EXPERIMENTAL INVESTIGATIONS ON RECENT *SELAGINELLA* SPORES

M. KEDVES

(Manuscript received 7 May, 1990; revised version accepted 7, August, 1990)

Abstract: By the TEM method, on the partially degraded wall of the microspores of *Selaginella bellula* Moore, the basic biopolymer units in angstrom dimension were observed. These results are the first on Pteridophyta spores in this field. Using the modified Markham rotation method in the outmost layer of the wall (perispore) a hexagonal, in the exospore a regular pentagonal polygon biopolymer unit was established. On the basis of the recently elaborated methods of the biopolymer organization of the sporoderm the hexagonal biopolymer organization may be modelled with the TICOS polyhedra. The effect of high temperature was investigated to the qualitative and quantitative morphological characteristic features of micro- and megaspores. In comparison to previous results on gymnosperm and angiosperm pollen grains, the alterations of the spores of the genus *Selaginella* are not so striking.

INTRODUCTION

The heterosporous Pteridophyta represented an important degree in the evolution of vascular plants. Regarding the micro- and megaspores of recent and fossil taxa several papers were published. In the important work by Stainier (1965) the so-called classical results of the mostly LM investigations were reviewed. From more recent publications with light microscope as important establishments, the following are of mention: Wehman (1970) at the spores of *S. pygmaea* (Kaulf.) Alston; p. 19: "there is a tendency for the spores to remain united in tetrad". Huang (1981) described the spores of the genus *Selaginella* of Taiwan and pointed out that the spores of some species are dimorphic in size. The first transmission electron microscopical data on the wall of the *Selaginella* megaspores were published by Afzelius, Erdtman & Sjöstrand (1954); p. 158: "The wall is here composed of a three-dimensional network of rounded bars (Fig. 5)". The differences in the wall ultrastructure of the genus *Lycopodium* and *Selaginella* were also pointed out. Martens (1960) described radially oriented polygonal structures from the megaspore wall of *Selaginella myosurus* (Sw.) Alston, with the following remarks; p. 1599: "Ce type de structure n'a été trouvé jusqu'ici dans aucune paroi cellulare végétale". Similar structure was described by W. A. Taylor & T. N. Taylor (1987) from the wall of Cretaceous megaspores of Argentia. The reconstruction of the subunits of the construction of the megaspore wall of fossil and extant *Selaginella* spores was also published. Important results were published in this field by Kempf (1970), and by Minaki (1984). In the latter mentioned paper the SEM method was used.

Regarding the ultrastructure and the nomenclature of the *Selaginella* microspores and the isosporous Pteropsida spores the publications of Lugardon (1965,

This work was financially supported by OTKA 1/2, 24/88. Research councilor and titular professor, Department of Botany J. A. University Szeged, Hungary.

1969, 1971, 1972a, b) and Tryon & Lugardon (1978) are basically important.

As regards the subunits and the basic biopolymer structure and the organization of the sporoderm our data comes firstly from the exines of gymnosperm and angiosperm pollen grains; cf. Rowley (1967, 1978) Rowley, J. R., Dahl & Rowley, J. S. (1981), Southworth (1974, 1985a, b), Kedves (1988, 1989, in print, manuscript).

The purposes of the present paper are as follows:

1. To investigate the biopolymer organization of the partially degraded sporoderm of the microspores of the genus *Selaginella* and to compare of these data with the previous results.
2. To investigate the high temperature effect on the micro- and megaspores of the genus *Selaginella.*

MATERIALS AND METHODS

The spore material for our investigations was collected in the Greenhouse of the Botanical Garden of the Department of Botany of J. A. University, Szeged.

TEM investigations

Microspores of *Selaginella bellula* Moore, collected by Dr. L. Técsi (15 June 1989) were investigated by the following method; experiment No: 111 (17 June 1987); 20 mg air dried microspore+1 ml 2-aminoethanol; temperature 30°C, length of time 24 h, washing with water until neutralization+10 ml $KMnO_4$ aq. dil., temperature 30°C, length of time 24 h. After washing H_2O, fixation in OsO_4 aq. dil., embedding in Araldite (Durcupan, Fluka). The ultra-thin sections were made on a Porter Blum ultra-microtome in the EM Laboratory of the Department of Biophysics of the Biological Center of the Hungarian Academy of Sciences. The TEM pictures were taken in the EM Laboratory of the J. A. University on a TESLA BS-500 transmission electron microscope, resolution 6Å.

Light-microscope investigations

Spores of the following species were the subjects:

