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Microspore Wall Structure in *Selaginella kraussiana* (Lycophyta)

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ABSTRACT: We have examined fresh and macerated microspores of *Selaginella kraussiana* (Kze.) A. Br. using scanning electron microscopy and chemically fixed spores prepared for transmission electron microscopy. These examinations indicated that the outer spiniferous part of the microspore wall (exospore) is composed of rods that are 70 to 130 nm in diameter and it has numerous conduits of variable size, that pass through the exospore. The structural rods of the exospore are deflected around the conduits. The inner part of the exospore has radial conduits (channels) and it has the same rod-structural units as the outer part. The spines on the outer exospore increase in number and size during development and develop many branches. The outer part of the exospore is separated from the inner part of the exospore by a gap.

KEY WORDS: Exospore units, Lycophyta, Microspores, *Selaginella*, Ultrastructure.

INTRODUCTION

While *Selaginella* is the only genus of Selaginellaceae there are ca 700 species that occur in all landforms except Antartica and some far north islands. About 25 species are cultivated domestically as ornamentals (Lawrence 1951). *S. kraussiana* is one of the species that is widely cultivated.

Perhaps the first study of *Selaginella* microspores was by Millardet (1869) on *S. kraussiana*. He described the formation of antherozoids. Pfeffer (1871) worked mostly on microspores of *S. martensii* and *S. caulescens* but studied *S. kraussiana* to check on Millardets results and he confirmed them. Belajeff (1885) studied ten species of *Selaginella* and seems to have been the first to consider spore wall layers. He determined that microspores of *S. kraussiana* and *S. poulteri* had three spore wall layers and the others only two layers but all developed their antheridia as had been described by Millardet and Pfeffer. Lyon (1901) and Campbell (1902, 1918) studied *S. kraussiana* with regard to development and dispersal of sperm cells.

Slagg (1932) described and illustrated development of *S. kraussiana* microspores. This author wrote that his purpose was to obtain, if possible, a more reliable account than was available of microspore development in a single species. There is now considerably more information about *Selaginella* microspores due to work by Stainiér (1965), Pettitt (1966), Robert (1970, 1971), Gullvåg (1971), Lugardon (1978, 1986, 1990) and Tryon and Lugardon (1991).

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Erdtman (1957: Fig. 179) has a drawing showing the laesura of the proximal surface and spines on the equator and the distal surface and there are internal cavations observable in them with light microscopy.

The scanning electron microscope (SEM) figure of *S. kraussiana* in Foster and Gifford (1974: Fig. 9-23B) suggests that the spines have rod-like surface structures. Our aim in this study was to determine the basis for this rod-like surface texture and the relationship of the rod structures to the internal cavations.

MATERIAL AND METHODS

Material was obtained from the greenhouses of the Kew Botanical Garden, England and the Botany Department of Stockholm University, Sweden. In the last case all samples were taken from one plant.

For TEM fresh material was fixed using 0.003% ruthenium red, 3% glutaraldehyde, and 2% paraformaldehyde in 0.1M phosphate buffer (pH 7, 48 h, 4℃). After decanting these fixatives the material was transferred to 1% osmium tetroxide plus 0.003% ruthenium red for 1 h. Dehydration was with an acetone series before embedding in Spurr hard mixture (Spurr 1969). Some sections were stained using uranyl acetate followed by lead citrate (UA-Pb). Other sections were stained with 1% periodic acid followed by 0.1% phosphotungstic acid in 10% chromic acid (PA-PTA-C); a simple and clean contrasting method giving results similar to the PAS reaction or the Thiéry procedure for carbohydrates. "PA-TCH-C" procedure was introduced by Roland *et al.* (1972) to contrast polysaccharides and carbohydrates on the plant cell plasma membrane. Observations were with a Zeiss 10A TEM.

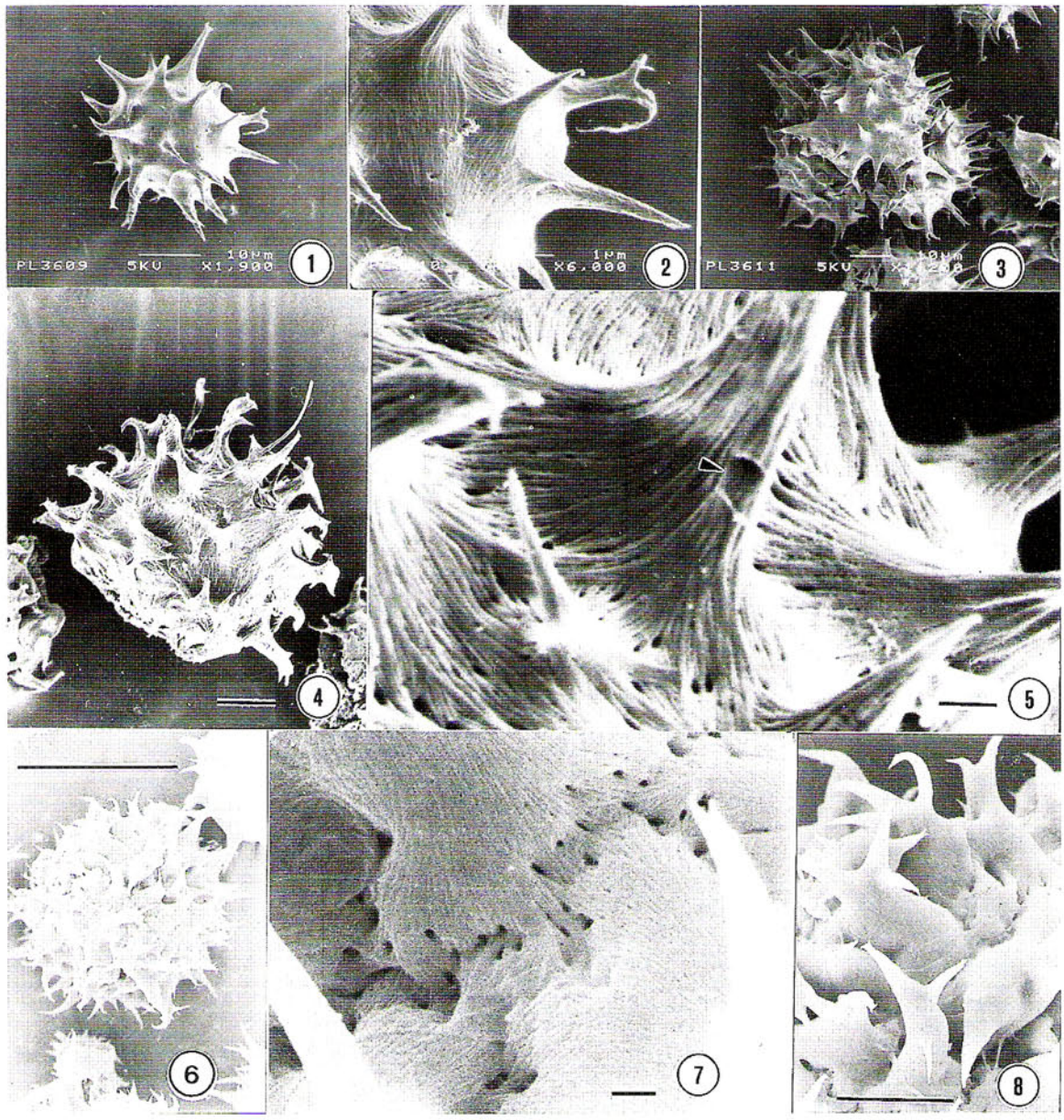
For SEM studies the spores were prepared either fresh and sputter coated with gold/palladium or by a freeze fracture and cytoplasmic maceration technique (Barnes and Blackmore 1984; Blackmore and Barnes 1986). The specimens were examined with Cambridge Stereoscan 600, JEOL JSM-6300 and Hitachi S800.

