

SCANNING ELECTRON-MICROSCOPIC INVESTIGATIONS ON THE SPOROMORPHS OF THE UPPER PANNONIAN IN HUNGARY

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Abstract

We have carried out scanning electron-microscopic investigations on the sporomorphs of the brown coal layers of the Upper Pannonian in Túrkeve, Emőd, Szerep. Our results are the following:

- (1) A sure demonstration of the *Cathaya* genus.
- (2) *Psophosphaera pseudotsugoides* is heterogeneous on the basis of the submicroscopic surface ornamentations.
- (3) The proper botanical affinity of the pollen grains of *Inaperturopollenites hiatus* is not decided finally on the basis of the scanning electron-microscopic investigations, either.
- (4) A more exact knowledge of the germinal area in *Arecipites vancampoae* and *Monogemmites pseudosetarius*.
- (5) At the fossil forms of Amentiflorae the occurrence of ridges, as well as the number of coni per square micron are characters of taxonomical value.

Introduction

The marshy-belted vegetation of the coal layers of Túrkeve, Emőd and Szerep from the Upper Pannonian, which can be reconstructed on the basis of sporomorphs, was described by the author (1962). Later some new taxa were described as well (KEDVES and RÁKOSY, 1964; KEDVES and BOHONY, 1966). The spore-pollen assemblage is in a very good state of preservation and, therefore, it is a suitable for electron-microscopic investigations. The scanning electron-microscopic investigations have so far mainly been confined to the sporomorphs of older ages. From the younger Tertiary we have but very few literary data of this character. The scanning electron-microscopic investigation into the sporomorphs, and mainly into the pollen grains from the younger Tertiary, is justified by that this gives a comparative basis for the developmental evaluation of the submicroscopic formations of the Upper Cretaceous and Lower Tertiary. In addition to this, the knowledge of the sporomorphs of the subtropical vegetation of the Upper Tertiary is made more perfect by the scanning electron-microscopic data, being in this way comparable with the recent taxa as well.

Materials and Methods

From among the three localities the preparations made of the coaly layers of Túrkeve and Emőd are particularly suitable for scanning electron-microscopic investigations. For making the preparations, we took the work of LEFFINGWELL and HODGKIN (1971) for our basis. Dry sporo-

morphs were carried with a glass needle on a cover plate covered with a polyvinylchloride adhesive and coated with gold. The investigations took place in the electron-microscopic laboratory in the Department of Zoology of ELTE (Loránd Eötvös University in Budapest). For the kind help, I wish to express my thanks, in this way, too, to Dr. J. Kovács, lecturer at and head of the Department.

Results

1. *Laevigatosporites haardti* (R. POT. et VEN. 1934) TH. et PF. 1953 subfsp. *haardti* (Plate I, 1)

The surface magnified mildly, corresponds to the light-microscopic results: it is smooth. Magnified strongly, it is covered with small granules, taking place densely, their size being 0.15–0.2 μ .

2. *Pityosporites pristinipollinius* (TRAV. 1955) W. KR. 1971 (Plate I, 2–5)

On photomicrographs of great magnification the surface ornamentations of some parts of the pollen are different. The surfaces of the pecten and bladder are by and large identical, finely corrugated. On the other hand, the pollen body is verrucate, here and there granulated, the size of ornamental elements is 0.3–0.5 μ .

On the basis of UENO's (1974) scanning electron-microscopic data the pollen body of the recent *Pinus thunbergii* PARL. is verrucate-undulated. Thus, the connection of the fossil form with the *Pinus* genus is supported by the submicroscopic surface as well.

3. *Pityosporites alatus* (R. POT. 1931b) TH. et PF. 1953 (Plate I, 6)

The pollen body is generally ornamented with granules of 0.2 μ diameter, placed in a distance of 0.7–0.9 μ from one another. The surface of the bladder is similar, too, but the ornamentation elements take place densely.

SIVAK (1975) described the diagnostic features of the pollen grains with bladders with light- and scanning electron-microscopic methods. By reason of his scanning data, this form-species is identical with the *Cathaya* type. From the French Tertiary sediments, *Cathaya* pollen was first demonstrated by Caratini, M. VAN CAMPO and SIVAK (1972). Then SIVAK (1976) described several new species in this genus, on the basis of pollen grains from Oligo-Miocene sediments. The genus occurred in the Far East at present, was described by CHUN and KUANG (1958) after the concise work of FERGUSON (1967) who classified here the cone *Keteleeria loehri* ENGELHARDT and KINKELIN 1911, as well, from the Pliocene (CF. FLORIN, 1963). A further Pliocene macrofossil is known from SVECHNIKOVA (1964) from the environs of the Black Sea.

