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ADAM URBANEK

ULTRASTRUCTURE OF MICROFUSELLI AND THE EVOLUTION OF GRAPTOLITE SKELETAL TISSUES

Abstract. — Ultrastructure of microfusellar tissues has been studied in *Neocucullograptus kozlowskii*, and compared with that in normal fuselli. Microfusellar tissue is composed of both fully developed and reduced microfuselli. The former consists of the fusellar and the cortical components and may pass into reduced microfuselli due to skipping the fusellar phase of secretion. This demonstrates a possible mechanism of the transition from the fusellar to the cortical tissue and sheds some light on principles governing the morphogenesis of graptolite skeletal tissues. Formation of particular fabrics and patterns was determined by control of a certain innate potential of secretory cells. Modes of changes in this control are identified and a working hypothesis concerning the evolution of graptolite skeletal tissues is advanced.

INTRODUCTION

Recent studies on ultrastructure of peridermal derivatives in Graptolithina (Towe & Urbanek, 1972; Urbanek & Towe, 1974, 1975; Urbanek & Rickards, 1974) provided entirely new data concerning the nature of the unit elements recognized in the fabrics of the graptolite skeleton. They also enable a classification of a variety of observed materials. A comparison of submicroscopic structure of the skeleton in Pterobranchia and Graptolithina seems to be of great significance for a better understanding of the affinities and the systematic position of the latter group (Urbanek, 1976).

The present paper deals with light and electron microscopy of a separate and rather sparsely distributed peridermal tissue — the microfusellar tissue, found so far only in a few graptolites. In spite of its rather rare occurrence, the microfusellar tissue proved to be of crucial importance for understanding the mode of formation and presumable evolution of the graptolite skeletal tissues.

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MATERIAL AND TECHNIQUES USED

The specimens studied and illustrated in the present paper were etched from some erratic boulders of Baltic origin and from bore core samples of deep boring at Mielnik on the Bug.

Material of *Monoclimacis micropoma* (Jaekel) has been obtained from erratic boulder from Śrem (Central Poland) numbered S. 220 in the collection of graptolite bearing erratic boulders in the Palaeontological Institute of Warsaw University, and from the bore core of a deep boring at Mielnik on the Bug (Eastern Poland) from a depth of 1019.30 m. The associated graptolite fauna is indicative of a Lower Ludlovian age for this material (*Lobograptus progenitor* Zone).

Material of *Neocucullograptus kozlowskii* Urbanek comes from the bore core of the Mielnik on the Bug deep boring (depth 873.40 m, lower part of the Siedlce Beds — Upper Ludlovian, *N. kozlowskii* Zone). More details on the stratigraphical setting of this fauna are given in Urbanek (1970, p. 184—187).

The etching and bleaching technique used is much the same as that described earlier by the author (Urbanek, 1966, pp. 302—304). Scanning electron micrographs were taken at the Laboratory of the Electron Microscopy of the Polytechnic in Warsaw, with use of a Cambridge Stereoscan M. K. II. Specimens were gold-coated for study under the microscope. Ultrathin sections, their scoping and photographing with Phillips EM 200 transmission electron microscope were made in the Department of Paleobiology, Smithsonian Institution, Washington D. C. Methods used were the same as those described by Urbanek and Towe (1974, 1975).

LIGHT MICROSCOPY OF THE MICROFUSELLAR TISSUE

Characteristics of microfusellar tissue. — The microfusellar tissue as a separate peridermal material was first recognized in *Monoclimacis micropoma* Jaekel (Urbanek, 1958, pp. 23 and 93, fig. 68) and later technically defined by Urbanek (1966, 1970) as a "peridermal fabric consisting of very narrow, densely crowded strips (microfuselli), producing dark-pigmented, thick-walled periderm, that is, the microfusellar tissue proper, or consisting of wider, irregularly arranged strips making up a membranous, attenuated periderm, that is, the pseudo-microfusellar tissue". The present paper deals only with the light and electron microscopy of the former variety of the microfusellar tissue.

Structures made of microfusellar tissue occur sporadically in various graptoloids, lineages represented by Upper Silurian monograptids — *M. micropoma* and *Neocucullograptus* being so far the only known case of extensive utilization of this tissue. The evolution of neocucullograptids as analysed by Urbanek (1970) is closely related to the appearance and utilization of the microfusellar tissue, as it served in this group for formation of different microfusellar additions superimposed, usually with a distinct delay, over the fusellar parts of thecae. The order of appearance (introduction) of these phylogenetic novelties in a rhabdosome as well as different morphological forms of terminal microfusellar additions were described and defined earlier (Urbanek, 1970, pp. 194—200). In some monograptids this tissue was eventually used to produce complex apertural apparatus of thecae, clearly an adaptive feature not attainable morphogenetically with use of normal fusellar tissue in this particular group.

Microfusellar tissue forms terminal additions to the thecae (rarely also siculae) in form of apertural lobes or spines, in certain cases producing complex apertural apparatuses. These show a remarkable homoeomorphy to apertural apparatuses produced independently in other lineages on the base of normal fusellar tissue. Such homoeomorphic pairs are (1) *Monograptus uncinatus* Tullberg — *Monoclimacis micropoma* Jaekel and (2) *Cucullograptus aversus rostratus* Urbanek — *Neocucullograptus kozlowskii* Urbanek. In spite of a striking similarity of outer shape of apertural apparatuses the underlying structural principle is quite different.

The exploitation of certain new possibilities opened by microfusellar tissue was evidently the source of evolutionary success for some groups of graptolites. This fact emphasizes the significance of this particular skeletal tissue. It has also a great bearing for understanding the mode of secretion, morphogenetic interrelations and evolution of main skeletal tissues in graptolites.

Light microscopic features of microfusellar tissue. — After bleaching the microfusellar tissue proper examined with a light microscope in tran-

smitted light reveals numerous, rather narrow strips (approx. 8—2 μ, in average some 5 μ in width), called the microfuselli. In certain parts of microfusellar additions the arrangement of microfuselli is fairly regular, while in some others distinct irregularities and discrepancies between particular bundles (bunches) of microfuselli are observed. Microfuselli are fairly long (some 300 μ in length), sometimes much shorter and wedge-shaped. They taper irregularly at different places, without producing any suture, so characteristic of normal fusellar tissue (pl. I, figs 2, 4).

The surface of unbleached and usually "carbonized" microfusellar additions is indistinguishable from the surface of the fusellar part of the thecae, while bleached specimens reveal a sharp difference between both parts of rhabdosome.

Structural characters of microfusellar additions and normal fusellar tissue from the metathecal wall are here confronted in *Monoclimacis micropoma* (pl. I, figs 3, 4), and *Neocucullograptus kozlowskii* (pl. I, figs 1, 4). For more details see Urbanek (1970, pls. 44—45).

ULTRASTRUCTURE OF MICROFUSELLAR AND FUSELLAR TISSUE IN *NEOCUCULLOGRAPTUS*

Morphology of microfusellar tissue studied with SEM. — Studies on the surface morphology of the microfusellar additions in *Neocucullograptus kozlowskii* and closely related *N. inexspectatus* as observed in a scanning electron microscope (SEM) proved to be of little value for understanding the underlying structures. The SEM micrographs show, in the best case, a number of delicate ridges on the surface of periderm which correspond to junctional lines between microfuselli (pl. IV, fig. 3). The information offered by SEM is in fact inferior both to that obtained under the light microscope and the transmission electron microscope (TEM). The only noteworthy result is a remarkable conformity of the SEM picture showing the end of a rostral process with that observed on ultrathin sections with TEM (comp. pl. IV, fis 3 and 4).

