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THE ULTRASTRUCTURE OF RIBBON-LIKE DEPOSITS OVER THE THECAE IN *ORTHOGRAPTUS GRACILIS* ROEMER

Abstract. — The periderm of *Orthograptus gracilis* has bee studied with an electron microscope (TEM and SEM). Four components have been recognized within the thecal wall: 1. endocortex, 2. fusellar layer, 3. cortex and so-called 4. taeniocortex. Taeniocortex covering the outer surface of the thecal wall consists of ribbon or sometimes roller-like elements and is produced of a peculiar material. The data obtained do not confirm Andres' belief that ribbons are made of cortical material and that entire cortex was produced by deposition of ribbon-like units.

INTRODUCTION

For the first time the bandages were found on the outer and inner thecal wall of *Orthograptus gracilis* Roemer by Kraft (1926), who called them "Chitinverdickungsbänder". These enigmatic structures were described also by Kühne (1955) on the periderm of *Monograptus dubius* Suess and by Eisenack (1959) on the sicula of *Orthograptus gracilis*. Urbanek and Teller (1974) described a number of delicate lines crossing the fusellar boundaries in *Monograptus testis* Barrande. Crowther and Rickards (1977) recognized the presence of rather narrow and elongated belts which they called "bandages" on the graptolite periderm. Their observations were made with a scanning electron microscope. Similar investigations have been conducted independently by Andres (1976, 1977) with a light microscope. Ribbons were recognized on the surface of rhabdosome, forming a characteristic pattern of criss-crossing secretions produced by cephalic disc of particular zooids, creeping over the surface of rhabdosome. He considers that in diplograptids all the cortex is produced by bandages.

The primary aim of our work was to study the ultrastructure of the bandages in *Orthograptus gracilis* and to clarify their relations to the other periderm components.

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MATERIAL AND METHODS

Specimens of *Orthograptus gracilis* were etched from erratic boulder number 0.212 in the collection of the Institute of Palaeobiology in Warsaw, found in Zakroczym the Vistula valley (Central Poland). They were subsequently cleaned of mineral impurities by being immersed in a 20 per cent solution of the hydrofluoric acid for 48 hours. Dried specimens were used after coating them with coal and gold, for further scoping with a SEM. The specimens for scoping with a TEM were dried in the standard graded alcohol series and propylene oxide. After embedding the samples in Epon 812, the standard ultramicrotome techniques were used. The Tesla 490A and LKB-III ultramicrotomes provided with a diamond knife (DuPont) were used to obtain sections of an approximate thickness of 400—600 A. The sections were placed on grids (100 and 200 mesh), which were coated with a Formvar film. The material was studied with a Cambridge Stereoscan 180 at 20—23 kV and a Tesla BS500 transmission microscope at 60 kV.

SEM OBSERVATIONS

Under the SEM the specimens are covered by a network of ribbons (pl. 31 : 1). Bandages can be seen over the whole surface of the sample without being recorded however on the basal spines (pl. 31 : 2). Most of them are situated near the medial line of rhabdosome on the proximal part of colony. The ribbons are usually placed obliquely in respect to the fuselli and pass over a number of them. The course of the ribbons is either straight or more often slightly sinous. The width of a given ribbon is constant throughout, varying from ribbon to ribbon between 55 μm and 75 μm.

The cortex bandages often display a "rail-way-track" appearance. This is due to bandages margins being distincly elevated in respect to the middle part, and often roller-like (pl. 31 : 1, 2). In many cases it is impossible to recognize any substance filling the space between the parallel margins of the bandages. The roller-like margins are not always paired (pl. 32 : 1). The roller diameter is not stable varying along the length of bandage from 3 to 4,5 μm. At junctions, the underlying margins are often flattened (pl. 34 : 2). Sometimes we can see ribbons vanishing on the thecal surface (pl. 32 : 1).

TEM OBSERVATIONS

The transverse sections of *Orthograptus gracilis* periderm, studied with a transmission electron microscope reveal four components within a fully grown thecal wall, namely: 1. the endocortex, 2. the fusellar layer, 3. the cortex and what will be called 4. taeniocortex, which is the term we suggest for entirety of the ribbons or rollers (pl. 35 : 1).

Particular layers of the cortical deposits are continous over the apertural margin of thecae, pass from outer into the inner cortical coating of the theca and penetrate deeply into thecal cavity. Our observations also indicate the presence of a layer of cortical tissue on the inner surface of the thecal cavity (pl. 37 : 2). The endocortex and cortex are formed due to a strong overlap of outer lamellae of subsequent fuselli. This is, therefore, a dependent mode of cortex formation (Urbanek 1976*a*). The cortex material is typical, composed of straight, unbranched fibrills embedded in an electron-homogeneous and discontinously distributed ground substance (pl. 35 : 1; pl. 37 : 1, 2). Thus, a typical cortical layer can be observed between the fusellar component of the thecal wall and the overlying taeniocortex.

The fusellar component is typical too, the fuselli being of *Acanthograptus* type ($ph_1 + ph_2 + ph_3$) (comp. Urbanek 1976). The characteristic pattern of fusellar fabric is a three-dimensional, loose network with a spongy appearance. The ground substance has not been preserved.