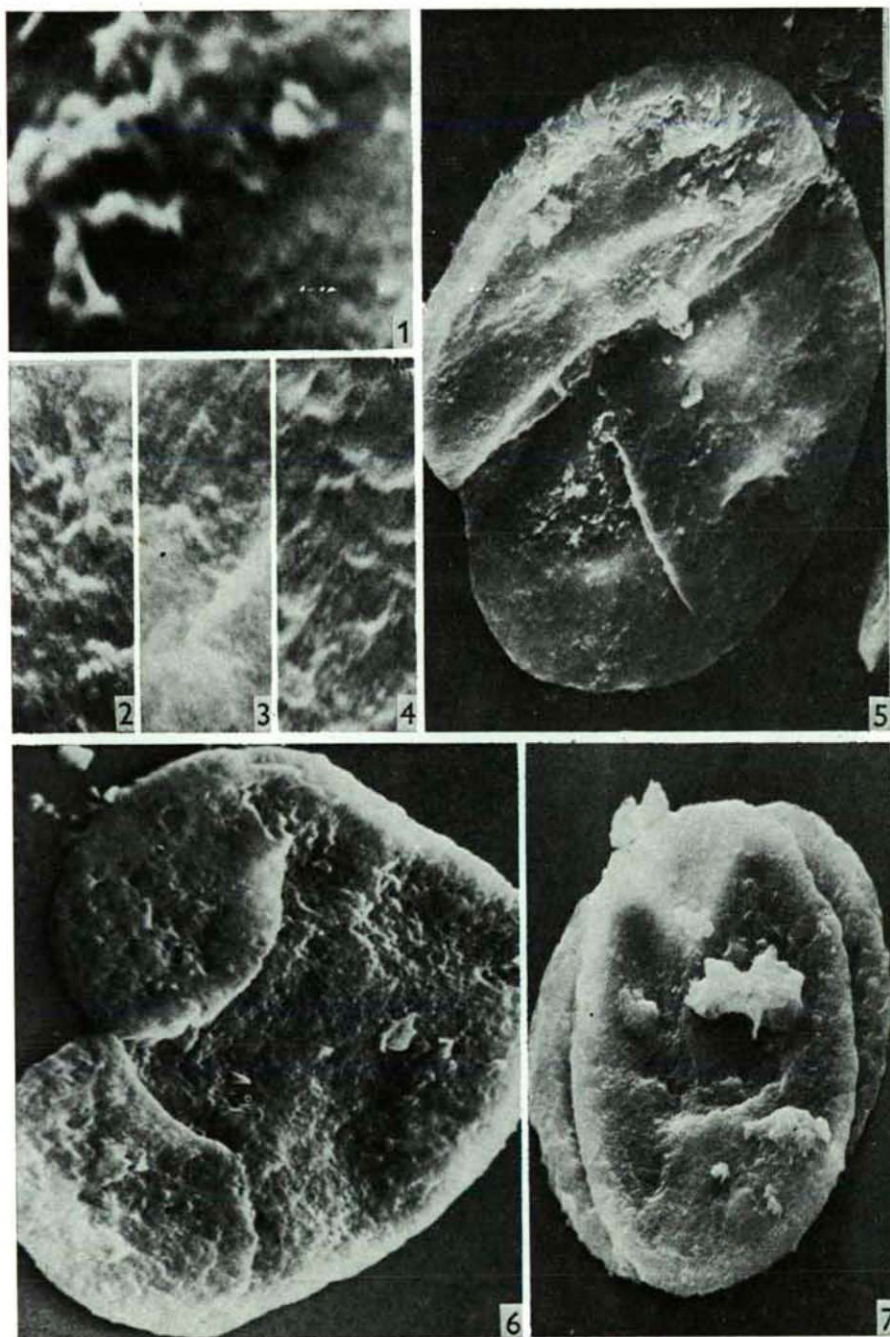
4. *Pityosporites pactovae* W. KR. 1971 (Plate I, 7)

The bladder and the surface of the pollen body are equally corrugated, the width of elements is only different. The sculpture elements are 0.2–0.3 μ wide on the pollen body, 0.4–0.5 μ wide on the bladders

Plate I

1. *Laevigatosporites haardti* (R. POT. et VEN. 1934) TH. et PF. 1953 subfsp. *haardti*, Emőd, $\times 10000$.
2. *Pityosporites pristinipollinius* (TRAV. 1955) W. KR. 1971, pecten, Túrkeve, $\times 10000$.
3. *Pityosporites pristinipollinius* (TRAV. 1955) W. KR. 1971, pollen body, Túrkeve, $\times 10000$.
4. *Pityosporites pristinipollinius* (TRAV. 1955) W. KR. 1971, bladder, Túrkeve, $\times 10000$.
5. *Pityosporites pristinipollinius* (TRAV. 1955) W. KR. 1971, Túrkeve, $\times 1000$.
6. *Pityosporites alatus* (R. POT. 1931b) TH. et PF. 1953, Emőd, $\times 1000$.
7. *Pityosporites pactovae* W. KR. 1971, Túrkeve, $\times 1000$.

Plate I



By reason of SIVAK's data (1975), this pollen type cannot be brought into connection, on the basis of its submicroscopic sculpture, with any recent genus.

5. *Pityosporites scopulipites* (WDH. 1933) W. KR. 1971 (Plate II, 1—3).

On the pollen body and the bladder there are equally granules of 0.15—0.2 diameter. These are placed rather densely. The ornamentation is denser on the surface of the bladders than on the pollen body.

From among the recent taxa — after HO and SZIKLAI (1972), NILSSON, S., PRAGLOWSKI and NILSSON, L. (1977) — the surface of the *Picea* genus is finely granular. According to UENO (1974), the texture of the *Pinus* and *Picea* genera is very fine. On the basis of SIVAK's (1975) work, the surface of the pollen grain of *Microcachrys tetragona* HOOK is similar.

6. *Abiespollenites absolutus* THG. 1937 (Plate II, 4)

The pollen body is ornamented with anastomosing granules giving a rugulate surface. The granules are sporadically in a heap. The surface of the pollen body is rugulate, the width of the sculpture elements is generally 0.3 μ .

The submicroscopic surface of this pollen grain resembles the type of SIVAK's (1975) *Abies nebrodensis* Mattel. It is worth mentioning that the scanning electron-microscopic picture of *Abies nordmanniana* (STEV.) SPACH. differs from the above mentioned ones very much.

7. *Piceapollenites planoides* W. KR. 1971 (Plate II, 5, 6).

