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ULTRASTRUCTURAL INVESTIGATION OF UPPER CRETACEOUS ANGIOSPERM EXINES II.

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Introduction

The first publication of this character concerning Upper Cretaceous fossil angiospermous pollen grains was that of LEFFINGWELL, LARSON and VALENCIA (1970), who carried out an ultrastructural electron microscopic examination (TEM) of the exine of *Wodehouseia spinata* STANLEY 1961, and a scanning electron microscopic examination (SEM) of its surface formations. They found essentially that this pollen, which is extremely distinct as regards its light microscopic morphology, originates from *Angiosperms*.

In an earlier publication we discussed the extragerminal exine ultrastructure of some Upper Cretaceous Normapolles taxa from phylogenetic and functional points of view (HEGEDŰS, KEDVES and PÁRDUTZ, 1971). The present paper sums up the recent results in this field.

Materials and Methods

The investigation material was from the Upper Turonian or Lower Coniacien layer at Carrajao, the Santonian/Campanian layer at Aveiro (Portugal), the Campanian layer at Herend (Hungary) (drilling: No. H—458; 250,0—250,8 m.) and from the Maastrichtian layer at Farafra (Egypt: U. A. R.). For the methods of preparing the samples and ultra-thin sections, see KEDVES and PÁRDUTZ (1970a, b).

Results and discussion

Complexiopollis praeatumescens W. KR. 1959 (Plate I, 1—7).

The investigation material originates from a findspot at Carrajao. For a description of the extragerminal exine, see HEGEDŰS, KEDVES and PÁRDUTZ (1971).

Germinal exine. — The tectum becomes somewhat thinner in the vicinity of the exopori, while the columella layer becomes thicker, at a maximum being twice as thick as the tectum. In the germinal region, the elements of the columellae are of the *Juglandaceae*/*Myricaceae* type, consisting mainly of short, ellipsoidal and more rarely spherical anastomosing ultrastructural elements. The foot layer is separated from the columella layer and is parallel to the tectum. On it is to be found the endogerminalia, which according to light microscopic examination is a transverse colpus. The foot layer is a little thicker than extragerminally. The lamellar ultrastructure of the endexine, which is extremely thin in the extragerminal region, is more expressed, and its elements are strongly multiplied their course being parallel to the foot layer.

On comparison with the drawings of KRUTZSCH (1959), the ultrastructural data exhibit some differences. Layer No. 1 corresponds to the tectum, layer No. 2 to the columella layer. The latter does not consist of straight elements, and is not as thick as appears from the light microscopic data. The light microscopically-established lamella system Nos. 3—7 corresponds in effect to the uniform foot layer that can be demonstrated electron microscopically. Layers Nos. 8—10 are the elements of the endexine. The characteristic curved formations in the germinal duct of the species were created, according to the electron microscopic data, by the multiplication of the lamellar elements of the endexine. Summing up, the exine is formed by an ectexine and a lamellar endexine, the substance of the ectexine being homogenous and triply divided. The tectum and foot layer in the germinal and extra-germinal regions are essentially identical. The columella layer definitely represents two different types. The germinal columella layer indicates the *Myricaceae/Juglandaceae* development direction, in contrast with that of the extragerminal region. Taking into consideration that this pollen grain represents a primitive type even among Brevaxones and the ancient *Angiosperm* pollen grains, the fact that some layers of the germinal and extragerminal exine represent different lines of development must be regarded as a sign of primitiveness.

Atlantopollis reticulatus W. KR. 1967 (Plate II, 1—6).

The investigation material originates from a findspot at Carrajao. For the description of the extragerminal exine, see HEGEDŰS, KEDVES and PÁRDUTZ (1971).

Germinal exine. — The tectum in the vicinity of the exopori becomes only a little thinner, while the columella layer is by and large identical with that in the extragerminal region. The thickness of the foot layer does not change, either, but in the pore-duct it partially breaks up into more or less spherical or ellipsoidal elements. The number of lamellae of the endexine is strongly multiplied; they are arranged densely in a centripetal direction and create a characteristic curved formation.

The light microscopic drawings of KRUTZSCH (1967) (in GÓCZÁN, GROOT, KRUTZSCH and PACLTOVÁ, 1967) are essentially supported by the ultrastructural data. The ectexine is triply divided, with an endexine below it. Only in

Plate I

Complexiopollis praeatumescens W. KR. 1959

1—3. — Light microscopic picture of a sample under ultrastructural examination, in the embedding substance. × 1000.

4. — Detail of the ultrastructure of the germinal exine. × 10 000.