RESULTS

We will refer to the spiniferous part of the *S. kraussiana* microspore covering as the outer-exospore and the wall component close to the spore cytoplasm as the inner-exospore. The space between inner- and outer-exospore is termed the gap. The layer on the cytoplasm (homologous to the intine of pollen) is referred to as endospore.

In SEM micrographs there are rods in interspine parts of microspores and on the surface of spines from their base to the tip (e.g., Figs. 2, 5, 8, 14, 20-22). There are perforations between these rods, notably around spine bases (Figs. 5, 7 & 15). Most rods are ca 100 nm in width and their height is as great as the 10 μm or more height of spines.

In TEM sections of the outer exospore spinules, where glancing (tangential) exposures are more common than in the inner exospore, rods are exposed with great frequency (Figs. 9-12). Their orientation is mostly radial in spines (Figs. 9 & 10) but variable in spine bases (Figs. 11 & 12) and in the inner exospore (Fig. 11). It can be seen that the rods do not pass across (through) conduits (Figs. 9-11, 12, 13 & 15).



Figs. 1-8. SEMs of fresh *S. kraussiana* microspores. Fig. 1. Young microspore with spines that are mostly undivided (unbranched). The diameter of the body (without spines) is less than 24 μm. Bar=10 μm. Fig. 2. Part of the microspore in Fig. 1 at higher magnification. The surface is striated and there are perforations. Bar=1 μm. Fig. 3. Tetrad of young microspores. Bar=10 μm. Fig. 4. Equatorial view of a middle stage in microspore development. Many spines are branched. There are only a few short spines evident on the proximal side. Bar=10 μm. Fig. 5. This SEM illustrates the continuity of the rods of the exospore structure. The rods by-pass the openings of the conduits. Rods can be seen inside of the spine in a chipped site (arrowhead). Bar=1 μm. Fig. 6. A distal surface showing that by late stages of development there has been a great increase in number of spines and their branches. There is also a great increase in the frequency of perforations (conduits) (please see figure 7). Bar=50 μm. Fig. 7. The rods of the exospore structure are apparent as are the broad bases of spines and the numerous conduit openings in mature microspores. Bar=1 μm. Fig. 8. In mature microspores there are many branches on the now broad spines. Bar=10 μm.