A strongly magnified picture could only be made of the bladder. The surface of this is finely corrugated.

This submicroscopic surface essentially agrees with SIVAK's (1975) *Picea excelsa* LINK type.

At the pollen grains with bladders, it can be established that the fine surface formations are suitable for ascertaining the botanical connections. In our material, this is particularly important in case of the *Cathaya* genus. The SEM ornamentation of TAYLOR and MILLAY's (1969) *Pityosporites* fgen. from the Pennsylvanian fundamentally differs from that of the species from the Tertiary. The light-microscopic characteristics, the alveolar structure (VAN CAMPO and SIVAK 1972), together with the submicroscopic surface characteristics may have a phylogenetical significance. In this relation many more Mesozoic pollens are to be investigated.

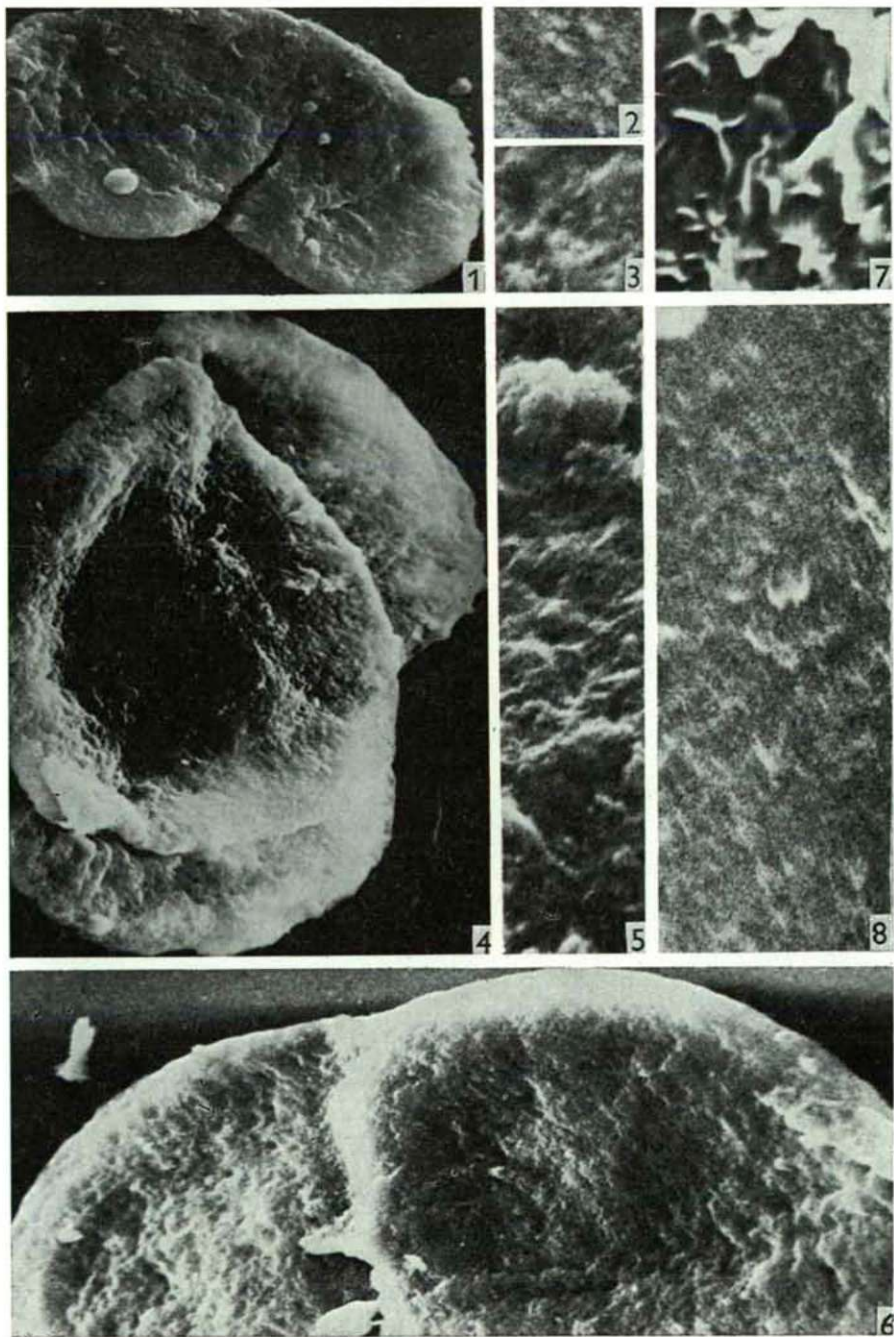
8. *Psophosphaera pseudotsugoides* W. KR. 1971 (Plate II, 7, 8)

Several specimens of this were investigated. We could separate among the light-microscopically identical forms two types by scanning electron-microscopic method. One of these was expressedly rugulate-corrugate with 0.3—0.5 μ wide elements (Plate II, 7), the other type is nearly smooth, ornamented with small, 0.15—0.2 μ wide granules, resp. with narrow verrucate elements, the width of which was below 0.2 μ .

Plate II

1. *Pityosporites scopulipites* (WDH. 1933) W. KR. 1971, Túrkeve, x1000.
2. *Pityosporites scopulipites* (WDH. 1933) W. KR. 1971, pollen body, Túrkeve, x10000.
3. *Pityosporites scopulipites* (WDH. 1933) W. KR. 1971, bladder, Túrkeve, x10000.
4. *Abiespollenites absolutus* THG. 1937, Túrkeve, x1000.
5. *Piceapollenites planoides* W. KR. 1971, bladder, Túrkeve, x10000.
6. *Piceapollenites planoides* W. KR. 1971, Túrkeve, x1000.
7. *Psophosphaera pseudotsugoides* W. KR. 1971, Emöd, x10000.
8. *Psophosphaera pseudotsugoides* W. KR. 1971, Emöd, x10000.

