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ULTRASTRUCTURAL STUDIES ON AMENTIFLORAE POLLEN GRAINS, II

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Abstract

This paper is the second part of our TEM investigations on Amentiflorae taxons. The genera *Carpinus, Ostrya, Zelkova, Ulmus, Humulus, Morus* and *Urtica* were investigated. It is concluded that some of the fine structural features in the Amentiflorae taxons are of general, while others of special character. The ultrastructural features can be used for elucidation the question of relationship between different genera.

Introduction

In a previous paper (KEDVES and PÁRDUTZ, 1973) we touched briefly on the necessity of ultrastructural studies on the exines of Amentiflorae taxons. Our results on the exine ultrastructure of some Brevaxones pollen grains were reported earlier. These studies have been continued in accordance with the points of view put forward. The material in the present examinations extended to *Carpinus, Ostrya, Zelkova, Ulmus, Humulus, Morus* and *Urtica* genera. The method was the same as described previously.

Results

Carpinus L. Fig. 1.

Examinations were made on *Carpinus betulus* L. and *C. duinensis* SCOP. No essential ultrastructural difference was observed between the two species. Extragerminal exine. — Tectate, perforated with narrow channels. The surface of the tectum is uneven, and sparsely ornamented with spinae. The elements of the columellae are of various shapes: spherical, ellipsoid and columnar, and are mostly situated in one, or rarely two rows. The foot layer is very thin, and it did not prove possible to observe a marked endexine under it on our ultrathin sections. T/C/F (ratios of the thicknesses of the tectum, the columellae and the foot layer)= =3—4/2—3/1 (Fig. 1,1). Pore wall exine (Fig. 1,2—4). The tectum is attenuated in the vicinity of the pores, inclines in the centripetal direction, and breaks around the middle of the annulus. The elements of the columellae accumulate strongly, generally comprise 7—8 rows and form the annulus. The foot layer breaks at the level of the beginning of the annulus, and thus an atrium is formed. Before the atrium, below the foot layer, an endexine of pronounced lamellar ultrastructure appears, and this by and large runs intermittently through below the annulus.

Ostrya Scop. (Fig. 2)

Examinations were made on *Ostrya carpinifolia* Scop.

Extragerminal exine. — Tectate, perforated with extremely narrow channels. There are large, wide-based spinae on the surface of the tectum. The elements of the columellae are generally spherical, and arranged in 1—2 rows. The foot layer is narrow. T/C/F=3—4/1,5/1. (Fig. 2,1).

Pore wall exine. — The tectum inclines in the centripetal direction along the pores, attenuates and breaks. The elements of the columellae accumulate only slightly in the pore wall region and form the annulus. The columellae here are generally 4-rowed. The foot layer breacks around the base of the annulus, and thus in essence an atrium is formed. No endexine was observed in the pore wall region either.

Zelkova Spach (Fig. 3)

Examinations were made on *Zelkova cretica* Spach.

Extragerminal exine. — The tectum is perforated with relatively narrow, frequently difficulty observable channels. The surface is uneven, and ornamented sparsely with small spinae. The columellae below the tectum consists of spherical or ellipsoid anastomizing elements, the latter being very small and arranged in 10—16 rows. Before the foot layer the elements of the columellae are larger and sparsely arranged. They are 2—3 times as large as the previous ones, and similarly spherical (Fig. 3,2—5). The foot layer is narrower at the tectum too, and below it there is sporadically endexine of narrow granular ultrastructure. T/C/F= =1.5/10—15/1.

Pore wall exine. — In the pore wall region the endexine of granular ultrastructure is pronounced. The foot layer similarly breaks before the pores, but the endexine takes over its place, and thus the atrium forms an interesting case. Before the pores, in the vicinity of the pore-channel, it is mainly spherical, and there is a formation corresponding to the foot layer. The tectum inclines at the pores. The elements of the columellae are strongly accumulated and form the annulus.

Ulmus L. (Fig. 4)

Examinations were made on *Ulmus americana* Willd. and *Ulmus japonica* Sarg.

Extragerminal exine. — Tectate, perforated with narrow channels, and the surface of the tectum is ornamented with small spinae. The surface is strongly undulated, a consequence of the light-microscopially known sculptura. The foot layer is extremely narrow. For the columellae essentially the same could be established as with the examined species of the *Zelkova* genus; as regards its size the columellae above the foot layer differs from the other parts of this layer. The columellae are arranged in 6—15 rows. T/C/F=1.5/10—20/1. (Fig. 4,1—3).

Pore wall exine. — The tectum inclines centripetally along the pores, and then breaks. The elements of the columellae accumulate and form the annulus. The foot layer breaks at the level of the pore, and thus we can speak of an atrium. Endexine could not be observed with certainty even in the pore wall region (Fig. 4,4).

Humulus L. (Fig. 5)

Examinations were made on *Humulus japonicus* Sieb. and Zucc.

