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Morphological variability and botanical affinity of some species of the genus *Tricolporopollenites* Pf. et Thoms. from the Middle Miocene Lignite association at Lubstów (Konin region – Central Poland)

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ABSTRACT. From the abundant and very well-preserved pollen assemblages from the brown coal open-cast workings at Lubstów near Konin we were able to perform detailed morphological studies of pollen grains by means of the SEM (Scanning Electron Microscope) and LM (Light Microscope). The studies concerned the following species: *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug sensu lato, *T. dolium* (Potonié) Thomson et Pflug, *T. theacoides* (Roche et Schuler) comb. nov. and *T. villensis* (Thomson) Thomson et Pflug. Within the collective taxon *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug sensu lato one can distinguish four species: *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug sensu stricto, *T. lubstovensis* sp. nov., *T. leonensis* sp. nov., and *T. scutulensis* sp. nov. The species listed above especially *Tricolporopollenites theacoides* (Roche et Schuler) comb. nov. and *T. dolium* (Potonié) Thomson et Pflug revealed changes in the morphology of the tectum sculpture, clearly visible under the SEM and illustrating the process whereby the vallum structures gradually become separated to form loose, irregularly distributed rodlets (after Gortemaker 1986). The sculpture of these grains has been compared to the tectum sculpture of pollen of the Fagaceae and was found to be closest to that of the subfamily Fagoideae. Additionally the tectum sculpture of *Tricolporopollenites villensis* (Thomson) Thomson et Pflug is characterised. This species is considered to be intermediate between the subfamilies Fagoideae and Castaneoideae.

KEY WORDS: pollen grains, tectum sculpture, Fagoideae, Castaneoideae, SEM, Middle Miocene, Poland

INTRODUCTION

In the lowland area of Central Poland, the continental (fluvial and lacustrine) Neogene sediments bearing brown coal seams of various thickness occur on the marine beds of the Upper Cretaceous and Palaeogene. In the Konin area two of them are of commercial importance. The lower seam is exploited only in the Lubstów area, the upper one in several open-cast workings near Konin (Kohlman-Adamska & Ziembińska-Tworzydło 1999). A palynological description of stratigraphic type was carried out for the lower seam on the basis of material obtained from drilling cores (Ciuk & Grabowska 1991).

The brown coal from the lower seam at Lubstów is earthy (detritic), compact, with conchoidal fracturing, without traces of xylites and other plant fragments. The uniform structure of the coal visible to the naked eye has been confirmed microscopically. The whole coal mass consists of amorphous humus with very numerous and perfectly preserved pollen grains and scattered fungal hyphae and spores.

Among the pollen grains of the Angiospermae are very numerous and well-preserved tricolporate ones, which have usually been included in a fossil collective species whose bo-

tanical affinity has not been established until now. They are:

Tricolporopollenites pseudocingulum (Potonié) Thomson et Pflug,

Tricolporopollenites dolium (Potonié) Thomson et Pflug,

Tricolporopollenites villensis (Thomson) Thomson et Pflug.

The studies of the taxa listed above were aimed et elucidating, whether it is possible to distinguish them by differences in their exine sculpture visible under the SEM and to determine their possible affinity to recent families and genera on the basis of their pollen exine structure.

The species *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug and *T. dolium* (Potonié) Thomson et Pflug and *T. villensis* (Potonié) Thomson et Pflug (Thomson & Pflug 1953) had been interpreted differently by Potonié (Potonié 1931a, b). The present authors, having compared the descriptions and illustrations in the available references, accept the species in the sense of Thomson and Pflug (1953). Detailed remarks concerning the nomenclature of the individual taxa have been given in the species descriptions.

SYSTEMATIC PART

Tricolporopollenites lubstovensis sp. nov.

Pl. 1, figs 1–3

Holotypus. Pl. 1, figs 1a, b; 2a, b, c.

Locus typicus. Open-cast working, Lubstów.

Stratum typicum. Lower Miocene, II group of seams – Lusatia

Derivatio nominis. From the village of Lubstów

Material. About twelve specimens, housed in the Institute of Geology, Warsaw University.

Diagnosis. **LM –** Pollen grains tricolporate, in equatorial view 35 × 29 μm, subprolate in outline (P:E 120), polar areas small, broadly-rounded. Colpi long, with gentle curves almost reaching the poles and slightly bent in the equatorial plane. The margins of the colpi are thickened throughout their length. Colpus pores at the equator deep and elongated longitudinally (depth 3 μm, height 5μm). Pollen grains with tectum verrucose. Verrucae densely packed, flat, ca 1 μm in height and 2 to 3 μm in diameter. Exine two-layered about 3 μm thick. Ectoexine about twice as thick as endoexine.

SEM – The sculpture consists of thinly distributed irregular pseudovalla formed from the adhering rodlets, with free endings visible in places. The pseudovalla have a tendency to curve and the fissures between them are moderately deep.

Remarks. *Tricolporopollenites lubstovensis* sp. nov., distinguished among the morphological forms of the pollen grains included in *Tricolporopollenites pseudocingulum* sensu lato, is similar to *T. dolium* (Potonié) Thomson et Pflug in the equatorial view it presents and in the arrangement of the colpi. However, it differs distinctly in its thicker sculpture formed by large, flat verrucae of irregular outline, in the flat and broadly rounded polar areas, and large colpus pores.

Tricolporopollenites leonensis sp. nov.

Pl. 1, figs 4–5, Pl. 2, fig. 1

Holotypus. Pl. 1, figs 4a, b; 5a, b, c.

Locus typicus. Open-cast working, Lubstów.

Stratum typicum. Lower Miocene, II group of seams – Lusatia.

Derivatio nominis. From the forename of Professor Leon Stuchlik, an outstanding Polish palynologist.

1934 *Pollenites pseudocingulum* Potonié; Potonié, p. 74, 75, Pl. 3, fig. 28.
1953 *Tricolporopollenites pseudocingulum* Potonié; Thomson & Pflug, Pl. 12, fig. 111 only.
1962 *Rhooidites pseudocingulum* Potonié; Mamczar, Pl. 4, fig 14, Pl. 6, figs 62, 63.
1974 *Rhoipites pseudocingulum* (Potonié) Potonié; Ziembińska-Tworzydło, Pl. 23, fig. 2.

Material. Roughly a dozen specimens housed in the Institute of Geology, Warsaw University.

Diagnosis. **LM –** Pollen grains tricolporate, in equatorial view 33 × 24 μm, prolate in outline (P:E 140), polar areas narrowly-rounded. Colpi long, almost reaching the poles. Pollen grains asymmetric, one colpus curving outwardst in the equatorial plane more than the other. Pores in the colpi at the equator elongated longitudinally. Pollen grains with tectum

scabrate. Projections densely packed and less then 1 μm in both height and diameter. Exine two-layered of thickness ca 2 μm, ecto- and endoexine of equal thickness.

SEM – Sculpture in the form of pseudovalla consisting of fine rodlets, loosely and irregularly forming a flabellate arrangement, laterally contiguous. The holes and fissures visible among the pseudovalla form a labyrinth. Some pseudovalla are curved, forming a torus.

Remarks. *Tricolporopollenites leonensis* sp. nov. was distinguished among the morphological forms of pollen included in *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug. From *T. pseudocingulum* (Potonié) Thomson et Pflug sensu stricto it differs in the asymmetric arrangement of the colpi and the less acuminate outline of the polar areas, and in the SEM image the distinctly discernible elements forming the pseudovalla. *Tricolporopollenites leonensis* sp. nov. is most similar to *T. lubstovensis* sp. nov., from which, however, it differs under the LM by the asymmetric arrangement of the colpi, the more convex polar areas and the finer scabrate sculpture. The tectum in the SEM image appears as small pseudovalla consisting of fine rodlets. All the elements of the sculpture are distinctly finer than in *T. lubstovensis* sp. nov. and exhibit a more regular vallum sculpture.

Tricolporopollenites pseudocingulum (Potonié 1931) Thomson et Pflug 1953 sensu stricto

Pl. 2, figs 2–4; Pl. 3, figs 1–5

1931a *Pollenites pseudocingulum granulatum* n. f.; Potonié, p. 332, Pl. 1, figs 19, 24, 26, 27.
1931a *Pollenites dolium solum* n. sp.; Potonié, p. 332, Pl. 2, fig. 21.
1931b *Pollenites* cf. *dolium* n. sp.; Potonié, p. 26, Pl. 1, fig. V45d.
1934 *Pollenites pseudocingulum* Potonié; Potonié, p. 74, 75, Pl. 3, fig. 38.
1950 *Rhooidites pseudocingulum* Potonié; Thomson in Potonié, Thomson & Thiergart, p. 57, Pl. B, figs 41, 42.
1950 *Rhoipites pseudocingulum* Potonié; Thiergart in Potonié, Thomson & Thiergart, Pl. C, figs 25, 26.
1953 *Tricolporopollenites pseudocingulum* (Potonié) n. comb.; Thomson & Pflug p. 99, Pl. 12, figs 95–105, 108–111.
1962 *Rhooidites pseudocingulum* Potonié; Mamczar, Pl. 4, figs 4, 5, 8, 9, 16–19, 25; Pl. 5, figs 29, 31, 35, 41, 42; Pl. 6, fig. 56.
1974 *Rhoipites pseudocingulum* (Potonié) Potonié; Ziembińska-Tworzydło, Pl. 23, figs 3, 4.
1980 *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug; Thiele-Pfeiffer, p. 150, Pl. 12, figs 4, 5.
1980 *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug; Ollivier-Pierre, p. 60, Pl. 22, figs 14, 15.
1984 *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug; Mohr, p. 87, Pl. 15, figs 7.1, 7.2, 8.
1993 *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug; Kohlman-Adamska, p. 159, Pl. 31, fig. 1a, b.