Microfusellar tissue studied with TEM. — Ultrathin sections through the apertural apparatus of *N. kozlowskii*, made of microfusellar tissue, reveal a distinct pattern of the submicroscopic structure of the microfusellar strips. Viewed on sections oriented parallelly to the longitudinal axis of the theca, the microfusellar strips look like parabolic (pl. II, fig. 1; pl. V, fig. 3) or "V"-shaped (pl. IV, fig. 1) structures, much lower than the normal fuselli of the theca proper (see below).

When fully developed, each microfusellus is parabolic in cross-section and composed of a body, an outer lamella and an outer pellicle, not unlike the majority of growth bands in normal fusellar tissue. The body of the microfusellus (pl. II, figs 2—4) is made of a typical fusellar fabric as defined by Urbanek and Towe (1974, p. 5). It is a rather loose,

meshwork of interconnecting fibrils, each some 500 Å in diameter. The outer lamella (pl. II, figs 2, 3*o*) is a layer situated marginally and produced by dense packing of irregular fibrils being a continuation of those within the body (pl. V, fig. 1,*o*). In other cases it displays raher a regular arrangement of parallel-oriented fibrils, fused at places by rare interconnecting rods (pl. III, fig. 4; pl. V, fig. 4,*o*). Both inner components of the microfusellus are coated by an outer pellicle, seen as a single electron dense line (pl. II, figs. 2, 3,*p*) or sometimes as a triple-unit element, being composed of two electron dense lines separated by a less dense middle layer (pl. V, fig 2,*p*) Such microfuselli are therefore built of the same subunits which were earlier recognized in normal fusellar tissue of some dendroids (Urbanek & Towe, 1974) and graptoloids (Urbanek & Towe, 1975). The only difference is in the narrowness of the particular growth bands in microfusellar tissue as well as a smaller share of the fusellar fabric.

A characteristic feature of the microfusellar tissue, however, is a fairly irregular secretion of a series of fully developed microfuselli, followed by a multiple deposition of the r e d u c e d m i c r o f u s e l l i. These are usually "V"-shaped in cross section, with little or no fusellar fabric inside (pl. III, figs. 1, 2, *r*). In the latter case, the only components of microfusellar strips are an outer lamella and an outer pellicle (pl. III, fig. 4, *o*, *p*), i.e. the same units that are found in cortical tissue. The width of reduced microfuselli is usually some 1—0.5 μ.

Sections through periderm in the dome of the left apertural lobe show a common sequence of the above mentioned parts. A more or less regular deposition of a number of fully developed microfuselli frequently produces a distinct convexity, or club-like, bulbous thickening (corresponding to separate bundles of microfuselli as defined above) (pl. II, fig. 1; pl. IV, fig. 1, *th*). This is followed by the deposition of usually numerous reduced microfuselli, forming much thinner parts of peridermal wall and being composed mainly of outer lamellae and outer pellicles, with little amounts of fusellar fabric, sometimes present asymmetrically in one limb only (pl. IV, fig. 2; pl. V, fig. 3, *th*). Some spots of the apertural dome are made of multiple deposition of reduced microfuselli, fully deprived of their fusellar component, usually with obliterated boundaries between particular growth bands. They show a gradual passage to almost homogenous tissue, with a few patches of a more spongy aspect due to reappearance of some fusellar fabric (pl. III, fig. 3, *h*).

A similar multiple deposition of the reduced microfuselli which are composed of outer lamellae and outer pellicles only, has been observed at the free ends of microfusellar additions in *N. kozlowskii*, namely at the edge of the ventral apertural lobe (pl. VI, figs 3, 4, *e*) and at the end of the rostral apertural process (pl. IV, fig. 4, *e*). This accumulation of reduced microfuselli in terminal structures of the apertural apparatus may be

indicative of some cessation of growth in the proliferation zone of the secretory epithelium. Smaller depositions of the outer lamellae, however, may be observed as intercalations even between fully developed microfuselli in the dome of the ventral lobe (pl. II, fig. 4, *i*).

A remarkable feature of both fully developed and reduced microfuselli is the great degree of their overlapping. This is especially striking when compared with the degree of overlapping in the normal fusellar growth bands of the thecal wall of *N. kozlowskii* (see below). This overlap is distinctly asymmetric in places. In the ventral part of apertural lobe (pl. V, figs 1, 2, *c*, *ec*; pl. VI, fig. 3) an accumulation of 5—10 overlapping outer lamellae produces an inner cortical coating (endocortex) some 3 μ thick. This inner cortical deposit is made of a number of layers, each being an extension of an outer lamella of a given microfusellus. It has a vesicular aspect due to a number of vesicles scattered between fibrils or fused with the outer pellicles and due to a number of fusellar intercalations. As a result of a lesser degree of overlap on this side of microfuselli, the outer cortical coating (cortex) is distinctly thinner and looks rather dense, because of the scarcity of vesicles and the tight packing of the fibrils (comp. pl. V, figs 1, 2, *c*, *ec*). Elsewhere, for example the dome of the lobe, the degree of asymmetry in overlapping of the outer lamellae seems smaller or none, the thickness of endocortex and cortex being about the same.

The formation of the cortical deposit over microfusellar additions of the thecae in *N. kozlowskii* differs therefore from that laid down over the fusellar part of the thecae. The former is essentially produced according to a mode recognized earlier in *Didymograptus* sp. (Urbanek & Towe, 1975), involving a simultaneous formation of a given microfusellus and a corresponding layer of the cortical deposit. This is due to the overlapping of the outer or/and the inner limbs of microfuselli. The latter, in contrast to the former, is laid down independently over the preformed fuselli.

The evidence available seems to suggest that at different places of the same rhabdosome, cortical deposits may be secreted according to either independent or dependent mode (comp. observations by Urbanek and Towe, 1975, pp. 21—22). There is no good reason to follow Kirk (1975, p. 3) and insist that because cortical coating on virgella of *Pristiograptus dubius* (as shown by Urbanek and Towe, 1975, pl. 16) is formed due to overlapping of outer lamellae, the same is true for the rest of rhabdosome. The empirical evidence clearly suggests the different modes of formation of cortical deposit even within a single rhabdosome. This does not contradict, in present author opinion, that entire periderm was secreted within a single secretory organ, namely the perithecal membrane (Urbanek, 1976; see below for more data and discussion).

Ultrastructure of the fusellar tissue in Neocucullograptus. — The nor-

mal fusellar tissue and the cortical coating of the thecal wall in *Neocucullograptus kozlowskii* were studied for comparison.

The fusellar component of the thecal wall seen on longitudinal sections, is made of fuselli, morphologically similar to those found in *Pristiograptus dubius* (Urbanek & Towe, 1975, pl. 14, figs 1—3). Each fusellus may be subdivided morphologically into a broader *base*, resting immediately over the head of preceding fusellus, a much narrower and elongated *trunk* and broader, club-like *head*. The width (1) of a normal fusellus is some 25 μ, while microfusellar strips in average are only 5 μ wide (1).

Structurally, each fusellus is composed of a body, formed by spongy fusellar fabric, which does not differ from that in fully developed microfuselli; an outer lamella produced by tightly crowded fibrils showing rather irregular arrangement, and an outer pellicle (pl. VI, figs 1, 2, *b*, *o*, *p*). The outer lamella is a band which is wider within the head of the fusellus and gradually decreases in width towards the base. The outer pellicle is a delicate electron dense line indiscernible at places, especially at head (pl. VI, fig. 1, *o*, *p*).

