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SCANNING ELECTRON MICROSCOPY OF SESSILE GRAPTOLITES

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The surfaces of rhabdosomes in dendroid and tuboid graptolites and in *Mastigograptus* were investigated with SEM. In general the surfaces are remarkably smooth and essentially featureless, even around the apertures. The only exception are subparallel rollers recognized on one specimen of *Dictyonema* sp., which pass at places into accumulations producing a reticulated network. The evidence available indicates a foreign nature these structures which cannot be considered units of secretion of graptolite cortex. The opinion is advanced that the recent data are suggestive of collagen fibrillogenesis occuring immediately adjacent to the surface coat of epithelial cells. The lack of bandages in sessile graptolites and the lack of foreign agglutinated material on their rhabdosomes, the intimate control of fibrillogenesis by epithelial cells in extracellular secretion of collagen are all presented as evidence in favour of the membrane model of graptolite periderm secretion.

Key words: graptolites, scanning electron microscopy, rhabdosome surface, bandages, inclusions, collagen fibrillogenesis, models of secretion.

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INTRODUCTION

Recent light and scanning electron microscopic investigations (Andres 1976, 1977, Crowther and Rickards 1977) on well preserved graptoloids chemically isolated from rock matrix established the presence on the periderm surface of peculiar ribbon-like units (termed also cortical bandages). A considerable number of graptoloid species investigated exhibits a cortex surface composed largely of bandages or similar ribbon-like units. A hypothesis has been advanced that these bandages are universal secretory units of graptolite periderm inherited from pterobranch ancestors. The presence of bandages is considered by their discoverers to be crucial also for understanding the mode of secretion of graptolite periderm (comp. discussion in Urbanek 1978). The cortical bandaging however has not been convincingly established so far in sessile orders of Graptolithina which are generally regarded as representatives of the most primitive adaptive type within the class. The aim of this paper therefore is to present the results of our SEM work on some dendroid (*Dictyonema* Hall, *Acanthograptus* Spencer) and tuboid (*Epigraptus* Eisenack (= *Idiotubus* Kozłowski), *Dendrotubus* Kozłowski, *Kozlowskitubus* Mierzejewski and *Discograptus* Wiman) graptolites, as well as on aberrant (*incertae ordinis*) *Mastigograptus* Ruedemann. *Tubicamara coriacea* Kozłowski, the only representative of Camaroides investigated supplied quite unexpected data concerning the surface structures and fabric involved and will be described separately.

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MATERIAL AND METHODS

The specimens studied and illustrated in the present paper were etched from calcareous erratic boulders of the Baltic origin with the use of 10—15% acetic or hydrochloric acid. They were subsequently cleaned of mineral impurities by immersion in a 20 per cent solution of hydrofluoric acid for 48 hours. The dried specimens were carbon and gold coated for further examination with the SEM. The specimens were studied with a Cambridge Stereoscan 180 at 20—23 kV.

The drift material used in the present paper stems from the collection of boulders at the Institute of Palaeobiology of the PAN in Warsaw (boulders marked O.) and from the collection housed in the Museum of the Earth of the PAN in Warsaw (marked MZ).

The specimens of *Dictyonema* sp. were etched from an erratic boulder found between Wyszogród and Zakroczym, Valley of the Vistula River (60 km north of Warszawa, central Poland) and numbered O.129. The age of the boulder is probably Ordovician.

Specimens of *Acanthograptus* sp. were etched from an erratic boulder found in Jarosławiec (Western Pomerania, Baltic coast) and numbered O.107. The age of the boulder is probably Ordovician.

The specimen of *Mastigograptus* sp. was etched from an erratic boulder found in Mochty, Valley of the Vistula River (comp. above O.129) numbered O.181. It is probably of Middle Ordovician (Viruan) age.

Specimens of *Epigraptus* sp. were found in an erratic boulder collected in Zakroczym, Valley of the Vistula River and numbered O.242. The association with *Palaeotuba polycephala* Eisenack is indicative of its Middle Ordovician (Viruan) age (probably an equivalent of the Kukruse stage, C_{II} in Estonian sequence).

Discograptus schmidti has been isolated from two boulders, namely O.495 found in Mochty, Valley of the Vistula River, and in MZ/24 found in Orzechowo, Western Pomerania, Baltic coast. *Discograptus* is Upper Ordovician (see Bulman and Rickards 1966: 67).

The specimens of *Dendrotubus* sp. were etched from MZ/88 found in Poddębie, Baltic coast. The occurrence of *Mochtyella cristata* Kielan-Jaworowska indicates the Ordovician age of the boulder.

Kozlowskitubus erraticus was isolated from the boulder MZ/47, found in Orzechowo (Western Pomerania, Baltic coast) and being Upper Silurian (probably Late Ludlovian) in age.

SEM OBSERVATIONS

Dictyonema sp.

The predominant patterns recognized with the SEM on the rhabdosome of *Dictyonema* sp. are almost smooth surfaces (pl. 9: 1) or surfaces with faint traces of striation due to a regular arrangement and parallel orientation of the underlying fibrils (pl. 12: 2).

The apertural margins of autothecae are also smooth with faint traces of bowlike striation seen places (pl. 9: 2). A thecal wall broken just beneath the aperture reveals a series of superimposed and overlapping fuselli. Within a given fusellus, a body filled with spongy material and a dense outer pellicle may be recognized (pl. 9: 4, *p*). The cortical coating of the aperture (pl. 9: 4, arrowed) is again smooth and bears no traces of "bandages". Also the area around the aperture shows no traces of bandages or other ribbon-like structures, although admitting the pterobranch model of secretion as postulated by Crowther (1978), one could expect an accumulation of them (pl. 9: 2).

Only a few spots of rhabdosome show specific surface structures, which tentatively may be classified into: 1) parallel or subparallel structures delimiting ribbon-like areas (pl. 9: 5), 2) more or less irregular rollers delimiting lobate areas, at some places crowded enough as to produce a reticulated network (pl. 9: 6), 3) surface structure of the periderm proper in contrast to 1) and 2) which are structural features superimposed on the periderm.

Category 1) deserves special attention as it bears close resemblance to a particular variety of ribbon-like structures described in *Orthograptus gracilis* (Roem.) and named "railway tracks" (Andres 1976, 1977; Crowther and Rickards 1977; Crowther 1978). Delimiting margins are roughly parallel and distinctly protruding over the surface (pl. 10: 2, 3; pl. 11: 1, 2). They show a quasi-segmentation (pl. 10: 4) or dense growth lines (pl. 10: 6), only sometimes being smooth (pl. 10: 5). The presence of growth lines might be a primary feature, the remaining being most probably preservational ones.

There are no traces of material deposited within a given ribbon-like structure (between two "rails"). The surface of the periderm delimited by the two parallel rollers does not differ from the surface of adjacent areas and certain local structural features of the periderm (like lines, small discontinuities, margins) pass across the "tracks" (comp. pl. 11: 2; pl 12: 3). This may indicate that the ribbon-like structures observed in *Dictyonema* sp. have in fact nothing in common with the units of secretion of the cortical portion of periderm. They consist only of rollers ("rails") clearly deposited over the surface and bear no traces of material between them — so one can hardly speak of "railway tracks". This problem is discussed in greater detail on p. 204.

In a few cases the rollers join each other to form closed, loop-like terminations. These closed ribbon-like structures form a transition toward category 2) of surface structures observed in *Dictyonema* sp.

Category 2) consists of generally short, fairly irregular rollers delimiting the area of periderm with lobate outline (pl. 9: 6). Sometimes isolated (pl. 10: 1), they frequently are rather densely packed to produce an irregular network of "rails" (pl. 9: 6). The structure of the rollers seems to be the same as described above. Like in category 1) there are no traces of individual deposits within the area delimited by the rollers, and a number of structural lines of the underlying periderm may continue across many of the lobate areas (pl. 12: 3). The probable significance of this observation is discussed below (pp. 204—205).

Some of the patterns observed may be considered to be the surface structures of the periderm proper, accounting for the primary architecture of the cortex. These are namely: 1) parallel arrangements of coarse fibers (most probably bunches of cortical fibrils) sometimes showing a criss-cross pattern due to the exposure of different layers of cortical tissue (pl. 12: 2), 2) large homogenous areas covered with numerous pits (pl. 12: 4). These pits may be interpreted as intrasheet vesicles of cortical tissue (Crowther and Rickards 1977: 17) as described by Urbanek and Towe (1974: 4, pl. 11: 1), which were exposed due to destruction and removal of the upper part of the sheet fabric separating two adjacent cortical layers. A closer examination of the distribution of these pits reveals that they are grouped into clusters (pl. 12: 5). Similar pits were recognized by Crowther and Rickards (1977: pl. 9: 6) in *Dendrograptus oelandicus* Wiman. Their nature is largely enigmatic but a possible biological interpretation is discussed below (p. 204).

At one spot of the rhabdosome faint traces of orthogonal fibril arrangement have been recognized (pl. 9: 3). These rather narrow belts (packages, bunches) of fibrils might be suggestive of genuine bandages as recognized by Crowther and Rickards (1977) in *Climacograptus typicalis* Hall. However, abrupt and uneven border lines of this structure (see arrows on pl. 9: 3) indicate their secondary origin due to partial destruction and removal of a given cortical layer ("delapidation") as pointed out by Urbanek (1978: 616—617, fig. 8).

Acanthograptus sp.

SEM micrographs of the periderm, both on the stipe and on isolated autothecae, abound in roughnesses of the surface (pl. 13: 1—2), but do not reveal any traces of bandages. These roughnesses were formed most probably due to corrosion of the primary surface prior to fossilization. The majority of them outline a certain kind of elevations or saddle-like structures, convex toward the apertures of the thecae (pl. 13: 1, arrowed). This might account for the features of periderm deposition in the form of fairly large overlapping lobate areas which were exposed due to corrosion of the surface.

Mastigograptus sp.

