4. TRANSMISSION ELECTRON MICROSCOPY OF THE PARTIALLY DEGRADED POLLEN GRAINS FROM THE THANETIAN LAYERS OF MENAT (FRANCE) I.

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Abstract

Gymnosperm and *angiosperm* pollen grains were partially degraded with merkaptoethanol during 2.5 and 5 hours, and investigated with the TEM method. The saccate *gymnosperm* pollen grains *(Pityosporites alatus, P. pristinipollinius)* are relatively resistant against the experimental and embedding processes. The tectum and the infratectal layer at the investigated *Longaxones (Monocolpopollenites tranquillus, Cupuliferoidaepollenites quisqualis, C. liblarensis, Cupuliferoipollenites insleyanus, C. oviformis, C. pusillus, Retitricolpites thomsonii)* taxa are also resistant. The granular infratectal layer of the two *Normapolles (Plicapollis, Stephanoporopollenites)* taxa is less resistant, in opposition to this, the granular infratectal layer of the *Platycaryapollenites (Postnormapolles)* is well preserved after the partial dissolution experiment. The resistance of the pollen grains of the recent *Platycarya* against different kinds of experimental influences was emphasized previously. The ultrastructure of the pollen grains embedding organic material was also investigated and interpreted.

Key words: Palynology, Paleocene, Menat, France, experimental ultrastructure.

Introduction

EHRLICH and HALL (1959) in its pionnering paper on the transmission electron microscopy of fossil pollen grains among others called attention to the preservation of the ultrastructure of the fossil organic material. KEDVES, STANLEY and ROJIK (1974) observed the partial degradation of fossil pollen grains during fossilization processes from some *angiosperm* pollen grains isolated from the Eocene layers of Missisippi. Larger globular molecular structures were published from the infratectal layer of *Restioniidites hungaricus* (KEDVES 1965) ELSIK 1968 and from the ectexine of *Thomsonipollis magnificus* (PFLUG and THOMSON 1953) KRUTZSCH 1960. In several papers it was emphasized, that the preservation of the fossil organic material depends from several factors, such the basic chemistry of the organic material, the sedimentation processes, after the treatment of the sediments, the experiments and the fixation and embedding processes for transmission electron microscopical investigations. ROWLEY and SRIVASTAVA (1986) investigated the exine of *Classopollis* after oxidative etching. Biopolymer structure of this pollen grain was also established. Later ROWLEY, J.R., ROWLEY, J.S. and SKVARLA (1990) described the ultrastructure of the corroded exines from the HAVINGA's experiments.

The Paleocene (Thanetian) layers of Menat are very rich in well preserved sporomorphs. Some previous papers, and the monographical elaboration of this spore-pollen assemblage was previously published by KEDVES and RUSSELL (1982). Later some ultrastructural data from the partially degraded pollen grains from Menat were published (KEDVES, 1986, 1988) and two kinds of experiments were made on this material but till this time without systematic study and publication.

The aim of this paper is to investigate in detail the ultrastructure results of the so-called moderatedly degraded pollen grains in comparison to other fossil and recent pollen data.

Materials and Methods

The locality was described previously by RUSSELL (1982) in KEDVES and RUSSELL. The sediments were treated with HCl and HF. The organic residue was dried. 20 mg organic material was used for all experiments. 1 ml merkaptoethanol was added for the dry organic material and the length of time was 2.5 and 5 hours. For TEM studies the washed material was postfixed with OsO_4 aq.dil. and embedded in Araldite (Durcupan, Fluka). The ultrathin sections were made with glass knives, the TEM pictures were taken with a Tesla BS 500 instrument, resolution 5 Å.

The investigated pollen taxa with the length of time and the block numbers are as follows:

Pityosporites alatus (2.5h: 85/48), *Pityosporites pristinipollinius* (2.5h: 85/45, 5h: 85/36), *Monocolpopollenites tranquillus* (2.5h: 85/51), *Cupuliferoidaepollenites quisqualis* (2.5h: 85/64, 85/66, 86/4, 5h: 85/8, 85/37). *Cupuliferoidaepollenites liblarensis* (2.5h: 85/49, 85/60b, 86/6, 5h: 85/41, 86/2), *Cupuliferoipollenites insleyanus* (2.5h: 85/63), *Cupuliferoipollenites oviformis* (2.5h: 85/55, 5h: 85/35), *Cupuliferoipollenites pusillus* (2.5h: 85/31, 85/56, 85/57, 85/58, 5h: 85/38), *Retitricolpites thomsonii* (2.5h: 85/62, 86/1, 5h: 85/40, 85/42, 86/3), *Stephanoporopollenites hexaradiatus* (2.5h: 85/61), *Plicapollis pseudoexcelsus* (2.5h: 85/47), *Platycaryapollenites platycaryoides* (2.5h: 85/54, 85/60a, 85/65).

Results

Gymnosperm pollen grains

Two saccate *gymnosperm* pollen grains was investigated:

1. *Pityosporites alatus* (POTONIÉ 1931) THOMSON et PFLUG 1953, *Abietaceae, Pinus* (Plate 4.1.)

2. *Pityosporites pristinipollinius* (TRAVERSE 1955) KRUTZSCH 1971, *Abietaceae, Pinus* (Plate 4.2., figs. 1,2)

Remark. - The ultrastructure of fossil saccate *gymnosperm* pollen grains was summarized in the monograph of KEDVES (1994).

Based on our present results, the molecular system of the sporopollenin of the saccate *gymnosperm* pollen grains is resistant. The alveolar ectexine of the corpus is well shown in Plate 4.2., fig. 2, the saccus is represented on both investigated species (Plate 4.1., and Plate 4.2., fig. 1). The different kinds of alveoli (a_1, a_2, a_3) are well shown. On the other hand it is worth mentioning, that the outer surface is covered with organic material with fine lamellar or spongy ultrastructure. There are globular electron dense particles

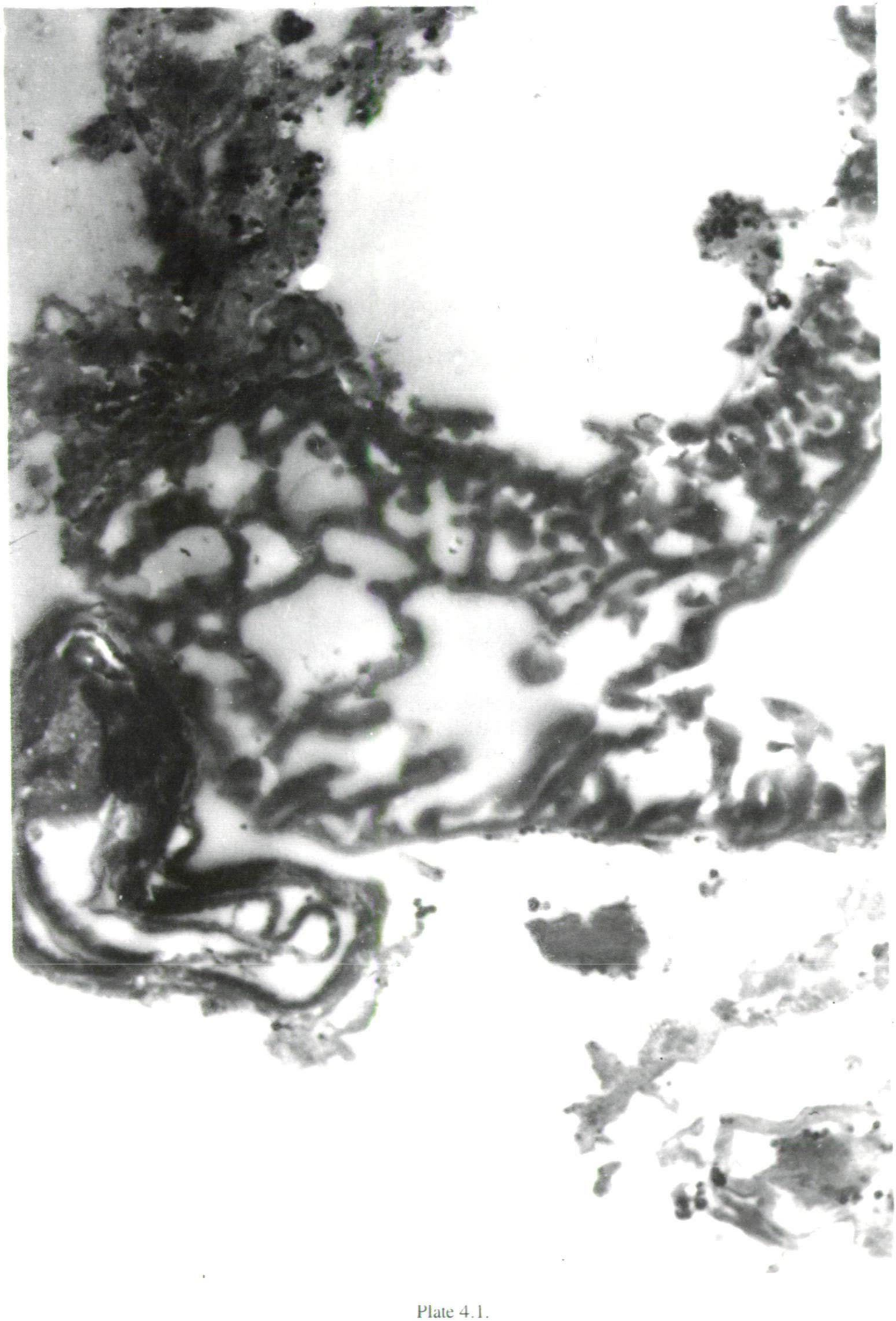

Plate 4.1.