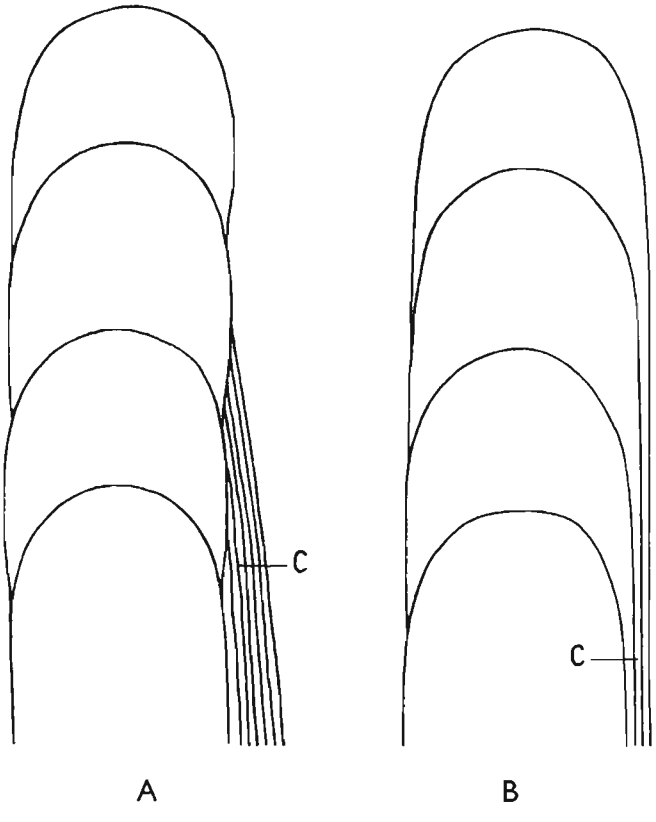

Fig. 1. Diagram showing an independent (*A*) and dependent (*B*) mode of cortex (*c*) formation, as recognized by ultrastructural studies.

In contrast to microfusellar strips, the fuselli show only a small overlap, the base of a given fusellus embracing at a certain distance the head of the preceding one (pl. VI, fig. 2, *b*, *h*). This overlap is somewhat asymmetric, greater from the outer side, than on the inner. Generally, however, the overlap is negligible and the fuselli produce closed systems independently from overlying and underlying layers of cortical coating. There is no doubt therefore that both the cortex and endocortex were laid down secondarily over the surface of the primary fusellar component. In *Neocucullograptus kozlowskii* two modes of cortex formation have been found. In the first mode the cortex formation is inseparable from the secretion of particular microfuselli, each layer of cortical deposit being an extension of the outer lamella of a given fusellus. This mode of formation of the cortical deposits may be termed as d e p e n d e n t. The second mode, which may be classed as i n d e p e n d e n t, has been recognized in the fusellar part of the thecae (text-fig. 1). In this case, successive layers of cortical deposit were laid down secondarily over the surface of the previously formed fuselli. A concurrence of both modes of the cortex formation within a single rhabdosome has been noted earlier (Urbanek & Towe, 1974, 1975). In the case of *N. kozlowskii* these differences are, however, closely related to those found in secretion of fusellar and microfusellar tissue.

SIGNIFICANCE OF ULTRASTRUCTURAL STUDIES ON MICROFUSELLAR TISSUE FOR UNDERSTANDING THE EVOLUTION OF SKELETAL BUILDING MATERIALS IN GRAPTOLITES

Nature of microfusellar tissue. — On the basis of light microscopy the microfusellar tissue has been classified by Urbanek (1970) as a variety of fusellar tissue, mainly because it is composed of numerous narrow growth bands, superficially resembling fuselli, but also because of the presence of certain transitions towards normal fusellar periderm. The electron microscopy and ultramicrotomy enable determination of the submicroscopic composition and fabrics involved. This leads to the conclusion that the microfusellar tissue, as defined by Urbanek (1970), may be actually considered as a variety of fusellar tissue. Such reasoning is based on the homology between the secretionary units of both tissues, namely the fuselli (growth bands) of the normal fusellar tissue and the microfuselli (growth strips) of the microfusellar tissue. A fusellus and a fully developed microfusellus are composed of the same fabrics and the same parts, thus being equivalent structures from the view-point of comparative anatomy.

The term "tissue" suggested previously in respect to the microfusellar component of the graptolite periderm (Urbanek, 1970) is justified by the fact that it is a structural system defined morphogenetically, i.e. by its mo-

de of formation. This fullfils the requirements of the notion of "tissue" as applied to graptolite skeleton by Urbanek and Towe (1974, 1975) in contrast to the notion "fabric". There is no unique fabric (defined by the nature of unit elements and their pattern) specific to the microfusellar component, but it is a peculiar morphogenesis that produces the differences between the fusellar and the microfusellar tissue (see above).

Morphogenetic position of microfusellar tissue. — The microfusellar tissue being essentially a variety of the fusellar one occupies, nevertheless, a particular position among graptolite skeletal tissues. It is truly intermediate between the two major components of graptolite skeleton — the fusellar and the cortical tissues.

This intermediate position is due to the ability of the secretionary units of the microfusellar tissue to be reduced by an omission of the fusellar phase of secretion, and thus to form some simplified units. Such reduced microfuselli may be formed of cortical components only as described above

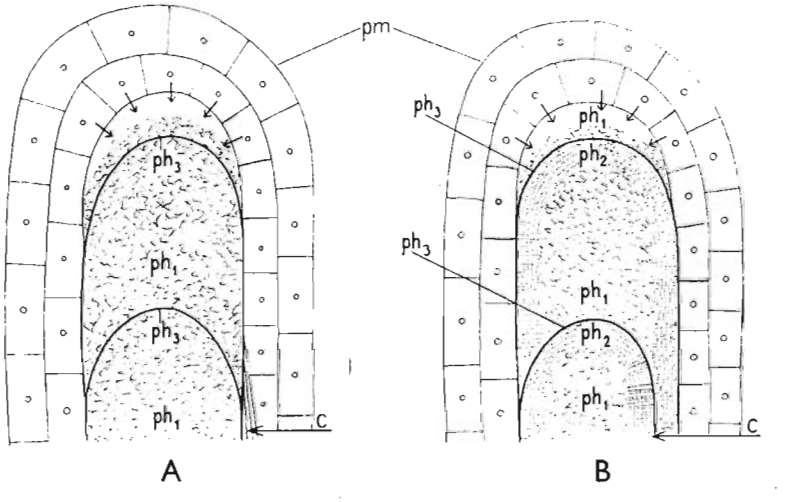

Fig. 2. Ideogram showing presumable relation of secretory part of the perithecal membrane (*pm*) to the growing edge of a thecal wall. *A* — in the case of *Dictyonema* type with fuselli lacking the cortical phase of secretion (ph_1-ph_3) and with independent mode of cortex (*c*) formation; *B* — in the case of *Acanthograptus* type with fuselli showing the cortical phase of secretion (ph_1-ph_2-ph_3) and with dependent mode of cortex (*c*) formation. Arrows indicate the secretionary activity of epithelial cells and directions of extrusion of their products. Mesodermal component of the perithecal membrane not visualized for the sake of convenience. Note the phase control in formation of fuselli (ph_1, ph_2, ph_3).

(see p. 319, and pl. III, figs 3, 4). A graded series of reduction of this fusellar phase, as well as progressive stages of "corticization" of microfusellar tissue may be observed within a single microfusellar addition (pl. III, figs 1, 2).

The data obtained from ultrastructural studies, combined with previous

reports on regeneration or repair of the damaged thecal walls strongly suggest that the formation of the entire graptolite periderm takes place inside a soft tissue evagination which may be termed the perithecal membrane (Urbanek, 1976). This may be visualized as a soft tissue membrane enveloping the thecal wall from both sides and composed most probably of outer and inner layer of epithelium with some mesodermal middle component (text-fig. 2). The layered structure of cortical derivatives of periderm and a considerable share of sheet fabric in the graptolite skeleton are indicative of the presumably epithelial nature of the secretory portion in the perithecal membrane.