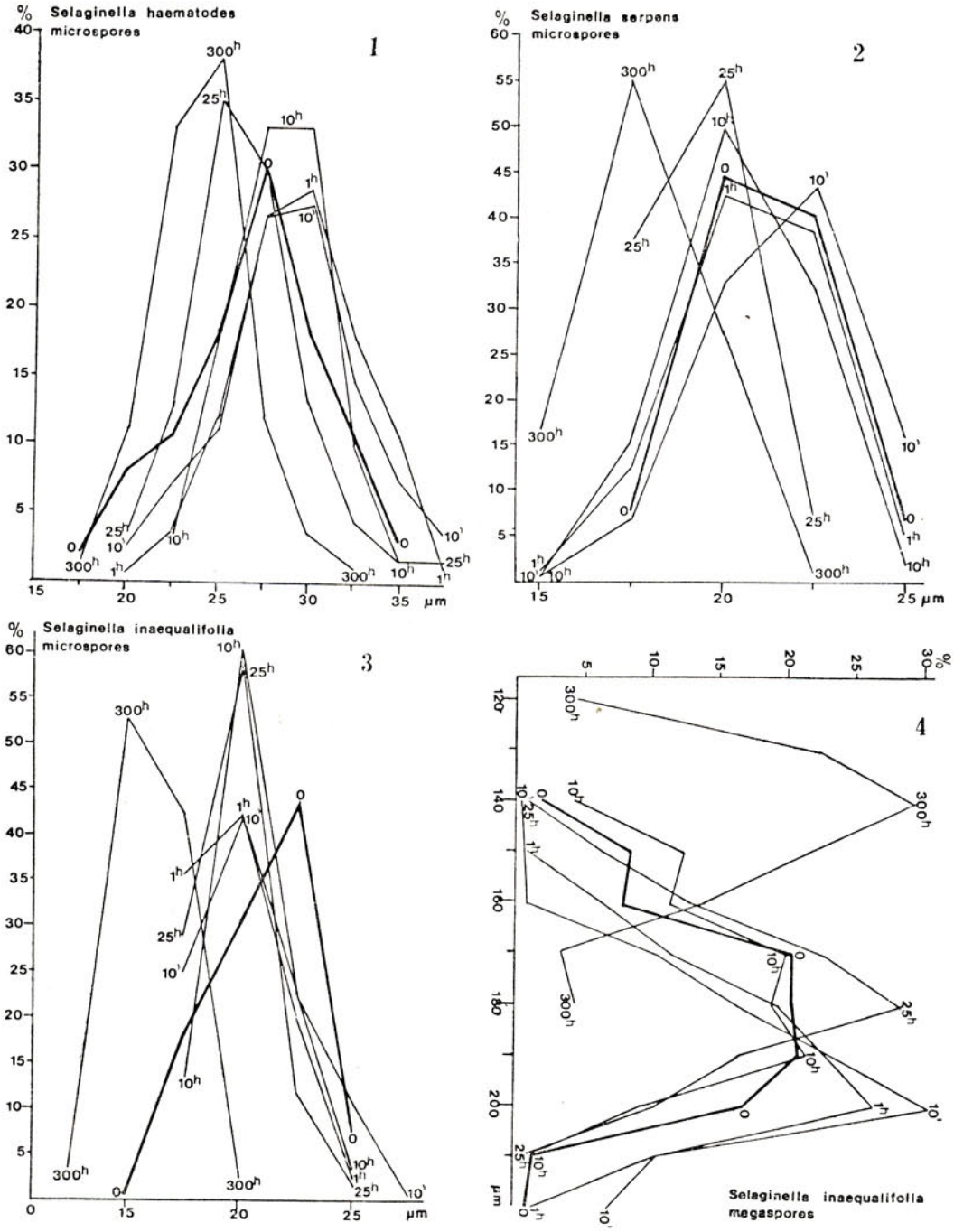
S. haematodes Spring., *S. inaequalifolia* Spring., *S. serpens* Spring.

The investigations material was collected by Dr. J. Széll, on February 8, 1990. Experiments were made or started on February 17, 1990. The maximum diameter of the spores without experiment, and heated at 200°C during 10′, 1 h, 10 h, 25 h and 300 h were measured, 200 specimens at each sample. As regards the so-called "Thermal Alteration Index" the publication of Utting, Goodarzi Dougherty & Henderson (1989) was used.

RESULTS

(1) Ultrastructure and biopolymer organization of the exospore of *Selaginella bellula* Moore

On the TEM picture (Pl. 1, Fig. 1), a fragment of the spore wall was partially degraded. Different layers of the spore wall are well shown. The thin perispore (P) is much more electron dense than the exospore. The outer (Ee), middle (Em) and the inner (Ei) part of the exospore distincts also well by its electron affinity. Here the innermost layer is the strongest from the point of view of electron



Figs. 1-4. Variation-statistical diagrams of the diameter of the spores investigated.

affinity. Beneath the exospore the fragments of the plasmolemma sporal occurs (Pe).

On the basis of our ultra-thin sections of the partially degraded exospore the following can be established:

The experimental process degraded differentially the different parts of the exospore (Pl. 1, Figs. 2, 3).

The basic biopolymer units were well shown on different parts of the exospore layers. These are tiny granular elements arranged into polygon systems.

Beneath the surface of the spore wall, a hexagonal basic biopolymer unit was observed (Pl. 1, Fig. 2). To establish the truth of the symmetry, the modified Markham rotation method was used. C. P. 6. A. 6. 6. rotation was successful. (Pl. 1, Fig. 2A, and 2C). The incomplete rotation was also arbitrary from this point of view (Pl. 1, Fig. 2B). Hexagonal basic biopolymer unit was first observed at the intine layer of the pollen grains of *Encephalartos ferox* Bertol. On the basis of the newest results of our plant cell wall biopolymer organization and modeling the TICOS-like biopolymer arrangment near the surface of the sporoderm can be presumed (Kedves, manuscript).

Beneath the surface in the outer part of the exospore (Ee), a pentagonal polygon biopolymer basic unit was observed (Pl. 1, Fig. 3). The C. P. 5. A. 5. 5. rotation (Pl. 1, Fig. 3A, 3B) resulted in a characteristic regular pentagonal polygon and secondary points of symmetry, too (Pl. 1, Fig. 3B). The rotation C. P. 5. A. 5. 10. resulted in not so characteristic secondary biopolymer units as at the previous taxa, in particular at the so-called etalon basic biopolymer of the partially degraded exine of *Pinus griffithii* McClell.

