Acta Biologica Szeged. 19 (1—4), pp. 19—32 (1973)

ULTRASTRUCTURAL STUDIES ON AMENTIFLORAE POLLEN GRAINS I

M. KEDVES and Á. PÁRDUTZ

Department of Botany, Attila József University;
Electron Microscope Laboratory, Institute of Biophysics, Biological Research Center
Hungarian Academy of Sciences, Szeged

(Received May 29, 1972)

Introduction

In our ultrastructural studies on Lower Eocene *Normapolles* exines it was found that these are derived from primitive *Amentiflorae* taxons (KEDVES and PÁRDUTZ, 1970a,b). In the *Normapolles* taxons the occurrence of the endexine as a function of the geological period is of evolutionary importance (KEDVES, HEGEDŰS and PÁRDUTZ, 1971a, HEGEDŰS, KEDVES and PÁRDUTZ, 1971; 1972). Our ultrastructural examinations have permitted the elucidation of frequently complex pore-wall exines of fossil pollen grains.

In spite of the fact that numerous literature data are known on the ultrastructures of the recent Amentiflorae taxons (AFZELIUS, 1956 – in ERDTMANN, 1956; UENO, 1963a,b; TAKEOKA and STIX, 1963; STONE, REICH and WHITFIELD, 1964, STONE and BROOME, 1971), we considered it necessary to carry out studies in accordance with the following points of view:

1. The description of the exine ultrastructure in those taxons where our knowledge is incomplete.

2. The exact study of the endexine in the species under examination.

3. Interpretation of the concepts of pore, atrium and vestibulum used in the description of fossil taxons in the pore-wall region, on the basis of the ultrastructural data in the recent taxons.

4. Establishment of the ultrastructural nature of special exine formations.

Materials and Methods

The species examined were the following: *Corylus avellana* L., *C. colurna* L., *C. sieboldiana* BLUME, *Cannabis sativa* L., *Carya amara* NUTT., *C. ovata* (MILL.) C. KOCH, *Juglans californica* WATSON, *Myrica gale* L., *Betula alba* L., *B. pubescens* EHRH., *Alnus glutinosa* (L.) GAERTN. The examination material originates from the Botanical Collection of the Natural Science Museum, and we should like to take this opportunity to express our grateful thanks to the Director, JULIA LACZA-SZUJKÓ.

Taking into account the work of STONE and BROOME (1971), our ultra-thin sections were prepared from acetolyzed pollen grains. With more complex light-microscopic morphology serial sections were used in the pore-wall region, as introduced on the Casuarina genus exine, where this was necessary (KEDVES, HEGEDŰS and PÁRDUTZ, 1971b). The results are described genus-wise.

Results

Corylus L. (Fig. 2/1–4)

Interpore-wall exine. – Tectate, perforated with narrow channels, spinae on the surface. The elements of the columellae are varied, mainly ellipsoid and columnar. An endexine can not be distinguished below the foot layer. T/C/F= 3–4/1.5–2/1. (Fig. 2/1)

Pore-wall exine. – The tectum is unchanged in the pore-wall region. The elements of the columellae are accumulated, and small, mainly spherical formations appear below the tectum. The lamellar endexine is marked in the pore-wall region (Fig. 2/2–4). Thus, the annulus is a formation of the columellae and the endexine in this genus. The tectum bends inwards along the pore and combines or almost combines with the foot layer (Fig. 2/4).

Cannabis L. (Fig. 4/1–4).

Interpore-wall exine. – Tectate non-perforate, large spinae on the surface of the tectum. The elements of the columellae are mainly columnar. An endexine can not be discerned below the foot layer. T/C/F=3–4/2/1. (Fig. 4/4).

Pore-wall exine. – The tectum is unchanged in the pore-wall region. The elements of the columellae are strongly increased, mainly by small, spherical elements (Fig. 4/1). The annulus is formed in this way (Fig. 3; 4/2, 3). The foot layer becomes extremely thin at the annulus, and almost breaks, and under it appears endexine with a granular ultrastructure. The tectum bends inwards along the pore, and combines with the tapered foot layer (Fig. 4/2, 3).

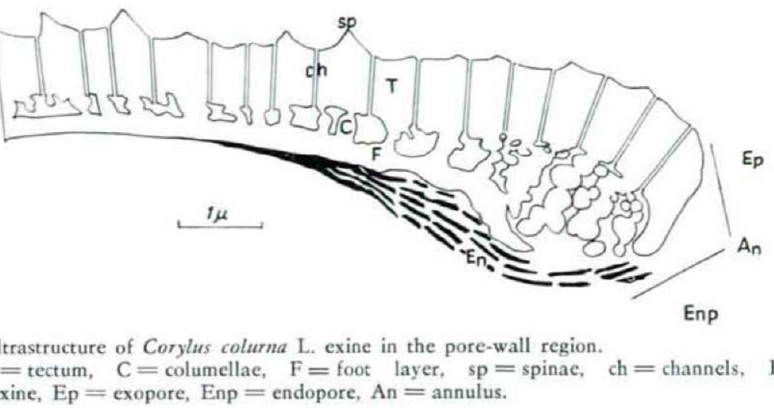

Fig. 1. Ultrastructure of *Corylus colurna* L. exine in the pore-wall region.
T = tectum, C = columellae, F = foot layer, sp = spinae, ch = channels, En = endexine, Ep = exopore, Enp = endopore, An = annulus.

Carya NUTT. (Fig. 6/1–4)

Note. – The pore-wall openings are situated sub-equatorially, and the exine becomes thin at the poles. Interpore-wall exine. – Tectate, perforated with narrow channels, the tectum with spinae. The elements of the columellae are spherical or ellipsoid, and frequently anastomize. Along the poles, where

Fig. 2. *Corylus colurna* L.

1. — Ultrastructure of the interpore-wall exine. M : 25,000x.