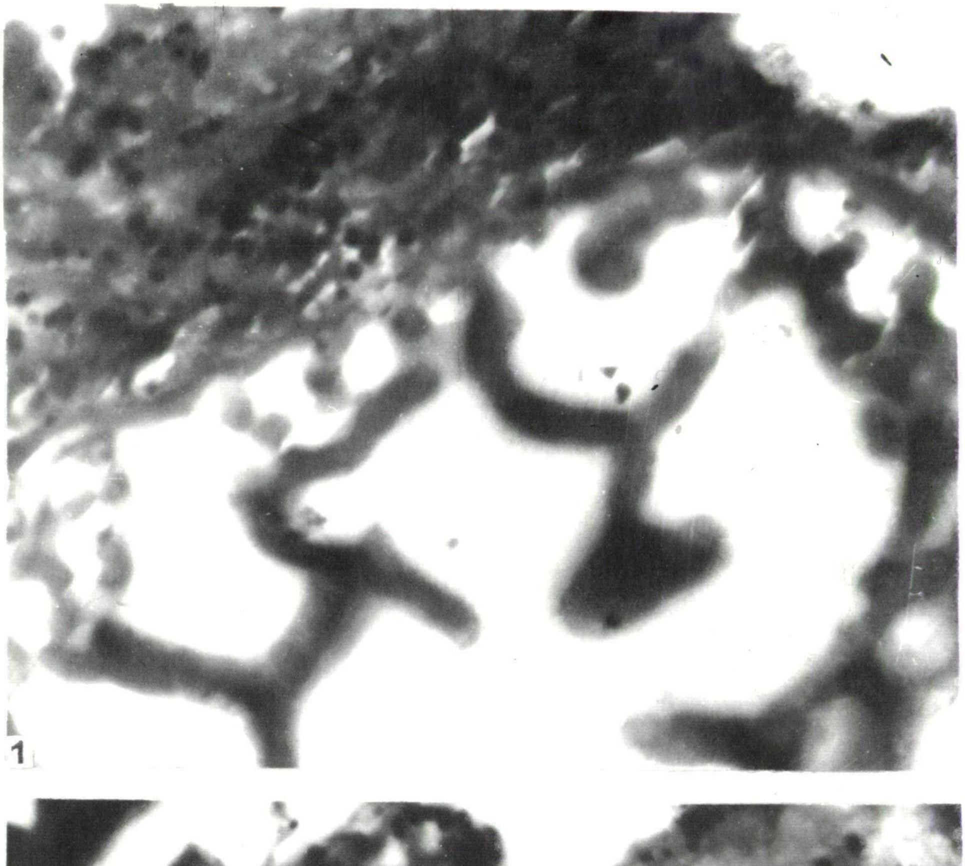

Plate 4.2.

Plate 4.1.

Pityosporites alatus (POTONIÉ 1931) THOMSON et PFLUG 1953, *Abietaceae, Pinus*, block number: 85/45, negative no: 5340, 10.000x.

Plate 4.2.

1,2. *Pityosporites pristinipollinius* (TRAVERSE 1955) KRUTZSCH 1971, *Abietaceae, Pinus*, block number: 85/48.
1. Negative no: 5346, 25.000x.
2. Negative no: 5344, 25.000x.

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within the spongy and/or lamellar organic matrix. Similar ultrastructure was published by GLIKSON and TAYLOR (1986), p. 276, fig. B,C, p. 272: "bacterial remains as a part of main component of vitrinite-like organic matter (TEM)," But this embedding matrix may be also in consequence of the electrostatic charge of the surface.

Angiosperm pollen grains
Longaxones

Monocolpopollenites tranquillus (POTONIÉ 1934) THOMSON et PFLUG 1953 subfsp. *tranquillus, Palmae* (Plate 4.3., figs. 1-4)

Remark. - This fossil pollen grain was compared to recent taxa by KEDVES and BOHONY (1966) to establish the nearer botanical affinity. SEM pictures were published by KEDVES (1979) and from specimens of the Middle Eocene layers of the Dorog coal basin.

The tectate perforate ectexine is well illustrated in picture 1 and 3 of Plate 4.3. The tangential section of the infratectal layer represents well the columellar character of this middle ectexine layer. Two layers may be distinguished on the highly magnified picture (Plate 4.3., fig. 4) of the foot layer. The inner one may be endexine with degraded lamellar system. Granular units are also present in this part, which represents the larger molecular structures. Worth mentioning is that the embedding organic material is not closely connected to the tectum.

Cupuliferoidaepollenites quisqualis (POTONIÉ 1934) POTONIÉ 1960, *Fagaceae* or *Leguminosae* (Plate 4.4., figs. 1,2)

Three blocks (85/64, 85/66 and 86/4) were treated during 2.5 hours, another two (85/37 and 85/40) during 5 hours. Partial degradation was observed at the last mentioned experiment we present one example from these pollen grains (Plate 4.4., figs. 1,2).

The surface of these pollen grains is covered with the organic material. This may be a more or less amorphous layer with the thickness of the ectexine. The desintegration of the ectexine is well shown (Plate 4.4., figs. 1,2) in particular it is the infratectal layer which is sometimes completely destroyed (Plate 4.4., figs. 1,2).

Cupuliferoidaepollenites liblarensis (THOMSON, in POTONIÉ, THOMSON et THIERGART, 1950), POTONIÉ 1960, *Fagaceae* or *Leguminosae* (Plate 4.5., figs. 1-4)

Five blocks (85/41, 85/49, 85/60, 86/2 and 86/6). The pollen grains embedded into the blocks no: 85/49, 85/60 and 86/6 were treated during 2.5 hours, the other two; 85/41, 86/2, during 5 hours. As the best example we present the results of the 86/2 block.

