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Research papers

Morphology and wall ultrastructure of some Middle Devonian dispersed megaspores from northern Poland

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ABSTRACT

Specimens of dispersed Middle Devonian megaspores have been isolated from core samples from the Miastko 1 borehole in Western Pomerania. Comprehensive investigations using light, scanning and transmission electron microscopy supplement previous information on morphology and gross structure and provide data on spore wall ultrastructure of four megaspore species. *Corystisporites acutispinosus* is azonate; the inner layer is laminate, and the lumen is lined by a thick, laterally continuous lamina. The outer layer consists of small, tangentially aligned tabular elements that become wider, more extensive and irregularly arranged toward the outside. *Coronispora variabilis* is a coronate megaspore; the inner layer appears homogenous and is probably lamellate. The outer layer consists of elongate, cylindrical, branching elements that are overlaid within the proximal part of the body by a lamellate, compact, almost homogenous layer. *Grandispora ciliata* is pseudosaccate. The inner body is laminate with laminae thickening and becoming less continuous and less tightly packed toward the outside. The outermost region of the inner body and the innermost region of the outer envelope consist of tabular and cylindrical elongate units. The bulk of the outer wall is almost homogenous, and near the surface it is granular. *Pomeranisporites subtriangularis* is pseudozonate. The inner layer appears homogenous except for the presence of a single innermost lamina. The inner part of the outer layer may represent small tabular and cylindrical elements, and the outer part comprises folded laminae. The megaspores studied share numerous features of morphology and wall ultrastructure with the lycopsids, putative lycopsids, and some enigmatic Devonian plants.

1. Introduction

The Middle Devonian is the critical epoch for diversification and evolution of heterosporous plants. In spite of this, the knowledge of Eifelian and Givetian megaspores is fragmentary. Devonian spores have been studied extensively for more than fifty years, but the focus of these studies was mostly stratigraphical, and the laboratory techniques used were not aimed at recovery of megaspores. Therefore, there are only a few monographs concerning Middle Devonian megaspores (Allen, 1972; Chi and Hills, 1976; Fuglewicz and Prejbisz, 1981; Marshall et al., 2007; Steemans et al., 2011; Stockmans and Streel, 1969; Turnau and Karczewska, 1987; Ville de Goyet et al., 2007). There is even less known about the spore wall ultrastructure of dispersed and in situ Middle Devonian megaspores and putative megaspores, so far, the only contributions in that area are those provided by Wellman (2009) and Turnau et al. (2009). Regarding Middle Devonian dispersed seed megaspores, wall ultrastructure has been reported by Meyer-Melikian and Arkhangelskaya (2002), Marshall and Hemsley (2003), and Turnau et al. (2009).

With this paper, we continue our study of dispersed megaspores from the Devonian of Poland. The specimens studied here are from the megaspore collection described by Fuglewicz and Prejbisz (1981). This material was recovered from Eifelian and Givetian deposits in the Miastko 1 borehole in northern Poland. In addition to the first part of our study (Turnau et al., 2009), specimens of four more species have been studied ultrastructurally: *Corystisporites acutispinosus* (Fuglewicz and Prejbisz) Turnau, 1996, *Coronispora variabilis* (Fuglewicz and Prejbisz) Turnau and Karczewska, 1987, *Grandispora ciliata* Fuglewicz and Prejbisz, 1981, and *Pomeranisporites subtriangularis* Fuglewicz and Prejbisz, 1981, emend. Our objective is to document spore wall ultrastructure and gross morphology of these megaspore taxa in the hope of providing evidence for their affinities.

In comparison with the first part of our work, which included *Granditetraspora zharkovae* Arkhangelskaya and Turnau emend. Turnau and Prejbisz, 2006, *Contagisporites optivus* (Chibrikova) Owens, 1971, and *Biharisporites*? *capillatus* Fuglewicz and Prejbisz, the present study is more challenging. Seed megaspores, such as

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Granditetraspora, are currently under rather intensive study (including TEM), focused on understanding their parent plants, and megaspores of *Contagisporites* morphology were repeatedly found in situ in archeopteridalean macroremains. On the contrary, the megaspores discussed in our present study belong to species that have not, so far, been encountered in situ in plant reproductive organs. Some light on their affinity can be shed by comparing their morphology, architecture and spore wall ultrastructure with those of latest Emsian and Middle Devonian large spores and Devonian and Carboniferous megaspores. Although a dispersed spore which has never been found in association with macro-remains is not a rare case, the situation is hampered even more by the fact that the spores under study are Devonian, which is the period of many enigmatic plants of uncertain affinities, with unknown or insufficiently studied spores.

2. Material and methods

2.1. Locality and geology

The palynological material described herein was isolated from Eifelian and Givetian deposits in borehole Miastko 1 drilled in northern Poland (Fig. 1). The Middle Devonian, continental and marine deposits of that area are dated on spores, and, partly, on marine fauna. Information on the biostratigraphy and lithostratigraphy of these strata is to be found in Turnau (1996), and Turnau and Prejbisz (2006). The Devonian sequence from the Miastko 1 borehole has been assigned, on spore data, to upper Eifelian and lower to middle Givetian (Turnau, 1996). The species discussed in this paper appear in strata assigned to the Eifelian, except for *Pomeranisporites subtriangularis* that appears in the sequence that may be either Eifelian or basal Givetian. The stratigraphic position of the palynological samples concerned in this paper is shown in Fig. 2.

2.2. Preparation and techniques

Samples of mudstone were palynologically processed by standard techniques involving treatment with HCl and HF. The organic matter was recovered by heavy liquid flotation. The residues were washed and dried, and megaspores were picked with a fine brush. Specimens for LM study were oxidized using fuming HNO_3. Unoxidized specimens were mounted on standard SEM stubs with carbon disks, coated with platinum, and examined at 20 kV using a JEOL JSM-840A microscope.

After SEM, specimens were removed from stubs and embedded in epoxy resin mixture. Since the studied specimens were considerably large for TEM processing, larger specimens were cut in two to three pieces before embedding to achieve proper embedding and sectioning. Some of the specimens were treated with butyl acetate for about half an hour to remove remnants of the carbon disk adhesive that stuck to the lower surfaces of spores hampering proper embedding. The specimens were polymerized for 2 days at 60 °C, orientated, and cut using an LKB 3 ultramicrotome with a diamond knife. The sections were viewed with a Jeol-100B TEM unstained. Most ultramicrographs were taken with an Olympus CO-770 digital camera, some high mag images were captured on film, and subsequently digitized using an Epson Perfection V700 Photo Scanner. Photo montages were produced using Photoshop 7.0. All materials (digital images, film, sections) are stored at the Laboratory of Paleobotany of PIN RAS (Moscow).

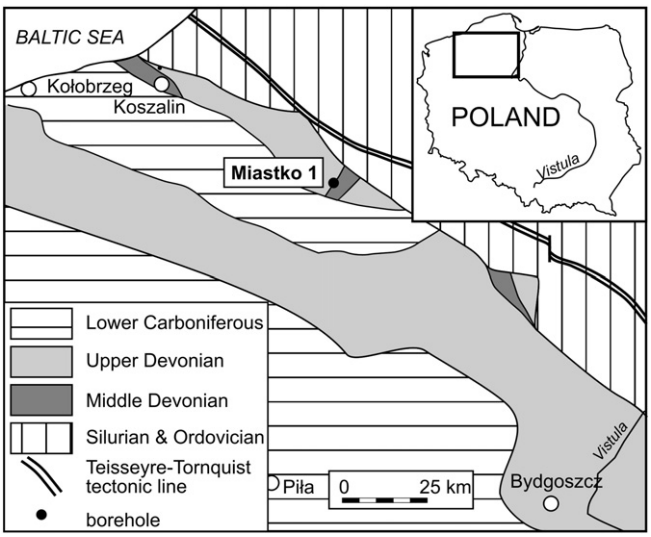


Fig. 1. Geological map of Western Pomerania showing the subsurface extent of sub-Permian deposits (adopted from Matyja et al., 2000) with location of the Miastko 1 borehole shown.

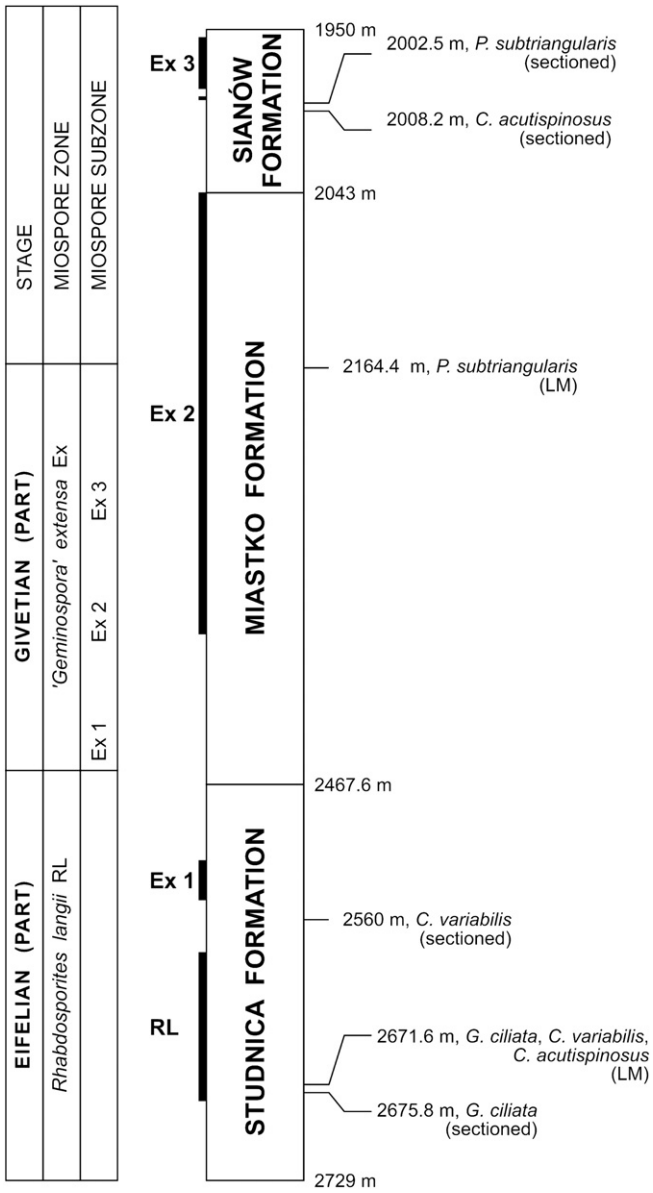


Fig. 2. Stratigraphy of the Devonian sequence from the Miastko 1 borehole, and position of the palynological samples.

3. Taxonomy and descriptions

3.1. Terminology

Pseudosaccus — a saccus-like separation in the wall of a spore resembling a saccus, but lacking the characteristic alveolate structure (after Grebe, 1971). The pseudosaccus may be developed in equatorial area or all around that area and the distal spore side.

Pseudozona — equatorial spore feature, where both the proximal and distal parts of the outer wall extend beyond the inner body, and are closely adpressed (after Wellman, 2001).

Zona — wide, membranous, equatorial flange which is not wedge-shaped in cross section (Potonié and Kremp, 1955). The structure of the zona (of Carboniferous, zonate spores like *Cirratriradites* and *Zonalesporites*) has not been sufficiently studied. Karczewska (1976) supposed that in *Zonalesporites* the zona is an extension of a membranous outer layer of the tri-layered outer wall. Karczewska called that layer a perispore. The median sections of in situ megaspores of *Selaginellites crassicinctus*, shown by Cottnam et al., 2000 (pl. I, 1, 2), seem to confirm that the inflated equatorial structure in that specimen is constructed of the outermost, compact, layer of the outer wall.

Lamina — we have used the term lamina in the sense recommended by Taylor (2009).

3.2. Descriptions using LM, SEM and TEM

Genus ***Corystisporites*** Richardson, 1964

Corystisporites acutispinosus (Fuglewicz and Prejbisz) Turnau, 1996 (Plates I, II, IV, V)

1981 Heliotriletes acutispinosus Fuglewicz and Prejbisz, p. 65, pl. 11, figs. 2, 5, 7; pl. 12, fig. 4.

1996 Corystisporites acutispinosus (Fuglewicz and Prejbisz) Turnau, p. 115, 117, pl. I, fig. 6.

Occurrence. Miastko 1 borehole, Studnica, Miastko, Sianowo Formations, late Eifelian to middle Givetian.

3.2.1. Material

We have examined several specimens using LM and five using SEM. The 3-D arrangement of the spore wall in a fractured specimen was studied using SEM, and we have sectioned five specimens preserved in equatorial compression. They were cut, as near as possible, perpendicular to the megaspore equatorial plane.