2—4. — Ultrastructure of the pore-wall exine in serial section. M : 25,000x.

T = tectum, C = columellae, F = foot layer, sp = spinae, ch = channels, En = endexine, An = annulus, P = pore.

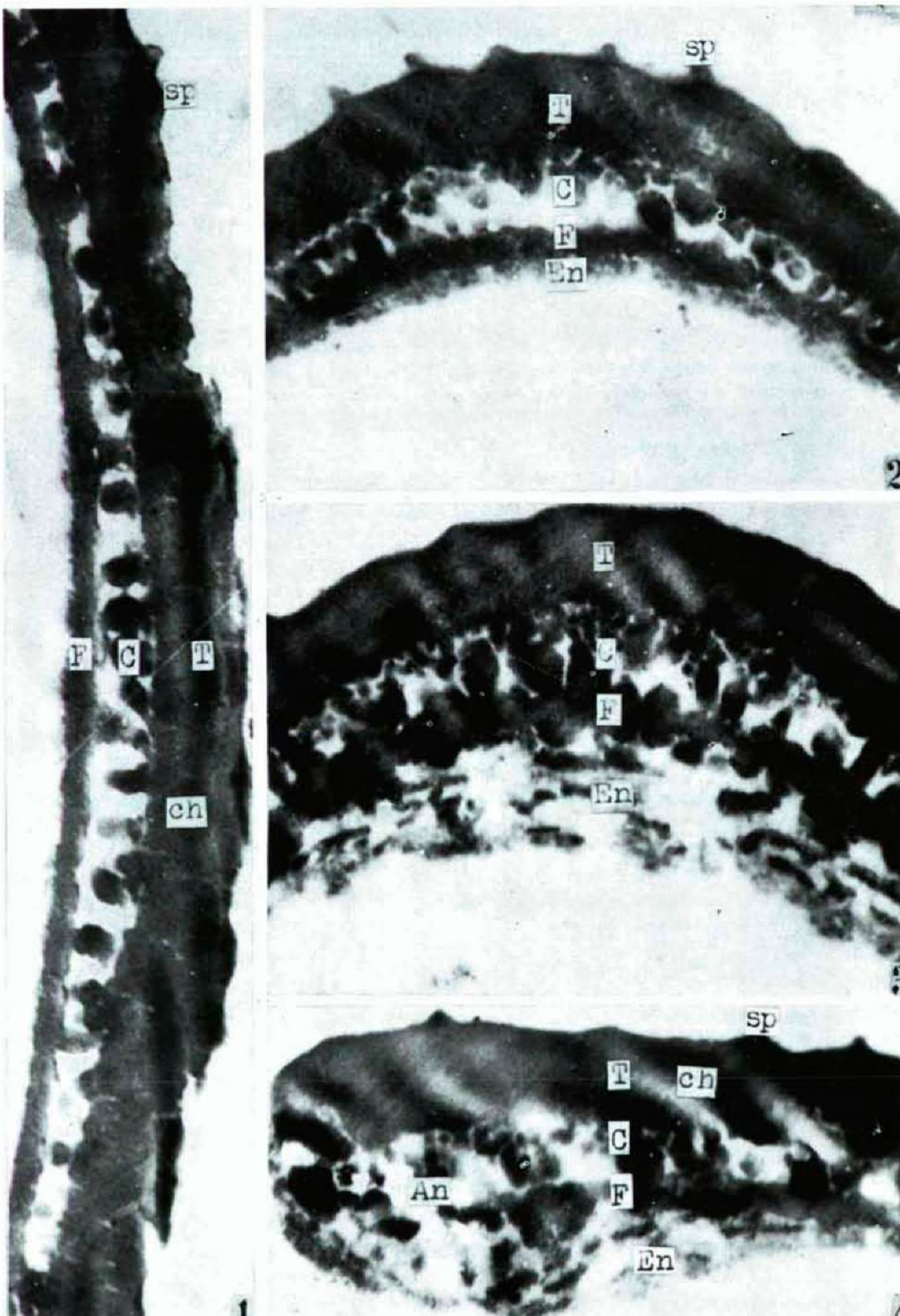

Fig. 2

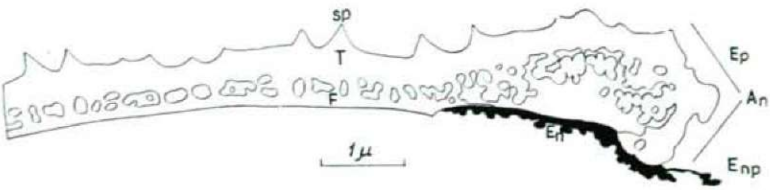

Fig. 3. Ultrastructure of *Cannabis sativa* L. exine in the pore-wall region.
T = tectum, C = columellae, F = foot layer, sp = spinae, En = endexine, Ep = exopore, Enp = endopore, An = annulus.

Fig. 4. *Cannabis sativa* L.

1. — Ultrastructure of the pore-wall exine in the vicinity of the pore-wall region. M : 25,000x.
2. — Ultrastructure of the pore-wall exine in the pore-wall region. M : 50,000x.
3. — Ultrastructure of the pore-wall region in the pore-wall region. M : 25,000x.
4. — Ultrastructure of the interpore-wall exine. M : 25,000x.

T = tectum, C = columellae, F = foot layer, sp = spinae, En = endexine, An = annulus, P = pore.

