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ADAM URBANEK and GRAŻYNA MIERZEJEWSKA

THE FINE STRUCTURE OF ZOOIDAL TUBES IN SABELLIDITIDA AND POGONOPHORA WITH REFERENCE TO THEIR AFFINITY

Abstract. — Organic tubes of Sabelliditidae are a characteristic element of Lower Cambrian faunas. They were commonly compared with tubes of sedentary polychaetes, until Sokolov (1965) suggested their close affinity with Recent pogonophores.

The aim of the present paper is to verify the latter hypothesis through a better understanding of ultrastructural features of zooidal tubes in both groups considered.

The ultrastructure of the tube in Sabelliditida recognized for the first time by Urbanek, 1976 (in press), reveals that the wall of the tube is composed of two almost homogenous layers — the outer one and the inner one, and of the middle distinctly laminar layer. Characteristic wrinkles on the outer surface of the tube are made solely of the outer layer which is almost homogenous or with faint traces of some lammiation.

The tubes in all Pogonophora under study display an entirely laminar structure. Wrinkles observed on certain areas of the tube are due to foldings involving numerous layers of the tube wall. Earlier biochemical and ultrastructural data and results of our ultrahistochemical observations are indicative of the presence of chitin, proteins (probably sclerotins) and mucopolysaccharides in the pogonophore tubes.

The above results contribute to a better knowledge of the organic skeleton in both groups in question, but the problem of sabelliditid/pogonophore affinities remains unresolved. The degree and specificity of resemblance recognized at the submicroscopic level is not sufficient to confirm or disprove the hypothesis on close relationship between both groups considered.

Introduction. — The aim of this paper is to present the results of ultrastructural investigations on skeletal remains of Lower Cambrian Sabelliditida and the tubes of Recent Pogonophora in order to verify the hypothesis advanced by Sokolov (1965, 1969) on close phylogenetic relation of both groups in question.

The ultrastructural data concerning the sabelliditids are preliminary (Urbanek, in press). The ultrastructural features of pogonophore tubes were likewise only preliminarily known prior to the present investigations (Gupta & Little, 1975), although much is known on submicroscopical anatomy of the zooid body.

Material. — The sabelliditids described in the present paper were obtained from a number of samples collected from the boreholes (Ludza 15 and Vishki 25) drilled in Eastern Latvia (USSR).

A detailed description of the sequence encountered in the drillhole Ludza 15 can be found in Birkis *et al.* (1972). The most abundant sample (Ludza 15/21) was collected from the depth of 775—777 m and is made of greenish-gray laminated and finely laminated clays, assigned by the above authors to the Lower Cambrian, and namely to the Lonyovaskiy horizon of the Lontovaskaya suite.

The sequence found in the drillhole Vishki 25 is described in the paper by Kirsanov (1974). The most abundant material was found in two samples — 9 and 16 which correspond to the depth of 730.0 and 722.6 m respectively. They are made of greenish-gray clays or finely laminated mudstones showing alternation of clayey and quartzitic material and were assigned to the Lower Cambrian.

The zooidal tube of a recent pogonophore *Zenkevitchiana longissima* Ivanov was collected during one of the cruises of the Soviet R/V "Vityaz" from the depth of 8.820—9.220 m in the Kuril Trench. Specimens investigated come from the material housed in the Institute of Oceanography of the Academy of Sciences of the USSR, Moscow. The tube of the other pogonophore *Siboglinum* sp. has been obtained from collection of Prof. A. V. Ivanov (Leningrad) through courtesy of Prof. A. M. Obut (Novosibirsk). Its origin is unknown to the present writers.

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Methods of study. — The sabelliditids described in the present paper were obtained by etching in HF a number of samples. Their subsequent

treatment included cleaning in concentrated HF. Dried specimens were used for further scoping with SEM, while specimens washed in 70% ethanol were used for subsequent graded alcohol series. The latter treatment was also used for *Zenkevitchiana* tube stored in alcohol. After embedding the samples in "Durcupan" ACM (Fluka) the standard ultramicrotome techniques were followed. The Porter-Blum and LKB ultramicrotomes provided with a diamond knife were used to obtain sections of an approximate thickness of some 900 — 1000 Å. Sectioning the sabelliditids proved to be an uneasy task. Staining was ineffective in the case of sabelliditid remains while some sections of *Zenkevitchiana* tubes were stained with lead citrate, 1% uranyl acetate or 4% phosphotungstig acid. Especially effective was staining with 1% potassium hypermanganate of a longer duration (1—5 minutes). The *Siboglinum* sections were stained with 4% potassium hypermanganate followed by destilled water and 0.025% citric acid. Scoping was done with the Philips EM-200 and JEM-100B transmission electron microscopes.

SUBMICROSCOPIC STRUCTURE OF SABELLIDITID TUBES

Micromorphology of sabelliditid tubes. — The sabelliditid tubes are usually strongly flattened, being transformed into a sort of ribbons, usually 1.20 — 0.30 mm wide and up to 120 mm long. Frequently, the samples from which the mineral residuum has been washed out, contain abundant delicate membranes. These are colourless and semitransparent or yellowish -brownish networks or felts composed of densely crowded threads, visible as misty spots (pl. 1:2). They make an impression of remnants of saprophytic fungi, living on decaying organic matter. Other samples are almost free of these membranous material (pl. 1:1). This somewhat enigmatic material deserves more attention.

Typical representatives of Sabelliditida have their tubes characteristically wrinkled (family Sabelliditidae Sokolov) although they could pass gradually into an almost smooth portion at one end of the tube. Particular genera differ but slightly in wrinkled ornamentation of the outer surface of the tube as described and classified by Sokolov (1972). Morphological characteristic of such surface sculpture is seen on light (pl. 2:4—5) and SEM micrographs (pl. 2:1—3). Tubes covered with fibrous felt-like or "mossy" outer layer have been recognized in the material etched from deep boring Ludza 15. According to Prof. B. S. Sokolov (personal information) they also belong to Sabelliditida.

Ultrastructure of sabelliditid tubes. — Wrinkled tubes of typical sabelliditids were used to obtain transverse (pl. 3:1—2) and longitudinal (pl. 3:3) sections. They reveal rather a clear picture of their ultrastructure.

Black strongly flattened tubes (some 1 mm wide) were sectioned tran-

sversely. Micrographs show remains of a strongly compressed internal cavity of tube (pl. 3:1,c). The wall of the tube is distinctly tripartite with an outer and inner component made of an essentially homogenous substance (pl. 3:2, o, i) and the middle component with a distinctly laminar structure (pl. 3:2, m). The outer and inner components show only very faint, hardly discernible traces of layering in form of fairly wide bands (pl. 4:4, arrows). The middle portion of the tube is distinctly and rather densely layered due to the presence of thin, electron dense layers, separated by a less dense material of varying thickness (pl. 3:2, 1). The inner surface of the tube wall (the surface of the tube cavity) is smooth. The inner surfaces of the tube wall are so intimately fused that they do not leave even a trace of a joint line (pl. 3:1).

More information of the ultrastructure of sabelliditid tube was supplied by longitudinal sections of smaller specimens (approx. 0.5 mm in diameter). Sections were taken shallow-tangentially and show therefore only the outer and the middle components of the tube wall (pl. 3:3, o, m).

The outer component forms on its surface a number of distinct folds, some of them being gently-sloped, some sharp and pointed (pl. 5:1, w). They are cross sections of transverse wrinkles seen on the surface of the tube. Some bigger wrinkles show the presence of smaller secondary protuberances. These are crossections of secondary, smaller wrinkles found on the slopes of the bigger ones (pl. 5:1, p). At certain places the outer component displays faint, hardly discernible traces of layering (pl. 5:1; pl. 6:2a). In certain cases, this rudimentary layering shows discordance with the overlying surface morphology (pl. 5:1, arrows). The significance of this rudimentary layering is not clear. It may equally well represent the remnants of primary layering, or be an entirely preservational feature which originated in primarily homogenous tissue due to fossilisation (comp. discussion on p. 233 and pl. 18:A).

The middle component, as seen on longitudinal sections, consists of numerous thin layers, separated from each other by narrow electron dense lines. The material within a given layer is medium electron dense, almost homogenous or with faint traces of irregularly dispersed densities giving, however, no indication of a fibrous fabrix (pl. 4:1—3; 5:2—3; l, m). This layering is frequently irregularly distorted to produce intense undulations and foldings, with numerous holes and fissures due to tearing and separation of adjacent layers. These irregularities may be, at least partly, preservational features (pl. 5:2—3).

SUBMICROSCOPIC STRUCTURE OF ZOOIDAL TUBE IN POGONOPHORES

Morphology and microstructure of the tube in Zenkevitchiana. — The tubes of *Zenkevitchiana longissima* are usually long (1.5 m) and narrow (width 0.4 mm in distal and 1.6 mm in anterior part) structures. (Ivanov,

1960, 1963). While their most anterior parts are membranous and attenuated tubes with transparent walls, the middle and posterior portions are more rigid and thick-walled. We have examined fragments of the middle part of a tube. They are characteristically whitish (milky), flexible and semitransparent. The whole tube, except its most posterior part, is segmented, namely, it consists of numerous 1) wide annular bands with a fairly smooth surface, separated by 2) narrow, wrinkled interspaces. Similar segmentation of the tube with wrinkled interspaces have been noticed in numerous pogonophores which form a group that has segmented but unringed tubes as defined by Ivanov (1963).

The longitudinal microtome sections through the tube reveal its structural principle (pl. 6:1, 3—4). The annular bands are made of a number of layers running parallel to each other. The layered nature of the tube wall is distinctly visible on SEM micrographs showing the broken surfaces (pl. 2:8). The interspaces are somewhat depressed furrows with their outer surfaces covered with some 10—12 delicate wrinkles (pl. 2:6—7); (pl. 18: B-C). The interspace areas display an unusual structure — particular layers produce a number of angular folds with a peculiar "V"-shaped arrangement of growth layers. Sharply pointed folds of a number of internal layers are directed outwards to produce a kind of "hills" covered with intense and more gentle undulations of superficial layers of the interspace areas (pl. 7:1—4).

The structure of interspace areas (see diagram pl. 18:B-C) is strongly suggestive of their functioning as a kind of flexible articulations between rigid and sclerotized annular bands, thus producing a system of joints responsible for elasticity of an extremely elongated tube.

Ultrastructure of the tube wall. — The unstained longitudinal and transverse sections through annular bands show a distinctly but irregularly layered structure of the tube wall, each layer being delimited by somewhat denser lines (pl. 6:1, 3—4). The material within layers looks homogenous with a number of small irregularly scattered vesicles. Slightly larger fissure-like vesicles are associated with denser lines delimiting particular layers (pl. 6:3). The outer surface of the tube looks characteristically corroded, most probably because of the environmental influences, with granular material of foreign bodies sticking out to the surface (pl. 6:1).

The longitudinal sections through interspace areas reveal a distinct picture of V-shaped infolding, with sometimes gentle but frequently sharp and angular arrangement of the growth layers (pl. 7:1, 4). The outer wrinkles are produced by a dense superposition of rather narrow growth lines, thus forming narrow undulations (pl. 18:B-C, is).

A number of longitudinal sections through interspace regions, showing such a V-shaped arrangement of layers, were stained with phosphotungstig acid. The micrographs obtained display an emphasized layering, due to

accumulation of an electron dense material on the boundaries of particular growth bands (pl. 7:1—4). The lines delimiting a given layer abound in fibrils arranged longitudinally. Each fibril is made of electron lucent material framed by narrow bands of electron dense substance (see pl. 7:4, arrow). The matrix within a given layer is essentially homogenous and electron lucent, serving as a background for scattered, rather indistinctly marked fibrils. They display a more or less regular V-shaped arrangament which results in a feather-like appearance of interlayer fibrous material (pl. 7:3).

As the phosphotungstig acid stains first of all polysaccharides, the results obtained may be interpreted on the assumption of crystalline nature of the chitinous fibrous component and a carbohydrate nature of electron dense material immediately surrounding the fibrils.

