

Morphological variability and botanical affinity of *Fususpollenites* Kedves 1978 (LM and SEM investigations)

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Received 23 May 2001; accepted for publication 18 August 2001

ABSTRACT. Tricolporate (“fusoid”) pollen grains of small size (20–30 µm) are commonly found in the Lower Oligocene deposits of Central Europe. Several morphological forms belonging to this group have been uncovered in such deposits in Central Poland. Examination of grains of this fossil pollen was carried out under both the LM and SEM. As a result of these observations the diagnosis of the genus *Fususpollenites* Kedves 1978 is emended and three species are distinguished, namely: *Fususpollenites fusus* (Potonié) Kedves, *Fususpollenites recollectus* (Doktorowicz-Hrebnicka) comb. nov. and *Fususpollenites residuus* (Doktorowicz-Hrebnicka) comb. nov. It was found that the structure of the exine surface (tectum) in the three species was of quercoidal type permitting their inclusion in the subfamily Quercoideae; they possibly are pollen of plants closely related to the genus *Trigonobalanus* Forman.

KEY WORDS: pollen grains, tectum sculpture, *Trigonobalanus*, Quercoideae, Fagaceae, SEM, LM, Lower Oligocene, Poland

INTRODUCTION

In the Palaeogene sediments of Europe, especially the Lower Oligocene beds, tricolporate pollen grains of small size (20–30 µm) have frequently been found. The first remarks on this pollen type were made in relation to the Eocene sediments in Geiseltal when Potonié (1931) described these grains as *Pollenites fusus*. A more extensive diagnosis was given by Potonié (1934) and Potonié and Venitz (1934), under the name *Pollenites cingulum fusus* (lowering the taxonomic rank to subspecies). According to these authors, the grains were tricolporate with an oval outline, polar areas rounded, polar axis ca. 25 µm long. The outline was almost smooth, with the colpi possessing pores and the costae colpi forming a cingulum.

Thomson and Pflug (1953) when morphologically systematizing spores and pollen grains from the Tertiary sediments of Europe, assigned *Pollenites cingulum fusus* Potonié to their morphogenus *Tricolporopollenites* (as *T. cingulum fusus*). These authors extended the

diagnosis of the taxon *fusus* from that formulated in the 1930s by Potonié (1931, 1934) and Potonié and Venitz (1934), including here also forms with tapering polar areas, colpi slightly curved in the equatorial area and exine structure of infrarugulate type. These features are distinctly visible in the illustrations in Thomson and Pflug (1953, Pl. 12 figs 15–27).

Krutzsch (1957) distinguished the group “112 (fusoid forms)” as comprising heterogeneous tricolporate, small “fusoid” forms with very variable morphology and sculpture, of which the germinal structure was insufficiently known. These are abundant from the Upper Eocene to Upper Oligocene.

Doktorowicz-Hrebnicka (1961), during pollen studies of the Palaeogene sediments from the Rogóźno deposit (Central Poland), distinguished several morphological forms within the morphospecies *Pollenites cingulum*, from completely smooth grains to those with a distinct sculpture of the exine surface. She com-

pared two of them (forma *refota* and forma *reliqua*) to the subspecies *Pollenites cingulum fusus* Potonié.

Kedves (1978), when elaborating the Palaeogene pollen flora from Hungary, asserted that the abundantly occurring subspecies *Tricolporopollenites cingulum fusus* (Potonié) Thomson & Pflug has sufficiently characteristic features to form the basis for a new morphogenus *Fususpollenites*, with *Pollenites fusus* Potonié (1931) as type.

Konzalová (in Knobloch et al. 1996) included in *Fususpollenites* Kedves the species *Tricolporopollenites incrassatus* Manykin (Manykin 1973), i.e. grains with a thick exine and narrow pores, which she had found in Eocene sediments in the Czech Republic. Konzalová (op. cit.) suggested the botanical affinity of this species to the recent genera *Castanopsis* (D. Don) Spach or *Trigonobalanus* Forman from the Fagaceae.

The inadequately brief diagnosis of the genus *Fususpollenites* Kedves 1978, and the wide diversity of pollen grains which Kedves (1978, Pl. 13 figs 1–9) considered as belonging to the species *Fususpollenites fusus* (Potonié) Kedves, induced the present authors to a detailed re-evaluation of the pollen grains assigned to the genus *Fususpollenites*. The material for this study came from the Lower Oligocene sediments in Central Poland. The same pollen grain specimens were photographed under both the LM and SEM.

SYSTEMATIC PART

Fususpollenites Kedves 1978, here emended

Emended diagnosis. Pollen grains tricolporate, tectate, in equatorial view prolate with rounded or slightly tapering poles. Polar axis 22–30 μm , equatorial diameter 14–20 μm . Colpi with thickened edges running parallel or slightly curved in the equatorial part. When colpi reach the poles, apocolpium is narrow; in some cases apocolpium is wide. Colpi with pores and with costae colpi forming cingulum. Pores in the middle of the colpi, round or rounded-square, 3–4 μm in diameter. Exine 1.5–3.0 μm thick, infrarugulate to distinctly rugulate. Thickness ratio of ectexine to endexine variable. Ectexine surface psilate to con-

sisting of elongated and irregularly spaced elements. SEM: sculpture formed of densely spaced verrucae fused into irregular rugulae. Rugulae sometimes toroid, fissures between them narrow or broad, deep or shallow. Rugulae surface covered with microgranula. This type of sculpture is quercoidal, comparable with that characteristic for pollen of the subfamily Quercoideae.

Remarks. When Kedves (1978) established the genus *Fususpollenites*, with the type *Pollenites fusus* Potonié 1931, he included into synonymy the subspecies *Tricolporopollenites cingulum fusus* (Potonié) Thomson & Pflug. The diagnosis of this new genus was as follows: "Pollen grains tricolporate. Surface smooth, exine intrarugulate". However, in the illustrations in Kedves's paper (1978, Pl. 13 figs 1–9) he presented various types of pollen, but none of them is true to the holotype *Pollenites fusus* Potonié 1931. For this reason Jansonius and Hills (1980, card No. 3858) expressed their doubts concerning the correctness of the designation of the species *Pollenites fusus* Potonié 1931 by Kedves (1978), as the type. The forms illustrated by Kedves (1978) differ significantly from the holotype. Because of such significant differences in the concept of the type of the genus *Fususpollenites*, the present authors decided to emend the generic diagnosis. With the extended diagnosis, the genus *Fususpollenites* now includes some of the pollen forms included by Kedves (1978, Pl. 13 figs 1–6 only) as well as the holotype *Pollenites fusus* Potonié (1931, Pl. 1 fig. 13) and various forms determined by Thomson and Pflug (1953) as *Tricolporopollenites cingulum fusus* (Pl. 12 figs 15–27).