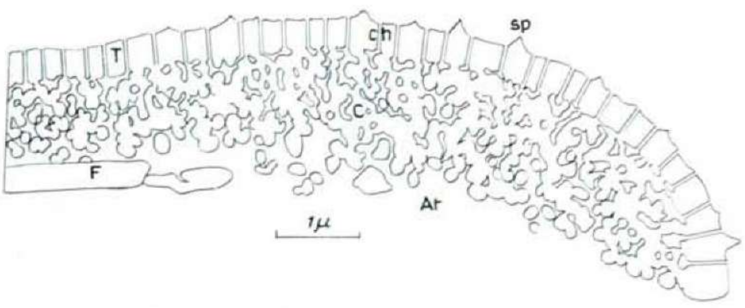

Fig. 5. Ultrastructure of *Carya amara* NUTT. exine in the pore-wall region.
T = tectum, C = columellae, F = foot layer, sp = spinae, ch = channels, At = atrium.

the exine becomes thin, the tectum and the foot layer are unchanged, and the elements of the columellae are generally in two rows – T/C/F=1.5/1/1 – but in the vicinity of the equator they are generally observed in eight rows – T/C/F=1.5/4/1 (Fig. 6/1, 4).

Pore-wall exine. – The tectum bends inwards along the pores, its thickness unchanged, and the columellae too become narrow only along the pores. There is no annulus, the foot layer is broken in the pore-wall region, and hence there is in essence an atrium (Fig. 5; 6/2, 3).

Juglans L. (Fig. 8/1–3)

Interpore-wall exine. – Tectate, perforated with narrow channels, relatively large spinae on the tectum. The elements of the columellae are spherical or ellipsoid, and are arranged in four rows on the tapering polar part of the exine, and generally in six rows in the vicinity of the equator. T/C/F=1.5–2/1.5/1 or 1.5–2/2–2.5/1. There is no endexine below the foot layer.

Pore-wall exine. – The tectum agrees with that of the Carya genus in the pore-wall region. The elements of the columellae are accumulated, however, in 10–14 rows, and form an annulus. The foot layer is broken in the pore-wall region, and an atrium is formed (Fig. 7; 8/1).

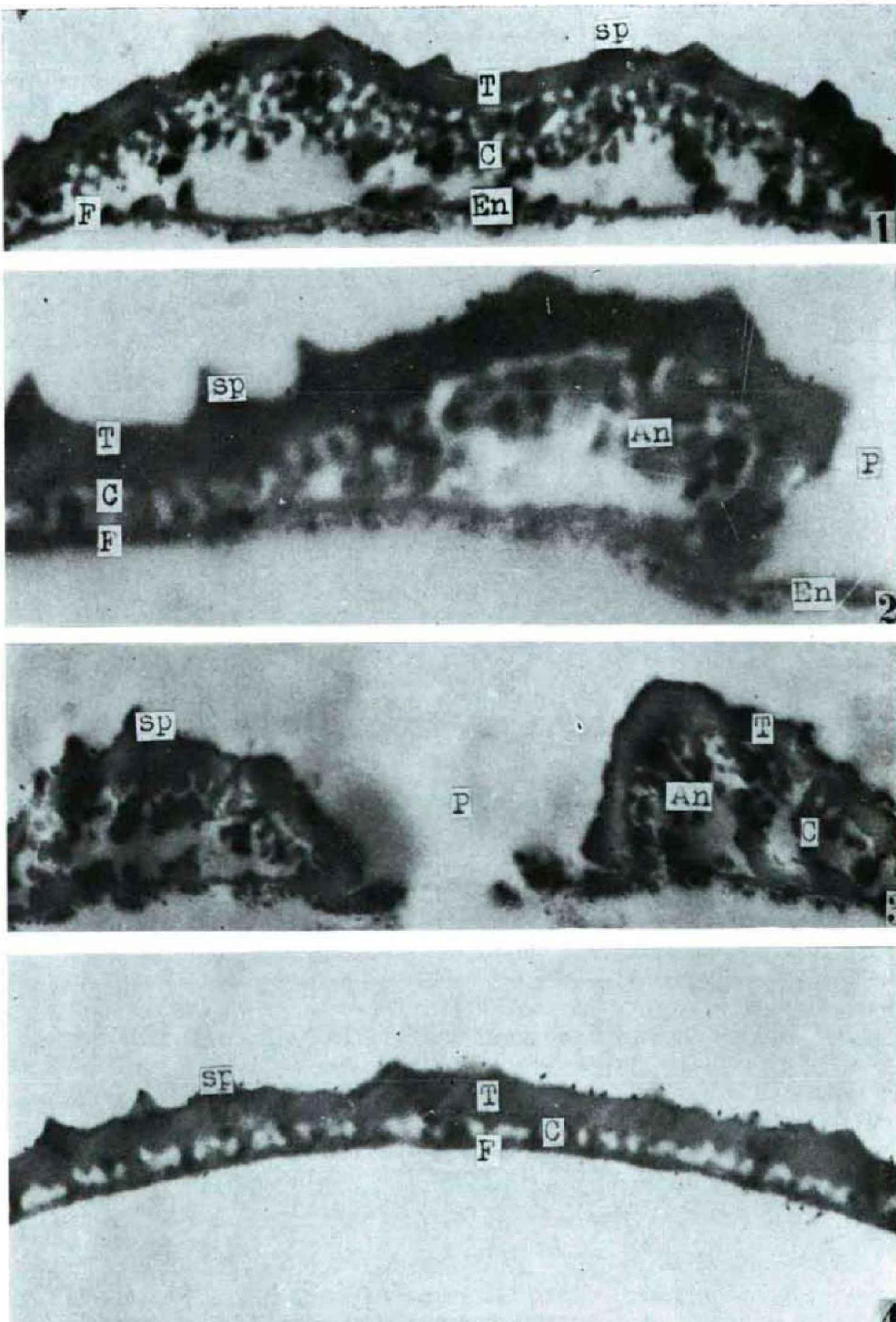

Fig. 4

Fig. 6. 1. — Ultrastructure of *Carya amara* NUTT. interpore-wall exine with the tapering columellae at the poles. M : 25,000x.
2. — Ultrastructure of *Carya alba* NUTT. pore-wall exine. M : 10,000x.
3. — Ultrastructure of *Carya amara* NUTT. exine in the pore-wall region. M : 10,000x.
4. — Ultrastructure of *Carya amara* NUTT. interpore-wall exine in the equatorial region. M : 50,000x.
T = tectum, C = columellae, F = foot layer, sp = spinae, ch = channels, At = atrium.