Material. Many well-preserved specimens housed in the Institute of Geology, Warsaw University

Description. **LM –** Pollen grains tricolporate, in equatorial view 35 to 40 × 28 to 35 μm, subprolate in outline (P:E 125), the polar areas slightly sharped. The pollen grains are symmetric with the colpi curved strongly outwards in the equatorial plane. These have thick margins, with additional thickening around the pores. The colpus pores are elongated latitudinally at the equator. The pollen grains possess a scabrate tectum of irregular large granulae whose diameters sometimes exceed 1 μm. The exine is two-layered of thickness ca 2,5 μm.; the ectoexine is distinctly thicker than the endoexine.

SEM – The sculpture takes the form of irregularly curved valla splitting into rodlets which in places become toroid. The surfaces of the valla have distinct incisions which represent traces of the splitting into rodlets, the basic elements composing the valla. The fissures between the valla are deep and they form a labyrinth.

Remarks. These specimens only were included in the synonymy of this species. Illustrations confirm this to be the species *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug *sensu* Potonié, Thomson & Thiergart (1950) and Thomson & Pflug (1953). The works of Potonié from the 1931a cannot provide a sufficient basis for *T. pseudocingulum* (Potonié) Thomson et Pflug, because Potonié illustrated various morphological types of tricolporate pollen, of which be attributed to *T. pseudocingulum*. Of the specimens illustrated by Potonié (1931a) only a few may be considered as belonging to *T. pseudocingulum* sensu Thomson et Pflug 1953.

Potonié, Thomson and Thiergart (1950) il-

lustrated *T. pseudocingulum* and included it in a new genus *Rhooidites*. However, the illustrations from their work (except for Pl. C, fig. 26) fully conform to the concept of *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug 1953. Even more complications were introduced as a result of a later publication by Potonié (1960), in which *Tricolporopollenites pseudocingulum* and *T. dolium* were included in the genus *Rhoipites* Wodehouse 1933. In his comment on this change Potonié (op. cit.) wrote that the holotype of the species *Rhoipites pseudocingulum* from his earlier publication (Potonié 1931a, Pl. 1, fig. 3) was illustrated again in Pl. 6, fig. 114. Furthermore, pollen of this morphological type had been considered earlier by Thomson and Pflug (1953, Pl. 12, figs 112–117) as typical for *Tricolporopollenites dolium* Thomson et Pflug. To make matters worse, the holotype of *Rhoipites dolium*, presented in the work by Potonié (1931b) in Pl. 1, fig. V45d and quoted by him in his publication of 1960, is in agreement with the morphological type accepted by Thomson and Pflug (1953) as the characteristic one for *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug 1953.

It would appear, from the above discussion, that the concepts of *T. pseudocingulum* (Potonié) Thomson et Pflug and *T. dolium* (Potonié) Thomson et Pflug, accepted by Thomson and Pflug (1953) reversed the definitions of these two species given by Potonié (1960). Potonié's ideas have not been accepted in the palynological literature, in which the concepts of these two species proposed by Thomson and Pflug (1953) have become established.

Thiele-Pfeiffer (1980), on the basis of observations of recent material, has found that pollen taxa of the same morphology as the fossil *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug do not occur in contemporary plants. Mohr (1984) has expressed a similar opinion; she illustrated by means of SEM (Pl. 15, figs 7.1, 7.2) the sculpture of specimens of the species *T. pseudocingulum* (Potonié) Thomson et Pflug. It is the same as that of the Lubstów material, which the present authors have accepted as characteristic for the species *T. pseudocingulum* (Potonié) Thomson et Pflug sensu stricto.

Tricolporopollenites dolium (Potonié 1931) Thomson et Pflug 1953

Pl. 4, figs 1–5

1931a *Pollenites dolium megaventricosum* n. f.; Potonié, Pl. 2, fig. 22.
1931b *Pollenites dolium* n. sp.; Potonié, Pl. 1, fig. V38a.
1934 *Pollenites pseudocingulum* Potonié; Potonié, p. 74, 75, Pl. 3, fig. 29.
1934 *Pollenites dolium* Potonié; Potonié & Venitz, p. 30, Pl. 3, figs 77, 78.
1953 *Tricolporopollenites dolium* (Potonié) n. comb.; Thomson & Pflug, p. 98, Pl. 12, figs 112–117.
1960 *Rhoipites pseudocingulum* (Potonié) nov. comb.; Potonié, p. 101, Pl. 6, fig. 114.
1962 *Rhooidites pseudocingulum* Potonié; Mamczar, Pl. 4, figs 22, 23.
1980 *Tricolporopollenites dolium* (Potonié) Thomson et Pflug; Ollivier-Pierre, p. 59, Pl. 22, fig. 11.

Material. Approximately twelve specimens housed in the Institute of Geology, Warsaw University.

Description. **LM** – Pollen grains tricolporate, in equatorial wiev 30 to 35 × 20 to 25 μm, subprolate in outline (P:E 140–150), rounded at the poles. Colpi long, almost parallel, curved slightly outwards in the equatorial plane, almost reaching the poles. Colpi margins thick with additional fine swellings visible around the pores. Colpus pores narrow at the equator, are elongated latitudinally with costae colpi. Pollen grains tectate, verrucate. Verrucae irregular with diameter exceeding 1 μm. Exine two-layered, ca 2 μm thick, both layers of equal thickness at the equator but in the polar areas the ectoexine is thicker than the endoexine.

SEM – The sculpture is formed of distinct valla, flat and broad, tightly coiled or irregularly toroid. The valla surface is finely and shallowly cut, revealing distinct traces of the splitting of the valla into individual elements (rodlets). The fissures between the valla form a labyrinth.

Remarks. Potonié (1931a) created a new species *Pollenites dolium* with three subspecies: *P. dolium solum*, *P. dolium megaventricosum* and *P. dolium clarum*. He neither distinguished the nominal subspecies *P. dolium dolium* nor indicated the holotype. In his next publication he again referred to *Pollenites dolium* as a new species (Potonié 1931b Pl. 1, fig. V38a).

In 1934 Potonié and Venitz gave the complete synonymy of the species *Pollenites do-*

lium Potonié with references to the following illustrations:

Pollenites dolium Potonié 1931b, Pl. 1, fig. V38a

Pollenites cf. *dolium* Potonié 1931b, Pl. 1, fig. V45d

Pollenites caroli Potonié 1931b, Pl. 1, fig. V51c

Pollenites dolium solum Potonié 1931a, p. 229, Pl. 2, fig. 21

Pollenites dolium megaventricosum Potonié 1931a, p. 229, Pl. 2, fig. 22

Pollenites ventricosum Potonié 1931a, p. 229, Pl. 2, fig. 30

Pollenites dolium clarum Potonié 1931a, p. 229, Pl. 2, fig. 35

Pollenites cf. *dolium solum* Potonié 1931a, p. 229, Pl. 2, figs 36, 38

Pollenites cf. *dolium* Potonié 1931a, p. 229, Pl. 2, fig. 39

It appears from the above list, that Potonié and Venitz (1934) included in the synonymy of *Pollenites dolium* the three subspecies earlier distinguished by Potonié (1931a) and they expanded the common diagnosis to morphological forms with very different sculptures and a range of courses of the colpi. Pollen dimensions varying between 20 and 24 μm provided the only common feature.

Later, in 1953, Thomson and Pflug established the new genus *Tricolporopollenites* and they accepted *Tricolporopollenites dolium* (Potonié) comb. nov. as the type species. They included *T. pseudocingulum* (Potonié) comb. nov. in this genus as well. They provided new diagnoses for both species, which were completely different from those of Potonié (1931a, b). In defending Thomson and Pflug (op. cit.) one must point out, that the diagnoses in Potonié (op. cit.) and Potonié and Venitz (1934) were ambiguous and the specimens illustrated showed essential differences, even within the same species.

According to the new diagnoses of Thomson and Pflug (1953), *Tricolporopollenites dolium* and *T. pseudocingulum* share a common class size (30–40 μm). These two species differ mainly in the colpi pattern: *T. dolium* has colpi almost parallel but in *T. pseudocingulum* the colpi in the equatorial plane are strongly curved and displaced outwards. The polar areas of *T. dolium* are rounded but these of *T. pseudocingulum* are slightly sharped. The ectoexine of *T. dolium* is thicker at the poles than at the equator, but that of *T. pseudocingulum* has the same thickness all over. It appears from Thomson and Pflug's description (1953), that the sculpture of *T. pseudocingulum* is finer than that of *T. dolium*.

The paper by Thomson and Pflug (1953) became very popular among palynologists because of the clear rules of application of morphological features to the systematics of Tertiary pollen and because of the good illustrations. Most palynologists accepted their definitions of *T. dolium* (Potonié) Thomson et Pflug and *T. pseudocingulum* (Potonié) Thomson et Pflug.

The present authors' studies have indicated that the scanning images of *T. dolium* (Potonié) Thomson et Pflug and *T. pseudocingulum* (Potonié) Thomson et Pflug sensu stricto display similar types of surface structure and distinct differences occur only in the size and thickness of the sculpture elements. That of *T. dolium* (Potonié) Thomson et Pflug (visible under the SEM) consists of thicker and larger elements in the form of valla with obscurely marked cuts on the surface. *T. pseudocingulum* (Potonié) Thomson et Pflug sensu stricto has smaller valla with a densely cut surface. Both species have their sculpture elements separated by deep labyrinthine fissures. These sculpture differences are clearly visible under the SEM at a magnification of ca × 10 000. Under the light microscope (LM) distinct differences between the two species are apparent in the structure and course of the colpi, the exine thickness and the outline of the polar areas.