Staining of a number of longitudinal sections with lead citrate has produced largely comparable with those obtained with phosphotungstig acid (pl. 8:1—2). The layering is rather distinct, the border lines showing abundance of electron dense material with a number of fibrils longitudinally oriented (pl. 8:2, 1). The bulk of the material confined within particular layers can be differentiated into 1) narrow lines and bands of electron dense ground substance, d 2) lucent fibrils showing a V-shaped or chevron arrangement, v 3) circular, rather densily packed lucent spots against the electron dense background, these spots being most probably cross-sections of numerous fibrils embedded into the ground substance and oriented perpendicularly to the plane of the section, f (pl. 8:1—2).

As the lead citrate is known to stain the ground substance, glycogen and related polysaccharides, the electron dense material on the micrographs may be interpreted as mucopolysasscharide-protein complex of the matrix. The dense lines outlining the fibrils are probably surface coats containing proteins and carbohydrates which have been stained with lead citrate, while fibrils themselves remain unstained.

Some longitudinal sections through the wrinkled area of the interspace were stained with uranyl acetate and the results are shown on pl. 9:1—2. The boundaries between particular layers are blurred electron dense bands, while the matrix within each layer shows densely packed fibrils, sometimes irregularly arranged but frequently more or less ordered so as to produce a featherlike or chevron arrangement (pl. 9:2, arrow).

The results obtained may be interpreted on the assumption of an acidic nature of the material accumulated closely to the boundaries of growth layers and an acidic nature of the ground substance in general.

Staining of transverse sections with potassium permanganate gave remarkable results owing to a sharp contrast between the electron dense reduction products and a rather lucent background (pl. 10:1—4). While the boundaries of particular layers are delimited by longitudinally placed fib-

rils, the material within each layer consists of a kind of reticulated tissue produced by a dense packing of circular, or irregularly elongated spots surrounded by electron dense bands (pl. 10:1—2). The matrix within each spot and between the adjacent ones is medium dense, thus producing a nebulous surrounding around the accumulation of "reticulated tissue" (pl. 10:3—4). These results may be interpreted presuming that the electron opacity in this case is due to reaction with a less packed matrix surrounding the crystalline areas of chitin. Neville and Luke (1969) have resolved microfibrils of chitin in the locust cuticle by means of negative staining using potassium permanganate followed by lead citrate. The electron lucent spots of "reticulated tissue" may be interpreted best as cross-sections of chitin fibrils arranged in the same way as in Bouligand's model established for the cuticle of Cructaceans (see also Gupta and Little, 1975; Wainwright *et. al.*, 1976).

Morphology and microstructure of Siboglinum tube. — The tube of *Siboglinum* sp. under study was flexible and ringed, composed of golden-brownish rigid rings alternating with transparent and clearly elastic interspaces (pls 11—12). In the main part of the tube these rings are equal and regular with even edges an uniform spacing (pl. 11:2a-b). While the surface of the rings is rather smoth, the surface of transparent interspaces is distinctly wrinkled (pl. 11:2b). The anterior part of the tube, as in the majority of Pogonophora, is membraneous and provided with faint incipient rings (pl. 12:2-3). Being too flimmy to carry its own weight this part collapsed. On the contrary, the posterior end is strongly sclerotized with rings much wider than in the medial part, probably as a result of fusion of neighbouring rings (pl. 11:1). Supposedly, such fusion of primarily rather narrow annular rings is also responsible for the formation of longer rigid portions of the tube called "segments" and characteristic perhaps of most Pogonophora (comp. *Zenkevitchiana*).

Longitudinal (Jägersten, 1956) and transverse (Southward and Southward, 1966) microtome sections show that the tube wall in *Siboglinum* is composed of numerous layers, which are more distinct in the flexible, interspace portions of the tube than within rigid and tanned rings. The wrinkles on the interspace area are formed by an undulation of such layers (Diagram, pl. 18:D).

Ultrastructure of the Siboglinum tube. — Transverse ultrathin sections show a distinct layering of the tube wall (pl. 13:1—4) emphasized by difference in electron density of particular layers. A number of ultrathin lucent lines separate some of these layers, being probably a sort of discontinuities of fissures. The outermost layers show some traces of corrosion (holes, cavities etc.) probably due to the environmental influences (pl. 13:1—2). The innermost layers are delicate, electron lucent, partly discontinuous and made of accumulations of a particulate matter (pl. 13:4).

This agrees with observations by Southward and Southward (1966) with light microscope who found similar differences between the inner layer and the rest of the tube. Higher magnification micrographs show little trace of ordered structure, displaying a fairly irregular distribution of electron dense and lucent spots and lines (pl. 13:3).

Longitudinal sections show two rather different patterns (comp. pl. 14 and pls. 15—16:1—2). Pattern 1 displays rather a distinct layering, with some layers composed of compact substance, and others — more lucent or made of dispersed dense particles against a lucent background (pl. 14:1—4). The denser layers display at places a faintly fibrous structure with some indication of a chevron arrangement or "Bouligand" pattern recognized in chitinous exoskeleton of some invertebrates (pl. 14:4). This pattern may be compared with layered, nonsclerotized portions of the tube in *Siboglinum* as revealed by light microscopy (Southward & Southward, 1966).

The other pattern (2) shows an obliterated layering or only a coarse zonation of the wall with numerous round or oval structures within a given layer (pl. 14, pl. 15:1—2). These structures form bodies outlined by lucent lines with a lucent middle part and recurring, dense central spots (indicated by arrows on pl. 15:2). The nature of these bodies is enigmatic. Pattern 2 probably corresponds to the nonlayered, sclerotized portion of the tube (rings).

Longitudinal sections through a number of wrinkles were also obtained (pl. 16:4; pl. 17). Each wrinkle is a protuberation made of angular folding of numerous layers, involving more than 2/3 of the thickness. The base of a wrinkle is produced by a few undulated layers, which form a fissure separating the base from the rest of the wall (pl. 17:1—4). The outer layers are electron dense, the density gradually decreasing inwards so as to produce a faintly layered portion. The outer surface is rough and shows some destruction most probably due to environmental agents (pl. 16:4; pl. 17:1—2).

Biochemistry of pogonophore tubes and histochemical interpretation of results obtained. — Chitin and some proteins associated with it have been found in the tubes of three species of *Siboglinum* and in *Zenkevitchiana longissima* by Brunet and Carlisle (1958). The presence of chitin was established by a number of characteristic reactions and confirmed by enzymic degradation with fungal chitinase yielding N-acetyl-glucosamine. This was later confirmed by Blackwell, Parker and Rudall (1965) by X-ray diffraction methods and infrared spectrophotometry. Similar results were obtained by Foucart *et al.* (1965) using tubes of *Siboglinum* sp. Chitin and proteins were found as the main constituents of the tubes (33 per cent and 47 per cent of dry substance respectively), probably bound to a great extent in the form of glycoproteic complexes.

The nature of proteinaceous component of pogonophore tubes is less clear. The presence of keratin group was excluded for *Zenkevitchiana* by Carlisle (1964) and for *Siboglinum* by Foucart *et al.* (1965) since no sulphur-containing amino acids were found in hydrolysates. The amino acids derived from the protein of *Siboglinum* tube are not indicative of the collagen group either. Some data speak in favour of Carlisle's assumption that the proteinaceous component of pogonophore tubes may be sclerotin ss in the insect cuticle and sclerotization may be due to quinonoid links (Carlisle *in* Ivanov, 1963; Carlisle 1964). The presence in *Siboglinum* tubes (Foucart *et al.* 1965) of considerable quantities of tyrosine and phenylalanine, the chief precursors of tanning agents in the insect cuticle, may be indicative of quinone tanning as the factor responsible for the rigidity of pogonophore exoskeleton. The sclerotized rings in *Siboglinum* tube are rich in tyrosine or other phenolic groups as found with Millon test (Southward & Southward, 1966).

The relation of chitin to the proteinaceous (sclerotin?) component of pogonophore tubes requires more investigations. Foucart *et al.* (1965) suggested that most of the chitin (63 per cent) in *Siboglinum* tube is bound with proteins to form a glycoproteic complex, while only 37 per cent occur as the free chitine, hydrolysable by chitinase without previous treatment with NaOH. This conclusions sheds some light on the results presented by Blackwell, Parker and Rudall (1965), who obtained from deproteinized tubes of *Zenkevitchiana* a skeletal framework made of pure, chitinous fibres rather loosely and irregularly interconnected. These fibres may correspond to "chitine libre" in *Siboglinum* tubes while "chitine masque" (bound with proteins) has been probably removed as a result of treatment (boiling in KOH).

The total chitin and proteins represent no more than about 80 per cent of dry substance of the tube (data for *Siboglinum;* Foucart *et al.* 1965), the third main component being acid mucopolysaccharides as indicated by histochemical studies by Southward and Southward (1966). A considerable amount of acid mucopolysaccharides were found in the inner lining, the interspaces and the membraneous anterior part of the tube. Some of our results are also indicative of acid mucopolysaccharides in *Zenkevitchiana* tube.

The formation of the tube may be related to the various types of epidermal glands described in Pogonophora (Southward & Southward 1966; Southward, 1975). The chitinous component of the tube is secreted in association with some mucopolysaccharides by peculiar pyriform glands, and the fibrous extracellular secretion is later transformed into threads which the animal can incorporate into the wall of tube. These glands are believed to be responsible for the formation of the major part of the tube, while some other glands producing strongly sulphated mucopolysacchari-

des and proteins rich in tyrosine (sclerotins?) help to bind together the excretion of pyriform glands and are responsible for later sclerotization of the excretions. Southward and Southward (1966) visualize the formation of the tube suggesting a deposition of subsequent layer of chitin-containing fibres bound together by sulphated acid mucopolysaccharides. Later sclerotization (as in brownish rings of *Siboglinum* tube) involves desulfating of the mucopolysaccharides to produce a basic ground substance and tanning of chitin-protein complex due to polyphenol cross-linkages, similar to the chitin-sclerotin systems in the insect cuticle.

Taking into account the previously quoted results of staining of the ultrathin sections of the *Zenkevitchiana* tubes and the above biochemical studies one could conclude that the lucent fibrous component of these tubes is most probably chitin. Much of interfibrillar matrix, especially that stained with potassium permanganate and lead citrate, may be considered as a mucopolysaccharide-protein complex although its microfibrils were not resolved. Most of fibrous material within a given growth layer is — as observed on longitudinal sections — gathered into bunches or bundles producing a feather-like or chevron pattern due to their conical divergence. A similar pattern has been recognized in pogonophore tubes by Gupta and Little (1975) and compared with the "Bouligand pattern" seen in the electron micrographs of somewhat obliquely taken sections of arthropod cuticle (comp. Wainwright *et al.*, 1976 for detailed explanation). This may suggest that in pogonophores the tube wall is also made of a series of very thin sheets, oriented longitudinally within a given layer. Each sheet consists most probably of a single layer of uniformly oriented chitin fibrils. The neighbouring sheets differ in the direction of their fibrils, so as to produce a progressive rotation of fibrils in a thick series of sheets, whose oblique sections produced a "helicoid" or "Bouligand" pattern.

The interpretation of ultrahistochemical results offered in the present paper is in line with earlier opinion of Gupta (1975, p. 47) who was convinced "that the transparent cores of the fibrils are the chitin component while the electron opaque material around and between them is protein".

The decisive data for a safe interpretation of stained micrographs, however, are lacking and the problem needs further investigations. It must be emphasized that isolated system of chitinous fibrils in *Zenkevitchiana longissima* obtained by Blackwell, Parker and Rudall (1965) does not fit into the patterns produced by lucent fibrils on cross-sections of the zooidal tube in the same species.

RELATIONSHIP OF SABELLIDITIDS AND POGONOPHORES IN THE LIGHT OF ULTRASTRUCTURAL STUDIES

The present investigation is designed to recognize the electron microscopic structure of zooidal tube in the Lower Cambrian Sabelliditida in

order to compare it with the ultrastructure of zooidal tube in Recent Pogonophora. This should provide a verification of an intriguing hypothesis advanced by Sokolov (1965, 1972) on close relationship between both groups considered. As suggested by him, sabelliditids were fossil pogonophores and their abundance in the Lower Cambrian rocks may be evidence of an early and extensive radiation of this group. The resemblance of sabelliditid tubes to sedentary polychaetes has been treated by Sokolov as purely superficial without phylogenetis implications. He points out a number of resemblances between both groups in question (1965, 1972): 1) organic ("chitinoidal") nature of zooidal tubes and their similar physical properties, 2) cylindrical shape, absence of annelid annulation and branching of tubes, 3) presence of transition from wrinkled to smooth portion of the tube, 4) extreme elongation of tubes, 5) presence of collar-like, protruding upper margins of tube segments ("funnels") in some sabelliditids and pogonophores.