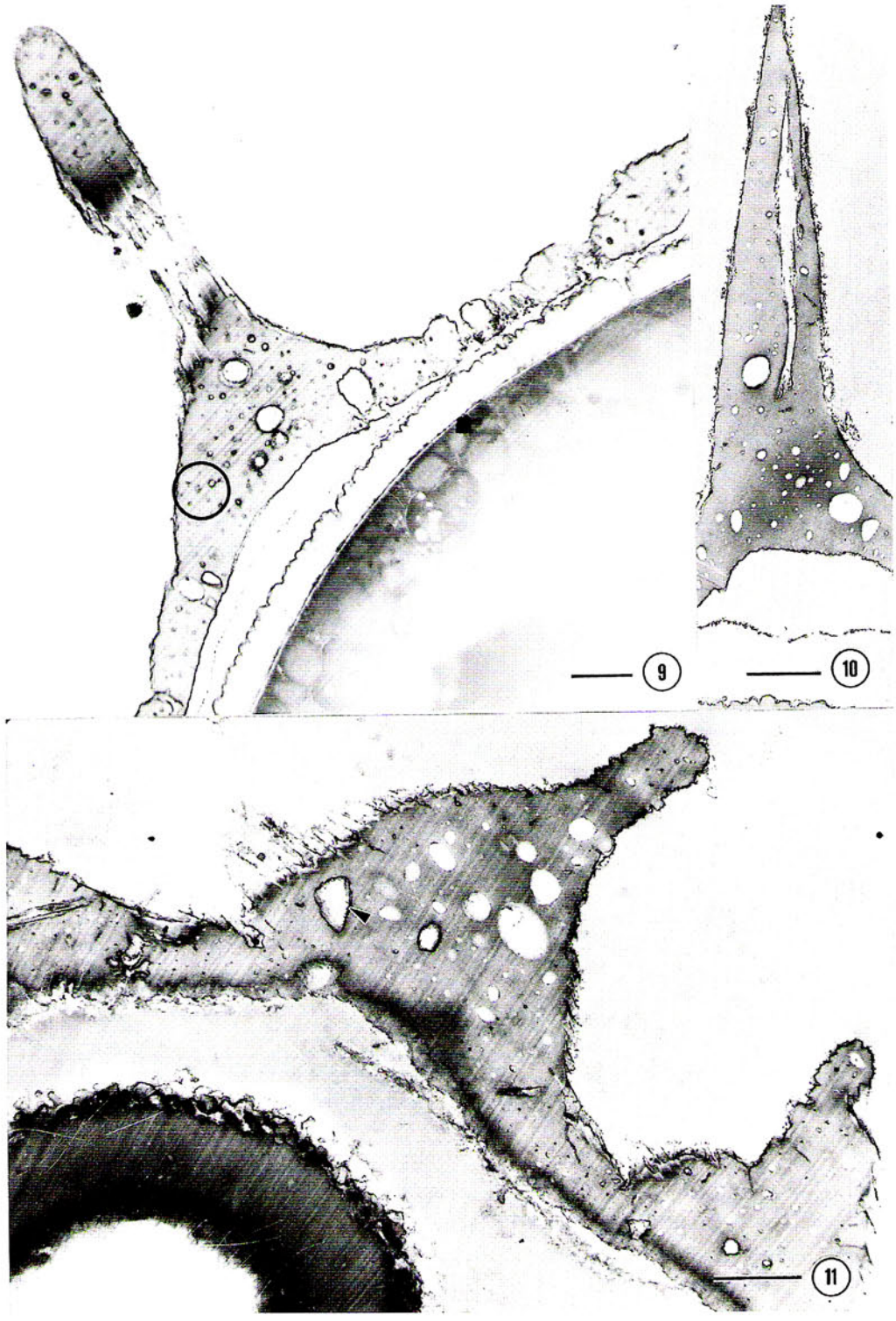


Fig. 9. The spines in the outer exospore consist of rods that are orientated radially for the most part. Rods sectioned obliquely or in cross-section appear as small circles (several are circled). The inner exospore has surface irregularities that are similar in dimensions with the radial rods of the spines. Stain: P-PTA-C. Bar=1 μm. Fig. 10. Tangential (grazing) section of a spine surface show two rods at the base of the long gap and one rod at its top. Stain: P-PTA-C. Bar=1 μm. Fig. 11. The micrograph shows that the inner and outer exospores consist of rods of similar dimensions. Rods do not cross conduits (e.g., arrowhead). Stain: P-PTA-C. Bar=1 μm.

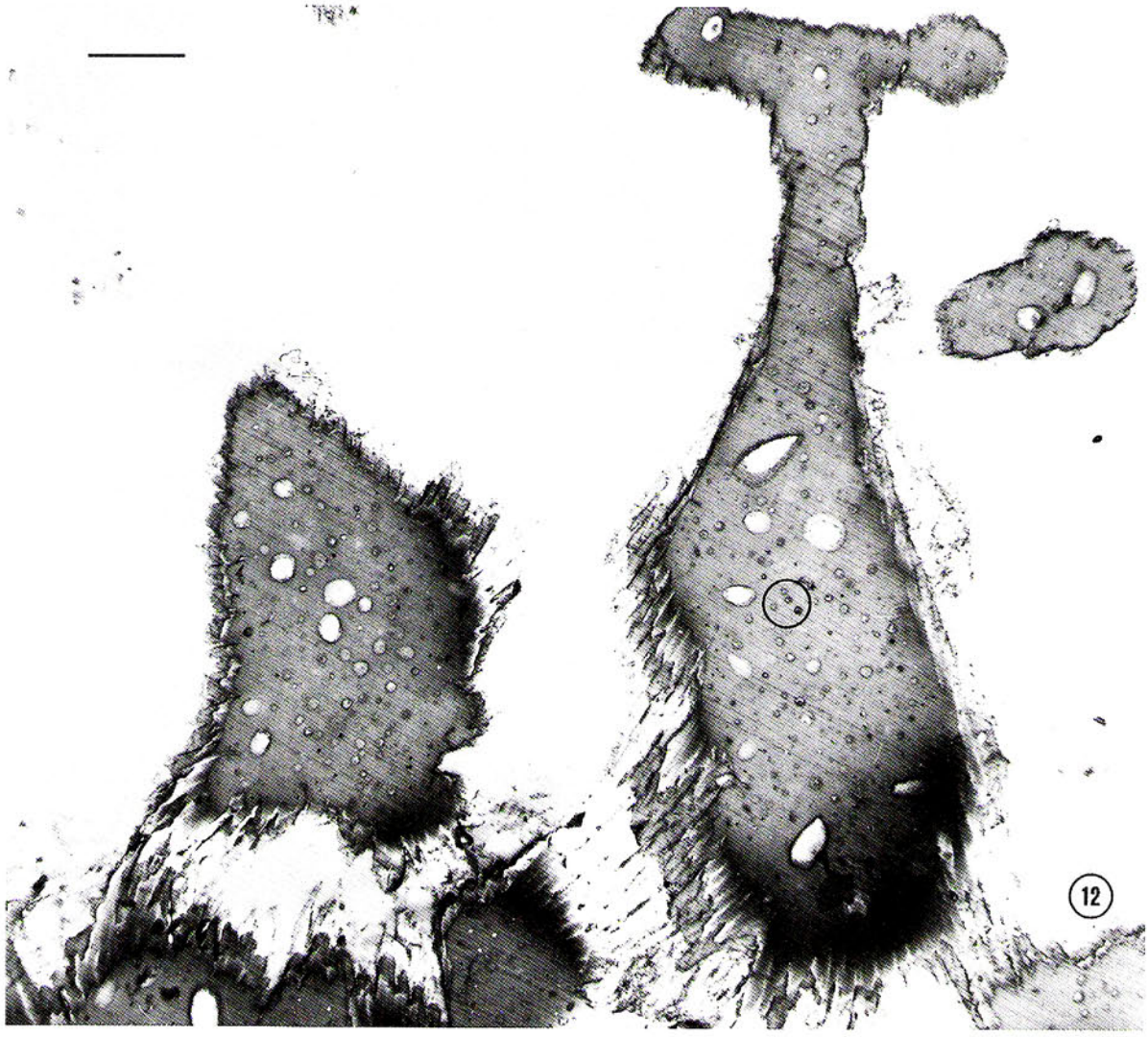


Fig. 12. A grazing section across the basal enlarged portion of two spines in the outer exospore. A multitude of rods pass into and out from these structures and connect between them. The small circles, ca 40 nm in diameter,(four are circled) are considered to be oblique or cross-sections of part of the structural rods. Stain: P-PTA-C. Bar=1 μm.

The spiniferous, outer part of the exospore is seen to be separated by a gap from the inner part of the exospore (Figs. 9, 13, 16, 17 & 23). Conduits are readily seen by light microscopy in the outer-exospore (Fig. 23).