Extragerminal exine. — Tectate, perforated sparsely with narrow channels; the surface is ornamented with wide-based large spinae. The elements of the columellae are of various shapes: spherical, ellipsoid and columnar, they frequently anastomize, and are arranged in 1—2 rows. Compared to the previous two layers the foot layer is extremely thin. T/C/F=6—8/4—5/1.

Pore wall exine. — The tectum inclines along the pores and generally breaks at the level of the foot layer without attenuation. The elements of the columellae accumulate strongly and form the annulus, but there is an appreciable drop-shaped cavity below the thickening columellae. The foot layer generally breaks at the base of the annulus and its place is assumed by endexine with difficulty distinguishable granular ultrastructure (Fig. 5,1). At times the breaking of the foot layer can not be observed with certainty, and the endexine is difficult to distinguish from the foot layer.

Morus L. (Fig. 6)

Examinations were made on *Morus nigra* L. and *Morus indica* L. In this case noteworthy differences were observed in the pore wall regions of the two species.

Extragerminal exine. — Tectate, perforated with narrow channels. There are wide-based large spinae on the surface of the tectum. The elements of the columellae are arranged in 2—3 rows, and are small and generally spherical. In this genus too the foot layer is very narrow compared to the other layers. T/C/F= =5—6/3/1. (Fig. 6,1).

Pore wall exine. — In *Morus nigra* there is an endexine of extremely developed, lamellar ultrastructure in the pore wall region. The tectum and the columellae are unchanged in the pore wall region, and break at the level of the pores. The foot layer breaks at the base of the thickening endexine, and thus there is an atrium, but without an annulus of ectexine origin. The elements of the endexine form a developed endannulus. In *Morus indica* the difference primarily lies in the fact that part of the pore wall endexine carries an "operculum" in the pore, and part of the ectexine, the tectum and the columellae, a small part of it, probably spherical in shape. The endannulus is not so pronounced as in the former species (Fig. 6,4).

Urtica L. (Fig. 7)

Examinations were made on *Urtica diodica* L. Its pores are arranged strongly subequatorially, and thus there was no means of studying the entire ultrastructure of the pore wall region. The extragerminal exine is tectate and not perforated, the surface of the tectum is undulated, and on it there are blunt or sharp-ended ornamental elements. The elements of the columellae are spherical, and generally arranged in 2 rows. T/C/F=2—3/2/1. In the pore wall region the foot layer breaks (Fig. 7,1—2), and the elements of the columellae accumulate a little.

Discussion

Comparison of the present data with the earlier results leads to the following conclusions: The new data too show the channels in the tectum to be extremely widespread; only in the *Cannabis* and *Urtica* genera did they not appear. Spinae occurred without exception in the Amentiflorae species previously examined. Two types can be distinguished here; the extremely narrow-based, relatively short *Carpinus, Ostrya, Zelkova* and *Ulmus*, and the relatively large and wide-based *Humulus, Morus* and *Urtica*. The columellae are very characteristic in the *Zelkova* and *Ulmus* genera, in that the ultrastructural elements in the part directly above the foot layer are larger than in the part above this. In spite of the fact that it proved possible to detect endexine in *Zelkova cretica*, which is not known for the hitherto examined pollen exines of the Juglandaceae, the exine ultrastructures of the *Ulmus* and *Zelkova* genera resemble those of the Juglandaceae *Carya* and *Juglans* genera, but definitely differ from the other Amentiflorae in their characteristic columellae. Also similar to one another are the columellae of the *Carpinus* and *Humulus*, and the *Ostrya* and *Morus* genera.

Endexine of granular ultrastructure can also appear independently of the other features of the ectexine, e.g. in *Zelkova cretica, Humulus japonicus* and the previously studied *Cannabis sativa*. A developed lamellar endexine occurred in the *Morus* genus, and is also known in the pore wall region of Corylaceae and Betulaceae. The development of the endannulus is similarly characteristic in the *Morus* pollen grains by way of the strong accumulation of the endexine lamellae.

Our new data have confirmed that the annulus is formed in the Brevaxones pollen grains by the accumulation of the elements of the columellae, and with the exception of the *Morus* genus occurred in every species examined. A difference can be observed in *Humulus japonicus*, where there is a consequential cavity between the pore wall columellae and the endexine. Pores appeared in the *Zelkova, Ulmus* and *Humulus* genera, and from this respect too this latter genus differs from the type regarded as general, for the foot layer breaks in the pore wall region and its place is taken over by the endexine. In contrast with the earlier data, of interest is the operculum of ectexine origin above the pores of *Morus indica*. The atrium in the *Carpinus* and *Ostrya* genera is a new ultrastructural addition as regards the pore wall exine of *Myrica* type, since the exact demonstration of this on the basis of light-microscopic examinations is fairly problematical.

Reference

KEDVES, M. — PÁRDUTZ, Á. (1973): Ultrastructural studies on Amentiflorae pollen grains, I. — Acta Biol. Szeged. *19*, 19–32.