The present study may have only a limited significance for verification of the phylogenetic hypothesis advanced by Sokolov. This is first of all due to a relatively uncertain significance of the ultrastructural features for tracing phylogenies. The nature of similarities and differences at the submicroscopic level, their value for establishing homology is in many ways unclear and should be checked up in each case against the background of other evidence (comp. Urbanek, 1976). In the other hand, only a few pogonophores were studied as far as their ultrastructure is concerned. In the light of a considerable variation in zooidal tube morphology, appearance and properties within this group the knowledge of a few forms only cannot produce a safe basis for establishing a picture of ultrastructure truly representative for the whole group.

Some points deserve, however, to be emphasized:

1) The entirely laminar structure of zooidal tubes in pogonophores studied so far, contrasts with the structure of sabelliditid tube which is only partly laminar. In the latter case it is only the middle component of the tube that is laminar, while the tubes of all pogonophores are distinctly laminar throughout the thickness. The significance of this difference is difficult to evaluate because of the presence of some traces of layering within both homogenous components of the tube. These may be interpreted either as traces of primary lamination obscured by fossilization or as preservational features of the primarily homogenous material due to fossilization. The first possibility seems especially probable in the light of the unpublished data obtained by Dr. B. Gupta (personal communication). He has found pogonophores with zooidal tubes distinctly layered only in the middle portion, while showing obscured lamination within its outer and inner portions. When fossilized such tubes might produce a pattern not unlike those observed in sabelliditids.

2) Characteristic wrinkles of pogonophores are produced by undulations involving a great number of underlying layers, while in sabelliditids they are produced solely by the outer homogenous or almost homogenous component of the tube wall. Certain faint traces of layering observed within such wrinkles are in a few cases discordant with the surface morphology. It seems therefore that wrinkles are of a different nature in both groups considered.

The significance of differences in the ultrastructural pattern of sabelliditid and pogonophore tubes (pl. 18), could be better evaluated when associated with different chemical compositions of organic skeleton in both groups. Studies on the chemical composition of sabelliditid tubes are thus necessary to complete the morphological studies, particularly so as according to Brunet and Carlisle (1958), some organic compounds (chitin) may be preserved in skeletal remains as old as the Lower Cambrian.

At the moment, conclusions regarding the affinities between Sabelliditida and Pogonophora in the light of ultrastructural studies remain open. They do not supply any specific data to support the hypothesis on their close relationship, but they do not exclude their affinity either.

Uniwersytet Warszawski
Instytut Geologii Podstawowej
02-089 Warszawa
Al. Żwirki i Wigury 93
March, 1977

Polska Akademia Nauk
Zakład Paleobiologii
02-089 Warszawa
Al. Żwirki i Wigury 93
March, 1977

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ADAM URBANEK I GRAŻYNA MIERZEJEWSKA

ULTRASTRUKTURA SZKIELETU SABELLIDITIDA I POGONOPHORA ORAZ PROBLEM ICH ZWIĄZKÓW FILOGENETYCZNYCH

Streszczenie

Sabeliditida stanowią charakterystyczny element faun dolnokambryjskich. Ich rurki zbudowane z substancji organicznych porównywano powszechnie z rurkami osiadłych pierścienic, do momentu gdy B. S. Sokołow (1965) zwrócił uwagę na podobieństwo sabelliditidów do współcześnie żyjących Pogonophora. Zdaniem Sokołowa Sabelliditida to kopalna grupa Pogonophora.

Niniejsze badania mają na celu zweryfikowanie interesującej hipotezy Sokołowa przez lepsze poznanie ultrastruktury szkieletu u przedstawicieli obu wspomnianych grup. W tym celu zbadano dolnokambryjskiego *Sabellidites* sp. i współczesnych przedstawicieli Pogonophora z rodzajów *Zenkevitchiana* i *Siboglinum*.

Po raz pierwszy rozpoznana ultrastruktura rurki Sabelliditida wykazuje, że jej ściana składa się z dwu prawie zupełnie homogenicznych warstw — zewnętrznej i wewnętrznej, oraz ze środkowej warstwy laminarnej. Charakterystyczne zmarszczki na powierzchni rurki *Sabellidites* są utworzone wyłącznie z zewnętrznej warstwy homogenicznej, wykazującej tylko w niektórych miejscach niewyraźne ślady warstwowania.

Wszystkie dotychczas zbadane Pogonophora mają ściankę rurki całkowicie laminarną, zaś widoczne na jej powierzchni zmarszczki są utworzone z zafałdowania bardzo licznych warstewek. Otrzymane rezultaty badań ultrahistochemicznych, w połączeniu z wcześniejszymi wynikami badań biochemicznych i ultrastrukturalnych innych autorów, pozwalają sądzić, że u *Zenkevitchiana* i *Siboglinum* rurka składa się z chityny, białek (przypuszczalnie sklerotyn) oraz mukopolisacharydów.

Chociaż badania nasze w pewnym stopniu uzupełniają wiedzę o budowie szkieletu obu grup, nie rozwiązują one jednoznacznie zagadnienia ich związków rodowych. Stwierdzone podobieństwa w anatomii submikroskopowej są niewystarczające do bezpośredniego potwierdzenia hipotezy o bardzo bliskich związkach filogenetycznych między Sabelliditida i Pogonophora, ale też nie wykluczają ich pokrewieństwa.

АДАМ УРБАНЕК, ГРАЖЫНА МЕЖЕЕВСКА

УЛЬТРАСТРУКТУРА ТРУБОК SABELLIDITIDA И POGONOPHORA И ПРОБЛЕМА ИХ ФИЛОГЕНЕТИЧЕСКИХ СВЯЗЕЙ

Резюме

Sabelliditida представляют собой своеобразную группу животных, характерных для нижнекембрийской фауны. В течение долгого времени было принято сравнивать их трубки, состоящие из органического вещества, с трубками седентарных кольчатых червей. Однако в 1965 году Б. С. Соколов обратил внимание на сходство между Sabelliditida и современными Pogonophora. По мнению Б. С. Соколова Sabelliditida являются не чем иным, как ископаемой группой Pogonophora.

Настоящие иследования имели целью проверку интересной гипотезы Соколова последством детального изучения ультраструктуры скелета у представителей обеих групп. Были изучены нижнекембрийский *Sabellidites* sp. и современные представители Pogonophora относящиеся к родам *Zenkevitchiana* и *Siboglinum*.

Выполненные впервые ультраструктурные исследования трубки сабеллидитид обнаружили, что стенка трубки состоит из двух почти полнностью гомогенных слоев — наружного и внутреннего, а также средней ламинарной части. Характерные морщинки на поверхности трубки *Sabellidites* образованы исключительно наружным гомогенным слоем, на котором лишь кое-где отмечаются слабые следы слоистости.

Стенки же трубок всех до сих пор изученых имеют полностью ламинарную структуру, а морщинки, выступающие на их поверхности, складываются из многочисленных слоёв ткани.

На основании настоящих ультраструктурных исследований и раннее опубликованных биохимических данных можно утверждать, что трубки *Zenkevitchiana* и *Siboglinum* состоят из хитина, белков (повидимому, склеротина) и мукополисахаридов. Данные исследования существенно дополняют имеющиеся сведения о строении скелета обеих групп, однако, при этом не дают оснований для однозначного решения вопроса об их родстве. Элементы сходства, обнаруженные в их субмикроскопической анатомии, недостаточны для прямого подтверждения гипотезы о весьма близких филогенетических связях между Sabelliditida и Pogonophora, хотя и не исключают полностью возможности их родства.

EXPLANATION OF THE PLATES

Plate 1

Samples with sabelliditid remain etched by HF and stored in glycerine; *A* — almost free of associated membranous organic material (saprophytic fungi?); drillhole Vishki 25, depth 725.4 - 730.0 m, Lower Cambrian, Eastern Latvia, USSR; *B* — with abundant membranous organic material (saprophytic fungi?) seen as misty places; drillhole Ludza 15, depth 775.0 - 777.0 m, Lower Cambrian, Eastern Latvia, USSR. *A* — *B* approx. x 3.

Plate 2

Micromorphology of zooidal tubes in Sabelliditida (Lower Cambrian) and Pogonophora (Recent); 1 2 SEM micrograph of a tube in *Sabellidites* sp. showing characteristic wrinkles on the surface (1) and their details (2); 3 SEM micrograph of a "shaggy" sabelliditid tube covered by a felt-like layer; 4-5 Light micrograph of *Sabellidites* sp. showing a thinner and wider portions of the tube; 6-8 SEM micrographs of a zooidal tube in *Zenkevitchiana longissima* Ivanov, showing wrinkled portion of an internode and adjacent smooth areas (6), details of the wrinkled portion (7) and broken edge of the tube (8).
1-2, 4-5: deep boring Vishki 25, Eastern Latvia, depth 730.0 m; 3: deep boring Ludza 15, Eastern Latvia, depth 775-777 m; 6-8: Kuril Trench, depth 8.820-9.220 m.

Plate 3

Ultrastructure of the zooidal tube in *Sabellidites* sp.; 1-2 transverse sections, 3 longitudinal (shallow tangential) section, showing outer wrinkles on the surface and the tube wall. Further explanation in text. Deep boring Vishki 25, Eastern Latvia, depth 725.4 m.

Plate 4

Ultrastructural details of layered portion of the *Sabellidites* sp. tube (1-3) and faint traces of lamination observed in homogenous portion of tube (4). All seen on longitudinal sections. Deep boring Vishki 2, Eastern Latvia, depth 725.4 m.

Plate 5

Ultastructural details of the zooidal tube in *Sabellidites* sp., showing a surface wrinkle with faint traces of cryptolamination (1, arrow) and layered portion fo the tube with spongy appearance due to undulation and partial tearing of the laminae (2-3). Further explanations in text. Deep boring Vishki 25, Eastern Latvia, depth 725.4 m.

Plate 6

Ultrastructure of zooidal tubes in Sabelliditida (2, a-b) and Pogonophora (1, 3-4); 1, 3-4 an outer (1) and inner (4) surface and middle portion of the tube (3) in *Zenkevitchiana longissima* as seen on unstained longitudinal (1, 3) and transverse sections (4); 2 shows details of wrinkled surface portion of the tube in *Sabellidites* sp. Note faint traces of layering (arrows). *Zenkevitchiana*, Kuril Trench, depth 8.820-9.220 m; *Sabellidites*, deep boring Vishki 25, Eastern Latvia, depth 725.4 m.

Plate 7

Ultrastructure of zooidal tube in *Zenkevitchiana longissima* as seen on longitudinal sections through the internodal area and stained with PTA (1-4). Note the V-shaped arrangement of layers (1, 3).

Plate 8

Ultrastructure of zooidal tube in *Zenkevitchiana longissima* as seen on longitudinal sections (1-2) stained with lead citrate for 10 minutes. *d*—electron dense ground substance, *f*—presumed chitin fibrils, *v*—fibrils showing chevron arrangement.

Plate 9

Ultrastructure of zooidal tube in *Zenkevitchiana longissima* as seen on longitudinal sections (1-2) stained with 1% uranyl acetate for 4 hours.

Plate 10

Ultrastructure of zooidal tube in *Zenkevitchiana longissima* as seen on transverse sections (1-4) stained with potassium permanganate, for 5 minutes (1, 3) and 1 minute (2, 4).

Plate 11

Light micrographs of *Siboglinum* sp. zooidal tube showing details of thinner proximal part (1) and its medial portion (2a, b).

Plate 12

Light micrographs of *Siboglinum* sp. zooidal tube showing its anterior portion passing gradunlly from ringed part (1) into a flimsy part with indistinct incipient rings (2, 3).

Plate 13

Ultrastructure of zooidal tube in *Siboglinum* sp. as seen on transverse sections (1-4) stained with 4% potassium hypermanganate followed by citric acid; 1-1 wall of the tube, 3-4 its medial and inner parts.