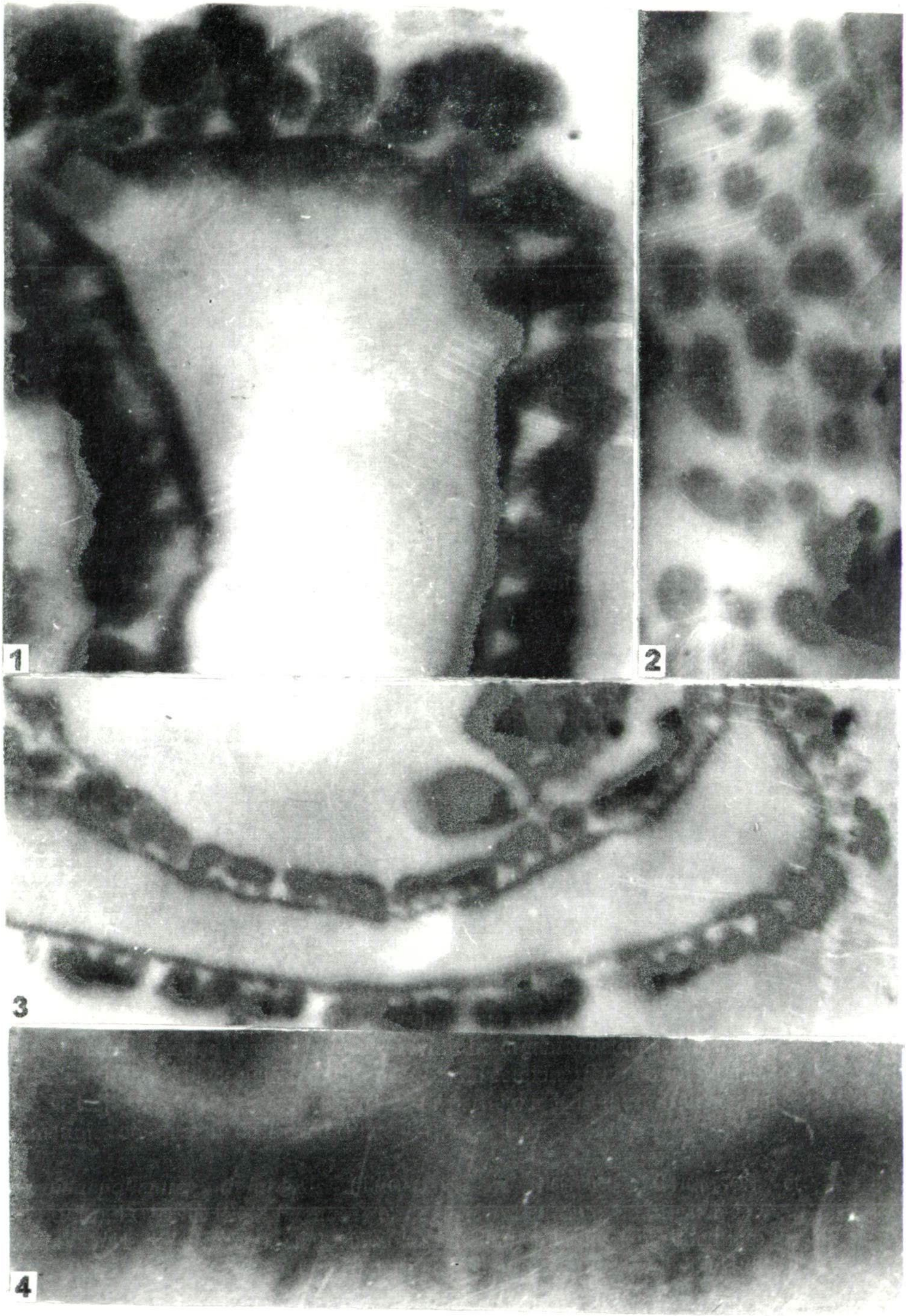

Plate 4.3.

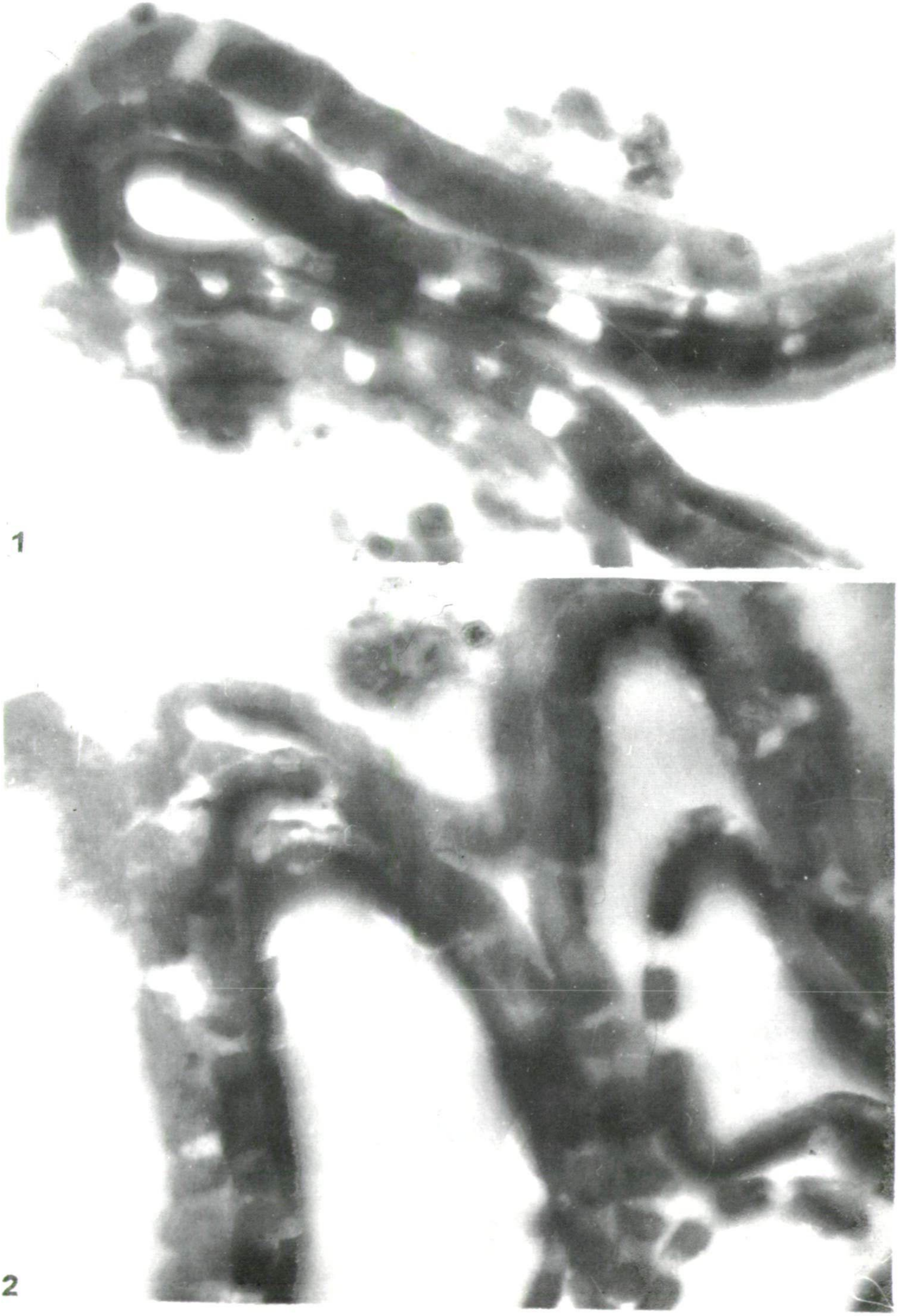

Plate 4.4.

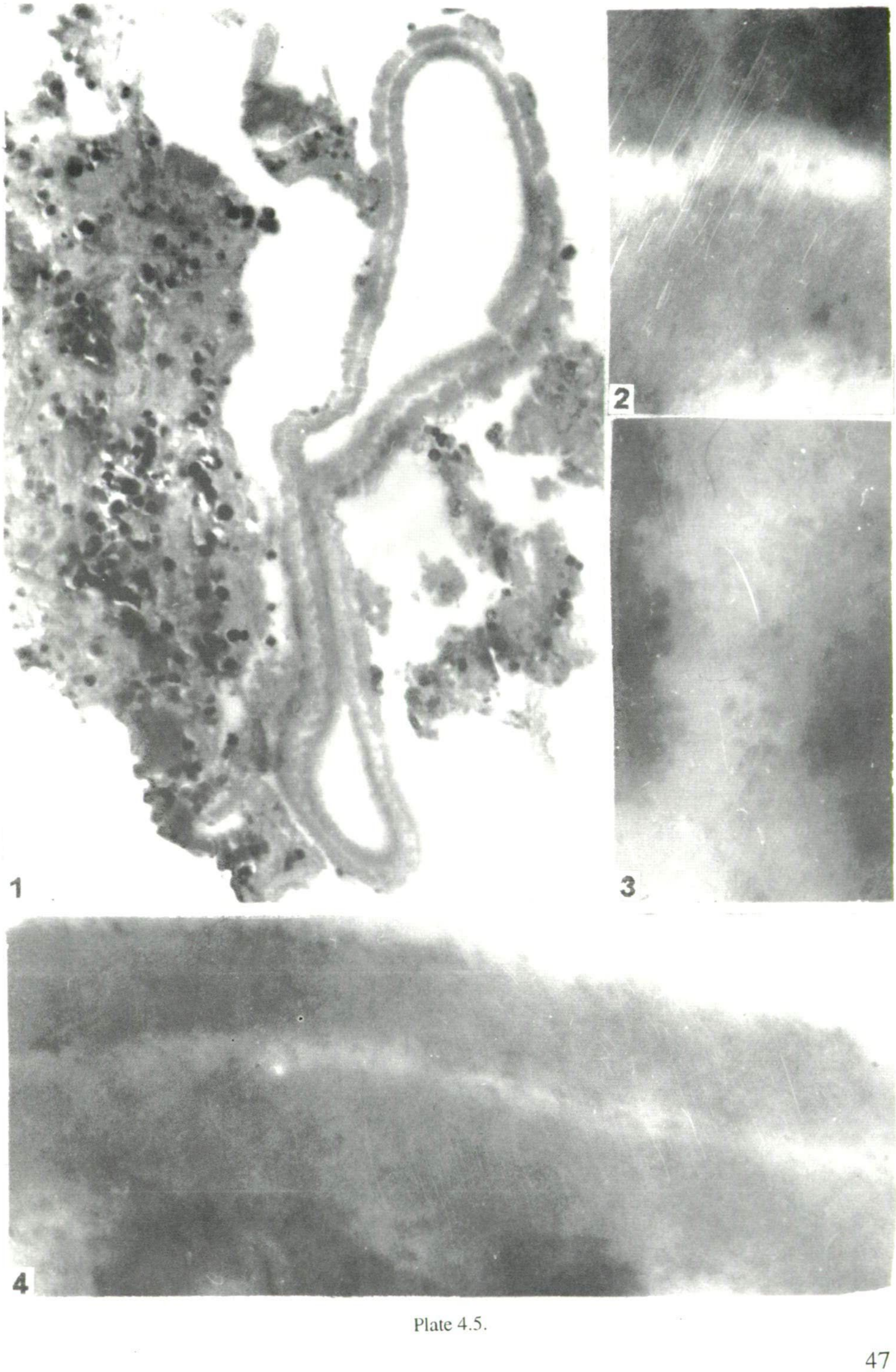

Plate 4.5.