Fususpollenites fusus (Potonié 1931)
Kedves 1978

Pl. 1 figs 1–4, Pl. 2 fig. 1

- 1931 *Pollenites fusus* n.sp.; Potonié, p. 556, Pl. 1 fig. 13; holotype.
1934 *Pollenites cingulum fusus* Potonié; Potonié p. 82, 83, Pl. 4 fig. 20.
1934 *Pollenites cingulum fusus* Potonié; Potonié & Venitz, p. 38, 39, Pl. 3 fig. 96.
1953 *Tricolporopollenites cingulum* subsp. *fusus* (Potonié) n. comb.; Thomson & Pflug, p. 100, pl. 12 figs 16, 19, 27 only.
1961 cf. *Castanopsis* forma *refota* (*Pollenites cingulum fusus* Potonié); Doktorowicz-Hrebicka, p. 233, Pl. 11 fig. 165.

- 1961 *Pollenites cingulum* Potonié forma *reliqua*; Doktorowicz-Hrebnicka, p. 234, Pl. 11 fig. 167.
 1965 *Tricolporopollenites cingulum* subsp. *fuscus* (Potonié) Thomson & Pflug; Grabowska, Pl. 2 fig. 28.
 1966 *Pollenites cingulum* Potonié; Ziemińska & Niklewski, p. 37, Pl. 6 fig. 8.
 1968 *Tricolporopollenites* (Potonié) Thomson & Pflug; Grabowska, Pl. 2 fig. 51.
 1976 *Scabratricolporites scheffleroides* n. sp.; Roche & Schuler, p. 24, Pl. 10 figs 12, 13 only.
 1980 *Psilatricolporites cingulum fuscus* (Potonié) Roche & Schuler; Olivier-Pierre, p. 65, Pl. 25 fig. 9.
 1990 *Fususpollenites fuscus* (Potonié) Kedves; Konzálóvá, p. 85, Pl. 37 fig. 13.

Material. Budki Janowskie, 185.5 m, Lower Oligocene; Dąbrowa 157.4–157.5 m, Lower Oligocene, more than ten specimens; housed in the Institute of Geology, Warsaw University.

Description. Pollen grains tricolporate, tectate, in equatorial view prolate with rounded poles. Measurements: polar axis 20–28 μm , equatorial diameter 14–20 μm . Colpi with thickened edges, running parallel to polar axis and not reaching the poles; apocolpium wide. Colpi with pores and with costae colpi forming cingulum. Pores in the middle of the colpi, rounded-square, 3–4 μm in diameter. Exine 1.5–2.0 μm thick, infrarugulate. Ectexine slightly thicker than endexine, surface psilate. SEM: sculpture formed by densely spaced verrucae fused into irregular rugulae. Rugulae rarely toroid, fissures between them narrow and deep. The surface of rugulae covered in places with rounded and flat microgranula. This type of sculpture is quercoidal.

Remarks. The material investigated by the present authors, and illustrated in Pl. 1 figs 1–4 and Pl. 2 fig. 1 as *Fususpollenites fuscus*, is closest to the holotype *Pollenites fuscus* Potonié 1931 (= *Pollenites cingulum fuscus* Potonié 1934). The same pollen type may be found among the illustrations of *Tricolporopollenites cingulum fuscus* in Thomson and Pflug (1953, Pl. 12 figs 16, 19 and 27 only) and among the pollen grains determined as *Pollenites cingulum* Potonié forma *reliqua* (Doktorowicz-Hrebnicka 1961, Pl. 1 fig. 167; see also the present paper Pl. 1 fig. 3) as well as in those classified as cf. *Castanopsis* forma *refota* (Doktorowicz-Hrebnicka 1961, Pl. 11 fig. 165; see also the present paper Pl. 1 fig. 2). We include all these forms in the species *Fususpollenites fuscus* on the basis of the same morphology observed under the LM and the same quercoidal type sculpture, indistinct under the LM, but very

clearly observable under the SEM (Pl. 1 figs 1d, 4d; Pl. 2 fig. 1d).

Fususpollenites relictus

(Doktorowicz-Hrebnicka 1961) **comb. nov.**

Pl. 3 figs 1–8

- 1953 *Tricolporopollenites cingulum* subsp. *fuscus* (Potonié) n. comb.; Thomson & Pflug, p. 100, Pl. 12 figs 15, 20, 22, 26 only.
 1961 *Pollenites cingulum* Potonié forma *relicta*; Doktorowicz-Hrebnicka, p. 234, Pl. 12 figs 168–172, (fig. 168 – holotype).
 1964 cf. genus *Ptelea*, *Tricolporopollenites cingulum fuscus*; Stuchlik, p. 55, Pl. 16 figs 26–28.
 1965 *Tricolporopollenites cingulum* subsp. *fuscus* (Potonié) Thomson & Pflug; Grabowska, Pl. 2 fig. 30.
 1978 *Fususpollenites fuscus* (Potonié) n. comb.; Kedves, p. 65, 66, Pl. 13 figs 1–6 only.

Material. Dąbrowa 157.4–157.5 m, Lower Oligocene, about twenty specimens; housed in the Institute of Geology, Warsaw University.

Description. Pollen grains tricolporate, tectate, in equatorial view prolate with tapering poles. Measurements: polar axis 20–28 μm , equatorial diameter 15–18 μm . Colpi with thick edges, running parallel to the grain margin although somewhat bent in the equatorial area. Colpi reaching the poles; apocolpium is narrow. Colpi with pores and with costae colpi forming cingulum; pores in the middle of colpi, square, 3–4 μm in diameter. Exine about 2.0 μm , ectexine and endexine equally thick or endexine somewhat thicker. Ectexine surface with a fine sculpture consisting of elongated and irregularly spaced elements. Under the SEM the sculpture is formed of densely spaced verrucae fused into irregular rugulae. Fissures between them narrow. Rugulae surfaces densely covered by elongated micro-elements with rounded ends. The sculpture is of quercoidal type.