3.2.2. Morphology and architecture

Azonate, acamerate megaspores, diameter 120–330 μm (Fuglewicz and Prejbisz, 1981) or 85–330 μm (Turnau, 1996), ornamented distally and equatorially by closely set, long spines. The specimens vary by having more or less numerous spines. It is visible under LM that the spines consist of two different portions, the basal part that is translucent and the distal part that is opaque and appears solid (Plate I, 1). SEM images show that the labra of the trilete mark are high, narrow and flexuous, reaching the equatorial spore margin (Plate II, 1). The proximal spore surface and the labra of the trilete mark are covered by irregularly shaped, more or less globular elements, about 4 μm in width, assembled into clusters (Plate II, 5); the distal surface is covered with spines projecting at the equatorial margin (Plate II, 2, 3). Those situated at the equator are up to 1/3 of spore body diameter in length (Plate I, 1). A broken basal portion of a spine shows that it is hollow (Plate II, 4). TEM images of the sections show that the spore wall is bilayered, consisting of a thin, inner layer and the outer layer that is 6 to 10 times thicker. (Plate IV, 1; Plate V, 1). Both layers are firmly attached to each other. The trilete mark is an extension of the outer layer (Plate IV, 4) with no internal slit (but the section does not pass near the polar axis). It is tall and narrow, tapering, with a rounded crest. The proximal spore surface is undulating due to the presence of the surface sculpture. A transverse section of a spine is hollow (Plate V, 1, lower left).

3.2.3. Ultrastructure

An SEM image of a fractured spore wall (Plate II, 7) shows that the spore wall is bilayered, with an inner, apparently homogenous, layer, and an outer, thicker layer, consisting of tangentially aligned elements. This image (lower part of the figure) also shows small tabular units that have irregular outlines, and short appendages or knobs at the margins. They belong to the inner portion of the outer layer. TEM observations show that the thickness of the inner layer is constant being about 1.7 μm (in specimens st2-11, st2-12 and st2-15), and the outer layer is approximately as thick distally as proximally, measuring from 10 to 19 μm. Precise measurements are hampered by the indistinctness of the junction between the layers. Under low magnification, the inner layer looks almost entirely homogenous but higher magnification reveals that in some places a lamellate structure is visible. In specimen st2-15 in equatorial areas about a dozen laminae 0.18–0.24 μm in thickness may be discerned (Plate V, 2). In specimen st2-11, the innermost part of the inner layer is a distinct lamina 0.13–0.20 μm in thickness (Plate IV, 3, 5). It is traceable all around the perimeter of the inner layer. The lamina is overlaid by a layer 0.6–0.85 μm in thickness that appears homogenous, except for minute perforations present around the lamina (Plate IV, 2) analogous to those we described in *Biharisporites* (Turnau et al., 2009) and considered as a preservation effect. Toward the outside, about five laminae 0.07 μm in thickness are traceable. Some short small alveolae are present in this part of the layer (Plate IV, 3). These laminae are not

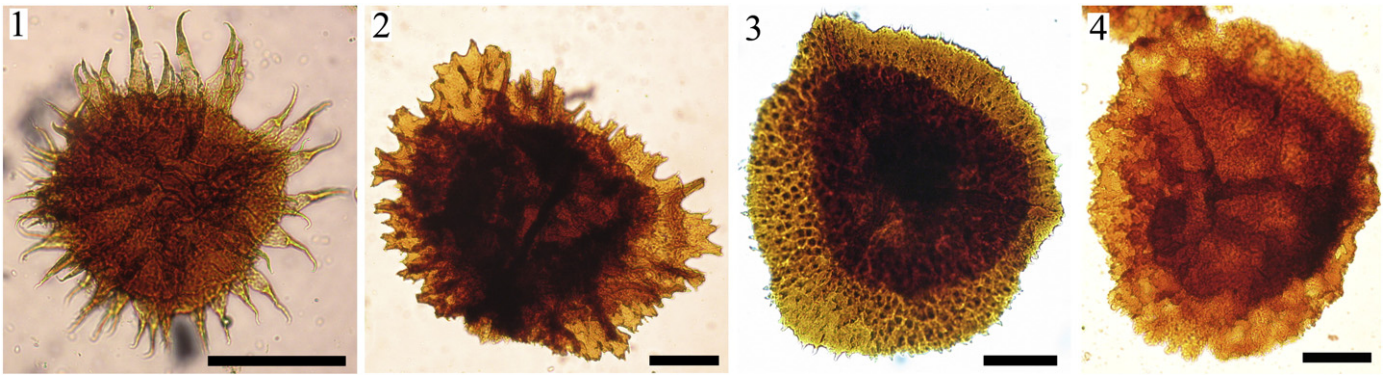


Plate I. LM images of the megaspores studied. Scale bar = 100 μm.

1. *Corystisporites acutispinosus*, distal focus. Note the nature of the ornamentation processes (upper center).
2. *Coronispora variabilis*, equatorial focus.
3. *Grandispora ciliata*, equatorial focus. Note folds of the inner body at its periphery.
4. *Pomeranisporites subtriangularis*, proximal focus. Note presence of darker streaks and circles representing folds of outer wall.

discernible under low magnification and appear to constitute the inner layer. There is no sharp boundary between the inner and outer layer, and we accept the level of appearance of more numerous and larger alveolae as the junction between the two layers. The innermost part of the outer layer is composed of elongate elements that become thicker and thicker (from 0.1 to 0.2 to 0.3 μm) toward the outside. The innermost, thinnest, elements are aligned parallel to the spore lumen, toward the outside the alignment is more irregular, the elements are undulating and the spaces between them become larger though less numerous (Plate IV, 5). Within the clusters of elements present on the proximal surface (see 3.2.2. Morphology and architecture), and on the labra (Plate IV, 1, 4) the irregular elements are about 0.4 μm, undulating, and some of the intervening voids are perpendicular to the spore surface. In specimen st2-11, ultrastructure of the distal wall is similar to that of the proximal one except that it is slightly denser (Plate IV, 1) but in specimen st2-14, the outermost portion of the distal outer layer is very dense: rare alveolae occur in a nearly homogeneous wall, though it is impossible to discern the individual structural elements (Plate V, 1).

The basal parts of the spines are hollow with a space that is lined with elements like those forming the outer wall. The spine apices are solid (Plate V, 1).

Considering both the fractured wall and all ultrathin sections, we suppose that the structural elements constituting the outer wall are plate-like, thin, laterally discontinuous laminae of irregular outline, with short appendages or knobs at the margin. Under TEM they

Plate II. SEM images of *Corystisporites acutispinosus* and *Coronispora variabilis*
1–7. *C. acutispinosus.* (see on page 5).

1. Proximal view, specimen st2-11.
2. Distal view, specimen st2-14. Note the close spacing of spines.
3. Distal view, specimen st2-12. Note the wide spacing of spines.
4. Detail of distal surface showing a hollow in a broken spine. Specimen st2-12.
5. Detail of proximal surface showing sculpture of elevated trilete rays and contact faces. Specimen st2-11.
6. Proximo-equatorial area, specimen st2-15.
7. Detail of fractured megaspore wall, specimen st2-13. Proximal and distal portions of the inner layer appear homogeneous and are closely appressed to each other; arrow indicates the position of the lumen. Below the arrow, the inner surface of the outer wall displays presence of tabulate units with uneven margins decorated by short appendages or knobs. They correspond to short, elongate, tangentially arranged units (see Plate IV, 5).

8–13. *Coronispora variabilis*

8. Proximal view, specimen st1-15.
9. Area of the corona, specimen st1-13.
10. Distal surface showing processes connected by bridges, specimen st1-16.
11. Fragment of megaspore, proximal surface, specimen st1-17; asterisk indicates position of image showed in Plate II, 13.
12. Detail of proximal surface in the area of the corona, showing the nature of sporopollenin units, specimen st1-15.
13. Detail of fractured proximal wall showing a pile of plate-like units, specimen st1-17. The section appears as some 6 μm in thickness, but is in fact thicker because this wall fragment is tilted. Arrows show appendages of tabular units of the inner, more open part of the compact laminate sublayer.
Scale bar (1–3, 8, 10, 11) 100 μm, (4–7, 9, 12) 10 μm, and (13) 1 μm.

Plate III. SEM images of *Grandispora ciliata* and *Pomeranisporites subtriangularis.*
1–6, 9. *Grandispora ciliata.* (see on page 6)

1. Proximal surface, specimen st2-1.
2. Distal view, specimen st2-2.
3. Proximal view of broken specimen st2-5; arrow indicates the position of the detail shown in Plate III, 6.
4. Detail of image in Plate III, 1 showing granules on the labra.
5. Enlargement of Plate III, 6.
6. Detail of image in Plate III, 3 showing fractured labrum of the trilete mark. Note that most part of the outer envelope is homogenous and the inner part has some tangentially arranged units; tabulate, anastomosing units are present on the exposed surface of the inner body.
9. Detail of image in Plate III, 1, showing granules on the proximal surface and spines at equator.

7, 8, 10–12. *Pomeranisporites subtriangularis.*

7. Proximal surface, detail of image in Plate III, 10, specimen st2-17.
8. Distal surface, specimen st1-28. Note the presence of folds.
10. Proximal surface, specimen st2-17.
11. Proximal surface, specimen st2-16. At the apex a possible microspore is partly covered by the labra (compare section of apical area in Plate X, 3).
12. Distal surface, specimen st2-18. Most folds are compressed and not visible.
Scale bar (1–3, 8, 10–12) 100 μm, (4, 6, 7, 9) 10 μm, and (5) 5 μm.

Plate IV. Ultrastructure of *Corystisporites acutispinosus*, TEM, specimen st2-11 shown in Plate II, 1. (see on page 7)

1. Section across the entire wall, proximal face to the right. Scale bar 2 μm.
2. Detail of inner lamina, supposedly preservational perforations are visible. Scale bar 0.2 μm.
3. Inner layer and the lowest portion of the outer layer. Note the presence of the inner lamina. Scale bar 1 μm.
4. Section across the labrum, proximal face to the right. Scale bar 2 μm.
5. Detail of image in Plate IV, 1 showing changing of constructing elements, distal face to the left. Scale bar 1 μm.

Plate V. Ultrastructure of *Corystisporites acutispinosus*, TEM. (see on page 8)

1. Section of distal wall and ornamentation processes, specimen st2-14. Scale bar 2 μm.
2. Laminae of the inner layer, specimen st2-15. Scale bar 0.5 μm.

Plate VI. Ultrastructure of *Coronispora variabilis*, TEM. Proximal surface facing right in Plate VI, 1, 2, 4–6. Black line visible in Plate VI, 1, 2 is remnants of SEM coating. (see on page 9)

1. Part of section across the periphery of the body. Arrows indicate position of the lumen, black asterisk is inserted over the labrum, three processes are visible distally (one of them is indicated with white asterisk, i — inner wall, a — alveolate layer of the outer wall, l — laminate layer of the outer wall, specimen st1-17. Scale bar 5 μm.
2. Section showing dense outer part of wall in the region of the trilete ray marked by asterisk. Arrow indicates position of the lumen, specimen st1-13. Scale bar 5 μm.
3. A portion of a distal spine, specimen st1-17. Scale bar 0.667 μm.
4. Detail of proximal wall showing part of the alveolate layer and the laminate sublayer, specimen st1-17. Scale bar 1 μm.
5. Distal wall, a sculptural element (white asterisk) is cut, specimen st1-13. Scale bar 5 μm.

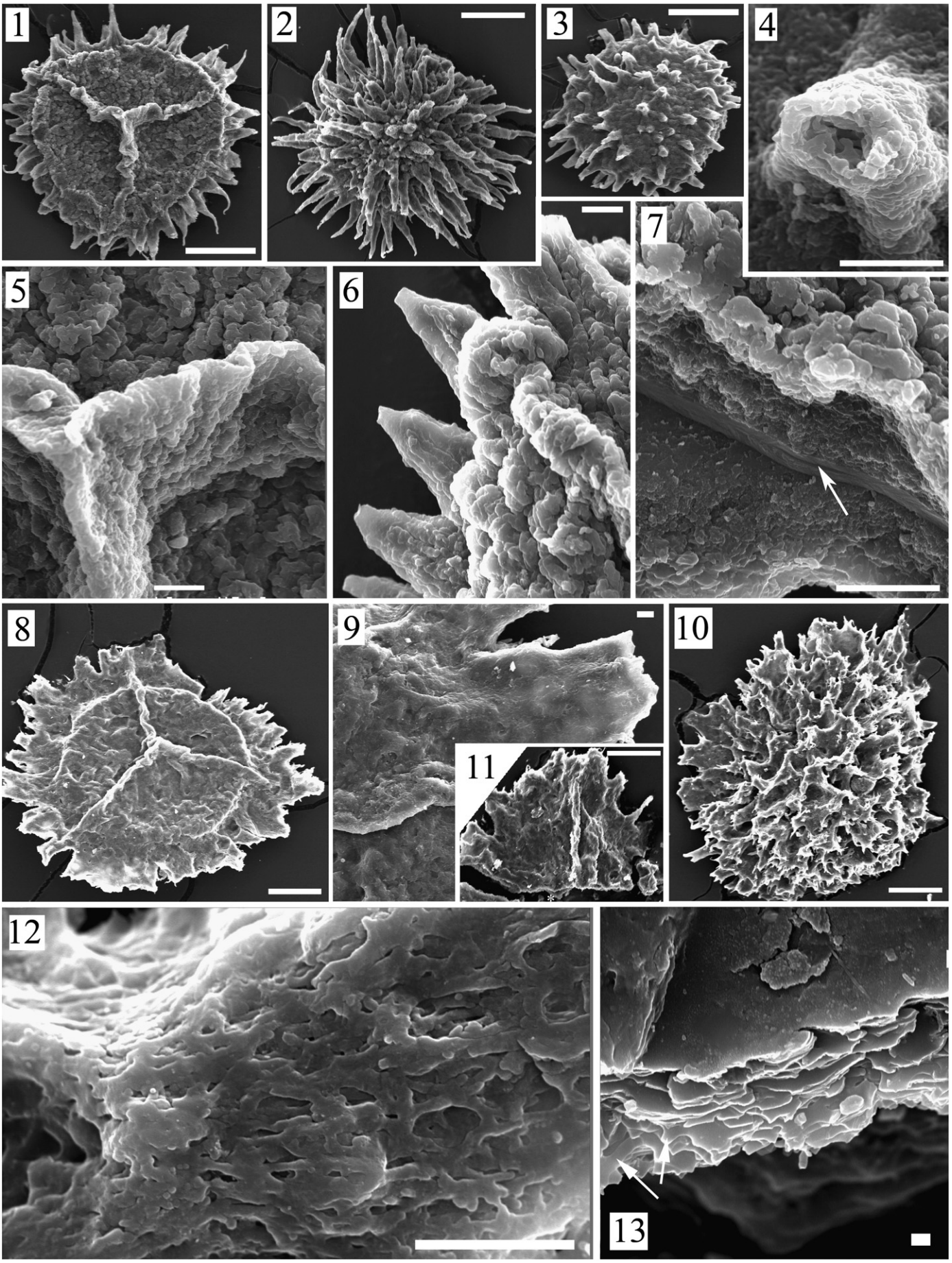


Plate II (*caption on page 4*).