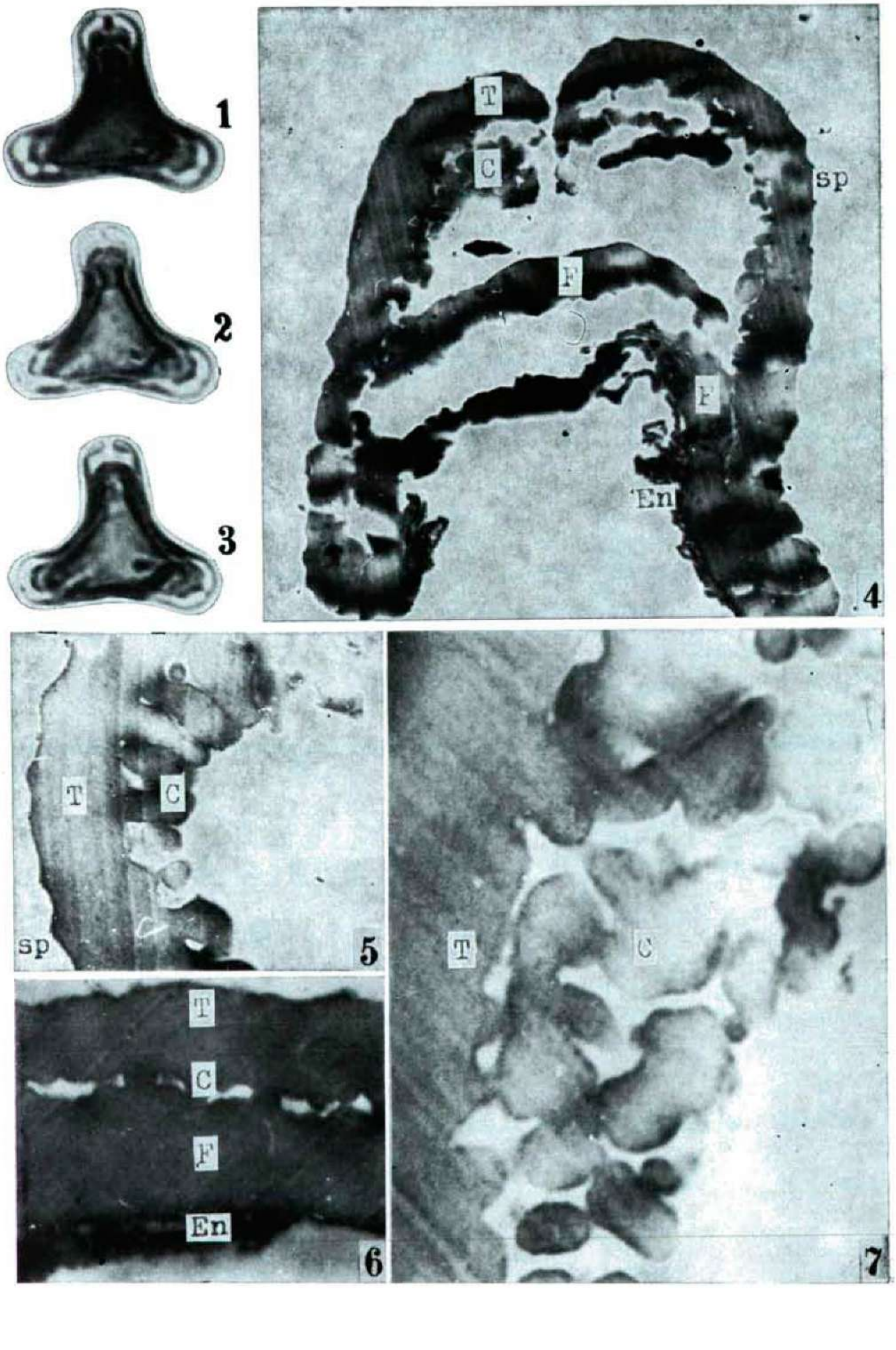
5. — Tectum and columella layer in the pore region. × 25 000.

6. — Detail of the ultrastructure of the extragerminal exine. × 25 000.

7. — Ultrastructure of the columella layer in the vicinity of the exoporus. x50000.

T = tectum, C = columella layer, F = foot layer, En = endexine, sp = spinae.

Plate I



the germinal region is there some difference: in contrast to the light microscopic findings the foot layer does not thicken in the vicinity of the germinaliae, and the endexine does not break in the pore-duct, either; on the contrary, it becomes much thicker due to the multiplication of its elements. In contrast to *Complexiopollis praeatumescens* W. KR. 1959, the ectexines in the germinal and extragerminal regions are much the same. The characteristic breaking up of the foot layer in the ultrastructure of the Upper Cretaceous *Angiosperm* pollen grains, reminiscent of the ultrastructure of the columella layer of *Myricaceae/Juglandaceae,* is interesting and so far unique.

From a taxonomical point of view the following must be mentioned:

a) The light microscopically found differentiating marks, that the form-genera *Complexiopollis* W. KR. 1959 and *Atlantopollis* W. KR. 1967 could be well distinguished by the absence or presence of the columella layer, can no longer be upheld. The perforated tectum in the form-genus *Atlantopollis* W. KR. 1967 and the concomitant characteristic sculpture are the only distinguishing features light microscopically.

b) Apart from the light microscopic differences on the basis of electron microscopic data, we may mention the germinal and extragerminal differences observed in the columella layer of *Complexiopollis praetumescens* W. KR. 1959; these could not be observed in *Atlantopollis reticulatus* W. KR. 1967.

c) Due to the essential differences between the light microscopic diagnosis of *Complexiopollis praeatumescens* W. KR. 1959 and the electron microscopic results, it is necessary to establish the TEM diagnoses of the form-genus and species.

Fgen.: *Complexiopollis* W. KR. 1959.

TEM diagnosis:

The exine consists of ectexine and endexine. The ectexine is tectate inperforate, and divided into tectum, columellae and foot layer. In the germinal region, the foot layer separates from the columella layer, on which is the endogerminal opening. The elements of the endexine multiply in the pore region.

Complexiopollis praeatumescens W. KR. 1959.

TEM diagnosis:

The tectum is decorated with small spinae, the columella layer of the extragerminal exine is narrow, and the endexine has a lamellar ultrastructure. Close to the germinal aperture, in the part after the separation of the columella layer from the foot layer, it has an ultrastructure differing from the extragerminal exine, its elements increase, are ellipsoidal, sometimes spherical, and often anastomose. The foot layer is parallel to the tectum, and the endogerminalia is a transverse colpus. The elements of the endexine too multiply, and are parallel to the foot layer.

Plate II

Atlantopollis reticulatus W. KR. 1967

1, 2. — Light microscopic picture of a sample under ultrastructural examination in the embedding substance. × 1000.