Remarks. The pollen grains we illustrated in Pl. 3 fig. 1 are morphologically close to those described by Doktorowicz-Hrebnicka (1961) as *Pollenites cingulum* Potonié forma *relicta* (Doktorowicz-Hrebnicka op. cit., Pl. 12 figs 168–172, see also the present paper Pl. 3 figs 2–6). Doktorowicz-Hrebnicka compared this form to the pollen grains *Tricolporopollenites cingulum fuscus* illustrated by Thomson and Pflug (1953, Pl. 12 fig. 26). Grains of the same structure also appear in other illustrations of the Thomson & Pflug paper (1953, Pl. 12 figs

15, 20, 22), all of them regarded by Thomson and Pflug (1953) as typical for *Tricolporopollenites cingulum fusus*.

Stuchlik (1964, Pl. 16 figs 26–28, see also the present paper Pl. 3 fig. 8) determined this type of pollen grain as cf. genus *Ptelea* – *Tricolporopollenites cingulum fusus* (Potonié) Thomson & Pflug. The pollen grain of the recent genus *Ptelea* L. has similar outline, shape of colpi and pores to that of *Tricolporopollenites cingulum fusus* (sensu Thomson & Pflug, 1953), but its tectum is formed as a tiny reticulum (Pl. 3 figs 9–11). The completely different tectum structure in the pollen grains of the recent genus *Ptelea* (Rutaceae) and *Tricolporopollenites cingulum fusus* Thomson & Pflug, preclude any possible botanical relationship of both taxa.

The identical pollen grain morphology of the taxa: *Pollenites cingulum* Potonié forma *recolleta* Doktorowicz-Hrebicka (1961), *Tricolporopollenites cingulum fusus* sensu Thomson & Pflug (1953), cf. genus *Ptelea* – *Tricolporopollenites cingulum fusus* (Potonié) Thomson & Pflug (in Stuchlik 1964) and *Fususpollenites fusus* (Potonié) Kedves (1978, Pl. 13 figs 1–6) justifies their combination as one species. On this basis the taxon *Pollenites cingulum* Potonié forma *recolleta* Doktorowicz-Hrebicka has been raised to species rank as *Fususpollenites recollectus* (Doktorowicz-Hrebicka) comb. nov. Under the SEM the tectum of this species is revealed as of the quercoidal type (Pl. 3 fig. 1d).

Fususpollenites residuus

(Doktorowicz-Hrebicka 1961) **comb. nov.**

Pl. 2 figs 2, 3

1953 *Tricolporopollenites villensis* (Potonié) n. comb.; Thomson & Pflug, p. 100, Pl. 12 fig. 13 only.

1961 *Pollenites cingulum* R. Pot. forma *residua*; Doktorowicz-Hrebicka, p. 235, Pl. 12 figs 173, 174.

1976 *Scabratricolporites scheffleroides* n. sp.; Roche & Schuler, p. 24, Pl. 10 fig. 14.

Material. Dąbrowa 157.4–157.5 m, Lower Oligocene, five specimens; housed in the Institute of Geology, Warsaw University

Description. Pollen grains tricolporate, tectate, in equatorial view prolate with slightly tapering poles. Measurements: polar axis 20–30 μm , equatorial diameter 16–20 μm . Colpi with very thick edges, running parallel to the grain margin and reaching the poles,

apocolpium narrow. Colpi with pores and with indistinct costae colpi forming cingulum; pores in the middle of colpi, rounded, 2–3 μm in diameter. Exine about 3 μm , ectexine somewhat thicker than endexine. Ectexine surface with a distinct sculpture consisting of irregularly spaced flat verrucae, which under the SEM revealed as consisting of densely spaced irregular verrucae. Sometimes the verrucae fused into irregular, frequently toroid rugulae. Verrucae surfaces densely covered by wide, flat microgranula. Fissures between verrucae narrow and shallow, sometimes containing deep holes. This type of sculpture is quercoidal.

Remarks. The described pollen grains, illustrated in Pl. 2 fig. 3 are morphologically close to the specimens determined as *Pollenites cingulum* Potonié forma *residua* (Doktorowicz-Hrebicka 1961, Pl. 12 figs 173, 174, see also the present paper Pl. 2 fig. 2). Doktorowicz-Hrebicka compared them to *Tricolporopollenites villensis* Thomson in Thomson and Pflug (1953, Pl. 12 fig. 13). She stated in the description that the grains possessed a thick exine and “an abundantly granulated surface”. However, the comparison with *Tricolporopollenites villensis* was not apt, because the pollen grains of *T. villensis* are larger and exhibit differences in both their sculpture and pores. The forma *residua* distinguished by Doktorowicz-Hrebicka differs distinctly from other “fusoid” forms. The similarity of the specimens illustrated in the present paper (Pl. 2 fig. 3) to those determined by Doktorowicz-Hrebicka (1961, Pl. 12 figs 173, 174) as forma *residua* is so significant, that it justifies raising forma *residua* to species rank as *Fususpollenites residuus* (Doktorowicz-Hrebicka) comb. nov. Under the SEM the tectum of this species reveals features characteristic of the quercoidal type (Pl. 2 fig. 3d).

DISCUSSION

The three fossil pollen species described above may be distinguished under the LM by differences in the equatorial grain outline, colpi arrangement, pore shape and exine surface.

The SEM observations of the surface of pollen grains generally determined as *Tricolporopollenites cingulum fusus* reveal that, in these small (20–30 μm) tricolporate forms, two types

of tectum formation occur. One has a quercoidal character, possessing irregular verrucae fused into rugulae, which sometimes form toroid structures. Microgranula are visible on the verrucae surfaces. Pollen grains structured thus are included in the genus *Fususpollenites* (in a broader sense of our emendation).

Another group of the pollen grains has a surface structure that has been recognized as ancestral for the pollen of the subfamily Fagoideae (Kohlman-Adamska & Ziemińska-Tworzydło 2000). In these the tectum reveals toroid forms, developed from the fused rodlets. Fossil pollen grains with this type of surface structure have already been partially described (Kohlman-Adamska & Ziemińska-Tworzydło 1999, 2000).