Plate II



On the basis of the ultrasculpture data, obtained with a carbon replica method by YAMAZAKI and TAKEOKA (1962), the first type (Plate II, 7) resembles the *Pseudotsuga* genus, while the second (Plate II, 8) the *Larix* genus. These are fossil forms and thus, at any rate, heterogeneous, but their separation is only possible by studying the submicroscopic surface.

In connection with the fossil *Tsuga* pollen grains, to be discussed below, it is to be mentioned that, unfortunately, we could only examine one of the sides of the fossil forms by scanning electron-microscopic method.

There were carried out SEM investigations by SIVAK (1973) on the recent and fossil pollen grains of this genus. The method is of differentiating value.

9. *Zonalapollenites rueterbergensis* W. KR. 1971 (Plate III, 1,2)

Concerning the taxonomy the form-genus, we are following POCKOCK's work (1968).

The ornamentation of the pollen body is double on the basis of scanning data; verrucate and rugulate. Sculpture is expressed, consisting of elements of 0.4—0.6 μ size. The surface of the zone is differently corrugated, ornamented with granules.

In respect of the SEM surface, *Tsuga van campoae* SIVAK 1973 is similar to the investigated species.

10. *Zonalapollenites verruspinus* W. KR. 1971 (Plate III, 3)

It has an expressedly verrucate ornamentation with small spinae. The zone is extremely narrow, its ornamentation does not differ from that of the pollen body.

On the basis of SEM data, it is similar to *Tsuga gaussenii* SIVAK 1973.

11. *Zonalapollenites pliocaenicus* W. KR. 1971 (Plate III, 4)

The surface of the pollen body is granular. According to KRUTZSCH (1971), this is the proximal surface. The ornamental elements sporadically anastomose. The ornamentation of the narrow zone is different, it is here and there verrucate.

Of the recent species, the SEM surface of *Tsuga brunoniana* is the most similar to the fossil form (SIVAK 1973). The submicroscopic ornamentation of the *Zonalapollenites* specimens, investigated by REYRE (1973) from the Mesozoic sediments in the Sahara, does not differ essentially from the forms from the Upper Pannonian which are in an unquestionable connection with the *Tsuga* genus. This does not refer unconditionally to an identical origin; the possibility of convergence is, namely, not excluded either.

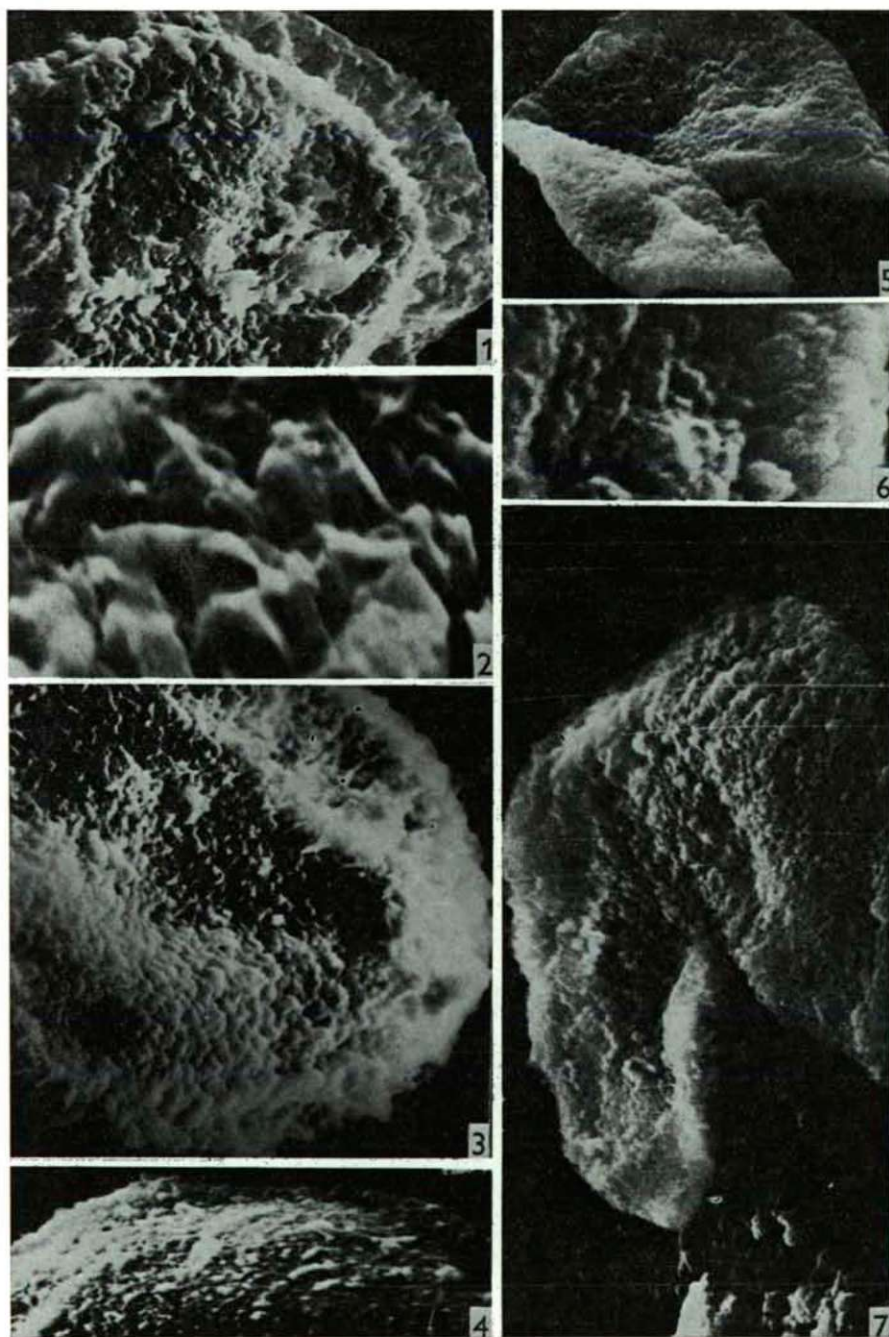
12. *Inaperturopollenites hiatus* (R. POT. 1931b) TH. et PF. 1953 (Plate III, 5—7)