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Fig. 1. *Carpinus duinensis* SCOP.

1. — Ultrastructure of the extragerminal exine. M: x25 000.
2. — Ultrastructure of the pore wall exine. M: x25 000.
3. — Exine ultrastructure in the vicinity of the pore well region. M: x25 000.
4. — Tectum and columellae in the vicinity of the pore wall region. M: x25 000.

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

Fig. 2. *Ostrya carpinifolia* SCOP.

1. — Ultrastructure of the pore wall exine. M: x25 000.
2. — Ultrastructure of the extragerminal exine. M: x50 000.

sp=spinae, ch=channels, T=tectum, C=columellae, F=foot layer.

Fig. 3. *Zelkova cretica* SPACH.

1. — Ultrastructure of the pore wall exine in the vicinity of the pore wall region. M: x25 000.

2—5. — Details from the ultrastructure of the extragerminal region. M: x25 000.

sp=spinae, ch=channels, T=tectum, C=columellae, F=foot layer.

Fig. 4. *Ulmus americana* WILLD.

1—3. — Ultrastructure of the extragerminal exine. M: x25 000.

Ulmus japonica SARG.

4. — Ultrastructure of the pore wall region. M: x25 000.

sp=spinae, ch=channels, T=tectum, C=columellae, F=foot layer.

Fig. 5. *Humulus japonicus* SIEB. and ZUCC.

1. — Ultrastructure of the pore wall region. M: x50 000.
2. — Outline picture of the ultrastructure of the pore wall and extragerminal exines. M: x25 000.

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

Fig. 6. *Morus nigra* L.

1. — Ultrastructure of the extragerminal exine. M: x50 000.
2. — Ultrastructure of the pore wall region in the vicinity of the pore wall region. M: x25 000.
3. — Ultrastructure of the pore wall region in the pore wall region. M: x25 000.

Morus indica L.

4. — Ultrastructure of the pore wall region in the pore wall region. M: x25 000.

sp=spinae, ch=channels, T=tectum, C=columellae, F=foot layer.

Fig. 7. *Urtica dioica* L.

3,2. — Exine ultrastructure in the vicinity of the pore wall region. M: x50 000.

1,4. — Ultrastructure of the extragerminal exine. M: x50 000.