The arcuate shape and bilateral overlap of the fuselli are strongly suggestive of the fact that they were produced within a fold of soft tissue, close to the presumed proliferation zone of the perithecal membrane (cf. also earlier suggestions by Kirk, 1972). In some cases, as discussed below, these cells were capable of secreting fusellar and sheet fabric only, while, in others they produced at this spot also some amount of cortical fabric (text-fig. 2, *B*). Secretion of a greater amount of this latter fabric as a cortex was due to a later polarization of the secretionary activity of the above cells, after they were displaced from the proliferation zone onto the surface of the perithecal membrane proper (text-fig. 2, *A*).

The formation of a single fusellus may be described in terms of succession of certain secretionary phases in the activity of epithelial cells in such perithecal membrane. The formation of the body of fusellus made of the fusellar fabric only is thus phase 1 (ph_1). Formation of the outer lamella, an essentially cortical element, is phase 2 (ph_2), and secretion of an outer pellicle, made of sheet fabric, is phase 3 (ph_3) respectively (text-fig. 2, *A*, *B*). These phases correspond to the successive changes in secretionary activities of epithelial cells responsible for the secretion of skeletal material.

The fuselli of some graptolites, e.g. in *Dictyonema* sp. described by Urbanek and Towe (1974), are relatively simple being composed of the body and an outer pellicle only. Thus, the formation of their fuselli may be described as a simple succession:

$$ph_1\text{-}ph_3 \text{ (see text-fig } 2A)$$

omitting phase 2 (ph_2) responsible for formation of an outer lamella. This omission is most probably a primitive character of some dendroids (*Dictyonema* type of secretion) and the lack of an outer lamella in fuselli may also be an ancestral character of all graptolites. The fuselli in an other dendroid (*Acanthograptus* sp.) and some other graptolites described by Urbanek and Towe (1974, 1975) have all three components resulting from a secretion due to formula:

$$ph_1\text{-}ph_2\text{-}ph_3 \text{ (see text-fig. } 2B)$$

The fuselli in the theca proper in *Neocucullograptus kozlowskii* belong to

this *Acanthograptus* type of secretion. The fully developed microfuselli in this species show the same succession of secretionary phases:

$$ph_1\text{-}ph_2\text{-}ph_3$$

phase 1 being only distinctly abbreviated which results in a lesser amount of the fusellar fabric produced and respectively in a greater narrowness of the strips. The above secretionary phase may undergo a further abbreviation up to a complete reduction and skipping of ph_1. This is how reduced microfuselli are formed according to the sequence:

$ph_2\text{-}ph_3$ (see text-fig. 3).

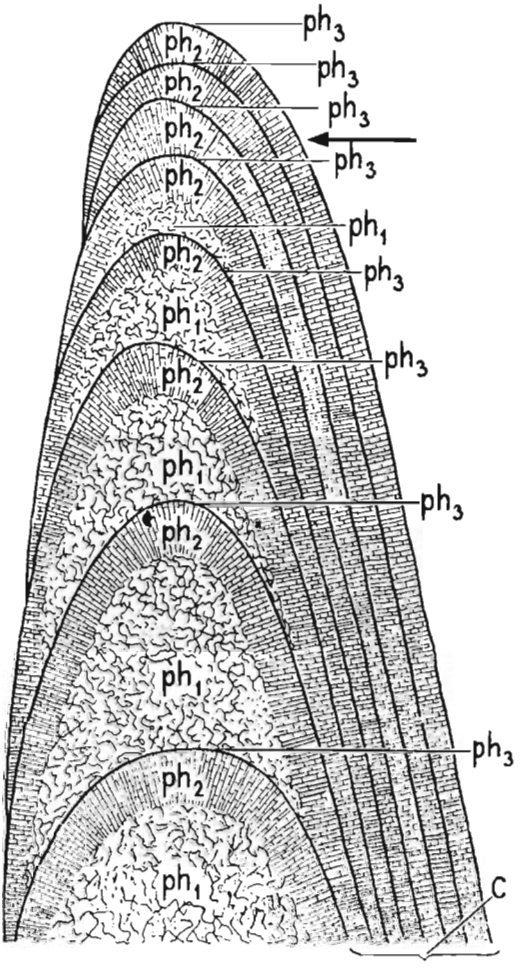

Fig. 3. Diagram showing a gradual depression of fusellar phase of secretion (ph_1) in a series of eight microfuselli seen on a longitudinal section. In result of the above process the fully developed microfuselli pass into reduced ones (at the top). The onset of a complete skipping of ph_1 (indicated by an arrow) results in formation of reduced microfuselli made solely of cortical components (ph_2, ph_3). Note a strongly asymmetric overlap of microfuselli producing in this way a heavy cortical coating (*c*) on one side.

Such composition does not differ, however, from that in the cortical tissue. The microfusellar tissue composed of reduced microfuselli still retains therefore a structural organization of fusellar tissue (the presence of V-shaped growth bands due to formation within the proliferation zone of the perithecal membrane) acquiring at the same time an essentially cortical composition (fabric, nature of unit elements).

As indicated by the sections studied, this transition from an essentially fusellar to an essentially cortical tissue may take place either as a gradual change or an abrupt shift in the secretory activity of epithelial cells. A necessary precondition for this transformation of fusellar tissue into its cortical derivative is the appearance of a cortical phase within an act of secretion of a single fusellus (as described by Urbanek and Towe, 1974, 1975). An outer lamella is composed of the tightly crowded, more or less ordered fibrils, interconnected by transverse rods, i.e. it bears all the characters of the cortical fabric, although it is secreted as a part of the fusellus and sealed by its outer pellicle. The origin of the outer lamella could be visualized (text-fig. 4) as an intensification and ordering of the primarily isolated and dispersed centers of corticization, which had been observed sporadically within the top of fuselli in *Dictyonema* sp. (Urbanek & Towe, 1974, pl. 13, fig. 1). The appearance of the outer lamella produced a prerequisite for the dependent mode of formation of the cortical deposits, especially the outer cortical coating (cortex) as recognized in the thecae of *Didymograptus* sp. (Urbanek & Towe, 1975), and in the microfusellar additions in *Neocucculograptus kozlowskii*.

It seems, therefore, that the independent mode, as defined above, was phylogenetically the primary one, and initially the fuselli were probably closed systems with cortex laid down on them secondarily. The develop-

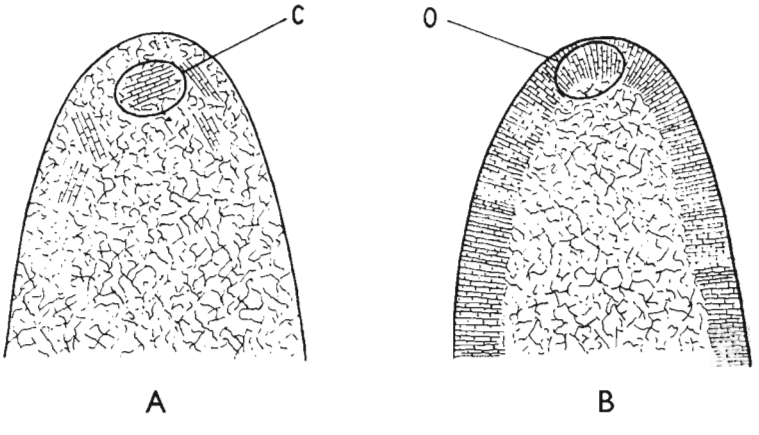

Fig. 4. Ideogram showing the possible origin of continuous outer lamella (*B*, *o*) made of cortical fabric, from primarily scattered centers of corticization (*A*, *c*), by means of intensification and rigid timing of the secretionary activity responsible for formation of the cortical fabric.

ment of an outer lamella accounts for a later appearance of a dependent mode of cortex formation, due to the overlapping of the fusellar limbs made of cortical fabric. In this way, the fuselli were secondarily transformed into systems opened towards the cortex, each extending into a corresponding layer of the cortex (text-fig. 2, *A-B*). Although more data are needed to substantiate the above working hypothesis, the suggested direction of changes from independent to dependent mode of cortex formation seems more probable than the reversed one.