Several specimens were examined and this led to the same results. We could not observe any orbicules, characteristic of recent Taxodiaceae; these probably perished as a result of fossilization. The ornamentation of the surface is granulate, verrucate, sporadically rugulate. The size of the sculptural elements is also varied, their size is 0.2—0.4 μ .

Plate III

1. *Zonalapollenites rueterbergensis* W. KR. 1971, Szerep, x1000.
2. *Zonalapollenites rueterbergensis* W. KR. 1971, central body, Szerep, x5000.
3. *Zonalapollenites verruspinus* W. KR. 1971, Túrkeve, x1000.
4. *Zonalapollenites pliocaenicus* W. KR. 1971, Emőd, x2000.
5. *Inaperturopollenites hiatus* (R. POT. 1931b) TH. et PF. 1953, Emőd, x2000.
6. *Inaperturopollenites hiatus* (R. POT. 1931b) TH. et PF. 1953, Emőd, x10000.
7. *Inaperturopollenites hiatus* (R. POT. 1931b) TH. et PF. 1953, Emőd, x2000.

Plate III



ERDTMAN (1965) investigated into several Gymnospermatophyte pollens with carbon replica method. On the basis of his data, in fossil forms, the *Cryptomeria* genus can also be taken into consideration. The first SEM data on inaperturate Gymnospermatophyte pollen grains are known by REYRE (1968). By reason of his work, the heteromorphous ornamentation occurs in the *Sequoiadendron*, *Cryptomeria* and *Taxodium* genera within the Taxodiaceae family. The *Taxodium* genus is the most probable. On the other hand, it is to be mentioned, as well, that a similar surface occurs in Cupressaceae, too. According to UENO (1973), the connection with *Cunninghamia lanceolata* HOOK cannot be regarded as excluded, either. According to HO and SZIKLAI (1973), the submicroscopic surface of the Taxodiaceae and Cupressaceae pollen grains investigated by them is similar — with the exception of *Sciadopitys verticillata*. According to DUHOUX (1975), the SEM surface of the Cupressaceae pollen is granular with orbicules. From among fossil forms, *Taxacites sahariensis* REYRE 1973, from Neocomian sediments, has a smooth surface or it is a little uneven, with orbicules. The surface of *Cupressacites oxycedroides* REYRE 1973 (Liassic-Neocomian) is granular, with orbicules. It is interesting that *Inaperturopollenites* sp.₂, from the Trias-Dogger sediments of the Sahara, has a similar surface to that of our form. The SEM surface of *Taxodiaceapollenites distichiforme* (SIMPSON) SRIVASTAVA 1975 is, according to SRIVASTAVA (1975) granulate, sporadically with orbicules. In connection with the phylogeny of orbicules, TAYLOR's paper (1976) is important. This demonstrated orbicules and tapetal membrane on the Pennsylvanian in situ *Schopfiipollenites*.

13. *Arecipites vancampoeae* (KDS. et BOH. 1966) W. KR. 1970 (Plate IV, 1—3)

The perforated tectum, which forms a reticulum, is perfectly proved by the scanning method. In the neighbourhood of the colpus perforations are rare, their diameter is 0.2—0.3 μ . Here there is no reticulate structure, the diameter is extragerminally 0.8—1 μ , there is a typically net-like surface.

14. *Monogemmites pseudosetarius* (WEYL. et PF. 1957) W. KR. 1970 (Plate IV, 4, 7)

Several specimens were investigated. It is unequivocally proved by these, that in case of this species the slit of germ is a peculiar, curved colpus. The surface is not smooth. It is covered with granules of varied size, with a 0.05—0.1 μ diameter. The surface of sculptural elements is not entirely smooth, either. It is covered with tiny granules.

15. *Trivestibulopollenites betuloides* PF. 1953a (Plate IV, 5)