The microspores enlarge from less than 25 μm (less spines) in diameter in early stages (Fig. 1), to 40-45 μm in middle stages (Figs. 18, 20 & 23), and to 50 to 60 μm at maturity (Figs. 6 & 19). The number of spines and their basal diameter increase very much as do the branches and connections between spines (compare Figs. 1 & 2 with Figs. 3, 4, 6, 8 & 20-22).

The endospore is darkly contrasted by the PA-PTA-C procedure, indicating polysaccharides (Fig. 16). In figure 16 there are low contrast sites under several conduits and the darkly contrasted endospore up into other conduits.

The inner part of the exospore has radial conduits. These are seen, in some sections, to coincide with conduits in the outer exospore (Figs. 9 & 16).

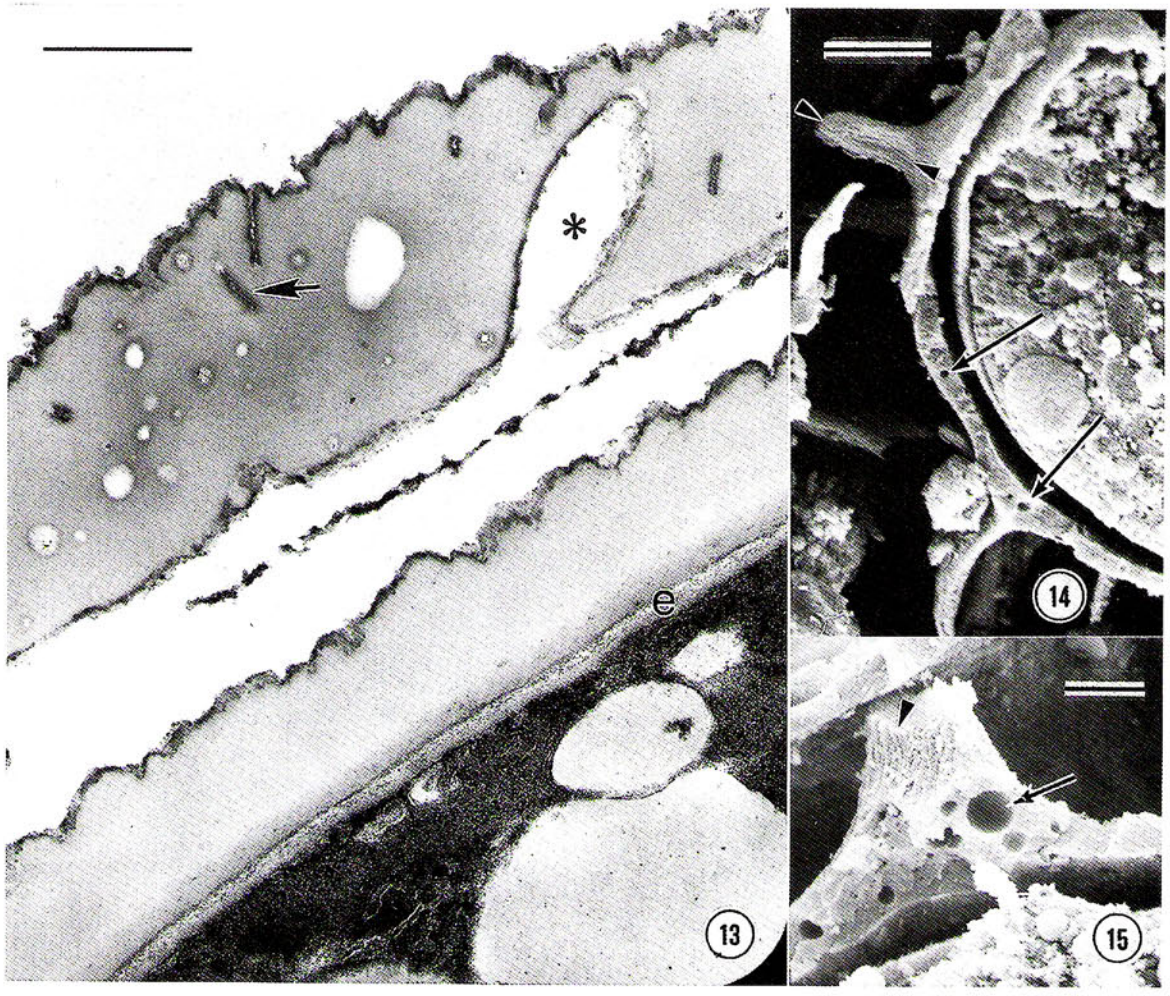


Fig. 13. Section of the inner and outer exospore. The section stain has penetrated part of several of the rod structures (arrow) that form the exospore. The central (core) part of the rods appears to be without contrast. There are many conduits of varing size. A large one (asterisk) is open in this thin section to the inner surface of the outer exospore. There is an endospore (e) and the microspore cytoplasm in the lower part of the figure. Stain: UA-Pb. Bar=1 μm. Fig. 14. This fracture shows several conduits (arrow) in the outer exospore. The inner part of the split (fractured) spine shows radial rods (between arrowheads). Rods are also evident on the surface of the inner part of the exospore at the top and on the left of this fracture. Bar=5 μm. Fig. 15. There are rods on the fractured spine (arrowhead) and several openings of conduits; one that opens onto the inner surface of the outer exospore (arrow). Bar=1 μm.

In all TEM sections stained with UA-Pb there is a very thin darkly contrasted layer between the outer and inner exospore (Figs. 13 & 17). This layer is contrasted by procedures considered to contrast proteins (not shown). A developmental study is needed to indicate the role of this thin layer.

By a middle stage of development (when microspores are 40-45 μm in diameter) the cytoplasm became packed by globular material (Figs. 14, 16, 17 & 23) and plastids containing large starch grains (Fig. 17).

In our illustrations we show tetrads (Fig. 3), two oblique views of the proximal side (Figs. 4 & 20), two images of the proximal surface (Figs. 18 & 19) and a thin section of the proximal side of a microspore (Fig. 17).