Most authors (Doktorowicz-Hrebicka 1961, Kedves 1978, Nagy 1985, Konzalová 1990) considered that, though the botanical affinity of the pollen grains included within *Tricolporopollenites cingulum fusus*, that are frequent in Palaeogene and Lower Neogene strata in Europe, is unknown, nevertheless they might be related to various genera of the Fagaceae, e.g. *Castanopsis* (Nagy 1985) or *Trigonobalanus* (Konzalová in Knobloch et al. 1996).

Another suggestion of the botanical affinity of *Tricolporopollenites cingulum fusus* was proffered by Stuchlik (1964), who included these forms in the Rutaceae (cf. *Ptelea*). Subsequently, this opinion was quoted by Gruas-Cavanetto (1977) and Olivier-Pierre (1980), but it now appears to be incorrect on the basis of the present investigations.

SEM studies of the pollen surface of *Fususpollenites fusus* as now understood, has solved the uncertainty concerning the botanical affinity of this fossil taxon, linking it to the subfamily Quercoideae.

Two recent genera are contained in the Quercoideae: the genus *Quercus* L., widely distributed with numerous species, and the relic genus *Trigonobalanus* Forman, with three species (Jones 1986). Pollen of the recent *Quercus* L., studied in detail under the SEM (Crepet & Daghljan 1980, Solomon 1983), shows large tectum variation within the same type of surface structure which consist of microverrucae arranged in various ways, forming either rugulae or verrucae, smooth or covered by microgranula. This quercoidal type of sculpture is characteristic for the subfamily Quercoideae.

Pollen grain studies for *Trigonobalanus* Forman, were performed under the SEM by Erdtman (1967), Nixon and Crepet (1989) and Konzalová (1990). Nixon and Crepet (1989) considered the differences between the recent three species *Trigonobalanus verticillata* Forman, *T. doinchangensis* (Camus) Forman and *T. excelsa* Losano so important that they divided the whole genus into three new monotypic genera.

Trigonobalanus pollen grains are tricolporate with a rugulate surface. Rugulae in the recent species form somewhat different patterns, the most typical rugulate sculpture occurring in *T. doinchangensis*. The grains of the three species differ in outline (in *T. verticillata* and *T. excelsa* the outline in the equatorial position is prolate, and in *T. doinchangensis* it is peroblate), the peculiar structure of the pores and in the different thicknesses of the footlayer (Nixon & Crepet 1989).

Macrofossils of *Trigonobalanus* (Mai 1970, 1981) are known from the Eocene to Lower Miocene, but fossil pollen data for this genus is lacking. Konzalová (Knobloch et al. 1996), suggested that the fossil pollen *Fususpollenites in-crassatus* (Manykin) Konzalová might be related to that of the recent *Trigonobalanus*, but she did not publish any supporting evidence.

Crepet and Nixon (1989) described male catkin inflorescences of *Amentogerdiopollenites* Crepet & Nixon and *Amentoplexipollenites* Crepet & Nixon with pollen in situ from the Oligocene sediments in Texas (North America). These inflorescences, according to them, (Crepet & Nixon 1989), are comparable to those of the recent species *Trigonobalanus verticillata*. However, the SEM images and descriptions of the pollen grains found in the fossil anthers of the male inflorescences of *Amentogerdiopollenites* and *Amentoplexipollenites* (Nixon & Crepet 1989 and Crepet & Daghljan 1980), are (in our opinion) completely different from the pollen grains of the recent species *Trigonobalanus verticillata*. The fossil anther pollen has a tectum structure of vermiculate type, consisting of twisted vermiform elements or rodlets with free ends. Crepet and Nixon (1989) thought that such a pollen surface structure was intermediate between the Castaneoideae and Fagoideae, and that it could be intermediate between the pollen surface structures of the recent *Fagus* and *Trigonobalanus*.

The surfaces of the pollen grains prepared

from the anthers described by Crepet and Nixon (1989) as *Amentogerdipollenites* and *Amentoplexipollenites*, especially the latter, have many features in common with that of *Tricolporopollenites villensis* (Potonié) Thomson & Pflug (= *Eotrigonobalanus eischmanii* Zetter in Walther & Zetter 1993) from the subfamily Fagoideae (see Kohlman-Adamska & Ziemińska-Tworzydło 2000). According to these authors (Kohlman-Adamska & Ziemińska-Tworzydło 2000), the structure of the pollen surface of *Tricolporopollenites villensis* (Potonié) Thomson & Pflug is intermediate between those of the subfamilies Castaneoideae and Fagoideae. This is in agreement with observations made by Nixon and Crepet (1989).

However, the authors of the present paper disagree with Crepet and Nixon (1989) concerning the claim that the nature of the pollen surface structure of *Amentogerdipollenites* and *Amentoplexipollenites* is intermediate between those of *Fagus* L. and *Trigonobalanus* Forman.

The tectum of the recent *Trigonobalanus* pollen has a quercoidal type sculpture (cf. Erdtman 1967, Nixon & Crepet 1989, Konzalová 1990), whereas that *Amentogerdipollenites* and *Amentoplexipollenites* is fagoidal.

Unfortunately, detailed comparison of the fossil pollen grains found in sediments with those prepared from the anthers is not possible, because the publication of Nixon and Crepet (1989) lacked LM images.

The SEM studies of the surface of the dispersed fossil pollen grains presented in present publication, indicate that the forms with quercoidal surface structure similar to the surface of the pollen of *Trigonobalanus* rather than *Quercus*, occur in the group of fossil pollen grains of the genus *Fususpollenites* Kedves as here emended. They might have come from the Tertiary species of *Trigonobalanus*, which was an important component of mesophilous mixed forest in the Palaeogene and Early Neogene times in Europe (Mai 1981)

ACKNOWLEDGEMENTS

We wish to thank Dr Tatiana Rylova (Institute of Geology, National Academy of Sciences of Belarus, Minsk) for help in the preparation of specimens for observations under the SEM. The authors are very indebted to Dr Cyprian Kulicki (Institute of Palaeobiology of the Polish Academy of Sciences) for his help with observations and taking photographs of pollen grain surfaces under the scanning electron micro-

scope. Most sincere thanks are due to Professor Ewa Zastawniak (W. Szafer Institute of Botany of the Polish Academy of Sciences) for discussion and critical reading of the manuscript and to Mr. Arthur Copping for linguistic verification of the English text.