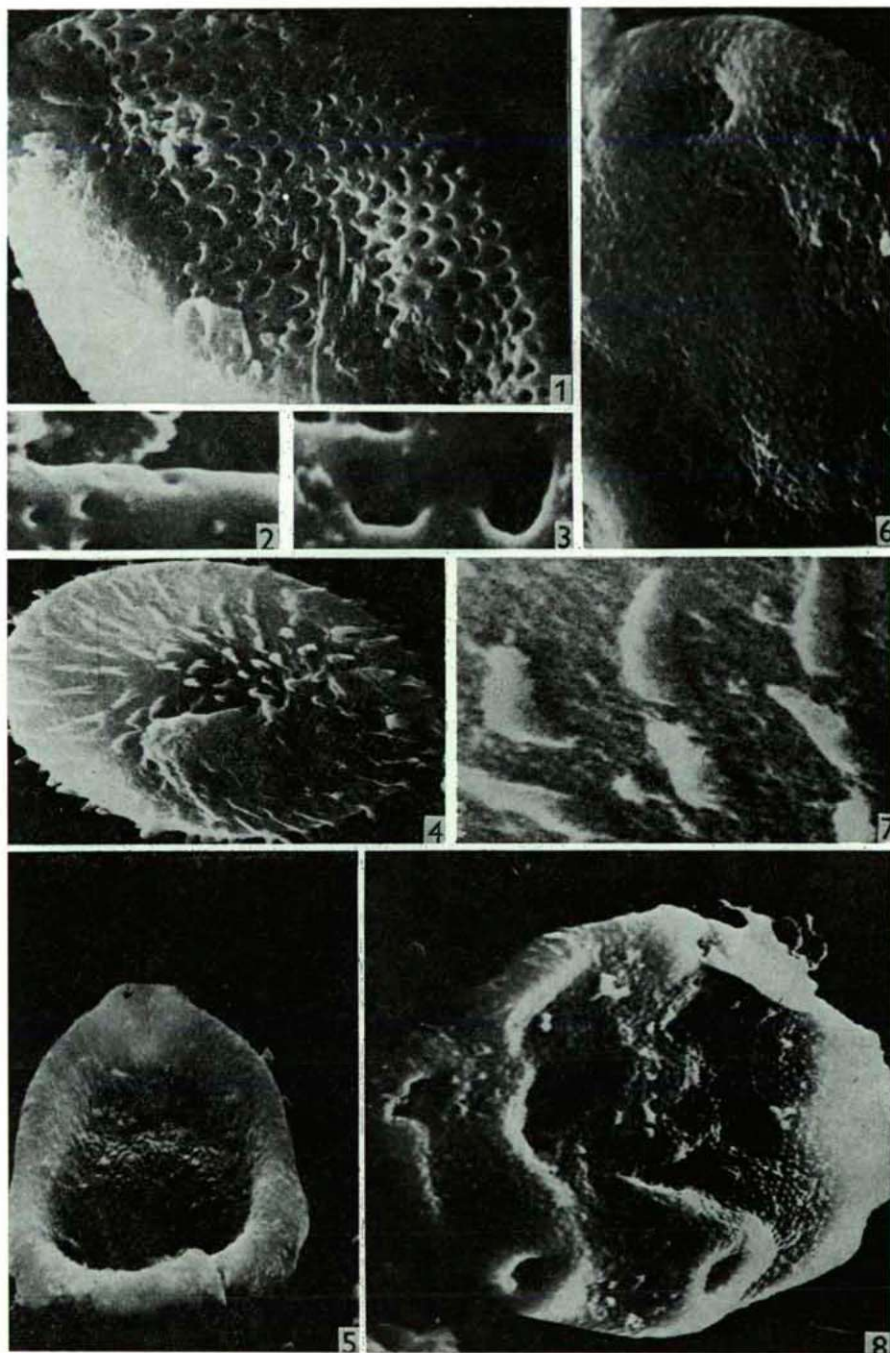
It is visible in the weakly magnified picture, too, that the surface ornamentation consists of short ridges, on which there are small coni. The width of ridges is 0.1—0.2 μ .

ERDTMAN, PRAGLOWSKI and NILSSON (1963) demonstrated ridges and spinae with the carbon replica method. UENO (1975) emphasized spinae in this genus; cf.

Plate IV

1. *Arecipites vancampoeae* (KDS. et BOH. 1966) W. KR. 1970, Emöd, x2000.
2. *Arecipites vancampoeae* (KDS. et BOH. 1966) W. KR. 1970, Emöd, colpus, x10000.
3. *Arecipites vancampoeae* (KDS. et BOH. 1966) W. KR. 1970, extragerminal exine, Emöd, x10000.
4. *Monogemmites pseudosetarius* (WEYL. et PF. 1957) W. KR. 1970, Türkeve, x1000.
5. *Trivestibulopollenites betuloides* PF. 1953a, Emöd, x2000.
6. *Caryapollenites simplex* (R. POT. 1931) RAATZ 1937, Emöd, x2000.
7. *Monogemmites pseudosetarius* (WEYL. et PF. 1957) W. KR. 1970, Türkeve, x10000.
8. *Pterocaryapollenites stellatus* (R. POT. 1931) RAATZ 1937, Emöd, x2000.

Plate IV



SUROVA (1975). In the *B. papyrifera* SEM picture of KOZAR and AARON (1976) ridges can hardly be recognized. On the basis of the work of NILSSON, S., PRAGLOWSKI and NILSSON, L. (1977), ridges are not expressed in every species investigated. VISET (1972) identified his fossil forms with recent species. According to DAMBLON's SEM data (1975), the coni of *Betula pubescens* are on ridges. The fossil *Betula* pollen, examined by us, corresponds to the SEM results published by SUROVA (1975), particularly to those found in the specimens in Plate 51, figs. 1, 2.

For a summary it is to be mentioned that this problem may be cleared up in detail by the SEM investigation into the recent *Betula* species.

16. *Caryapollenites simplex* (R. POT. 1931) RAATZ 1937 subfsp. *simplex* (Plate IV, 6).

The surface is covered with coni characteristic of Juglandaceae. The diameter of the basis of coni is 0.2—0.3 μ . Coni density 3—4 per square micron.

KEDVES and STANLEY (1975) demonstrated, on recent pollen grains, the taxonomical importance of the number of coni per square micron, in this genus. The number of coni per square micron is higher (4—5) on the surface of *Caryapollenites triangulus* (Pf. 1953a) W. KR. 1961 at the Mississippi, from the Lower Eocene, investigated by the scanning electron-microscopic method. In the diameter of the coni basis there is no difference between the fossil *Carya* pollen grains from the Lower Eocene and Upper Pannonian.