The concept of "lateral corticization", i.e. a gradual passage from fusellar into cortical fabric within the outer limbs of mutually overlapping fuselli suggested by Kirk (1974), finds, therefore, no support in the present investigations on microfusellar tissue. The model of cortex formation proposed by Kirk (1974, Diagram 2) was based on an erroneous interpretation of ultrastructural data presented by Urbanek and Towe (1974). It is wrong for graptolites with an independent mode of cortex formation, and is also inadequate for the graptolites with dependent mode of its formation. In this latter case no gradual lateral corticization within the outer limbs of overlapping fuselli was observed, each layer of the cortex being only an extension of an outer lamella of a given fusellus, that is a strip of cortical fabric present already within the fusellus proper.

The mechanism of the appearance of phase 2 (ph_2) as a separate stage in the formation of a fusellus may be imagined as merely a change in control of secretory behaviour of epithelial cells in perithecal membrane (soft tissues enveloping the thecal wall from both sides). In the independent mode of formation of the cortex, the cortical fabric was laid down with certain delay by cells which were moved over from the proliferation zone to the outer layer of the perithecal infolding (see text-fig. 2, *A*). The control of the secretion was therefore determined by p o s i t i o n a l displacement from the proliferation zone and t e m p o r a l (delay in the secretion) factors. The formation of an outer lamella means a complete elimination of positional control (deposition of cortical fabric by cells already within the proliferation zone) and a drastic reduction of significance of temporal factors (strong acceleration in the secretion of cortical material, however, with preservation of the previous sequence in the secretory phase; see text-fig. 2, *B*).

CONCLUSIONS

The ultrastructural studies of the graptolite skeleton provide convincing evidence of the great versatility of secretory tissues, which cells were capable of an easy shift from the secretion of one fabric to the other. Moreover, these studies demonstrate also that there is a graded series of the tran-

sients between the extreme modes of morphogenesis of the tissues in which these fabrics are involved.

The ultrastructural studies on microfusellar tissue shed in particular a new light on mechanisms of transition from the fusellar to the cortical tissue. The microfusellar tissue is an evolutionary elaboration of the graptolite skeletal tissues making the transition from the fusellar to the cortical tissue especially easy, due to a preliminary depression of the fusellar phase (ph_1) of secretion.

In the light of the above considerations, the organization of the graptolite skeleton, that is the formation of particular fabrics and patterns, was determined within a certain framework of innate potential of secretory cells. A limited set of possible structures that could result from such a potential has been distributed in a number of ways in space and time due to changes in control of the activity (secretory behaviour) of corresponding cells. These changes may be identified as (1) omissions (skipping) or (2) accelerations of secretory phases through which every cell might have passed, and as changes in (3) localization of cell activity (space dependent control). All changes in morphogenesis of graptolite skeletal tissues may be explained by the combination of these basic factors.

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

ULTRASTRUKTURA UTWORÓW MIKROFUSELLARNYCH I EWOLUCJA TKANEK SZKIELETOWYCH GRAPTOLITÓW

Streszczenie

Zbadano ultrastrukturę tkanki mikrofusellarnej u górnosylurskiego monograptida *Neocucullograptus kozlowskii* oraz przeprowadzono porównanie budowy submikroskopowej mikrofusellusów i zwykłej tkanki fusellarnej. W tkance mikrofusellarnej występują normalnie wykształcone i zredukowane mikrofusellusy. Pierwsze składają się z tworzywa fusellarnego i kortykalnego i mogą przechodzić w zredukowane mikrofusellusy dzięki ominięciu fusellarnej fazy sekrecji. Zjawisko to ilustruje możliwe przejście od tkanki fusellarnej do tkanki korowej oraz rzuca światło na zasady rządzące morfogenezą tkanek szkieletowych u graptolitów.

Należy sądzić, że powstawanie poszczególnych tworzyw i typów ultrastruktury było określane przez wrodzony potencjał sekrecyjny komórek. Określono sposoby zmian w przejawianiu się tego potencjału oraz wysunięto hipotezę roboczą odnoszącą się do ewolucji tkanek szkieletowych u graptolitów.

АДАМ УРБАНЕК

УЛЬТРАСТРУКТУРА МИКРОФЮЗЕЛЛЯРНОЙ ТКАНИ И ЭВОЛЮЦИЯ ФОРМИРОВАНИЯ СКЕЛЕТА У ГРАПТОЛИТОВ

Резюме

Ультраструктура микрофюзеллярной ткани была изучена у верхнесилурийского монограптида *Neocucullograptus kozlowskii* в сравнении с обычной фюзеллярной тканью. Микрофюзеллярная ткань состоит из вполне развитых и редуцированных

цированных микрофюзеллюсов, причём первые складываются из фюзеллярных и кортикальных компонентов и могут переходить в редуцированную форму в результате выпадения фюзеллярной стадии секреции. Такое протекание процесса является иллюстрацией одного из возможных механизмов перехода от фюзеллярной к кортикальной ткани и раскрывает некоторые принципы, управляющие морфогенезом скелетной ткани граптолитов. Образование отдельных тканей и их пространственная организация зависят от регулирования определенного врождённого секреторного потенциала клеток. В настоящем исследовании были определены модусы изменений данного регулирующего механизма и выдвинута рабочая гипотеза относительно эволюции скелетных тканей граптолитов.

EXPLANATION OF PLATES

Plate I

Light microscopic features of fusellar (2, 4) and microfusellar (1, 2) tissue compared in *Monoclimacis micropoma* (Jaekel) (figs 3, 4) and in *Neocucullograptus kozlowskii* Urbanek (figs 1, 2).

All specimens strongly bleached and seen in transparent light. Deep boring Mielnik I. G. 1, depth 1019,50 m (fig. 4) and 874.00 m (figs 1, 2) and from erratic boulder S. 220, Śrem (3).

m microfusellar part of theca, *t* transient zone between the fusellar and microfusellar parts of theca

Plate II

Ultrastructure of microfusellar tissue in *Neocucullograptus kozlowskii* (Upper Silurian, Poland) as seen on longitudinal sections through the apertural lobe observed with TEM.

Fig. 1. A portion of microfusellar tissue with a gradual passage from the fully developed microfuselli (bottom and middle) to partly reduced ones (top).

Figs 2—4. Details of the fully developed microfuselli from the above portion.
b base of microfusellus, *i* intercalary deposition of outer lamellae, *o* outer lamellae, *p* pellicle of microfusellus, *th* thickened portion of microfusellar structure.

Plate III

Ultrastructure of partly and strongly reduced microfuselli in *Neocucullograptus kozlowskii* (Upper Silurian, Poland) as seen on longitudinal sections through the apertural lobe observed with TEM.

Fig. 1. Sequence of microfuselli from fully developed to partly reduced and "V"-shaped (*r*).