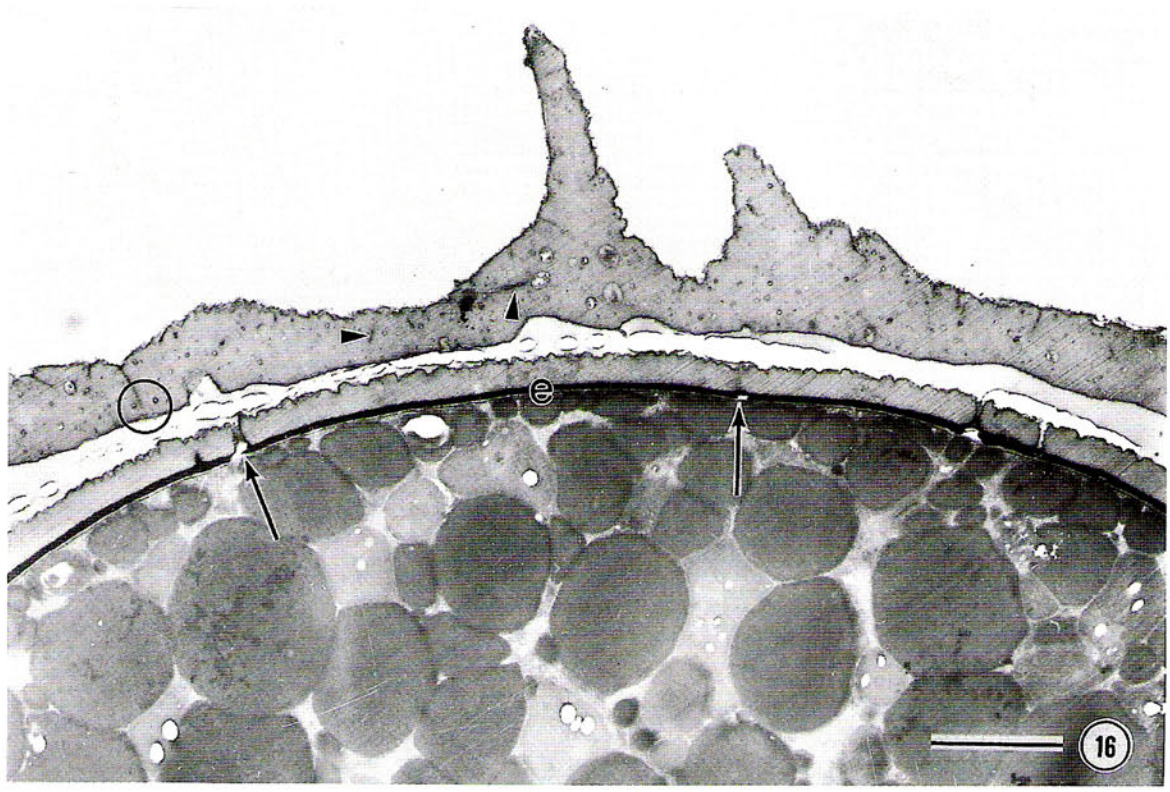


Fig. 16. Section of the distal part of the wall including two spine bases. There are two examples of conduits in the outer exospore opening over conduits (arrows) in the inner exospore. Many of the small structures in the outer exospore seen in cross section (circled) and longitudinal sections (arrowheads) are similar in size to the rods making up the exospore. The endospore (e) is darkly contrasted at this stage. The cytoplasm contains many large globules which may be lipoidal. Stain: PA-PTA-C. Bar = 1 μm.

DISCUSSION

For microspores of *S. kraussiana* Erdtman (1957) and Erdtman and Sorsa (1971) referred to the spiniferous part as a supposedly perinous cover. They noted that it was seemingly unbroken over the aperture and that spines or spine-like processes were up to 15 μm long. They refer to Fig. 179-f in Erdtman (1957) as an example that "shows the 'non-perinous' parts of two microspores confined within a supposedly perinous cover common to them both". The "non-perinous" part of the drawing is, according to our arbitrary terminology, the inner part of the exospore.

Lugardon (1978, 1986) defined the sporoderm in microspores of *S. kraussiana* as consisting of a perispore (our outer exospore), exospore (our inner exospore) and endospore and illustrated them in TEM micrographs. The "perispore" term was based on ontogenetic studies (see below Slagg, 1932 and Robert, 1970, 1971) showing that the perispore forms after completion of the exospore. This "perispore" was found to be independent of the (inner) exospore and continuous over the proximal aperture (Lugardon 1978, 1986, 1990 and Tryon and Lugardon 1991). Lugardon's micrographs in these reports show through the sections of the "perispore" what we call "conduits" in our Figs. 13 and 17.

The space between the outer, spiniferous, part of the exospore and the inner part of the exospore is a gap similar to that described for microspores of some *Selaginella* species and in