The surface of the periderm on the main stipe and on lateral thecae examined with the SEM appears rather smooth, with numerous shallow fissures and minute pits (pl. 14: 1). These fissures show usually an irregular distribution with predominantly horizontal and oblique orientation in respect to the main axis of the thecae, dividing the surface into innumerable small fields (pl. 14: 1, arrowed). This effect is caused, most probably, by a sort of corrosion of the periderm. In some cases one could observe, on the same portion of the stipe, numerous parallel lines corresponding most probably to the fibrils on the exposed cortical layer (pl. 14: 2; pl. 16: 3).

Epigraptus sp.

The thecorhiza examined with SEM reveals smooth, almost enamel-like surfaces with a faint stration suggestive of a fibrous nature of the underlying structure (pl. 15: 2).

The bithecae and basal parts of autothecae are also rather smooth, having, however, a number of coarse fibers, frequently twisted or creased and showing horizontal or longitudinal orientation (pl. 15: 1, arrowed). A distinct annulation is evidence of thecal fusellar structure, its wider portions (rings) corresponding to the protruding margins of fuselli so-called heads (pl. 18: 1, arrowed). The same pattern has been recognized in the upper portion of autothecae (pl. 16: 2). Their apertural part shows similar annulation, the surface being covered by numerous coarse fibers oriented longitudinally or obliquely and crossing a number of underlying fuselli (pl. 16: 2, f). A broken apertural margin seen at higher magnification shows numerous coarse fibers and may correspond to the section through apertural thickening (cortical derivative) or to the edge of fuselli (pl. 16: 1).

In spite of the satisfactory state of preservation no traces of bandages were recognized.

Discograptus schmidti Wiman, 1902

Except for numerous cracks and fissures due to the state of preservation, thecorhiza is very smooth, almost enamel-like (pl. 17: 1). At some spots examined under high magnification one can see a coarse fibrous structure, with a parallel arrangement of fibers (pl. 17: 2).

The bithecae, rising only somewhat above the thecorhiza, have also a smooth surface, except in one case where parallel lines placed horizontally might correspond to the traces of fuselli (pl. 17: 3).

The autothecae gathered into thecal groups and producing characteristic branches (twigs) are perfectly smooth, from their bases to the upper portions inclusively (pl. 20: 1). The apertural parts of autothecae are usually adnate to the wall of the adjacent autotheca of a given thecal group (pl. 18: 2). A detailed examination of the entire apertural area shows only a smooth apertural thickening and equally featureless surface of the neighbouring thecal wall (pl. 18: 2). Some autothecae show parallel horizontal lines all along from their bases to the upper portions. These lines, distinctly protruding over the surface, correspond to the traces of fuselli (pl. 20: 1). In some cases one could observe a characteristic oblique suture between fuselli (arrow). In spite of an excellent state of preservation of the specimens examined no traces of bandages of any sort were found within the apertural area of the autothecae.

On the internal surface of the encrusting portion of a specimen regarded as a single autotheca one could observe a small area covered with a spongy-reticulated material (pl. 20: 2). This material might be classified as a surface structure of the periderm proper as observed in *Dictyonema* sp. (p. 200) and bears a superficial resemblance to sheet fabric with pits.

Kozlowskitubus erraticus (Kozłowski, 1963)

The material under study consists of two complete old colonies. The surface of all colony elements does not reveal any traces of "bandages". It resembles closely the rough surface of *Acanthograptus* sp. periderm (pl. 19: 2). These roughnesses might be interpreted as corrosion of the primary surface prior to fossilization. The boundaries of fuselli are visible only on the youngest autothecae, whereas on the older ones they are completely masked by the cortical tissue.

Dendrotubus sp.

The specimen under study consists of only two incomplete autothecae. The periderm examined with SEM reveals a smooth, almost enamel-like surface, with indistinct traces of fuselli (pl. 19: 1). No traces of "bandages" were recognized in spite of an excellent state of preservation of the periderm.

SCANNING ELECTRON MICROSCOPY AND THE MODE OF SECRETION OF GRAPTOLITE PERIDERM

The two conflicting theories of skeletal tissue secretion in graptolites are based on a rather limited number of observations and allow different predictions concerning the structural pattern of periderm in sessile graptolites (comp. Urbanek 1978). The pterobranch model suggests that sessile orders of graptolites preserved an ancestral mode of secretion. Their cortex, therefore, should be made of distinct and ample bandages or ribbon-like structures, considered in the light of this theory as units of secretion produced by glands situated on the cephalic discs of zooids. It is believed that these units formed as a result of the animal creeping and dragging its cephalic disc over the surface of rhabdosome (Andres 1976, 1977; Crowther and Rickards 1978; Crowther 1978).

The present preliminary survey of scanning electron microscopy of sessile graptolites is an attempt at providing more data and at checking the evidence in favour or against this theory. The following main conclusions may be draw from the material investigated:

1) The surface of rhabdosome in sessile graptolites (Dendroidea, Tuboidea and *Mastigograptus*) is in most cases fairly smooth and bears no traces of ribbon-like structures.

A conclusion may be advanced that the periderm in sessile orders of graptolites is free of the well defined scarp edged bandages, so characteristic of e.g. many diplograptids. The smooth appeavance of periderm surface does not exclude, however, the presence of ribbon — like units of secretion with indistinct tapered lateral margins (as suggested already by Crowther and Rickards, 1977: 12). It should be stated, that the presence of such "hidden" cortical bandaging has not yet been demonstrated in sessile graptolites.

2) The surface structures similar to the "railway tracks" described

by Andres (1976) in *Orthograptus gracilis* (Roem.) occur sporadically on the surface of *Dictyonema* sp. Closer examination of the structures in question reveals, however, that they consist of "rails" only, namely of parallel or subparallel rollers, protruding over the surface of the periderm proper, without any material deposited within the rollers. It is clear therefore, that these structures cannot be considered as basic units of secretion of genuine graptolite periderm as they do not containt any cortical material and do not contribute to the formation of the rhabdosome cortical coating.

The very nature of these structures is obscure but it might well be that they are secondary and foreign to the graptolite skeletal tissues. This is indicated also by their sporadic and scanty distribution and gradual passage into irregular rollers delimiting the lobate fields of the surface. One cannot exclude their *post mortem* formation due to some non-graptolite organisms and prior to the burial or rhabdosomes in the sediment.

The relation to the genuine "railway tracks" as described in *Orthograptus gracilis* (Roem.) is unclear. Urbanek and Mierzejewska (1978) found on ultrathin sections that their ribbon-like structures consist or parallel rollers and a thin layer of material spread between them. Such ribbons provide therefore, some additional material for the surface of rhabdosome, which, however, differs distinctly from the cortical fabric. Certain general resemblance between the "rails" in *Dictyonema* sp. and the "railway tracks" in *Orthograptus seems* incidental but a final solution is impossible without further investigations.

The material described in the present paper does not confirm, in our opinion, the pterobranch model of graptolites periderm secretion, but, giving exclusively negative evidence, it cannot be considered crucial for the solution of the entire problem. On the other hand, it does not confirm Urbanek's (1978: 624) prediction either. This latter was based on the "membrane model" and postulated that in sessile graptolites the periderm surface should bear traces of broad areas of secretion. It seems, however, that smoothness of rhabdosome surfaces in sessile graptolites is indicative of gradual thinning (tapering) of layers, usually sealed with sheet fabric. This is why the surface of sessile graptolite rhabdosome is rather featureless. But it does not provide any crucial evidence as far as the shape of secretory units is concerned.

The presence of numerous pits which correspond to intrasheet vesicles recognized with TEM may be explained as a trace of particular glands gathered into clusters within the perithecal membrane (comp. p. 200). Such vesicles or their traces (pits) are a characteristic graptolite feature which has not been encountered within the peridermal structures in pterobranchs.

Our studies on surface micromorphology provide a certain argument concerning the possible microenvironmental conditions of graptolite skeleton. Admitting the "pterobranch model", one postulates at the same time a steady exposure of a growing skeleton to the external environment. Thus *Rhabdopleura* displays a special outer layer of the zooidal tube which shows traces of destructive influences of external environment upon the primary wall of the tube (Dilly 1971). In cephalodiscid pterobranchs, in turn, the surface of the coenecium is frequently covered with foreign material (grains of sand, spiculae of sponges, diatoms, minute fragments of shells etc.) so as to give them an almost "arenaceous" look (Andersson 1907; Ridewood 1918; John 1931). This is a result of these particles, sticking to the soft and viscous surface of the coenecium. Andersson (1907) observed that many cephalodiscids were covered with inclusions of foreign particles, while the tubes of *Cephalodiscus (Orthoecus) rarus* Andersson were perfectly clean and devoid of sand grains. This was considered a species specific character by Andersson (*ibidem*). Ridewood (1918 *a*, *b*) observed that the inclusion of foreign particles was not a constant character of any species of *Cephalodiscus*, but is purely local, depending rather on immediate surroundings. In unsheltered spots where particles constantly rain from above, coenecia are encrusted with them, but, when sheltered, the animals have their coenecia perfectly clean and "leathery" (nonarenaceous). John (1931) shared the above opinion of Ridewood and indicated that colonies of the same species differ markedly in the quantity of foreign material embedded into the coenecium, which seems to depend on the local conditions of their growth. He has described (*ibidem*) *Cephalodiscus (Orthoecus) fumosus* which is buried in the common mass, formed of a dense agglutination of minute sand grains. John (*ibidem*: 239—40) does not exclude that sand grains may be considered a regular character of that species and believes it possible that the first zooid of the colony always selected loose sandy bottom. While this opinion remains controversial and cannot be definitely established, it is safe to generalize that the inclusion of foreign material and in some cases also the presence of epifauna (Andersson 1907 mentions ctenostomate bryozoans which frequently settle on coenecia of cephalodiscids) is an ecological marker of the steady exposure of the growing skeleton to the outer environmental agents.

The model of secretion of graptolite periderm advocated by Crowther (1978) is to a large extent based on cephalodiscids and consequently presumes a similar secretionary behaviour in graptolite zooids. In both groups, a growing skeleton would be directly exposed to the outer environment, being continuously covered by fresh secretions of the zooids cephalic discs.

Observations made with TEM on graptolites do not indicate the presence of an outer layer changed by "abrasive" influences of an external environment. The outermost layer of cortex is sealed with normal sheet fabric, which does not differ from the sheet fabric of the underlying layers. There are no traces of secondary decomposition of cortical fibrils in peripheral parts of a given layer suggestive of destructive environmental influences (comp. Urbanek and Towe 1974).