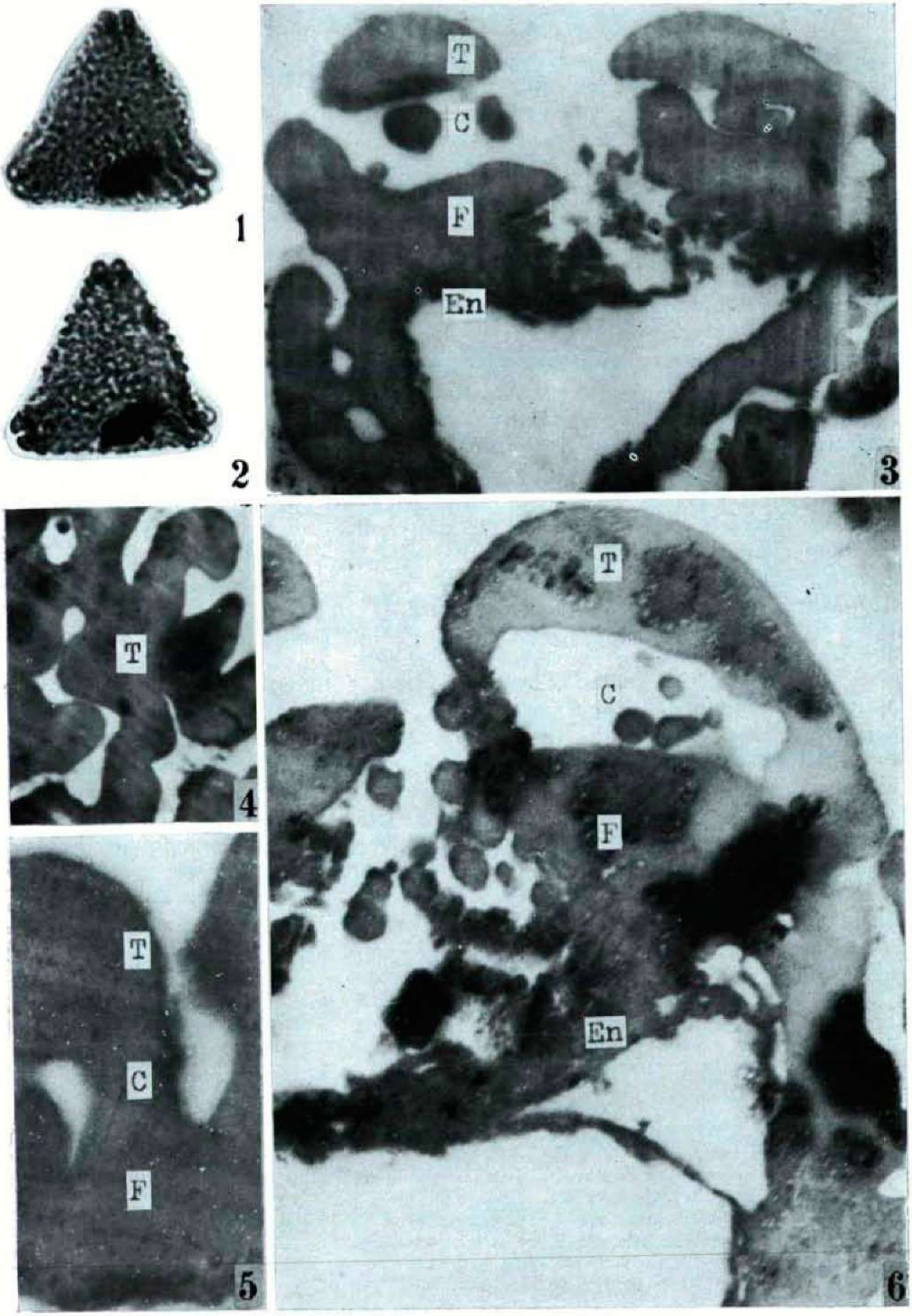
3. — Ultrastructure of the germinal exine. × 10 000.

4. — Tangential section from the tectum. × 10 000.

5. — Detail of the utrastructure of the extragerminal exine. × 25 000.

T = tectum, C = columella layer, F = foot layer, En = endexine.

Plate II



Trudopollis mechanicus PF. 1953 (Plate III, 1—5).

The investigation material originates from a findspot at Herend.

Extragerminal exine. — Tectate inperforate. On the surface of the tectum there are smaller and larger protrusions and recesses, and it is decorated with small spinae. The columella layer consists mostly of uniseriate, at times biseriate elements, of varied shape: spherical, ellipsoidal or irregularly elongated. The thickness of the foot layer is much the same as that of the tectum, T/C/F = = 2 · 5 — 3/1/2 · 5 — 3. Its endexine could not be observed.

Germinal exine. — The tectum gradually becomes thinner in the direction of exopori; its structure is identical with that of the extragerminal region. The elements of the columella layer are extremely multiplied and form an annulus, In contrast with the extragerminal exine, the elements of the columella layer are somewhat larger and anastomose. The thickness of the foot layer does not change; it bends back towards the centre, producing a formation characteristic of the form-genus.

This ultrastructure, particularly that of the tectum and columella layer, indicates a relationship to *Amentiflorae*. A certain degres of similarity may also be found to *Nudopollis terminalis* (PF. et TH. 1953) PF. 1953 (KEDVES and PÁRDUTZ, 1970b), known from Lower Eocene deposits. The possible connection between the origins of the two pollen form-genera is supported by the light microscopic morphology.

Interporopollenites endotriangulus n. fsp.
(Plate IV, 1—3, Plate VII, 1—3, Fig. 1.)

The investigation material originates from a findspot at Aveiro. 80 examplars were examined by light microscope. The contour is triangular with rounded corners and convex sides. Both surfaces of the pollen grains have essentially the same morphology, with pores of a diameter smaller than 1 μ, in the vicinity of the corners by and large opposite one another. The external wall around the pores projects only a little. In optical section, the internal contour is approximately triangular. The innermost layer thickens strongly in the pore region. The external pores open into the internal cavity and then, through the radial duct, into the central cavity. The two external layers can be well distinguished light microscopically, but their finer structures can not.