REFERENCES

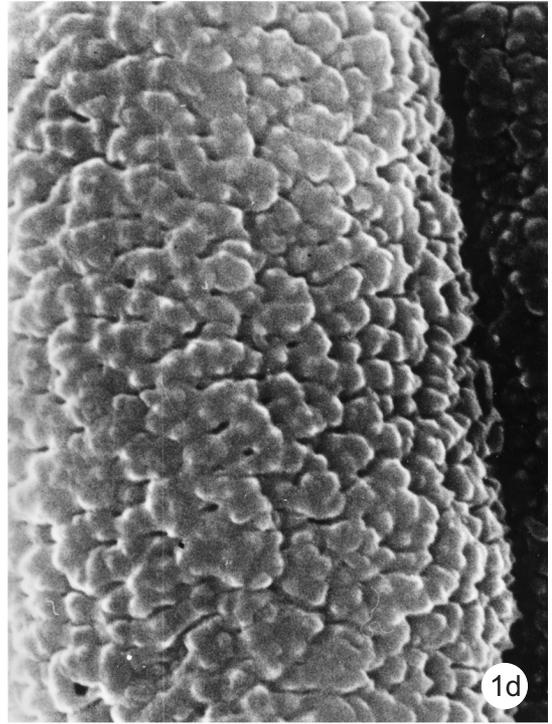
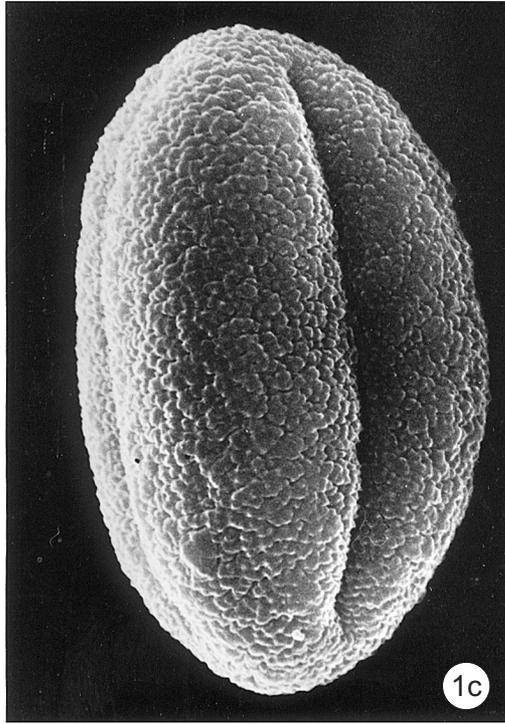
- CREPET W.L. & DAGHLIAN C.P. 1980. Castaneoid inflorescences from the Middle Eocene of Tennessee and the diagnostic value of pollen (at the subfamily level) in the Fagaceae. *American Journal of Botany*, 67(5): 739–757.
- CREPET W.L. & NIXON K.C. 1989. Extinct transitional Fagaceae from the Oligocene and their phylogenetic implications. *American Journal of Botany*, 76(10): 1493–1505.
- DOKTOROWICZ-HREBNICKA J. 1961. Paleobotaniczne podstawy paralelizacji pokładów węgla brunatnego ze złoża Rogóżno pod Łodzią. Część 1, 2. (summary: Palaeobotanical bases for the correlation of brown coal seams from the Rogóżno deposit near Łódź. Part 1, 2). *Biuletyn Instytutu Geologicznego*, 158: 113–303.
- ERDTMAN G. 1967. On the pollen morphology of *Trigonobalanus* (Fagaceae). *Botaniska Notiser*, 120: 324–333.
- GRABOWSKA I. 1965. O środkowooligocenijskim wieku ilów toruńskich na podstawie analizy sporowo-pyłkowej (summary: The Middle Oligocene age of the Toruń clays, based on the spore and pollen analysis). *Kwartalnik Geologiczny*, 9(4): 815–836.
- GRABOWSKA I. 1968. Paleogen z wiercenia Szczecin IG-1 w świetle analizy sporowo-pyłkowej. (summary: Palaeogene in bore hole Szczecin IG-1 in the light of spore and pollen analysis). *Kwartalnik Geologiczny*, 12(1): 157–166.
- GRUAS-CAVAGNETTO C. 1977. La palynoflore du sondage du Mont Pagnotte (Oise). *Bulletin d'Information des Géologues du Bassin de Paris*, 14(2): 31–44.
- JANSONIUS J. & HILLS L.V. 1980. Genera file of fossil spores – supplement. Special publication. Dept. Geology University of Calgary, Canada.
- JONES J.H. 1986. Evolution of the Fagaceae: The implications of foliar features. *Annales Missouri Botanical Garden*, 73: 228–275.
- KEDVES M. 1978. Paleogene fossil sporomorphs of the Bakony Mountains. Part III. *Studia Biologica Hungarica*, 15: 5–166.
- KOHLMAN-ADAMSKA A. & ZIEMIŃSKA-TWORZYDŁO M. 1999. Microstructure of the tectum sculpture visible under SEM – a diagnostic feature for the botanical affinity of fossil pollen species. *Acta Palaeobotanica*, Supplement 2: 331–339 – Proceedings 5th EPPC.
- KOHLMAN-ADAMSKA A. & ZIEMIŃSKA-TWORZYDŁO M. 2000. 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) *Acta Palaeobotanica*, 40(1): 49–71.
- KONZALOVÁ M. 1990. Palynological investigation of the basal Tertiary sediments (Paleogene) in western Bohemia and their correlation with the Carpathian region. *Západné Karpaty, séria Paleontológia*, 14: 73–102.
- KNOBLOCH E., KONZALOVÁ M. & KVAČEK Z. 1996. Die obereozäne Flora der Staré Sedlo – Schichtenfolge in Böhmen (Mitteleuropa). *Rozprawy Českého Geologického Ústavu*, 49: 11–260.
- KRUTZSCH W. 1957. Sporen- und Pollengruppen aus Oberkreide und dem Tertiär Mitteleuropas und ihre stratigraphische Verteilung. *Zeitschrift für Angewandte Geologie*, 3(11/12): 509–548.
- MAI D.H. 1970. Die tertiären Arten von *Trigonobalanus* Forman (Fagaceae) in Europa. *Jahrbuch für Geologie*, [1967] 3: 381–409.
- MAI D.H. 1981. Entwicklung und klimatische Differenzierung der Laubwaldflora Mitteleuropas im Tertiär. *Flora*, 171: 525–582.
- MANYKIN S.S. 1973. Paleogen Belarussii (The Palaeogene of Belaruss). *Nauka i Technika*, Minsk. (in Russian).
- NAGY E. 1985. Sporomorphs of the Neogene in Hungary. *Geologica Hungarica, series Palaeontologica*, 47: 3–471.
- NIXON K.C. & CREPET W. 1989. *Trigonobalanus* (Fagaceae): Taxonomic status and phylogenetic relationships. *American Journal of Botany*, 76(6): 828–841.
- OLIVIER-PIERRE M.F. 1980. Études palynologique (spores et pollens) de gisements paléogènes du Massif Armoricaïn. *Stratigraphie et paléogéographie. Memoires de la Société Géologique et Minéralogique de Bretagne*, 25: 3–239.
- POTONIÉ R. 1931. Zur Mikroskopie der Braunkohlen. Tertiäre Blütenstabformen. *Braunkohle*, 30(16): 325–333.
- POTONIÉ R. 1934. Zur Mikrobotanik des eozänen Humodils des Geiseltals. *Arbeiten aus dem Institut für Paläobotanik und Petrographie der Brennsteine*, 4: 25–125.
- POTONIÉ R. & VENITZ H. 1934. Zur Mikrobotanik des miozänen Humodils der niederrheinischen Bucht. *Arbeiten aus dem Institut für Paläobotanik und Petrographie der Brennsteine*, 5: 5–54.
- ROCHE E., SCHULER M. 1976. Analyse palynologique (pollen et spores) de divers gisements du Tongrien de Belgique. *Service Geologique de Belgique, Professional Paper*, 11: 1–57.
- SOLOMON A.M. 1983. Pollen morphology and plant taxonomy of white oaks in Eastern North America. *American Journal of Botany*, 70(4): 481–494.
- STUICHLIK L. 1964. Pollen analysis of the Miocene deposits at Rypin (NW of Warsaw). *Acta Palaeobotanica*, 5(2): 3–111.
- THOMSON P.W. & PFLUG H. 1953. Pollen und Sporen des mitteleuropäischen Tertiärs. *Palaeontographica*, B, 94(1–4): 1–138.
- WALTHER H. & ZETTER R. 1993. Zur Entwicklung der Paläogenen Fagaceae Mitteleuropas. *Palaeontographica*, B, 230(1–6): 183–194.
- ZIEMBIŃSKA M. & NIKLEWSKI J. 1966. Stratygrafia i paralelizacja pokładów węgla brunatnego złoża Ścinawa na podstawie analizy pyłkowej. (summary: Stratigraphy and correlation of brown coal beds in the Ścinawa deposits on the basis of spore-pollen analysis). *Biuletyn Instytutu Geologicznego*, 202: 27–48.