17. *Pterocaryapollenites stellatus* (R. POT. 1931) RAATZ 1937 (Plate IV, 8)

The diameter of coni covering the surface is generally 0.2 μ . The number of coni per square micron is 4—6. Thus, the diameter of the basis of coni, as well as the number per square micron are considerably different in the same period in case of the two Juglandaceae genera.

The comparative SEM data see in the work of STONE and BROOME (1975).

18. *Alnipollenites verus* R. POT. 1934 (Plate V, 1,5)

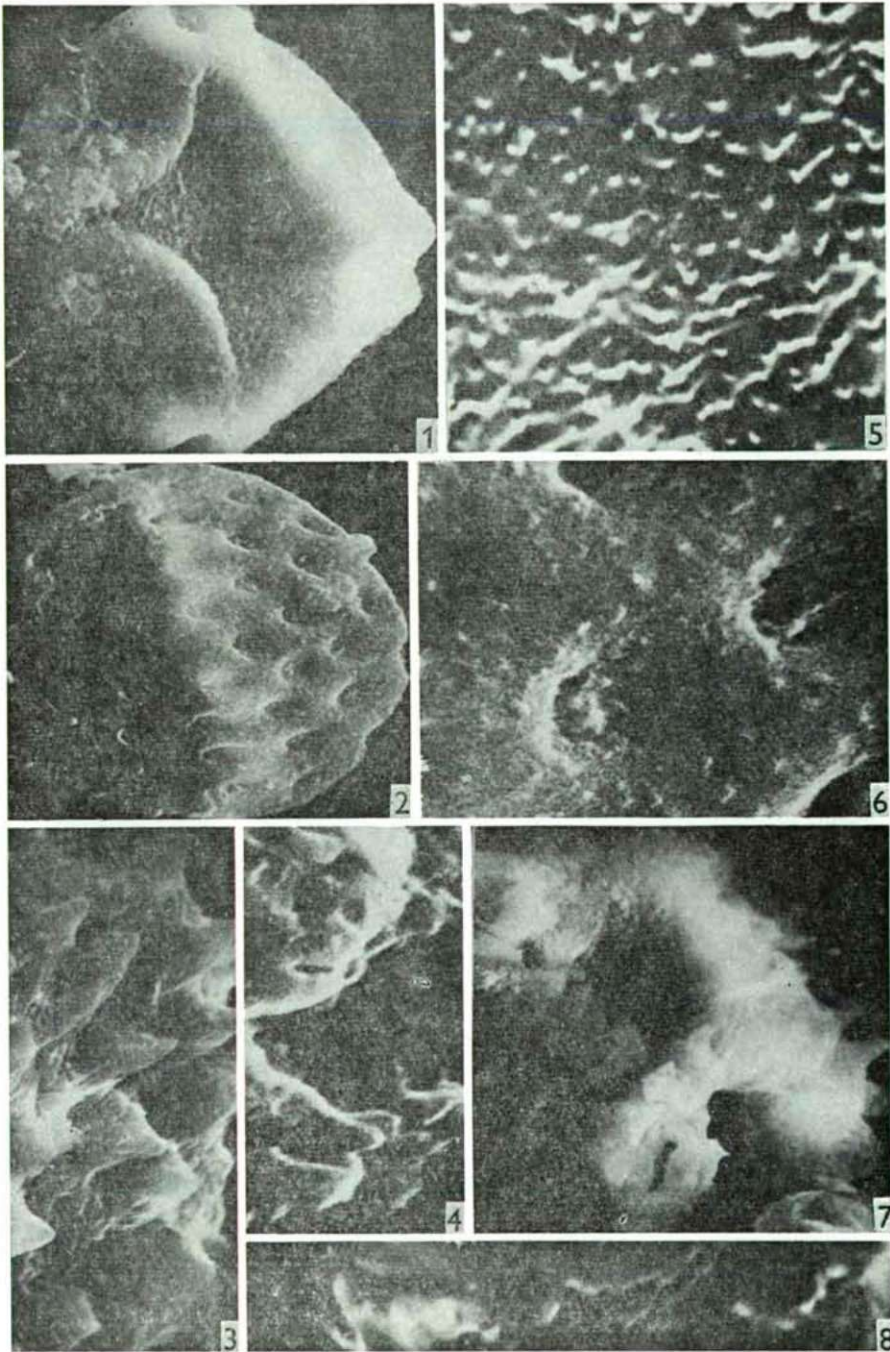
The investigated sediments are rich in fossil *Alnus* pollen grains and several specimens have got under scanning electron-microscopic investigation. Among these, there were pollens of three, four and five germinalia. The most frequent were those of four germinalia. These are, therefore, published. Between the number of pores on the surface sculpture no connection could be established. The surface is covered with coni, the diameter of the basis of which is 0.2—0.3 μ , and 5—6 per square micron. Coni take very often place on ridges.