***Tricolporopollenites scutulensis* sp. nov.**

Pl. 5, figs 1, 2

Holotypus. Pl. 5, figs 1a, b, 2a, b, c

Locus typicus. Open-cast working, Lubstów

Stratum typicum. Lower Miocene, II group of seams – Lusatia.

Derivatio nominis. From the Latin word "scutula" – vallum, describing the vallum sculpture.

1974 *Rhoipites pseudocingulum* (Potonié) Potonié; Ziembińska-Tworzydło, Pl. 23, fig. 3.

1980 *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug; Thiele-Pfeiffer, p. 150, Pl. 12, figs 6–10.

Material. More than fifty specimens housed in the Institute of Geology, Warsaw University.

Diagnosis. **LM –** Pollen grains tricolporate, in equatorial view the equator diameter ranges from 24 to 28 μm and the polar axis from 28 to 30 μm, the outline being prolate spheroidal to subprolate (P:E 110–113); the polar areas are broadly rounded and slightly flattened. The colpi are long, curved strongly outwards in the equatorial plane, with the margins thickening gradually from the poles towards the pores. The pores in the colpi at the equator are fissured and latitudinally elongate. The exine is two-layered up to 2 μm thick. The ectoexine has the same thickness as the endoexine or is slightly thicker. The tectum of the pollen grains is verrucose, with the verrucae flat and of diameter 1–2 μm, densely packed.

SEM – The sculpture consists of thick, irregular, broad valla with a distinctly ribbed surface. The individual ribs provide evidence of the splitting of the valla into the basic elements of the sculpture, i.e. rodlets. Toroid formation is rare. The fissures between the valla are broad and labyrinthine.

Remarks. Among the many morphological forms of pollen grains included in *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug sensu lato, a group of specimens with verrucose tectum structure, has been distinguished for which the new species *Tricolporopollenites scutulensis* sp. nov. has been established. The type of colpus and pore structure of the described specimens is similar to that of *T. pseudocingulum* (Potonié) Thomson et Pflug sensu lato. The specimen illustrated by Thiele-Pfeiffer (1980, Pl. 12, figs 6–10) and included by her, on acount of its colpus and pore structure, in the so-called short-axial *T. pseudocingulum* (Potonié) Thomson et Pflug of verrucose sculpture, is identical to the newly described species *T. scutulensis*.

Tricolporopollenites theacoides (Roche et Schuler 1976) **comb. nov.**

Pl. 5, figs 3–5

1974 *Rhoipites pseudocingulum* (Potonié) Potonié; Ziembińska-Tworzydło, Pl. 23, fig. 5.

1976 *Verrutricolporites theacoides* n. fsp.; Roche & Schuler, p. 27, Pl. 10, figs 31, 32.

Material. A dozen specimens housed in the Institute of Geology, Warsaw University.

Description. **LM** – Pollen grains tricolporate, in equatorial view the diameter of the equator ranges from 22 to 28 μm and the polar axis from 28 to 40 μm, forming a prolate outline (P:E 130–147), the polar areas narrowly rounded. The colpi are long, slightly curved in the equatorial plane with their margins gradually thickening from the poles towards the pores. At the equator the pores in the colpi are broad and almost round (slightly elongated longitudinally) of dimensions 3 × 4 μm. The exine is two-layered and up to 2.5 μm thick. The grains have a coarsely verrucose tectum, with verrucae 1.5–2 μm in diameter and 3–5 μm in height.

SEM – The sculpture consists of thick, irregular, flat and broad valla, finely ribbed on the surface. The valla are rarely toroid and the fissures between them are broad and labyrinthine.

Remarks. The specimens from Lubstów which were determined as *Tricolporopollenites theacoides* (Roche et Schuler 1976) comb. nov. have an identical morphology to that described by Roche and Schuler as *Verrutricolporites theacoides* (Roche & Schuler 1976, Pl. 10, figs 31, 32). The transfer of *V. theacoides* Roche et Schuler to the genus *Tricolporopollenites* resulted from the acceptance of the morphological systematics of Thomson and Pflug (1953) by the present authors. According to Roche and Schuler (1976), the tectum sculpture visible under the LM, as well as the structure of the colpi and pores of the pollen of *Verrutricolporites theacoides*, indicate its similarity to that of the recent species *Gordonia anomala* of the Theaceae. In the present authors' opinion however, the tectum sculpture of *Tricolporopollenites theacoides* (Roche et Schuler 1976) comb. nov. as revealed in the SEM images, differs completely from that of pollen of the Theaceae.

Tricolporopollenites villensis (Thomson in: Potonié, Thomson & Thiergart 1950) Thomson et Pflug 1953

Pl. 6, figs 1–6

1950 *Cupuliferoidae – poll. cingulum villensis* n. sp.; Thomson in Potonié, Thomson & Thiergart, p. 55, Pl. B, figs 28, 29.

1953 *Tricolporopollenites villensis* (Thomson) n. comb.; Thomson & Pflug, p. 99, Pl. 12, figs 5–14.

1962 *Rhooidites pseudocingulum* Potonié; Mamczar, Pl. 4, figs 1, 11, 12; Pl. 5, figs 38?, 50, 52, 53.
1980 *Tricolporopollenites villensis* (Thomson in Potonié, Thomson & Thiergart) Thomson et Pflug; Ollivier-Pierre, p. 60, Pl. 22, fig. 12.
1984 *Tricolporopollenites villensis* (Thomson) Thomson et Pflug; Mohr, p. 86, Pl. 15, fig. 3.
1993 *Eotrigonobalanus eiszmannii* n. sp.; Walther & Zetter, p. 187, Pl. 2, figs 1–15.
1998 *Eotrigonobalanus eiszmannii* Walther et Zetter; Gastaldo & al., Pl. 2, figs 8–12.

Material. More than fifty specimens housed in the Institute of Geology, Warsaw University

Description. **LM –** Pollen grains tricolporate, in equatorial view the diameter of the equator ranges from 18 to 20 μm and that of the polar axis from 25 to 30 μm, with prolate outline (P:E 150), the small polar areas being narrowly rounded or slightly sharped. The colpi are long, straight and parallel, almost reaching the poles. The colpus margins are thick, with additional thickening around the pores, but without sharp costae colpi. In the equatorial plane the colpus pores are large and of almost equal height and width (2.5×3 μm). The tectum of the grains is rugulose and the exine thick (2–2.5 μm), with the ectoexine thicker than the endoexine.

SEM – The sculpture consists of rodlets arranged in irregular toroid valla with the surface deeply and regularly cut to form flabella. The fissures between the valla are deep and labyrinthine.

Remarks. Zetter (Walther & Zetter 1993) observed a similar type of sculpture in pollen grains found on the leaves of the fossil species *Eotrigonobalanus furcinervis* (Rossmässler) Walther et Kvaček from the family Fagaceae. For this pollen Zetter described a new species *Eotrigonobalanus eiszmannii*. However, this name was not applied correctly, because the genus *Eotrigonobalanus* Kvaček et Walther had been formed earlier on the basis of macroscopic fossil remnants (Kvaček et Walter 1989).

CONCLUSIONS

The detailed observations of pollen of the collective fossil species *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug sensu lato described in the present paper have resulted in the recognition within this collective species of four clearly distinct species: *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug sensu stricto, *T. leonensis* sp. nov., *T. scutulensis* sp. nov. and *T. lubstovensis* sp. nov. These species and the taxa *T. theacoides* (Roche et Schuler) comb. nov. and *T. dolium* (Potonié) Thomson et Pflug which were also present, display similar exine surface structure, visible under the SEM. The sculpture of the fossil pollen of all the species listed above consists of the same basic elements, which are rodlets. However, the mode of orientation and growth of those rodlets differ in the individual species, giving rise to distinct images of sculpture structure visible under the SEM (Fig. 1).

In this respect the pollen resembles that of the recent Fagaceae, where the rodlets, arranged in various configurations, play a basic role in the pollen grain tectum structure. However, the pollen grains of recent representatives of the Fagaceae, as evidenced by SEM observations, are characterised by a different type of sculpture, i.e. by different rodlet arrangements in each of the three subfamilies: Castaneoideae, Fagoideae and Quercoideae (Crepet & Daghlian 1980, Praglowski 1982, 1984).

In the Fagoideae (genus *Fagus*) the horizontally arranged rodlets, forming vermicular, partly anastomosing structures, are the basic elements of the sculpture. Some rodlets agglomerate to form clusters and have their free ends curved upwards, as e.g. in *Fagus mexicana* (comp. Praglowski 1982, fig. 1, D, E) and *Fagus japonica* (comp. Gortemaker 1986, Pl. 3, figs 3, 4). A similar type of sculpture, visible under the SEM, occurs in the Miocene species *Faguspollenites verus* Raatz (Fig. 1; comp. Gortemaker 1986, p. 282, Pl. 3, figs 5, 6; Pl. 4, fig. 1; Kohlman-Adamska & Ziembińska-Tworzydło 1999, Pl. 1, figs 1, 2).

All the listed fossil and recent species display sculpture typical of the Fagoideae, as observable under the SEM. The tectum is formed of basic elements (rodlets) fused to various degrees. The fused rodlets form patterns with vary from valla with obscure, scarcely protruding basic elements through partly accreted pre-valla to separated or weakly accreted rodlets, which show an irregular, vermicular pattern as on the pollen grains of *Fagus*. The changes of sculpture in the studied fossil pollen species as seen under the SEM form a logical sequence, leading to gradual separation of the rodlets (Fig. 1).

