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Transmission electron microscopy of Mesozoic terrestrial microfossils

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Abstract. From the evolutionary point of view the most important ultrastructural characteristic features of the terrestrial microfossils are presented in this contribution. During the Mesozoic Era important innovations happened in the ultrastructure of the gymnosperm pollen grains. The earliest saccate elements represent the alveolar infratectal ultrastructure, which appeared in the Carboniferous, and remains in the present day gymnosperm species (*Pinus*, *Picea*). New events during the Mesozoic: 1. Appearance of the modern ultrastructure type in several inaperturate and monosulcate pollen grains (*Araucariacites* Cookson, *Cycadopites* (Wodehouse) Wilson and Webster). 2. Exclusively Mesozoic gymnosperm types with peculiar LM morphology and exine ultrastructure. The pollen grains of the Operculati (*Circulina* Malyavkina, *Classopollis* Pflug, *Classoidites* Amerom) are very isolated by their LM morphology, the wall ultrastructure is very complicated, similar to some angiosperm taxa. 3. Angiosperm-like exine ultrastructure appeared at the LM morphologically gymnosperm pollen grains of the *Spheripollenites* Couper fgen. 4. The gymnospermous *Eucommiidites* Erdtman has some angiosperm characteristics with the granular infratectal layer. Concerning the evolution of the vegetation the appearance of the angiosperms was the most important event. Regarding the ultrastructure of the pollen grains, the most important evolutionary alterations may be followed by the alterations in the ultrastructure of the infratectal layer. In the earliest Longaxones (Lower Cretaceous) the columellar infratectal layer is characteristic, this may be followed in some Brevaxones by the granular one, during the Senonian.

Key words. Palynology. Mesozoic. Ultrastructure evolution.

Introduction

The evolution of the Plant Kingdom may be followed at different levels of organization. The starting level is the molecular, this is followed by different biopolymer structures and the ultrastructure of the organic remains. The concept of the "ultrastructure evolution" of the plant cell wall was introduced by Ehrlich and Hall (1959) based on the first TEM data of fossil pollen grains from the Eocene layers of South Mayfield Kentucky, U.S.A. Several TEM results were published from different kinds of spores and pollen grains from different ages. Monographical works were also published by the writer of the angiosperm (1990), gymnosperm (1994) pollen grains and spores (1996). After these volumes several new data appeared and a new synthesis of the ultrastructure phylogeny seems necessary.

The aim of this contribution is to synthetise from an evolutionary point of view the most important alterations in the ultrastructural features of different taxa of the Mesozoic terrestrial ecosystems.

The earliest ultrastructure characteristic features

Based on TEM data from Silurian (Hemsley, 1992, 1994) the lamellar ultrastructure is the earliest. At the Devonian spores outer spongy and inner lamellar wall were established. But the evolved homogeneous wall appeared also in microspores of some heterosporous Pteridophyta during the Paleozoic Era.

Earliest and evolved ultrastructural characteristic features were described at the first saccate pollen grain (*Archaeoperisaccus* (Naumova) Potonié) by Meyer and Raskatova (1984) isolated from Devonian sediments. The endexine is lamellar, the saccus alveolar.

The most important alterations during the Mesozoic time

1. Differenciation of evolved Pteridophyta.
2. Differenciation of gymnosperms.
2.1. Evolution of the earliest disaccate types.
2.2. Appearance and extinction of peculiar gymnosperm types; Operculati (*Circulina* Malyavkina, *Classopollis* Pflug, *Classoidites* Amerom), *Eucomiidites* Erdtman.

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2.3. Appearance of pollen grains which are important for the evolution of angiosperms.

3. Appearance and early differentiation of the primitive angiosperms.

Evolutionary lineages in the sporoderm ultrastructure of the Mesozoic Cormophyta

Pteridophyta

In general, in heterosporous ferns, the ultrastructure of the megaspore wall represents the early type, in contrast to the evolved (homogeneous) exospore of the microspore. The microspore wall of *Nathorsisporites hopliticus* Jung from the Triassic is a modern homogeneous exospore with perispore. Wall ultrastructure of miospores of the Jurassic time is in general homogeneous sometimes transversed with radially oriented channels (*Paraconcavisporites* Klaus). Perispore remains were observed at the surface of the homogeneous exospore of *Saadisporites* (Kedves, 1986). During the Early Cretaceous homogeneous spore ultrastructure was described for several miospores [*Ruffordiaspora australiensis* (Cookson) Dettmann and Cookson, *Ruffordia goepperti* (Dunker) Seward *in situ* spores, *Plicatella distocarinata* (Dettmann and Playford) Davies, *Cyatheacidites tectifera* Archangelsky and Gamerro]. Spongy perispore and more or less compact exospore were observed in spores of the form-genus *Crybelosporites* Li Wen-ben and Batten. In the megaspore ultrastructure three types may be distinguished:

1. The early: spongy perispore, and lamellar exospore.

2. The intermediate: spongy outer layer, and filamentous inner one.

3. The evolved types are represented by a spongy perispore and an homogeneous exospore.

The wall ultrastructure of Upper Cretaceous spores presents mostly modern and intermediate types, particularly in the megaspores. In several Upper Cretaceous miospores homogeneous wall was described, but in the Lycopodiaceous *Zlivisporis* Pacltová lamellar perispore and exospore were established. The wall of the *Hydrosporis* Krutzsch form-genus (microspore of fossil *Azolla*) is homogeneous, but the spores are embedded in a unit-membrane like epispore.

Gymnospermophyta

1. The disaccate gymnosperm pollen type with alveolar infratectal layer is represented by different types during the Mesozoic. This pollen type is present from the Paleozoic until the present day vegetation (*Pinus*, *Picea*, etc.). The peculiar Mesozoic type *Parvisaccites radiatus* Couper may be pointed out, by the small sacci and radially oriented alveolar system.

2. The ultrastructure of the inaperturate pollen types represents three great types from an evolutionary point of view:

2.1. Early spongy ectexine composed of irregular rods of sporopollenin and lamellar endexine at the *Balmeiopsis* pollen grains (Kedves and Párdutz, 1974, Archangelsky, 1994), and at some taxa of *Araucariacites* Cookson (*e.g.*: *A. hungaricus* Deák; Kedves, 1985).

2.2. Granular ectexine which may represent the three layered ectexine, and lamellar endexine is at the evolved *Araucariacites* Cookson pollen grains. This is the modern inaperturate exine ultrastructure type which also occurs at several recent pollen taxa (Taxaceae, Taxodiaceae, Cupressaceae, etc.).

2.3. Angiosperm ectexine (tectum, columellar infratectal layer and foot layer) is characteristic for the pollen grains of the *Spheripollenites* Couper form-genus (probably extinct type of Taxaceae) pollen grain (*cf.* Kedves and Párdutz, 1973, Batten and Dutta, 1997). This pollen group is also of Mesozoic type.

2.4. The exine ultrastructure of *Eucommiidites* Erdtman is also of angiosperm character, but with granular infratectal layer (Doyle *et al.*, 1975, Batten and Dutta, 1997). There are a number of publications on this subject. The taxonomy and the botanical affinity were discussed for example by Batten and Dutta (1997). Worth mentioning is the *Eucommiitheca hirsuta* Friis and Pedersen (1996b), from the early Cretaceous of Portugal. TEM and SEM investigations were made on the associated pollen grains also. The electron dense endexine may be emphasized at this material.

2.5. Similar is the ultrastructure of the polyplicate gymnosperm pollen grains (*Ephedripites* Bolkhovitina).

2.6. The Operculati group (*Circulina* Malyavkina, *Classopollis* Pflug, *Classoidites* Amerom) which represents the Cheirolepidaceae (*Pagiophyllum, Brachyphyllum, Cheirolepis*) is an important constituent of the Mesozoic vegetation. *Circulina* Malyavkina is the earliest, *Classoidites* Amerom the most evolved type. The LM morphology is completely isolated without relation to other fossil and recent gymnosperm pollen grains. The exine ultrastructure as Pettitt and Chaloner (1964) pointed out "complexity is unmatched even among living angiosperms". There are several papers concerning the exine ultrastructure of this group, the most important are as follows: *Circulina* Malyavkina fspp. 1-3 (Médus, 1977), *Classopollis classoides* (Pflug) Pocock and Jansonius 1961 (Kedves, 1990), *Classoidites glandis* Amerom 1965 (Kedves and Párdutz, 1973). The pollen grains of the last two form-genera can be well distinguished by ectexine ultrastructure, infratectal layer is columellar in *Classopollis* Pflug, and irregular in *Classoidites* Amerom form-genus. Based on the concept of Lugardon (1985), the exine stratification may be summarized as follows: supratectum, tectum, infratectum, sole (foot layer), endexine. Very important results were published in this respect by Taylor and Alvin (1984). TEM investigations were made on associated pollen grains (isolated from *Classostrobus comptonensis* Alvin *et al.* 1978) of different level of maturity, in this way we have information about the ultrastructure ontogeny of these important and peculiar pollen type (Taylor and Alvin, 1984). An extremely particular pollen morphology is connected with a complicated angiosperm-like exine ultrastructure. But on the other hand Van Campo (1971) emphasized that the lamellar endexine allows to classify these pollen grains in the gymnosperms.