Plate 14

Ultrastructure of zooidal tube in *Siboglinum* sp. as seen on longitudinal sections revealing structural pattern 1 (1-4). Staining as on pl. 13.

Plate 15

Ultrastructure of zooidal tube in *Siboglinum* sp. as seen on longitudinal sections revealing structural pattern 2 (1-4). Staining as on pl. 13.

Plate 16

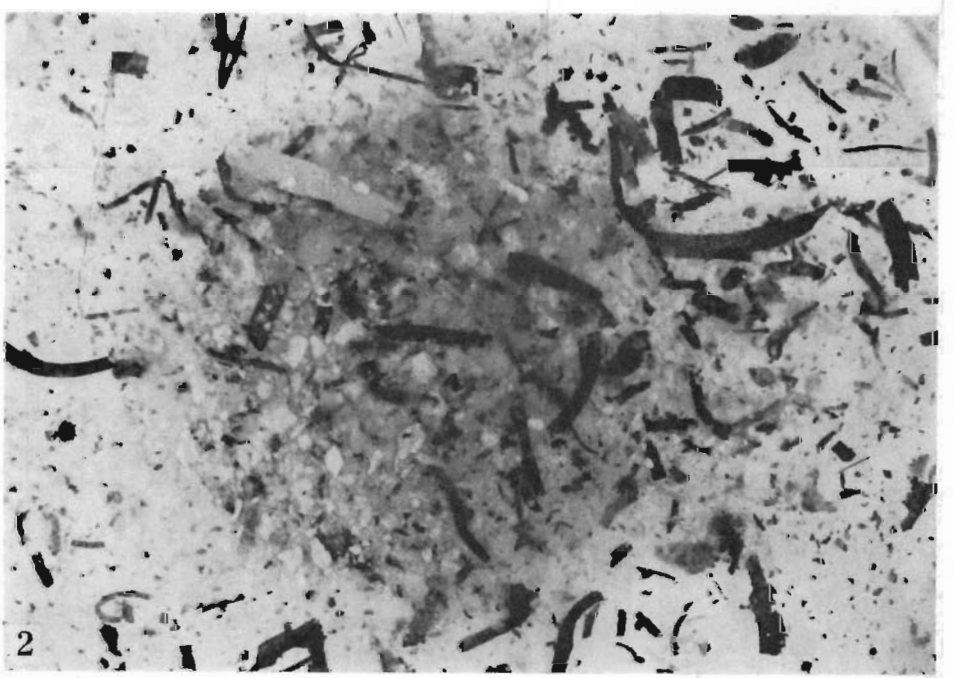
Ultrastructure of zooidal tube in *Siboglinum* sp. as seen on longitudinal sections and revealing structural pattern 2 (1-2) and wrinkled area of the tube (3-4). Staining as on pl. 13.

Plate 17

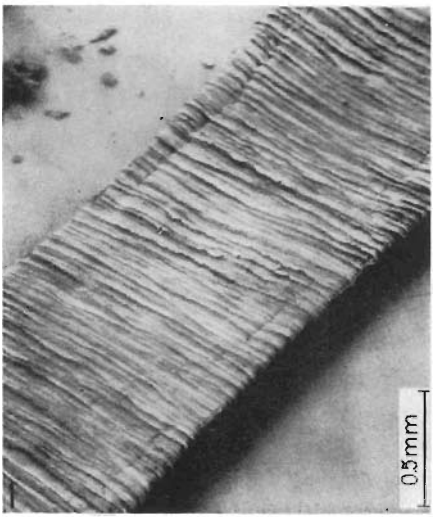
Ultrastructure of wrinkles on the zooidal tube of *Siboglinum* sp. Staining as on pl. 13.

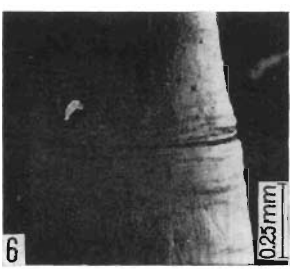
Plate 18

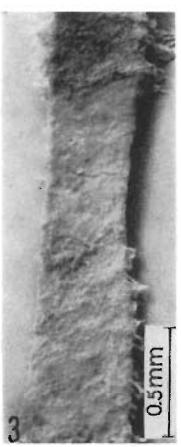
Diagram showing longitudinal sections through the wall of a zooidal tube in *Sabellidites* (*A*), *Zenkevitchiana* (*B,C*) and *Siboglinum* (*D*). Note the difference of structure observed in two neighbouring interspaces (*B,C*); *i* — inner component, *is* — wrinkled interspace area separating two adjacent annular bands, *m*—middle component, *o* — outer component. Arrows in *A* indicate the faint traces of layering observed at some places within the inner and outer components. Broken lines in *D* indicate the boundary between the interspace and adjacent annular areas. Empty spaces formed by tearing of layers are shown in solid black.

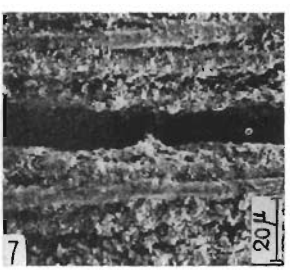


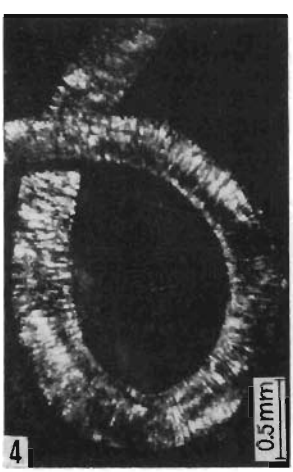
Phot. L. Łuszczewska

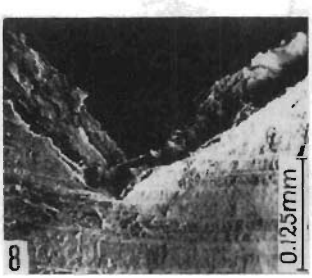


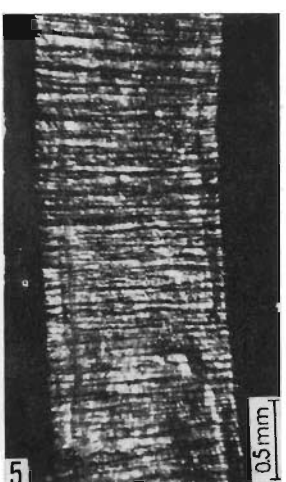












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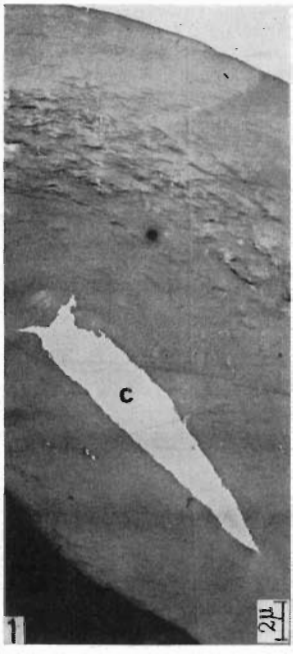
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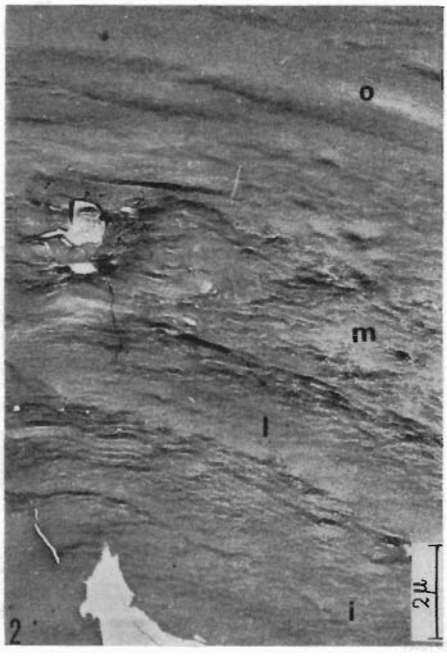
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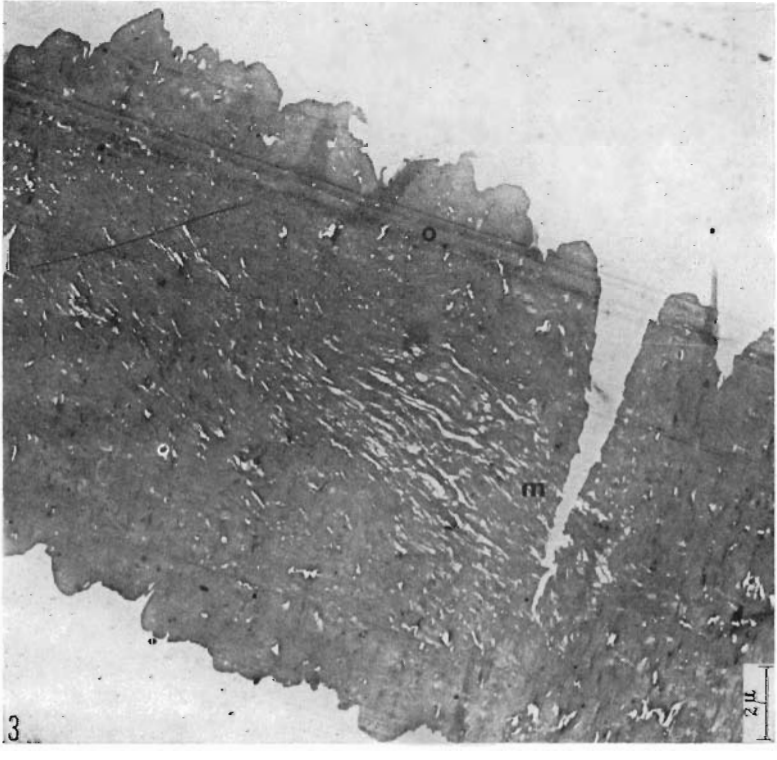
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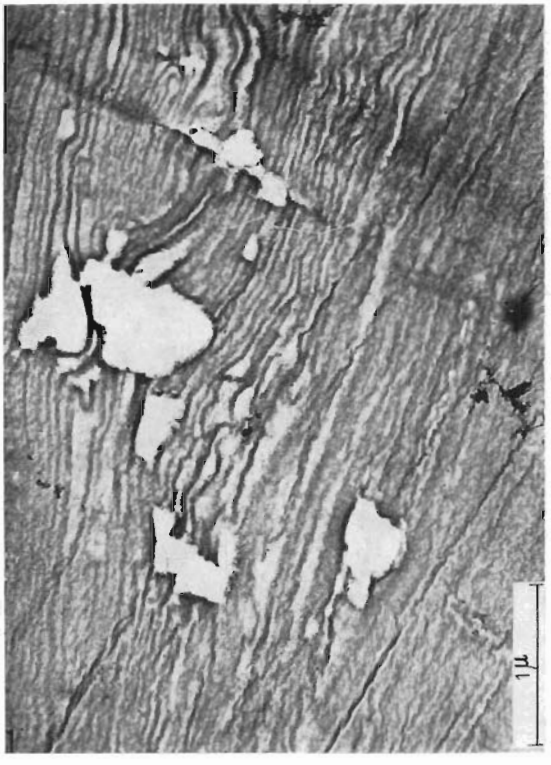

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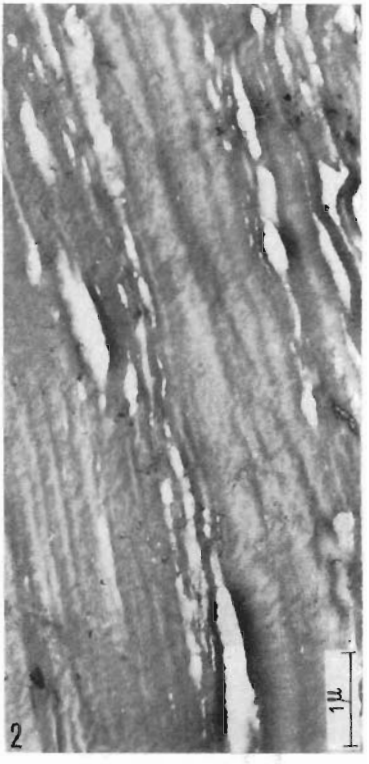