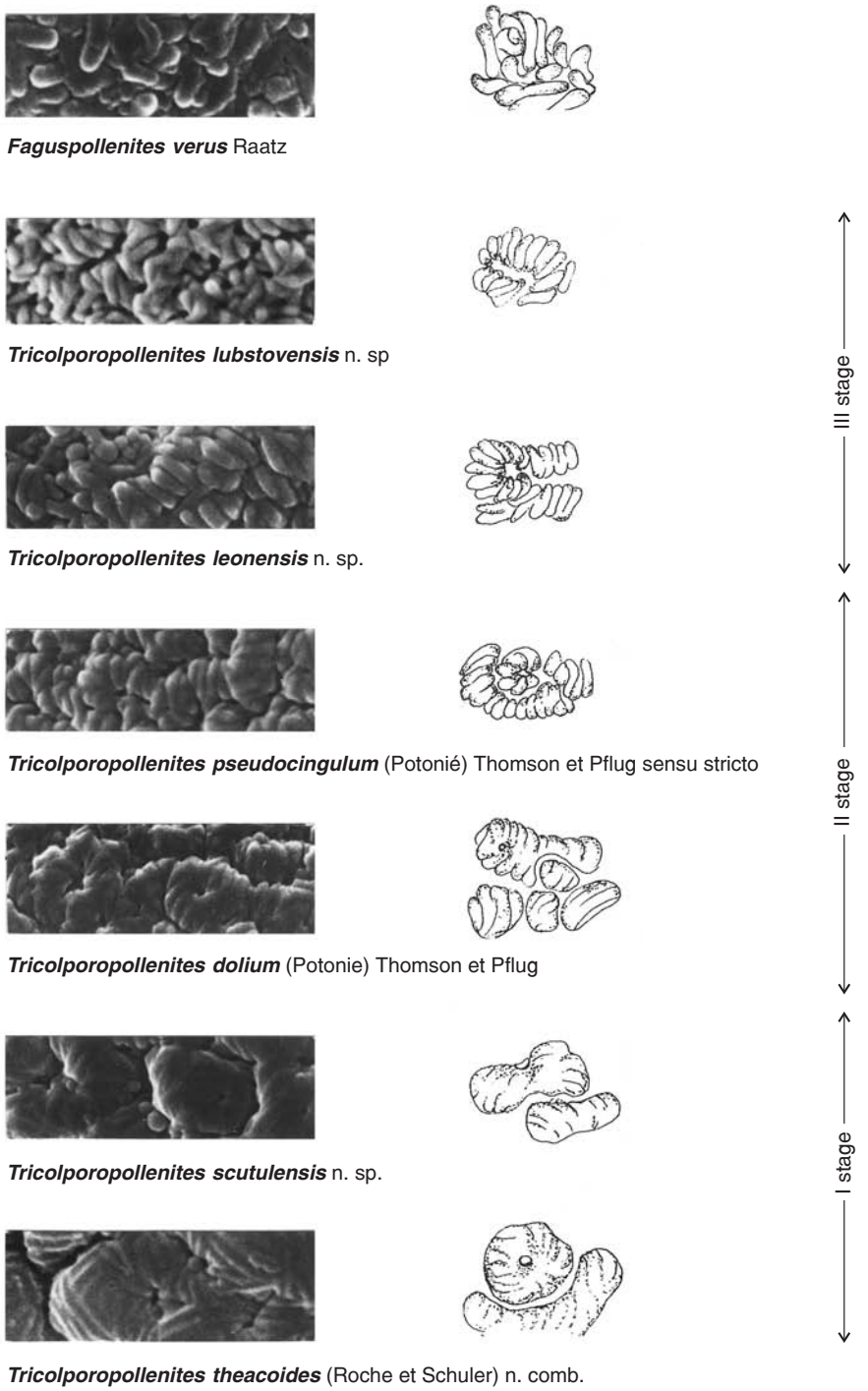

Fig. 1. Morphological sequence of tectum sculpture of some species in genus *Tricolporopollenites* observed under the SEM. (Lubstów, Middle Miocene lignite association). I stage – valla forming an almost flat surface with faintly marked cuts, whith indicate the beginnings of the separation of the basic elements to form rodlets (*Tricolporopollenites theacoides, T. scutulensis*). II stage – the valla are well-developed and their surfaces have relatively deep cuts, which clearly mark the separating rodlets (*Tricolporopollenites dolium, T. pseudocingulum*). III stage – the sculpture consist of loose, horizontally arranged rodlets, forming groups of wide, irregular pre-valla with deep cuts. (*Tricolporopollenites leonensis, T. lubstovensis, Faguspollenites verus*)

In the first stage the sculpture consists of valla forming an almost flat surface with faintly marked cuts, which indicate the beginnings of the separation of the basic elements to form rodlets. The following pollen grains:

1 – *Tricolporopollenites theacoides* (Roche et Schuler) comb. nov. (Fig. 1, Pl. 5, figs 3–5). The sculpture consists of wide valla forming an almost flat surface. Traces of rodlet separation appear as obscurely visible cuts on the

vallum surface. The valla are irregularly curved, in places forming a toroid pattern; the labyrinthine fissures between them are deep.

2 – *Tricolporopollenites scutulensis* sp. nov. (Fig. 1, Pl. 5, figs 1, 2). The sculpture takes the form of wide and almost flat valla with shallow cuts on the surface which are the poorly defined traces of separating rodlets. The valla are irregularly curved, in places forming tori. The fissures between the valla are large and labyrinthine.

In the second stage the valla are well developed and their surfaces have relatively deep cuts, which clearly mark the separating rodlets. Such a structure is characteristic for the following pollen grains:

1 – *Tricolporopollenites dolium* (Potonié) Thomson et Pflug (Fig. 1, Pl. 4, figs 1–5). The sculpture takes the form of distinct valla, flatter and wider than in *T. pseudocingulum* (Potonié) Thomson et Pflug sensu stricto and tightly coiled, creating a surface which is faintly and shallowly cut. These cuts provide distinct traces incipient rodlet separation. The valla are tightly curved and form tori. Between them labyrinthine fissures can be seen.

2 – *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug sensu stricto (Fig. 1, Pl. 2, figs 2–4, Pl. 3, figs 1–5). The elements of the sculpture (rodlets) are accreted in irregularly coiled valla, whose surface contains cuts representing the rudimentary rodlets. The valla are tightly curved, forming tori, with a labyrinth of fissures between them.

In the final stage the rodlets are arranged loosely and horizontally and accreted in pre-valla on whose surface they are distinctly visible. The pollen grains of the following have this structure:

1 – *Tricolporopollenites leonensis* sp. nov. (Fig. 1, Pl. 1, figs 4–5, Pl. 2, fig. 1). The individual sculpture elements are horizontally and irregularly arranged rodlets which are essentially accreted in groups to form pre-valla. In places the free ends of the rodlets, held perpondicularly to the surface, are visible. Some pre-valla are curved, forming tori. Between them holes and labyrinthine fissures are apparent.

2 – *Tricolporopollenites lubstovensis* sp. nov. (Fig. 1, Pl. 1, figs 1–3). The sculpture consists of loose, horizontally arranged rodlets, forming groups of wide, irregular pre-valla with deep cuts in their surface where the upwardly directed ends of the rodlets are clearly visible. The fissures between the valla are moderately deep.

3 – *Faguspollenites verus* Raatz (Fig 1; Kohlman-Adamska & Ziembińska-Tworzydło 1999, Pl. 1, figs 1, 2). The sculpture consists of loose, horizontally arranged rodlets whose numerous upwardly directed endings are clearly visible. The rodlets are arranged in a vermicular pattern and sometimes form clusters.

From the above observations, it results that the fossil species, which, on the basis of the similar morphology observable in transmitted light, have hitherto been included in the collective taxon *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug sensu lato as well as *T. theacoides* (Roche et Schuler) comb. nov. and *T. dolium* (Potonié) Thomson et Pflug, have the type of sculpture seen in the pollen grains of the Fagoideae. Most probably they are all genetically related. Of the fossil species listed above, the Miocene *Faguspollenites verus* Raatz and *Tricolporopollenites lubstovensis* sp. nov. (Fig. 1) are closest to the recent genus *Fagus*.

A different type of sculpture from that characterised above occurs in the fossil pollen species *Tricolporopollenites villensis* (Thomson) Thomson et Pflug (Fig. 1, Pl. 6, figs 1–6). Observation of the pollen grains under the SEM showed, that their sculpture consists of basic elements (rodlets), arranged differently from those in the species *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug sensu lato, *T. theacoides* (Roche et Schuler) comb. nov. and *T. dolium* (Potonié) Thomson et Pflug.

The sculpture of *Tricolporopollenites villensis* (Thomson) Thomson et Pflug as seen under the SEM (Pl. 6, figs 1, 4) consists of rodlets arranged horizontally and regularly to form a flabellate pattern. The accreted rodlets form irregular vallum structures in which the valla surfaces are deeply and regularly cut into flabella with a distinct tendency to coil and form of the tori. The fissures between the valla are deep and labyrinthine.