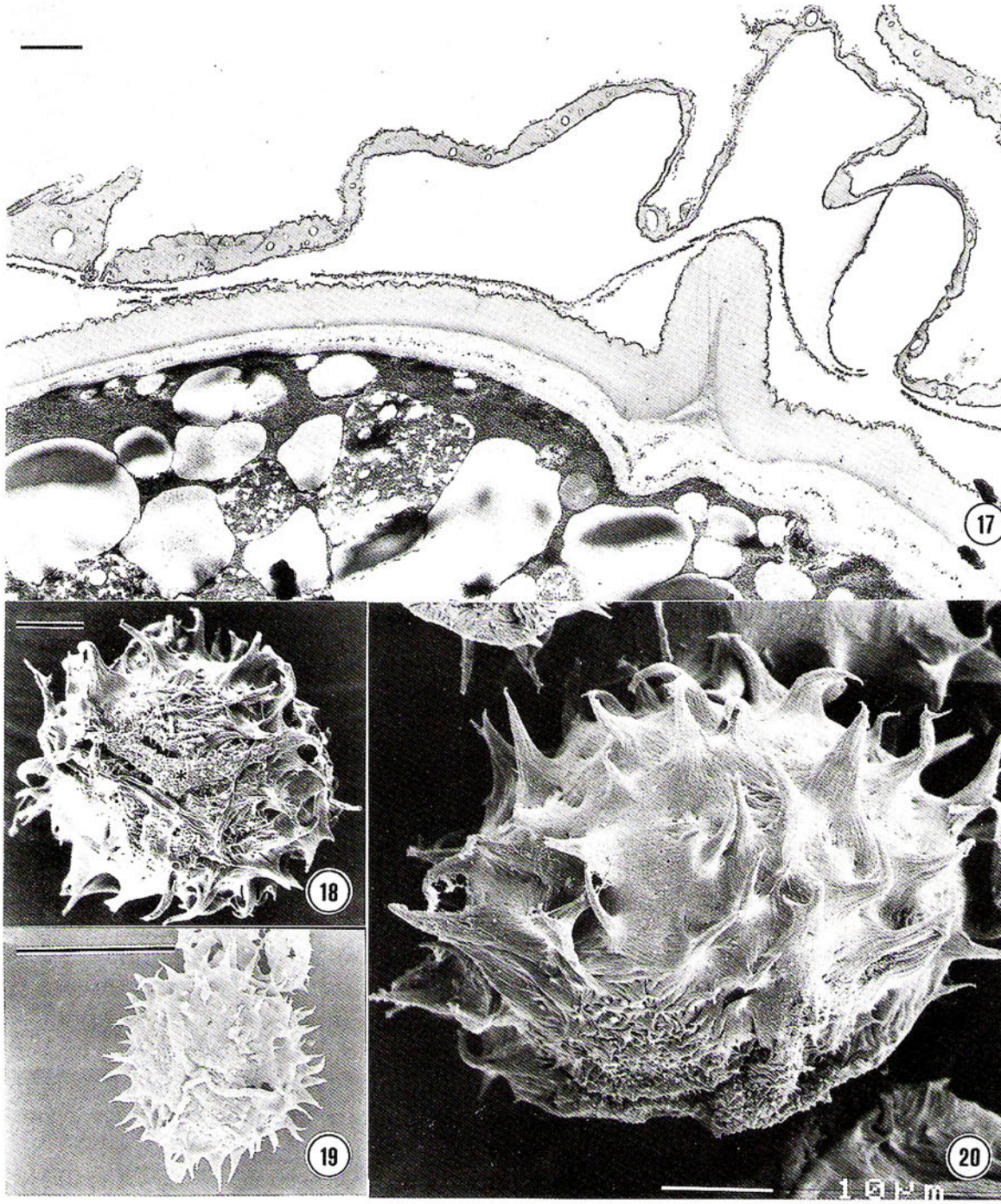


Fig. 17. A laesura sectioned near the proximal pole. The outer exospore is thin but continuous. The endospore (e) is thicker under the proximal swelling. A thin, darkly contrasted, layer is present between the outer and inner parts of the exospore and is continuous over the laesura. Two zones of different contrast can be distinguished on the inner exospore. A conduit open to the inside is evident at the left in the inner part of the exospore. Stain: UA-Pb. Bar=1 μm. Fig. 18. An equatorial view of a middle stage microspore. The surface at the proximal part of the microspore shows many rod-structures. The arms of the triradiate laesura radiate from the asterisk. Bar= 10 μm. Fig. 19. The proximal face of a mature microspore. There are only a few short spines toward the equatorial zone. Bar=50 μm. Fig. 20. An equatorial view showing some of the proximal surface. That equatorial/proximal surface shows a maze of rods. Bar=10 μm.