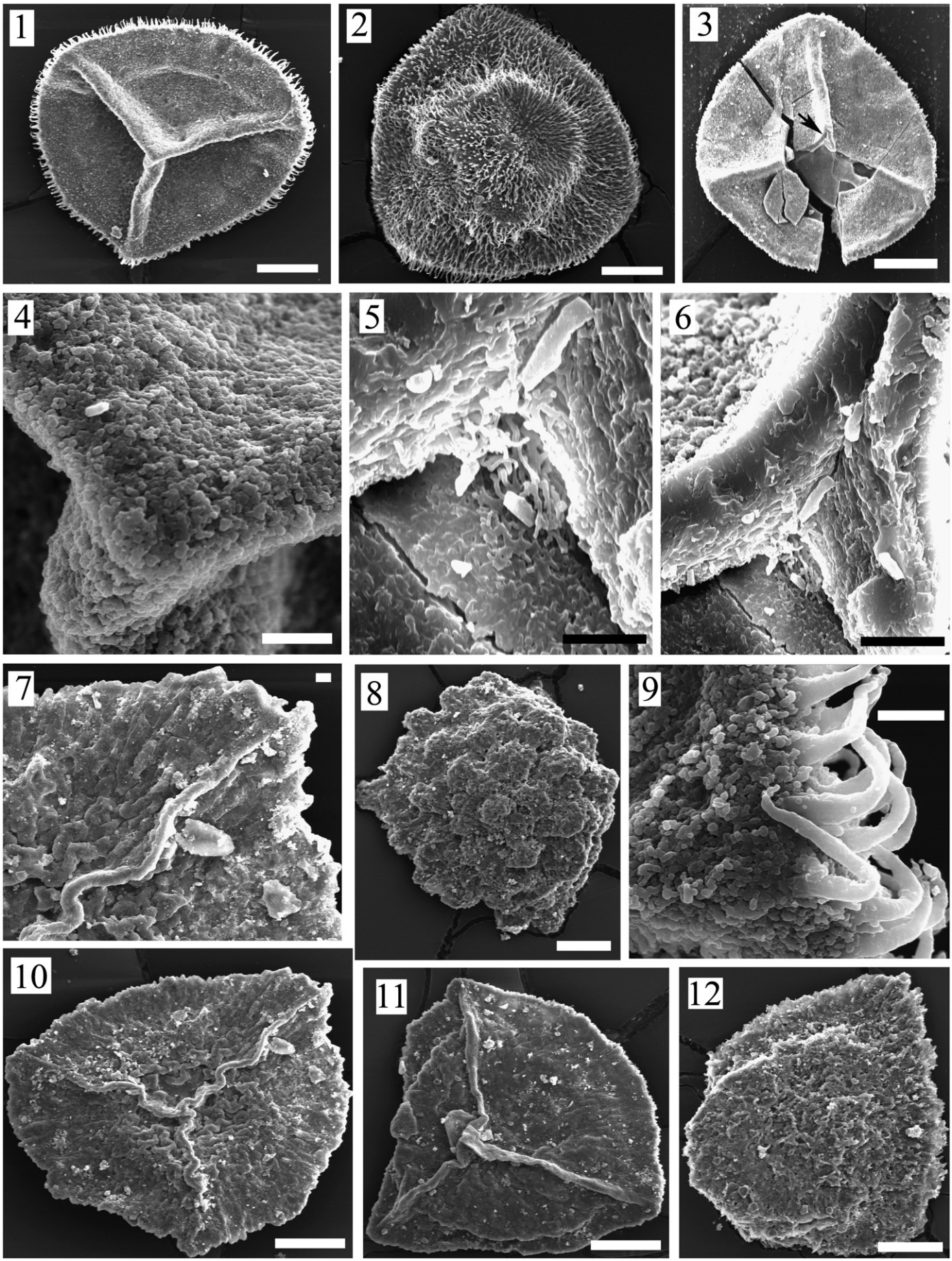


Plate III (*caption on page 4*).

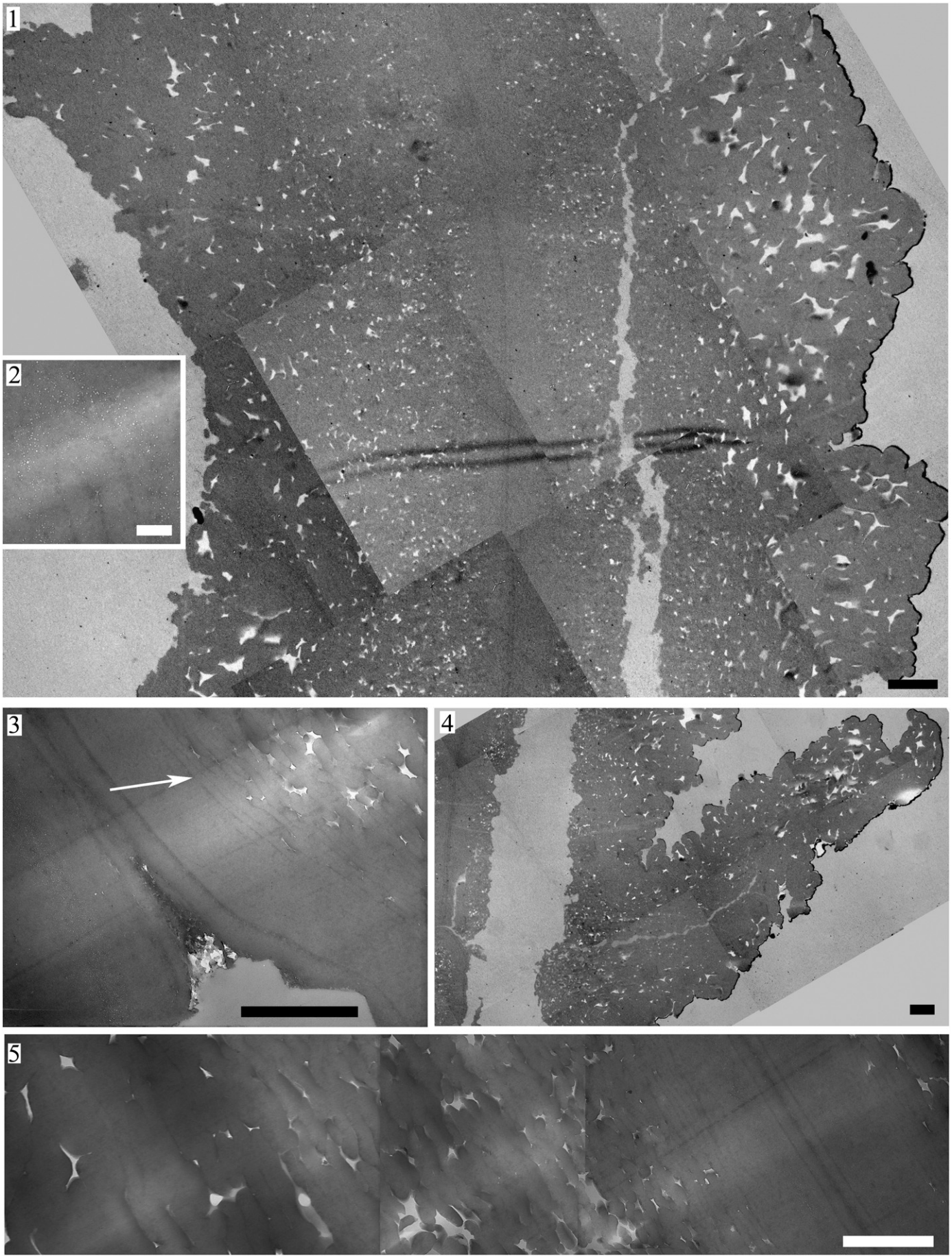


Plate IV (*caption on page 4*).

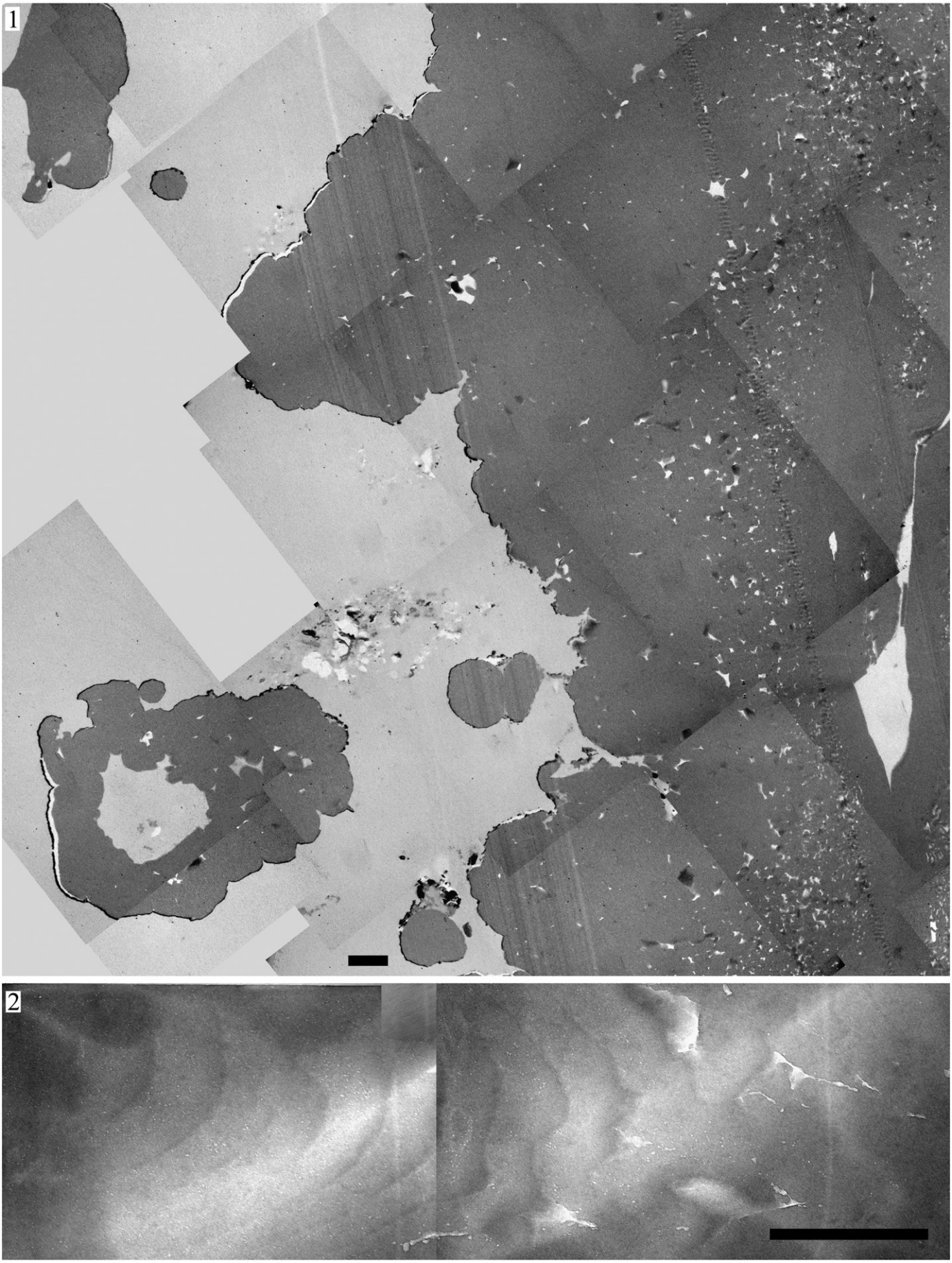


Plate V (*caption on page 4*).