Fig. 2. A reversed sequence from the strongly reduced to the fully developed microfuselli (top).
Fig. 3. Change from microfusellar (bottom) into structureless homogenous portion (*h*) of the lobe.
Fig. 4. Ultrastructural features of strongly reduced microfuselli (*r*) made of cortical components only (*o*, *p*).
h homogenous portion of the tissue, *o* outer lamella, *p* pellicle of the microfusellus, *r* reduced microfuselli.

Plate IV

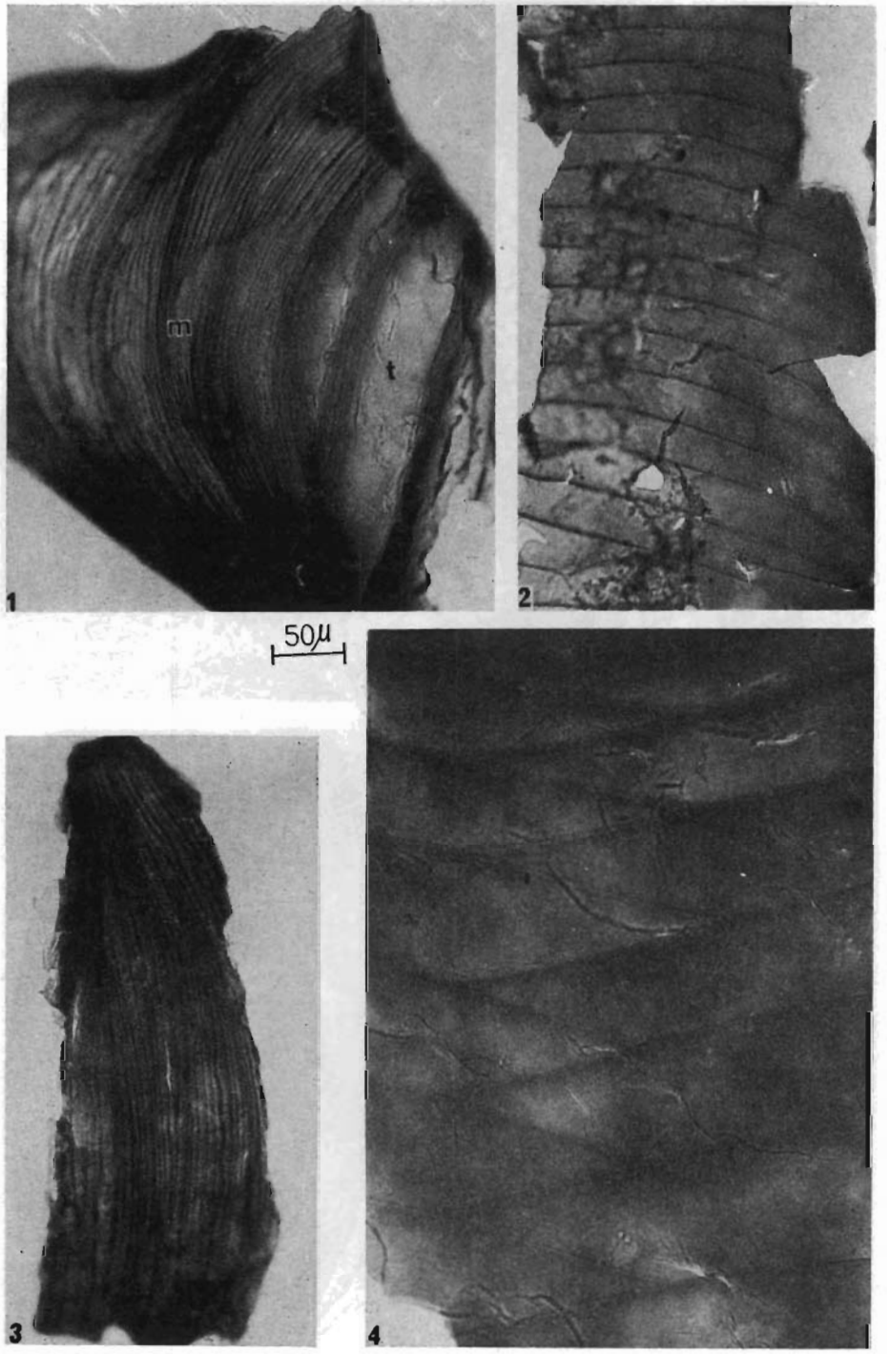
Ultrastructure of microfusellar tissue in *Neocucullograptus kozlowskii* (Upper Silurian, Poland) as seen on longitudinal sections through the apertural lobe observed with TEM (figs 1, 2, 4) or seen with SEM (fig. 3).
Fig. 1. Portion of microfusellar tissue showing a number of fully developed and slightly reduced microfuselli (top).
Fig. 2. Details of the above portion. Note the thick cortical deposit formed due to overlap of a number of outer lamellae (*d*).
Figs 3—4. SEM (3) and TEM (4) micrographs of the rostral apertural process.
d cortical deposit, *e* end of the rostral process with multiple deposition of outer lamellae, *p* pellicle of the microfusellus, *th* thickened portion of microfusellar structure

Plate V

Ultrastructure of microfusellar tissue in *Neocucullograptus kozlowskii* (Upper Silurian, Poland) as seen on longitudinal sections through apertural lobe observed with TEM.
Figs 1, 2. Portions of microfuselli in the ventral process of the lobe with adjacent cortex (*c*) or endocortex (*ec*).
Fig. 3. Bulbous thickening composed of a number of fully developed microfuselli, passing into a thinner portion made of strongly reduced ones (at the top).
Fig. 4. Fibrils in an outer lamella of a microfusellus (*o*).
c cortex, *ec* endocortex, *o* outer lamella, *p* pellicle of the microfusellus

Plate VI

Ultrastructure of fusellar (figs 1, 2) and microfusellar (figs 3, 4) tissue in *Neocucullograptus kozlowskii* (Upper Silurian, Poland) as observed with TEM.
Figs 1, 2. Longitudinal sections through fusellar portion of the theca showing the ultrastructure of normal fuselli.
Figs 3, 4. Portion and the free margin of the ventral process of the apertural lobe, showing irregular deposition and different degree of development of the microfuselli (fig. 3), and an accumulation of strongly reduced fuselli in the terminal part of the ventral lobe (fig. 4).
b base of the fusellus, *e* free edge of the ventral process, *h* head of the fusellus, *o* outer lamella, *p* pellicle of the microfusellus, *t* trunk of the fusellus