This sculpture structure, as revealed by the SEM, consisting of regularly arranged rodlets accreted in bunches, obliquely inclined to one another, occurs in the fossil pollen grains determined as *Castanopsis* sp. – "*Tricolporopollenites cingulum pusillus*" (Draxler & Zet-

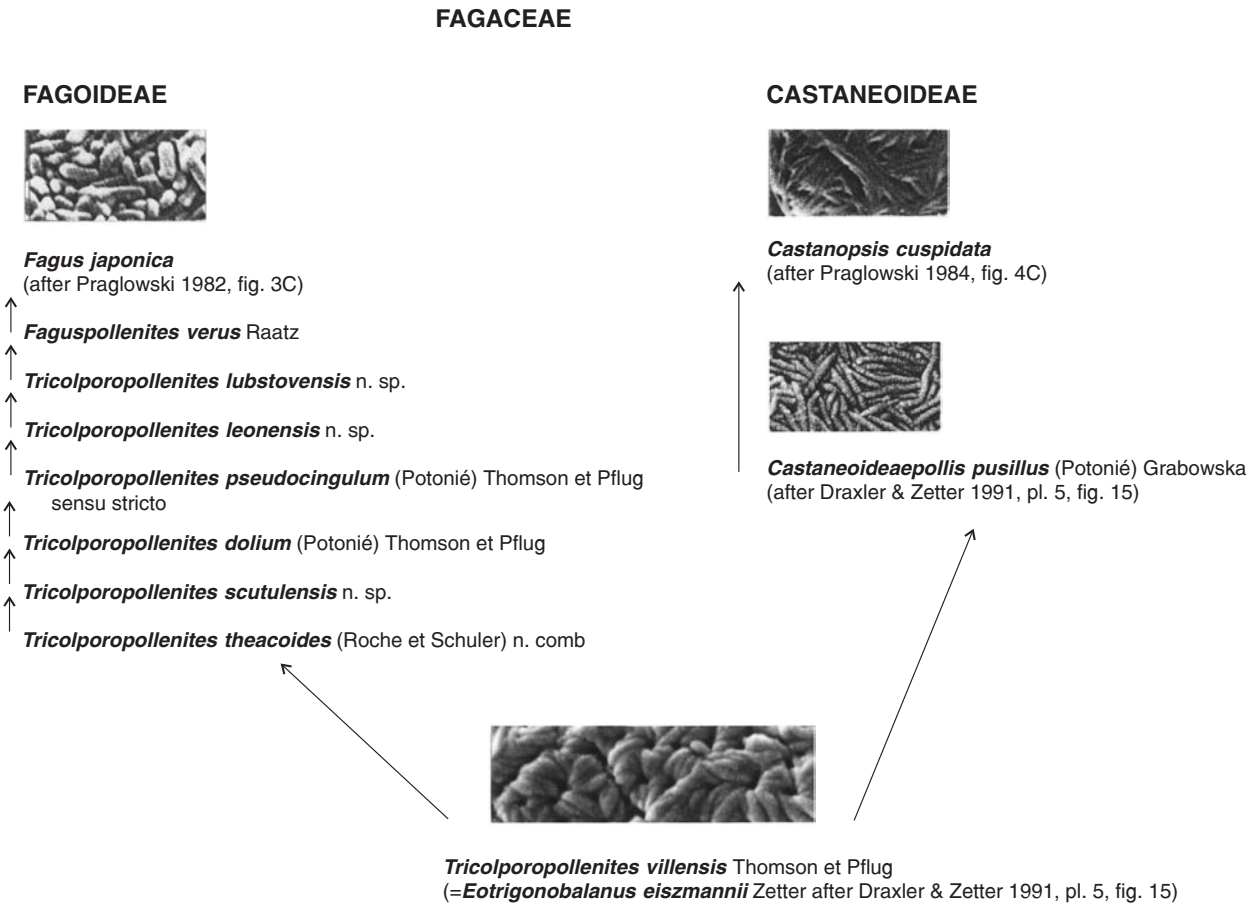

Fig. 2. Botanical affinity of some species in genus *Tricolporopollenites* (after sculpture structure visible under the SEM)

ter 1991, Pl. 5, figs 13–15) and *Castaneoideaepollis pusillus* (Potonié) Grabowska (Kohlman-Adamska & Ziembińska-Tworzydło 1999 Pl. 1, figs 5, 6) as well as in the recent Castaneoideae (comp. Praglowski 1984).

On the basis of these observations one may suppose that the pollen sculpture of *T. villensis* observed under the SEM is intermediate between the vallum structure which shows a distinct tendency to form tori and a deeply cut surface, typical of *Tricolporopollenites pseudocingulum* sensu lato, *T. theacoides* and *T. dolium* of the Fagoideae and that of flat and radially arranged rodlets which characterize the pollen grains of Castaneoideae (Fig. 2).

Pollen grains exhibing the same surface structure and general morphology as *Tricolporopollenites villensis* were observed by Zetter (Walther & Zetter 1993) on the leaves of *Eotrigonobalanus furcinervis* (Rossmässler) Walther et Kvaček, a fossil species of the Fagaceae. Zetter (Walther & Zetter 1993) described this pollen as *Eotrigonobalanus eiszmannii*. He found individual grains of the some pollen free of the parent plant, in Late Oligocene sediments from Bockwitz (Gastaldo *et al*. 1998, Pl. 2, figs 8–12).

The Palaeogene species *Eotrigonobalanus* created by Kvaček & Walther (1989) from macroscopic fossil remains, was accepted by Mai (1995) as the ancestral form of the subfamily Castaneoideae. This opinion is confirmed by the SEM observations of the sculpture of the pollen grains of *Tricolporopollenites villensis* (= *Eotrigonobalanus eiszmannii* Walther et Zetter). This sculpture represents a primitive type of structure, combining features characteristic of the pollen grain sculptures of the subfamilies Castaneoideae and Fagoideae (Fig. 2).

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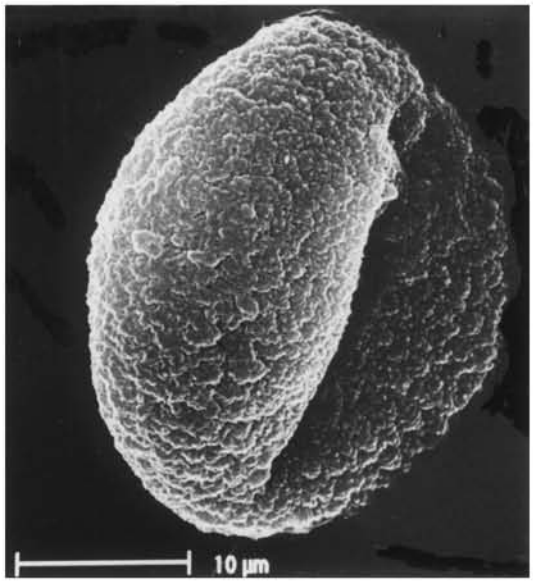
PLATES

Plate 1

1. *Tricolporopollenites lubstovensis* sp. nov.; Lubstów, Middle Miocene; SEM (holotype)
   1a. general view × 2500
   1b. part of sculpture × 8000
2. *Tricolporopollenites lubstovensis* sp. nov.; Lubstów, Middle Miocene; LM (holotype)
   2a, b. two optical sections × 1000
3. *Tricolporopollenites lubstovensis* sp. nov.; Lubstów, Middle Miocene; SEM
   3a. general view × 2500
   3b. part of sculpture × 11000
4. *Tricolporopollenites leonensis* sp. nov.; Lubstów, Middle Miocene; SEM (holotype)
   4a. general view × 2000
   4b. part of sculpture × 8000
5. *Tricolporopollenites leonensis* sp. nov.; Lubstów, Middle Miocene; LM (holotype)
   5a, b, c. three optical sections × 1000



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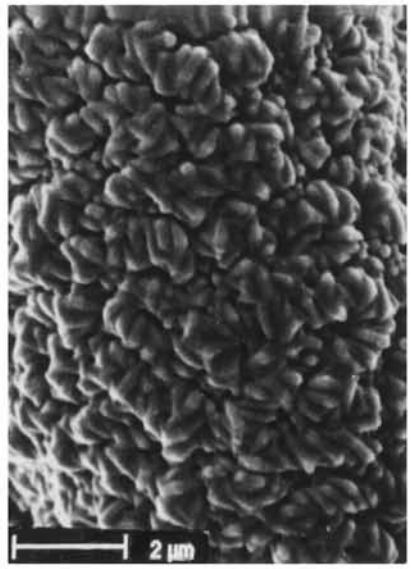

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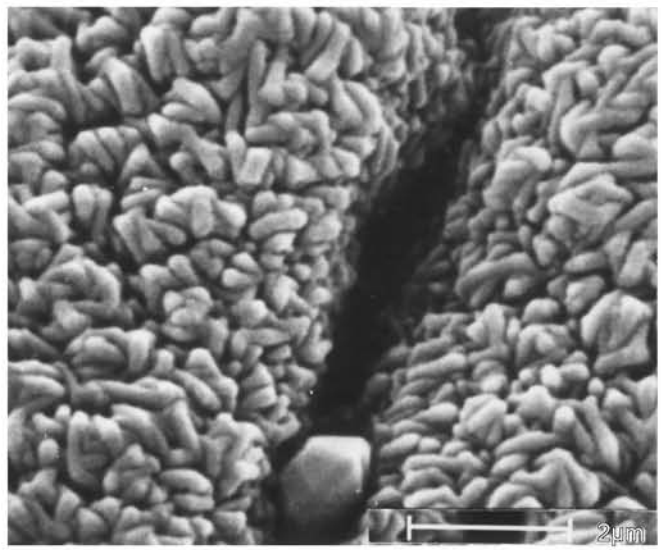

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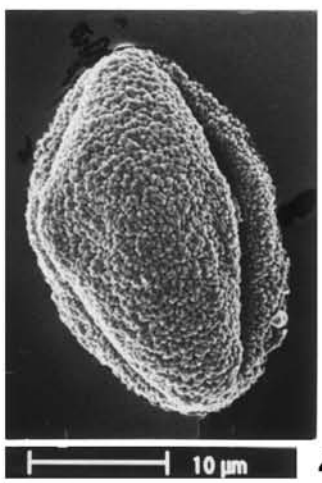