Plate 4.3.

1-4. *Monocolpopollenites tranquillus* (POTONIÉ 1934) THOMSON et PFLUG 1953 subfsp. *tranquillus, Palmae,* block number: 85/51.
1. Negative no: 5456, 50.000x.
2. Negative no: 5458, 64.000x.
3. Negative no: 5455, 20.000x.
4. Negative no: 5463, 250.000x.

Plate 4.4.

1,2. *Cupuliferoidaepollenites quisqualis* (POTONIÉ 1934) POTONIÉ 1960, *Fagaceae* or *Leguminosae*, block number: 85/40.
1. Negative no: 5277, 50.000x.
2. Negative no: 5279, 50.000x.

Plate 4.5.

1-4. *Cupuliferoidaepollenites liblarensis* (THOMSON, in POTONIÉ, THOMSON et THIERGART, 1950) POTONIÉ 1960, *Fagaceae* or *Leguminosae*, block number: 86/2.
1. Negative no: 5679, 15.000x.
2. Negative no: 5682, 150.000x.
3. Negative no: 5682, 150.000x.
4. Negative no: 5685, 150.000x.

The surface of the pollen grains is completely covered with the spongy or lamellar organic material. There are several electron dense globular particles in the embedding material. The ultrastructure of this kind of embedding organic matter is similar to those published by LUGARDON, RAYNAUD and HUSSON (1991); Planche I, fig. 6.: "Part of large mass of dense, heterogeneous MAT with a cluster of packed laminae (arrowhead) and scattered ovoid elements (arrows). Upper Cretaceous, Iran. x50.000." The degradation of the infratectal layer is well shown on the general survey picture (Plate 4.5., fig. 1) too. The more or less completely disparition of the infratectal layer is illustrated on the highly magnified pictures (Plate 4.5., figs. 2-4). There are electron dense granules in the inner part of the tectum and the outer part of the foot layer which are in the larger sporopollenin globular dimension. The innest part of the exine is electron dense, this is in all probability the endexine (Plate 4.5., figs. 1 and 4). In picture 4 of the Plate 4.5., the desintegration of the tectum is illustrated.

Cupuliferoipollenites insleyanus (TRAVERSE 1955) POTONIÉ 1960 *Fagaceae, Castanea* (Plate 4.6., figs. 1,2)

The surface of the investigated pollen grain was rarely covered with the organic embedding material with electron dense granular particles. Fig. 1 in Plate 4.6., illustrate the degradation in the apertural area. Strong degradation of the infratectal layer was also observed in particular in the highly magnified picture (Plate 4.6., fig. 2). Less characteristic molecular structures were also observed.

Cupuliferoipollenites oviformis (POTONIÉ 1931) POTONIÉ 1960, *Fagaceae, Castanea* (Plate 4.7., figs. 1-5)

Pollen grains of two blocks (85/35 and 85/55) were investigated. The general survey pictures (Plate 2.7., figs. 1,4) illustrate well the characteristic ectexine of this kind of pollen grain, namely the thick tectum and foot layer and the relatively thin infratectal layer. The embedding organic material is not always connected to the surface of the tectum. The characteristic lamellar ultrastructure of this material and the electron dense globular particles are well shown in fig. 5 of Plate 4.7., cf. LUGARDON, RAYNAUD and HUSSON (1991). The ectexine is resistant not so characteristic degradation was established at the ultrastructure of the infratectal layer.

Cupuliferoipollenites pusillus (POTONIÉ 1934) POTONIÉ 1960, *Fagaceae,* cf. *Castanea.* (Plate 4.8., figs. 1-3)

Pollen grains of the following blocks were partially dissolved during 2.5 hours: 85/31, 85/56, 85/57, 85/58, and one during 5 hours; 85/38. The exine ultrastructure is similar to the previous species including the interesting lamellar embedding organic material (Plate 4.8., fig. 2). The thin columellar infratectal layer more or less preserved. Beneath the foot layer the electron dense endexine is illustrated in picture 3, Plate 4.8. In several places the endexine is completely destroyed, and the inner surface of the foot layer is partially degraded and the globular larger molecular structures are well shown; Plate 4.8., fig. 1.

Retitricolpites thomsonii KEDVES 1982, in KEDVES and RUSSELL (Plate 4.9., figs. 1-3, plate 4.10., figs. 1,2, plate 4.11., figs. 1-3)

Pollen grains investigated from the blocks 85/62 and 86/1 were dissolved during 2.5 hours, 85/40, 85/42 and 86/3 during 5 hours. The characteristic exine ultrastructure of this exine is well shown in pictures no 1 in Plate 4.9. and 4.10. There are tangential sections also from the retipilate tectum (Plate 4.10., fig. 1) and from the columellar infratectal layer (Plate 4.1., fig. 1). The lamellar embedding organic material is in several places connected to the surface of the tectum. The electron dense granular particles are in the holes of the infratectal layer (Plate 4.10., fig. 2), cf. LUGARDON, RAYNAUD and HUSSON (1991). In general the exine of this kind of pollen grains is resistant, but degradation was observed in the infratectal layer (Plate 4.9., fig. 3).

In the apertural area the lamellar endexine is also degraded (Plate 4.9., fig. 3).

Brevaxones
Normapolles

Stephanoporopollenites hexaradiatus (THIERGART 1940) THOMSON et PFLUG 1953 cf. *tribinae* KRUTZSCH 1961 (Plate 4.12., figs. 1-3)

The investigated specimen was extremely damaged. The infratectal layer disappeared in consequence of the sedimentation or the experimental processes (Plate 4.12., figs. 1-3). The tectum is thinner than the foot layer, light, partial degradation zones were observed. The lower layer separate sometimes. The embedding organic material is not closely connected to the tectum, its ultrastructure is lamellar, with globular electron dense particles.

Plicapollis pseudoexcelsus (KRUTZSCH 1958) KRUTZSCH 1961 subfsp. *pseudoexcelsus* (Plate 4.13., figs. 1-3)

The lamellar embedding organic material is in general connected to the tectum. Worth mentioning is that in this case electron dense granular particles were not observed. The granular infratectal layer was completely destroyed. This is very characteristic at the annuli. Beneath the foot layer another electron dense layer is present with doubtful origin. This may be an inner embedding organic material or a peculiar inner