m
t
1
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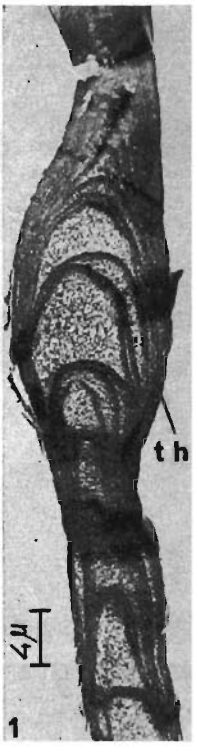
3
4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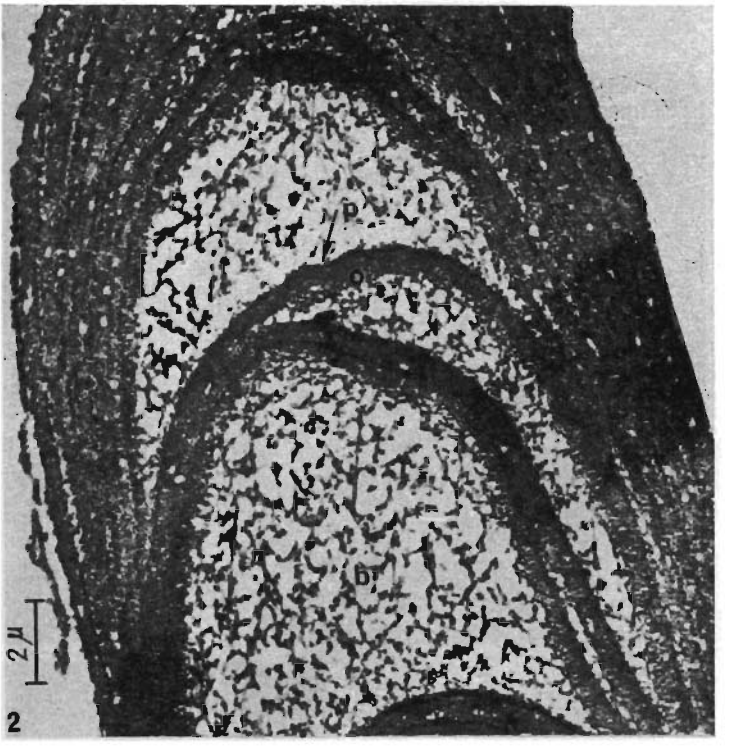
p
o
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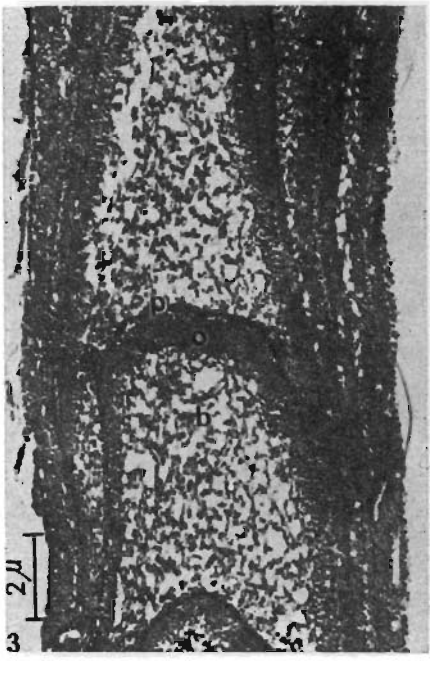
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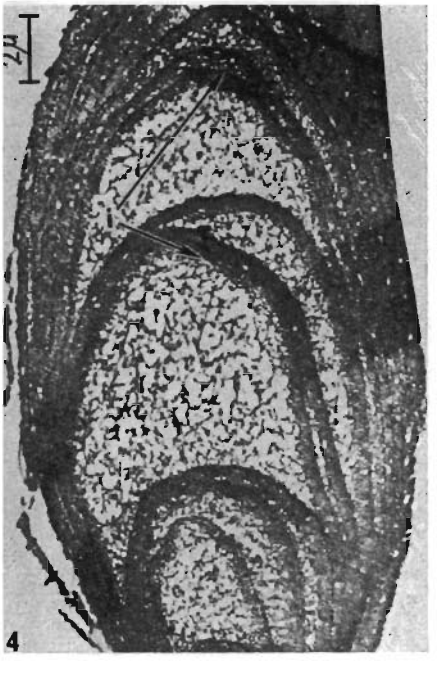
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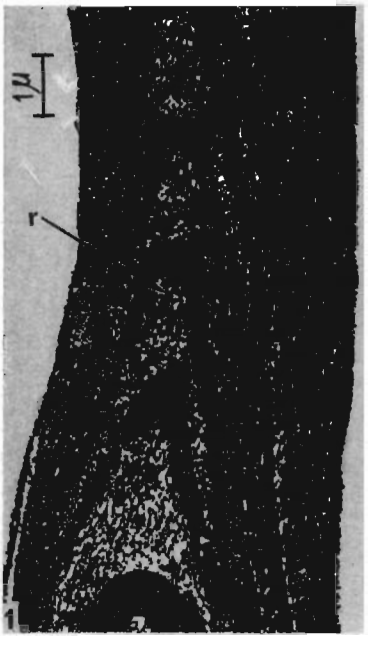
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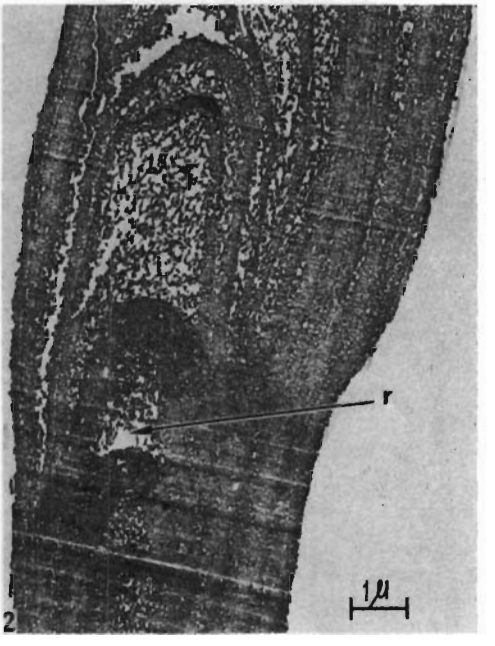
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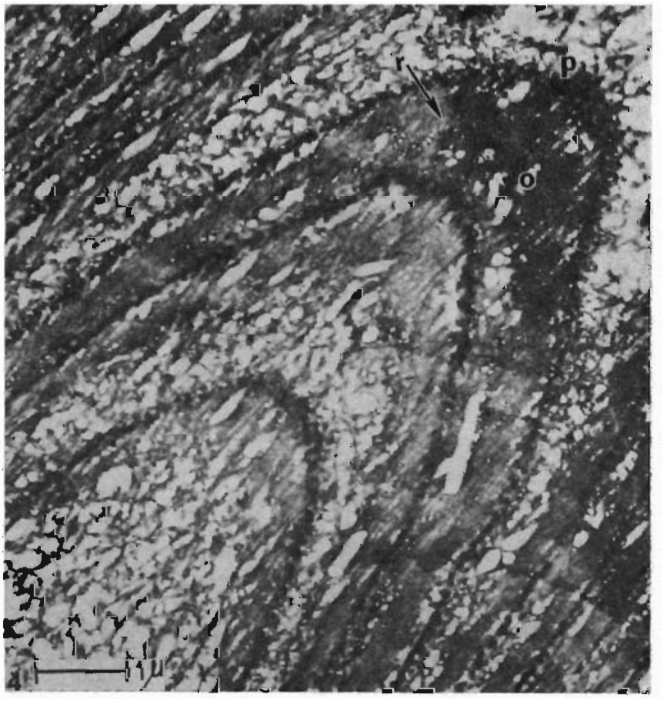