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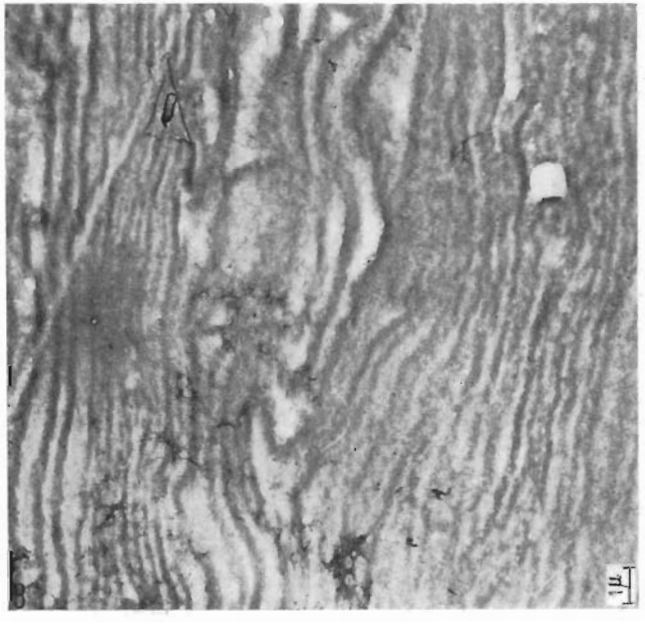

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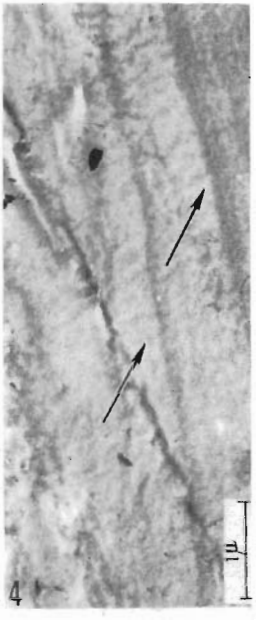

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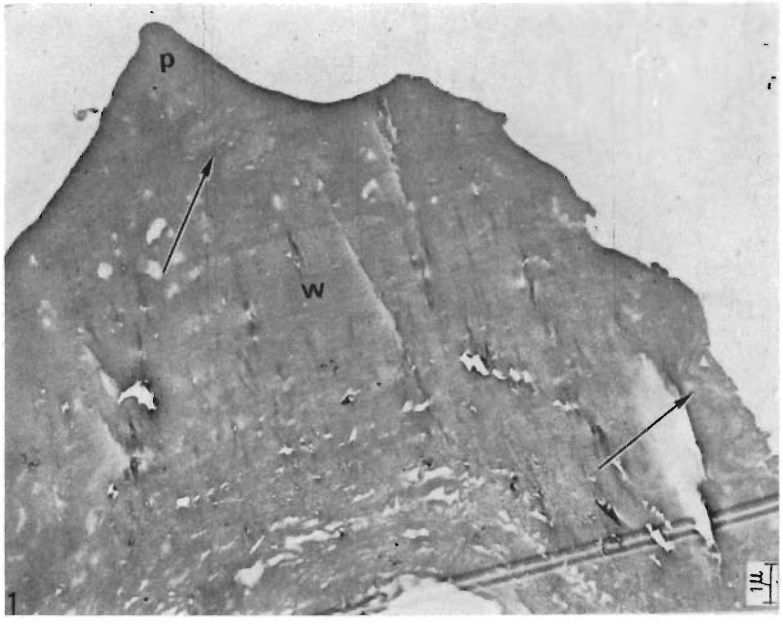
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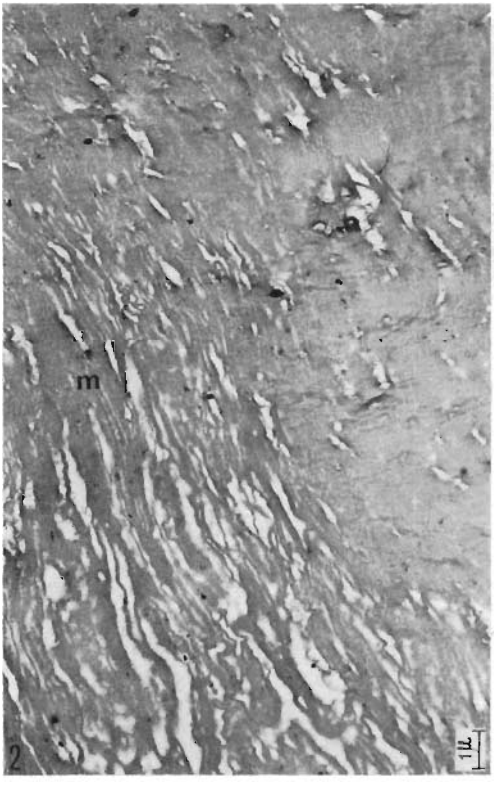
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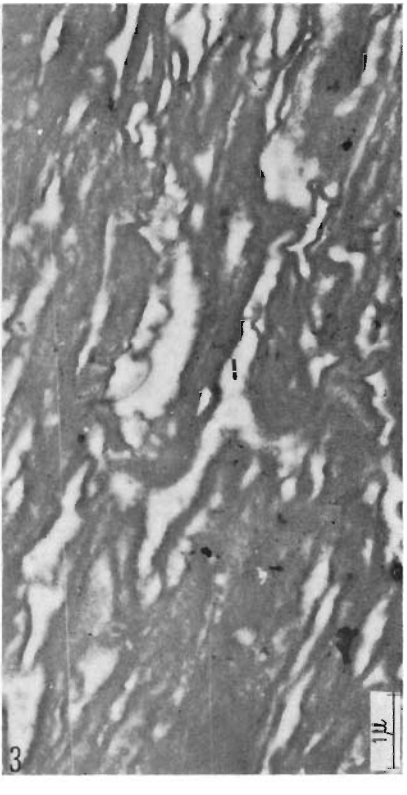
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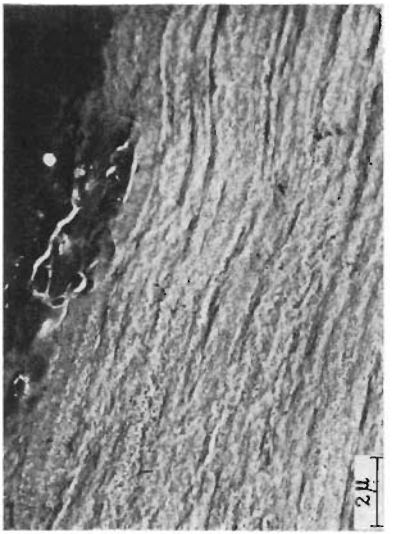
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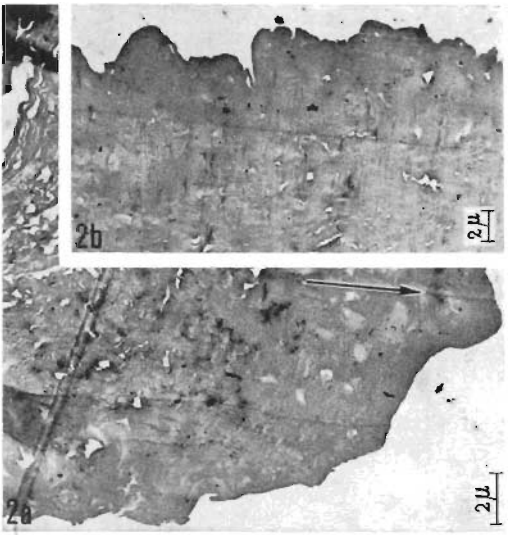
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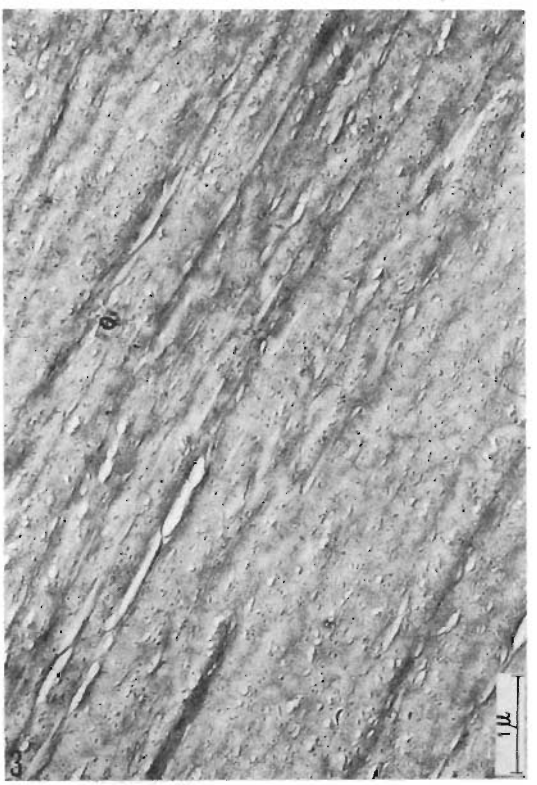
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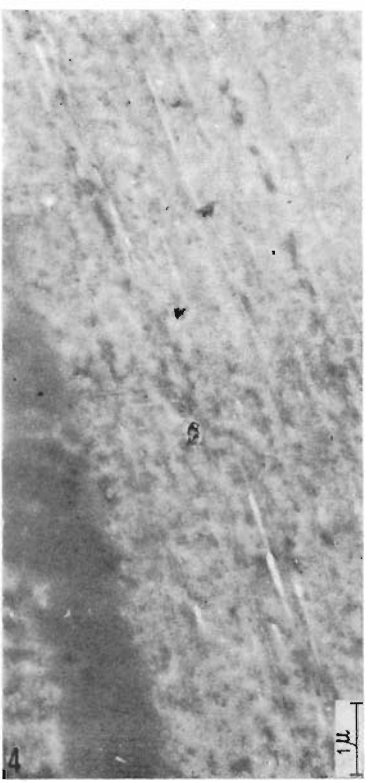
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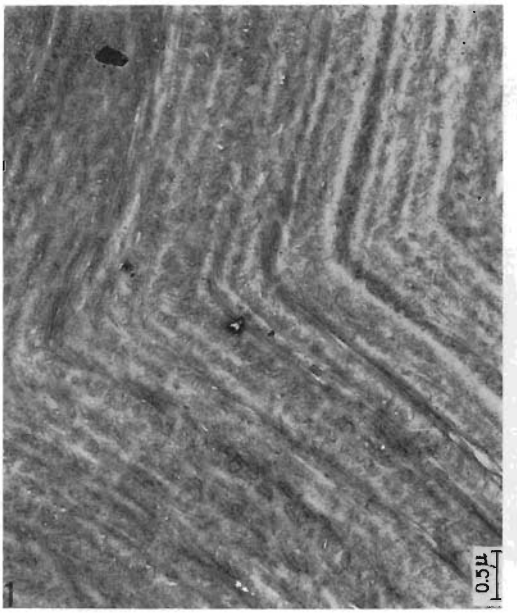

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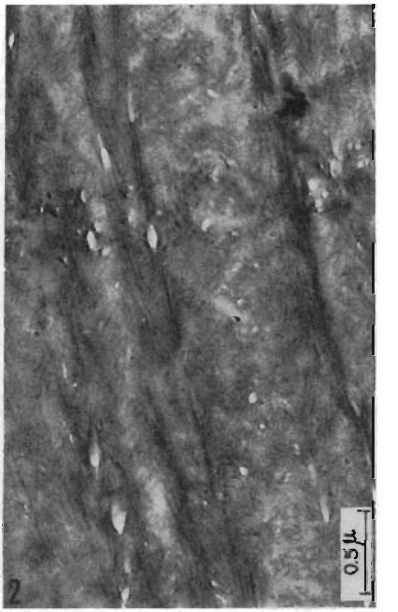