4a

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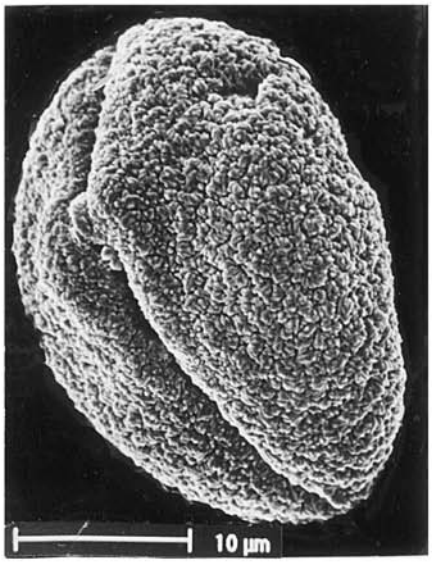
5a

5b

5c

Plate 2

1. *Tricolporopollenites leonensis* sp. nov.; Lubstów, Middle Miocene; SEM
   1a. general view × 2500
   1b. part of sculpture × 10000
2. *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug (sensu stricto); Lubstów, Middle Miocene; SEM
   2a. general view × 2500
   2b. part of sculpture x10000
3. *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug (sensu stricto); Lubstów, Middle Miocene; LM
   3a, b. two optical sections × 1000
4. *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug (sensu stricto); Lubstów, Middle Miocene; SEM
   4a. general view × 2500
   4b. part of sculpture × 8000



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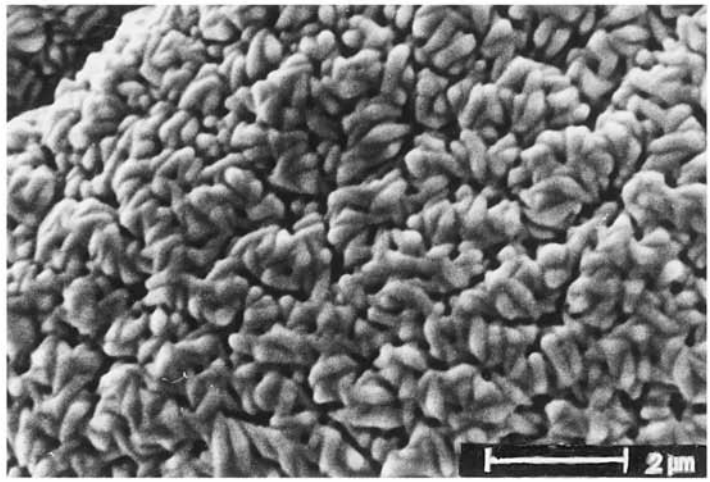

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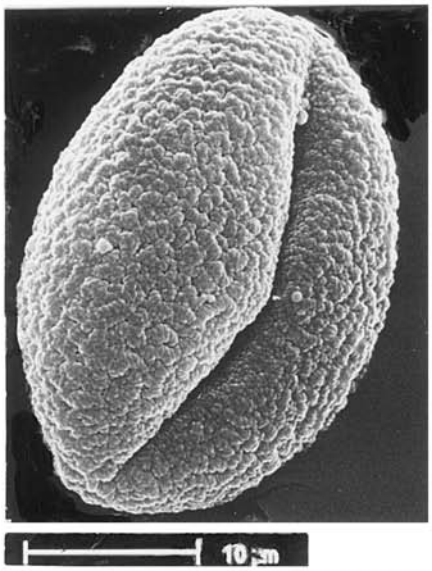

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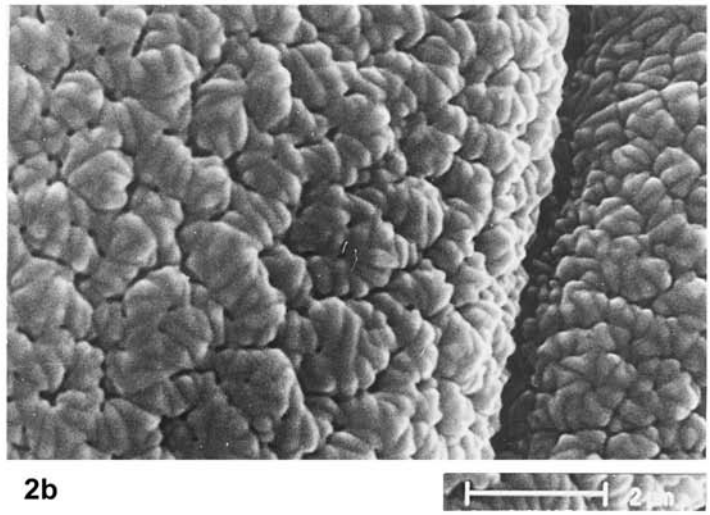

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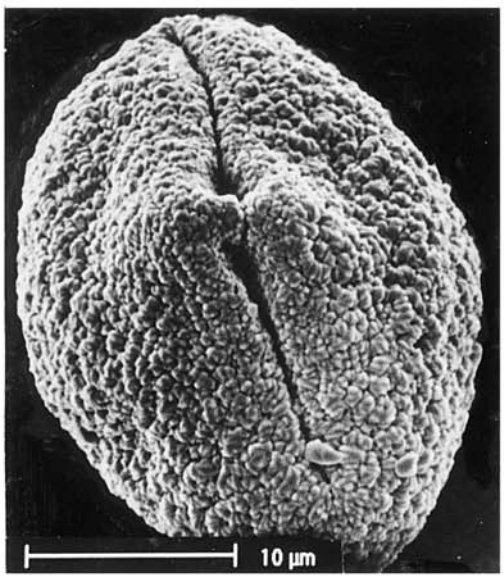


4a

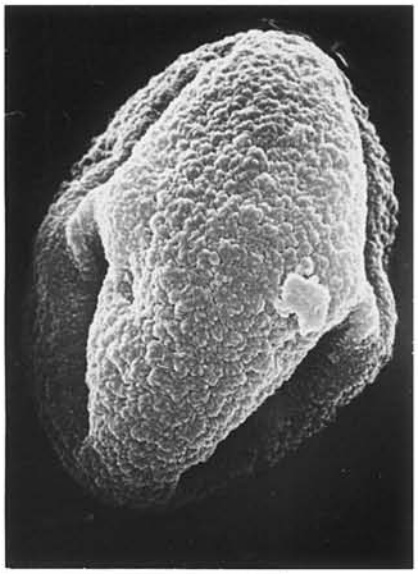
3a

3b

4b

Plate 3

1. *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug (sensu stricto); Lubstów, Middle Miocene; SEM
   1a. general view × 2500
   1b. part of sculpture × 12000
2. *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug (sensu stricto); Lubstów, Middle Miocene; LM
   2a, b. two optical sections × 1000
3. *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug (sensu stricto); Lubstów, Middle Miocene; LM
   3a, b. two optical sections × 1000
4. *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug (sensu stricto); Lubstów, Middle Miocene; SEM
   4a. general view × 2000
   4b. part of sculpture × 8000
5. *Tricolporopollenites pseudocingulum* (Potonié) Thomson et Pflug (sensu stricto); Lubstów, Middle Miocene; SEM
   5a. general view × 2000
   5b. part of sculpture × 4000



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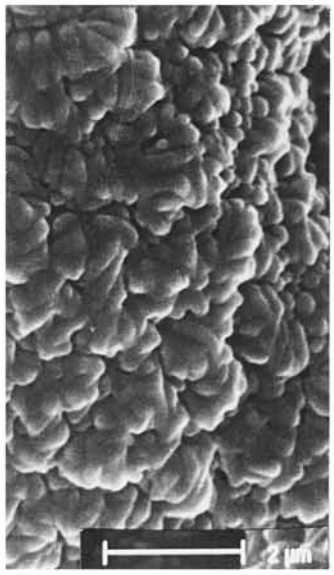

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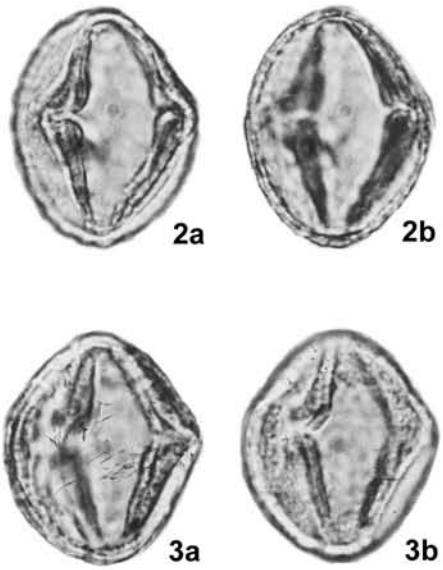