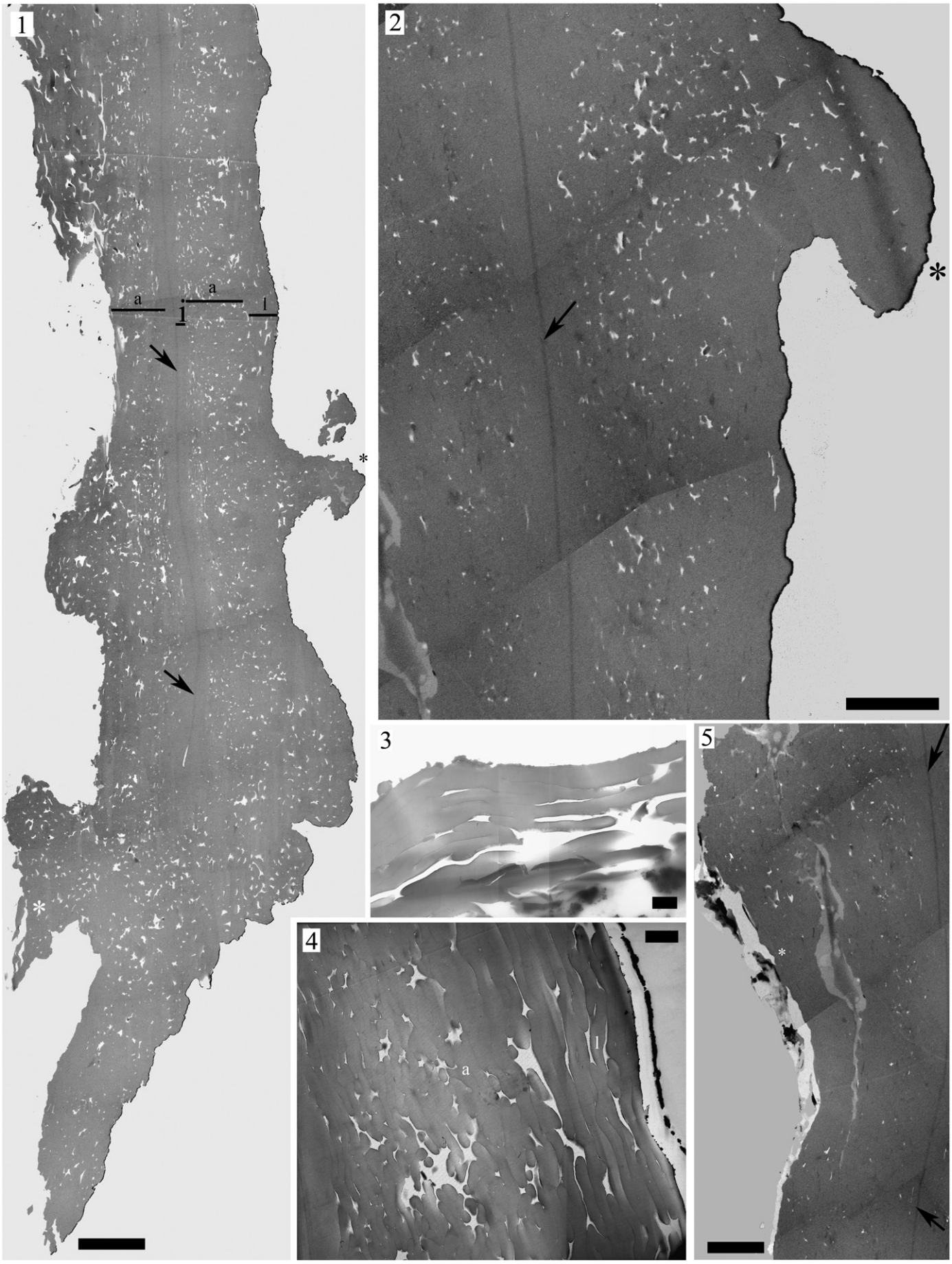


Plate VI (*caption on page 4*).

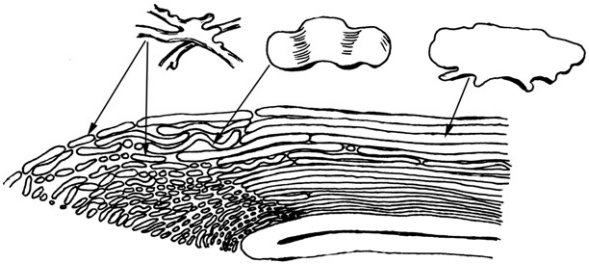


Fig. 3. Diagrammatic representation of the wall of *Coronispora variabilis*. Ultrastructure of proximal wall (to right); ultrastructure of proximo-equatorial, corona, and distal regions (to left).

appear as elongate elements and the appendages are represented by circular elements (granulae). Toward the outside, the laminae are more extensive, they thicken and fold, and become irregularly arranged.

Genus ***Coronispora*** Lu and Ouyang, 1978 (ex Jansonius and Hills, 1979)

Coronispora variabilis (Fuglewicz and Prejbisz) Turnau and Karczewska, 1987 emend. (Plates I, II, VI)

1981 ?*Pomeranisporites variabilis*, Fuglewicz and Prejbisz (? Fuglewicz and Prejbisz, 1981), p. 64, pl. 10, figs. 2, 4; pl. 14, fig. 4.

3.2.4. Occurrence

Miastko 1 borehole, Studnica, Miastko, Sianowo Formations, late Eifelian to middle Givetian.

3.2.5. Material

We have examined several specimens using LM and five using SEM. The 3-D arrangement of the spore wall in a fractured specimen was studied by SEM. Four specimens were cut, as near as possible, perpendicular to the megaspore equatorial plane, and studied by TEM. Two sections were situated near the periphery of the central area, and two other sections passed through the corona.

3.2.6. Original diagnosis

Trilete mark well developed. Proximal surface almost smooth. Distal surface uneven, covered with flattened appendages with strongly dissected tips.

3.2.7. Emended diagnosis

Acamerate, coronate spores. Trilete mark with high labra reaching onto the corona. Corona formed by wide processes branching in one plane, connected at bases. Over the distal hemisphere, processes of the same kind form a coarse reticulum.

3.2.8. Remarks

The original diagnosis does not mention the corona.

3.2.9. Morphology and architecture

These megaspores were studied by Fuglewicz and Prejbisz (1981), and Turnau and Karczewska (1987). The overall diameter given by Fuglewicz and Prejbisz is 340–700 μm while Turnau and Karczewska recognized two populations of this species of sizes 156–280 μm (presumably functional microspores) and 297–604 μm (presumably functional megaspores). Here we want to add some new details to the earlier descriptions. Under SEM, the contact areas are folded, the folds are irregularly distributed, straight or sinuous (Plate II, 8). The corona is formed by wide and flat processes bearing at the crest multiple, sharp spines 8–30 μm in length (Plate I, 2; Plate II, 9–11). The processes are connected at the base by bridges. On the distal hemisphere, similar chains of processes form a reticulum of wide lumina (five or six lumina may be counted along the megaspore diameter, Plate II, 10). Our TEM observations indicate that megaspore wall is two-layered, and both layers are closely adpressed (Plate VI, 1). The trilete mark (viewed in a section taken away from the polar axis) is wide, narrowing to a rounded edge, without a suture. It is formed by extension of the outer layer (Plate VI, 1, 2), similarly as the muri of the reticulum and corona. The inner layer is more or less constant in thickness and the outer layer is approximately ten times thicker proximally, and about six times thicker distally (Plate VI, 1, bars). The sectioned sculptural processes are wide at the base and taper to a narrow crest (Plate VI, 1).

3.2.10. Ultrastructure

SEM images of the fractured spore wall of the proximal pole area show that a portion of the outer layer is formed by extensive, stacked plate-like elements (Plate II, 13). The section appears to be 6 μm in thickness. It represents a considerable portion of, or the entire outer layer of the apical megaspore region (because the TEM measurements give the thickness of that layer as 6.5 to 11.5 μm. In the following discussion, this layer will be termed the laminate layer. The plates are entirely homogenous, and less than 0.5 μm thick. Rare, small,

Plate VII. Ultrastructure of *Grandispora ciliata*, TEM. Proximal surface facing right in all images. Black contours in some images are remnants of SEM coating. (see on page 11)

1. Enlargement of a peripheral section, shown in Plate VII, 5. Innermost elements of the outer layer line one of the labra of the trilete mark and the inner surface of the lumen. Specimen st2-5. Scale bar 1 μm.
2. Composite image of section situated within central megaspore part showing two-layered nature of the wall. Specimen st2-2. Scale bar 5 μm.
3. Detail of section of the labrum in central spore part showing the suture lined by the inner layer, specimen st2-1. The strip situated in the lumen (left upper corner) supposedly does not belong to the wall. Scale bar 1 μm.
4. Proximal sculpture, specimen st2-5. Scale bar 1 μm.
5. A portion of peripheral section, only the outer layer is present, specimen st2-5. Scale bar 2 μm.

Plate VIII. Ultrastructure of *Grandispora ciliata*, TEM, Plate VIII 1–4, 6–8 — enlargements of the image shown in Plate VII, 2, specimen st2-2, Plate VIII, 5 — specimen st2-1. (see on page 12)

1. The inner body and innermost region of the outer envelope of the proximal wall. The lumen is visible in the upper left. Note the various shapes of the sectioned units. The area of junction between the inner body and the outer envelope is marked with arrows. Scale bar 0.5 μm.

2, 3. Areas of the proximal wall near the laesura.

2. The hollow in the center of the figure is the split (artificial) between the inner and outer wall layers below the trilete mark. The outer layer is visible in the upper right and lower right of the figure, the inner layer is in the lower left, scale bar 0.667 μm. Compare with Plate VII, 2.
3. Fragments of proximal wall showing the inner body and inner part of the outer envelope (the area of junction shown by the arrow). The lumen is to the left. Scale bar 0.667 μm.
4. Fragment of proximal wall the detail of which is shown in Plate VIII, 1, showing the megaspore wall up to the lower portion of the homogenous part of the outer envelope. The lumen is to the left. Scale bar 1 μm.
5. Fragment of distal wall, showing homogenous and granular part of the outer envelope and fragment of the spine. Scale bar 0.667 μm.
6. Section of distal spine. Scale bar 1 μm.
7. Fold of equatorial part of inner body. The lumen is in lower left. Scale bar 0.667 μm.
8. Inner equatorial region. Note how the outer envelope diverges from the inner body visible at lower left, note also variable shapes of the sectioned structural elements at junction of the inner body and outer envelope. Scale bar 0.667 μm.

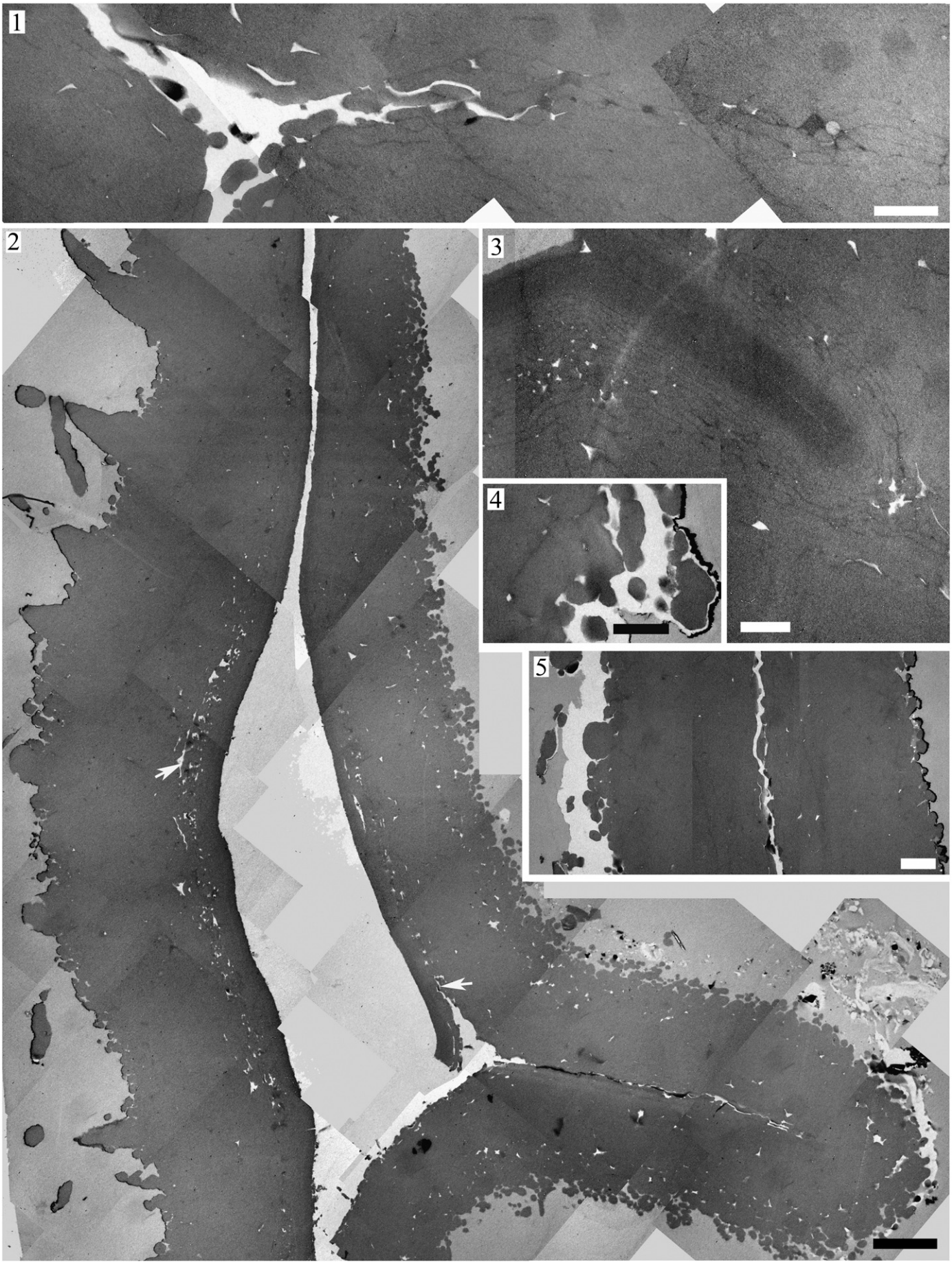


Plate VII.