The taeniocortex, covering the outer and sometimes inner surface of the thecal wall (pl. 37 : 2), is organized into ribbons and pillows. Sometimes it forms thin "enamel-like" coatings (pl. 36 : 1). The taeniocortex is seperated from the underlying cortical layer by a denser pelicle made of fibrils or grains (pl. 35 : 1; pl. 36 : 2, 3). During the study of bandages a number of ultrastructural patterns were recognized producing rather an unexpected picture of their differentiation. These are follows:

1. a delicate reticulated fabric: the taeniocortex of thus type consists of peculiar material being produced by a mesh of reticulated tissue made of medium-density fibrills tightly packed and embedded in homogeneous ground substance. The ground substance is formed by the material of lower density. Within the taeniocortex of this type there are

vesicles of both an irregular and regular oval shape. The irregular vesicles are enveloped by a pellicle made of dense bodies or grains (pl. 35 : 1; pl. 36 : 2; pl. 37 : 1).

2. a coarse reticulated fabric: in this case the taeniocortex is made of electron-denser material, no vesicles have been recognized (pl. 36 : 3).

3. a pseudofusellar fabric: this material shows close resemblance to the genuine fusellar fabric, at places passing longitudinaly into the coarse reticulated fabric (the taeniocortex of type 2) (pl. 36 : 1).

One can recognize the similarity of taeniocortex not only to the fusellar fabric, as noted above, but also to the structure of other graptolite tissues. Taeniocortex of type 1 displays similarities to the admembrane accumulations of reticulated tissue recognized within the cortex of *Dictyonema* sp. (Urbanek and Towe 1974: pl. 7 : 1), as well as to the fabric found in membraneous vesicles ("blisters") on the prosicula of *Didymograptus* sp. (Urbanek and Towe 1975: pl. 9 : 1, 2). Taeniocortex of type 2, in turn, resembles the accumulation of the reticulated tissue within the marginal disc in *Mastigograptus* sp. (Urbanek and Towe 1974: pl. 24 : 1, 2 — especially 2).

CONCLUSIONS

We have found so far no bandages formed by a typical cortical material in *Orthograptus gracilis*.

The results obtained do not confirm Andres' (1976, 1977) and Crowther's and Rickards' (1977) opinion as to the character of cortex formation. There are fundamental ultrastructural differences between the genuine cortex and cortical bandages in *Orthograptus gracilis*. The presence of genuine cortical layer beneath the bandages is evidence against the hypothesis that the formation of the bandages is the only way of secretion of cortical derivatives in *Orthograptus gracilis*.

The dependent mode of cortex formation in our graptolite is suggestive of secretion by a continous perithecal membrane (Urbanek 1976*a* and in this volume pp. 595—629) rather than by cephalic disc of the zooid presuming a painting method of deposition.

In conclusion, we would like to point out that one should be very careful when interpreting the structures under study on the basis of SEM investigations alone (Urbanek 1976*b*). Such interpretations may be only incomplete, but sometimes misleading, which is particulary true where fossil material is concerned. The micrographs of the hyphae of the fungus *Phytophtora infestans* may serve as an illustration (pl. 38 : 1, 2, 3). Had that micrographs been considered before the ultrastructural investigations of the bandages and before establishing the relationship of their material with the typical graptolite tissues, one might interprete the bandages as traces of saprophytic organisms which have been fossilized on the periderm surface.

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EXPLANATION OF THE PLATES 31—38

Plate 31

Ultrastructure of cortical bandages in *Orthograptus gracilis* Roemer (SEM)

1. A network of ribbons on the surface of rhabdosome.
2. The basal spine without a network of ribbons.
3. The cortical bandages. Showing the end of the bandage.

Plate 32

Ultrastructure of cortical bandages in *Orthograptus gracilis* Roemer (SEM)

1. The cortical bandages appearing as paired ridges. Bandages vanishing on the thecal surface.
2. The course of the ribbons: straight and slightly sinous.

Plate 33

Ultrastructure of cortical bandages in *Orthograptus gracilis* Roemer (SEM)
1, 2, 3, Details of ribbons structure.

Plate 34

Ultrastructure of cortical bandages in *Orthograptus gracilis* Roemer (SEM)
1, 2. The bandages with the roller-like margins. The flattened margins at junctions.

Plate 35

Ultrastructure of periderm in *Orthograptus gracilis* Roemer (TEM)
1. The transverse section of wall; ×1400.
   e endocortex, *f* fusellar layer, *c* cortex, *t* taeniocortex, *p* pellicle made of fibrills or grains, *iv* vesicles of irregular shape, *rv* vesicles of regular shape.

Plate 36

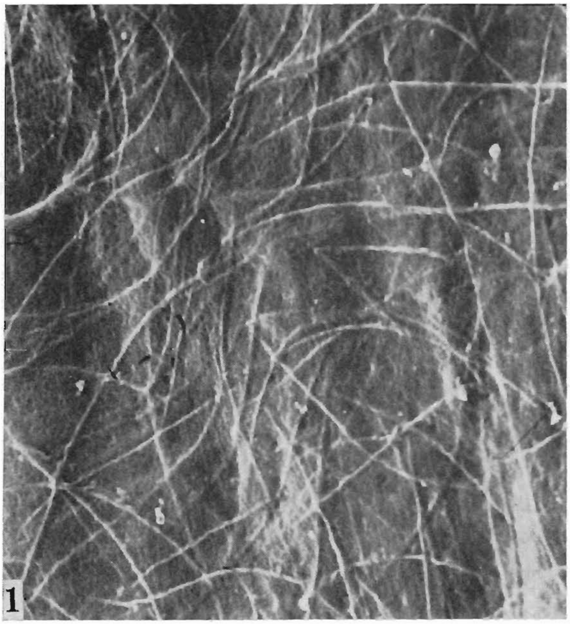
Ultrastructure of taeniocortex in *Orthograptus gracilis* Roemer (TEM)
1. Taeniocortex of type 3; ×13700.
2. Taeniocortex of type 1; ×16800.
3. Taeniocortex of type 2; ×21000.