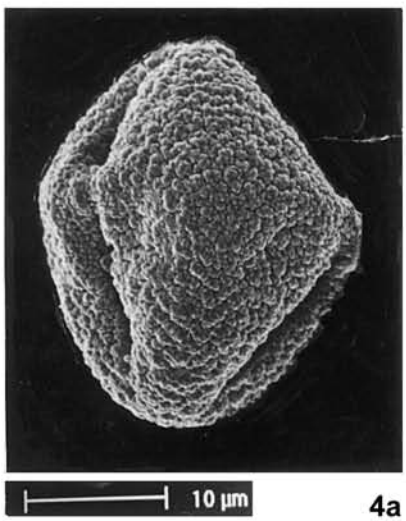

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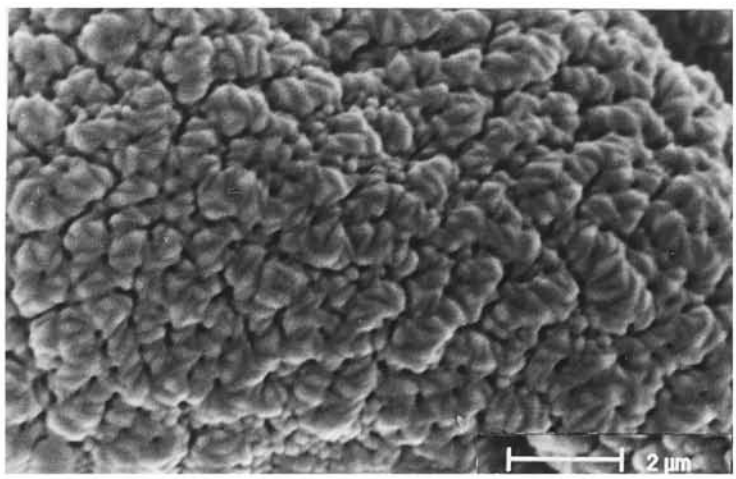

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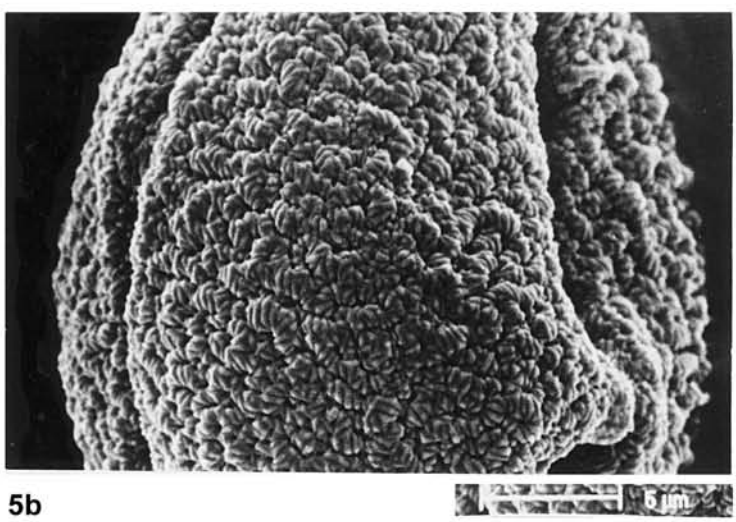
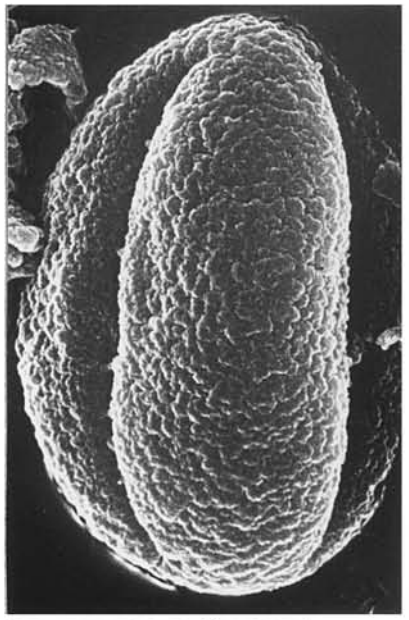


5b

Plate 4

1. *Tricolporopollenites dolium* (Potonié) Thomson et Pflug; Lubstów, Middle Miocene; SEM
   1a. general view × 2500
   1b. part of sculpture × 10000
2. *Tricolporopollenites dolium* (Potonié) Thomson et Pflug; Lubstów, Middle Miocene; SEM
   2a. general view × 2500
   2b. part of sculpture × 10000
3. *Tricolporopollenites dolium* (Potonié) Thomson et Pflug; Lubstów, Middle Miocene; SEM
   3a. general view × 2500
   3b. part of sculpture × 10000
4. *Tricolporopollenites dolium* (Potonié) Thomson et Pflug; Lubstów, Middle Miocene; LM
   4a, b. two optical sections × 1000
5. *Tricolporopollenites dolium* (Potonié) Thomson et Pflug; Lubstów, Middle Miocene; LM
   5a, b, c. three optical sections × 1000



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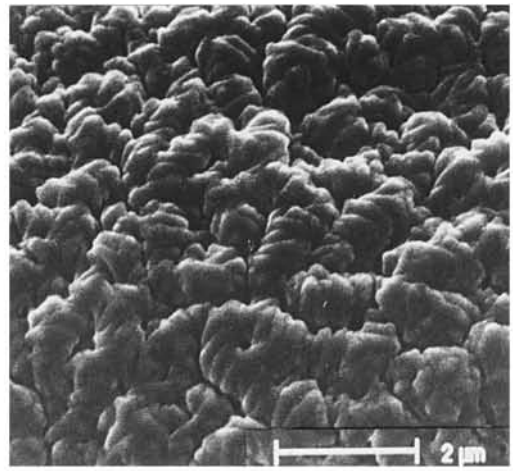
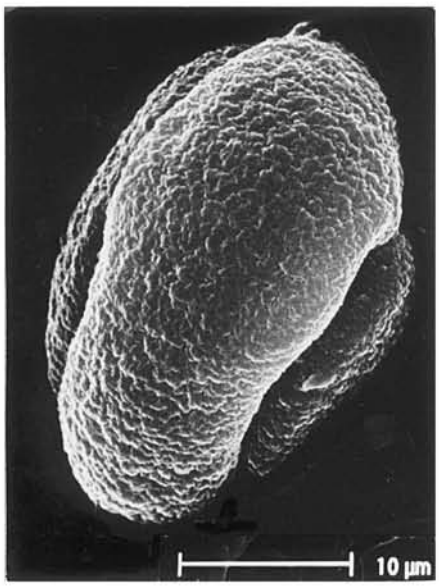


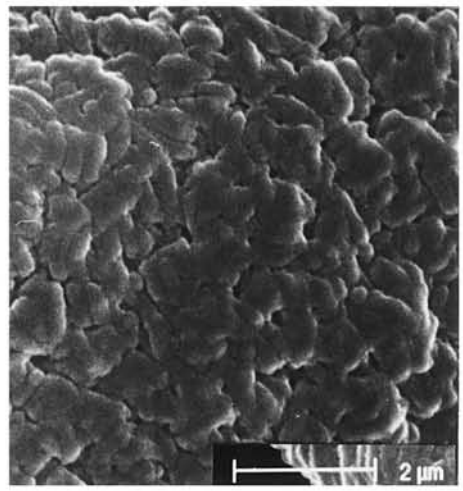
1b

4a

4b

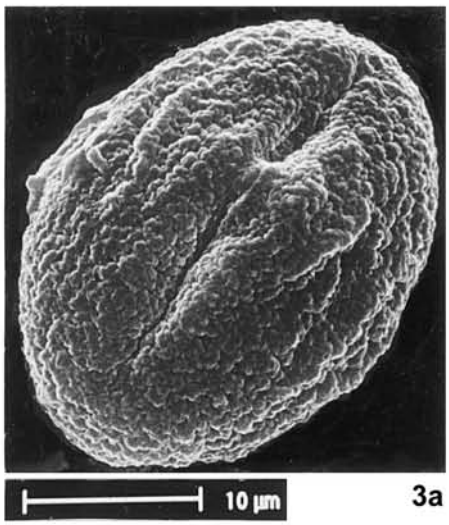


2a

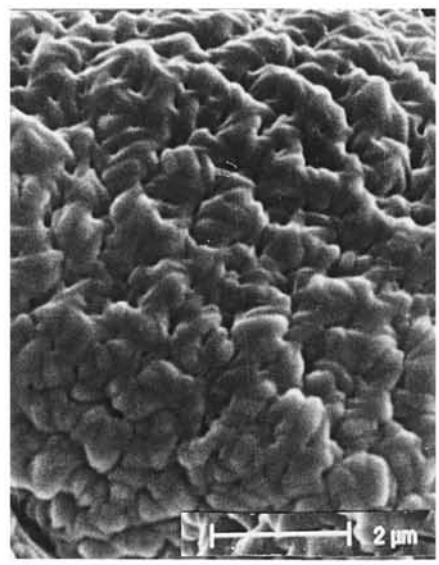


2b

5a



3a



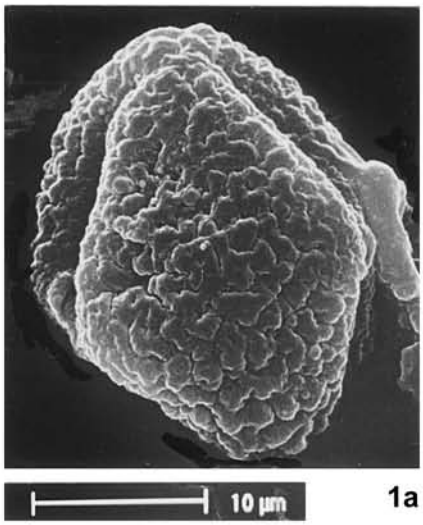
3b

5b

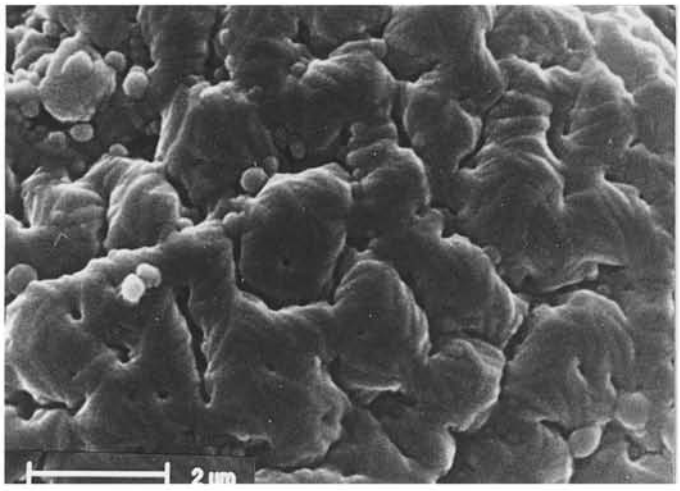
5c

Plate 5

1. *Tricolporopollenites scutulensis* sp. nov.; Lubstów, Middle Miocene; SEM (holotype)
   1a. general view × 2000
   1b. part of sculpture × 10000
2. *Tricolporopollenites scutulensis* sp. nov.; Lubstów, Middle Miocene; LM (holotype)
   2a, b. two optical sections × 1000
3. *Tricolporopollenites theacoides* (Roche et Schuler) comb. nov.; Lubstów, Middle Miocene; LM
   3a, b. two optical sections × 1000
4. *Tricolporopollenites theacoides* (Roche et Schuler) comb. nov.; Lubstów, Middle Miocene; LM
   4a, b, c. three optical sections × 1000
5. *Tricolporopollenites theacoides* (Roche et Schuler) comb. nov.; Lubstów, Middle Miocene; SEM
   5a. general view × 3000
   5b. part of sculpture × 8000