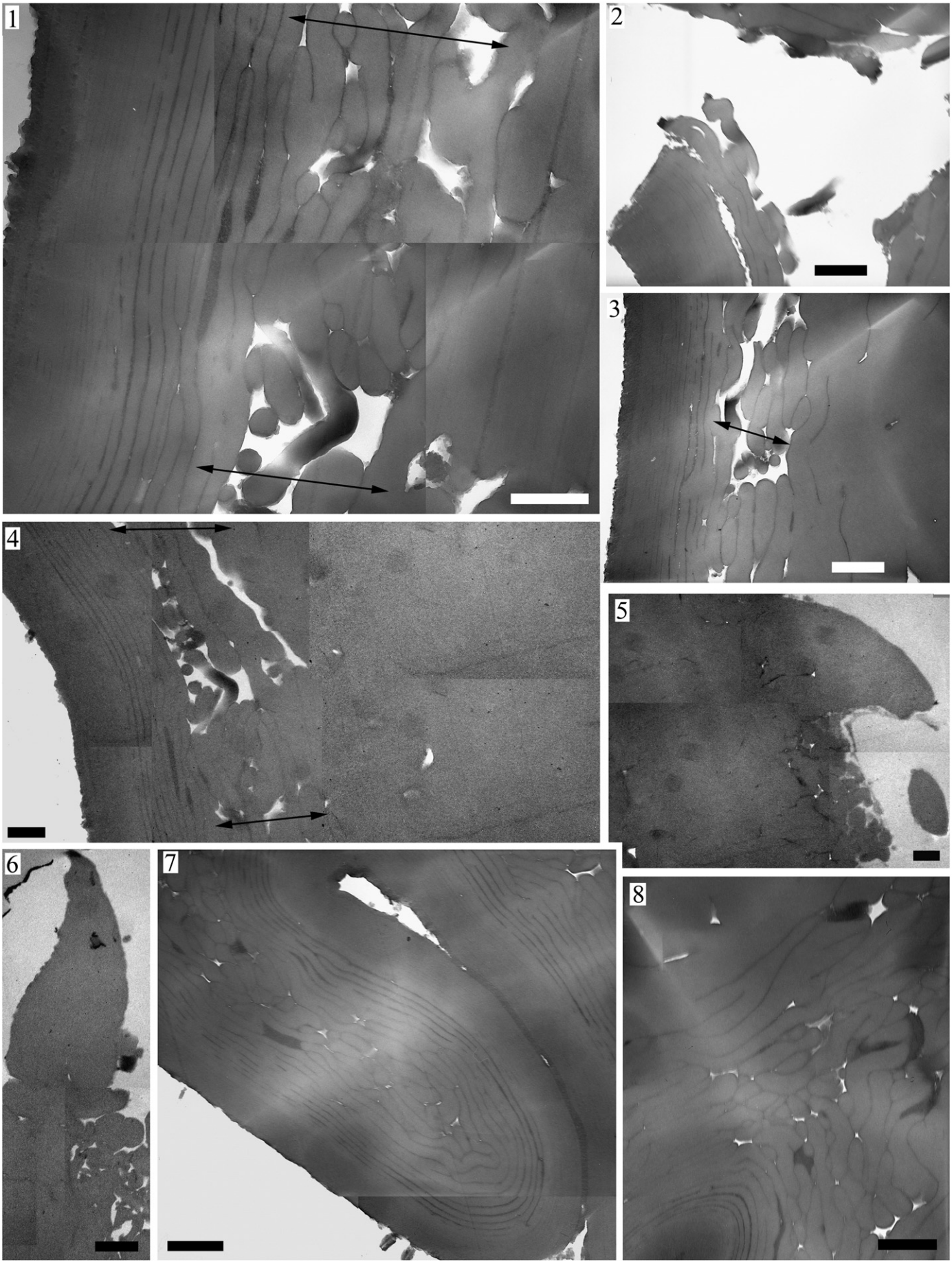


Plate VIII (*caption on page 10*).

rounded pits about 0.15–0.25 μm in diameter are visible on the surface of the topmost plate. Toward the spore lumen, there seems to be more open space within that layer, the plate-like laminae have some narrow appendages (Pl. II, 13, arrows) bordering rounded openings. The proximal spore surface near the junction of the spore body and corona, the surface of the corona, and the distal spore surface, show under higher magnification a peculiar pattern of elongate, branching and fusing elements of variable width (0.5–1.5 μm), enclosing lumina 0.8–2.5 μm in width (Plate II, 12). The width of the branching elements is comparable to that of the narrow, elongate units seen under SEM in the deeper part of the outer layer of the proximal, polar region.

The TEM images show that the spore wall consists of two main layers; both layers are firmly appressed to each other. The inner layer, about 0.96 μm in thickness, looks homogeneous under magnification ×5000, and the outer layer is quite dense, with alveolae of variable sizes, smaller than the intervening partitions (Plate VI, 1). The innermost part of the outer layer is constructed of fine elements 0.4 to 0.15 μm in diameter, showing faint tangential alignment (Plate VI, 2). Toward the outside, the sporopollenin units become wider and the intervening voids become larger (Plate VI, 1, 2). One may observe a constant alternation of elongate, undulating and rounded elements. They may be interpreted as cylindrical, branching units that appear as granules if cut transversely (Fig. 3). In the following discussion, this layer will be termed the alveolate layer. This trend in size and arrangement of sporopollenin units is traceable throughout the entire perimeter of the distal and proximo-equatorial outer layer. However, the outer layer of the proximal wall consists of two sublayers — the inner alveolate one, and the outer that is very dense and appears almost homogenous in a lower magnification (Plate VI, 1, 2). This sublayer consists of laminae (Plate VI, 4), closely spaced, tangential to the surface of the spore coat. The outermost lamina seems continuous over the proximal surface of the central area. The distal wall, corona, and the distal processes do not have this continuous coating. The porous nature of the proximal surface of the corona is well visible in SEM and TEM images (Plates II, 12 and VI, 1), but is not so evident where the distal side of corona is concerned (Plate VI, 1, down from the lower left asterisk). This, we think, is preservational effect. Due to the absence of this coating, the outer layer of the distal megaspore part is thinner than its proximal counterpart (Plate VI, 1).

Information about the three-dimensional organization of the alveolate layer may be seen in SEM images, of the part of megaspore surface lacking the continuous coat. Indeed, the reticulate pattern (Plate II, 12) apparently constitutes not only the surface areas of the spore wall, but also deeper areas. The repeatedly alternating elongate and granular elements observed in ultrathin sections could be explained by a reticulum of narrow elongate repeatedly branching and fusing elements. Taking into account all our sections (SEM and TEM), we suppose that a considerable part of the outer wall (or entire outer layer) of the proximal wall close to polar axis is formed by flat, thin plate-like elements stretching over a considerable area (Plate II, 13; Fig. 3). Closer to the corona such elements are present only in the surface area of the outer layer (Plate VI, 4), and near the corona the whole sublayer peters out. The sculptural elements are very dense, filled throughout with the same units that constitute the alveolate layer of the outer wall (Plate VI, 3, 5).

3.2.11. Remarks

It is not rare in Paleozoic megaspores that different areas of the spore wall of the same spore have different ultrastructure. In the Devonian spores *Ancyrospora ancyrea* (Eisenck) Richardson, 1962, the outermost layer (layer 3) is only patchy on the spore surface, best developed on the proximal surface and in the vicinity of the trilete mark (Wellman, 2002). Also in that species, the outer layer is variable between specimens. In the opinion of Wellman (2002) this is due to variations in the strength of compression of specimens, but another possibility is that differing specimens were cut across different regions of the spores. Variability of spore wall ultrastructure in a single specimen was observed by Glasspool et al. (2009), pl. 3, figs. 4–6) — in the Carboniferous megaspore *Rotatisporites rotatus* (Bartlett) Potonié and Kremp, 1954, the compact wall included pockets of more porous structure.

Genus ***Grandispora*** (Hoffmeister, Staplin and Malloy) emend. McGregor, 1973

Grandispora ciliata Fuglewicz and Prejbisz, 1981 (Plates VII, VIII)

1981 *Grandispora ciliata* Fuglewicz and Prejbisz, 1981, p. 62, pl. 10, figs. 3, 5; pl. 11, fig. 1; plate 13, fig. 2.

3.2.12. Occurrence

Miastko 1 borehole, Studnica, Miastko, Sianowo Formations, late Eifelian to middle Givetian.

3.2.13. Material

We have examined several specimens using LM and five specimens (preserved in equatorial compression) using SEM. Three of the specimens studied under SEM were further studied using TEM. They were sectioned, as near as possible, perpendicular to the megaspore equatorial plane, two of them were sectioned close to the polar axis and one along a more peripheral plane.

3.2.14. Morphology and architecture

The morphology of this species based on LM and SEM observations was provided by Fuglewicz and Prejbisz (1981) and Turnau and Karczewska (1987). The overall diameter given by the former authors is 340–600 μm while Turnau and Karczewska recognized two populations of this species of sizes 72–136 μm (presumably functional microspores) and 140–594 μm (presumably functional megaspores). Our present observations agree with the previous descriptions, but we want to emphasize some points of particular interest. Observations under SEM indicate that the proximal spore surface and the labra are covered with granules about 1 μm in diameter, often fused into groups (Plate III, 4). The distal surface is covered with biform spines up to 20 μm long, with wide bases about 5 μm in diameter, tipped by almost parallel-sided terminal portions with rounded or pointed ends; granules about 1–1.5 μm in diameter are situated between the spines (Plate III, 5). Our TEM observations indicate that the spores comprise a thin central body entirely enclosed within a thick outer layer (Plate VII, 2). The outer layer is about six times thicker than the inner body (inner separable layer) and distally is thicker than proximally. The trilete mark is wide, with a broadly rounded apex. It is essentially formed by the outer layer (Plate VII, 1), but at the base of the sutural prominence, the inner (electron dense) part of the inner body extends some distance up into the fold (Plate VII, 3). This feature was observed only in specimen st2-1, but not in specimen st2-2 (Plate VII, 2), in spite of the fact that both sections were situated more or less centrally. At the equator, the outer layer forms a pseudosaccus; the presence of a camera is well visible in the peripheral sections where the outer layer is only present and the inner layer is missing (Plate VII, 5). In other sections there is no gap between the layers due to diagenetic compression of the spores. We have observed using TEM the presence of a fold at the distal equatorial part of the inner body (Plate VIII, 7). Folding of the central body was also noted by Fuglewicz and Prejbisz (1981), and Turnau and Karczewska (1987). In compressed spores, the central body is often positioned eccentric to the outer envelope. This indicates that the spores were camerate, equatorially or both equatorially and distally.

3.2.15. Ultrastructure

The fractured part of the labrum of the trilete scar, studied by SEM, (Plate III, 3, 6) shows a homogenous wall with infrequent alveolae.

This wall has a tendency to break along surfaces perpendicular to that of the labrum. The innermost part of this fracture, representing the deeper part of the outer envelope, shows some units of tangential alignment. In the lower portion of the figure, the exposed surface of the inner body is visible. The surface displays variously shaped units corresponding to units B and C in Fig. 4. The type-C units anastomose with each other. Under TEM, the spore wall appears dense (with very high sporopollenin/lacunae ratio). It is about 10 μm thick in the non-apertural proximal area, 15.0–16.2 μm in the polar region of the distal area, and 9.7 μm equatorially. It consists of two main layers differing in thickness. The inner body exhibits a complex ultrastructure (Plate VIII, 1–4, 7, 8; Fig. 4). Its innermost portion is more electron-dense than the rest of the spore wall (Plate VII, 3; Plate VIII, 3); the thickness of this portion in a given specimen is 0.6–0.8 μm. It appears homogenous under low magnification, but laminae (about 0.03 μm in thickness) were detected in places under greater magnification (Plate VIII, 1, 3); however, no innermost, thicker lamina was observed. This sublayer (Fig. 4, unit A) is covered with paler, less electron-dense distinct laminae (Fig. 4, unit B). The innermost of these laminae are thin (0.07–0.08 μm), seem continuous, parallel to each other, and closely packed. They are overlain by thicker laminae (0.13 μm) that seem to be less tightly packed. The successive laminae are wider and less continuous, and they are followed by the zone of alternating circular and discontinuous, elongate, tangentially orientated elements with infrequent voids between them (Plate VIII, 1, 8; Fig. 4, unit C). They may be interpreted as cylindrical, branching units that appear as granules in section view (Fig. 4, units C, D). The junction between the inner body and the outer envelope is indistinct because the constituting elements of both layers in that area are of similar appearance (Plate VIII, 1, 3, 4). The complicated nature of the inner body is best seen where part of this layer has separated from the outer layer and has formed a fold (Plate VIII, 7), and in equatorial areas where the outer envelope extends away from the inner body to form the pseudosaccus (Plate VIII, 8). The bulk of the outer layer is nearly homogenous (Plate VIII, 4, 5, Fig. 4, unit E). However, the outlines of irregularly distributed, rarely present lacunae imply that they may be spaces between globular units that are densely packed and homogenized (Plate VIII, 5, lower left; Fig. 4, unit E). The succeeding sublayer consists of tightly packed granular elements, 1.0–2.0 μm in diameter, similar to those loosely arranged at the spore surface (Plate VIII, 5, Fig. 4, unit F). The distal spines often appear in sections as larger solid and homogenous granules 2.7–4.1 μm in diameter (Plate VII, 5, left); some of them are cut longitudinally along some portion of their length (Plate VIII, 6).