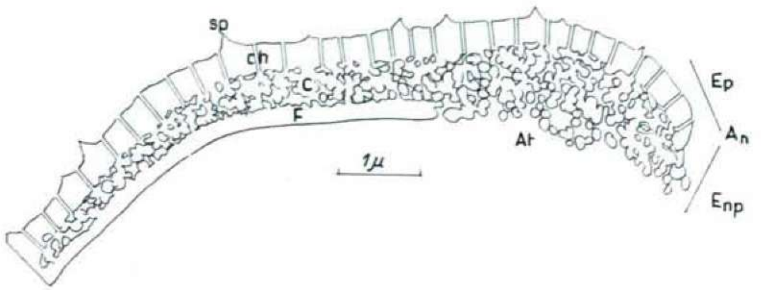

Fig. 7. Ultrastructure of *Juglans californica* WATSON exine in the pore-wall region.
T = tectum, C = columellae, F = foot layer, sp = spinae, ch = channels, At = atrium, An = annulus, Ep = exopore, Enp = endopore.

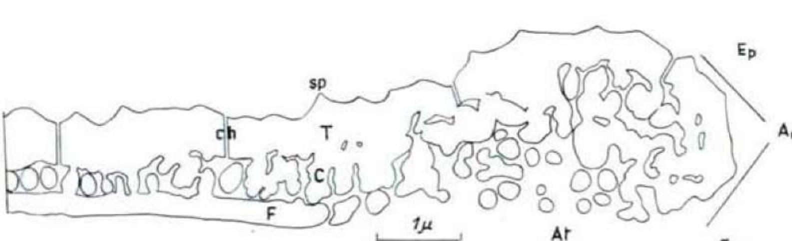

Fig. 9. Ultrastructure of *Myrica gale* L. [= *Gale palustris* (LAM.) CHEVAL.] exine in the pore-wall region.
T = tectum, C = columellae, F = foot layer, sp = spinae, ch = channels, At = atrium, An = annulus, Ep = exopore, Enp = endopore.

Myrica L. (Fig. 10/1–5)

Interpore-wall exine. – Tectate, rarely perforated with narrow channels, spinae also rarely situated on the surface. The elements of the columellae are spherical, ellipsoid, or rarely columnar, and arranged in one, or rarely two rows. There is no endexine below the foot layer (Fig. 10/5). T/C/F = 2–3/–1.5/1.

Pore-wall exine. – The thickness of the tectum is unchanged in the pore-wall region, and it bends inwards along the exogerminalia. The elements of the columellae form an annulus by their accumulation, and here the structural elements frequently anastomize. The foot layer breaks in the vicinity of the pore-wall region, partially divides up, and in this way the atrium is formed (Fig. 9; 10/1–4).

Betula L. (Fig. 12/1, 3, 4)

Interpore-wall exine. – Tectate, perforated with narrow channels, decorated with spinae on the surface (Fig. 12/1). The columellae and the foot layer