(2) "Thermal Alteration Index" at the spores investigated

Temperature: 200°C

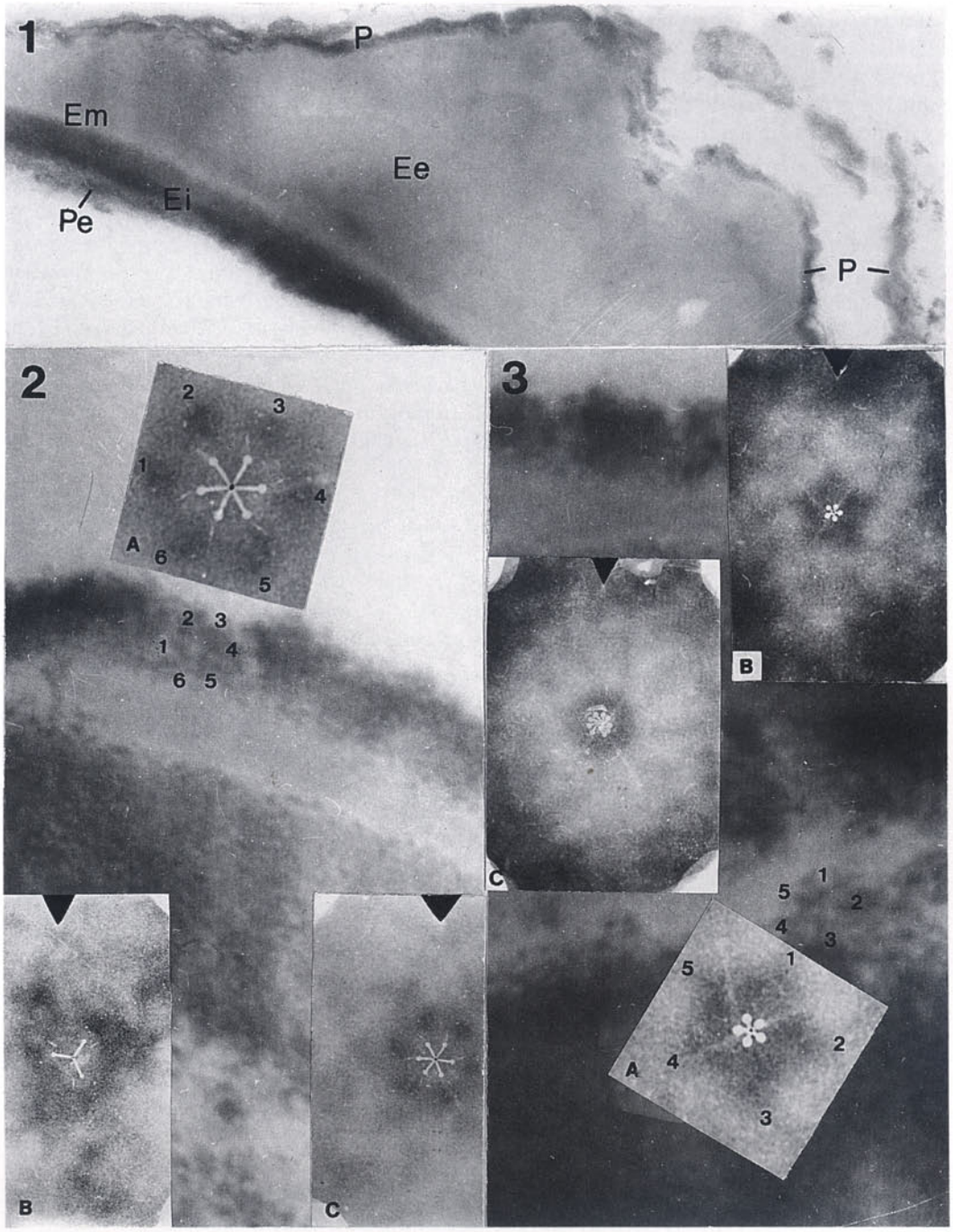
		Length of time						
		0	10′	1 h	10 h	25 h	300 h	
S. haematodes	microspore	1	1	2—	2	2+	2+	Perispore
		1	2	2+	3—	3+	3+	Exospore
S. inaequalifolia	microspore	1	2—	3—	3	4—	4—	Exospore
	macrospore	1	2	2+	3—	3—	3—	Perispore
		2+	2+	4—	4	4	4	Spore wall
S. serpens	microspore	1	1+	2+	3—	3	3+	Exospore
	macrospore	2+	3—	4	4	4	4	Spore wall

On the basis of the above enumerated results the following conclusions can be established:

The microspores, without experiment are of TAI: 1. The raw wall of the macrospores is darker; TAI: 2+, probably in consequence of the relatively thicker wall. In this way the TAI may be greater than 1, without thermal alteration of the chemical components of the sporoderm. The basic colour is an essentially thing.

When it is a cingulum-like perispore, its TAI is in general lower than those of the spore wall.

The increasing of the TAI values in the relationship of the growth of the


1
P
Em
Ee
Ei
Pe
P
2
1
2
3
4
5
6
A
1
2
3
4
5
6
B
C
3
B
C
1
2
3
4
5
1
2
3
4
5
A

length of time is not linear. Changes between 10′ and 1 h of the *S. inaequalifolia* and *S. serpens* macrospores can be pointed out as an extremely good example.

It is worth of mentioning that the spores, in particular, the megaspores investigated have not reached the highest TAI, the 5.