Genus ***Pomeranisporites*** Fuglewicz and Prejbisz, 1981 emend.

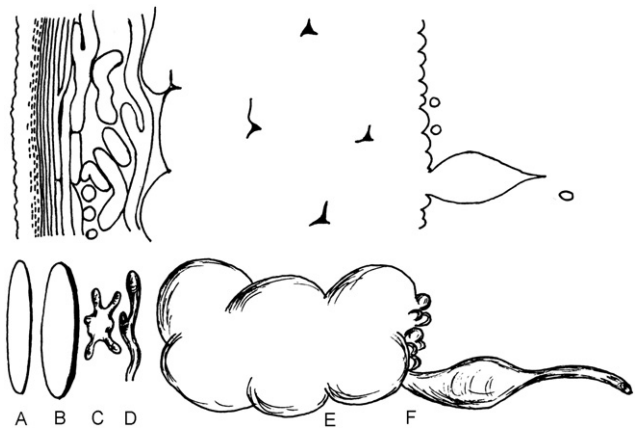


Fig. 4. Diagrammatic representation of the wall of *Grandispora ciliata* (top), and its constituent parts (bottom); A — thin laminate unit, B — thick laminate unit, C — tabulate unit with appendages, D — cylindrical forking unit, E — fused globular unit, F — granular unit.

3.2.16. Type species

Pomeranisporites subtriangularis Fuglewicz and Prejbisz, 1981.

3.2.17. Original diagnosis

Megaspores mostly of subtriangular amb. Trilete mark well developed. Curvaturae absent. Contact faces usually smooth or granulate. Distal surface often covered with hairlike processes.

3.2.18. Emended diagnosis

Spores acamerate, sutures bordered by high, flexuous labra extending to the equatorial spore margin. Outer wall extended equatorially to form a thinner walled pseudozona. Proximal and distal surfaces are folded.

3.2.19. Remarks

The diagnosis is emended to point out the presence of the equatorial feature and explain its nature. *Pomeranisporites* Fuglewicz and Prejbisz emend. is a monotypic genus. The creators of the genus included in it, though reluctantly, ?*Pomeranisporites variabilis*, but it was transferred later (Turnau and Karczewska, 1987) to *Coronispora*. The genus *Samarisporites* Richardson, 1964 differs in having unfolded contact areas, and *Triangulatisporites* Potonié and Kremp emend. Karczewska, 1976 has a zona, not a pseudozona, and the surface sculpture involves only the thin, uppermost portion of the outer layer.

Pomeranisporites subtriangularis Fuglewicz and Prejbisz, 1981 (Plates IX, X)

1981. *Pomeranisporites subtriangularis* Fuglewicz and Prejbisz, 1981. p. 63, pl. 9, figs. 4, 6, 7, 8; non plate 14, fig. 2.

Occurrence. Miastko 1 borehole, Studnica, Miastko, Sianowo Formations, late Eifelian (?), lower and middle Givetian.

3.2.20. Material

We have examined several specimens using LM, five specimens using SEM, and we have sectioned five specimens preserved in equatorial compression. They were cut as near as possible perpendicular to the spore surface. One of the specimens was cut into pieces which were subsequently embedded separately; sections of two different regions of that specimen were obtained. Six sections were finally studied with TEM, four of those passed across the central part of the spore body, and two across the periphery of the body.

3.2.21. Original diagnosis

Megaspores most commonly of subtriangular amb. Trilete mark well developed. Contact faces smooth or scabrate, occasionally wrinkled. Distal surface uneven, rugged, often covered by numerous, fine spines.

3.2.22. Emended diagnosis

Acamerate spores with equatorial pseudozona. Trilete mark with high labra extending to spore margin. Proximal and distal surfaces are ornamented by folds; these are irregularly distributed over most of the contact area while near its equatorial part and on the proximal surface of the flange their alignment is radial. Distal folds are dome-shaped or irregular. Additionally, the distal surface is ornamented by fine spinose processes projecting at the spore equator.

Remarks. The diagnosis is emended to point out the presence of the equatorial feature and explain its nature. The sculpture of the spore surface is described more precisely.

3.2.23. Morphology and architecture

The megaspores are 290–464 μm in diameter (Fuglewicz and Prejbisz, 1981). Viewed with LM, the megaspores comprise a dark, subcircular central body and a lighter equatorial extension one-fifth to one-third of the spore radius in width. The amb is subtriangular or subcircular, the equatorial margin is often undulating. A reticulate or irregular pattern of darker and lighter streaks and rings is present

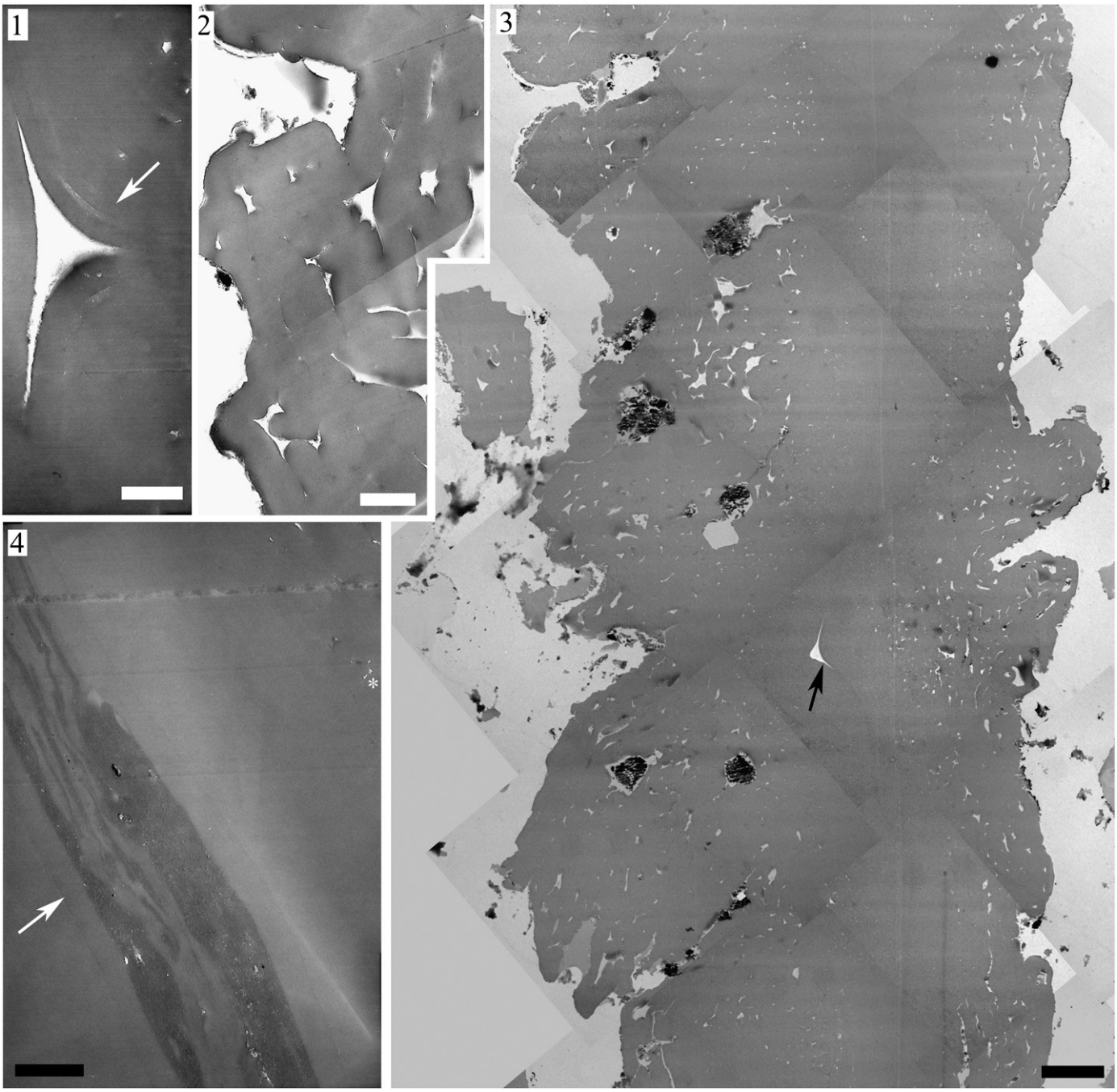


Plate IX. Ultrastructure of *Pomeranisporites subtriangularis*, TEM.

1. Detail showing compressed lumen and the inner lamina of the inner layer (white arrow), specimen st2-18. Scale bar 0.667 μm.
2. Outermost portion of the distal wall, specimen st1-28. Scale bar 1 μm.
3. Composite image of section showing two-layered nature of the wall, and proximal and distal folds of the outer layer, specimen st2-17. Strongly compressed lumen detectable only in places (black arrow). Proximal surface facing right. Scale bar 5 μm.
4. Detail of the inner layer and compressed lumen, the inner lamina is visible (white arrow), alveolae of the outer layer are visible in the upper right corner (white asterisk), specimen st2-18. Scale bar 0.667 μm.

over the spore body and the equatorial extension (Plate I, 4). It corresponds to overlapping proximal and distal folds of the outer wall described below. The distal surface of intact specimens is ornamented with spines up to 15 μm in length, with wide bases and very slender, sharp stems. The slender parts are almost always broken off, and the spines or spine bases appear as cones with rounded tips, mostly detectable in equatorial regions (Plate I, 4; Plate III, 12).

SEM observations show that laesurae have elevated, ridge-like labra extending almost to the equatorial spore margin (Plate III, 10, 11). The surface of the contact faces bears vermiculate folds or ridges of no preferred orientation while at the periphery of the central area and on the equatorial extension, the folds are straight and of radial arrangement (Plate III, 7, 10). The distal spore surface bears folds usually in the form of rounded protuberances (Plate III, 8).

TEM observations indicate that the spore wall is bi-layered, with a thin inner layer that appears homogenous, and a much thicker, structured outer layer (Plate IX, 3). The labra of the trilete mark are formed by the extension of the outer layer (Plate X, 3); they are narrow and

possess a suture that does not reach the surface. The outer layer is extended equatorially in the form of pseudozona (Plate X, 1). There is no trace of a space between the proximal and distal parts of the outer layer in the pseudozona and therefore we suppose that originally the spores were acamerate. The outline of sections of the proximal and distal surfaces is undulating due to the presence of folds (Plate IX, 3). The inner layer is more or less constant in thickness, several times thinner than the outer layer. The thickness of the outer layer varies.

3.2.24. Ultrastructure

The spore wall is very dense, so that the fractured spore wall observed under SEM appears homogeneous (not shown). TEM observations show that the inner layer of the spore wall is constant in thickness (about 2.2 μm), homogeneous, and in places the innermost part of that layer is a distinct lamina about 0.17–0.23 μm in thickness (Plate IX, 1, 4). The proximal outer layer measures 10.8–12.5 μm between the folds and 15.3–21.7 μm within folds. Distally it measures 13.6 μm between the folds and up to 27.7 μm within those. The outer layer is alveolate, very dense, and it is difficult to discern unequivocally the nature of the constituting elements (Plate IX, 3). In the inner region of the distal outer layer the sporopollenin units are 0.25 μm in width, and they are so closely packed that it is not possible to see whether they are elongate or granular. Toward the outside, the elements are 0.4–0.7 μm wide and appear elongated. It is not possible to point out the level where one type of element is replaced by the other, the transition is gradual. The succeeding elongate units are 1.25–1.6 μm wide, their alignment varies. In the outermost region of the distal wall, the constituting units (which fill the distal folds) reach 2.2 μm in width. They appear in sections as undulating, elongate elements that are so closely packed that the spaces between them occupy very limited, mostly triangular spaces (Plate IX, 2). This gradation in size of elements is observed in both the distal and proximal walls, but the elements of the proximal wall seem finer than those of the distal one (Plate IX, 3). The finest discernible elements of the proximal wall, circular and oval in shape (Plate X, 5), are about 0.25 μm in width. They may represent tabular and cylindrical units. Toward the outside, the units are elongate, undulating, and parallel to the spore surface. The thickest are 0.8 μm in width. In the specimen st2-16 the outermost proximal wall is in places almost homogenized (Plate X, 5); this was not detected in other studied specimens of this taxon. We suppose that the elongate, undulating units observed under TEM represent laterally continuous, folded laminae.