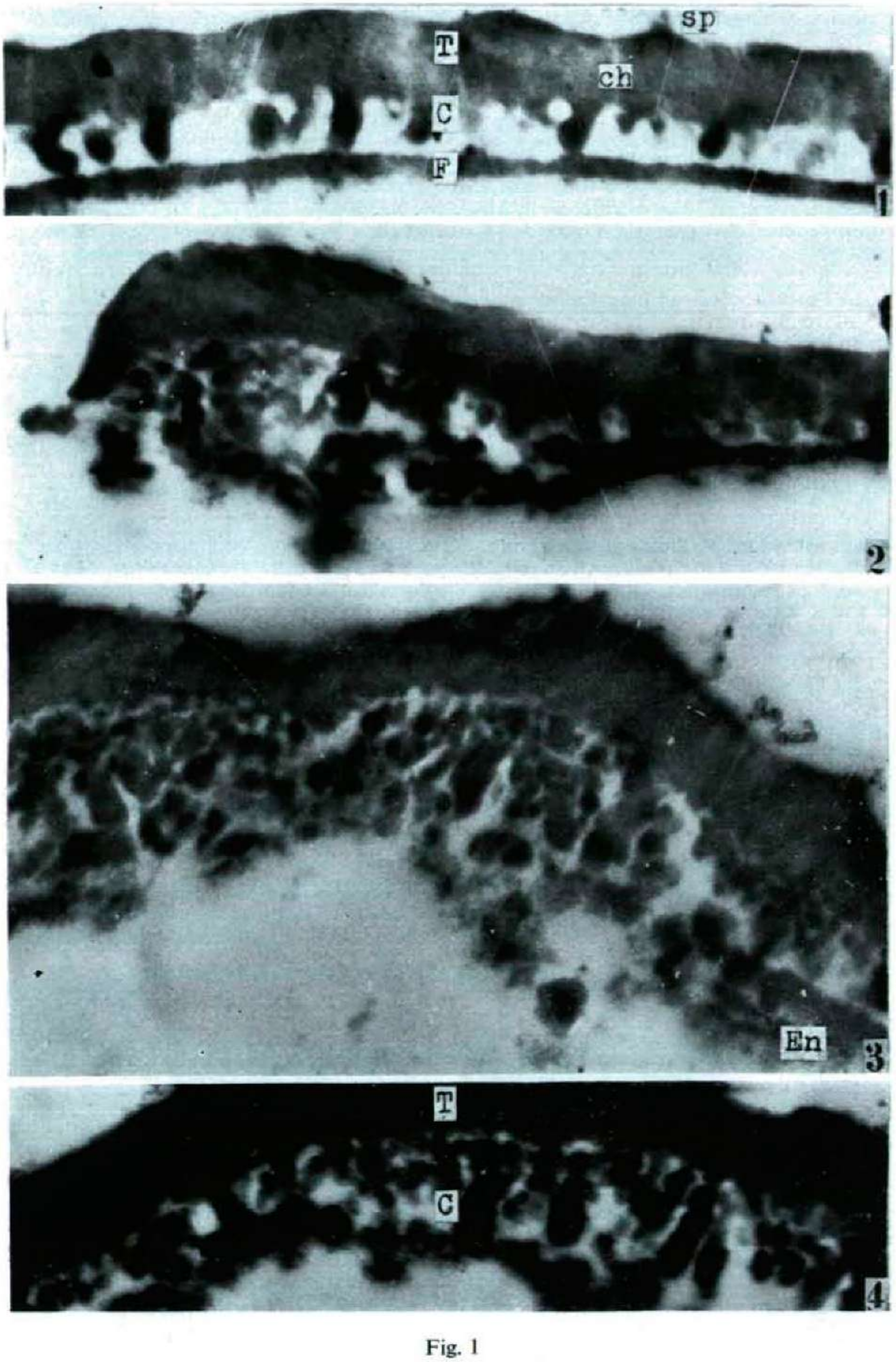


Fig. 1

