

THE PRESENT STATE OF ULTRASTRUCTURAL RESEARCH INTO FOSSIL SPOROMORPHS

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Introduction

After the pioneering studies by EHRLICH and HALL (1959), modern research into the ultrastructures of fossil sporomorphs began with the work of PETTITT and CHALONER (1964) and then PETTITT (1966). The essential advance in these latter two publications was that the objects of transmission electron-microscope (TEM) studies were predetermined. Later, KEDVES and PÁRDUTZ (1970a,b) strongly urged the need for light-microscopic documentation to be given on samples intended for examination, before the preparation of ultrathin sections, in order that it be possible to follow any changes in terminology even afterwards. The TEM examination of important sporomorphs is generally carried out with the following aims:

1. The elucidation of the wall-structure of the fossil sporomorphs, particularly in the pore-wall region where light-microscopic examinations have frequently led to contradictory results.
2. The use of ultrastructural data in taxonomic descriptions, or the supplementation or necessary revision of the earlier descriptions.
3. For a more precise establishment of the botanical relationships, together with the light-microscopic morphology.
4. To draw evolutionary conclusions on the basis of the ultrastructures between sporomorphs of various geological ages and belonging to various types.

Numerous such partial results have already been or are now being published. The aim of the present paper is to collate and systematize the available data, and to extract the most essential correlations from these in the hope that these will give new starting points for future studies.

The literature data available in the history of the development of the flora are listed in main groups according to the sporomorphs. After the names of the individual species or form-species comes the geological age, and then in brackets the number of the literature reference where the detailed descriptions can be found.

At present ultrastructural results are known for the following listed taxons:

I. *Isosporous Pteridophyta* spores
Psilopsida

1. *Archaeotriletes* sp., U. Devonian (15).
Tmesopsida

2. *Microfoveolatosporis pseudodentatus* W. KR. 1959, L. Eocene (9).
 Pteropsida
 Leptosporangiatae
 Filicales
3. *Leiotriletes adriennis* (R. POT. and GELL. 1933) W. KR. 1959 asp. *triplanoid* KDS. 1961, L. Eocene (9).
4. *Appendicisporites tricuspoidatus* WEYL. and GREIF. 1953, U. Cretaceous (9).
5. *Toroisporis (Toroisporis) eocenicus* KDS. 1966, L. Eocene (9).
 II. *Heterosporous Pteridophyta* spores
 Lycopsida
 Lepidodendrales
6. *Laevigatisporites cf. glabratus* (ZERNDT) R. POT. and KREMP 1954, VIRGILLIAN (15).
 Pteropsida
 Primo-filices
 Archaeopteridales
7. *Archaeopteris cf. jacksoni* DAWSON, Devonian (15).
 Hydropterides
8. *Azolla cf. aspera* DOROFEEV (1963), L. Pliocene (10).
9. *Azolla nana* DOROFEEV 1959, L. Miocene (10).
10. *Azolla tomentosa* NIKITIN ex DOROFEEV 1955 (10).
11. *Azolla teschiana* FLORSCHÜTZ 1945, L. Eocene - Palaeocene (10).
12. *Azolla tegliensis* FLORSCHÜTZ 1938, L. Pleistocene (11).
13. *Salvinia cerebrata* DOROFEEV 1955, Pliocene/Pleistocene (12).
14. *Salvinia rhenana* KEMPF 1971, Pliocene/Pleistocene (12).
 III. *Gymnospermatophyta* sporomorphs
 Pteridospermophytina
 Pteridospermopsida
15. *Schopfipollenites* sp., Virgillian (15).
16. *Trigonocarpus* sp., Virgillian (15).
17. *Cystosporites giganteus* (ZERNDT) SCHOPF 1938, L. Carboniferous (15).
18. *Didymosporites scotti* CHALONER, L. Carboniferous (15).
 Coniferophytina
 Cordaitopsida
19. *Florinites* sp., - (15).
 Coniferopsida
20. Cf. *Araucariacites* v. *Granulatisporites* fsp., U. Cretaceous (9).
21. *Spheripollenites scabratus* COUPER 1958, Jurassic (9).
22. *Classopollis* sp., *Cheirolepis muensteri*, Rhatic (16).
23. *Classoidites glandis* AMEROM 1965, U. Cretaceous (9).
24. *Wodehouseia spinata* STANLEY 1961, U. Cretaceous (13).
 IV. *Angiospermatophyta* pollen grains
 Dicotyledonopsida
 Brevaxones
 Normapolles
25. *Atlantopollis reticulatus* W. KR. 1967, U. Cretaceous (2, 3).
26. *Complexiopollis praeatumescentes* W. KR. 1959 emend. HEGEDŰS, KEDVES and PÁRDUTZ 1972, U. Cretaceous (2, 3).
27. *Trudopollis mechanicus* PF. 1953, U. Cretaceous (3).