(3) Morphological alterations in consequence of high temperature

As regards the qualitative changes in spore morphology it is necessary to emphasize, that at the species investigated such taxonomical and phylogenetical important changes found at some gymnosperm and angiosperm pollen grains were not observed (cf. Kedves, Tóth & Farkas, in print, and Kedves & Kincsek, 1989). The alterations in the size differ also from the inaperturate gymnosperm pollen grains. The dislocation of the variation-statistical graphs at the non-experimental and experimental spores was not established. As regards the details of the results the following may be summarized; Figures 1-4.

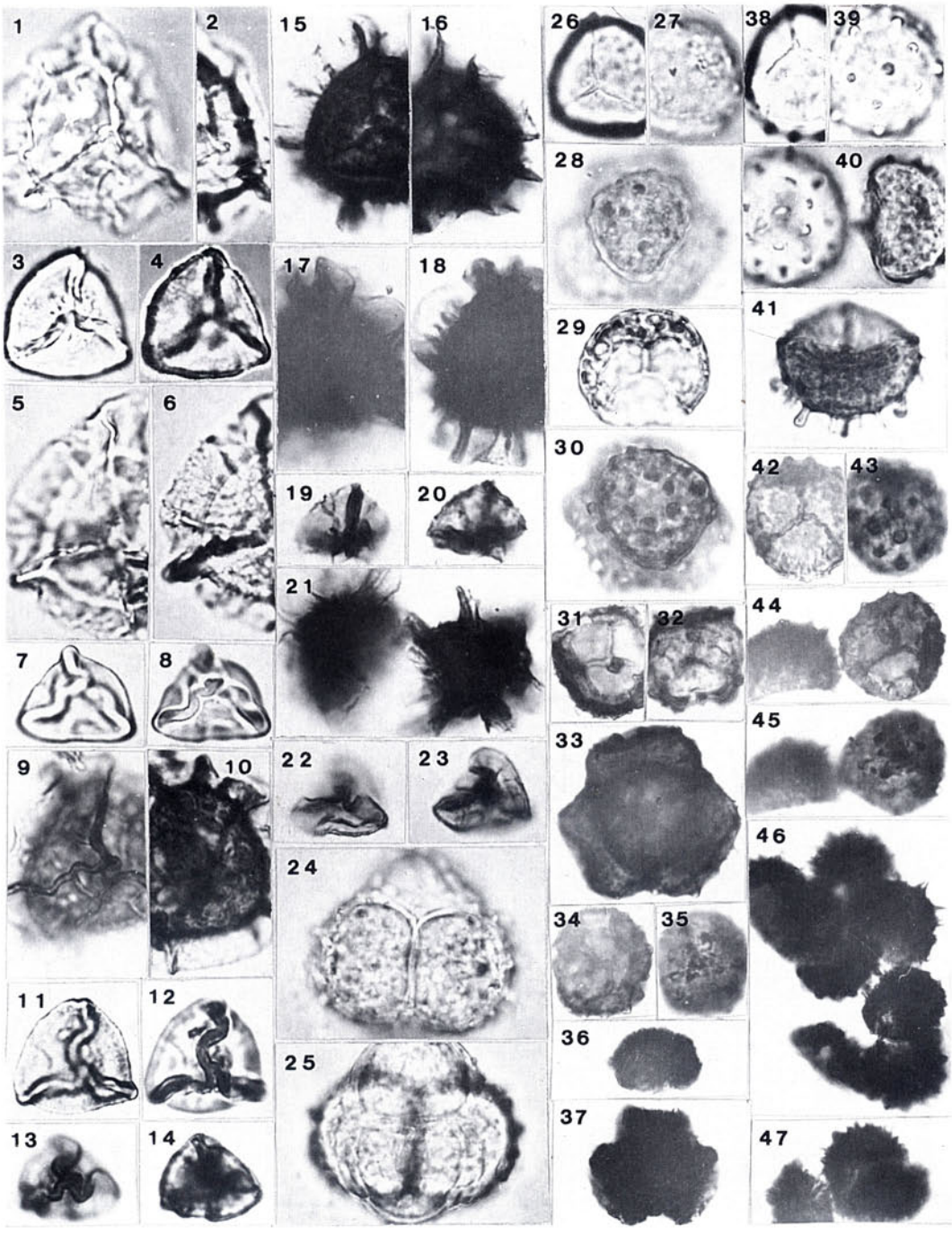
The non-experimental variation-statistical graphs at the microspores of *S. haematodes* and *S. inaequalifolia* have one prominent maximum. At the microspores of *S. serpens* this is not so characteristic, and at the megaspores of *S. inaequalifolia*, the highest per cents occur at different diameters. The variation-statistical graph is in this way flat.

An increasing of the diameter in consequence of the high temperature was established at the microspores of *S. haematodes*, *S. serpens*, and at the megaspores of *S. inaequalifolia*. The microspores of *S. inaequalifolia* are extremely characteristic from this point of view. A very typical decrease in diameter was observed after 10′ at high temperature. Moreower, all maxima are on the same value (20 μm), except the length of time of 300 h. The maxima of the graphs of 10′ and 1 h, respectively 10 h and 25 h are near the same. It is also to be emphasized that the maximum size of the spores, after the experiment during 300 h is in the middle of the variation-statistical graph of the non-experimental spores. This spore is the nearest to the dislocation of the variation-statistical graphs discussed previously.

It is probable, that the tendency of these microspores to remain in tetrads is one factor to the pecularities during the experiments at high temperature. The alterations in size at the other microspores investigated are different in contrast to the previously discussed species. It is interesting that the megaspores of *S. inaequalifolia* are intermediate in this respect among its own species, and of *S. haematodes*+*S. serpens*. The most restraint changes in size were observed at the microspores of *S. haematodes*. Probably this is in consequence of the perispore.