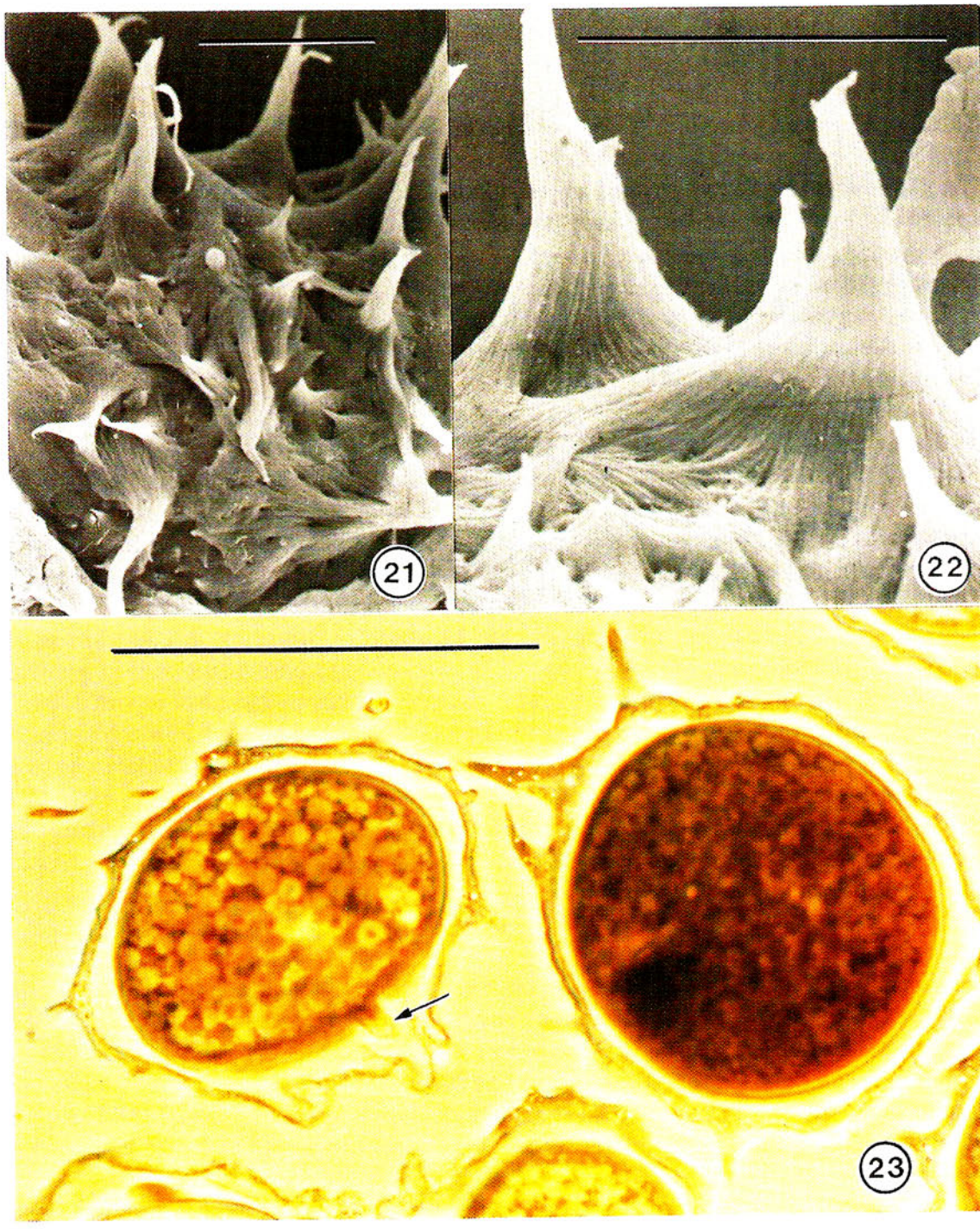


Fig. 21. SEM micrograph of the distal surface of a mature microspore. The change in spine bases, their spread and overlappment is much different from the simplicity and beauty of the condition in the young microspore in Fig. 1. Bar=10 μm. Fig. 22. SEM micrograph of a microspore surface similar to that in Fig. 21. The micrograph shows the bridges between spine bases and their rod-structures. Bar=10 μm. Fig. 23. Photomicrograph of a young microspore before the spines are much branched and their bases greatly expanded. Clearly there has been a great accumulation of nutrient material in the cytoplasm of these microspores. The molecules for these nutrients came from the tapetum and crossed the outer-exospore, the gap and the inner-exospore. An apertural arm (laesura) appears in the section as nipple (arrow) on one of the microspores. Bar=50 μm.

Selaginella megaspores (Morbelli and Rowley 1999). Species of *Selaginella* having microspores with two sporopolleninous walls and a gap between them have been described by Lugardon (1972, 1978, 1986, 1990) and Tryon & Lugardon (1991) for *S. kraussiana* and *S. selaginoides* and by Morbelli *et al.* (2001) for *S. peruviana* and *S. sellowii*.

The sporoderm structure of *S. selaginoides*, similar to that of *S. kraussiana,* but described as having a different sequence of development, was studied in detail with TEM by Lugardon (1972). He distinguished two layers: an outer para-exospore and the inner one termed the exospore. He found after acetolysis and potassium permanganate treatment and exposure to silver proteinate that the exospore and para-exospore had the same texture and contrast. Lugardon (1990) concluded that the two wall layers of *S. selaginoides* have perfect continuity when joined together. In mature microspores the para-exospore has the same texture and contrast as the exospore and Lugardon (1972) concluded that "les deux parois se confondent perfaitement" (the two layers are perfectly similar).

Development of spines in the outer exospore of *S. kraussiana* microspores

Slagg (1932) determined that the four microspores remained for a time in a thin microspore mother cell (MMC) wall. He suggested that this was made into the exospore by deposits from the tapetum. He found that the exospore was at first smooth then when microspore diameters became ca 20 μm papillate projections appeared upon the outer surface and then these grew into long spines. He showed in sections (Slagg 1932: Fig. 14) that both the new endospore within the exospore and the exospore --- were not in close apposition. Slagg considered that during growth of the microspore, the exospore outstrips it in growth of the endospore, and the gap between the two became widened. He also reported that in microspores still within a microsporangium the radial seam is puckered into a longitudinal crest which in section appears like a nipple. Then the outer layer thins at the apex to about half its thickness elsewere.

Slagg (1932) found that abortion was common in microspores and that frequently one, two or three of the members of a tetrad fail to develop. We found this to hold for microspores in the microsporangia of our plant.

Composition of the exospore layers

The inner and outer exospore contrast differently (Fig. 23) and are somewhat different with regard to density to electrons without any stain. The differences could, in our fresh samples, be due to nutrients crossing the exospore from the tapetum and locular sap.

Special consideration in this regard should be given to methods and solvents involved in preparation since great changes in contrast have been shown by Rowley *et al.* (1999: Figs. 11 & 12) in pollen grains of different stages of development and methods of preperation for microscopy.

The above idea may, however, be at odds with the experimental work of Stainiér (1965) with specimens of *Selaginella*. She found several differences in stain reactions between the two layers and also their appearance with polarised light and TEM.

Robert (1971) in reporting on his developmental studies with microspores of *S. kraussiana* has prudently avoided use of the usual, although in some cases differently applied, terms, e.g."exospore". His "leaflet I" (our inner-exospore, the endospore of Slagg) is in contact with the microspore cytoplasm during most of sporogenesis. This leaflet I becomes separated from the cytoplasm by the introduction of a cellulosic endospore ("the homologue of the intine in pollen"). Robert (1970, 1971) found that the nature and origin of the third wall layer "leaflet

II" (our outer-exospore, the exospore of Slagg) was very different from "leaflet I". Based upon its thickness, resistance and spinose ornamentation. Robert (1971) wondered if it was actually a part of the exospore. He considered "leaflet II" to originate exclusively from the tapetum and to be unlike any other spore wall that had been studied using electron microscopy. For him it was essentially "a lamella of condensation of material of the sporangial locule". An observation which may support Robert's (1970) interpretation of "leaflet II" formation by condensation of locular material was made by Erdtman (1957: Fig. 179f). Erdtman shows an example of two separated microspores of *S. kraussiana* each with a fully formed exospore (our inner-exospore) and both enveloped by a common cover that did not make contact between the two spores, as could be expected if the two spores were part of the usual connecting walls of tetrads.

In our illustrations we show tetrads (Fig. 3), two oblique views of the proximal side (Figs. 4 & 20), two images of the proximal surface (Figs. 18 & 19) and a thin section of the proximal side of a microspore (Fig. 17).

Our results show that the outer-exospore is thin proximally but does not extend to other spores. The Erdtman observation does not seem to be typical of spores in our plant.

Those that have studied the development in microspores of *S. kraussiana* have all found that what we term the outer-exospore was formed later in development than what we term the inner-exospore. This means that the outer-exospore is formed separated from the plasmamembrane and cytoplasm of the microspore, a distance that can not be known without observations of living microspores. Our interpretation of the rod subunits of the inner- and outer-exospore suggest a cytoplasmic nutrient and sporopollenin precursor supply source within the microspore protoplast. This is important as a source of genetic information with regard to species specific ornamentation.

The massive jumble of the spines in mature microspores (e.g., Figs. 21 & 22) compared with the simplicity of the early microspores (Figs. 1 & 2) would seem to indicate controlled growth and enlargement rather than condensation of locular material.

Radial 'canals', e.g., Figs. 9 and 16, across the inner exospore were illustrated by Tryon and Lugardon (1978) and they illustrated "canals" across the entire microspore wall in TEM micrographs of *S. galeottii*. In *S. martensii* microspores they found narrow "radial fissures" across the exospore of an apertural ridge.