PLATES

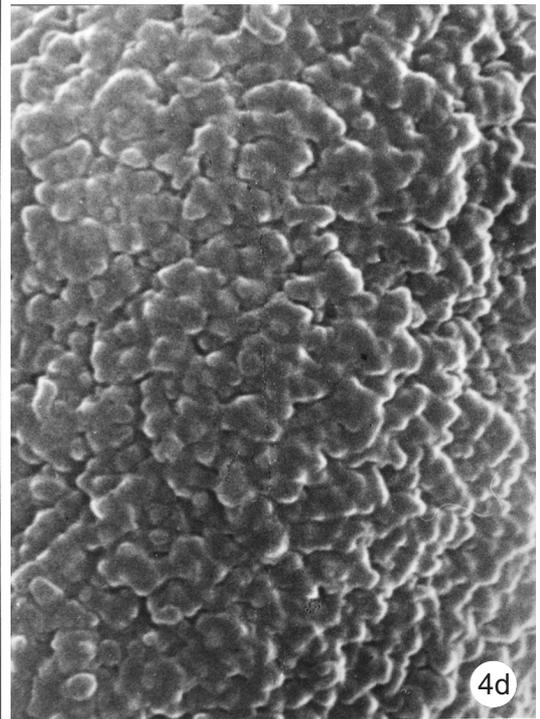
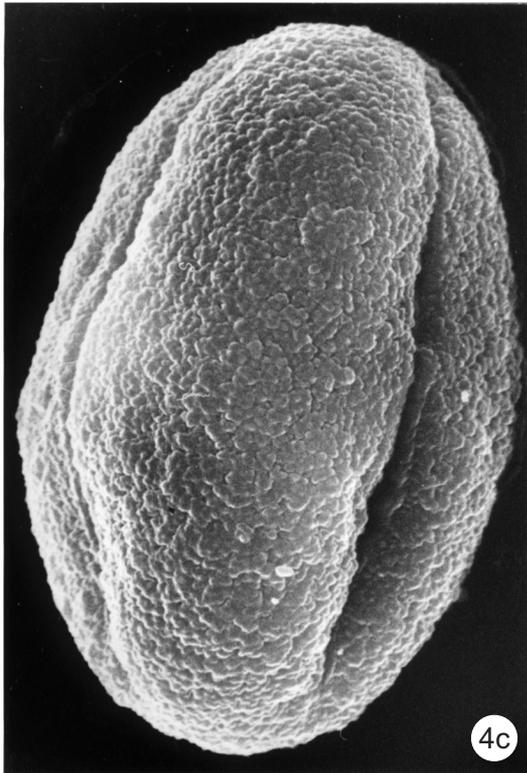
Plate 1