Plate 1. Fig. 1, ×50.000; figs. 2, 3, ×250.000; figs. 2A, 3A, ×1,000.000; figs. 2B, 2C, 3B, 3C, ×500.000.

1-3. *Selaginella bellula* More; 1. A transmission electron-microscopical picture of the microspore wall near the tetrad squar. This part of the wall is not degraded. Experiment, No.: 111, Negative No.: 7561. P=perispore, Ee=outer part of the exospore, Em=middle part of the exospore, Ei=inner part of the exospore, Pe=plasmolemma sporal. 2, 3. TEM pictures from the partially degraded outer part of the microspore wall. Experiment, No.: 111, Negative No.: 7581, 7680. 2A, 2C. C.P. 6. A. 6.6. rotation picture of the hexagonal biopolymer polygon of the outest layer of the sporoderm; 2B. I.P. 6. A. 6.3a. rotation picture of the hexagonal polygon; 3A, 3B. C.P. 5. A. 5.5. rotation picture from the basic pentagonal polygon of the outer part of the exospore; 3C. C.P. 5. A. 5.10. rotation picture from the previous basic pentagonal polygon biopolymer unit.


1
2
15
16
26
27
38
39
28
40
3
4
17
18
29
41
5
6
19
20
30
42
43
21
31
32
44
7
8
45
9
10
22
23
33
46
24
34
35
11
12
36
25
37
13
14
47

Worth of mentioning are the following: The maximum of the non-experimental variation-statistical graph is in the experimental ones. 10′ and 1 h resulted in almost the same alterations (+)=increase than 25 h and 300 h (−)=decrease, diminution. It is only the experiment during 10 h which is a little intermediate, but basically in the increasing (+) province. The changes in size at the experiments during 25 h and 300 h are not so different opposite each other.

Microspores of *S. serpens*: Increasing in size only at 10′. Maxima at 1 h, 10 h and 25 h, at the same value as the graph of the non-experimental spores. The graph of the experiment during 1 h is below the maximum of the non-experimental one, those of experiments during 10 h and 25 h are over. In this case the maximum of the graph of the experiment during 300 h is segregated, and different from the graph of the experiment during 25 h.

Finally, the megaspore investigated in detail is also peculiar (Fig. 4). Increasing in diameter may be established at 10′, and 1 h. The graph of the experiment at 25 h is funny, because its maximum is in the middle of the flat maximum of the non-experimental spores. As it was pointed out previously, the experiment during 300 h separates well, its maximum size is also in the middle of the non-experimental sample. This phenomenon is similar to those observed at the microspores of this species (cf. Fig. 3).

DISCUSSION AND CONCLUSIONS

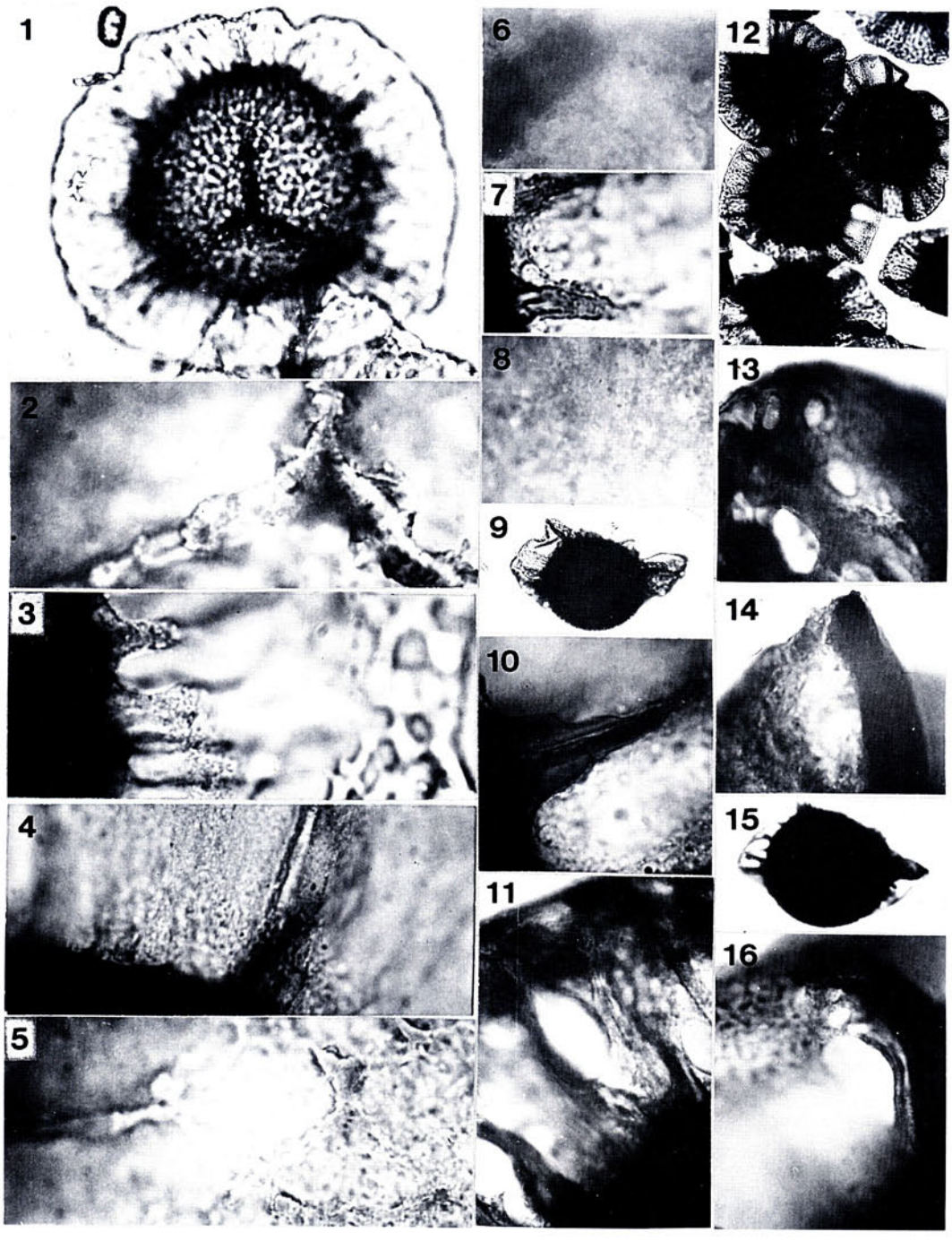
Taking into consideration the present results in comparison to the previously published ones, the following can be emphasized:

Basic biopolymer unit from the sporoderm of Pteridophyta discovered experimentally is published for the first time in this paper. The composition of the sporopollenin in every respects seems to be much more complicated at the Pteridophytes than those of the Gymnospermatophyta and Angiospermatophyta pollen grains. The basic regular pentagonal polygon described from the exospore is identical with the previously described ones. Its highly organized unit is an interesting subject of future investigations in phylogenetical point of view also

---

Plate 2. All figs., ×1000.

1-23. *Selaginella haematodes* Spring, microspores. 1-4. Microspores without experiment or staining; 5-8. Experiment, No.: 856, temperature: 200°C, length of time: 10′; 9-12. Experiment, No.: 857, temperature: 200°C, length of time: 1 h; 13-16. Experiment, No.: 858, temperature: 200°C, length of time: 10 h; 17-20. Experiment, No.: 859, temperature: 200°C, length of time: 25 h; 21-23. Experiment, No.: 860, temperature: 200°C, length of time: 300 h; 24-37. *Selaginella inaequalifolia* Spring, microspores. 24-27. Microspores without experiment or staining; 28, 29. Experiment No.: 881, temperature: 200°C, length of time: 10′; 30-32. Experiment, No.: 882, temperature: 200°C, length of time: 1 h; 33. Experiment, No.: 883, temperature: 200°C, length of time: 10 h; 34, 35. Experiment, No.: 884, temperature: 200°C, length of time: 25 h; 36, 37. Experiment, No.: 885, temperature: 200°C, length of time: 300 h; 38-47. *Selaginella serpens* Spring, microspores. 38, 39. Microspores without experiment or staining; 40. Experiment, No.: 876, temperature: 200°C, length of time: 10′; 41. Experiment, No.: 877, temperature: 200°C, length of time: 1 h; 42, 43. Experiment, No.: 878, temperature: 200°C, length of time: 10 h; 44, 45. Experiment, No.: 879, temperature: 200°C, length of time: 25 h; 46, 47. Experiment, No.: 880, temperature: 200°C, length of time: 300 h.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16

of the sporoderm organization. The superficial hexagonal unit is also a question to investigate in the future; it seems that the TICOS organization of the biopolymer units of the sporoderm may be of functional significance.

The Thermal Alteration Index (TAI) which was originally established and used to establish the maturity of the organic matter of the sediment in the researches of the Oil Industry applied to our recent experimental spores call newly the attention to the following: The original colour of the mature sporomorphs must be taken into consideration. So-called basic colour may indicate a TAI value higher than 1, cf. spores of Pteridophyta. The results of the experimental studies on the recent sporomorphs may be applied to the investigations of the Oil Industry.

Similarly, the basic variation-statistical graphs of the recent spores and pollen grains are extremely important, cf. Huang (1981), M. Van Campo-Duplan (1947), etc. This may be changed in consequence of several factors, as genetical or ecological.

Tetrads at the genus *Selaginella* probably may be useful in the reconstruction of the paleoenvironments at the fossil material.

ACKNOWLEDGEMENTS

The writer is grateful to Prof. Dr. T. C. Huang, Department of Botany, College of Science, National Taiwan University, Taipei, Taiwan, Rep. of China, for the translation of the Chinese summary, and his comments, to Dr. R. Zánthó, Dept. of Foreigin Languages at the J. A. University, Szeged, for the linguistic corrections of the English text and to Mrs. I. Biró-Halász for the technical assistance of these researches.