Observations made with TEM reveal that the surface of graptolite rhabdosomes (sessile and free-living) is fairly smooth and generally lacking such traces as could be ascribed to an adherent foreign material (e.g. cavities and impressions).

The essentially clean and smooth surface of rhabdosomes in sessile graptolites speaks in favour of some "protective" layer of soft tissues as suggested by the membrane model of graptolite skeletal tissue secretion.[1)]

Bjereskov (1978) who investigated some interesting cases of pyritization of graptolite remains with X-rays, has found accumulations of pyrite within the thecae and apertures. She interpreted them as traces of the zooid's body and presumable lophophore but failed to identify an outer layer of pyrite surrounding the rhabdosome and that might be indicative of the presence of cortical coating. As pointed out by Urbanek (1978, in a discussion of the paper submitted by Bjereskov), her observations are indecisive so far, and not unlike the case when the surface of rhabdosome was covered by fresh secretions and mucus substances exposed to the environment, they easily may serve as centers of pyrite nucleation. Bjereskov's observations do not supply, therefore, arguments capable to falsify one of the models of secretion of graptolite skeleton.

There is evidence of secondary deposits over the primary wall in cephalodiscid pterobranchs. Its value has been underestimated in earlier discussions on skeletal tissues secretion in graptolites. Whether these deposits are accumulation, of ribbon — like elements has not been established safely, except that they are composed of growth bands with spindle-like outline when seen on sections, and as such are considered to be equivalents of cortical bandages (Dr. D. Andres, unpublished data). However, the lack of direct evidence concerning the bandage-like units in *Rhabdopleura* is worth to be mentioned in view of its transient position in the series *Cephalodiscus* — *Rhabdopleura* — Crustoidea (the vertical fibres on the outer surface of *Rhabdopleura* tubes, recognized by Dilly (1976) are entirely inconvincing as equivalents of bandages, and their origin may be rather ascribed to the lophophore than to the cephalic disc). This is especially important in view of the great significance that the pterobranch model attaches to the shape of the presumed secretionary units in the secondary deposits of *Cephalodiscus* (while the fabric is considered as having small or no significance at all).

[1)] Crowther, P. R. (in press, The fine structure of graptolite periderm. Special Paper in Palaeontology, vol. 26) has independently inferred that the pterobranch model implies a possibility of foreign debris inclusion into the body of cortex in sessile graptolites. Moreover, he has found and example of a foreign inclusion in *Dendrograptus oelandicus* Wiman. His finding might weaken the value of our arguments against the pterobranch model as developed above.

What we could expect accepting the pterobranch model is, a frequent occurrence of foreign inclusions in sessile graptolites. In constrast to these expectations, we find smooth surface of periderm even on basal discs and similar basal structures like thecorhiza, which are immediately adjacent to the bottom sediments. It is worth mentioning that the well known Tremadocian fauna of sessile graptolites described by Kozłowski (1949) was embedded secondarily in colloidal mass of silica. Primarily they had lived on sandy bottom sediments, that were later transformed, due to diagenesis, into the glauconitic sandstone. Despite an environment abundant in mineral particles which could be incorporated into the rhabdosome wall, all this fauna has surprisingly smooth surfaces, usually pyritized. This smoothness can hardly be ascribed to the etching procedures. Thus, the presence of certain protecting film of soft tissue seems again probable as a factor responsible for the smooth and clean surfaces of planktonic and sessile graptolites.

When elaborating his version of the membrane model the senior author (Urbanek 1976) was trying to formulate an "all embracing theory", namely a theory which explains structural features common to both pterobranchs and graptolites, as well as the peculiar features of graptolites alone. The approach of the adherents of the pterobranchs model is piecemeal instead — they offer an explanation of certain features of graptolites, ignoring for the time being other important problems which a simple pterobranch model cannot adequately solve. The pterobranch model seems to offer a more adequate explanation of such a striking feature of graptoloids as cortical bandaging leaving, however, a number of important questions unresolved (e.g. the formation of nema and especially specialized derivatives of nema in particular; the problem of morphogenetic integration of zooids activity within a single colony). In these respects the membrane model demonstrates in our opinion certain prevalence over the competitive point of view. The membrane model, implies fibril formation in relative isolation from outer environment, perhaps beneath a sheet of soft tissue within "milieu intérieur" of the body. This may be particularly true when we take into account the probably collagenous nature of cortical fibrils (Towe and Urbanek 1972; Urbanek and Towe 1974). This view has been accepted and supported by Crowther and Rickards (1977). The formation of collagen fibrils (fibrillogenesis) on the free surface, open toward direct influences of an external environment seems less probable. Their formation in extant organisms occurs in the environment controlled by the living tissues.

This is also true in respect to *Lumbricus* and other annelids cited frequently as an example of an extracellular addition of new layer of collagen fibrils without any protection of newly formed fibrils from the external environment. Nevertheless, the material is deposited from the inside and microvilli extend through the annelid cuticle and therefore suggest a control of the entire structure by the underlying epithelial cells. The fibrillogenesis of collagen in small amounts of secretion "painted" immediately on to the outer surface of periderm provides therefore no true analogy to the secretion of the annelid cuticle. Such fibrillogenesis could be interpreted as occurring due to the self-assembly of tropocollagen molecules, but the instances of similar precipitation of soluble collagen "*in vitro*" provides evidence of high sensivity of this process to a number of physico-chemical agents (temperature, pH, ions). In each case somewhat differently organized fibrils appear responsible for the well known polymorphism of collagen. One could expect therefore that a variety of environmental factors interfering with fibrillogenesis would be responsible for a great variation in shape and size of the fibrils, which is directly contrary to the uniform composition of cortex in each given graptolite species examined.

The vertebrate fibril formation *in vivo* is a complex process most probably involving the enzymatic system of peptidases and proteases which could be also inhibited by a number of environmental factors (Bailey, Robins and Meat 1976). Similar enzymatic steps in collagen biosynthesis probably occur in the invertebrate collagen fibrillogenesis but are little known at present (Adams 1978). The evidence available is partly contradictory, but it seems safe to generalize that the collagen excreted by epithelial cells precipitates into fibrils immediately close to the cell surface and its fibrillogenesis occurs in the domain of their surface coat. Thus the epithelial cells control the extracellular morphogenesis of collagen macromolecules also by timing and determining the site of their discharge (Trelstad *et al.* 1974). A rather intimate relation between the secretory cells and collagen formation seems to be in support of the membrane model and reject the simple model of self-assembly in small packets of secretion exposed directly to the influence of the external environment.

REFERENCES

ADAMS, F. 1978. Invertebrate Collagens. — *Science*, **202**, 4368, 591—597.

ANDERSSON, K. A. 1908. Die Pterobranchier der Schwedischen Südpolar-Expedition 1901—1903, 132 pp. Stockholm.

ANDRES, D. 1976. Graptolithen aus ordovizischen Geschieben und die frühe Stammesgeschichte der Graptolithen. — Inaugural-Dissertion zur Erlangung der Doktorwürde des Fachbereiches 24, Freie Universität Berlin, 75 pp. Berlin 1976.

— 1977. Graptolithen aus ordovizischen Geschieben und die frühe Stammesgeschichte der Graptolithen. — *Paläont. Z.* **51**, 1/2, 52—93.

BAILEY, A. J., ROBINS, S. P. and MEAT, A. R. C. 1976. Current topics in the biosynthesis, structure and functions of collagen. — *Sci. Prog.*, **63**, 251, 419—444.

BJERESKOV, M. 1978. Discoveries on graptolites by X-ray studies. — *Acta Palaeont. Polonica*, **23**, 4, 463—471.

BULMAN, O. M. B., RICKARDS, R. B. 1966. A Revision of Wiman's Dendroid and Tuboid Graptolites. — *Publ. Pal. Inst. Uppsala,* **65**, 1—72.

CROWTHER, P. R. 1978. The nature and mode of life of the graptolite zooid with reference to secretion of the cortex. — *Acta Palaeont. Polonica,* **23**, 4, 473—479.

— and RICKARDS, R. B. 1977. Cortical bandages and the graptolite zooid. — *Geologica et Palaeontologica,* **11**, 9—46.

DILLY, P. N. 1971. Keratin-like fibers in the hemichordate *Rhabdopleura compacta.* — *Z. Zellforsch.,* **117**, 502—515.

— 1976. Some features of the coenecium of *Rhabdopleura compacta.* — *Cell. Tiss. Res.,* **170**, 253—261.

JOHN, C. C. 1931. *Cephalodiscus.* — *Discovery Reports,* **3**, 223—260.

KOZŁOWSKI, R. 1949. Les Graptolithes et quelques noveaux groupes d'animaux du Tremadoc de la Pologne. — *Palaeont. Polonica,* **3**, 1—235.

RICKARDS, R. B., CROWTHER, P. R. 1978. New observations on the mode of life, evolution and ultrastructure of graptolites. *In*: G. Jarwood and B. R. Rosen (eds.) "Biology and systematics of colonial organism". Systematic Assoc. Spec. Vol., **11**, 397—410. London and New York.

RIDEWOOD, W. G., 1918*a*. *Cephalodiscus.* British Antarctic ("Terra Nova") Expedition 1910, Zoology, **4**, 2, 11—82.

— 1918*b*. Pterobranchia. Australasian Antarctic Expedition 1911—1914, Series C, Zoology and Botany, **3**, 2, 1—25.

TOWE, K. M. and URBANEK, A. 1972. Collagen-like structure in Ordovician graptolite periderm. — *Nature,* **237**, 443—445.

TRELSTAD, R. L., HAYASHI, K. and TOOLE, B. P. 1974. Epithelial collagens and glycosamino-glycans in the embryonic cornea. Macromolecular order and morphogenesis. — *J. Cell. Biol.,* **62**, 815—830.

URBANEK, A. 1976. The problem of graptolite affinities in the light of ultrastructural studies on peridermal derivatives in pterobranchs. — *Acta Palaeont. Polonica,* **21**, 1, 3—36.