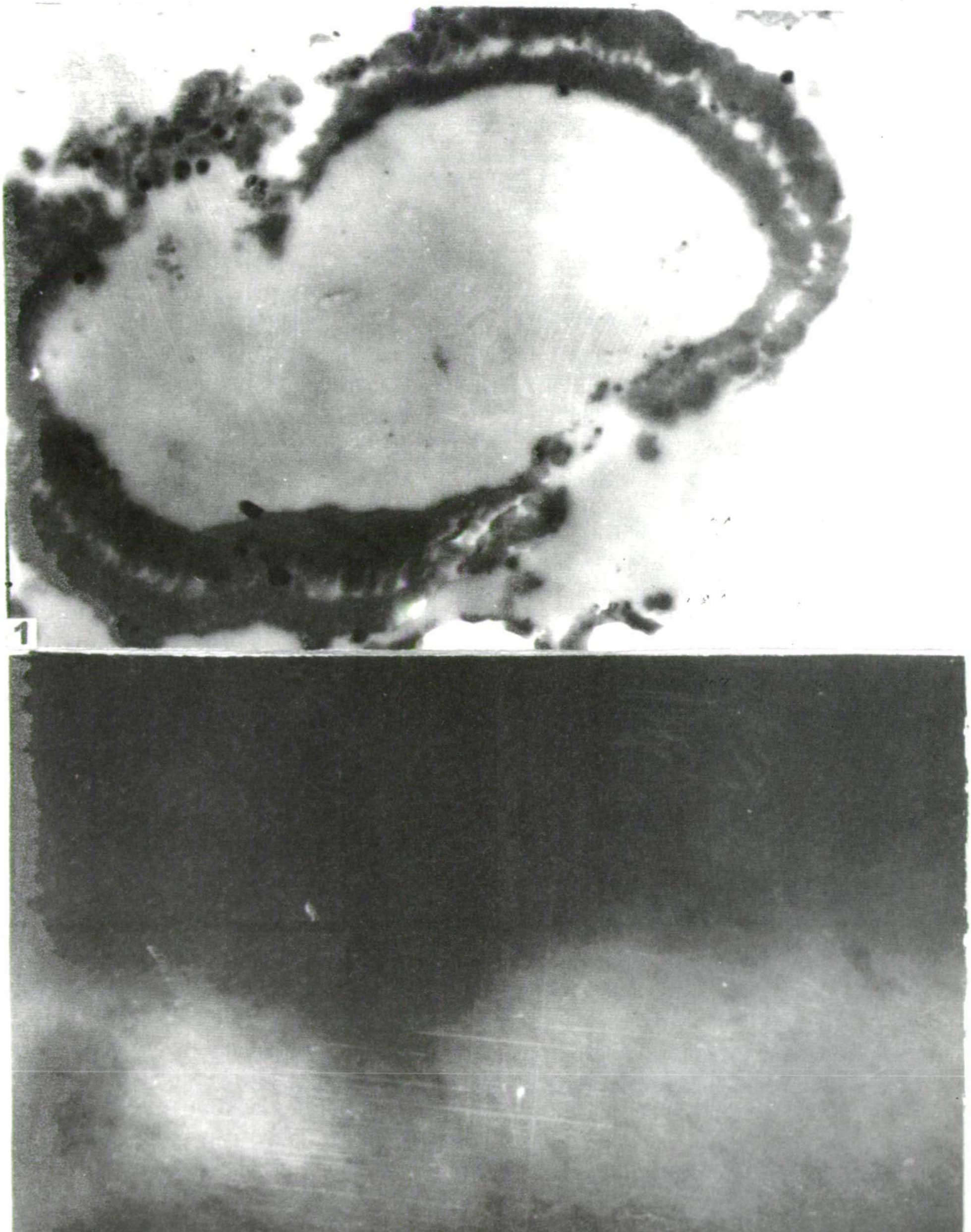

Plate 4.6.

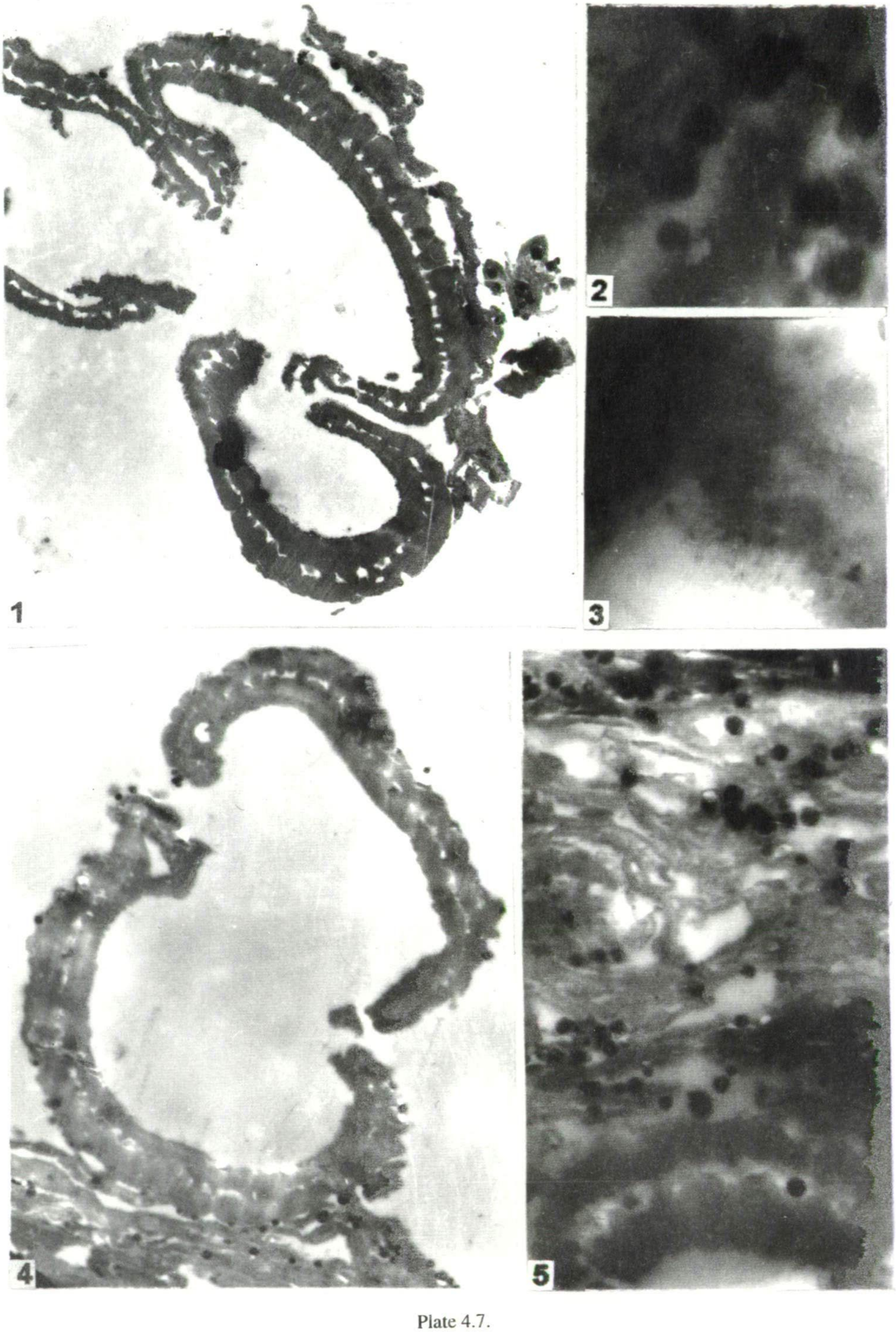

Plate 4.7.