Plate 37

Ultrastructure of thecal wall in *Orthograptus gracilis* Roemer (TEM)
1. The ultrastructure of the thecal wall with taeniocortex of type 1; ×28000.
2. The section of wall with taeniocortex (type 1) on the inner and outer thecal surface; ×16400.

Plate 38

The micrographs of the hyphae of the fungus *Phytophtora infestans* (SEM)
1, 2. Details of hyphae.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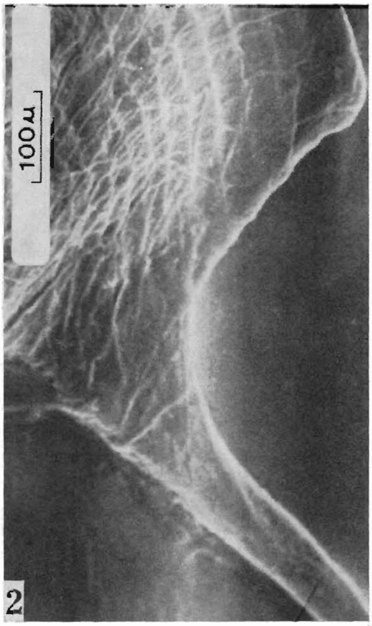
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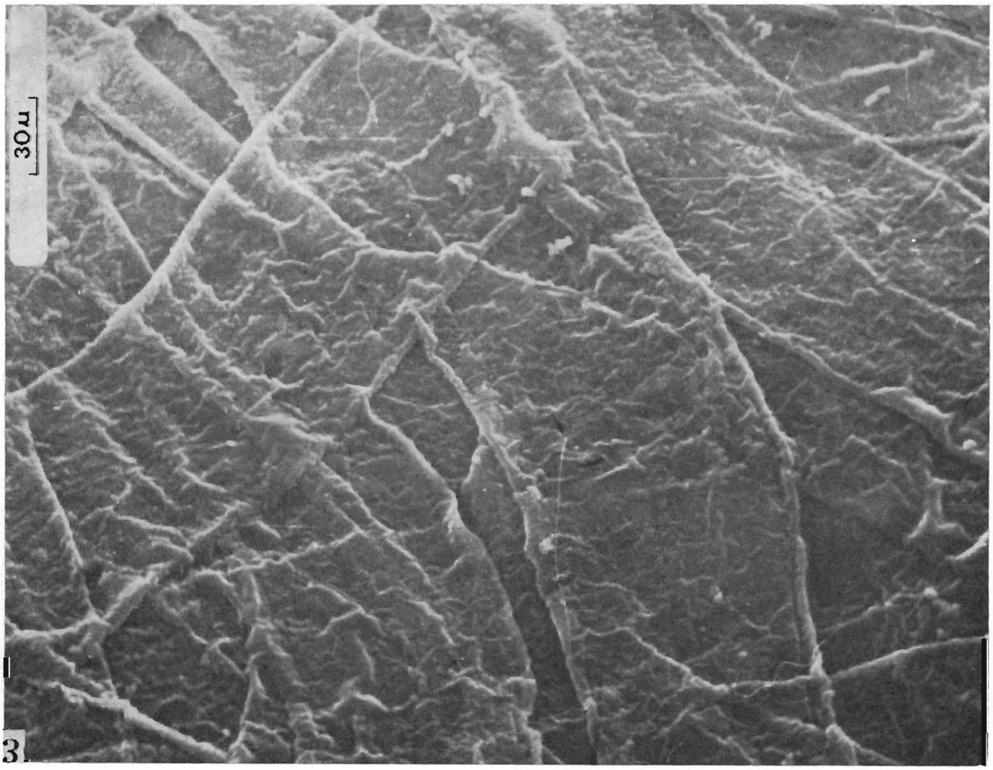
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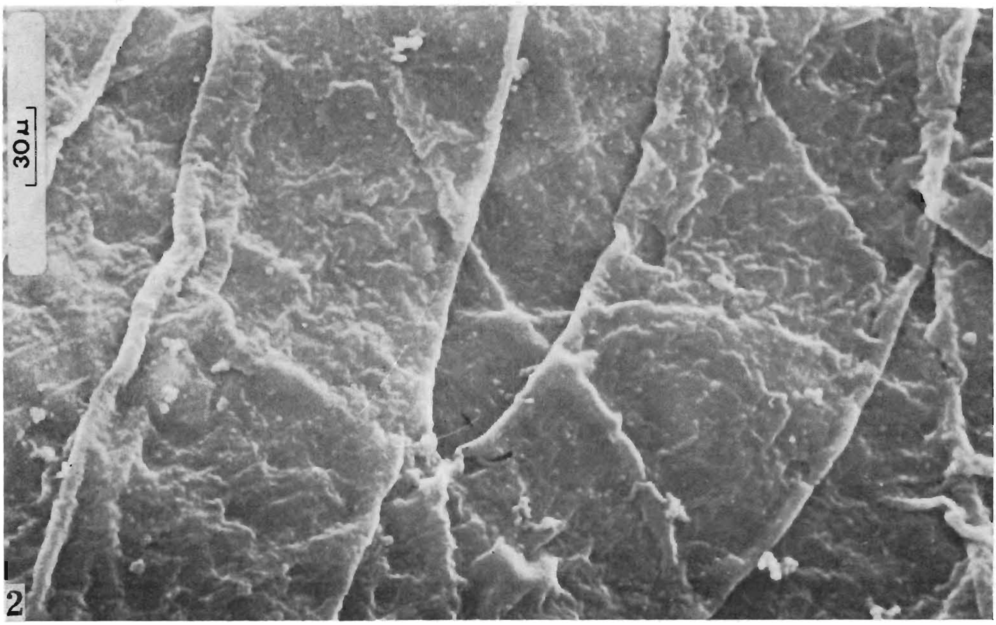