The section of specimen st2-16 that was taken very near the proximal pole demonstrates a very peculiar spore wall of several overlapping folds (Plate X, 3). Keeping in mind the SEM image of this specimen (Plate III, 11), we suppose that the inner, smaller object may represent a microspore attached to the megaspore under study. Its wall (1.8–2.4 μm thick) includes an outer, alveolate, and an inner homogeneous layers (about 0.3–0.6 μm each) that sandwich a layer of granular elements (about 0.8 μm thick, with the granules about 0.1–0.15 μm in diameter) (Plate X, 4). The outer, larger structure belongs to the megaspore labrum partly covering the microspore and keeping it attached to the megaspore. It is formed of elongate elements. The similarity between the ultrastructure of the supposed microspore and the megaspore implies that they could have been produced by the same parent plant. Another conceivable interpretation of this section is that it was the labrum that was repeatedly folded at the proximal pole and cut several times by this section, but it seems less probable. Besides, other specimens studied proximally show labra of insufficient size to allow repeated folding (e.g. Plate III, 10). An alternative interpretation might be that the attached structure may be an aborted megaspore.

4. Comparisons and affinity

The megaspores studied belong to species that have not, so far, been encountered in situ in plant reproductive organs. Some light on their affinity can be shed by comparing their morphology, architecture and spore wall ultrastructure with those characters of megaspores of known affinity.

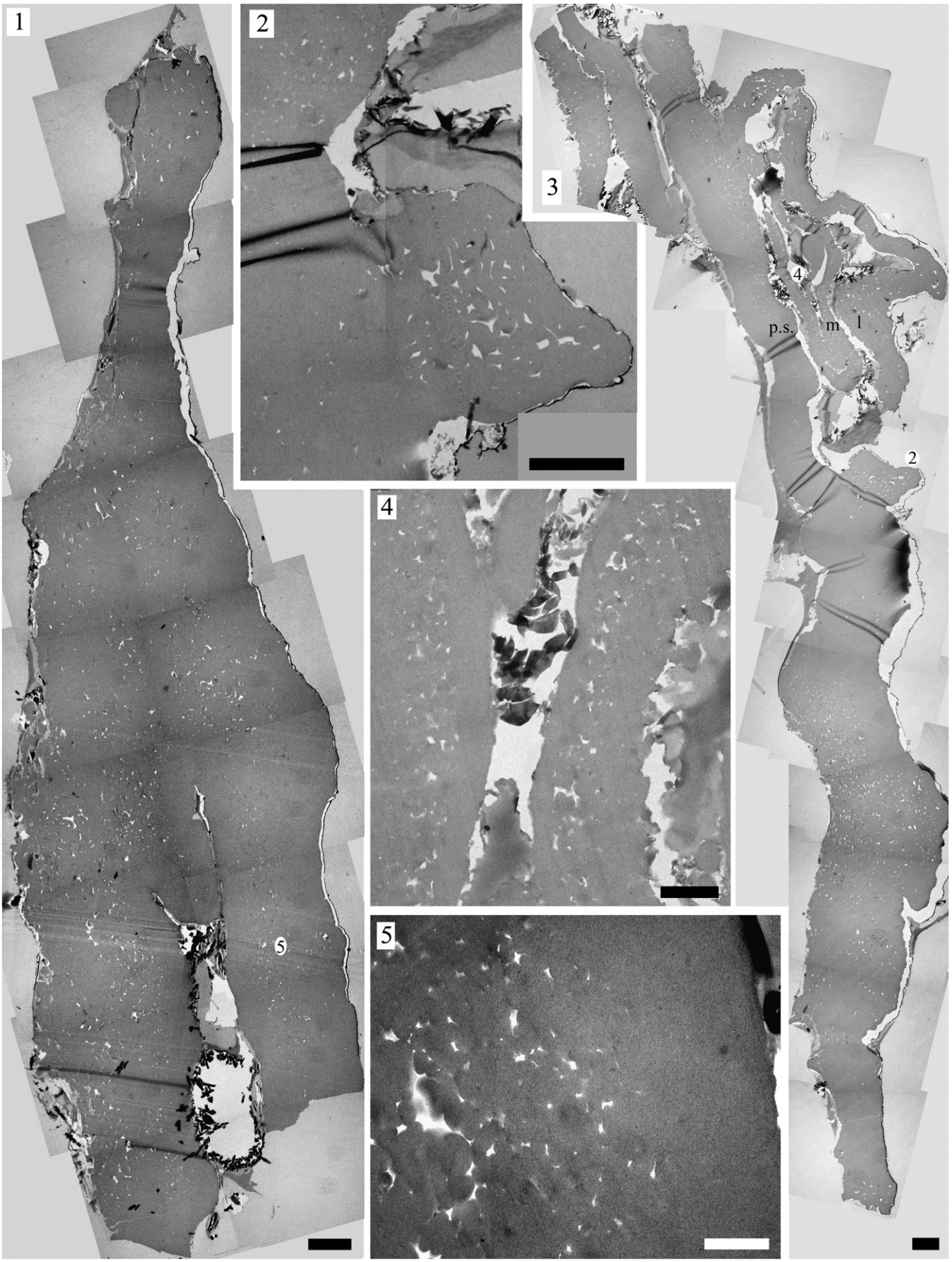
Very few heterosporous plants possessing spores of two distinct sizes have been described from the Middle Devonian or older strata. Existence of such plants in the Givetian is certain – *Contagisporites* and *Biharisporites* are megaspores of Frasnian archaeopteridaleans (see Allen, 1980; Edwards and Richardson, 1996; Gensel, 1980) – but the first appearance of these distinctive spore taxa is noted in the Givetian (e.g. Richardson and McGregor, 1986). The only heterosporous plant macrofossils found in Givetian rocks are *Enigmophyton superbum* (Vigran, 1964), *Mixostrobus givetensis* Senkevitsch, Jurina and Arkhangelskaya (Senkevitsch et al., 1993), and *Longostachys latisporophyllous* Cai and Chen (Cai and Chen, 1996), all three of lycopsid affinity. So far, wall ultrastructure was studied only in *Contagisporites* and *Biharisporites* (Pettitt, 1966; Telnova and Meyer-Melikian, 1993; Turnau et al., 2009).

The late Emsian and Middle Devonian palyno-floras include spores that are not definitely of megaspore size but are relatively large. Their overall equatorial diameter is generally between 100 and 200 μm, only in some cases it exceeds 200 μm, and the size of the inner body that originally contained the protoplast is in most cases around, and often more than 100 μm. Whether the Middle Devonian large spores were produced by homosporous plants, truly heterosporous ones or those with incipient heterospory, is uncertain. It is logical to believe that megaspores and microspores of the earliest heterosporous plants were quite similar in morphology and ultrastructure. This is evident, for example, in megaspores and microspores of *Archeopteris fimbriata* Nathorst and those of *Archeopteris* sp. 1 (Telnova and Meyer-Melikian, 1993), and in megaspores and microspores of *Tanaitis furcihasta* Krassilov, Raskatova and Istchenko (Krassilov et al., 1987 and unpublished data of NZ on their ultrastructure). If our interpretation of the specimen st2-16 as a megaspore of *Pomeranisporites subtriangularis* and attached microspore is correct, the ultrastructure of the microspore and megaspore produced probably by the same parent plant is similar. The successful dispersal of spores exceeding 115 μm requires acquisition of specific morphological and ultrastructural characters (Hemsley et al., 1999). Thus, whichever is the gender of the Middle Devonian large spores, their spore wall may share certain features with megaspores of related plants, and therefore data on their morphology and spore wall ultrastructure have been included in our discussion below.

A vast amount of information on affinity, morphology and wall ultrastructure of Carboniferous megaspores is now available. The data on those megaspores representing lycopsids (reviewed by Balme, 1995) are also used in our discussion. On the other hand, we have not included ultrastructural data concerning spores of the

Plate X. Ultrastructure of *Pomeranisporites subtriangularis*, TEM, specimen st2-16, proximal surface facing right in all images. Black line visible in Plate X, 1–3 is remnant of SEM coating. (see on page 17)

1. Composite image of section showing the pseudozona and part of the body. Number in white oval indicates position of relevant enlargement.
2. Detail of proximal outer layer showing an element of proximal sculpture.
3. Composite image of section through the proximal pole, distal wall is missing supposedly because of mechanical damage by our handling of the specimen; numbers in white ovals indicate positions of relevant enlargements; (m) wall of a supposed microspore; (l) labrum; (p.s.) proximal wall.
4. Detail of wall of the supposed microspore.
5. Detail of proximal outer wall showing oval and circular units. Scale bar (1–3) 5 μm, (4, 5) 1 μm.



other plants that achieved heterospory in the Paleozoic. We consider the wall ultrastructure of the stauropterid seed-megaspores and sphenopsid megaspores as completely different from that we have described (see Hemsley, 1990; Lugardon and Brousmiche-Delcambre, 1994).

4.1. Corystisporites acutispinosus

This azonate species, due to its wide contact faces comprising the entire proximal hemisphere, high, flexuous labra, and the distal ornament of densely set, prominent, acute appendages displaying the hollow basal part and solid distal one is closely comparable to *Acinosporites macrospinosus* Richardson, 1964. This species is thought to be of lycopsid affinity based on spore wall ultrastructure (Wellman, 2004). The ornamentation processes of our species are acute, but in construction they are similar to the bifurcate processes of *Ancyrospora* and *Hystricosporites*. The presence of the wide, hollow basal part and the distal solid part is apparent in larger representatives of *Hystricosporites*, like *Hystricosporites grandis* Owens, 1971 (see Chi and Hills, 1976, pl. 5, figs. 1, 2) or *Hystricosporites multifurcatus* Winslow, 1962 (see Higgs and Scott, 1982, pl. 2, figs. 2, 9). The ornamentation processes of *Ancyrospora grandispinosa* Richardson, 1960 and *Ancyrospora ancyrea* (Eisenack) Richardson, 1962 have a spongeous basal part and solid tip (Wellman, 2002). The basal spine part in *A.* cf. *ancyrea* is hollow (Urban, 1969). *Ancyrospora* and *Hystricosporites* are thought to be lycopsid spores because their processes are like those in megaspores of the Upper Devonian *Borysthenostrobus mirandus* Ishchenko and Semenova, 1982 (Wellman, 2002) and *Krishtofovichia africani* Nikitin, 1934 (Wellman, 2002). The former is a lycopsid fructification, the latter a putative lycopsid. Moreover, as noted by Marshall (2000), high abundance of *Ancyrospora* in the Orcadian Basin, in strata bearing the presumed lycopod *Thursophyton* suggests lycopsid affinity of the genus. Spore wall ultrastructure in *Ancyrospora* agrees with that supposition (Wellman, 2002).

Based on TEM observations, in *Corystisporites acutispinosus*, the innermost part of the inner layer is a concentric, continuous lamina bordering the lumen, appearing thicker than the overlying laminae. This lamina is followed by a laminate layer. This construction is not specific to this taxon, it has been noted in spores placed in distant plant groups like *Ancyrospora ancyrea* on one hand (see Wellman, 2002), and spores of the trimerophyt––progymnosperm intermediate *Oocampsa catheta* (see Wellman and Gensel, 2004) on the other. The outer exospore of *C. acutispinosus* resembles that of several megaspore taxa. The tabular elements with short appendages or knobs at the margin, present in the inner part of the outer layer of our species, recall the type-C elements (Fig. 4) of the outer part of inner body in *Grandispora ciliata*. In the Devonian *Valvisisporites auritus*-type megaspores from *Polysporia*-type sporangia, the elements forming the outer spore wall are elongate, short, parallel to the spore lumen, and toward the outside they thicken and become perpendicular to the spore surface (Bek et al., 2009, pl. IV, fig. 1, 2). In *Crassilagenicula agnina* (Zerndt) Dybova-Jachowicz et al., 1979, *Lagenicula acuminata* Dijkstra and Piérart, 1957, *Setosisporites brevispinosus* (Zerndt) Brzozowska, 1968, *Rotatisporites rotatus* (Bartlett) Potonié and Kremp, 1954, and *Rotatisporites dentatus* (Zerndt) Dybova-Jachowicz et al., 1977, the centrifugal gradation in thickness of the outer exospore units is very pronounced. The inner region where the units are aligned tangential to the spore lumen is wide, and the thick units of the outer region are perpendicular to the spore surface (Glasspool et al., 2000, pl. IV, VII, IX; 2009, pl. III, IV). The ornamentation processes in *L. acuminata* and *Crassilagenicula pseudoagnina* (Dijkstra and Piérart) Dybova-Jachowicz et al., 1979 are porous (Glasspool et al., 2009, pl. V), those in *Sublagenicula variabilis* (Winslow) Dybova-Jachowicz et al., 1979 have hollow bases (Arioli et al., 2007). The affinity of those Devonian and Carboniferous megaspore taxa is summarized in Balme (1995); see also Bek et al. (2009). *Valvisisporites* and probably *Rotatisporites* belong to isoetalean lycopsids, family Chaloneriaceae. *Lagenicula* is related to Lepidocarpaceae and lycopsids of uncertain affinity. *S. brevispinosus* is thought to have been produced by members of the Selaginellales.