Recent data are: MARTIN (1969), UENO (1975), NILSSON, S., PRAGLOWSKI and NILSSON, L. (1977). By KEMPF (1973), TEM and SEM data were published of fossil *Alnus* pollen grains from the Miocene (*A. metaplasmsus*). In SRIVASTAVA's (1975) SEM picture of the Maastrichtian *Polyvestibulopollenites verus* (R. POTONIÉ) THOM-

Plate V

1. *Alnipollenites verus* R. POT. 1934, Emöd, x2000.
2. *Chenopodiipollenites multiplex* (WEYL. et PF. 1957) W. KR. 1966, Túrkeve, x2000.
3. *Tubulifloridites grandis* E. NAGY 1969, Emöd, x2000.
4. *Tubulifloridites grandis* E. NAGY 1969, Emöd, x10000.
5. *Alnipollenites verus* R. POT. 1934, Emöd, x10000.
6. *Chenopodiipollenites multiplex* (WEYL. et PF. 1957) W. KR. 1966, Túrkeve x10000.
7. *Cichoreacidites* fsp. cf. *spinosus* SAH 1967, Emöd, x2000.
8. *Cichoreacidites* fsp. cf. *spinosus* SAH 1967, Emöd, x10000.

Plate V



SON et PFLUG 1953 no ridges can be recognized. The qualitative characters established by us can also be observed on SUROVA's (1975) fossil *Alnus* pollen grains (Pl. 50, 1,2).

19. *Chenopodiipollenites multiplex* (WEYL. et PF. 1957) W. KR. 1966 (Plate V, 2,6)

The surface is covered with coni, the diameter of which is 0.2μ . The density of coni per square micron is generally three. The surface of the operculum covering the pore is granular.

From the point of view of the botanical connection between the periporate pollen grains, it was an advancement when TSUKADA (1967) separated the Chenopodiaceae and Amaranthaceae pollen grains from each other with carbon replica method. On the other hand, RIOLLET and BONNEFILLE (1976) demonstrated convergence between Amaranthaceae, Chenopodiaceae, and Caryophyllaceae with scanning electron-microscopic method. There is some similarity between the *Celosia* and *Digera* genera and their fossil forms, the tectum of these is, however, perforated. Cf. with the SEM data of the *Celosia* pollen at ZANDONELLA and LECOQ (1972). Our species investigated, after SKVARLA and NOWICKE (1976), resembles *Beta trigyna*. From among NOWICKE's (1975) SEM data, the type *Amaranthus spinosus* may also come into consideration. The work of KOZAR and AARON (1976) raises the possibility of further connections.

MARTIN's (1969) pollen from the Pleistocene is similar to our fossil form. A further fossil datum is known from SUROVA (1975). The SEM picture of *Chenopodiipollis microporatus* (NAKOMAN) LIU 1978 is published by SUNG TZE CHEN and TSAO LIU (1978). The tectum of this is densely perforated. Thus the surface is essentially reticulate. It differs in this from the species investigated by us.

20. *Tubulifloridites grandis* E. NAGY (1969 Plate V, 3,4)

At the basis of the large sculpture elements and at the surface, the tectum is perforated what can generally not be demonstrated by light-microscopic method. The diameter of perforations is between 0.3 and 0.4μ .

21. *Cichoreacidites* sp. cf. *spinosus* SAH 1967 (Plate V, 7,8)

The taxonomy of the fenestrate Compositae pollen grains is not elaborated as yet. *Fenestrites spinosus* was invalidly described by VAN der HAMMEN (1956) and later validated by GERMERAAD, HOPPING and MULLER (1968), after separating the lectogenotype. On the other hand, Sah described the *Cichoreacidites* genus in 1967, using for the name of species similarly the name "spinosus". The validity of this latter genus is unquestionable. It is, however, necessary to describe the differentiating features of the pollen group exactly and elaborate this taxonomically in the last resort, so much the more because this is one of the developed angiospermous pollen types and is very considerable stratigraphically, as well, because it only occurred in the Upper Tertiary, in the Pannonian, within this first of all in the Upper Pannonian.

The arrangement of lacunae and characteristic spinae is well demonstrated by the scanning electron-microscopic data. The perforations of the tectum, which give a reticulate character to the interlacunar exine and to the basis of the large spinae, can only be demonstrated by this method. The diameter of perforations is $0.2-0.3 \mu$.

Discussion

As sporomorphs of heterogeneous character have got under scanning electron-microscopic investigation, the character of results and thus the value of SEM data are changing. At any rate, compared with the light-microscopic results, the scanning method has demonstrated qualitatively new characters in these cases as well. The sur-

face qualified as smooth with light-microscopic method, is sculptured *Laevigatosporites haardti haardti* with scanning method. Summarizing our experiences achieved so far, at miospores we can come to the conclusion that in the case of the surfaces strongly sculptured even light-microscopically, in most cases no further submicroscopic characters can be demonstrated by the scanning method either, opposite to the forms qualified for scabrate. It is not excluded that after the development of the scanning method, the results achieved so far must be put in a new light. The question of botanical connections in case of the pine pollen grains with bladders has considerably been promoted by SEM data. The *Pinus*, *Picea*, *Abies* genera were partly supported, the *Cathaya* genus was first demonstrated from the Carpathian basin with scanning method. Further on, the *Microcachrys* genus can also be supposed on the basis of the submicroscopic surface of the pollen grain.

Psophosphaera pseudotsugoides is heterogeneous by reason of SEM data; one part of it can be connected with the *Pseudotsuga*, the other part with the *Larix* genus. The fossil *Tsuga* pollen grains can be brought into connection with SIVAK's data (1973). The fossil Taxodiaceae-Cupressaceae (*Inaperturopollenites hiatus*) pollen grains demand further scanning electron-microscopic investigations, as well.

The surface morphology of *Arecipites vancampoae* and *Monogemmites pseudosetarius* was essentially improved by SEM data.

Within Amentiflorae, in case of the *Betula* genus the number of ridges, in case of *Carya* and *Pterocarya* the number of coni per square micron are particularly interesting taxonomical data. The SEM knowledge of the periporate pollen grains demands several investigations, as well, similarly also that of Compositae.

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