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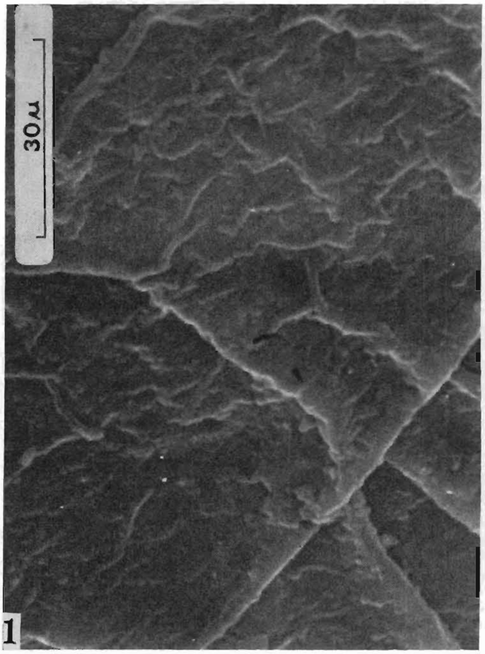
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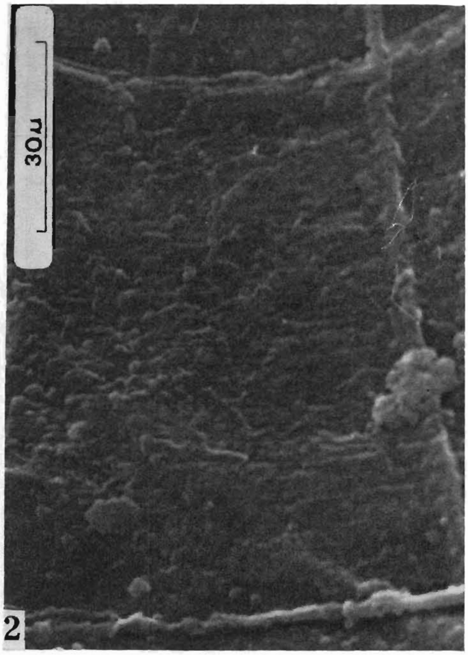
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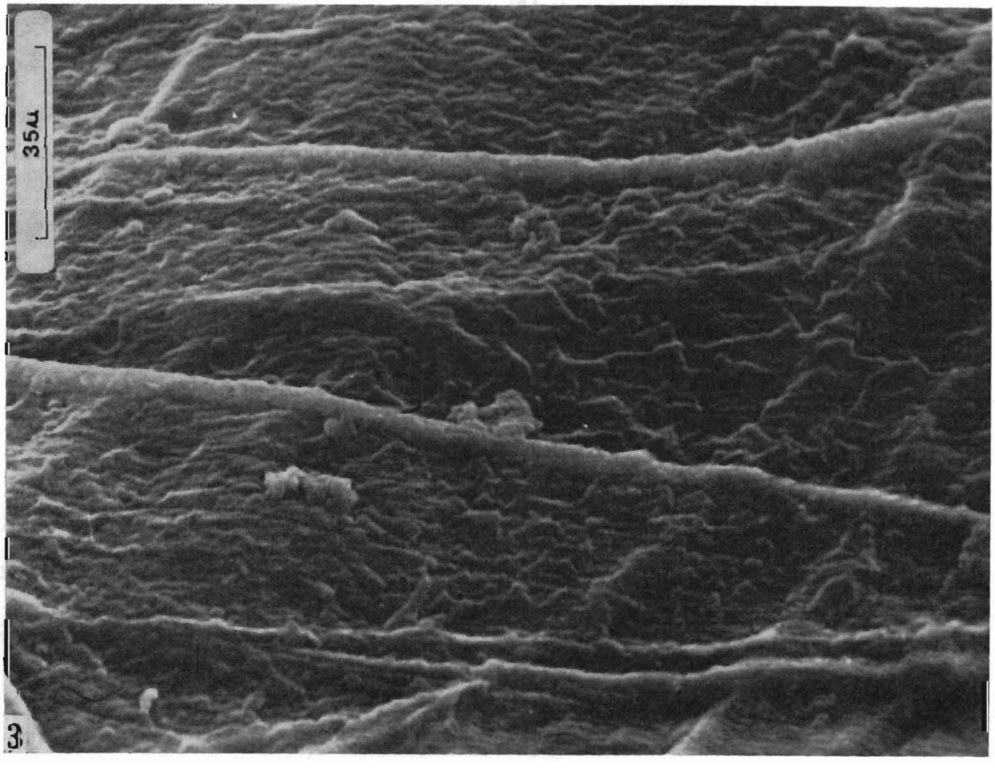