— 1978. Significance of ultrastructural studies of graptolite research. — *Ibidem,* **23**, 4, 595—629.

— and MIERZEJEWSKA, G. 1978. The ultrastructure of ribbon-like deposits over the thecae in *Orthograptus gracilis* Roemer. — *Ibidem,* **23**, 4, 637—642.

— and TOWE, K. M. 1974. Ultrastructural studies on graptolites. I. Periderm and its derivatives in Dendroidea and in *Mastigograptus.* — *Smith. Contr. Paleobiology,* **20**, 1—48.

— and — 1975. Ultrastructural studies on graptolites. II. The periderm and its derivatives in the Graptoloidea. — *Ibidem,* **22**, 1—24.

ADAM URBANEK, GRAŻYNA MIERZEJEWSKA i PIOTR MIERZEJEWSKI

BADANIA OSIADŁYCH GRAPTOLITÓW W SKANINGOWYM MIKROSKOPIE ELEKTRONOWYM

Streszczenie

Zbadano powierzchnię rabdozomów graptolitów dendroidowych, tuboidowych i *Mastigograptus* sp. za pomocą skaningowego mikroskopu elektronowego. Wykazano, iż w zasadzie powierzchnie te są zupełnie gładkie, nawet w okolicach apertur.

Tylko u jednego okazu *Dictyonema* sp. zaobserwowano na perydermie obecność niemal równoległych wałków występujących parami. Uzyskane wyniki wykluczają możliwość interpretowania tych wałków jako jednostek sekrecyjnych korteksu graptolitów. Wyraźnie gładkie, pozbawione „bandaży" powierzchnie rabdozomów graptolitów osiadłych ostro kontrasują z coeneciami Cephalodiscida, pokrytymi zazwyczaj obcymi ciałami przywierającymi do ich lepkiej powierzchni. Fakt ten może sugerować istnienie u graptolitów ochronnej warstwy z miękkich tkanek wokół rabdozomu, której obecność postuluje membranowy model sekrecji. Przedyskutowano możliwość depozycji małej ilości kolagenowego materiału szkieletalnego na powierzchniach otwartych na wpływ środowiska zewnętrznego. Wyrażono pogląd, iż dotychczasowe dane sugerują istnienie bezpośredniego związku fibryllogenezy kolagenu z powierzchnią komórek nabłonkowych. Takie fakty jak brak „bandaży" u graptolitów osiadłych, brak obcego, aglutynowanego materiału na rabdozomach oraz kontrolę fibryllogenezy przez komórki nabłonka w pozakomórkowej sekrecji kolagenu potraktowano jako przemawiające na korzyść membranowego modelu sekrecji peridermy graptolitów.

EXPLANATION OF PLATES 9—20

Plate 9

Dictyonema sp., erratic boulder No. O.129

1. Showing typical featureless surface of rhabdosome, × 990 (SEM 2222).
2. Apertural margin of autotheca revealing faint traces of bowlike striation (the arrow), × 406 (SEM 2257).
3. Surface of rhabdosome revealing an orthogonal superposition of two fibril systems. Arrows indicate broken edges due to mechanical abrasion. × 860 (SEM 1468).
4. Broken portion of theca beneath the aperture showing a series of fuselli demarcated by pellice (*p*) and covered by cortical deposit (the arrow), × 420 (SEM 2200a).
5. Subparallel rollers delimiting a ribbon-like area on the surface of rhabdosome, × 860 (SEM 2224).
6. Reticulate network made of irregular, densely packed rollers on the surface of rhabdosome, × 730 (SEM 2246).

Plate 10

Dictyonema sp., erratic boulder No. O.129

1. An isolated (single) irregular roller delimiting a lobate area on the periderm surface, × 1120 (SEM 2221).

2—3. Parallel rollers on the periderm surface, × 1200 and × 660 (SEM 2218 and SEM 2207).

4. Showing detail of a roller with quasi-segmentation, × 5720 (SEM 2200b).
5. Showing detail of a roller with smooth surface, × 730 (SEM 2237).
6. Showing dense growth lines on a roller, × 730 (SEM 2234).

Plate 11

Dictyonema sp., erratic boulder No. O.129

1—2. Parallel rollers seen on the periderm surface, × 2100 (SEM 2217) and × 1400 (SEM 2201).

Plate 12

Dictyonema sp., probably Ordovician, erratic boulder No. O.129

1—2. Different cortical layers exposed probably due to mechanical abrasion and showing orthogonal (1) and oblique (2) orientation of adjacent fibril, ×860 (SEM 2429, SEM 2251).

3. Discontinuities of periderm surface crossing the area between two rollers (indicated by arrows), × 2300 (SEM 2245).
4. Membrane (sheet) fabric exposed in successive layers showing numerous pits, × 3500 (SEM 2240).
5. Clusters of pits seen on the exposed membrane area, × 730 (SEM 2239).

Plate 13

Acanthograptus sp., Ordovician, erratic boulder No. O.107

1. Periderm surface on a rhabdosome stipe, × 600 (SEM 2191).
2. Surface of isolated autotheca, × 350 (SEM 2185).

Plate 14

Mastigograptus sp., Middle Ordovician, erratic boulder No. O.181

1. Surface of the stem with polygonal fields (the arrow), × 500 (SEM 2193).
2. Details of striation seen on the stem, × 2200 (SEM 1538).

Plate 15

Epigraptus sp., Middle Ordovician, erratic boulder O.242

1. Basal part of autotheca and bitheca with coarse fibers (arrows), × 400 (SEM 2183).
2. Surface of thecorhiza portion, × 300 (SEM 2180).

Plate 16

Epigraptus sp., Middle Ordovician, erratic boulder No. O.242

1. Broken apertural margin of autotheca showing traces of fuselli (the arrow), × 4300, (SEM 2171).
2. Upper portion of autotheca, × 620 (SEM 2172); f *fusellus*.

Mastigograptus sp., Middle Ordovician, erratic boulder No. O.181

3. Surface of stem showing striation, × 1400 (SEM 2194).

Plate 17

Discograptus schmidti Wiman, 1902, Upper Ordovician, erratic boulder No. O.495

1. Enamel-like surface of thecorhiza, × 340 (SEM 2163).
2. Traces of fibrous structure on thecorhiza, × 1330 (SEM 1510).
3. Surface of bitheca, × 570 (SEM 2166).

Plate 18

1. *Epigraptus* sp., Middle Ordovician, erratic boulder P. 242, × 70 (SEM 2170).
2. *Discograptus schmidti* Wiman, 1902, Upper Ordovician, erratic boulder 0.495, fragment of autothecal aperture, × 400 (SEM 2156/2157).

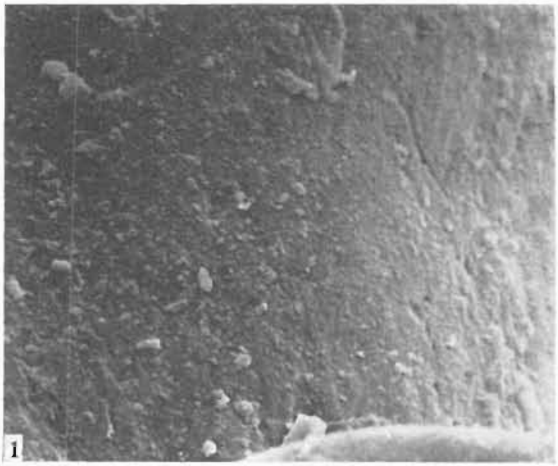
Plate 19

1. *Dendrotubus* sp., Ordovician, erratic boulder No. MZ/88, surface of central parts of two autothecae, × 250 (SEM 928).
2. *Kozlowskitubus erraticus* (Kozłowski, 1963), Upper Silurian, erratic boulder No. MZ/47, surface of autothecal part, × 720 (SEM 931).