The maximum size is 20—28 μ.

Electron microscope results:

Extragerminal exine. — Tectate, perforate. There are small spinae on the surface of the tectum, and the perforations are straight, narrow ducts. The

Plate III

Trudopollis mechanicus PF. 1953

1, 2. — Light microscopic picture of a sample under ultrastructural examination, in the embedding substance. × 1000.

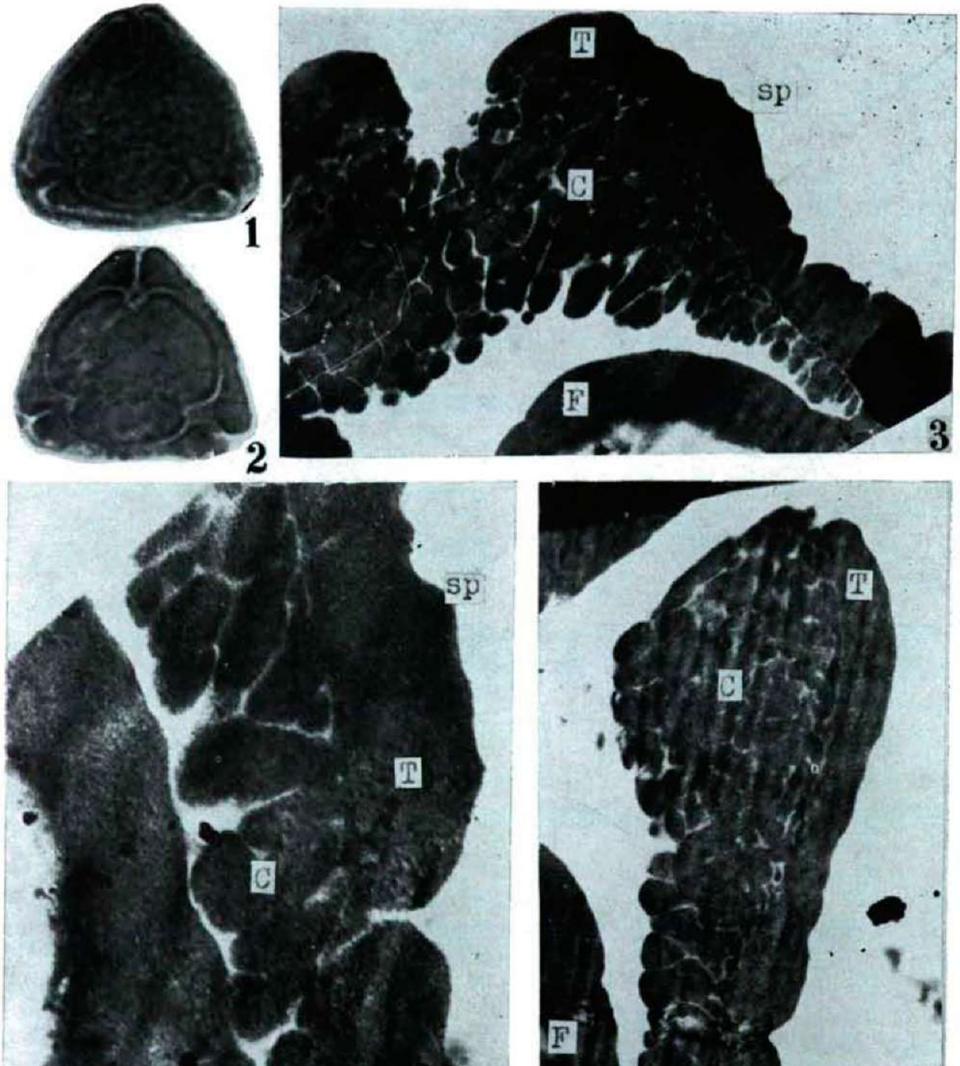
3. — Detail of the ultrastructure of the germinal exine. × 10 000.

4. — Detail of the ultrastructure of the extragerminal exine. × 25 000.

5. — Ultrastructure of the germinal exine in the pore region. × 10 000.

T = tectum, C = columella layer, F = foot layer.

Plate III



columella layer consists of small anastomosing elements of spherical or ellipsoidal form, arranged generally in three lines. The foot layer is extremely thick, and there is no endexine. $T/C/F = 1/1{,}5/5—6$.

Germinal exine. — Above the pores the tectum is unchanged. The columella layer, however, becomes thicker as a result of the multiplication of its

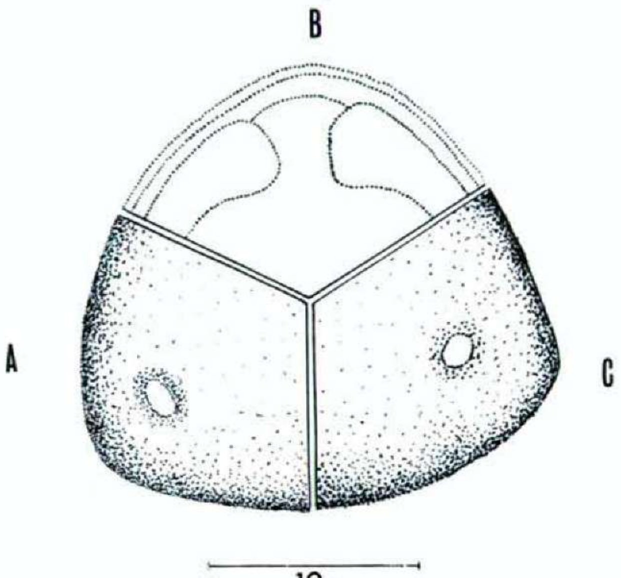


Fig. 1. *Interporopollenites endotriangulus* n. fsp., A and C are shematic drawings of the surfaces, B is the optical section.

elements; it is two-three times thicker than extragerminally. The foot layer, too, becomes very thick in the pore region. At the maximum, it is by and large twice as thick as in the exine part between the corners. Running from the surface towards the centre, the duct expands in the interior of the pollen grain, uniting with the inner lumen. The foot layer splits into elements arranged in a slightly radial direction at the junction of the duct and inner lumen.