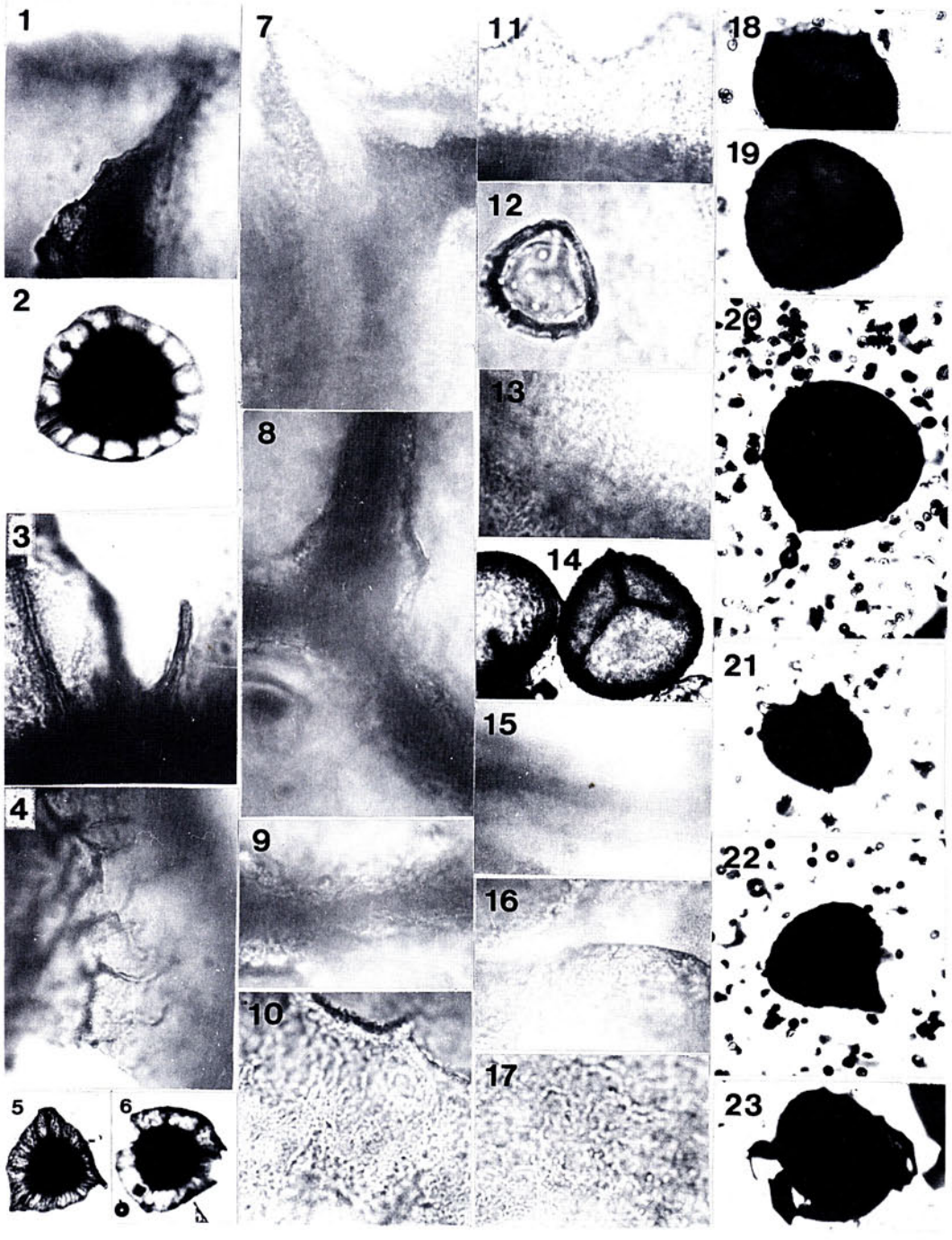
LITERATURE CITED

AFZELIUS, B. M., G. ERDTMAN and F. S. SJÖSTRAND, 1954. On the fine structure of the outer part of the spore wall of Lycopodium clavatum as revealed by the electron microscope. Svensk. Bot. Tidskr. **48**: 155-161.

HUANG, T. C., 1981. Spore Flora of Taiwan (Pteridophyta). National Taiwan University (Privately Published). Taipei. pp. 111 f. 12, pls. 120.

Plate 3. Fig. 1, ×250; figs. 2-8, 10, 11, 13, 14, 16, ×1000; figs. 9, 12, 15, ×100.

1-16. *Selaginella inaequalifolia* Spring, megaspores. 1-5. Megaspores without experiment or staining; 1. General aspect from the megaspore; 2. Detail from the tetrad squar of the proximal side; 3. Detail from the proximal side of the equatorial region; 4. Detail from the distal side of the equatorial region; 5. Distal surface of the spore; 6-9. Experiment, No.: 871, temperature: 200°C, length of time: 10′; 6. Detail from the tetrad squar of the proximal side; 7. Detail from the proximal side of the equatorial region; 8. Distal surface of the spore; 9. General aspect from the megaspore in equatorial view; 10-12. Experiment, No.: 872, temperature: 200°C, length of time: 1 h. 10. Detail from the proximal side of the equatorial region; 11. Detail from the distal side of the equatorial region; 12. Megaspores after experiment; 13-15. Experiment, No.: 873, temperature: 200°C, length of time: 1 h; 13. Detail from the distal side of the equatorial region; 14. Detail from the proximal side of the equatorial region; 15. General aspect from the spore in equational view; 16. Experiment, No.: 874, temperature: 200°C, length of time: 25 h, detail from the distal side of the equatorial region.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23

KEDVES, M., 1988. Quasi-crystalloid basic molecular structure of the sporoderm. 7th Internat. Palynol. Congr. Abstr.: 82, Brisbane.

_____, 1989. Méthode d'étude des biopolymères de la paroi pollinique à structure quasi-cristalloïde. Rev. de Micropaléont. **32**(3): 226-234.

_____, in print. First observations on the biopolymer organization of the intine. Acta Biol. Szeged **36**(1-4).

_____, manuscript. TICOS polyhedra as a model in the pentasporan organization.

_____ and I. KINCSEK, 1989. Effect of the high temperature on the morphological characteristic features of the sporomorphs I. Acta Biol. Szeged **35**(1-4): 233-235.

_____, A. TÓTH and E. FARKAS, in print: Effect of the high temperature on the morphological characteristic features on the sporomorphs II. Acta Biol. Szeged **36**(1-4).

KEMPF, E., 1970. Elektronenmikroskopie der Sporodermis von Megasporen der Gattung *Selaginella*. Rev. Palaeobot., Palynol. **10**: 99-116.