Plate 20

Discograptus schmidti Wiman, 1902, Upper Ordovician, erratic boulder No. MZ/24

1. Surface of the erect part of autotheca showing traces of zigzag suture (the arrow), × 700 (SEM 923).
2. Spongy-reticulated material covering the internal surface of the same autotheca, ×6670 (SEM 921).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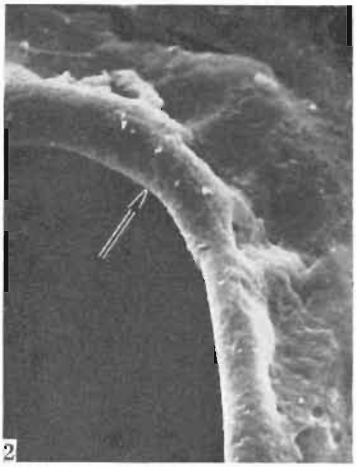
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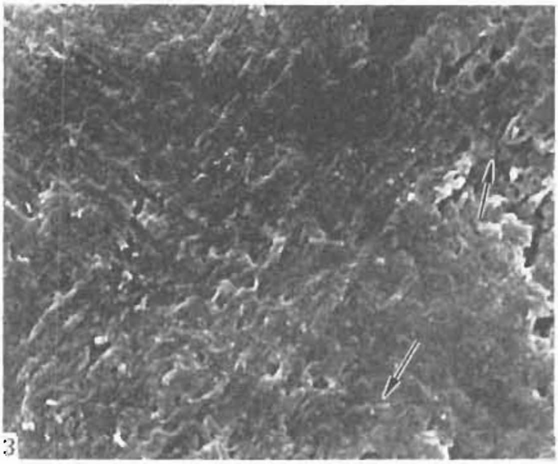
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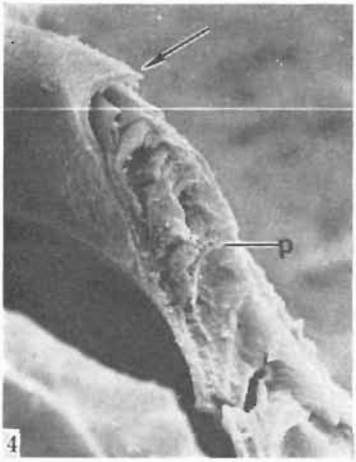
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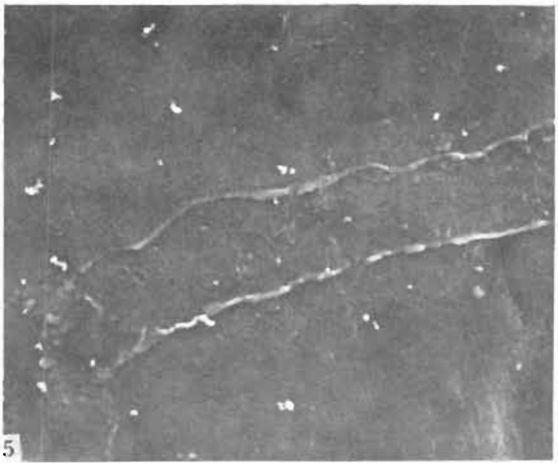
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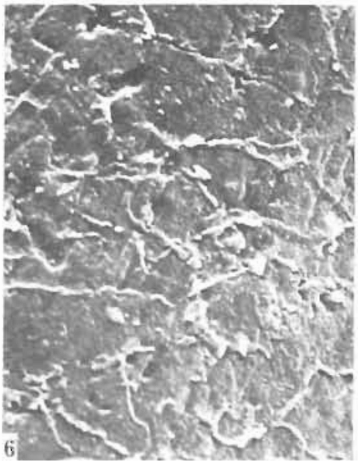
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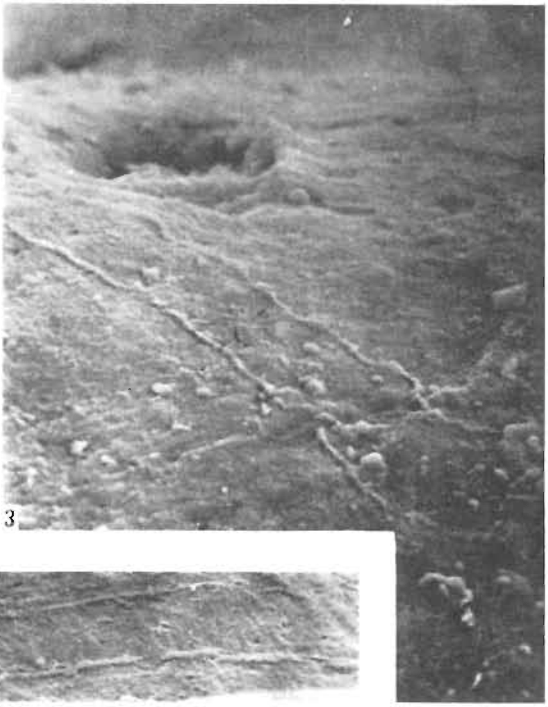
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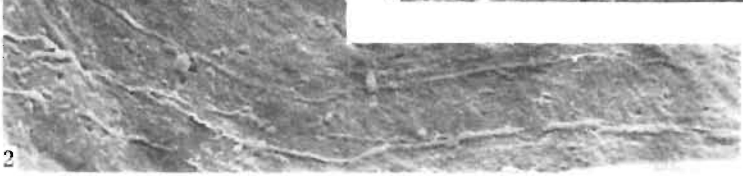
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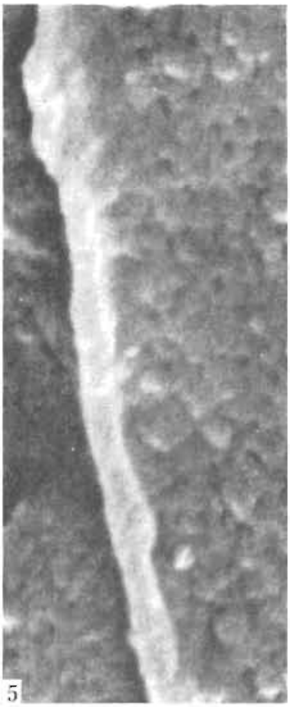
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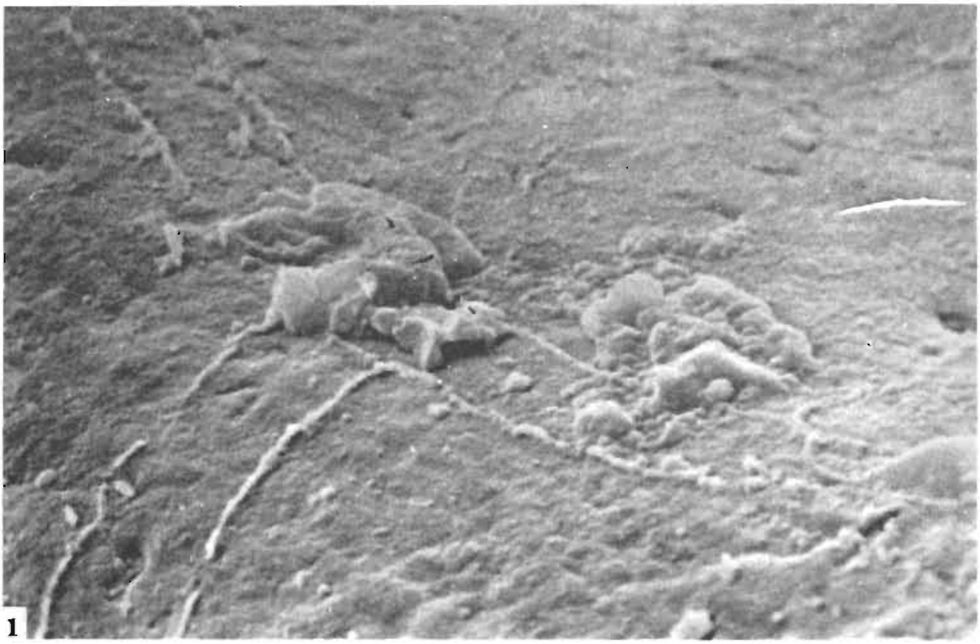

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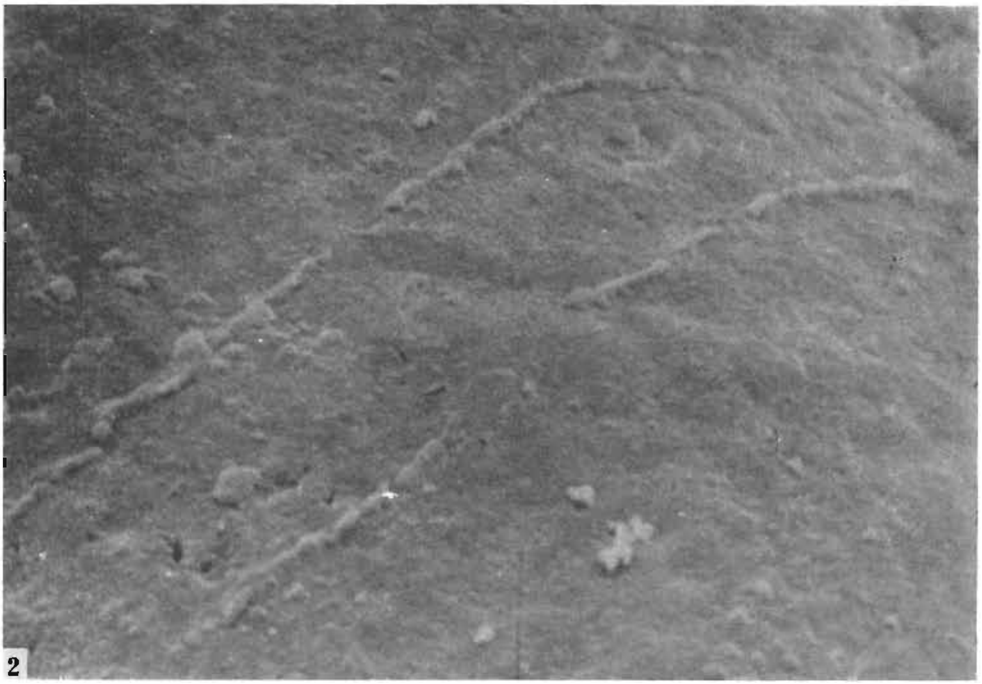