1. *Fususpollenites fusus* (Potonié) Kedves; Budki Janowskie 185.2 m, Lower Oligocene
1a, b. equatorial view, two optical sections, LM, $\times 1000$
1c. general view, SEM, $\times 4\ 000$
1d. part of sculpture, SEM, $\times 10\ 000$
2. *Fususpollenites fusus* (Potonié) Kedves (= cf. *Castanopsis* forma *refota* (*Pollenites cingulum fusus* Potonié) in Doktorowicz-Hrebicka 1961 Pl. 11 fig. 165), LM, $\times 800$
3. *Fususpollenites fusus* (Potonié) Kedves (= *Pollenites cingulum* Potonié forma *reliqua*, in Doktorowicz-Hrebicka 1961 Pl. 11 fig. 167), LM, $\times 800$
4. *Fususpollenites fusus* (Potonié) Kedves; Dąbrowa 157.4–157.5 m, Lower Oligocene
4a, b. equatorial view, two optical sections, LM, $\times 1000$
4c. general view, SEM, $\times 4000$
4d. part of sculpture, SEM, $\times 10\ 000$



Magn 4000x WD 6.8 Exp 27 | 5 μ m
st. 1

Magn 10000x WD 6.8 Exp 28 | 2 μ m
st. 1



Magn 4000x WD 6.7 Exp 44 | 5 μ m
st. 3

Magn 10000x WD 6.7 Exp 45 | 2 μ m
st. 3

Plate 2

1. *Fususpollenites fusus* (Potonié) Kedves; Dąbrowa 157.4–157.5 m, Lower Oligocene
1a, b. equatorial view, two optical sections, LM, $\times 1000$
1c. general view, SEM, $\times 4\ 000$
1d. part of sculpture, SEM, $\times 10\ 000$
2. *Fususpollenites residuus* (Doktorowicz-Hrebnicka) comb. nov. (= *Pollenites cingulum* forma *residua* ex Doktorowicz-Hrebnicka 1961, Pl. 12 fig 173), LM, $\times 800$ (holotype)
3. *Fususpollenites residuus* (Doktorowicz-Hrebnicka) comb. nov.; Dąbrowa 157.4–157.5 m, Lower Oligocene
3a, b. equatorial view, two optical sections, LM, $\times 1000$
3c. general view, SEM, $\times 4\ 000$
3d. part of sculpture, SEM, $\times 10\ 000$



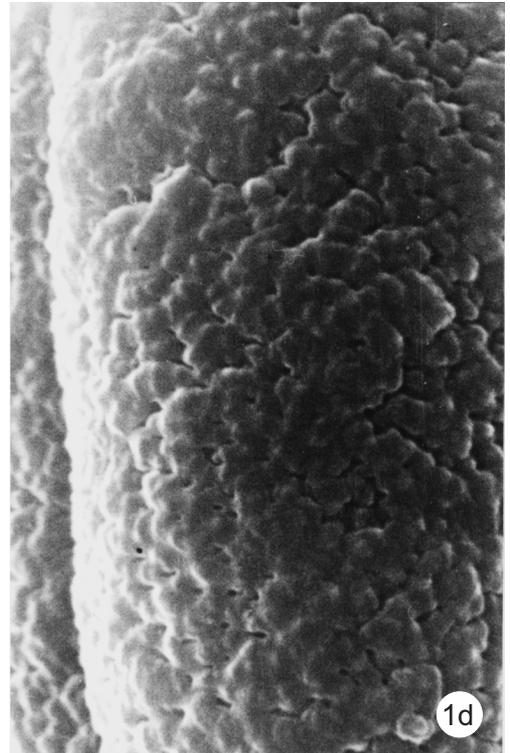
1a



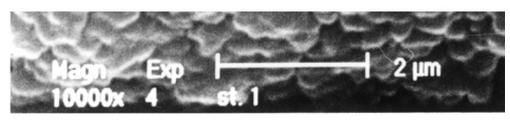
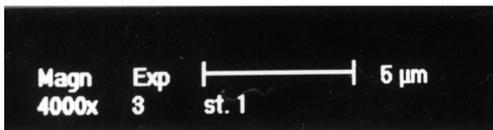
1b



