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

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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), 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 (Potonie) 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 (Potonie) 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 consisting 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 Potonie 1931, he included into synonymy the subspecies Tricolporopollenites cingulum fusus (Potonie) 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 Potonie 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 Potonie 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 Potonie (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** (Potonie 1931) Kedves 1978

Pl. 1 figs 1–4, Pl. 2 fig. 1

1931 Pollenites fusus n.sp.; Potonie, p. 556, Pl. 1 fig. 13; holotype.

1934 Pollenites cingulum fusus Potonie; Potonie p. 82, 83, Pl. 4 fig. 20.

1934 Pollenites cingulum fusus Potonie & Venitz, p. 38, 39, Pl. 3 fig. 96.

1953 Tricolporopollenites cingulum subsp. fusus (Potonie) n. comb.; Thomson & Pflug, p. 100, pl. 12 figs 16, 19, 27 only.

1961 cf. Castanopsis forma refota (Pollenites cingulum fusus Potonie); Doktorowicz-Hrebnicka, p. 233, Pl. 11 fig. 165.
1961 Pollenites cingulum Potonié forma reliqua; Doktorowicz-Hrebnicka, p. 234, Pl. 11 fig. 167.
1965 Tricolporopollenites cingulum subsp. fusus (Potonié) Thomson & Pflug; Grabowska, Pl. 2 fig. 28.
1966 Pollenites cingulum Potonié; Ziembirńska & Niklewski, p. 37, Pl. 6 fig. 8.
1968 Tricolporopollenites (Potonié) Thomson & Pflug: Grabowska, Pl. 2 fig. 51.
1976 Scabratricalporites schellendorfii nsp.; Roche & Schuler, p. 24, Pl. 10 figs 12, 13 only.
1980 Psilatricalporites cingulum fusus (Potonié) Roche & Schuler; Olivier-Pierre, p. 65, Pl. 25 fig. 9.
1990 Fususpollenites fusus (Potonié) Jedves; Konza-lová, p. 85, Pl. 37 fig. 13.

Material. Budki Janowskie, 185.5 m, Lower Oligocene; Dałbrowa 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 fusus, is closest to the holotype Pollenites fusus Potonié 1931 (=Pollenites cingulum fusus Potonié 1934). The same pollen type may be found among the illustrations of Tricolporopollenites cingulum fusus 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 fusus 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 recollectus
(Doktorowicz-Hrebnicka 1961) comb. nov.
Pl. 3 figs 1–8

1953 Tricolporopollenites cingulum subsp. fusus (Potonié) n. comb.; Thomson & Pflug, p. 100, Pl. 12 figs 15, 20, 22, 26 only.
1965 Tricolporopollenites cingulum subsp. fusus (Potonié) Thomson & Pflug; Grabowska, Pl. 2 fig. 30.
1978 Fususpollenites fusus (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 recollecta (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 fusus 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 (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-Hrebnicka (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-Hrebnicka has been raised to species rank as Fususpollenites recollectus (Doktorowicz-Hrebnicka) comb. nov. Under the SEM the tectum of this species is revealed as of the quercoidal type (Pl. 3 fig. 1d).

**Fususpollenites residua**

(Doktorowicz-Hrebnicka 1961) comb. nov.

Pl. 2 figs 2, 3

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

**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-Hrebnicka 1961, Pl. 12 figs 173, 174, see also the present paper Pl. 2 fig. 2). Doktorowicz-Hrebnicka 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-Hrebnicka 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-Hrebnicka (1961, Pl. 12 figs 173, 174) as forma residua is so significant, that it justifies raising forma residua to species rank as Fususpollenites residua (Doktorowicz-Hrebnicka) 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 Fagioideae (Kohlman-Adamska & Ziemińska-Tworyzdo 2000). In these the tectum forms, developed from the fused rodlets. Fossil pollen grains with this type of surface structure have already been partially described (Kohlman-Adamska & Ziemińska-Tworyzdo 1999, 2000).

Most authors (Doktorowicz-Hrebnicka 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 & Daghlian 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 Erdman (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 incrassatus (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 & Daghlian 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 verruculate type, consisting of twisted vermiciform elements or rodlets with free ends. Crepet and Nixon (1989) thought that such a pollen surface structure was intermediate between the Castaneoideae and Fagioideae, 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 Amentogerdiopollenites 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 Fagodeae (see Kohlman-Adamska & Ziembirńska-Tworzydło 2000). According to these authors (Kohlman-Adamska & Ziembirńska-Tworzydło 2000), the structure of the pollen surface of Tricolporopollenites villensis (Potonié) Thomson & Pflug is intermediate between those of the subfamilies Castaneoideae and Fagodeae. 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 Amentogerdiopollenites 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 Amentogerdiopollenites and Amentoplexipollenites is fagoidal.

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

The SEM studies of the surface of the dispersed fossil pollen grains presented in the 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 Kidves 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 (May 1981)

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PLATES

Plate 1

1. Fususpollenites fusus (Potonié) Kedves; Budki Janowskie 185.2 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 fusus (Potonié) Kedves (= cf. Castanopsis forma refota (Pollenites cingulum fusus Potonié) in Doktorowicz-Hrebnicka 1961 Pl. 11 fig. 165), LM, × 800

3. Fususpollenites fusus (Potonié) Kedves (= Pollenites cingulum Potonié forma reliqua, in Doktorowicz-Hrebnicka 1961 Pl. 11 fig. 167), LM, × 800

4. Fususpollenites fusus (Potonié) Kedves; Dąbrowa 157.4–157.5 m, Lower Oligocene
   4a, b. equatorial view, two optical sections, LM, × 1000
   4c. general view, SEM, × 4000
   4d. part of sculpture, SEM, × 10 000
Plate 1

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Plate 2

1. Fususpollenites fusus (Potonié) Kedves; 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 residuus (Doktorowicz-Hrebnicka) comb. nov. (= Pollenites cingulum forma residua ex Doktorowicz-Hrebnicka 1961, Pl. 12 fig 173), LM, × 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, × 1000
   3c. general view, SEM, × 4 000
   3d. part of sculpture, SEM, × 10 000
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


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