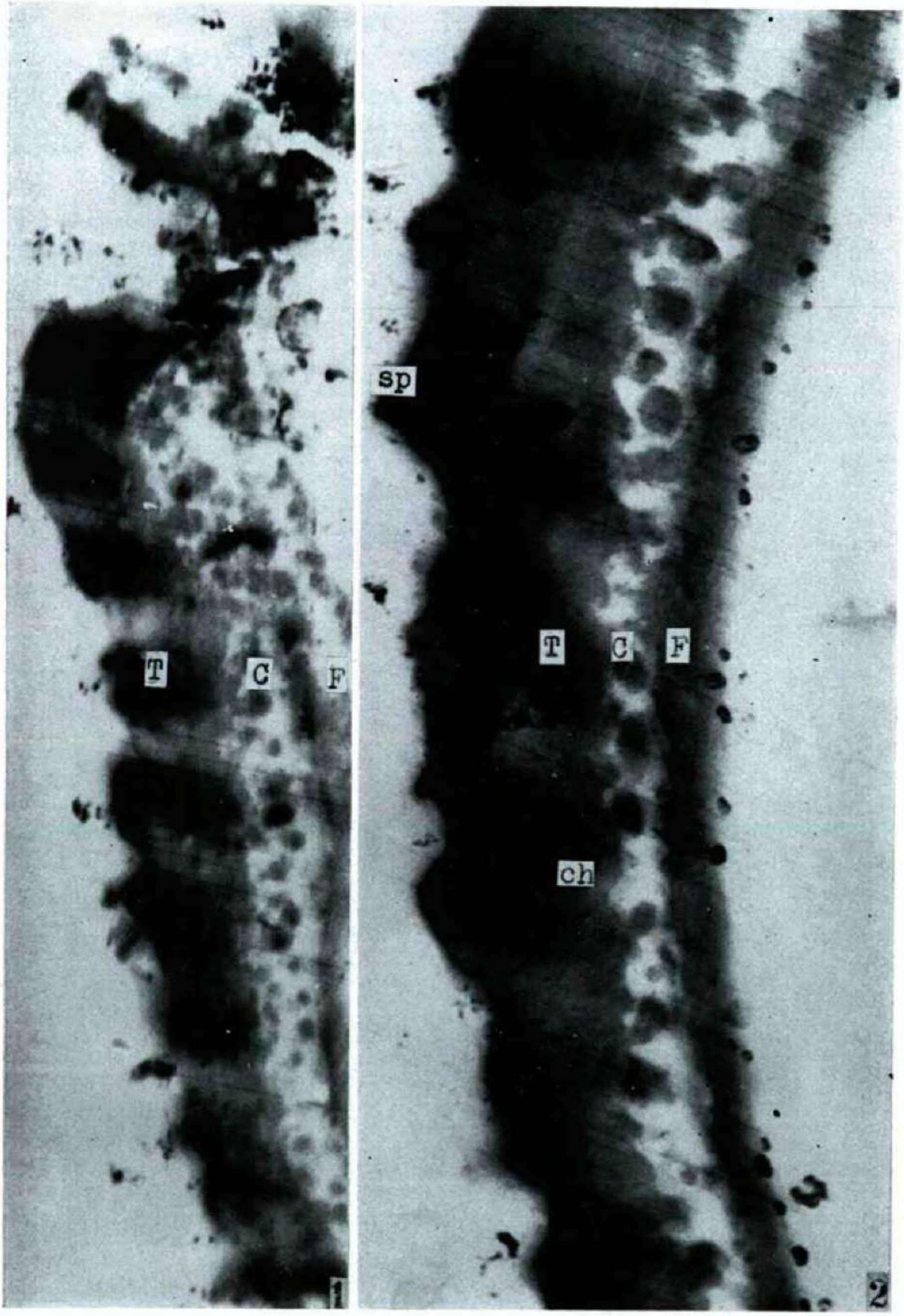
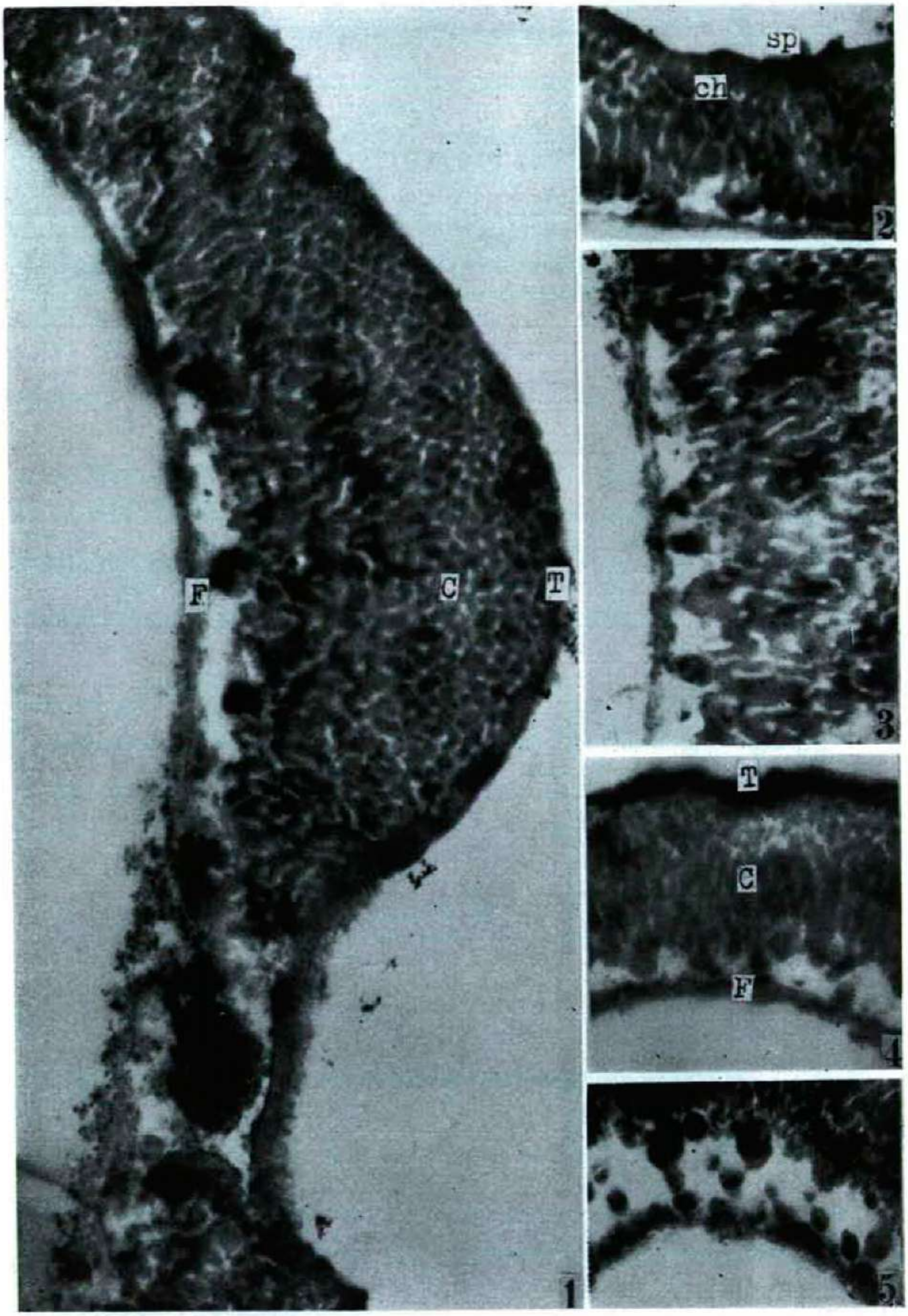