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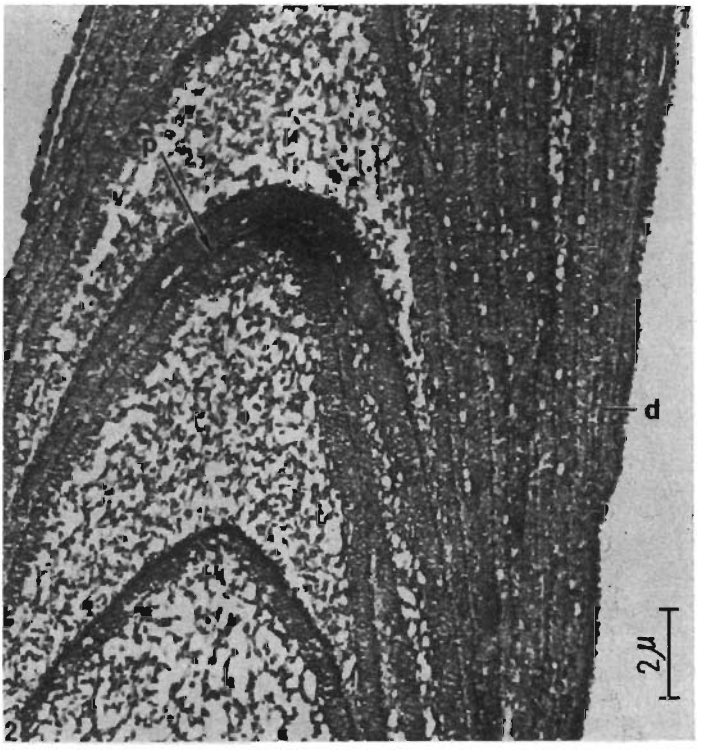
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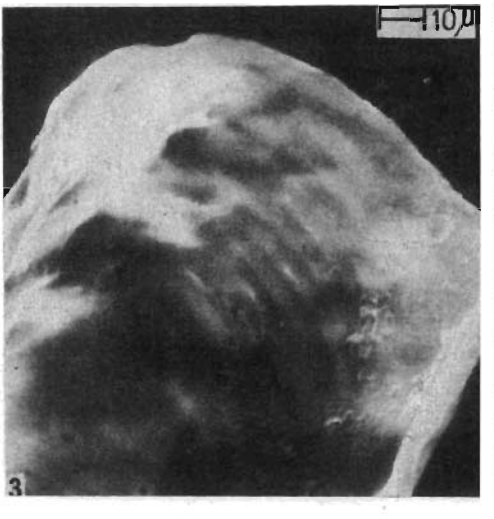
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e
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c
1
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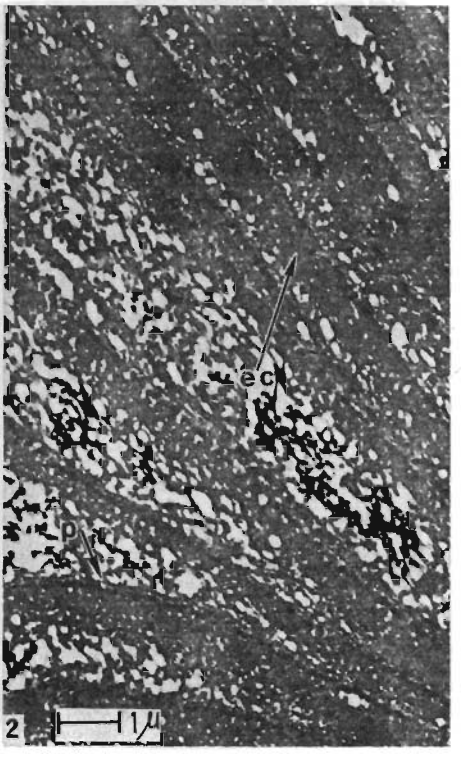
ec
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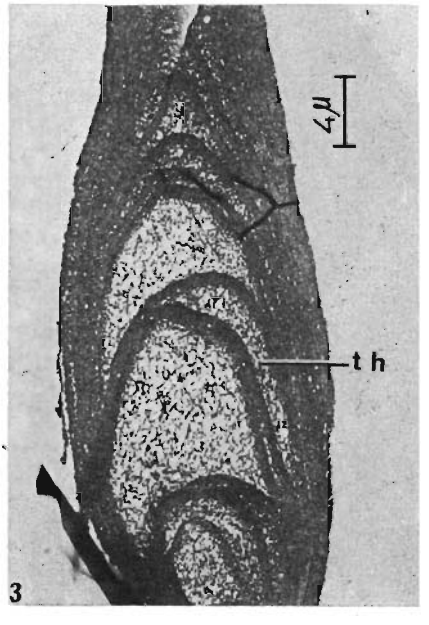
2
1μ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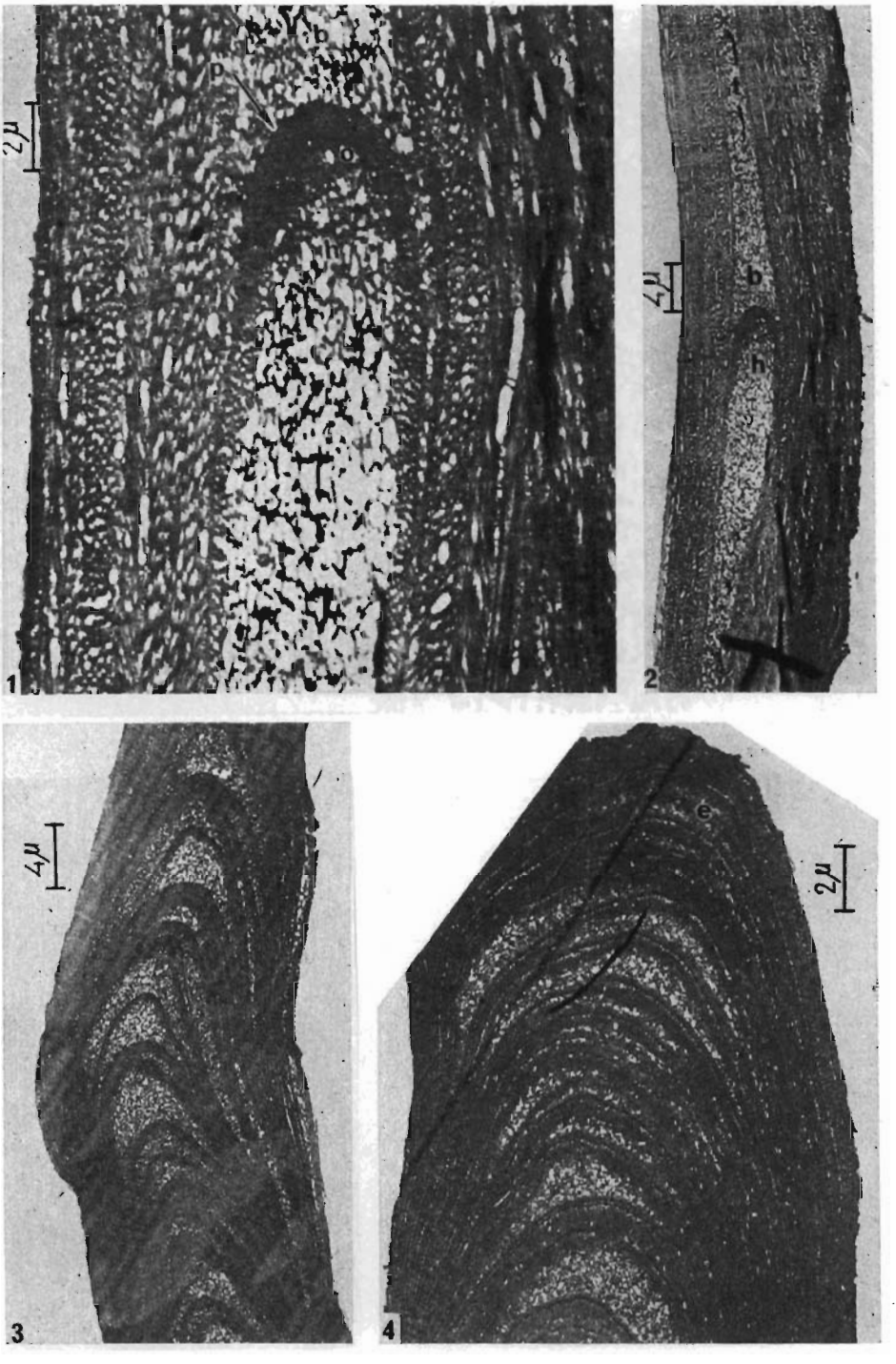
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