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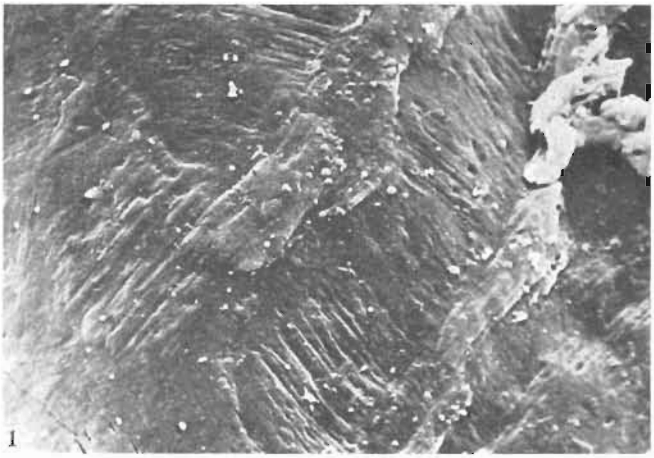
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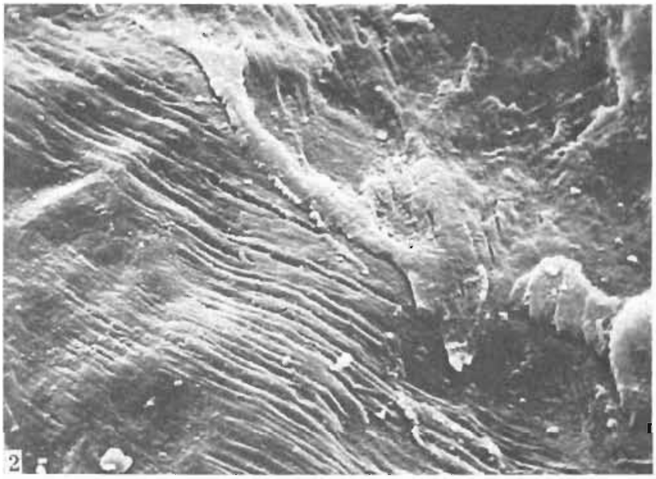
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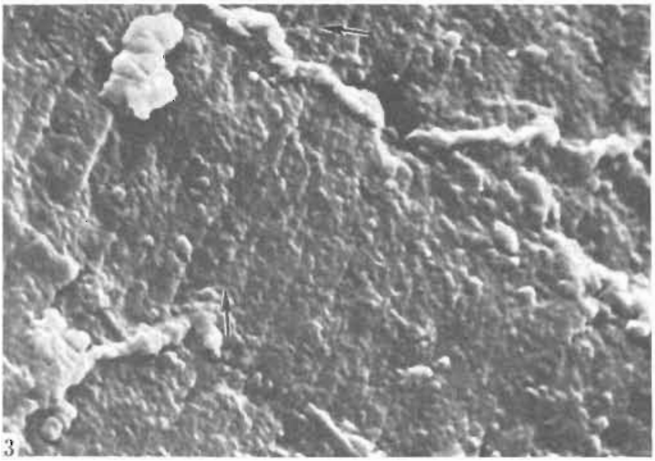
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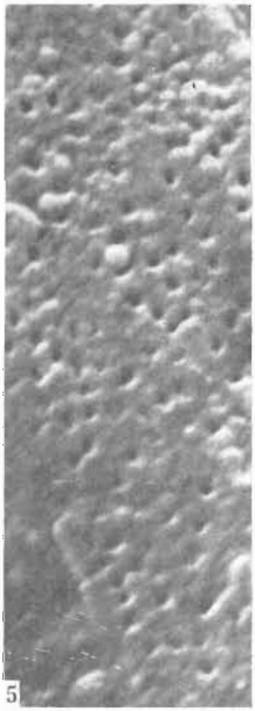
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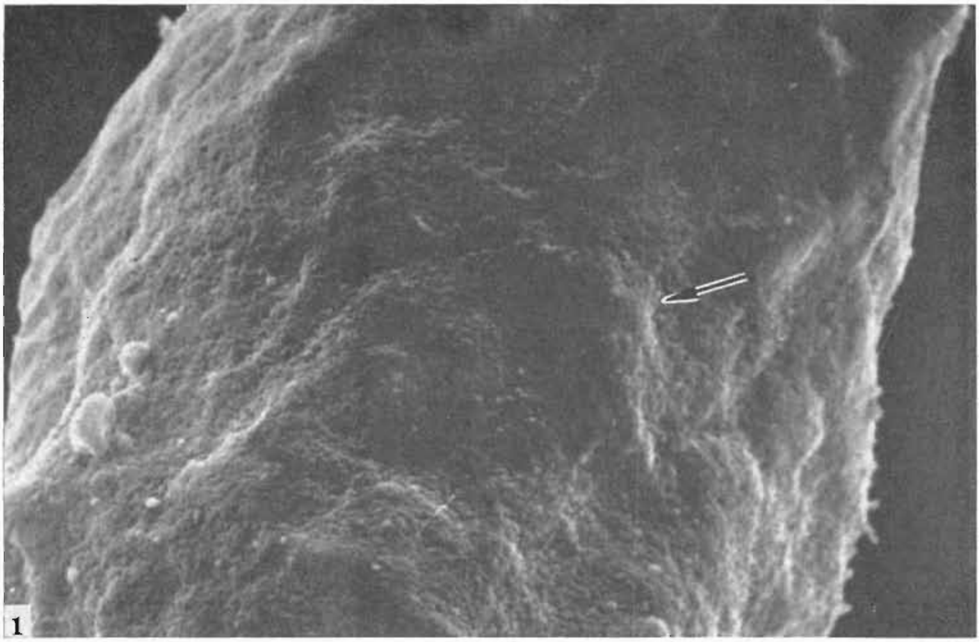
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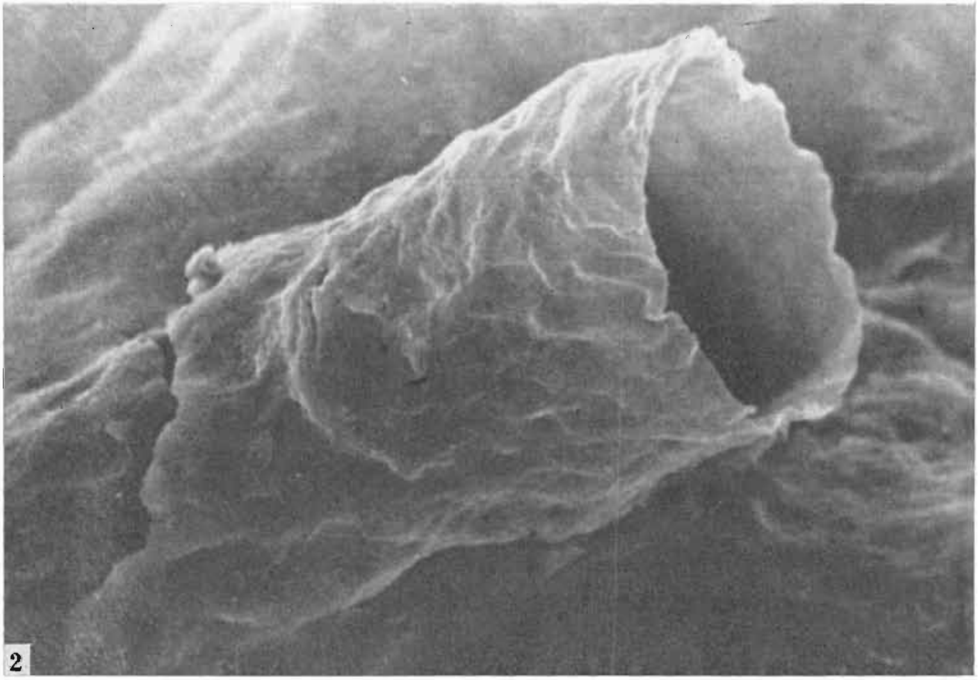
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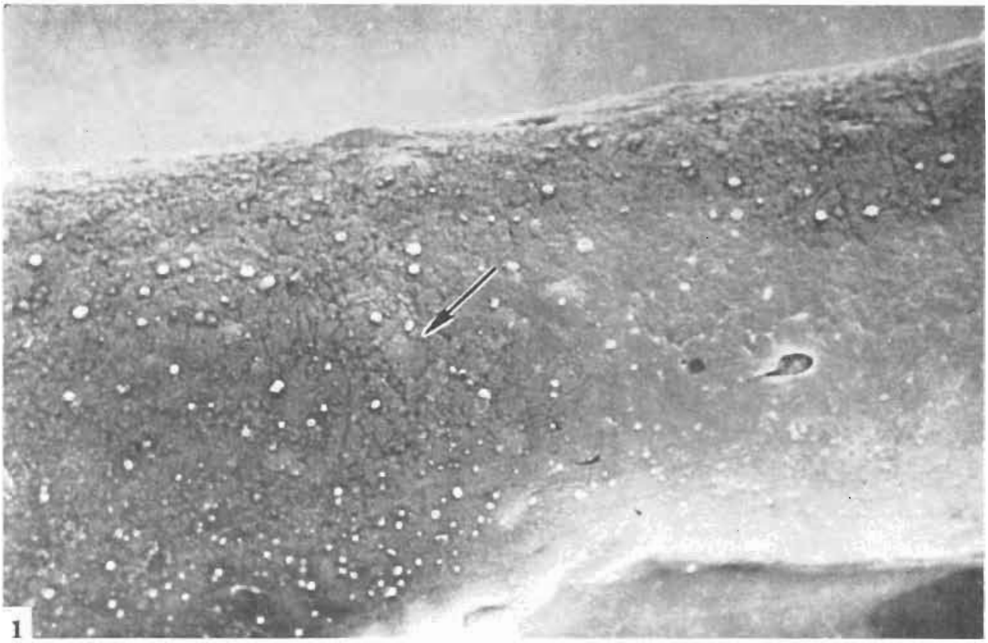

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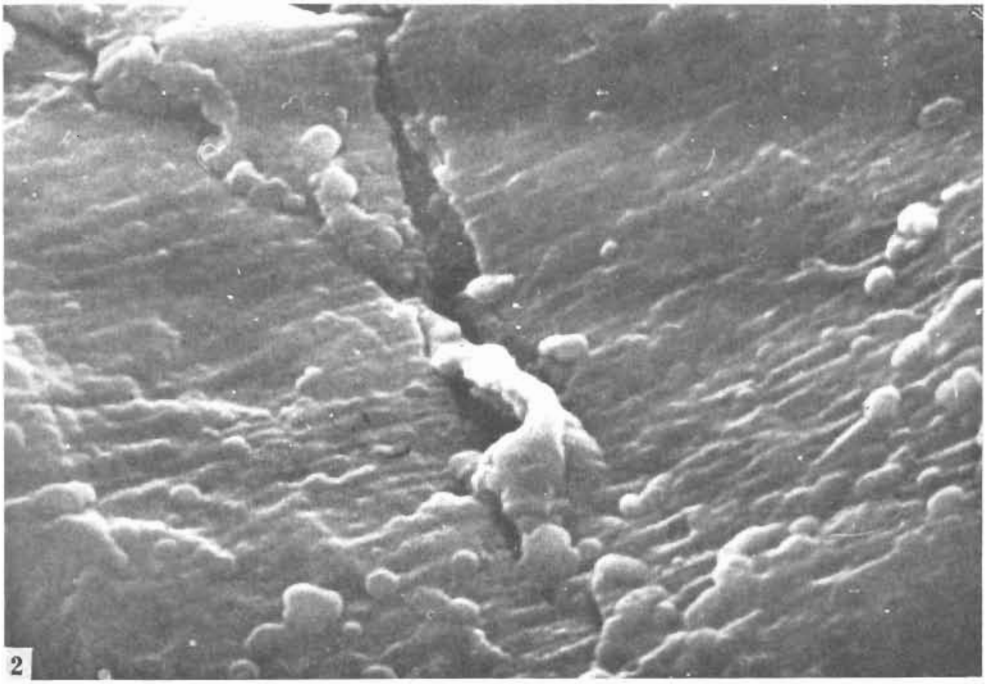