2.7. From the point of view of the angiosperm evolution the *Monosulcites* (Erdtman, Cookson) *ex* Couper pollen grains are the most important. The infratectal layer of monosulcate gymnosperm pollen grains is alveolar.

Angiospermophyta

3.1. The phylogeny of the angiosperm pollen grains was first elaborated in the Northern Hemisphere nearer to the Normapolles Province by Doyle and Hickey (1976) and Doyle (1977a) which may be summarized as follows: monosulcate-tricolpate-tricolporoidate tricolporate-Normapolles. There was a relatively long Longaxones period before the appearance of the Brevaxones. The change in the symmetry of the early angiosperm pollen grains was an important event. After the appearance of the first Brevaxonate pollen grains an extreme differenciation and diversification happened at the angiosperms (Kedves, 1981a, 1981b).

3.2. The ultrastructure of the early monosulcate is tectate, infratectum columellar; *Clavatipollenites* Couper fspp. (Walker and Walker, 1984; Khlonova and Surova, 1988; Eklund *et al.*, 1997; Friis and Pedersen, 1996a), *Retimonocolpites* Pierce fspp. (Doyle *et al.*, 1975; Walker and Walker, 1984), *Liliacidites* Couper spp. (Zavada, 1984), *Verrumonocolpites* Pierce fspp. (Zavada, 1984).

3.3. The infratectal layer of the tricolpate and tricolporate Early Cretaceous pollen grains is also columellar, *e.g.*: Doyle *et al.* (1975), Friis and Pedersen (1996a).

3.4. In the Senonian Normapolles taxa, the ultrastructure evolution may be followed with the reduction of the number of wall layers, and the earliest columellar (exceptionally alveolar) infratectal layer is granular in the evolved taxa.

3.5. In a further stage of evolution the columellar infratectal layer and the endexine appear, but at a higher level.

3.6. It is necessary to emphasize, that the evolutionary stages of angiosperm pollen grain are not yet elaborated for all the paleophytogeographical provinces of the World. The angiosperm evolution is different in the Monosulcate, *Aquilapollenites* or *Nothofagidites* Provinces.

Discussion and conclusions

During the Mesozoic Era the most important innovations in the evolution of the vegetation were the following:

1. Different kinds of evolutionary lineages in gymnosperms, with extremely constant (bisaccate) and peculiar Mesozoic types (Operculati, *Spheripollenites* Couper, *Eucommiidites* Erdtman).
2. In the Lower Cretaceous monosulcate pollen grains, the ultrastructure of the infratectal layer is frequently the unique character to distinguish the gymnosperm or angiosperm origin.
3. The appearance and the early evolution of the Longaxones and the extreme differentiation of the Brevaxones is an important event in the evolution of the Angiosperms.
4. Taking into consideration the palynological data the polyphyletical origin of the angiosperms may be probable (*cf.* Greguss, 1918, 1955). The *Spheripollenites* Couper lineage may represent the monoporate Monocotyledonous lineage. Monosulcate forms may represent the Magnoliophyta (Doyle, 1977b).
5. Finally it is necessary to emphasize several generalities:

5.1. The application of the transmission electron microscopic method for the fossil spores and pollen grains of different ages was not used with identical intensity. Some spores and pollen types were investigated by several methods, while others were poorly. In this way several cases our TEM data are insufficient.

5.2. The preservation is also an evergreen problem.

5.3. The evolutionary significance of the inner layers of the exine is important from a evolutionary point of view. The superficial elements are important in the first place for taxonomy.

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