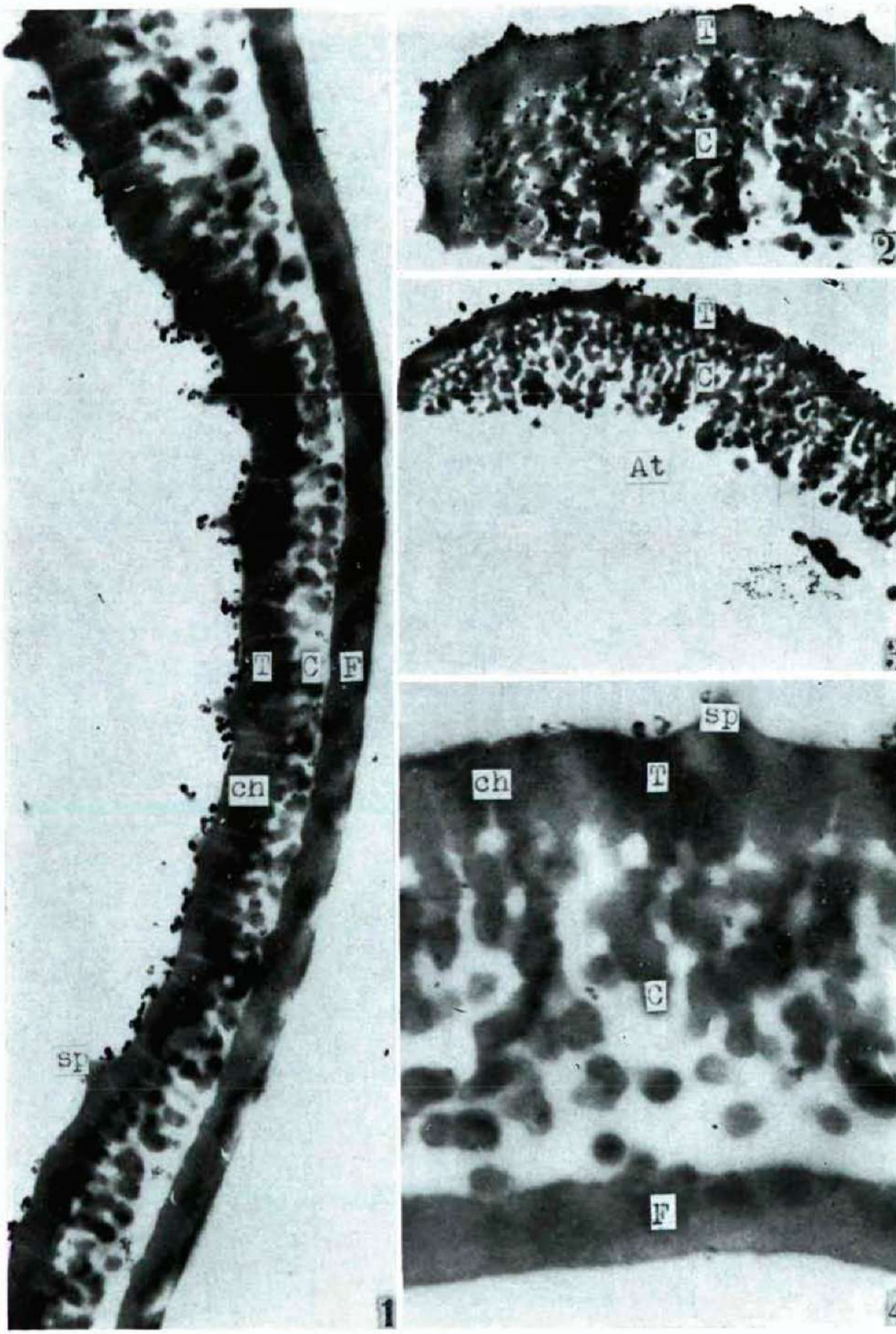

Fig. 6

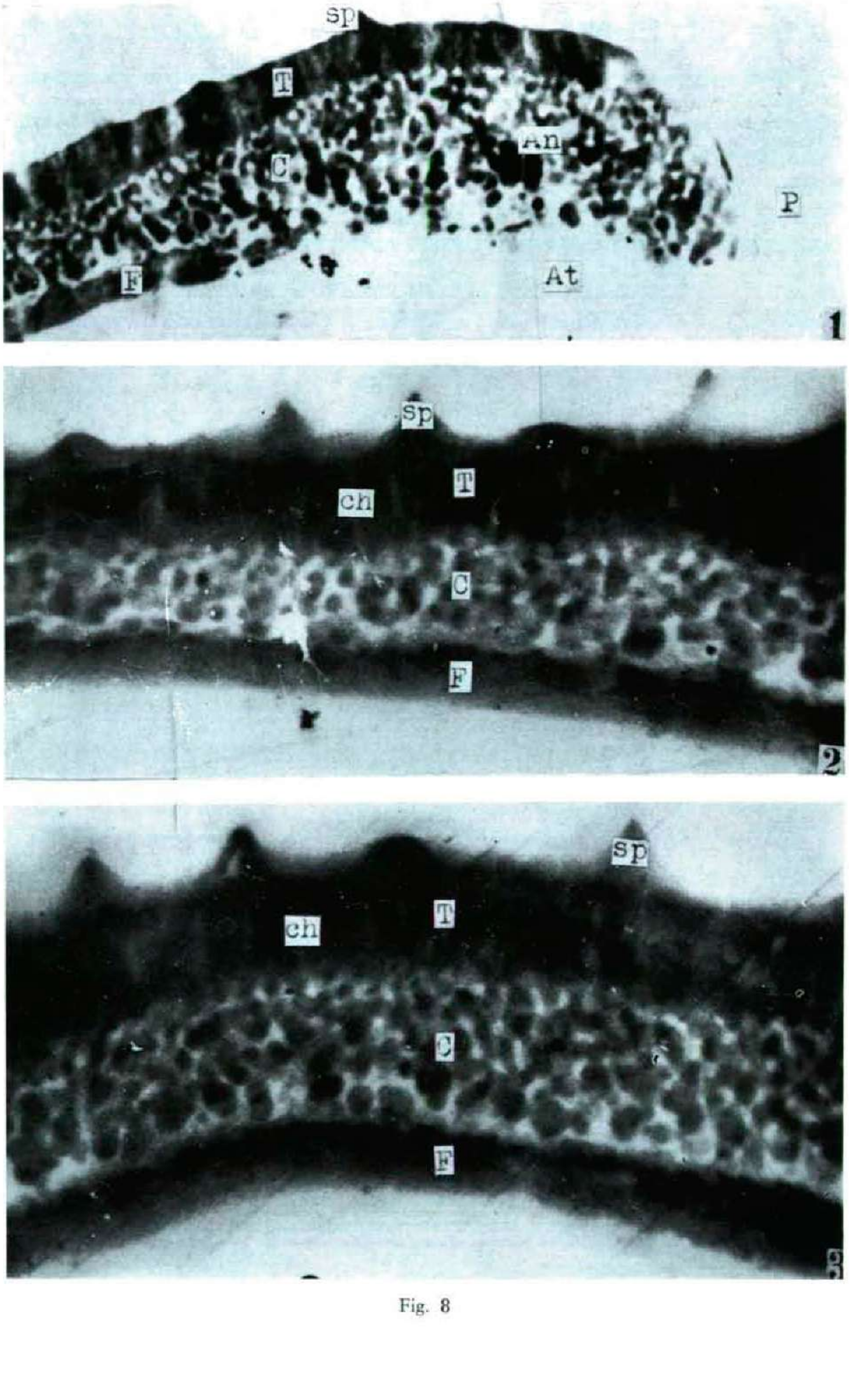

Fig. 8

Fig. 8. *Juglans californica* WATSON

1. — Ultrastructure of the pore-wall region. M : 25,000x.
2. — Ultrastructure of the interpore-wall region in the vicinity of the pole, with the tapering columellae. M : 50,000x.
3. — Ultrastructure of the interpore-wall exine in the equatorial region. M : 50,000x.

T = tectum, C = columellae, F = foot layer, sp = spinae, ch = channels, At = atrium, P = pore.

are very narrow, in contrast with the tectum. T/C/F=6–7/2/1. The columellae are single-rowed, and their elements have various shapes, ellipsoid, columnar, etc.

Fig. 10. *Myrica gale* L. [= *Gale palustris* (LAM.) CHEVAL.]