The great amount of material in the microspore cytoplasm, as seen in figures 14, 16, 17 and 23, shows that there has to be an extensive transport system across the inner-and outer-exospore and the gap between them as well as through the endospore. "Canals" or what we term conduits could allow also for transport of the molecules from the tapetum and loculus to the microspore protoplast.

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LITERATURE CITED

Barnes, S. H. and S. Blackmore. 1984. Freeze fracture and cytoplasmic maceration in botanical scanning electron microscopy. J. Microsc. **136**: 3-4.

Belajeff, W. 1885. Antheridien und Spermatozoiden der heterosporen Lycopodiaceen. Bot. Zeit. **43**: 792-802; 808-819.

Blackmore, S. and S. H. Barnes. 1986. Freeze fracture and cytoplasmic maceration of pollen grains. Grana **25**: 41-45.

Campbell, D. H. 1902. Studies on the gametophytes of *Selaginella*. Annals Bot. **16**: 419-428.

Campbell, D. H. 1918. Structure and development of mosses and ferns, 3rd. ed. Chicago.

Erdtman, G. 1957. Pollen and spore morphology/plant taxonomy. Gymnospermae, Pteridophyta, Bryophyta (An Introduction to Palynology. II). Almqvist & Wiksell, Stockholm.

Erdtman, G. and P. Sorsa. 1971. Pollen and spore morphology/plant taxonomy. Pteridophyts, text and additional illustrations. Almqvist & Wiksell, Stockholm.

Foster, A. S. and E. M. Gifford, Jr. 1974. Comparative morphology of vascular plants. W. H. Freeman, San Francisco, 2nd. edition.

Gullvåg, B. M. 1971. The fine structure of some pteridophyte spores before and during germination. In: Pollen and Spore Morphology IV. By Erdtman, G. and P. Sorsa, .pp. 252-295, 23 pl.

Lawrence, G. H. M. 1951. Taxonomy of vascular plants. Macmillan Co. N. Y.

Lugardon, B. 1972. Sur la structure fine et la nomenclature des parois microsporales chez *Selaginella denticulata* (L.) Link et *S. selaginoides* (L.) Link. C. R. Acad. Sc. Paris **274**: 1656-1659.

Lugardon, B. 1978. Isospore and microspore walls of living pteridophytes: Identification possibilities with different observation instruments. Proc. IV Int. Palynol Conf., Lucknow (1976-77) **1**: 152-163

Lugardon, B. 1986. Ultrastructural data of the exospore function in pteridophyte spores. In: Blackmore, S. and S. H. Barnes (eds.). Pollen and Spores: Form and Function. pp. 251-264. Linnean Society of London.

Lugardon, B. 1990. Pteridophyte sporogenesis: a survey of spore wall ontogeny and fine structure in a polyphyletic plant group. In: Blackmore, S. and R. B. Knox (eds.). Microspores: Evolution and Ontogeny. pp. 95-120. Academic Press, London.

Lyon, F. M. 1901. A study of the sporangia and gametophytes of *Selinella apus* and *Selaginella rupestris*. Bot Gaz. **40**: 285-295.

Millardet, G. 1869. Le prothallium male des cryptogames vasculaires. Strasbourg.

Morbelli, M. A. and Rowley, J. R. 1999. Megaspore development in *Selaginella* The gap and the mesospore. Plant Syst. Evol. **217**: 221-143.

Morbelli, M. A., J. R. Rowley and D. Claugher. 2001. Spore wall structure in *Selaginella* (Lycophyta) species growing in Argentina. Boletín de la Sociedad Argentina de Botánica. **36**: 315-368.

Pettitt, J. M. 1966. Exine structure in some fossil and recent spores and pollen as revealed by light and electron microscopy. Bull. British Museum (Nat. Hist.), Geology. **13**: 223-257.

Pfeffer, W. 1871. Entwicklung des Keimes der Gattung *Selaginella*. Bot. Abhandl. I No. 3. Bonn.

Robert, D. 1970. Participation des cellules de l' assise tapétale du sporange a 1' edification des parois microsporales chez une Sélginelle, *Selaginella kraussiana* A. Br. C. R. Acad. Sc. Paris, **271** (Serie D): 648-651.

Robert, D. 1971. Nouvelle contribution a l etude de l' origine des parois microsporales chez le *Selaginella kraussiana* A. Br. C. R. Acad. Sc. Paris, **272** (Serie D): 385-388.

Roland, J.-C., C. A. Lembi and J. Morre. 1972. Phosphotungstic acid-chromic acid selective electron-dense stain for plasma membranes of plant cells. Stain Technol. **47**: 195-200.

Rowley, J. R., D. Claugher and J. J. Skvarla. 1999. Structure of the exine in *Artemisia vulgaris* (Asteraceae): A review. Taiwania **44**: 1-21.

Slagg, R. A. 1932. The gametophytes of *Selaginella kraussiana* I. The microgametophyte. Amer. J. Bot. **19**: 106-126.

Spurr, A. R. 1969. A low-viscosity epoxy resin embedding medium for electron microscopy. J. Ultrastruct. Res. **26**: 31-43.

Stainiér, F. 1965. Structure et infrastructure des parois sporales chez deux Selaginélles (*Selaginella myosurus* et *S. kraussiana*. La Cellule **65**: 219-244.

Tryon, A. F. and B. Lugardon. 1978. Wall structure and mineral content in *Selaginella* spores. Pollen et Spores **20**: 315-340.

Tryon, A. F. and B. Lugardon. 1991. Spores of the Pteridophyta: Surface, wall structure and diversity based on electron microscope studies. Springer-Verlag, New York.

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摘　　要

以掃描式電子顯微鏡分別觀察新鮮和解離過的卷柏（*Selaginella kraussiana*）小孢子，另以穿透式電子顯微鏡觀察以化學固定處理後的小孢子。結果顯示小孢子壁外層刺狀部分是由直徑 70 至 130 奈米(nm) 的棒狀構造與有許多貫穿小孢子壁大小不一的管線構造組成，棒狀構造繞著管線周圍偏斜著生。小孢子壁的內層的管線構造則呈放射狀，並有與小孢子壁外層相似的棒狀構造。小孢子壁外層的刺狀構造的數目與大小會隨小孢子的發育而增加，形成分支狀。小孢子壁外層與內層是分離的，二者間有一空腔存在。

關鍵詞：孢子壁單位、石松門、小孢子、卷柏、超微細構造。

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