4.2. Coronispora variabilis

These zonate (coronate) megaspores are strikingly similar in ornamentation to two Mississippian azonate, gulate species, i.e. *Sublagenicula catenulata* (Winslow) Dybova-Jachowicz et al., 1979 (Dybova-Jachowicz et al., 1987, pl. 11, 12), and *Lagenicula multiapicalis* Hills, Hyslop, Braman, Lloyd (Hills et al., 1984, pl. 3). Both species share with *Coronispora variabilis* an ornament of chains of flat elements with spinose crests, connected by bridges, forming a reticulate distal pattern. As in *C. variabilis*, in *S. catenulata* the murus encircling the equator forms a corona (Dybova-Jachowicz et al., 1987, pl. 11, fig. 1, 1a, pl. 12, fig. 1, 1a). The parent plant of *S. catenulata* is not known, but another species — *Sublagenicula levis* (Zerndt) Dybova-Jachowicz et al., 1979 is a sigillariaceous megaspore (Opluštil et al., 2009).

The outer wall of *Coronispora variabilis* is partly formed of cylindrical, elongate, forking and anastomosing units. Elements of that shape, described as fibrous, tubular, rodlike, cylindrical or elongate-forking, form the spore wall or part of the spore wall of many Middle and Upper Devonian spore taxa. The large spores *Ancyrospora grandispinosa* Richardson, 1960, and megaspores of the putative lycopsid *Nikitinsporites canadensis* Chaloner are formed of such elements (Taylor et al., 1980; Wellman, 2002). Interlinking, elongate units like those that form a mesh on megaspore surface of *C. variabilis* were observed in megaspores of *Barinophyton citrulliforme* Arnold (Taylor and Brauer, 1983), and *Protobarinophyton pennsylvanicum* Brauer (Cichan et al., 1984), but the more advanced morphology of our taxa suggests their affinity to a group with a later point of origination. The mesh-like megaspore surface occurs also in the propagules of Late Devonian plants like the herbaceous lycopsid *Kossoviella timanica* Petrosjan (Telnova and Meyer-Melikian, 2002, pl. IV, fig. 2), the arborescent, eligulate lycopsid *Bisporangiostrobus harrisi* (Chitaley and McGregor, 1988), and the seed-like structure *Sphinxiocarpon wuhanium* (Li, Hilton and Hemsley) Wang, Xue and Prestiani (Li et al., 1997). Morphology of the latter fructification precludes assignment to any known group of plants. Cylindrical, forking and anastomosing units forming a mesh-like pattern on megaspore surfaces occur in many Carboniferous megaspore taxa related to lycopsids (summarized in Balme, 1995). Those are, for instance, *Lagenicula subpilosa* (Ibrahim) Potonié and Kremp, 1955 f. *major* Dijkstra ex Chaloner, 1954 (Scott and Hemsley, 1993), *Valvisisporites auritus* (Zerndt) Bhardwaj, 1958 (Gastaldo, 1981) and the seed megaspores *Cystosporites* (Hemsley, 1993). The proximal outer wall of *C. variabilis*, in the apical region, is composed of tangentially arranged, stacked laminae. Lamellate outer wall occurs in the Middle Devonian large spores *Ancyrospora ancyrea* (Eisenack) Richardson, 1962 (Wellman, 2002) and in *Acinosporites macrospinosus* Richardson, 1964 (Wellman, 2004).

4.3. Grandispora ciliata

The general morphology of this species makes it a member of the large group of the latest Emsian and Middle Devonian pseudozonate/pseudosaccate large spores with prominent labra and ornamentation of spines included in *Grandispora*, *Samarisporites*, and *Calyptosporites*. Gross structure of several of these taxa is known owing to studies by Allen (1965), Wellman (2001, 2002) and Wellman and Gensel (2004). The species *Grandispora ciliata* differs from *Grandispora douglastownense* McGregor, 1973, *Grandispora* ?*macrotuberculata* McGregor, 1973, and from in situ spores of the trimerophyte-progymnosperm intermediate *Oocampsa catheta* (Andrews et al., 1975) in the degree and mode of cameration. In those taxa, the cavity is not complete; in places the inner body and the outer layer are closely attached (Wellman and Gensel, 2004). The ornament of solid, homogenous processes in *G. ciliata* is very different from the

ornamentation processes of *Oocampsa* spores and representatives of *Grandispora* described by Wellman and Gensel (2004) that are formed by folding of the outer layer. Another species of this group is *Samarisporites orcadensis* (Richardson) Richardson, 1964. It is a pseudozonate form considered by Wellman (2001) to be acamerate, but in our opinion it may have an equatorial camera. The solid ornament of *G. ciliata* compares well with the solid verrucae, coni and spinae of *S. orcadensis* (see Wellman, 2001). The species *Calyptosporites proteus* (Naumova) Allen, 1965 including pseudosaccate, large spores ornamented by spines (Allen, 1965) is, in general terms, similar to *G. ciliata*. But in our specimens, the outer wall is at least six times thicker than that of the inner body, while in the taxa discussed above both layers are roughly of similar thickness. Comparing the relative thicknesses of the inner body and outer envelope, *G. ciliata* compares well with the dispersed Devonian pseudosaccate megaspores *Contagisporites optivus* (Chibrikova) Owens, 1971 known also from archaeopteridalean sporangia (Pettitt, 1965; Phillips et al., 1972). But in our species the camera is formed within the inner part of the outer layer, while in *C. optivus* it is formed between the inner and outer layer (see Turnau et al., 2009, pl. V, 1). The presence of a tangential gap within the inner part of the outer layer separating the former from the latter is a feature of many fossil and extant lycopsid megaspores (Taylor, 1994). As far as we currently know, members of progymnosperms (aneurophytes and archaeopterids) are similar to each other as far as ultrastructure of the outer wall is concerned. Descriptions vary (Pettitt, 1966; Telnova and Meyer-Melikian, 1993; Turnau et al., 2009; Wellman, 2009) but the spore wall is composed of fused granular elements. Only the fine structure of the outer spore wall of *Rhabdosporites langii* (Eisenack) Richardson described by Taylor and Scheckler (1996) seems to be different, but this may be explained by the laboratory treatment employed by these authors (HNO_3 and Schulze's solution). The outer spore wall of progymnosperms differs distinctly from that of *G. ciliata.*

Megaspores of morphology similar to our species are the Devonian and Carboniferous representatives of *Valvisisporites*. Although these megaspores are described as cingulate (following Potonié and Kremp, 1955) they are equatorially pseudosaccate which is obvious on examination of broken specimens (see Bek et al., 2009, pl. III, figs. 1, 3) or based on the way in which the auriculi collapse (see Taylor, 1990, pl. IV, fig. 24). In *Valvisisporites*, separation of the inner body from the outer envelope is within the outer wall layer (Bek et al., 2009, pl. V, 1), just like in *Grandispora ciliata*. The construction of the triradiate labra in some specimens of our species and in *Valvisisporites* (see Bek et al., 2009, pl. VI) is also similar. In both taxa the triradiate fold involves the inner and the outer spore wall layers. The inner wall of *G. ciliata* megaspores includes the inner part that appears homogenous but consists of fine, indistinct, tightly packed laminae, and the outer laminate part with laminae becoming thicker upwards. Similar construction of the inner wall characterizes the Devonian and Carboniferous representatives of *Valvisisporites* (Bek et al., 2009; Gastaldo, 1981; Glasspool et al., 2009; Taylor, 1990). In these taxa, the inner part of the inner layer appears homogenous, but in the opinion of Lugardon (in Bek et al., 2009) it may be formed by very fine laminae.

The tangentially orientated, elongate cylindrical and forking elements present in the outer part of the inner body and the inner part of the outer envelope of *Grandispora ciliata* (unit D in Fig. 4) are comparable to those forming most of the outer wall of *Coronispora variabilis*, though the region formed by those elements in *G. ciliata* occupies only a small part of the spore wall. This similarity is best seen in TEM images which show constant alternation of elongate and rounded elements (compare Pl. VI, 4 with Pl. VIII, 1, 4). Such elongate, cylindrical, forking units occur in many megaspore taxa (see the discussion of *C. variabilis* above). The type-C elements (Fig. 4) of the *G. ciliata* wall are somewhat similar to those of the inner part of the outer wall of *Corystisporites acutispinosus*. The bulk of the outer wall of *G. ciliata* is homogenous, but it is possibly formed of some large, fused, possibly globular elements. A homogenous outer wall layer or sublayer occurs in spores of distant plant groups like *Oocampsa catheta* (Wellman and Gensel, 2004) and *Ancyrospora grandispinosa* Richardson (Wellman, 2002). It is significant that in *A. grandispinosa*, it is the outer part of the outer layer that forms the equatorial pseudozona (see Wellman, 2002, Fig. 5, unit C) thus, in that species, the inner body, like that in *G. ciliata*, includes the inner layer and the inner part of the outer layer. The outermost granular layer present in our species may be compared with the globular layer developed randomly at the spore surface in *Ancyrospora ancyrea* (Eisenack) Richardson (Wellman, 2002).

4.4. Pomeranisporites subtriangularis

This species bears a superficial resemblance to the Carboniferous zonate megaspores included in *Triangulatisporites*, a genus generally associated with the Selaginellales (see Balme, 1995). Though superficially similar is *Triangulatisporites* cf. *bellus/regalis* that bears a proximal and distal, discontinuous reticulum with muri surmounted by spine-like projections (Cottnam et al., 2000). But *Triangulatisporites* megaspores differ in having a zona instead of pseudozona, and having sculptural elements formed by the surface layer of the outer wall (see Cottnam et al., 2000, pl. 1, figs.1–3). Externally, our species is strikingly similar to the uppermost Devonian (Strunian) megaspores *Triangulatisporites*? *leinsterensis* Higgs and Scott (1982) that have contact faces ornamented by convolute ridges and a radially ridged equatorial flange. Of some similarity is the Givetian, very large (1600 μm) megaspore ?*Triangulatisporites* sp. (Stockmans and Streel, 1969). Also similar are the Frasnian zonate, spinose, distally reticulate megaspores *Lagenicula devonica* var. *reticulatus* Chi and Hills, 1976, not really a representative of *Lagenicula*. So far, there is no information on affinity, architecture or ultrastructure of those Devonian taxa.

In *Pomeranisporites subtriangularis*, the innermost part of the inner layer is a concentric, continuous lamina bordering the lumen, thicker than the successive laminae. This lamina is followed by an apparently homogenous but presumably laminate layer. But in taxa placed with distant plant groups, such as *Ancyrospora ancyrea* (see Wellman, 2002), and spores of *Oocampsa catheta* and related forms (see Wellman and Gensel, 2004) the spore lumen is also bordered by a continuous lamina thicker than the successive laminae. The nature of the sporopollenin units forming the very dense inner part of the outer wall of *P. subtriangularis* is hard to evaluate. The elongate, undulating elements present more to the outside may represent laminae that are folded. Such units form part of the proximal outer wall in *Coronispora variabilis*, while the outer wall of *Ancyrospora grandispinosa* includes folded laminae (Wellman, 2002).

4.5. Discussion

The inner layer of spore wall in *Corystisporites acutispinosus*, *Coronispora variabilis* and *Grandispora ciliata* (possibly also in *P. subtriangularis*) consists of laminae that thicken and are less regularly orientated upwards. This construction is not specific to spores of one plant group, we find it in some Devonian progymnosperms (*Rhabdosporites langii* (Eisenack) Richardson, 1960, see Wellman, 2009) and some Devonian and Carboniferous lycopsids (*Valvisisporites*, see Bek et al., 2009).

The spore walls of four species described herein may be considered as typically lycopsid (cf. Wellman, 2009) i.e. including a narrow laminate inner exospore and wide, spongeous outer exospore (units small, globular to elongate or laminate. Our species also share several morphological and ultrastructural characters with various taxa of large spores and megaspores of assumed or proved lycopsid affinity. Moreover, *Grandispora ciliata* megaspores have a typical lycopsid inner separable layer. On the contrary, our megaspores differ, especially in spore wall ultrastructure, from those of trimerophytes and progymnosperms, and

from megaspores of other plants that achieved heterospory in the Paleozoic, i.e. sphenopsids and pre-ferns (reviewed in Balme, 1995). Thus, one could assume that all our taxa represent plants of lycopsid affinity. However, a firm assignment to any of the known plant clades would be premature because our knowledge of Devonian plants and their spores still contains many unanswered questions. There are quite a few so-called enigmatic Devonian plants, and only some have been studied in terms of ultrastructure. The results of those studies are confusing. For example, megaspores of still undescribed, Frasnian enigmatic plant informally called '*Ludovatia*' are zonate and their ornament is like that in *Ancyrospora* (Jurina and Raskatova, 2007). In transmitted light the megaspores are quite similar to *A. deltatus* Chi and Hills. The spore wall of the '*Ludovatia*' megaspores has a thin inner layer appearing homogenous but probably lamellate and a much thicker, spongeous outer layer formed of folded, anastomosing laminae increasing in thickness toward the outside. This is a similar ultrastructure to that in many lycopsid megaspores, for instance those of *Polysporia* described by Bek et al. (2009). The ornamentation processes of these megaspores have a spongeous basal part and solid distal part (Jurina et al., 2002, 2005). Dispersed megaspores of that morphology and ultrastructure would be considered as typically lycopsid, but the parent plant '*Ludovatia*' that has been studied by a large team of paleobotanists (see the introduction in Jurina and Raskatova, 2007), is considered to be anything but a lycopsid. The seed-megaspores of *Sphinxiocarpon wuhanium* (Li, Hilton and Hemsley) Wang, Xue and Prestiani display a spongeous fibrous construction of the outer spore wall (Li et al., 1997) typical of the lycopsids. But the morphology of *S. wuhanium* precludes assignment to any known group of plants.

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