1,2,4. — Ultrastructure of the pore-wall exine in serial section. M : 10,000x.
3. — The columellae in the pore-wall region. M : 25,000x.
5. — Ultrastructure of the interpore-wall exine. M : 50,000x.

T = tectum, C = columellae, F = foot layer, sp = spinae, ch = channels, At = atrium, An = annulus.

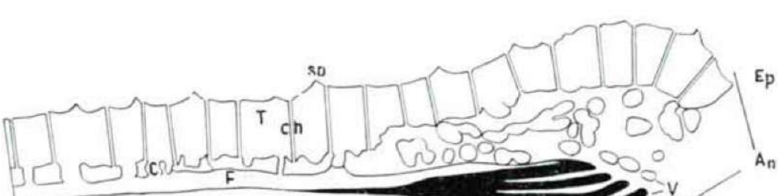

Fig. 11. Ultrastructure of *Betula alba* L. exine in the pore-wall region.
T = tectum, C = columellae, F = foot layer, sp = spinae, ch = channels, En = endexine, V = vestibulum, An = annulus, Ep = exopore, Enp = endopore.

Pore-wall exine. – The tectum is unchanged in the pore-wall region, while the elements of the columellae are in part larger than in the interpore wall, and in part accumulate and form an annulus. The foot layer breaks before the pores, and separates a little from the columellae (Fig. 11; 12/3, 4). There is an endexine of marked lamellar ultrastructure below the foot layer in the pore-wall region.

Alnus MILL. (Fig. 12/2, 5)

Interpore wall exine. – Tectate, perforated by narrow channels, with wide – – based spinae on the surface. The elements of the columellae are two- and three-rowed, spherical, ellipsoid, or irregular in shape (Fig. 12/2). T/C/F= 2–3/1–1.5/1.

Pore-wall exine. – The tectum becomes narrower in the direction of the exogerminalia. The elements of the columellae are strongly accumulated, in 10–12 rows, and also somewhat larger than in the interpore-wall region. The foot layer too is thicker before the pore-wall openings, and under it is a narrow endexine of lamellar ultrastructure. The foot layer and the endexine are a little separated from the columellae (Fig. 12/5; 13).

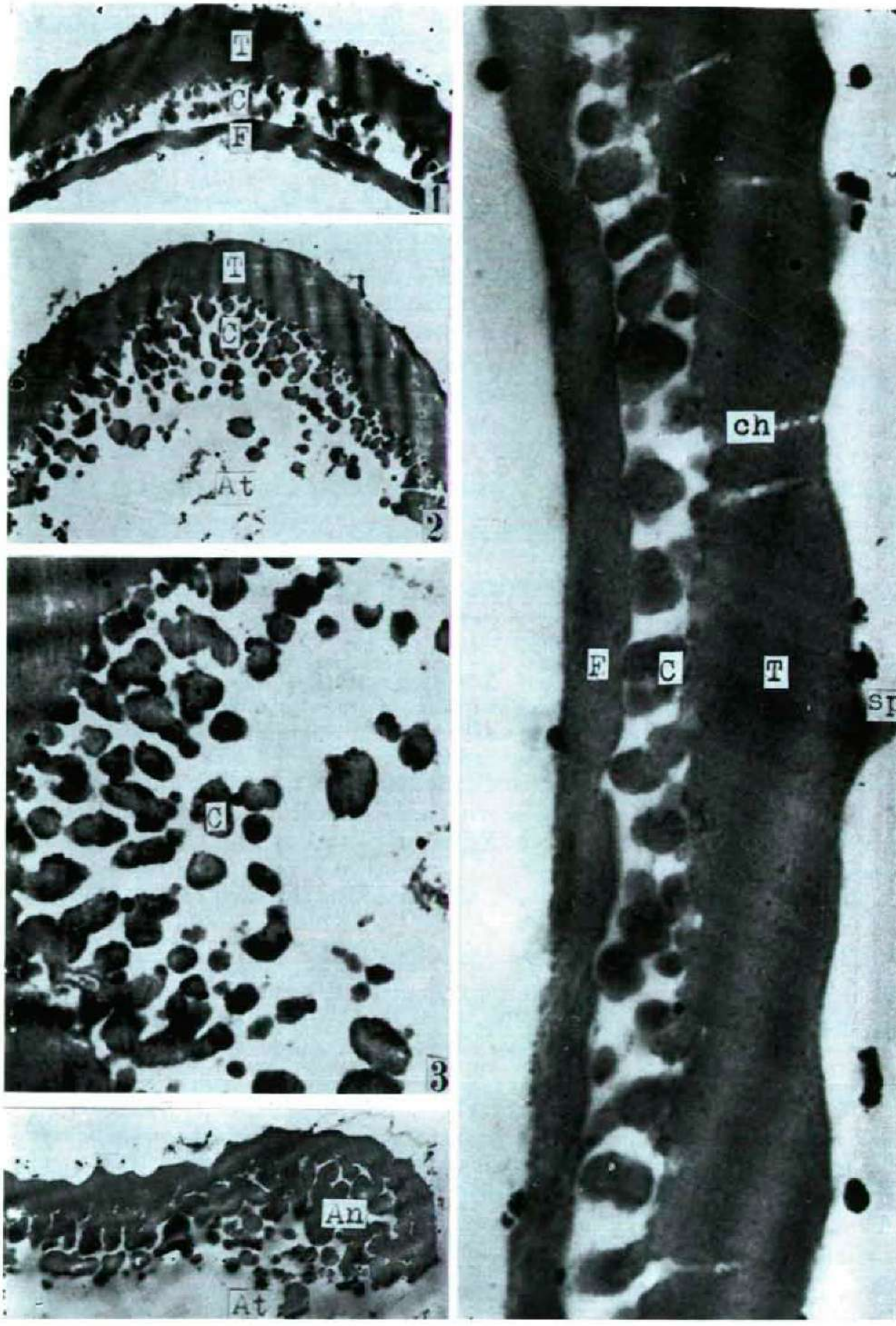

Fig. 10

Discussion of the results

From a comparison of our results with the findings of STONE and BROOME (1971), the following conclusions can be arrived at:

The occurrence of the channels is general in the tectum in the *Betulaceae, Corylaceae, Juglandaceae* and *Rhoipteleaceae* families, they are rare in the *Myricaceae* species studied, and they are not found in *Cannabis sativa;* thus, to a certain extent they are of taxonomic importance. The spinae on the surface are a general feature with Amentiflorae; they are probably of ecological significance, and a result of wind-pollination. According to TAKEOKA and STIX (1963), its finer morphology is of taxonomic value, but this can be evaluated primarily with a scanning electron-microscope method. On the basis of the species examined, the finer morphology of the columellae for taxonomic distinction, primarily of the genera.

According to our present knowledge, the endexine does not occur in the *Juglandaceae* genera *(Carya, Engelhardtia, Juglans)* and in the *Myricaceae.* In the Corylaceae and Betulaceae genera there is an endexine with lamellar ultrastructure in the pore-wall region, while in *Cannabis sativa* there is an endexine with granulated ultrastructure. As regards the ultrastructure, this latter species is very well distinguished not only by its characteristic endexine, but also by the fact that there are no channels in the tectum.

The annulus is generally formed by means of the accumulation of the elements of the columellae, and in the *Corylaceae* and the *Betulaceae* the endexine too participates in its formation. In *Cannabis sativa* the endexine is not important from this respect.

Fig. 12. 1. — Ultrastructure of *Betula alba* L. interpore-wall exine. M : 25,000x.
2. — Ultrastructure of *Alnus glutinosa* (L.) GAERTN. interpore-wall exine. M : 25,000x.
3,4. — Ultrastructure of *Betula alba* L. pore-wall exine. M : 10 000x.
5. — Ultrastructure of *Alnus glutinosa* (L.) GAERTN. pore-wall exine. M : 10,000x.
T = tectum, C = columellae, F = foot layer, sp = spinae, ch = channels, En = endexine, An = annulus.

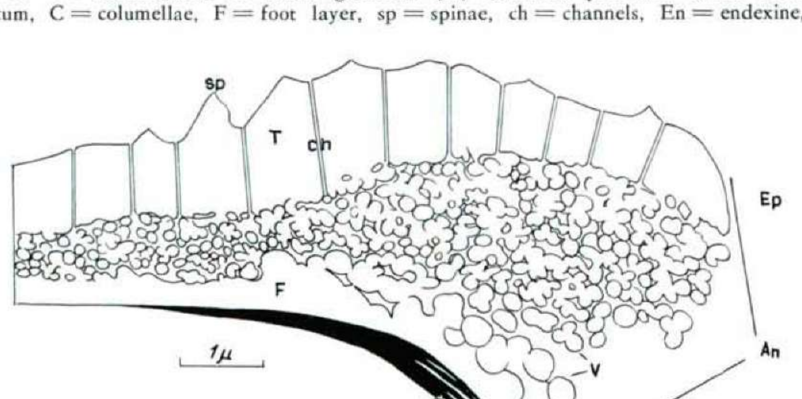

Fig. 13. Ultrastructure of *Alnus glutinosa* (L.) GAERTN. exine in the pore-wall region. T = tectum, C = columellae, F = foot layer, sp = spinae, ch = channels, En = endexine, V = vestibulum, An = annulus, Ep = exopore, Enp = endopore.