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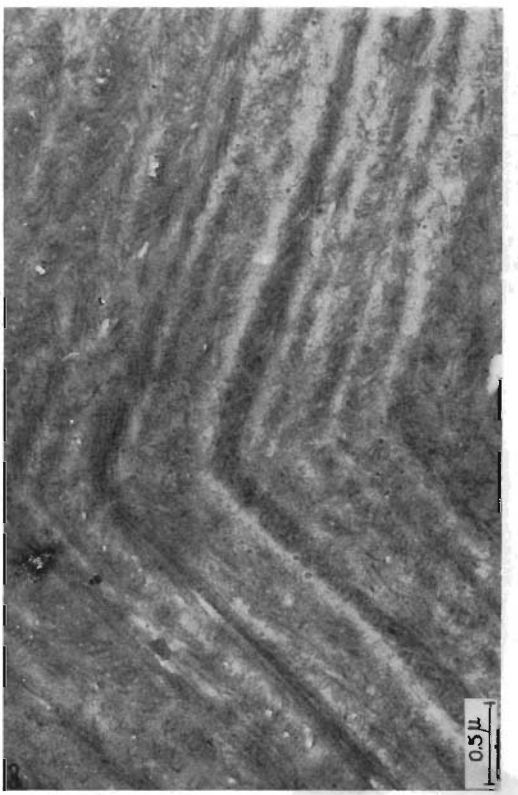

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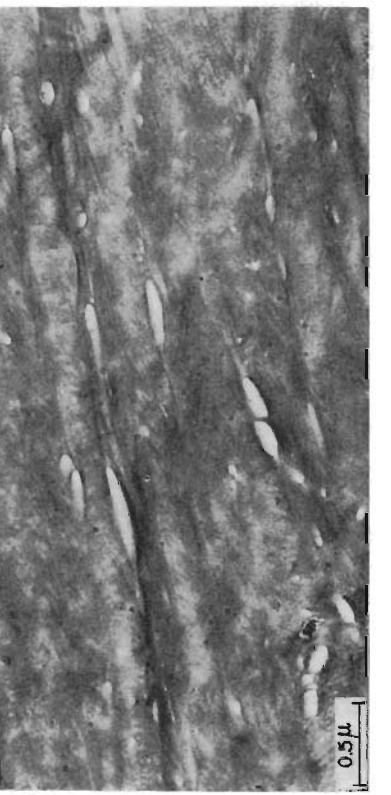

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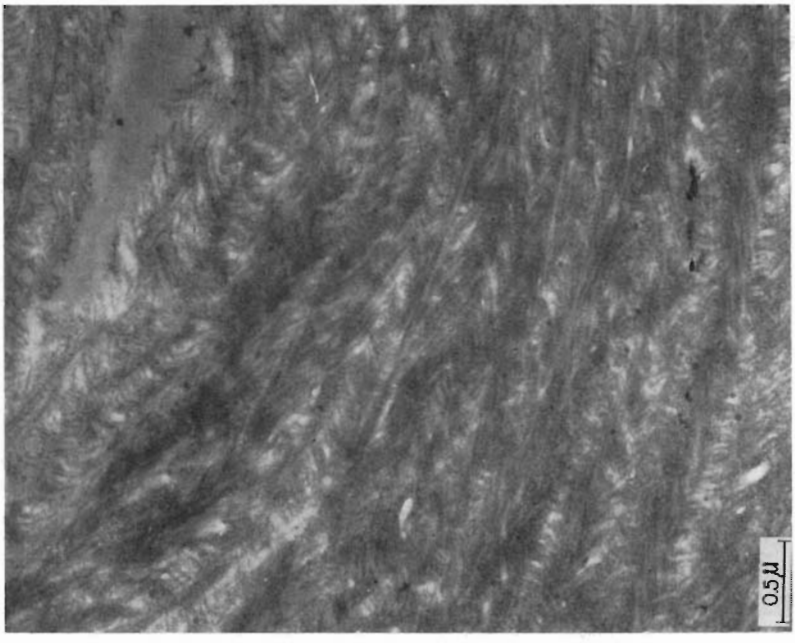
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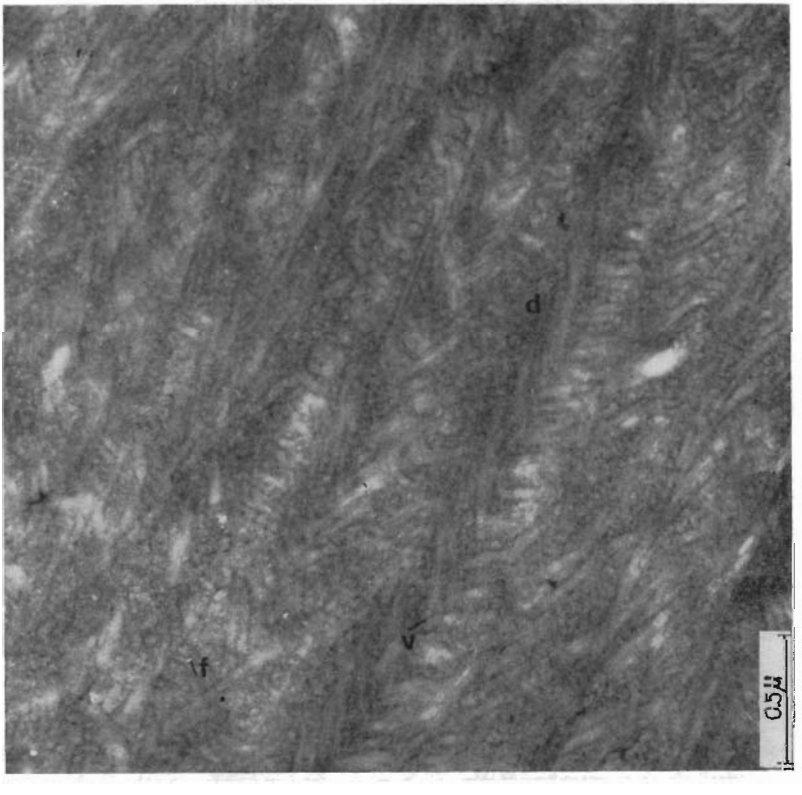
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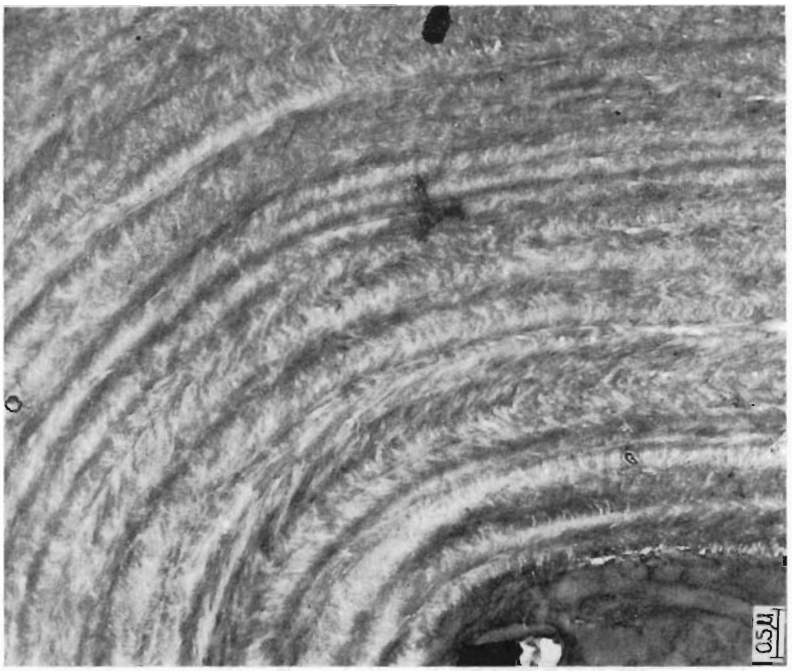
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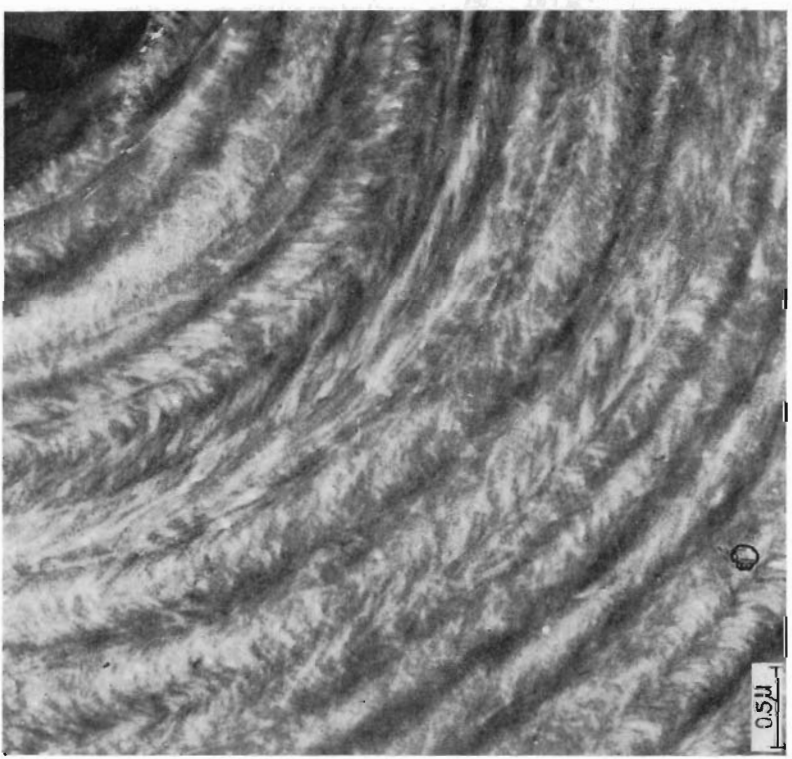
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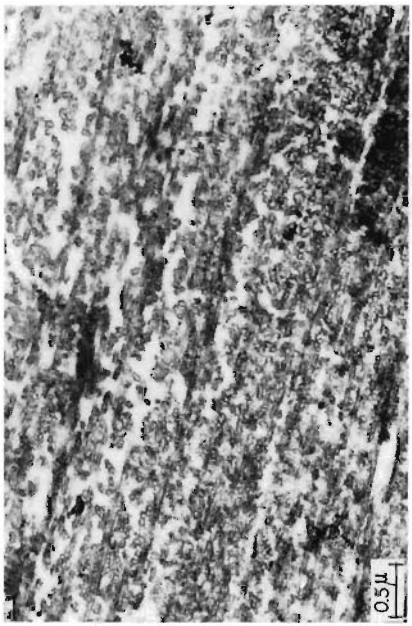

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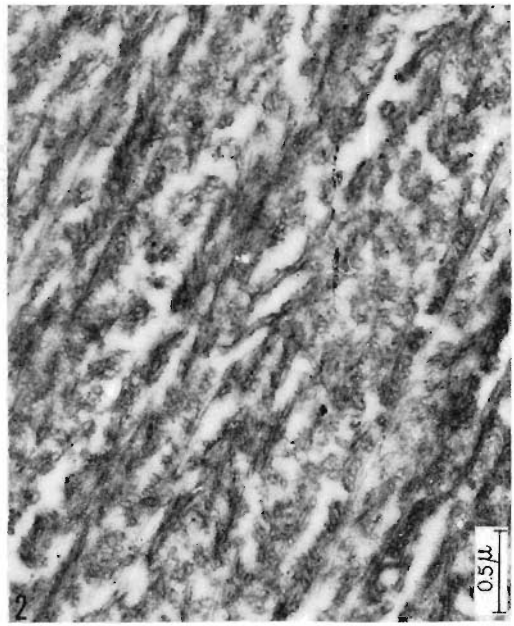

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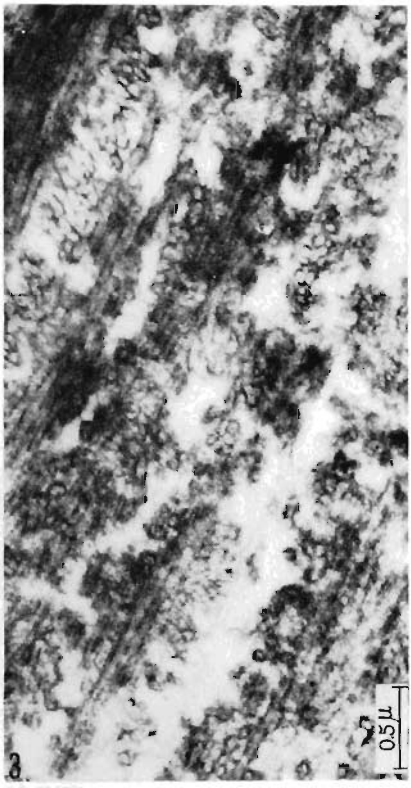