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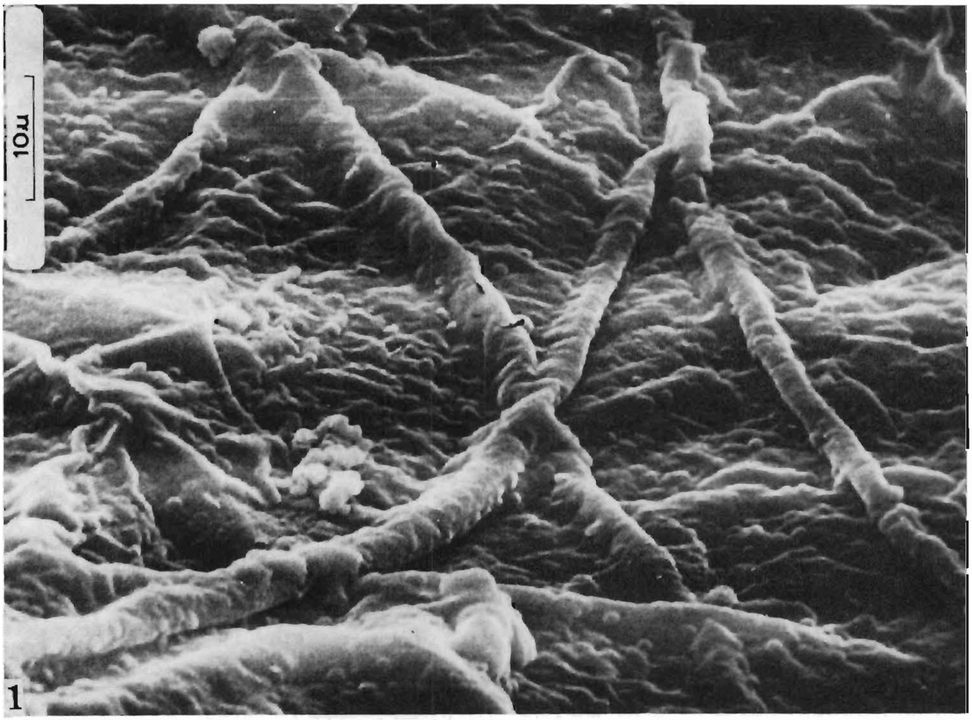
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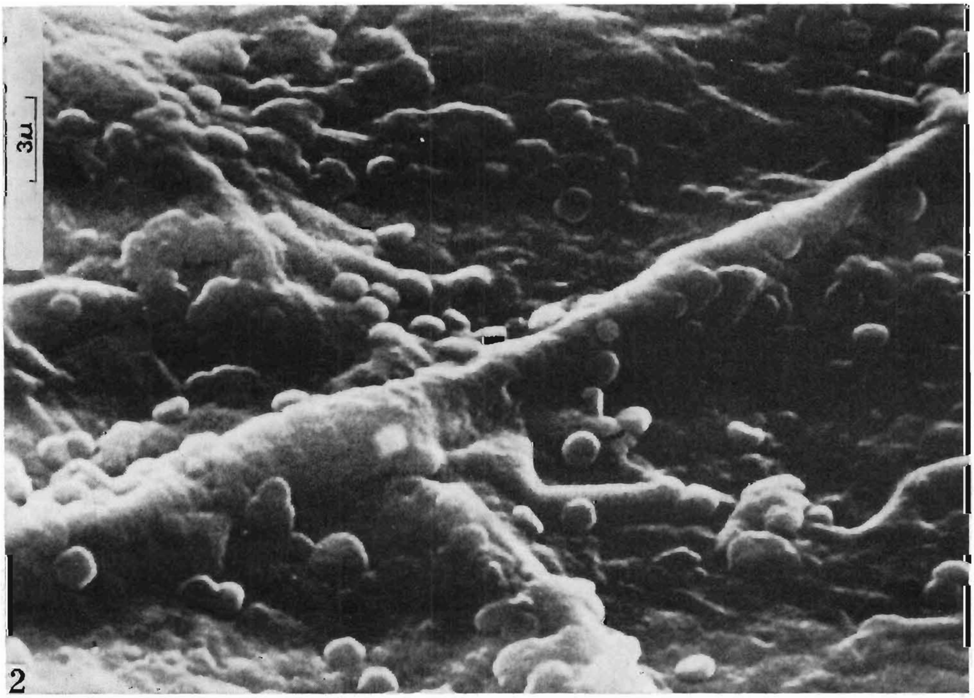
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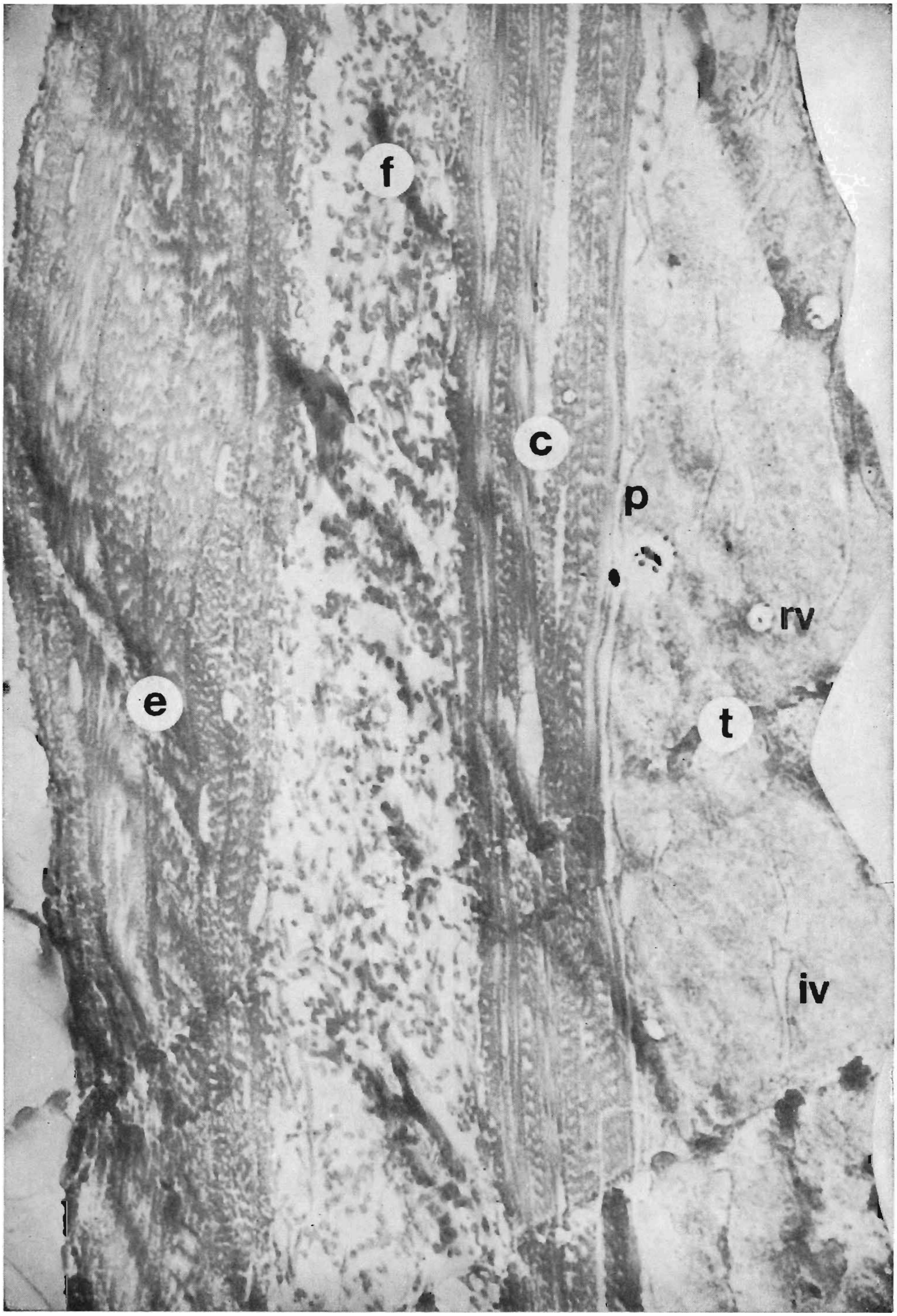