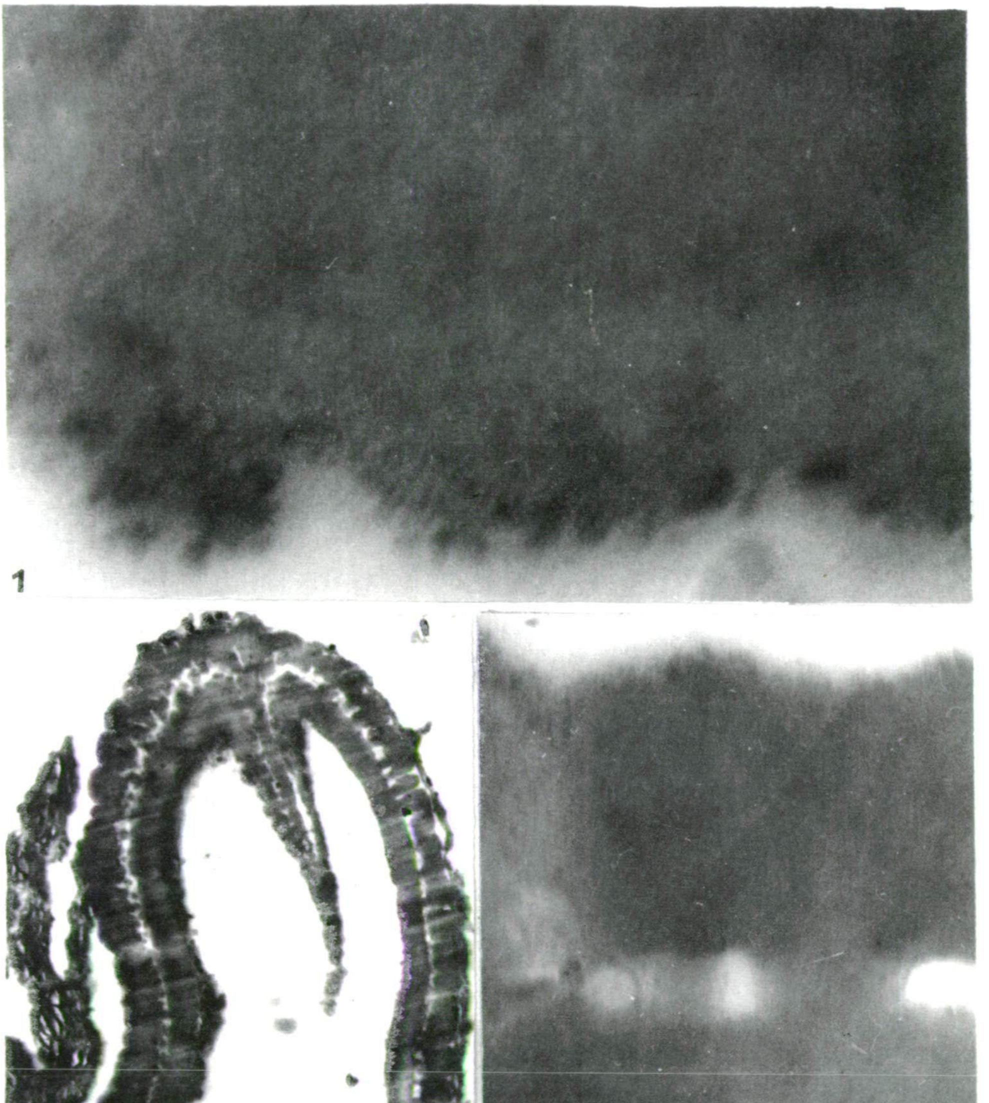

Plate 4.8.

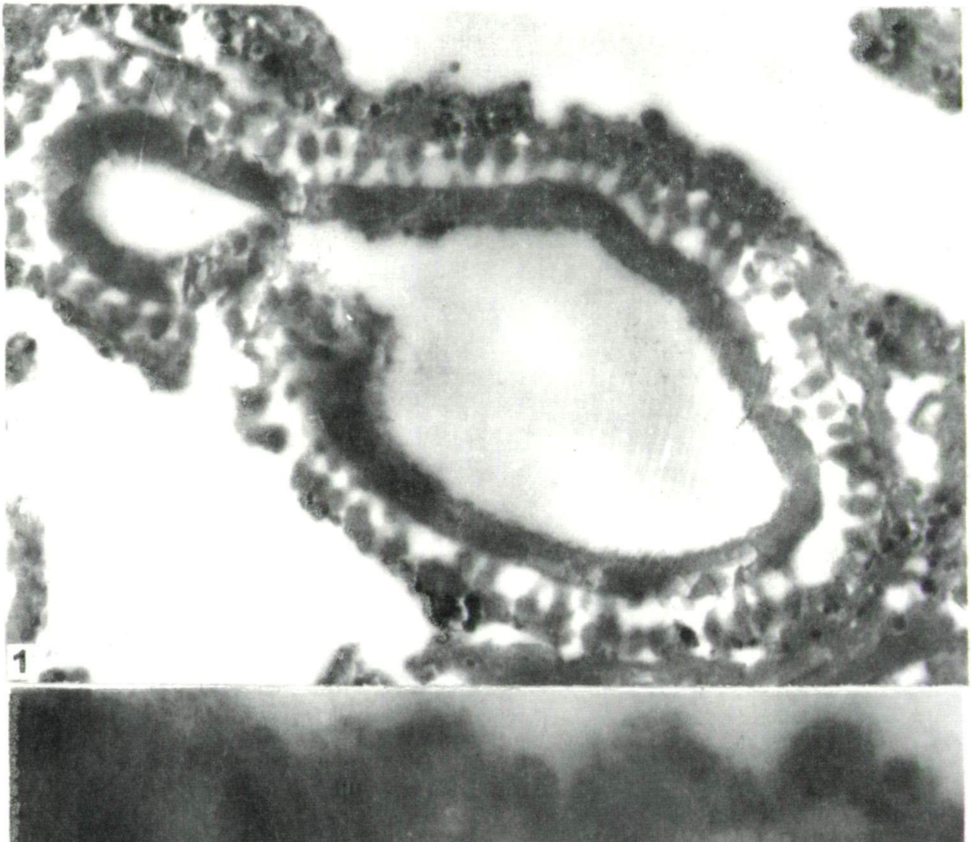

Plate 4.9.

Plate 4.10.

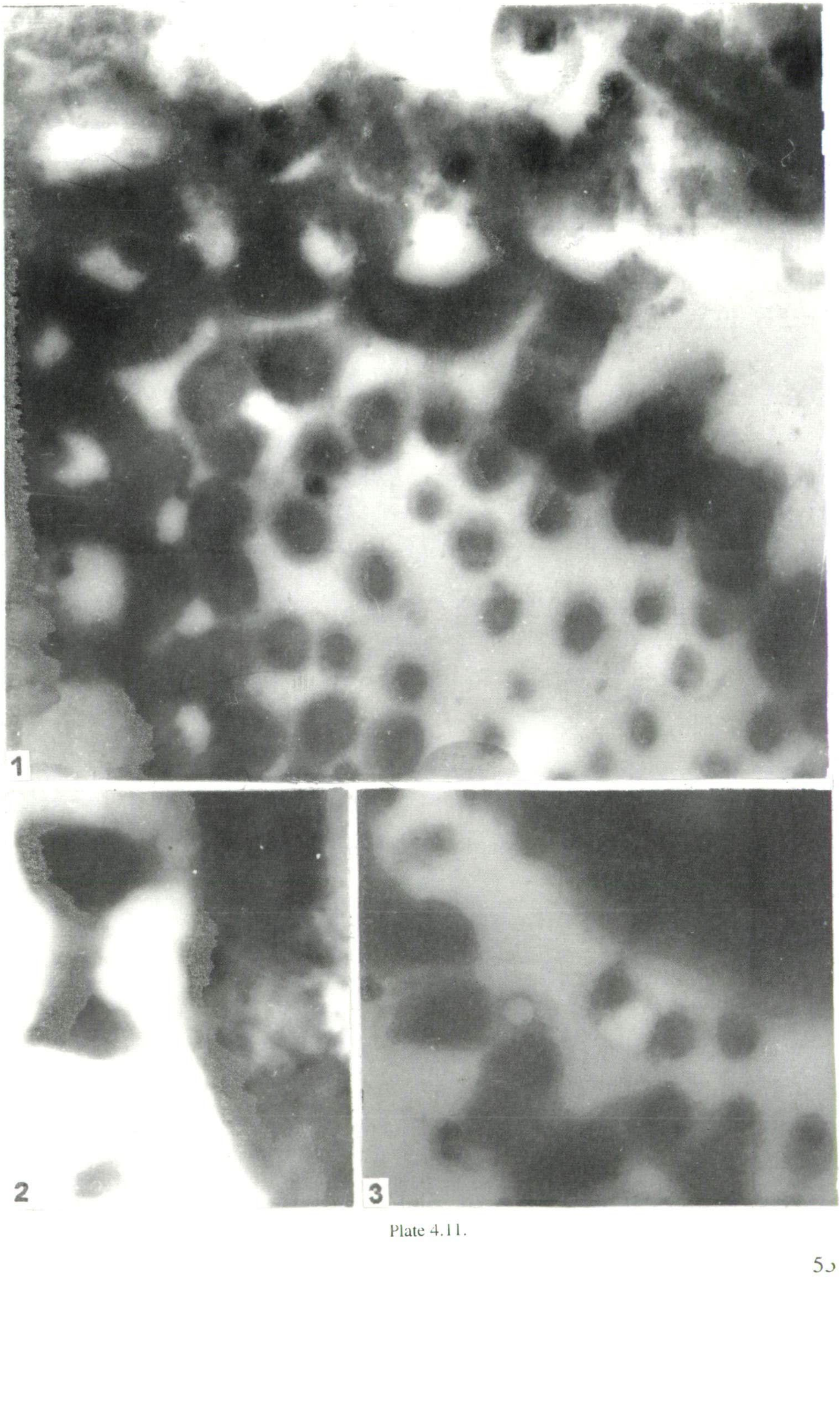

Plate 4.11.

Plate 4.6.

1,2. *Cupuliferoipollenites insleyanus* (TRAVERSE 1955) POTONIÉ 1960, *Fagaceae, Castanea*, block number: 85/63.
1. Negative no: 5615, 15.000x.
2. Negative no: 5619, 200.000x.

Plate 4.7.