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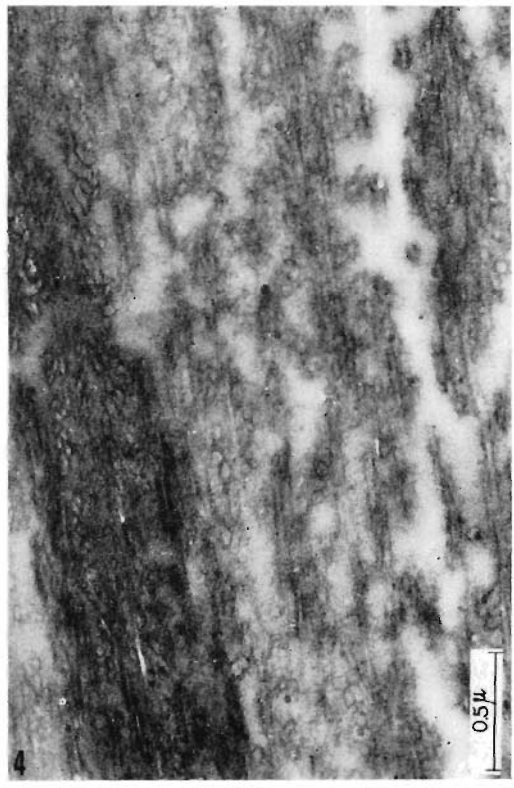

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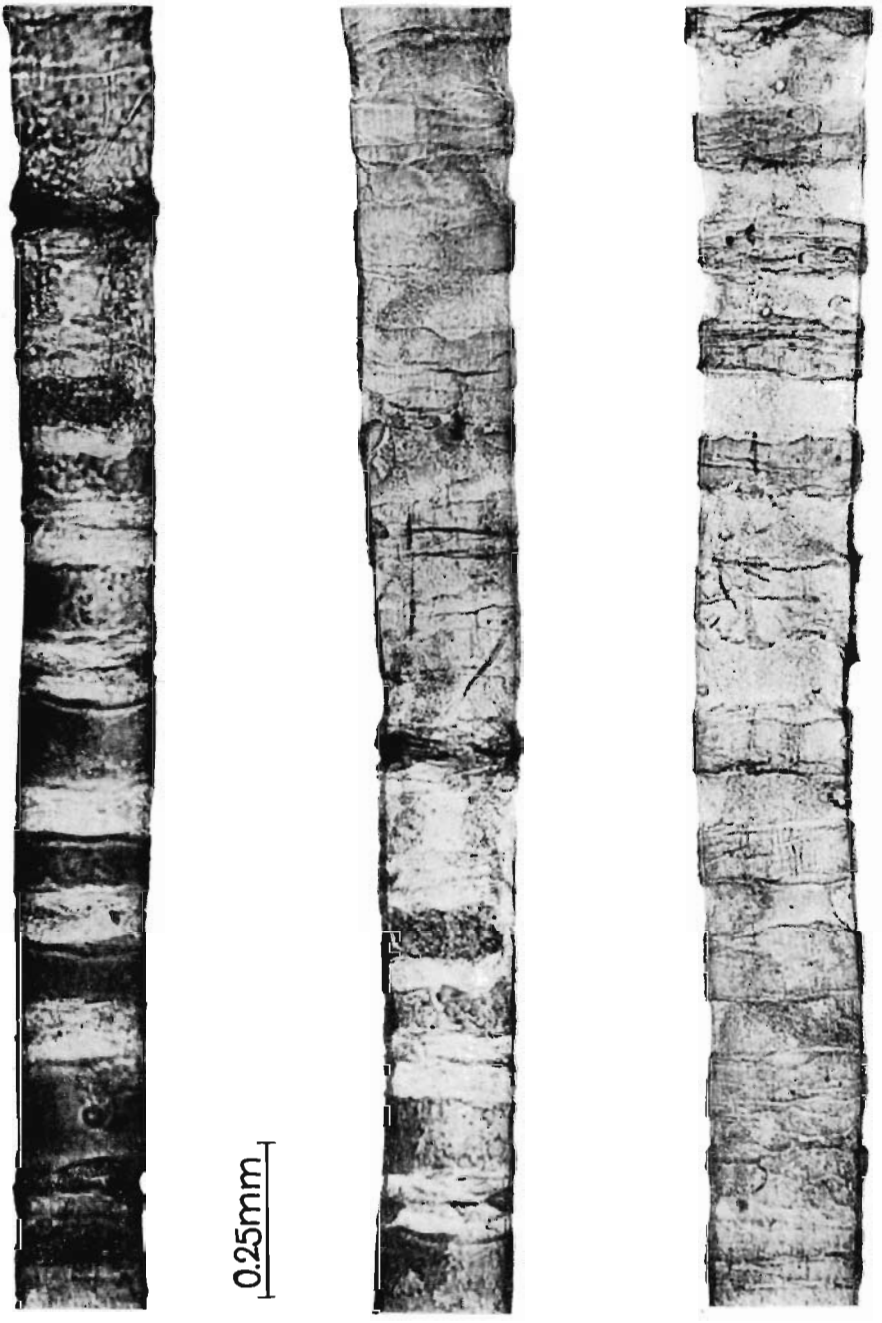
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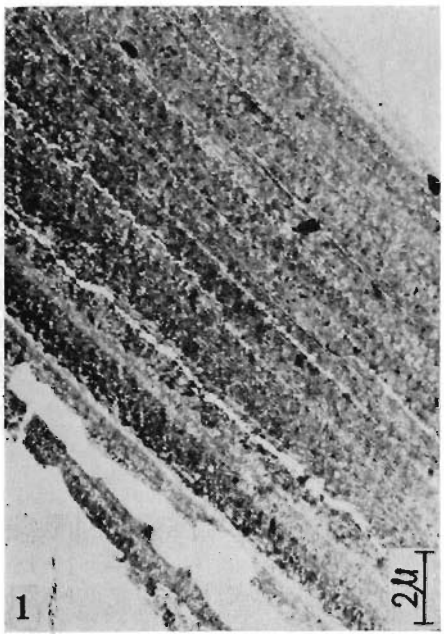
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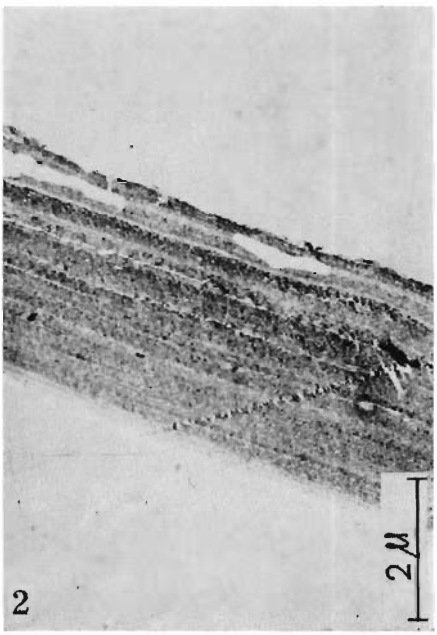
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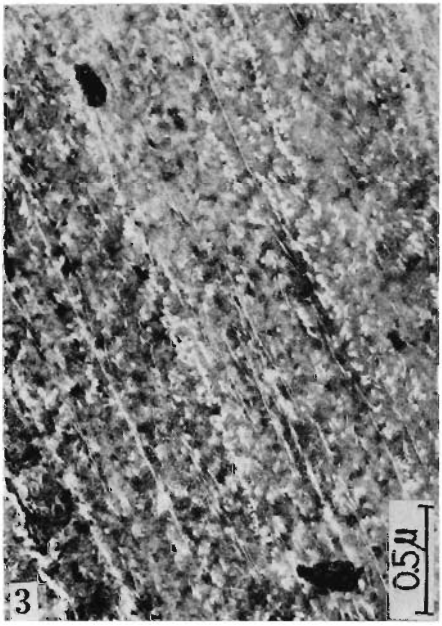
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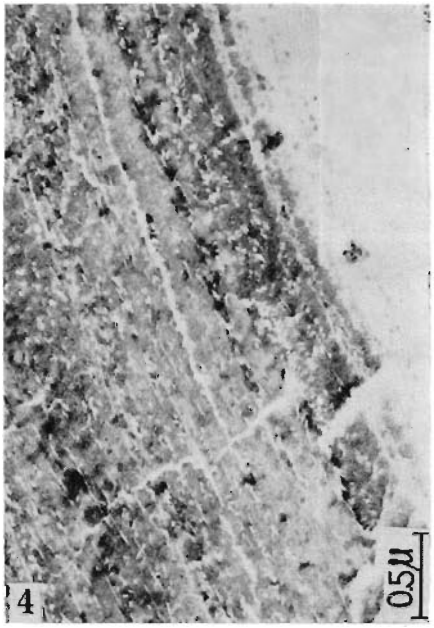
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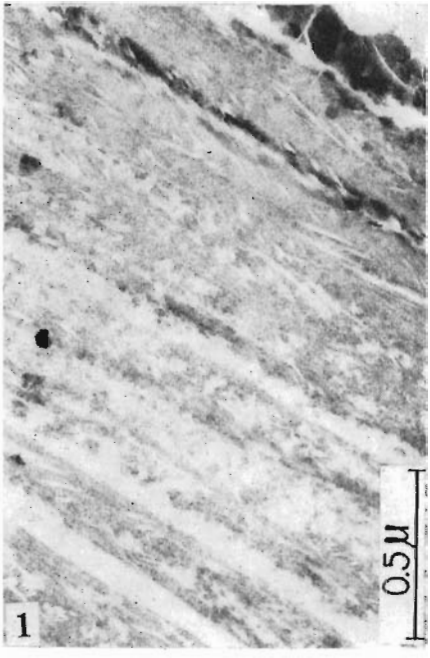
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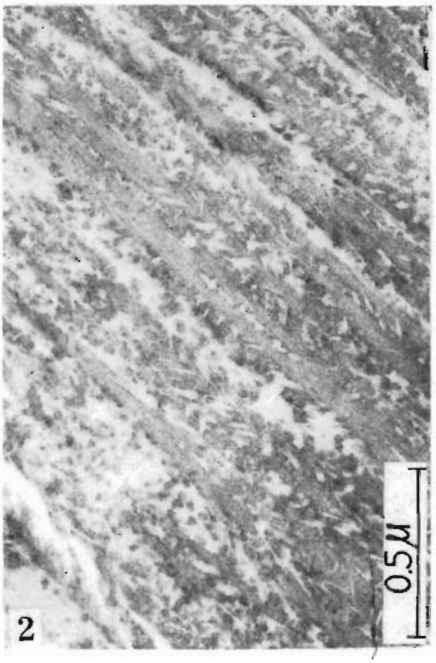
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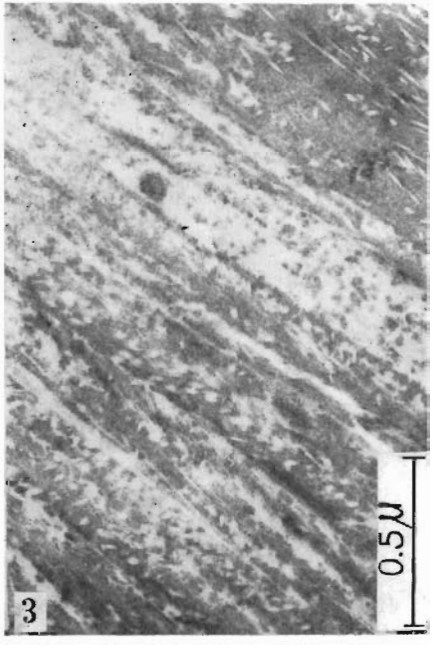
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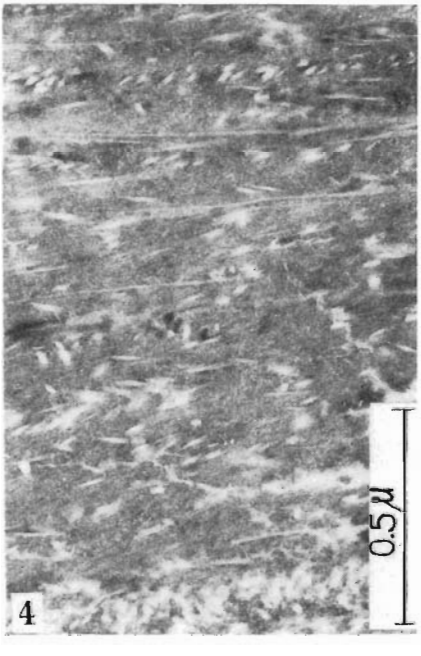
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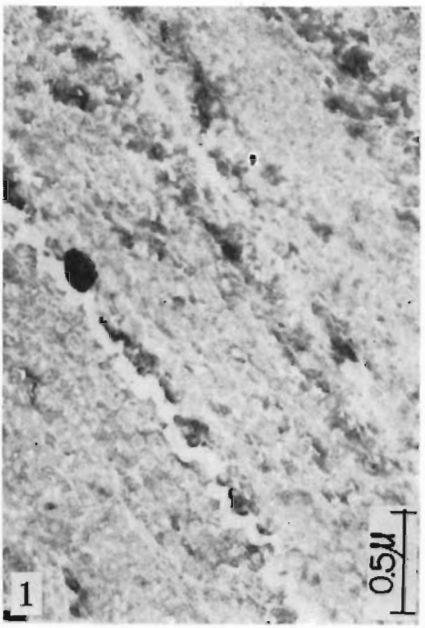
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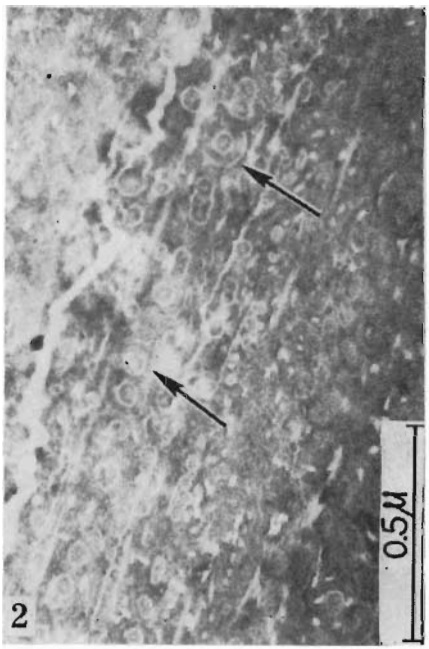
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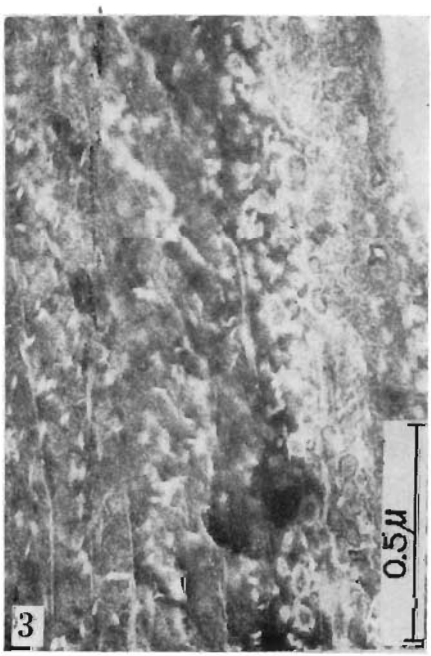
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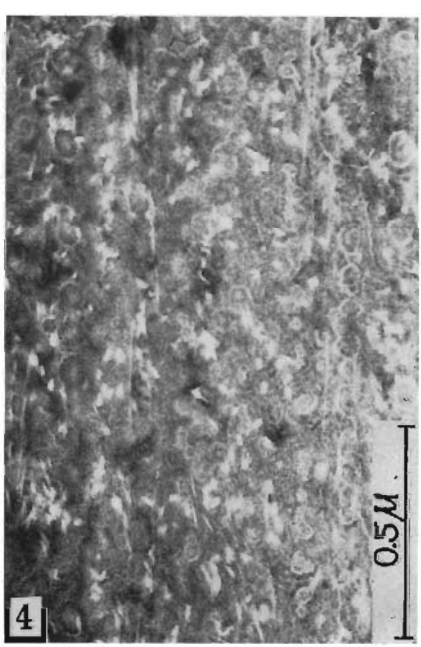
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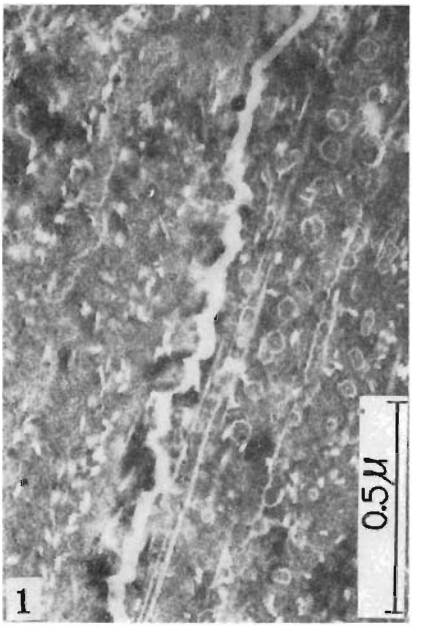
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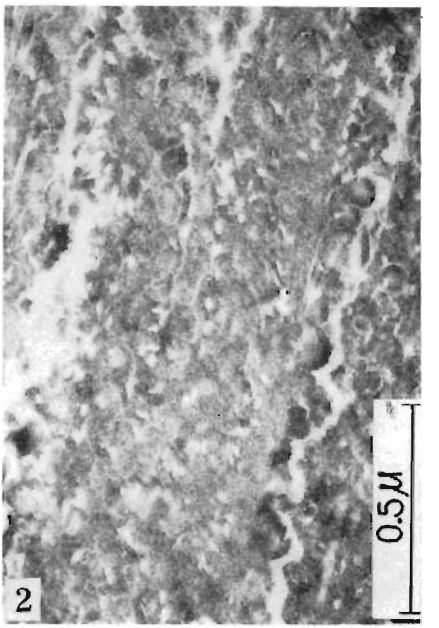
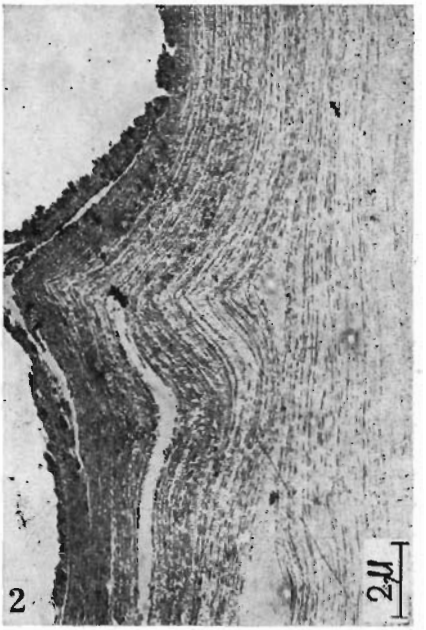