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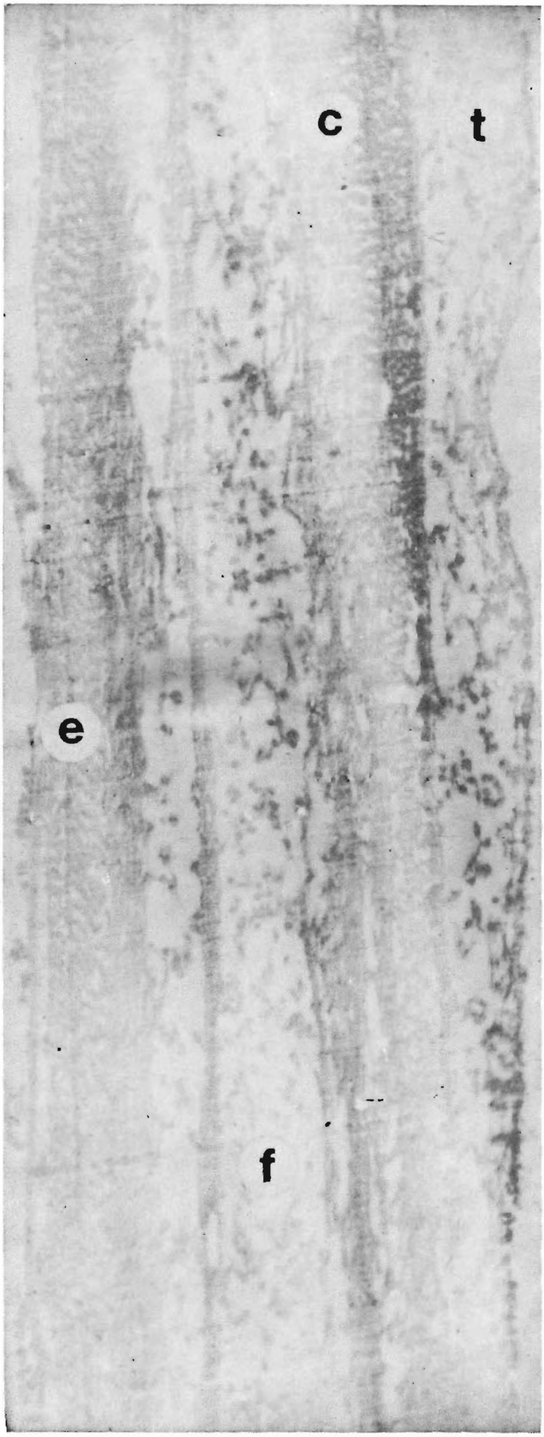
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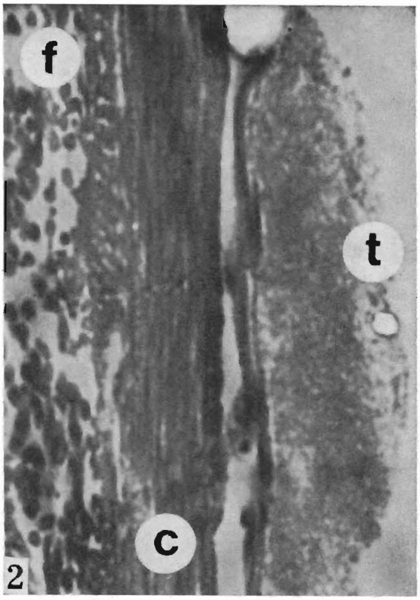
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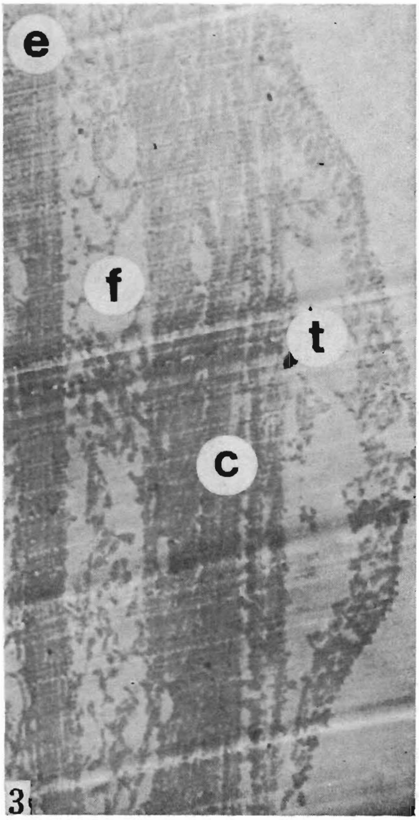