28. *Oculopollis zaklinskaiae* GÓCZÁN 1964, U. Cretaceous (2).
29. *Hungaropollis* fsp.₁, U. Cretaceous (2).
30. *Hungaropollis* fsp.₂, U. Cretaceous (2).
31. *Hungaropollis* fsp.₃, U. Cretaceous (2).
32. *Interporopollenites endotriangulus* HEGEDŰS, KEDVES and PÁRDUTZ 1972, U. Cretaceous (2).
33. *Vacuopollis orthopyramis* PF. 1953, U. Cretaceous (3).
34. *Basopollis basalis* (PF. 1953a) PF. 1953a, L. Eocene (7).
35. *Pompeckjoidaepollenites subbercynicus* (PF. 1953b) emend. W. KR. 1967, L. Eocene (6).
36. *Nudopollis terminalis* (PF. and TH. 1953) PF. 1953b subfsp. *bastajformis* PF. and TH. 1953, L. Eocene (6).
37. *Plicapollis pseudoexcelsus* (W. KR. 1958a) W. KR. 1961d subfsp. *turgidus* PF. 1953a, L. Eocene (6).
38. *Interpollis velum* W. KR. 1961d, L. Eocene (6).
Postnormapollis
39. *Tripoporopollenites robustus* PF. 1953a., L. Eocene (6).
40. *Subtripoporopollenites constans* PF. 1953a subfsp. *magnus* W. KR. 1961d, L. Eocene (6).
41. *Intratripoporopollenites microreticulatus* Mai 1961, L. Eocene (6).
42. *Compositoipollenites rhizophorus* (R. POT. 1934b) R. POT. 1960 subfsp. *burghasungensis* MÜRR. and PF. 1953, L. Eocene (6).
43. *Diporites iszkaszentgyörgyi* KDS. 1965, TEM diagnosis: KEDVES and PÁRDUTZ 1972a, L. Eocene (7).
44. *Teixeraipollenites globosus* PÁRDUTZ, JUHÁSZ, DINIZ and KEDVES 1972, U. Cretaceous (14).
Longaxones
45. *Transdanubiaepollenites magnus* KEDVES and PÁRDUTZ 1972a, L. Eocene (7).
46. *Tricolporopollenites sooi* KEDVES and PÁRDUTZ 1972 a, L. Eocene (7).
47. *Tricolporopollenites miniverrucatus* ROCHE 1968, L. Eocene (7).
48. *Tricolporopollenites kruschi* (R. POT. 1931) TH. and PF. 1953 subfsp. *accessorius* (R. POT. 1934) TH. and PF. 1953, L. Eocene (7).
49. *Tricolporopollenites cingulum* (R. POT. 1934) TH. and PF. 1953 subfsp. *pusillus* (R. POT. 1934) TH. and PF. 1953, L. Eocene (7).
50. *Tricolporopollenites margaritatus* (R. POT. 1931a) TH. and PF. 1953 f. *medius* PF. and TH. 1953, L. Eocene (6).
51. *Tricolporopollenites* cf. *microreticulatus* PF. and Th. 1953, L. Eocene (7).
52. *Polycolpites viesenensis* W. KR. 1961, L. Eocene (7).
Monocotyledonopsida
53. *Arecipites barakati* HEGEDŰS, KEDVES and PÁRDUTZ 1972, U. Cretaceous (3).

The examinations to date have led to the following essential conclusions:

The wall of the isosporous Upper Devonian *Archaeotriletes* sp. spore is uniform and composed of anastomosing rodlets of sporopollenin (PETTITT, 1966). Well-definable layers can not be distinguished in the walls of the Lower Eocene *Tmesopsida* and the Upper Cretaceous and Lower Eocene *Filicales* spores. Two parts can be discerned on the basis of the electron affinity,

the external ectexosporium and the internal endexosporium. The superficial ornamentation is exclusively a formation of the ectexosporium.