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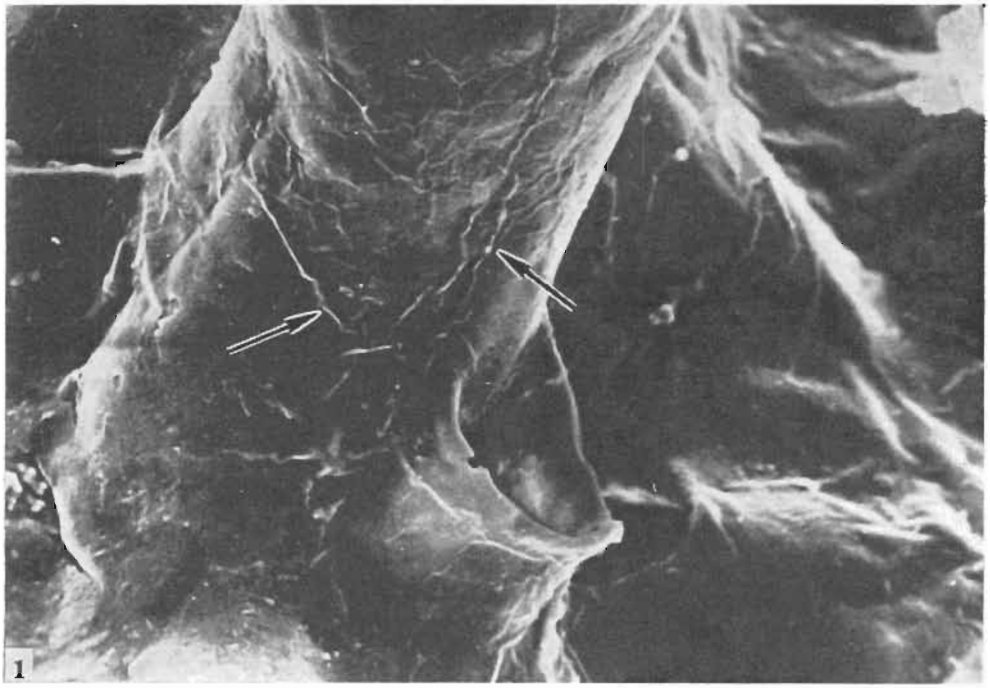
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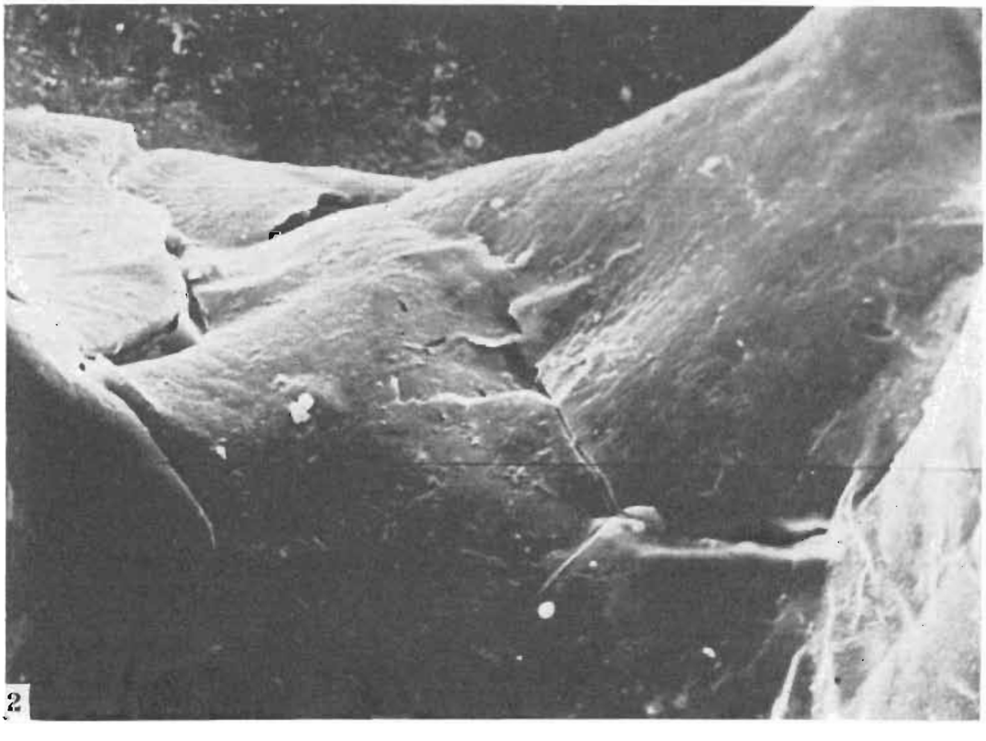
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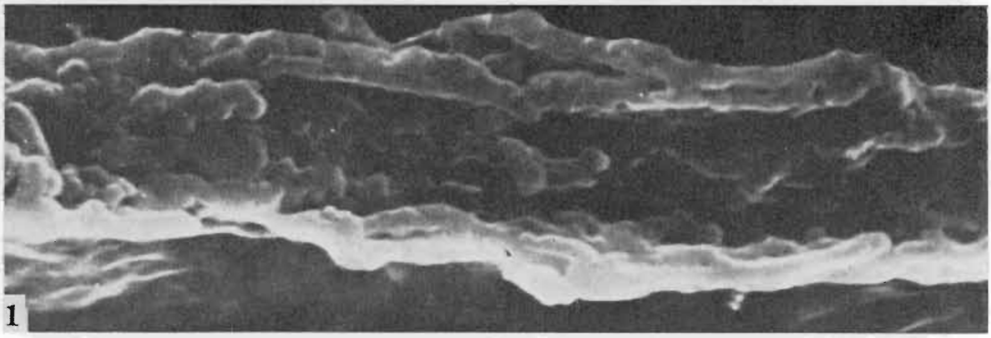

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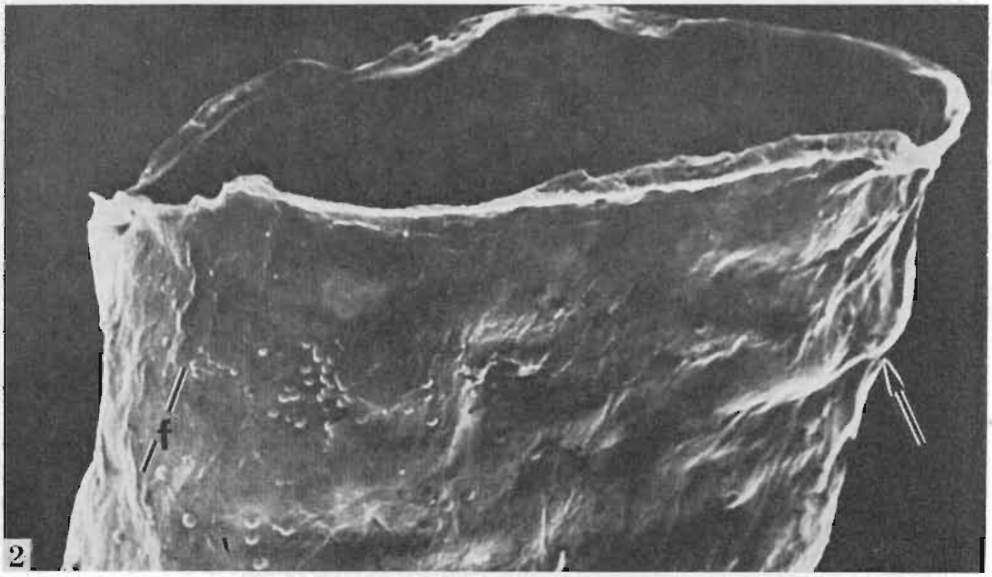

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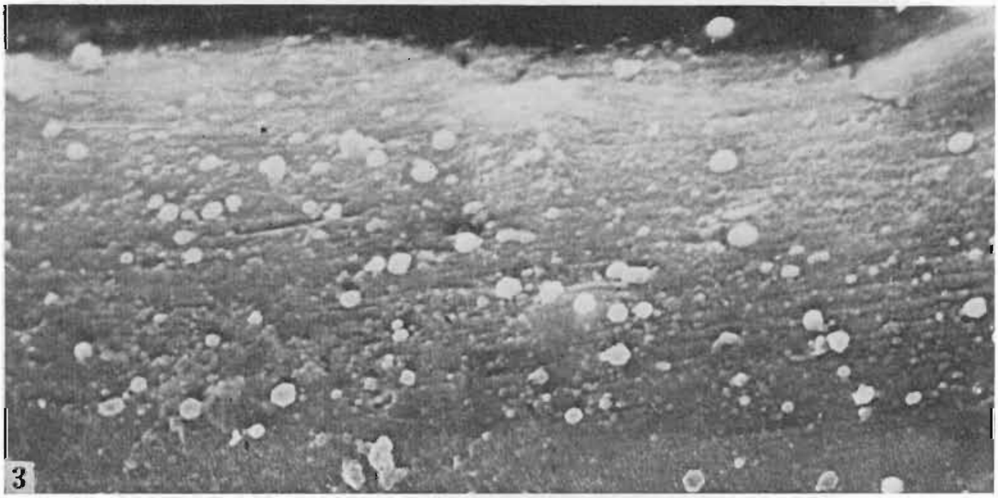