1-5. *Cupuliferoipollenites oviformis* (POTONIÉ 1931) POTONIÉ 1960, *Fagaceae, Castanea*,
1. Block number: 85/35, negative no: 5213, 10.000x.
2-5. Block number: 85/55.
2. Negative no: 5487, 100.000x.
3. Negative no: 5487, 100.000x.
4. Negative no: 5477, 10.000x.
5. Negative no: 5486, 20.000x.

Plate 4.8.

1-3. *Cupuliferoipollenites pusillus* (POTONIÉ 1934) POTONIÉ 1960, *Fagaceae* cf. *Castanea*.
1. Block number: 85/31, negative no: 5208, 250.000x.
2. Block number: 85/48, negative no: 9275, 8.000x.
3. Block number: 85/56, negative no: 5488, 100.000x.

Plate 4.9.

1-3. *Retitricolpites thomsonii* KEDVES 1982, in KEDVES et RUSSELL.
1,2. Block number: 85/57.
1. Negative no: 5496, 15.000x.
2. Negative no: 5493, 100.000x.
3. Block number: 85/57, negative no: 5609, 100.000x.

Plate 4.10.

1,2. *Retitricolpites thomsonii* KEDVES 1982, in KEDVES et RUSSELL, block number: 86/3.
1. Negative no: 5686, 10.000x.
2. Negative no: 5692, 50.000x.

Plate 4.11.

1-3. *Retitricolpites thomsonii* KEDVES 1982, in KEDVES et RUSSELL, block number: 85/40.
1. Negative no: 5283, 50.000x.
2. Negative no: 5281, 50.000x.
3. Negative no: 5285, 48.000x.

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part of the foot layer. In this case it is interesting, that it is a hiatus between the foot layer and the above mentioned layer.

Postnormapolles

Platycaryapollenites platycaryoides (ROCHE 1969) KEDVES 1992, *Juglandaceae, Platycarya* (Plate 4.14., figs. 1-3)

The investigated pollen grain is not completely closed in the lamellar embedding material (GLIKSON and TAYLOR 1986). The electron dense granular particles are sometimes on the outer surface of the tectum, or on the inner surface of the foot layer. The infratectal layer is granular, which are well preserved. Sometimes larger molecular structures were observed near the electron dense particles of the embedding material.

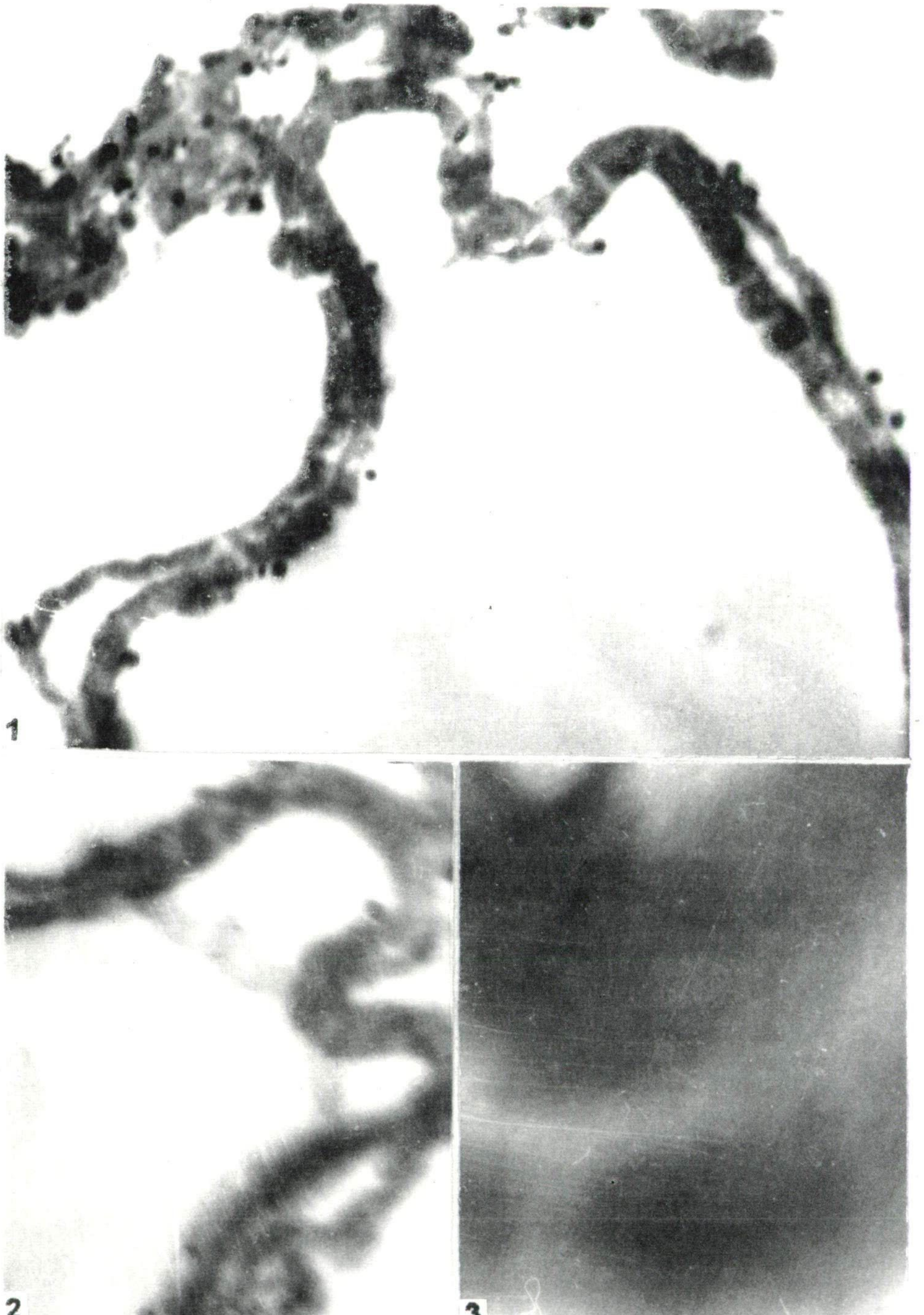

Plate 4.12.

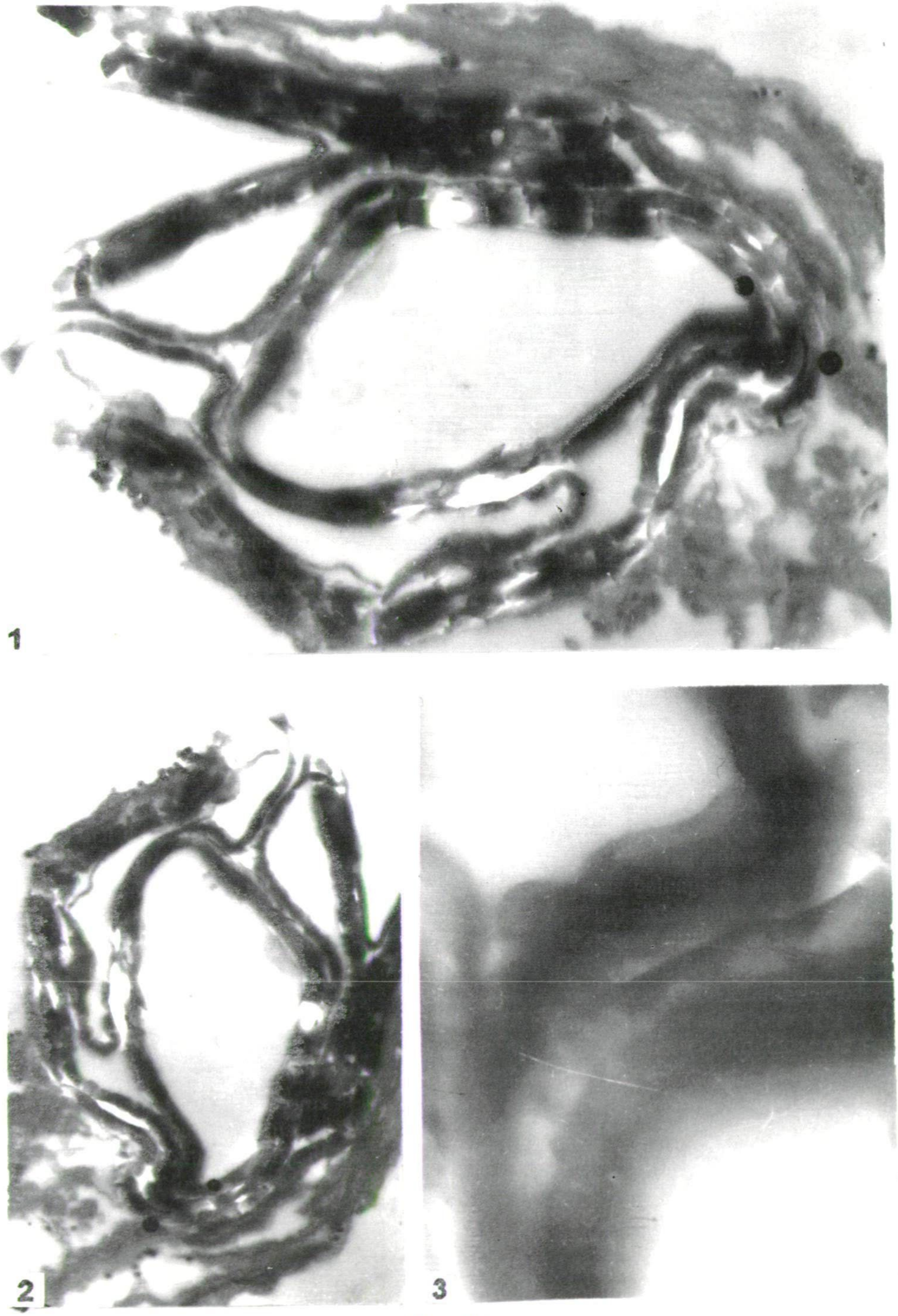

Plate 4.13.