Diagnosis:

The external contour is triangular, with rounded corners and convex sides. The surfaces of both sides of the pollen grains are identical, with pores always

Plate IV

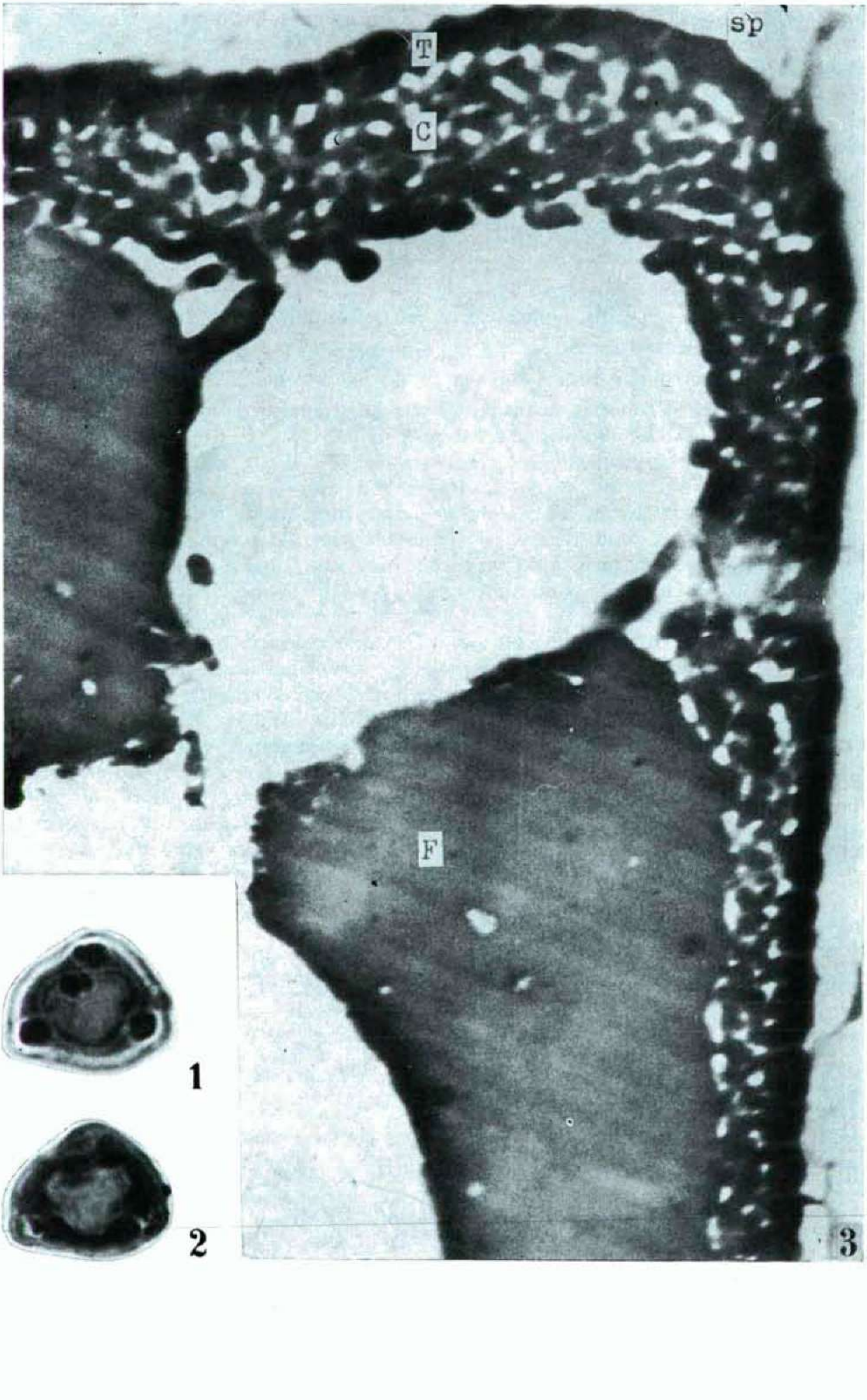
Interporopollenites endotriangulus n. fsp.

1, 2. — Light microscopic picture of a sample under ultrastructural examination, in the embedding substance. × 1000.

3. — Ultrastructure of the germinal region. × 25 000.

T = tectum, C = columella layer, F = foot layer, sp = spinae.

Plate IV



1

2

3

of diameter smaller than 1 μ in the vicinity of the corners. The external wall projects only a little around the pores. The inner contour is a triangle with rounded vertices, at times approximately spherical is shape. The extragerminal exine is about 3 μ thick, tectate, perforate, with small spinae on the tectum; the perforations are narrow ducts. The columella layer consists of anastomosing elements of spherical or ellipsoidal form, lying in three lines. The foot layer is extremely thick, and there is no endexine. T/C/F = 1/1,5/5—6. At the corners the columella layer becomes thicker due to the multiplication of its elements. It is two-three times thicker than extragerminally. The foot layer grows thicker to a similar extent and contains a wide duct of radial direction.

Maximum size: 20—28 μ.

Holotype. Plate VII, 1—3, prep. Aveiro—23, cross-table number 8,3/106,9.

Locus typicus: Aveiro, Upper Cretaceous; Santonien/Campanien.

Stratum typicum: Coaly clay.

Derivatio nominis: From the shape of the internal contour of the pollen.

Differential diagnosis: It can be well distinguished from the *Interporopoll. elector* PF. 1953 by means of its thicker wall.