0.5μ
2


1μ
3


0.5μ
4


1
1μ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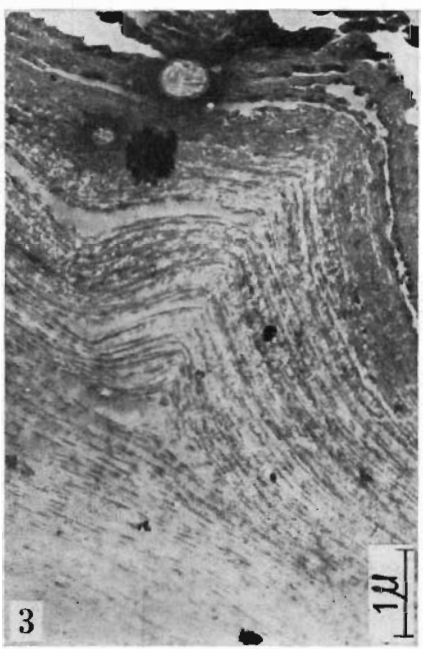
2μ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4
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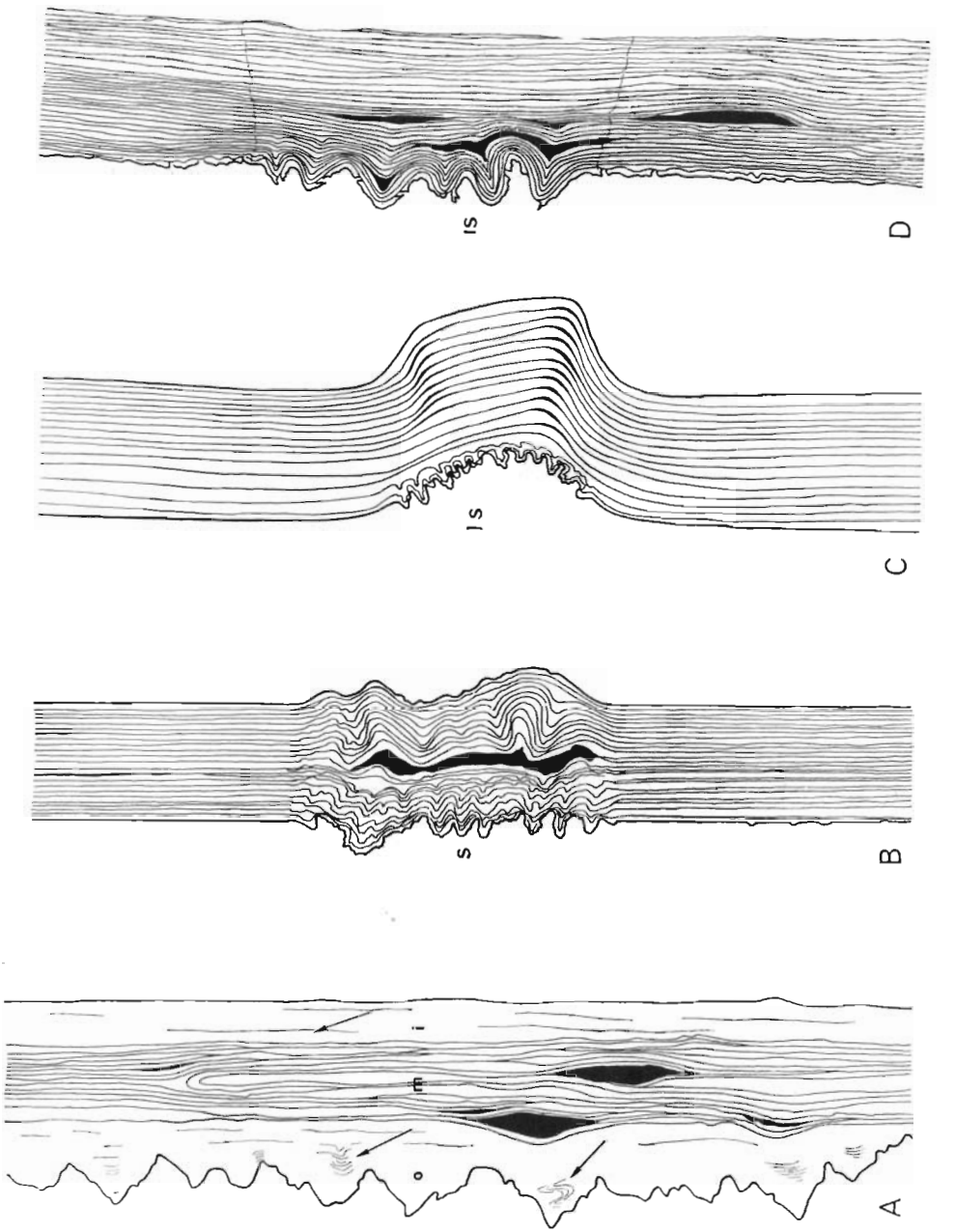
IS
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