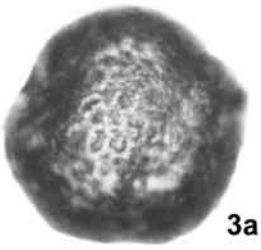
1a



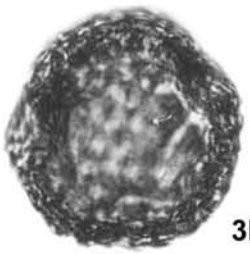
1b

2a

2b



3a

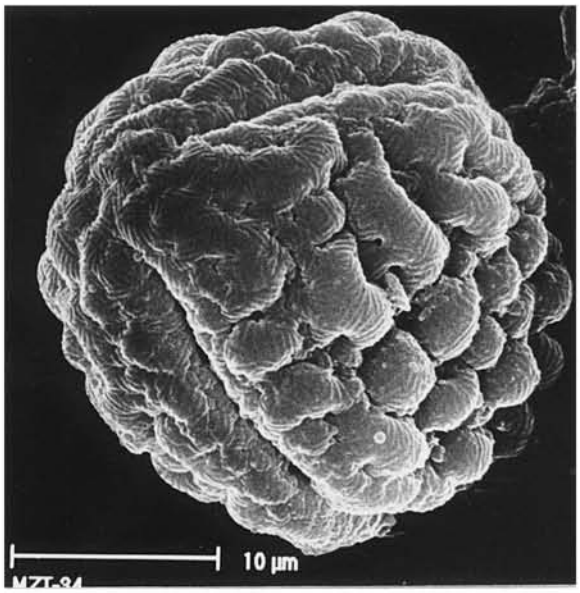


3b

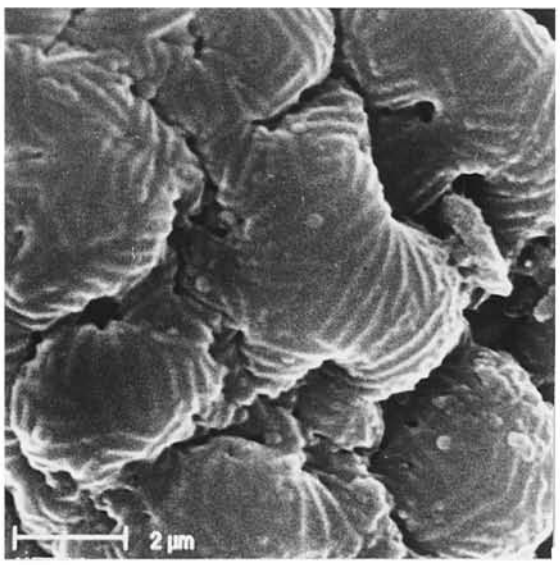
4a

4b

4c



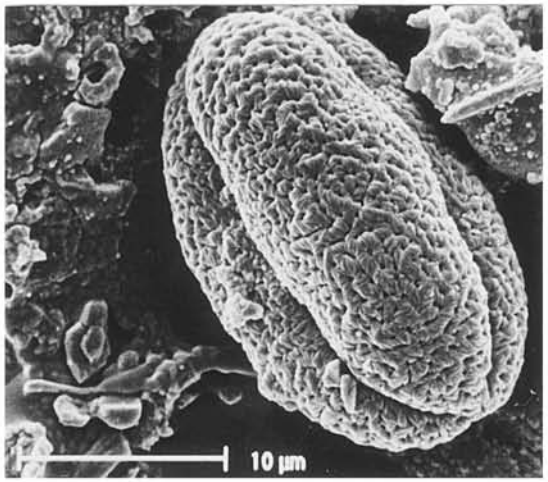
5a



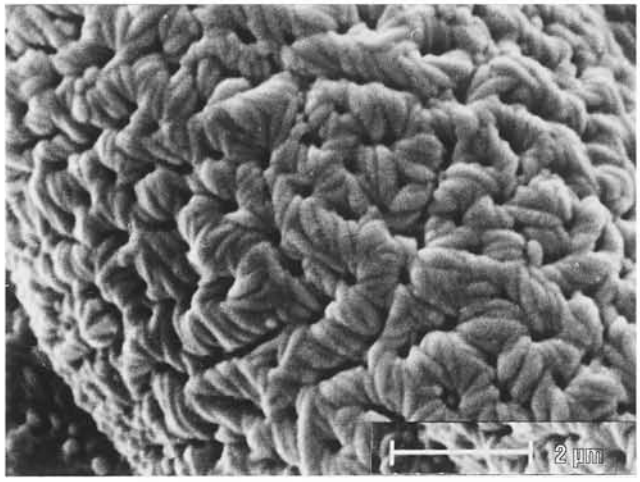
5b

Plate 6

1. *Tricolporopollenites villensis* (Thomson) Thomson et Pflug; Lubstów, Middle Miocene; SEM
   1a. general view × 2500
   1b. part of sculpture × 10000
2. *Tricolporopollenites villensis* (Thomson) Thomson et Pflug; Lubstów, Middle Miocene; LM
   2a, b. two optical sections × 1000
3. *Tricolporopollenites villensis* (Thomson) Thomson et Pflug; Lubstów, Middle Miocene; LM
   3a, b. two optical sections × 1000
4. *Tricolporopollenites villensis* (Thomson) Thomson et Pflug; Lubstów, Middle Miocene; SEM
   4a. general view × 4000
   4b. part of sculpture × 8500
5. *Tricolporopollenites villensis* (Thomson) Thomson et Pflug; Lubstów, Middle Miocene; LM
   5a, b, c. three optical sections × 1000



1a



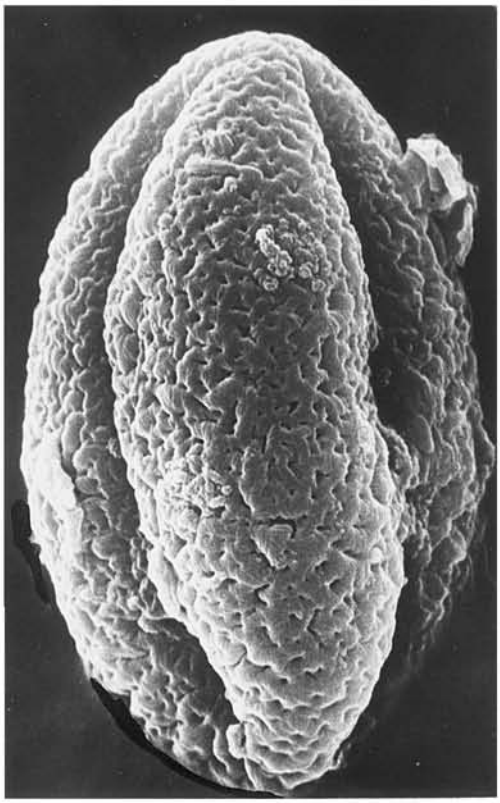
1b

2a

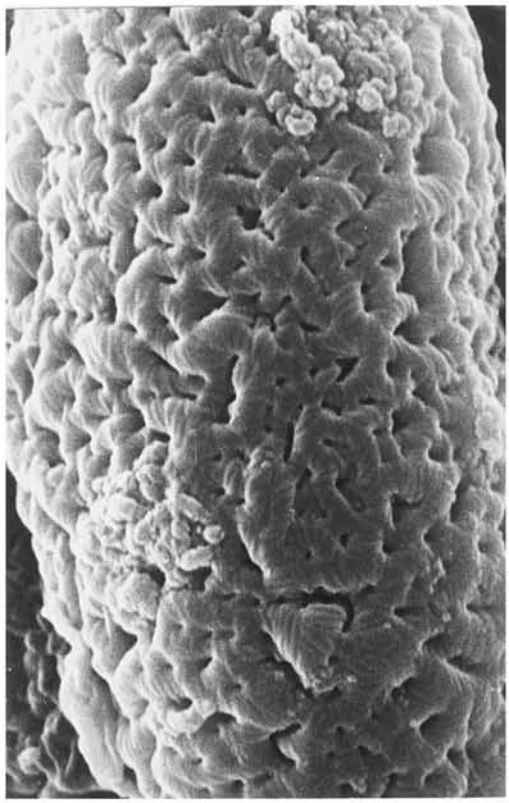
2b

3a

3b



4a



4b

5a

5b

5c