The first description of the form-genus (WEYLAND and KRIEGER, 1953) was checked by GÓCZÁN, GROOT, KRUTZSCH and PACLTOVÁ (1967), and a new diagnosis was given. The electron microscopic data agree with the light microscopic findings with regard to the outer layers (tectum, columella layer). Two important differences are, that the foot layer near the pores does not split into further lamellae, and that there is no endexine, in contrast with the light microscopic results.

With regard to its morphology, it is an extremely distinct pollen type. From a stratigraphic point of view it is a very significant form-genus, particularly with respect to the Upper Cretaceous. Morphologically some connection can be established with the form-genus *Interpollis* W. KR. 1961. The ultrastructural results so far achieved on the latter form-genus cannot be regarded as satisfactory (KEDVES and PÁRDUTZ, 1970b); the characteristic triple division of the ectexines has not yet been established. From the point of view of the evolutionary history of pollens it is highly problematical, probably representing a lateral branch of the *Angiosperms*, as it cannot be related with modern pollen types. The subtriporat pollen grains should perhaps be taken into consideration. Such a connection would be supported by the columella layer reminiscent of *Juglandaceae;* because of its very different light microscopic basic morphology, however, this is not probable. It may perhaps be assumed that the pollen grains of the primitive collateral *Angiosperms* which are similar to the recent *Juglandaceae* belong in this form-genus.

Plate V

Vacuopollis orthopyramis PF. 1953

1, 2. — Light microscopic picture of a sample under ultrastructural examination, in the embedding substance. × 1000.

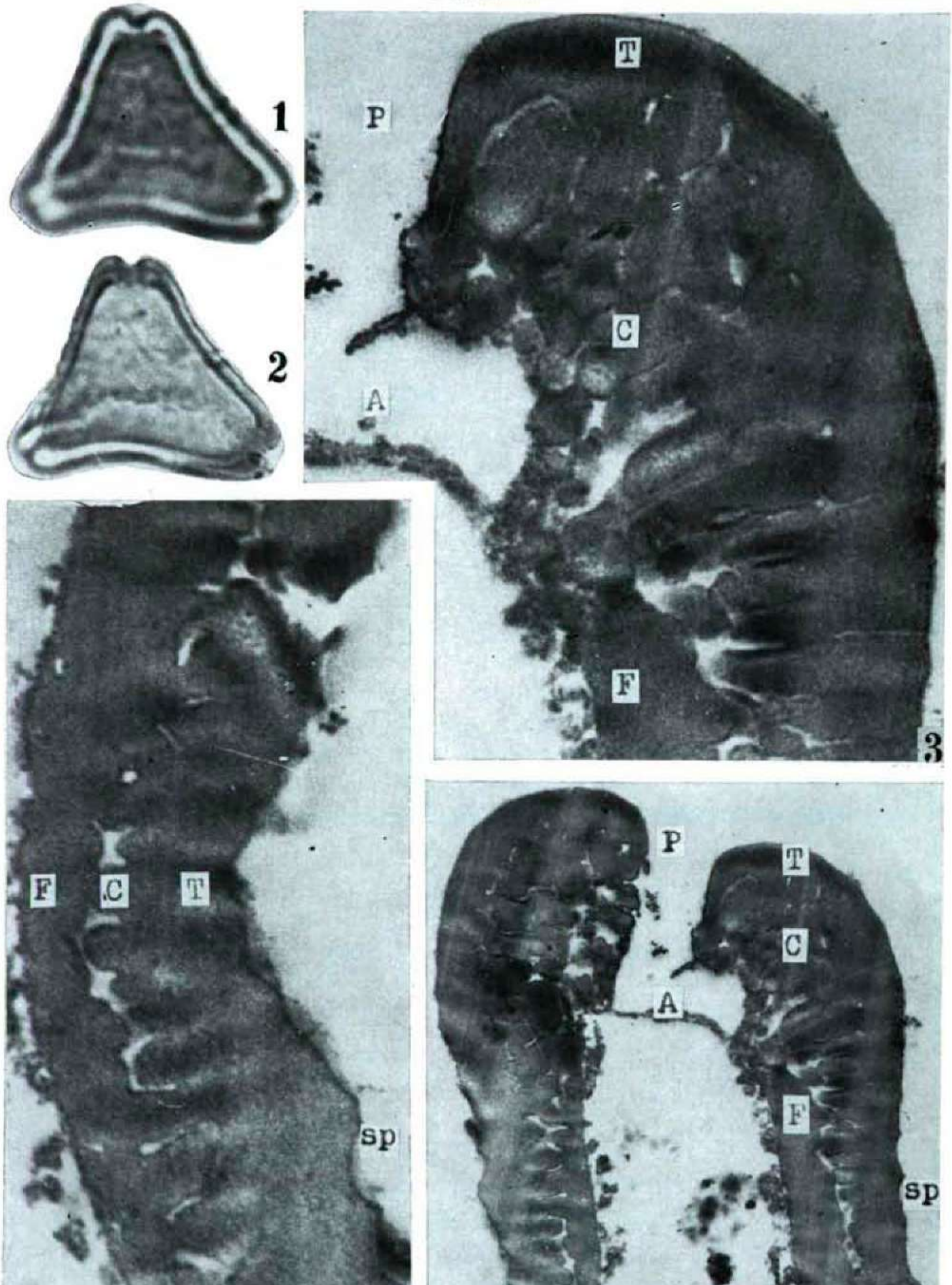
3. — Detail of the ultrastructure of the germinal exine. × 25 000.

4. — Detail of the ultrastructure of the extragerminal exine. × 25 000.

5. — A comprehensive picture of the utrastructure of the germinal region. × 10 000.

T = tectum, C = columella layer, F = foot layer, P = pore, A = atrium, sp = spinae.

Plate V



Vacuopollis orthopyramis PF. 1953 (Plate V, 1—5).