1c



1d



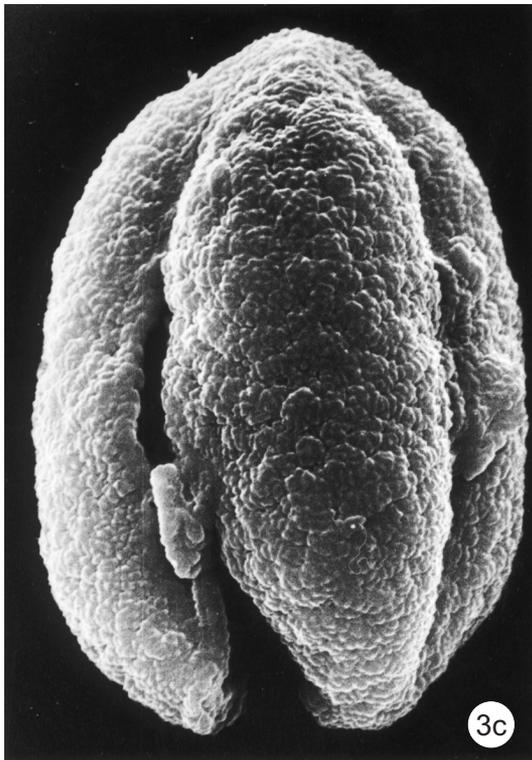
2



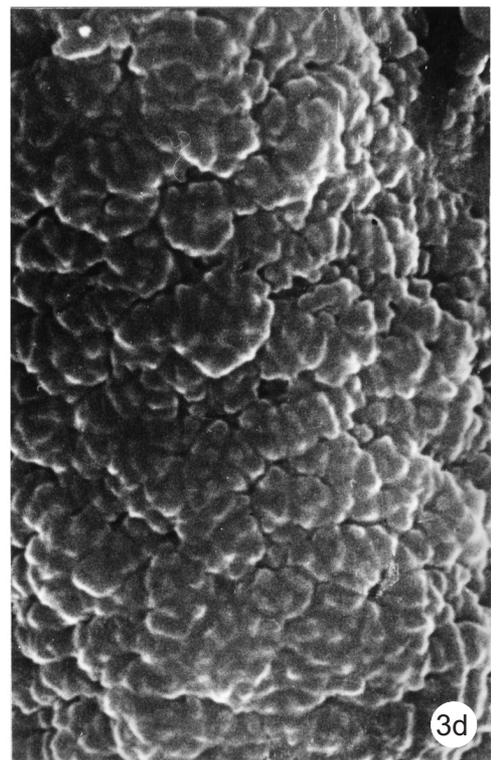
3a



3b



3c



3d

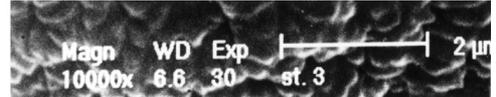


Plate 3

1. *Fususpollenites recollectus* (Doktorowicz-Hrebnicka) comb. nov.; Dąbrowa 157.4–157.5 m, Lower Oligocene
1a, b. equatorial view, two optical sections, LM, × 1000
1c. general view, SEM, × 4 000
1d. part of sculpture, SEM, × 10 000
2. *Fususpollenites recollectus* (Doktorowicz-Hrebnicka) comb. nov. (= *Pollenites cingulum* forma *recollecta* ex Doktorowicz-Hrebnicka 1961 Pl. 12 fig. 168), LM, × 800 (holotype).
- 3–6. *Fususpollenites recollectus* (Doktorowicz-Hrebnicka) comb. nov. (= *Pollenites cingulum* forma *recollecta* in Doktorowicz-Hrebnicka 1961 Pl. 12 figs 169–172), LM, × 800
7. *Fususpollenites recollectus* (Doktorowicz-Hrebnicka) comb. nov. Szczecin IG 1, LM, × 1000
- 8a, b, c. *Fususpollenites recollectus* (Doktorowicz-Hrebnicka) comb. nov. (= cf. *Ptelea* sp. – *Tricolporopollenites cingulum fusus* (Potonié) Thomson & Pflug ex Stuchlik 1964 Pl. 16 figs 26–28), three optical sections, LM, × 1000
- 9a, b. *Ptelea trifoliata* L. (recent), two optical sections, LM, × 1000
- 10a, b. *Ptelea trifoliata* L. (recent), two optical sections, LM, × 1000
11. *Ptelea trifoliata* L. (recent conglomerate of pollen grains), LM, × 1000



1a



1b



2



3



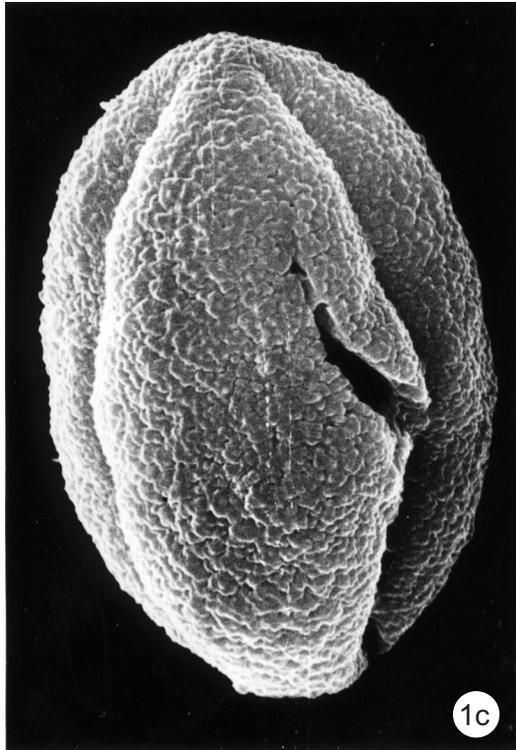
4



5

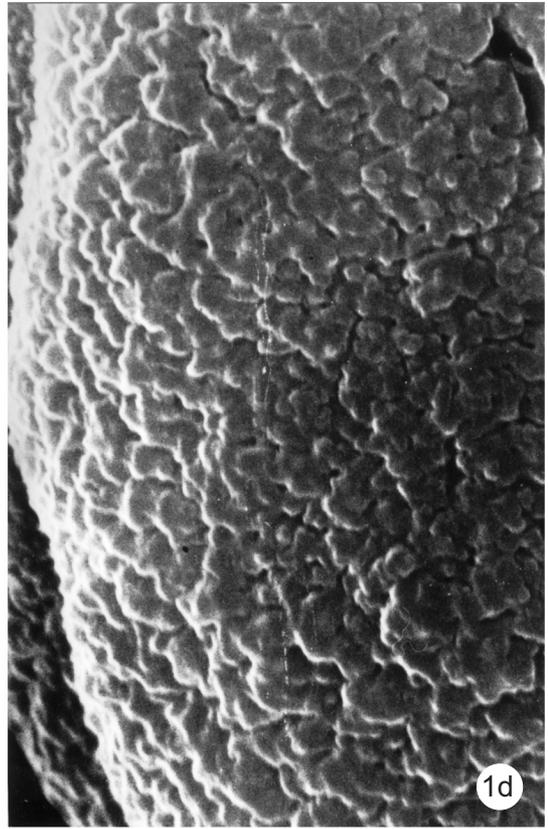


6



1c

Magn 4000x WD 6.8 Exp 31 | 5 μm | st. 3

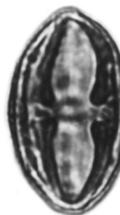


1d

Magn 10000x WD 6.8 Exp 32 | 2 μm | st. 3



7



8a



8b



8c



9a



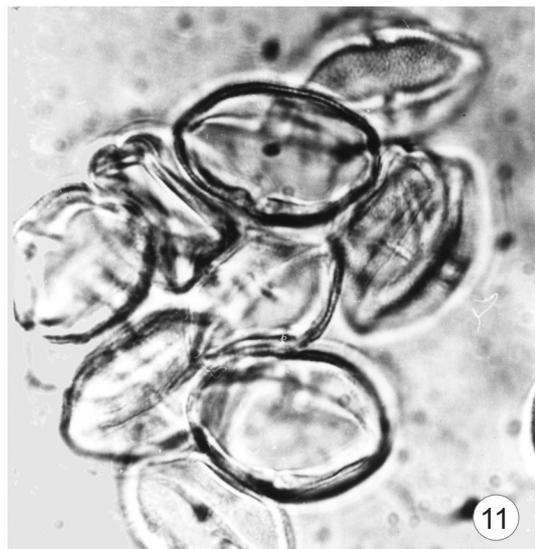
9b



10a



10b



11