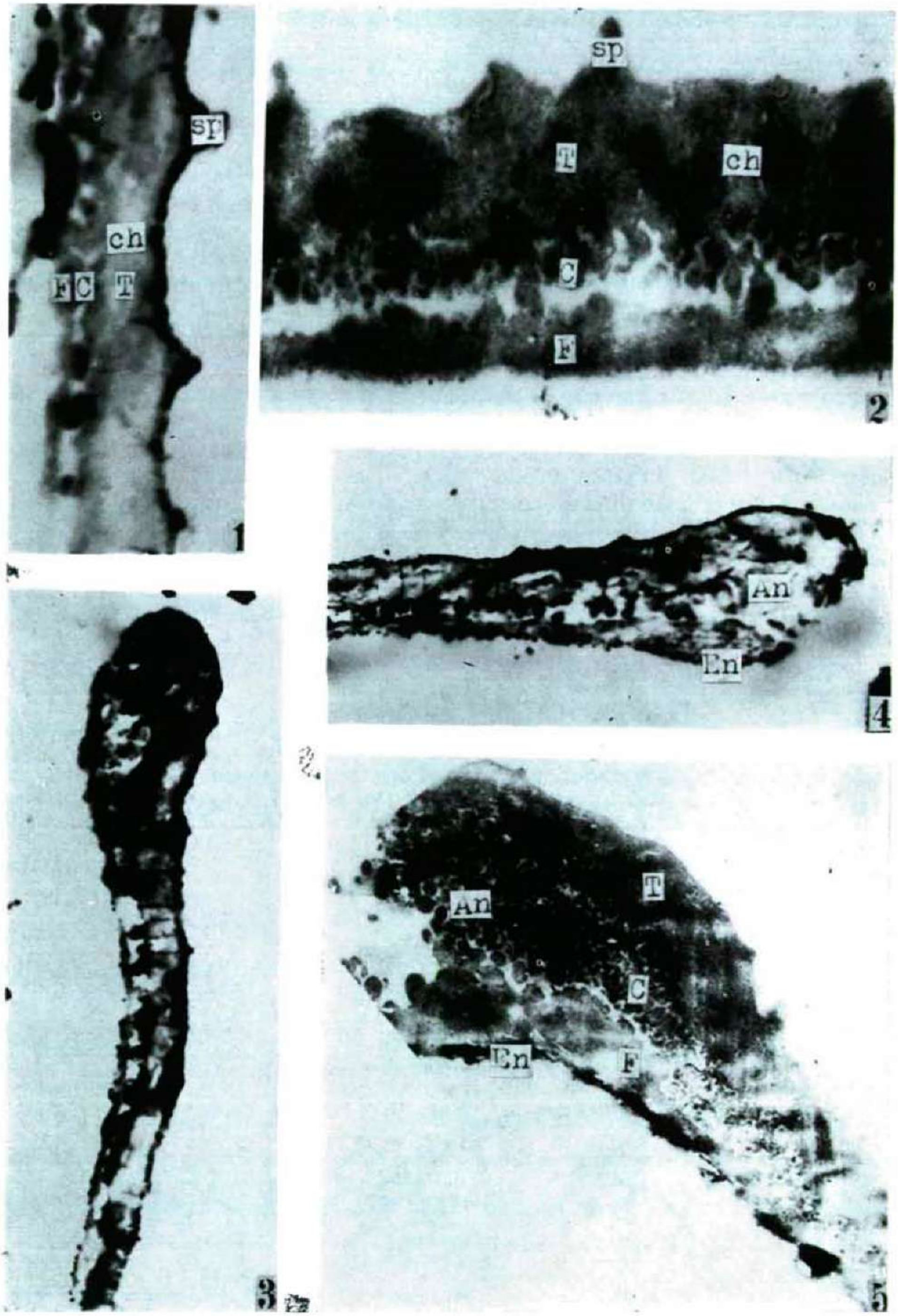

Fig. 12

In the pore the tectum and the foot layer combine *(Cannabis sativa),* or nearly combine: the two layer bend together (e. g. the *Corylus* genus). In the atrium the foot layer breaks before the pore-wall region; this is typical for the *Myrica* and the *Engelhardtia* genera, but essentially the same is found for the *Carya* and *Juglans* species too. In the case of the vestibulum the foot layer (together with the endexine) separates from the columellae in the pore-wall region and bends inwards towards the centre of the pollen. This is characteristic for the *Betula* and the *Alnus* genera. The „fainter zones" at the poles for the pollen grains of the *Carya* and *Juglans* genera are formed by the tapering of the columellae (cf. STONE, REICH and WHITFIELD, 1964).

Summary

1. In the Amentiflorae taxons the exine ultrastructural features are partially of ecologic value (e. g. the spinae on the tectum), and partially of taxonomic value.

2. From a taxonomic point of view the channels, the finer structure of the columellae, the endexine and the pore-wall region formations (pore, atrium, vestibulum) or the tapering zones sometimes occurring on the poles of the pollen grains can be used.

3. The features identified in the recent taxons are identical to the ultrastructural characteristics established on the fossil pollen grains (e. g. the atrium in *Plicapollis pseudoexcelsus).*

References

ERDTMAN, G. (1956): Current trends in palynological research work. — Grana Palynologica *1,* 128—139.

HEGEDŰS, M., KEDVES, M.—PÁRDUTZ, Á. (1971): Ultrastructural investigations on fossil Angiosperms exine of Upper Cretaceous. — Advancing Frontiers of Plant Sciences *28,* 317—329.

HEGEDŰS, M., KEDVES, M.—PÁRDUTZ, Á. (1972): Ultrastructural investigations of Upper Cretaceous Angiosperm exines II. — (in press).

KEDVES, M., HEGEDŰS, M.—PÁRDUTZ, Á. (1971a): Étude de l'ultrastructure des pollens fossiles des Angiospermes du Crétacé supérieur et du Tertiaire inférieur. — III. Internat. Palynological Conference. Sect. 2, Novosibirsk.

KEDVES, M., HEGEDŰS, M.—PÁRDUTZ, Á. (1971b): Ultrastructure investigations on the exine of the genus *Casuarina* L. (Short communication). — Acta Biol. Szeged *17,* 63—65.

KEDVES, M.—PÁRDUTZ, Á. (1970a): Az ultrastruktúra vizsgálatok jelentősége fosszilis Angiospermatophyta pollenszemek fejlődéstörténeti kérdéseinek megoldásában (The importance of ultrastructural studies in the solution of questions of the history of the development of fossil Angiospermatophyta pollen grains (preliminary communication). — Bot. Közlem. 57, 57—58.

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

KUPRIANOVA, L. A. (1965): The palynology of the Amentiferae (in Russian). — Moscow—Leningrad.

STONE, D. E., REICH, J.—WHITFIELD, S. (1964): Fine structure of the walls of *Juglans* and *Carya* pollen. — Pollen et Spores *6,* 379—392.

STONE, D. E.—BROOME, C. R. (1971): Pollen ultrastructure: Evidence for relationship of the *Juglandaceae* and the Rhoipteleaceae. — Pollen et Spores *13*, 5/14.

TAKEOKA, M.—STIX, E. (1963): On the fine structure of the pollen walls in some Scandinavian *Betulaceae*. — Grana Palynologica *4*, 161—188.

UENO, J. (1963a): On the fine structure of the pollen walls of Angiospermae. III. *Casuarina*. — Grana Palynologica *4*, 189—194.

UENO, J. (1963b): The stratigraphical structure of the pollen walls of Dicotyledoneae. I. Ranales and Amentiferae. — Acta Phytotax. Geobot. *19*, 137—141. (Japanese, with English summary.)

Addresses of the authors:

Dr. M. KEDVES

Department of Botany A. J. University
H — 6701 Szeged P. O. Box 428

Dr. Á. PÁRDUTZ

Electron Microscope Laboratory,
Institute of Biophysics, Biological Research Center, Hungarian Academy of Sciences, Szeged
H — 6701 Szeged P. O. Box 521
Hungary