Fig. 2



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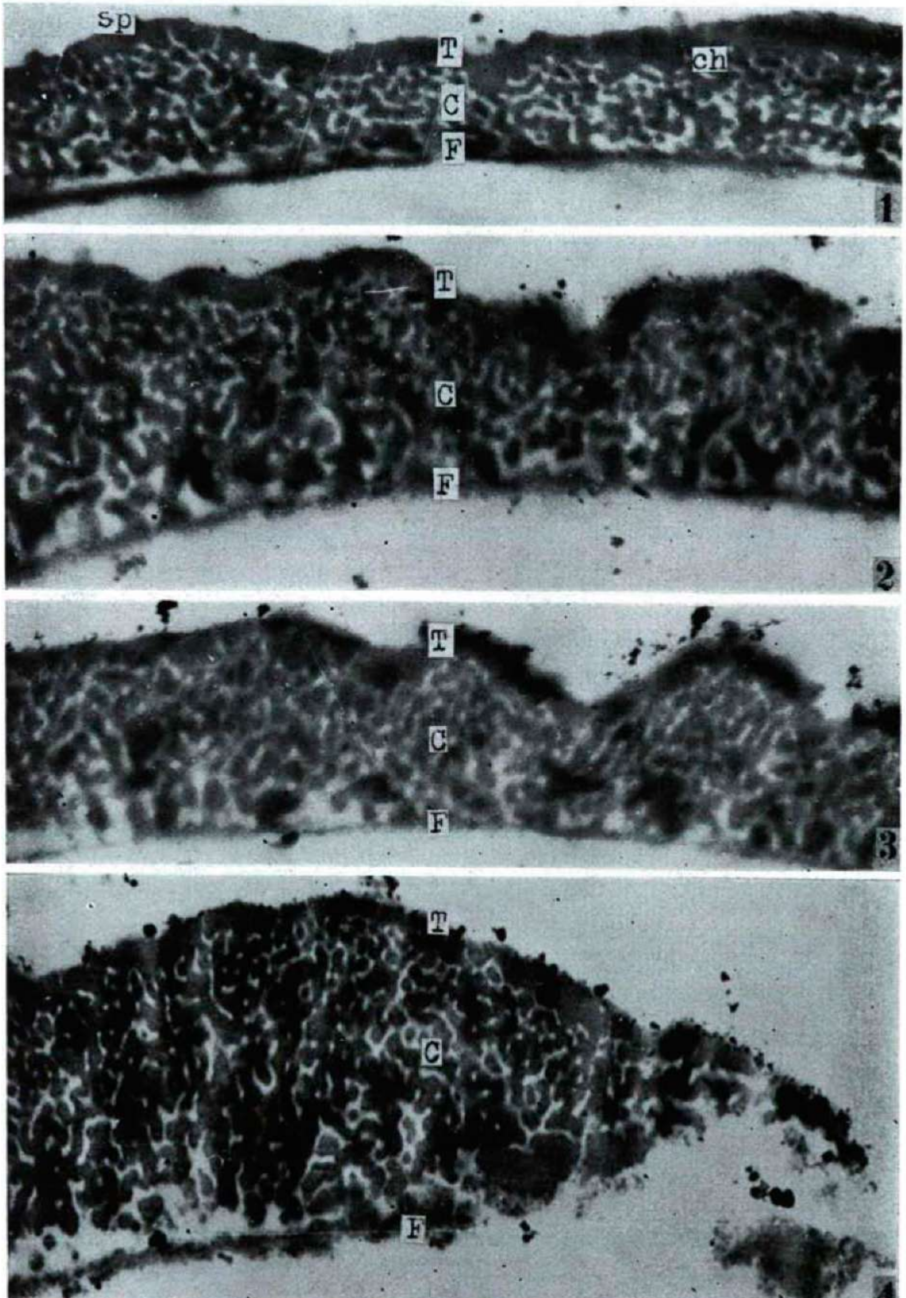