The investigation material originates from a findspot at Aveiro.

Extragerminal exine. — Tectate, perforate. The surface of the tectum is uneven, with occasional spinae. The columella layer is not sharply distinct from the tectum. The elements of the columella layer are in many cases followed by segments in the tectum and the ducts run along these. The foot layer in the vicinity of the columella layer has an uneven surface but is comparatively well distict; a transition similar to that towards the tectum is not found. T/C/F = 2/1/15. There is no endexine.

Germinal exine. — The tectum in the germinal region is strongly segmented, and in the direction of exopori it becomes very thin. The columella layer is strongly thickened, forming an annulus; in the direction of the germinal duct its elements split, partly into elements of spherical or ellipsoidal form. The foot layer ends at the height of the thickening of the columella layer and forms an atrium.

As regards its type, *Vacuopollis* PF. 1953 is of a transitional character towards *Triatriopollenites* PF. 1953. No ultrastructural data are available on the latter form-genus, but the similar *Plicapollis pseudoexcelsus* (W. KR. 1958) W. KR. 1961 resembles, with the exception of its columella layer, the investigated species of the form-genus *Vacuopollis* PF. 1953 in ultrastructure.

Arecipites barakati n. fsp. (Plate VI, 1—5, Plate VII, 4, 5).

Diagnosis:

Moncolpate pollen grains of ellipsoidal form. The colpi do not reach the apices of the pollen grain. The ectexine is tectate, perforate, and the tectum perforations are of varied shape, their diameters being 0,3—1,5 μ. The surface of the tectum is wavy. The columella layer consists mostly of columnar elements of variable thickness, and not always straight. The foot layer is sporadically perforated.

Maximum size: 26—45 μ.

Holotype: Plate VII, 4,5; prep. Farafra—6—2, S.—2, cross-table number 14,5/113.

Locus typicus: Farafra, upper level of the Nubian formation, Upper Cretaceous, Maastrichtian.

Stratum typicum: Foliated brown coal.

Derivatio nominis: In honour of Dr. M. G. BARAKAT (Institute of Geology, Cairo University), who made the samples available to us.

Differential diagnosis: It is distinguished from *Arecipites convexus* (THIERG. 1937) W. KR. 1970 by its shorter colpi.

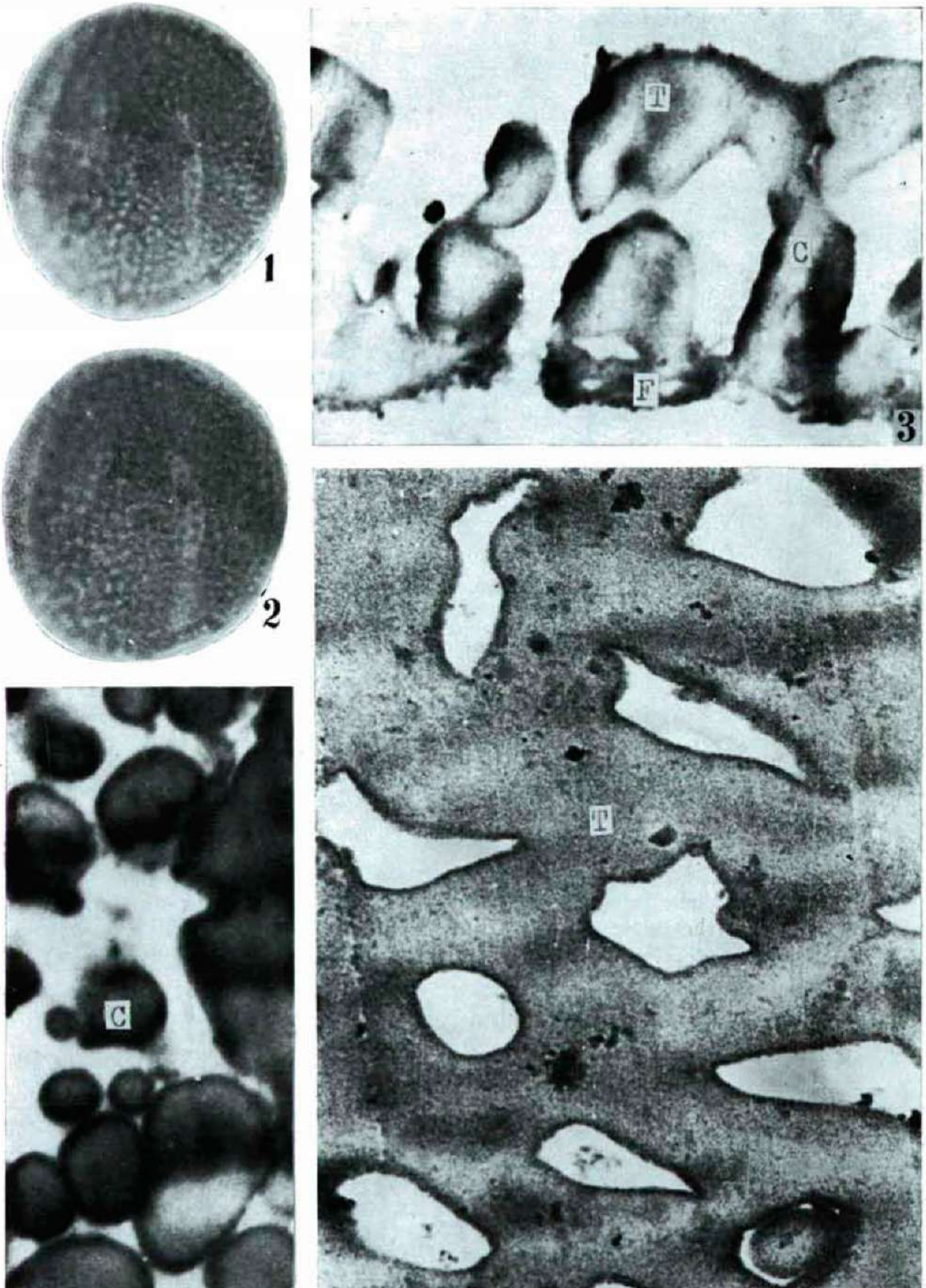
Plate VI

Arecipites barakati n. fsp.