LUGARDON, B., 1965. Structure des parois de la spore de *Blechnum* spicant (L.) Roth. Pollen et Spores **7**(3): 409-428.

_____, 1969. Sur la formation de l'exospore chez *Osmunda regalis* L. C.R. Acad. Sc. Paris **268**: 2879-2882.

_____, 1971. L'endospore et la "pseudo-endospore" des spores des Filicinées isosporées. C.R. Acad. Sc. Paris **273**: 675-678.

_____, 1972a. 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.

_____, 1972b. La structure fine de l'exospore et de la périspore des Filicinées isosporées I—Généralités. Eusporangiées et Osmundales. Pollen et Spores **14**(3): 227-261.

MARTENS, P., 1960. Sur une structure microscopie orientée, dans la paroi mégasporale d'une *Sélaginella*. C.R. Acad. Sci. Paris **250**: 1599-1602.

MINAKI, M., 1984. Macrospore morphology and taxonomy of *Selaginella* (Selaginellaceae). Pollen et Spores **26**(3-4): 421-480.

ROWLEY, J.R., 1967. Fibrils, microtubules and lamellae in pollen grains. Rev. Palaeobot., Palynol. **3**: 213-226.

_____, 1978. A model of exine substructure. Abstracts for Eleventh Annual Meeting of the American Association of Stratigraphic Palynologists: 31-32, Phoenix, Arizona.

_____, A.O. DAHL and J. S. ROWLEY, 1981. Substructure in exines of *Artemisia vulgaris* (Asteraceae). Rev. Palaeobot., Palynol. **35**: 1-38.

Plate 4. Figs. 1, 3, 4, 7-13, 15-17 ×1000; figs. 2, 5, 6, 14, 18-23, ×100.

1-6. *Selaginella inaequalifolia* Spring, megaspores. 1, 2. Experiment, No.: 874, temperature: 200°C, length of time: 25 h; 1. Detail from the proximal side of the equatorial region; 2. Megaspore after experiment; 3-6. Experiment, No.: 875, temperature: 200°C, length of time: 300 h; 3. Detail from the equatorial part of the megaspore; 4. Distal surface of one fractured spore; 5, 6. Megaspores, after experiment; 7-23. *Selaginella serpens* Spring, megaspores; 7-14. Megaspores without experiment or staining; 7-9. Portions of the proximal surface, the tetrad squar is in a different position; 10-12. Equatorial ornamentation and sculpture. On the figure 12, one microspore is also attached to the surface of the megaspore; 14. General aspect from the megaspore; 15-19. Experiment No.: 876, temperature: 200°C, length of time: 10′; 15. Detail from the proximal surface, with the tetrad squar; 16. Portion of the surface in equatorial view; 17. Sculpture of the distal hemisphere; 18, 19. General aspects from the megaspores and some microspores after experiment; 20. Experiment, No.: 877, temperature: 200°C, length of time: 1 h; one megaspore and several microspores after experiment; 21. Experiment, No.: 878, temperature: 200°C, length of time: 10 h; one megaspore and several microspores after experiment; 22. Experiment, No.: 879, temperature: 200°C, length of time: 25 h; one megaspore and several microspores after experiment; 23. Experiment, No.: 880, temperature: 200°C, length of time: 300 h; one megaspore after experiment.

SOUTHWORTH, D., 1974. Solubility of pollen exines. Amer. J. Bot. **61**(1): 36-44.

_____, 1985a. Pollen exine substructure. I. *Lilium longiflorum*. Amer. J. Bot. **72**(8): 1274-1283.

_____, 1985b. Pollen exine substructure. II. *Fagus sylvatica*. Grana **24**: 161-166.

STAINIER, F., 1965. Structure et infrastructure des parois sporales chez deux Selaginelles (Selaginella myosurus et S. kraussiana). Cellule **65**: 221-244.

TAYLOR, W. A. and T. N. TAYLOR, 1987. Subunit construction of the spore wall in fossil and living Lycopods. Pollen et Spores **29**(2-3): 241-248.

TRYON, A. F. and B. LUGARDON, 1978. Wall structure and mineral content in *Selaginella* spores. Pollen et Spores **20**(3): 315-340.

UTTING, J., F. GOODARZI, B. J. DOUGHERTY and C. M. HENDERSON, 1989. Thermal maturity of Carboniferous and Permian rocks of the Sverdrup Basin, Canadian Arctic Archipelago. Geological Survey of Canada Paper **89-19**: 1-20.

VAN CAMPO-DUPLAN, M., 1947. Considérations biométriques sur les grains de pollen de Abiétinées. Bull. Soc. Hist. Nat. de Toulouse **82**: 1-8.

WEHMAN, W. G., 1970. The South African fern spores. In Van Zinderen-Bakker, E. M. (ed.) South African Pollen Grains and Spores Part VI. A. A. Balkema 110 pp.

現生卷柏孢子之試驗研究

M. KEDVES

摘　　要

本研究爲蕨類孢子此類研究之首次報告，即以穿透式顯微鏡可觀察 *Selaginella bellula* 孢子壁之雙聚合體單位之結構。使用 Markham 牌旋轉機發現孢子外被層爲六角形而外壁爲五角形之多角聚合體單位組成，因此最新孢子壁之表示法爲 Ticos 多角型。高溫定性定量處理卷柏大小孢子後，發現其變化比從前研究發表之裸子植物及被子植物花粉較微。熱反應（變更）指標（TAI）與現生孢子顏色之研究成果可應用於石油工業。卷柏屬四分體孢子或有助於古環境之重建。