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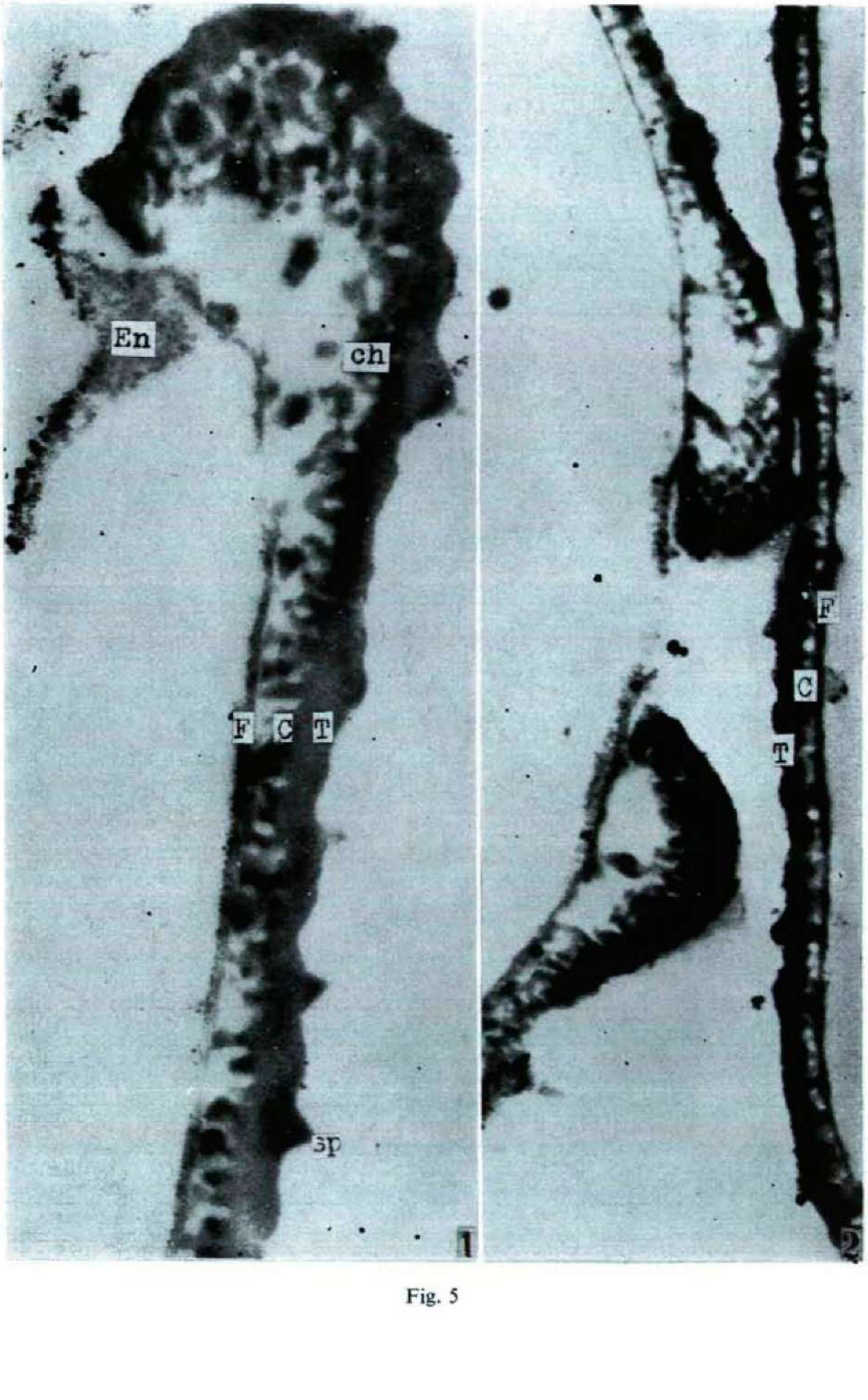