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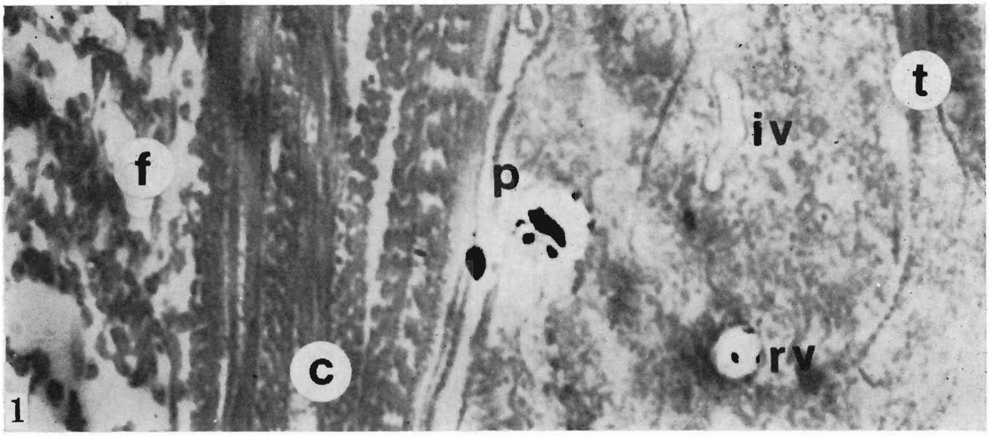
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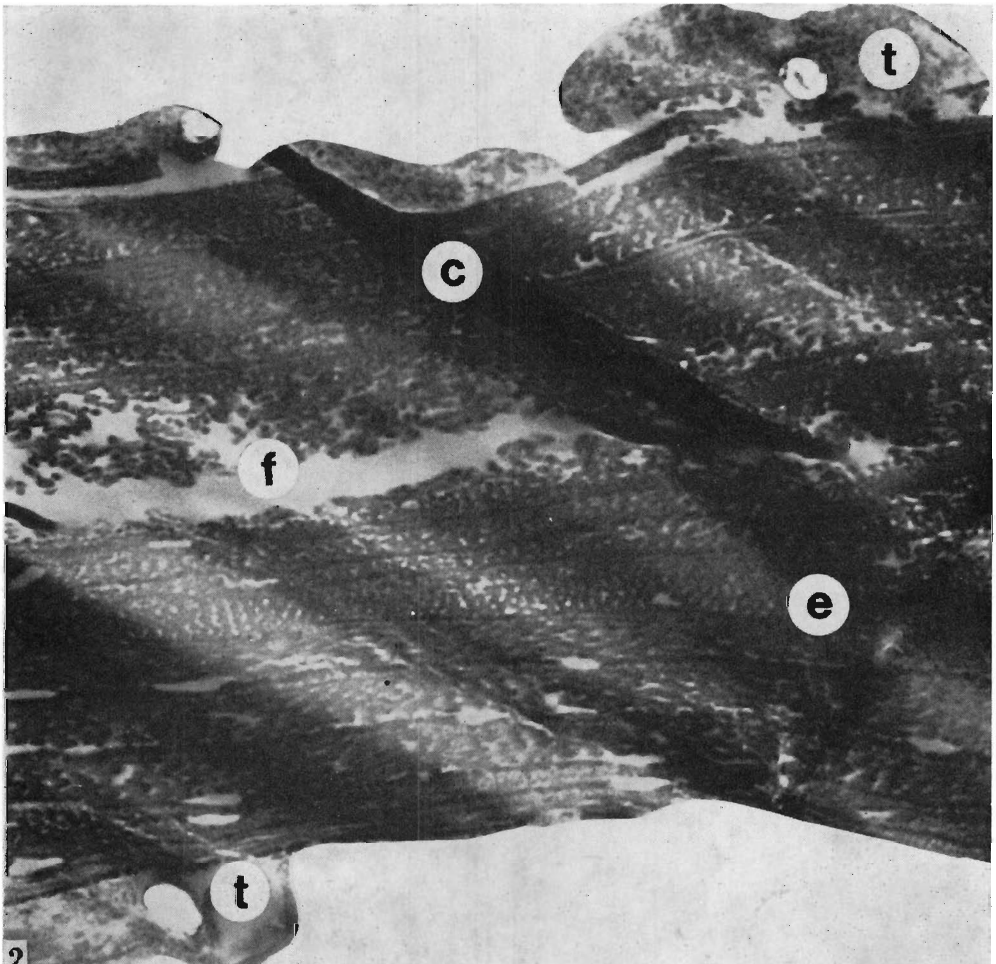
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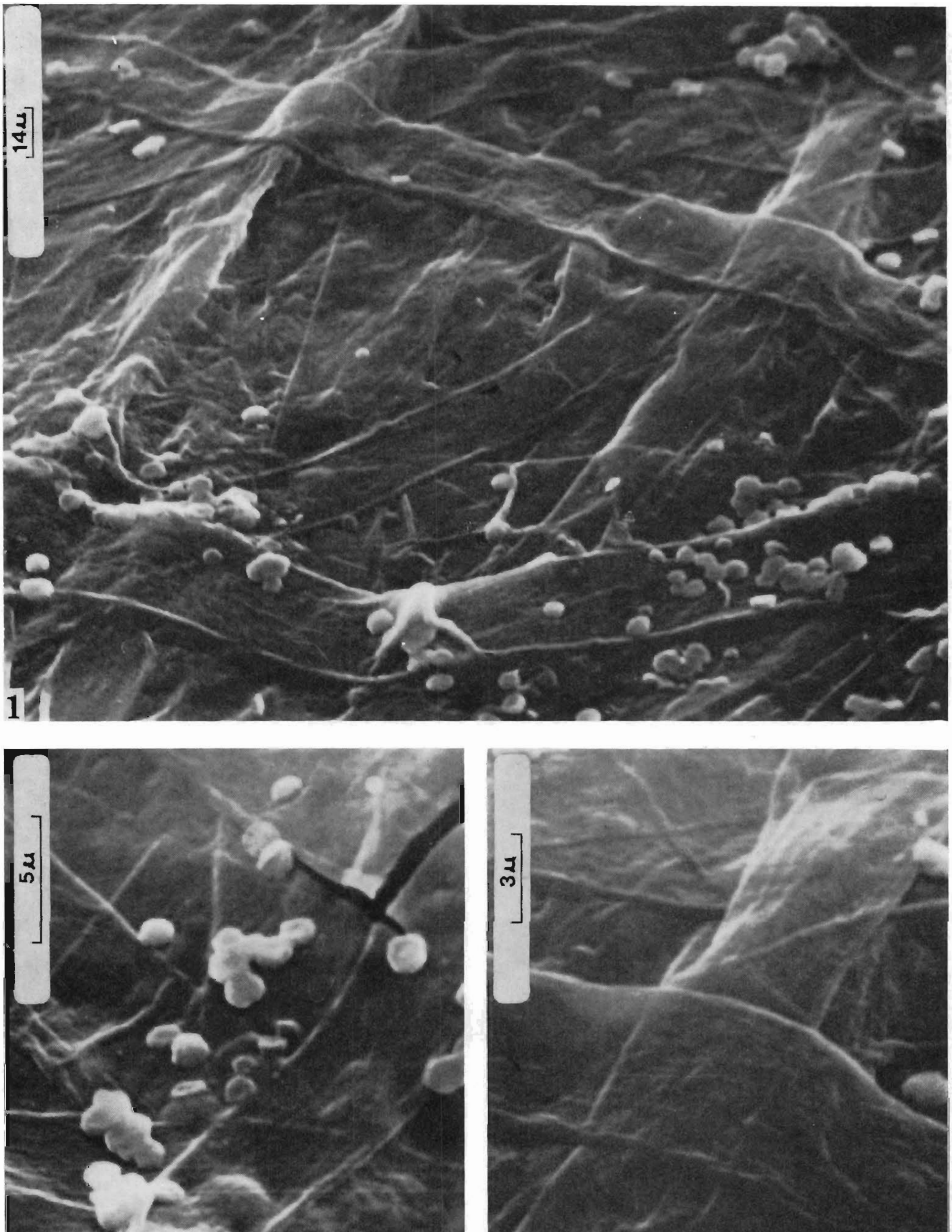
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