1, 2. — Light microscopic picture of a cample under ultrastructural examination, in the embedding substance. × 1000.
3. — Detail of the ultrastructure of the extragerminal exine. × 25 000.
4. — Tangential section of the columella layer. × 25 000.
5. — Tangential section of the tectum. × 25 000.

T = tectum, C = columella layer, F = foot layer.

Plate VI

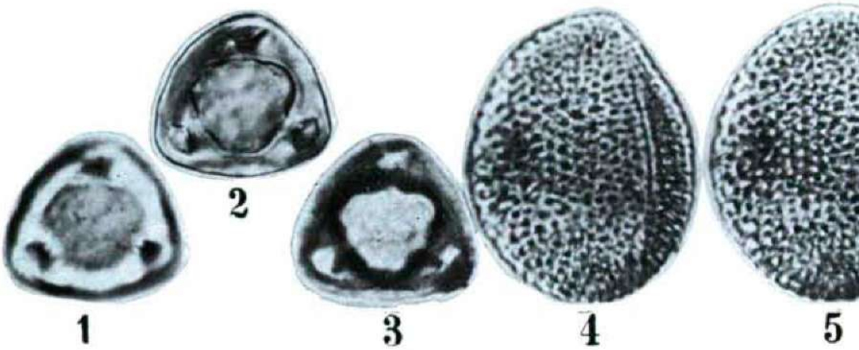


Botanical connection: *Palmae*.

Occurrence: Apart from the locus typicus, in the deposits at Abu Minquar of a similar age.

Note: It is frequent pollen grain, 100 samples were examined. It can be observed in our material with very varied forms, depending upon the state of preservation.

Plate VII



1—3. — Interporopollenites endotriangulus n. fsp., prep. Aveiro—23, cross-table number 8,3/106,9.
4, 5. — Arecipites barakati n. fsp., Palmae, prep. Farafra 6—2, S.—2, cross-table number 14,5/113.
N : × 1000.

Summary

1. The ultrastructures of the germinal exines of *Complexiopollis praeatumescens* W. Kr. 1959 and *Atlantopollis reticulatus* W. Kr. 1967 were described. There were essential differences between the light and electron microscopic data, particularly in the case of *Complexiopollis*, and it became necessary, therefore, to emend the form-genus, or form-species.

2. The ultrastructure of *Trudopollis mechanicus* Pf. 1953 points to extinct *Amentiflorae*. On the basis of results on the exine of *Vacuopollis orthopyramis* Pf. 1953, it is tectate.

3. In the cases of *Interporopollenites endotriangulus* n. fsp. and *Arecipites barakati* n. fsp., the results of the ultrastructure were used in the diagnoses.

References

Góczán, F., Groot, J. J., Krutzsch, W.—Pacltová, B. (1967): Die Gattungen des „Stemma *Normapolles* Pflug 1953b" *(Angiospermae)* Neubeschreibung und Revision europäischer Formen (Oberkreide bis Eozän). — Paläont. Abh. B, 2, 427—633.

Hegedűs, M., Kedves, M.—Párdutz, Á. (1971): Ultrastructural investigation on fossil *Angiosperms* exines of Upper Cretaceous. — Advancing Frontiers of Plant Sciences 28, 317—325.

Kedves, M.—Párdutz, Á. (1970a): Az ultrastruktura vizsgálatok jelentősége fosszilis *Angiospermatophyta* pollenszemek fejlődéstörténeti kérdéseinek megoldásában. — Bot. Közl. 57, 57—58.

KEDVES, M.—PÁRDUTZ, Á. (1970b): Études palynologiques des couches du Tertiaire inférieur de la Région Parisienne. VI. Ultrastructure de quelques pollens des *Angiospermes* de l'Eocène inférieur (Sparnacien). — Pollen et Spores *12*, 553—575.

KRUTZSCH, W. (1958): Sporen- und Pollengruppen aus der Oberkreide und dem Tertiär Mitteleuropas und ihre stratigraphische Verteilung. — Z. angew. Geol. *3*, 509—548.

KRUTZSCH, W. (1959): Einige neue Formgattungen und -arten von Sporen und Pollen aus der mittel-europäischer Oberkreide und dem Tertiär. — Palaeontographica B, *105*, 125—157.

KRUTZSCH, W. (1970): Atlas der mittel- und jungtertiären dispersen Sporen- und Pollen-sowie der Mikroplanktonformen des nördlichen Mitteleuropas VII Monoporate, monocolpate, longicolpate, dicolpate und ephedroide (polyplicate) Pollenformen. — Jena.

LEFFINGWELL, H. A., LARSON, D. A.—VALENCIA, M. J. (1970): A study of the fossil pollen *Wodehouseia spinata* I. Ultrastructure and comparison to selected modern taxa. Optical microscopic recognition of foot layers in differentially stained fossil pollen and their significance. — Bull. of Canadian Petroleum Geology *18*, 238—262.

PFLUG, H. D. (1953): Zur Entstehung und Entwicklung des angiospermiden Pollens in der Erdgeschichte. — Palaeontographica B, 95, 60—171.

STANLEY, E. A. (1961): A new Sporomorph Genus from Northwestern South Dakota. — Pollen et Spores *3*, 155—162.

THOMSON, P. W.—PFLUG, H. D. (1953): Pollen und Sporen des mitteleuropäischen Tertiärs. — Palaeontographica B, *94*, 1—138.

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