Fig. 5

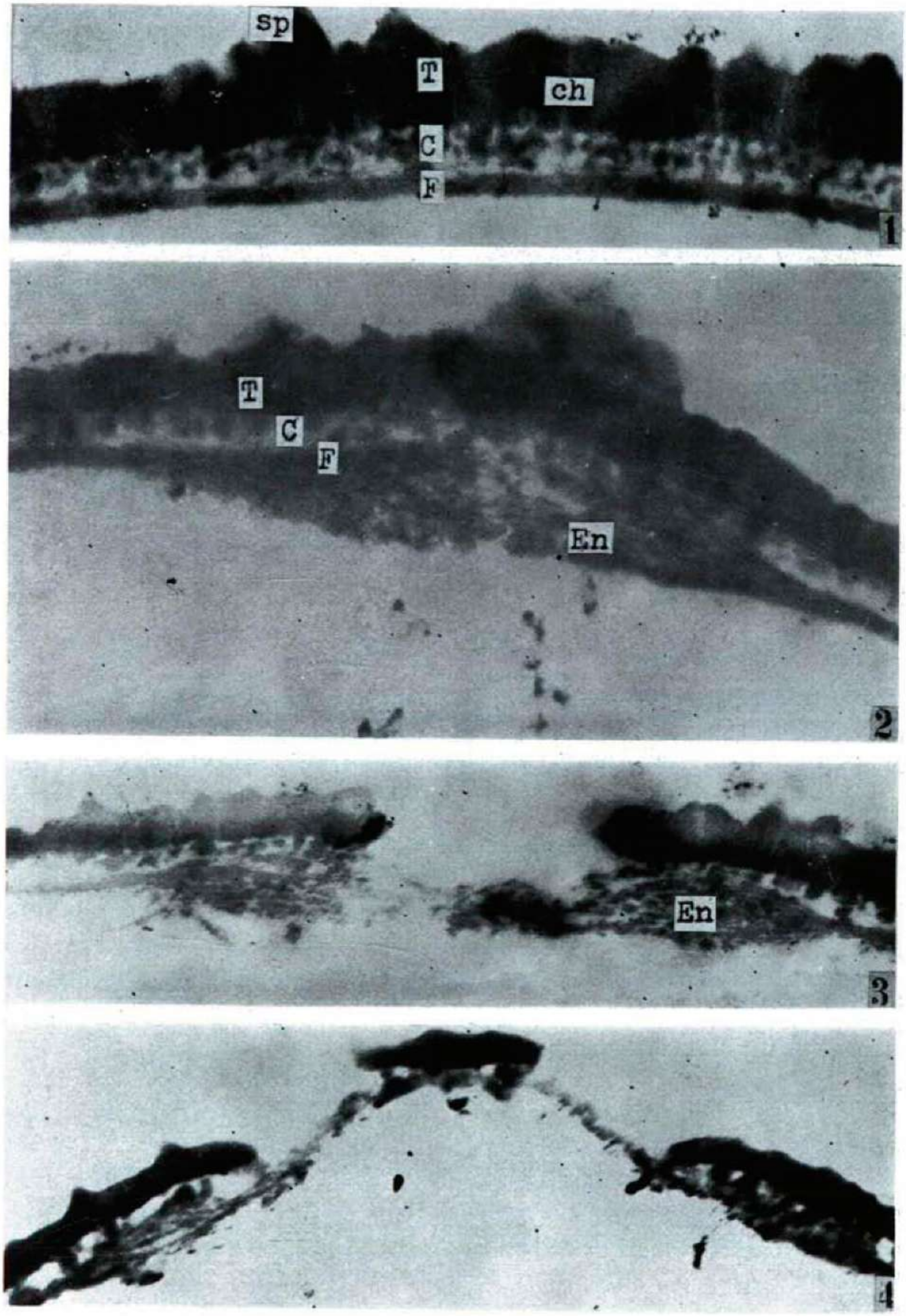

Fig. 6

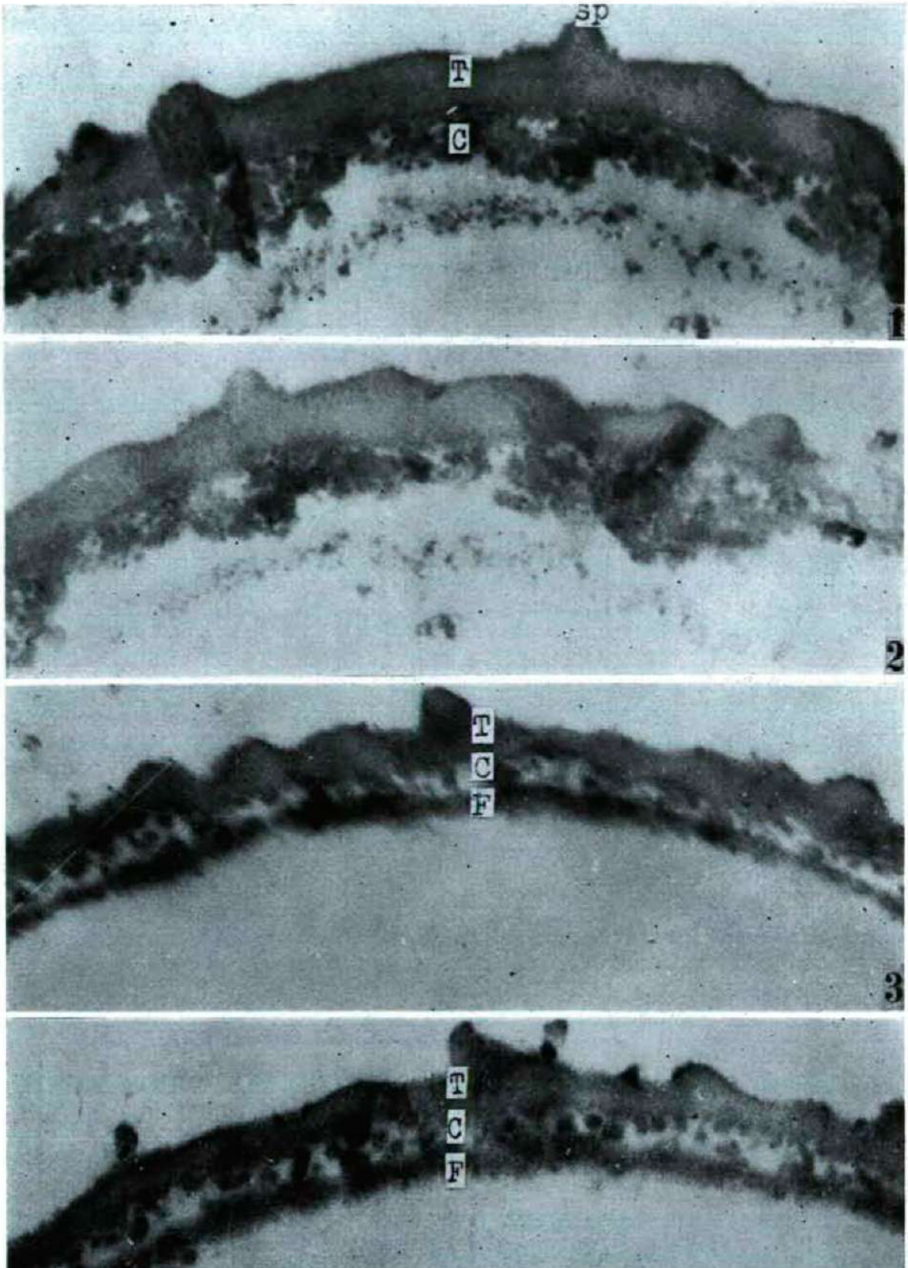

Fig. 7