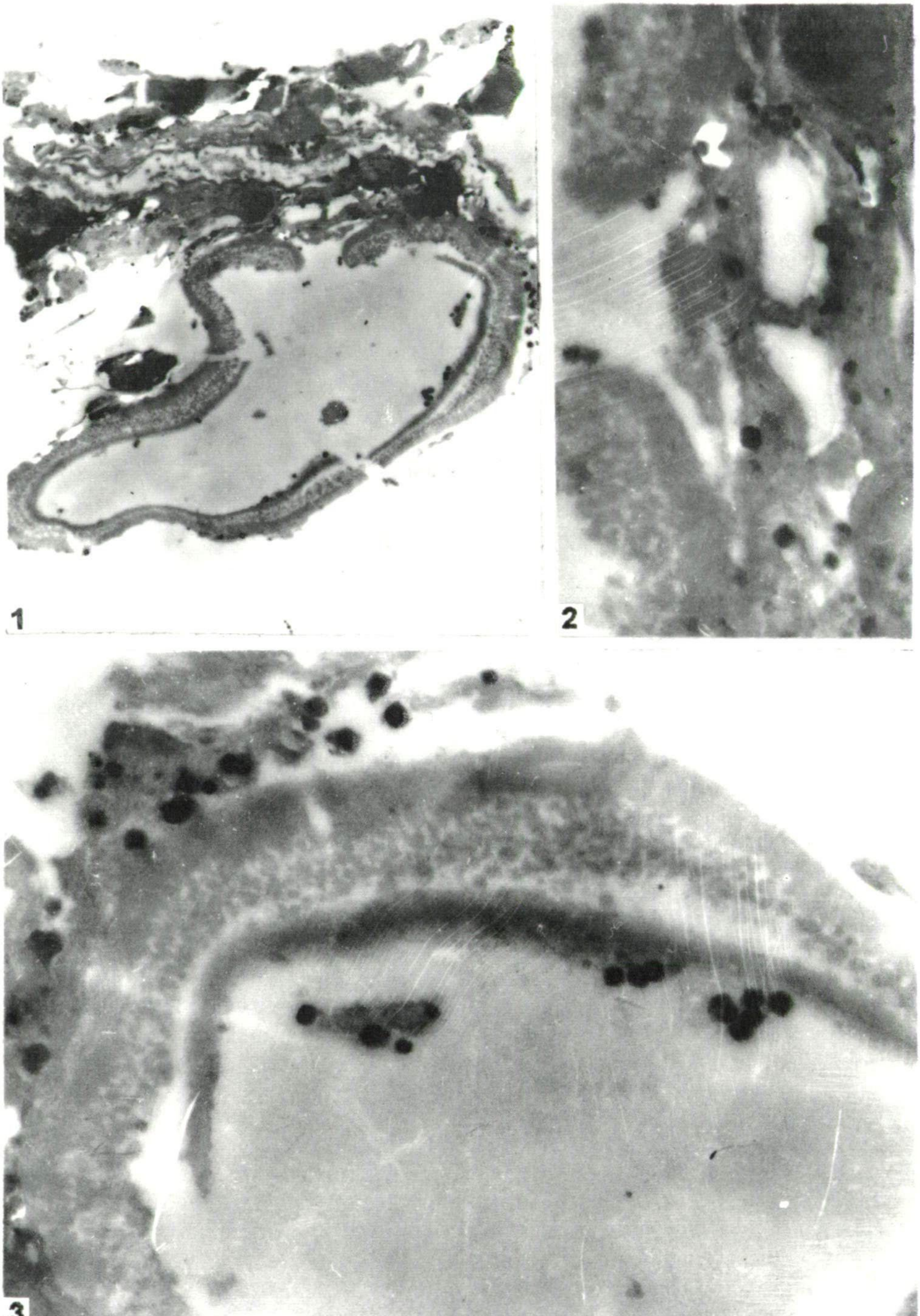

Plate 4.14.

Plate 4.12.

1-3. *Stephanoporopollenites hexaradiatus* (THIERGART 1940) THOMSON et PFLUG 1953 cf. *tribinae* KRUTZSCH 1961, block number: 85/61.
1. Negative no: 5587, 25.000x.
2. Negative no: 5581, 25.000x.
3. Negative no: 5582, 250.000x.

Plate 4.13.

1-3. *Plicapollis pseudoexcelsus* (KRUTZSCH 1958) KRUTZSCH 1961 subfsp. *pseudoexcelsus*, block number: 85/47.
1. Negative no: 5336, 5.000x.
2. Negative no: 5336, 2.500x.
3. Negative no: 5338, 100.000x.

Plate 4.14.

1-3. *Platycaryapollenites platycaryoides* (ROCHE 1969) KEDVES 1992, *Juglandaceae, Platycarya*, block number: 85/65.
1. Negative no: 5643, 5.000x.
2. Negative no: 5646, 25.000x.
3. Negative no: 5645, 25.000x.

Discussion and Conclusions

1. The molecular system of the investigated saccate *gymnosperm* pollen grains is very resistant. After the partial dissolution of the recent saccate *gymnosperm* pollen grains of *Pinus sylvestris* KEDVES, HORVÁTH, BORBOLA and TÓTH (1999) emphasized the same.

2. *Angiosperm* pollen grains

2.1. At the *angiosperm* pollen grains resistant tectum and the foot layer was observed in particular at the *Cupuliferoipollenites* fspp. KEDVES et al (1998) established, that the exine of *Castanea sativa* is resistant to the organic solvents, thinnings of the exine and protrusions in the apertural area were observed only.

2.2. Partial degradation of the *angiosperm* exines.

2.2.1. Degradation of the tectum is relatively rare (cf. *Stephanoporopollenites*).

2.2.2. Alterations in the ultrastructure of the infratectal layer.

Completely destroyed at *C. quisqualis* and *C. liblarensis* and at the two investigated *Normapolles* taxa. Worth mentioning is that the granular infratectal layer of the *myricaceous Plicapollis pseudoexcelsus* destroyed completely, and the also granular infratectal layer of *Platycaryapollenites* is very resistant. To this KEDVES, KÁROSSY and BORBOLA (1997) pointed out as follows, p. 54: "The resistance of the pollen grains of *Platycarya strobilacea* is also interesting."

Partial degradation was observed with larger biopolymer structures at *C. insleyanus* and *Retitricolpites thomsonii*.

Secondary lamellar ultrastructure appeared with molecular structures at the foot layer of *Monocolpopollenites tranquillus*. Larger globular molecular units at *Retitricolpites thomsonii* and at the inner surface of the foot layer of *Platycaryapollenites*.

3. The organic embedding material is also another subject for investigation. Till this time the following types may be established:

3.1. Lamellar structures without electron dense granular particles. This is not very often.

3.2. Lamellar structures with electron dense globular particles. According to GLIKSON and TAYLOR (1986) for the origin to these particles the microbial function may be presumed. To this the investigated *Platycaryapollenites* serve documents. Namely these granules are on the surface of the tectum or on the inner surface of the foot layer. The larger molecular structures were discovered near the electron dense particles.

3.3. Interesting and not so often when the embedding organic material is completely close to the surface of the pollen grains seemingly forming another outer layer of the exine. This may be in connection to the electrostatic charge of the surface of the pollen grain.

Finally, based on these present results it is necessary to continue further, stronger partial degradation experiment on this material.

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