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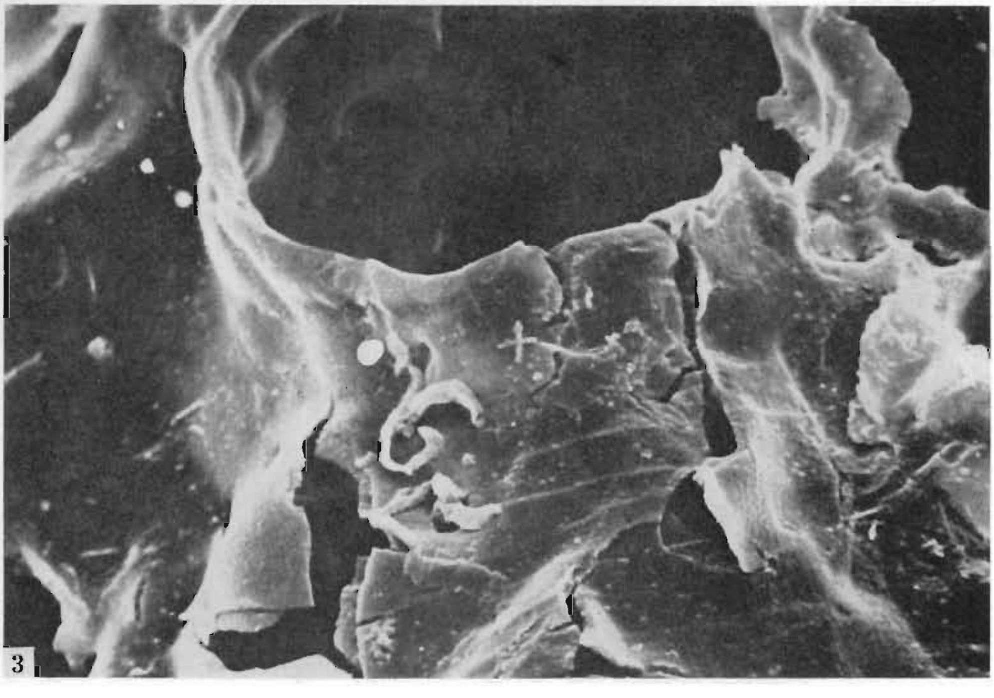

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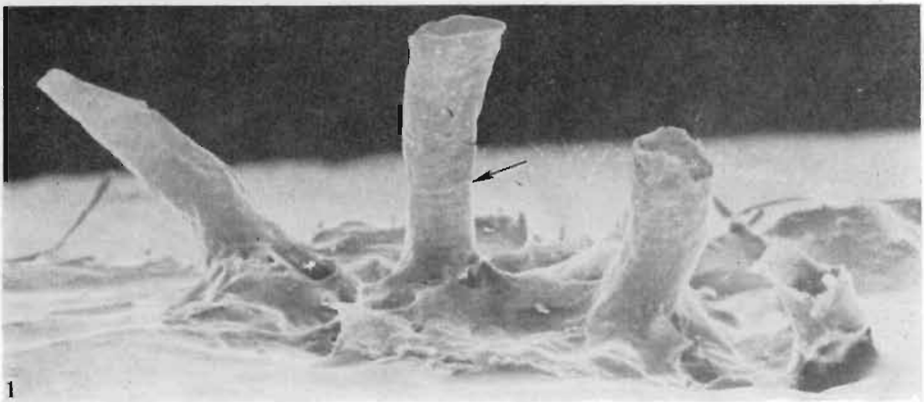

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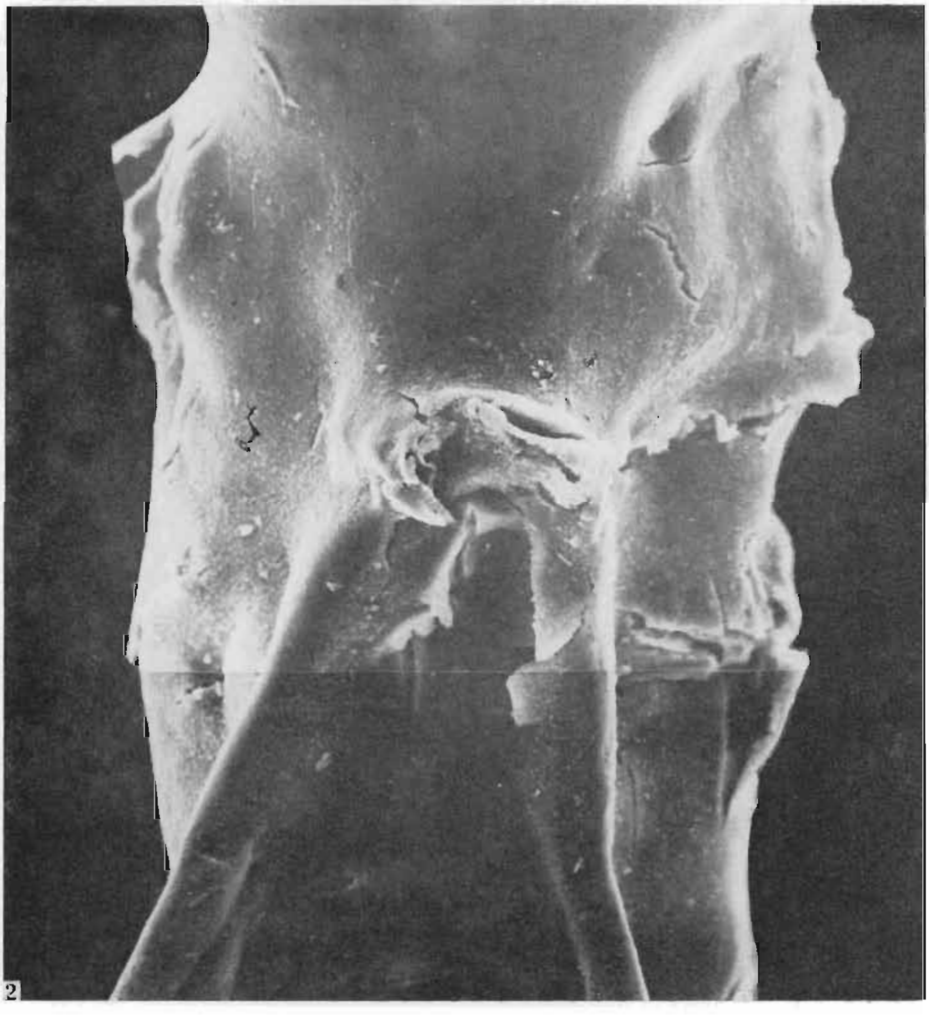

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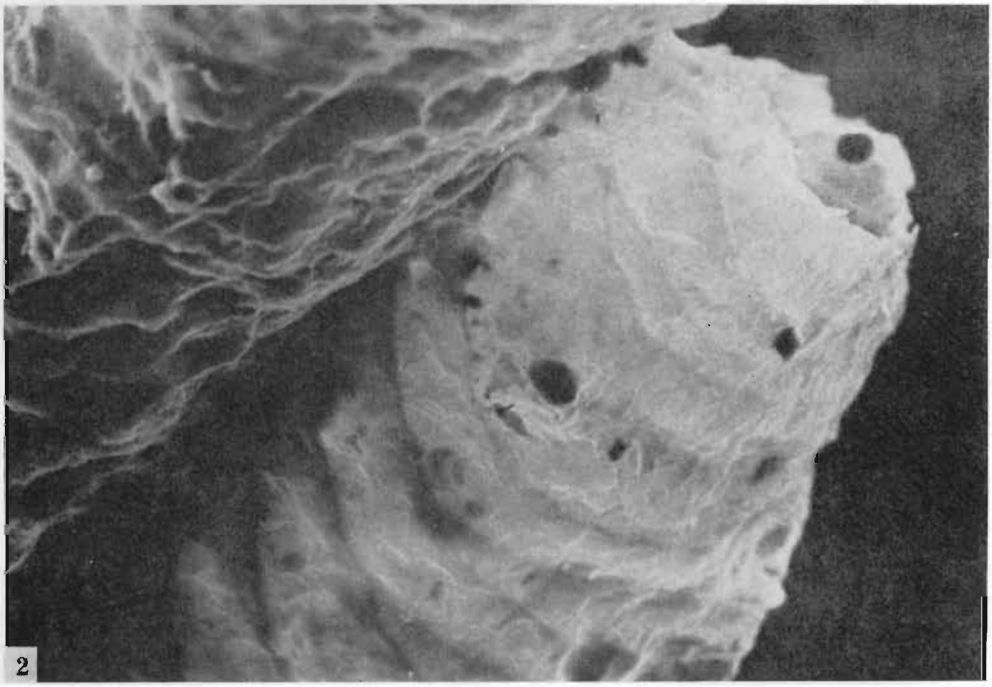

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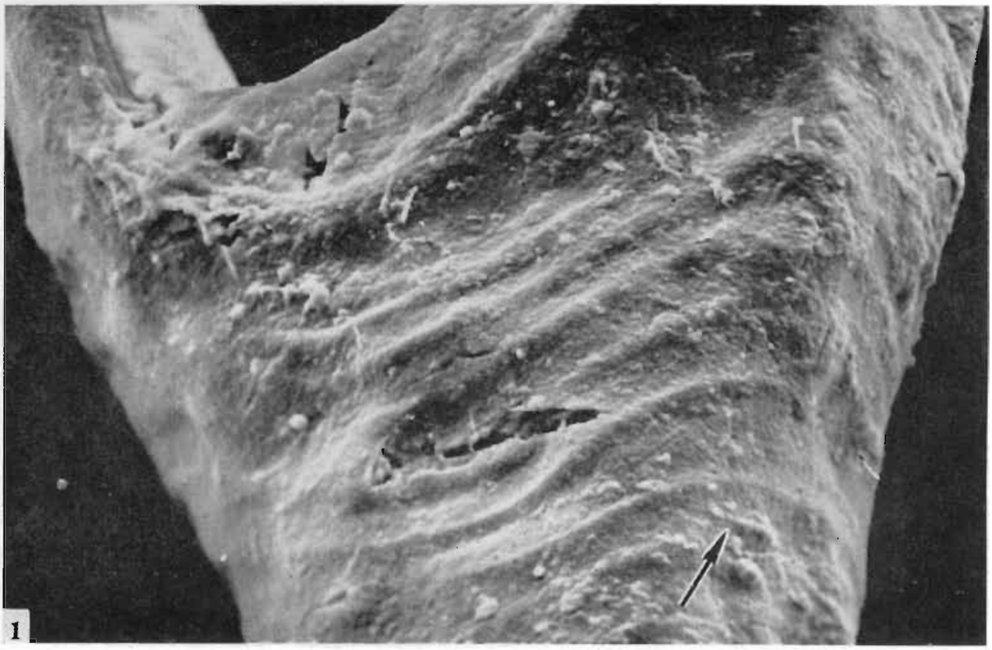
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