Similarly, separate layers can not be distinguished in the wall of *Laevigatosporites* cf. *glabratus* (ZERNDT) POTONIÉ and KREMP derived from the heterosporous *Sigillaria* fructification; the entire thickness of the exine is composed of the familiar ramifying units of sporopollenin (PETTITT, 1966). The walls of the heterosporous *Pteridophytae* are configured; PETTITT (1966) distinguished two layers in the wall of *Archaeopteris* cf. *jacksoni* DAWSON, and named them ectexine and endexine. Very many data are available on the ultrastructures of the spores of the *Hydropterides* species, which are derived primarily from younger, Tertiary deposits. In this connection, mention must be made of the finding of KEMPF (1969a) that the perinacum of the *Azolla* megaspore resembles that of the *Angiospermae* sporodermis in the arrangement of the foot layer, the columellae and the tectum.

As regards their ultrastructures, the *Pteridospermopsida* sporomorphs can be said to be heterogeneous. For *Schopfiipollenites* sp. it proved possible to detect an ectexine and an endexine, the external with a spongy, and the internal with a lamellar ultrastructure. Layers can not be identified for *Trigonocarpus* sp., while the wall consists of a three-dimensional network of sporopollenin giving a spongy appearance (PETTITT, 1966). Two layers can be discerned in the wall of the *Cystosporites giganteus* (ZERNDT) SCHOPF 1938 megaspore; the external one is composed of fibrils of two different dimensions, while the internal layer is very thin and homogeneous. Finally, the completely homogeneous wall-structure of *Didymosporites scottii* Chaloner is surprising.

Similar to the spore, a two-layered ultrastructure can be identified in the wall of *Florinites* sp. pollen belonging to the *Cordaitopsida*.

The fine structure of the wall of cf. *Araucariacites* v. *Granulatisporites* listed in the *Coniferopsida* is of an angiospermal nature; it is divided into tectum and columellae. The pollen wall of the Jurassic *Spheripollenites scabratus* is markedly of an *Angiospermatophyta* character, and contains tectum, columellae and foot layer. The exine ultrastructure of the *Classopollis* and *Classoidites* genus is extremely complicated, and even more complicated than that of the recent angiosperms. As regards ultrastructure, the two form-genera can be distinguished by the columellae above the endexine.

TEM data for the recent species have been interpreted in that the fossil *Angiospermatophyta* exines consist of ectexine and endexine. The ectexine is built up of three layers (tectum, columellae, foot layer). Thus, the terms ectexine and endexine, which are used in light-microscopic descriptions, do not agree with the ultrastructural results. In general the innermost layer of the ectexine (foot layer) is termed endexine. It must be noted that the detection of the endexine by light-microscopic methods is fairly difficult, because it differs from the ectexine in its ultrastructure or electron affinity. The main morphological types of the pore-wall exine had to be reassessed with the ultrastructural data, e. g. atrium, vestibulum, prevestibulum, colpore. It is a general phenomenon for fossil angiosperm pollen grains too that if there is an endexine below the ectexine, then this is thickened in the pore-wall region. In the *Brevaxones* and *Longaxones* taxons studied the evolutionary value of the endexine is different. In the most primitive *Brevaxones* - *Normapollis* form-genera (*Atlantopollis*, *Complexiopollis*) the endexine occurs fairly generally, whereas it is

absent from the more developed Lower Eocene types. Thus, the development within this group is revealed by the decrease of the number of layers. On the other hand, it may reappear in the more developed, modern angiosperm pollen grains, but naturally with another taxonomic value. It has so far not proved possible to establish a similar relationship for the *Longaxones* pollen grains, since the occurrence of the endexine is quite general. Three types of endexine occurred within the group; these may possibly also have evolutionary or taxonomic importance later. The ultrastructure of the primitive *Postnormapolles* taxons (e. g. *Subtriporopollenites constans magnus*) can be identified with that of the recent genera, and so the botanical connections can be established even in the cases when there was no possibility for this in the light-microscopic examinations. From an ultrastructural point of view a significant proportion of the Palaeocene – Lower Eocene *Normapolles* are of an *Amentiflorae* type. It was necessary to emend the light-microscopic diagnoses for several fossil *Angiospermatophyta* taxons, while the ultrastructural data too were used in the descriptions of the new taxons.

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- Note. — Only work dealing with the TEM study of fossil sporomorphs is given in the literature references. The manuscript was closed at the end of April 1972.

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