2. FIRST OBSERVATIONS ON THE BIOPOLYMER ORGANIZATION OF THE INTINE

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Abstract

During our experimental investigations on the recent and fossil sporomorphs characteristic biopolymer units were observed in the intine of partially degraded pollen grains of *Encephalartos ferox* BERTOL. The modified Markham rotation method was used to get information on the symmetry of the basic biopolymer units in Angstroem dimension. A hexagonal basic biopolymer unit was established. The five and/or ten-fold symmetry rotation of the hexagonal unit resulted in not pentagonal primary and secondary symmetry points against the biopolymer units of the ectexine. The quasi-crystalloid basic biopolymer units after 3–, 4–, 6–, 7–, 8–, and 9-fold rotation resulted in well defined secondary points of symmetry. This phenomenon also has been verified peculiar characteristic feature of the regular five-fold symmetry. In this way the regular pentagonal polygon includes all other kinds of basic symmetries, e.g.: the three-square and the square.

Key words: Palynology, *Gymnospermae,* intine, hexagonal basic biopolymer unit.

Introduction

The two principal layers of the pollen wall (exine, respectively intine) were recognized a long time ago. But most of the researches in Palynology were focused on the exine. Some selected opinions are as follows: MARTENS and WATERKEYN (1961), p. 1390: .."l'intine – c' est-à-dire la vrai membrane cellulaire – est encore mal connue". HORVAT (1969), p. 16: .."l'intine est resté jusqu'ici "le parent pauvre"". LE THOMAS (1981), p. 272: "Although still little studied, the intine is sometimes considered relatively homogeneous in structure." HESSE (1986), p. 315: .."the mature sporoderm consists of both exine and intine, the latter has been widely neglected through the years." As regards the most important characteristic features of the intine, the following may be mentioned. The earlier concepts on the basis of the paper of TOMSOVIC (1960):

I. Intina FRITZSCHE 1837 (the inner layer of the sporoderm which is composed of pectin and cellulose and is soluble by acids and alkalis).

A. Euintina KUPRIYANOVA 1955 = Endintine ELLIOT 1951 (Where the intina is two-layered, there the inner layer consisting of cellulose fibrills is impregnated with a pectinous matter).

B. Exintina FRITZSCHE 1837 (the outer layer of the two-layered intina is stronger than the euintina and is, composed of pectin).

Using the TEM method, ROWLEY (1959) established, p. 14: .."the intine ultrastructure was composed of a network oriented with the largest axis of the reticulations parallel with the endexine." SAAD investigated circumstantially the third, intermediate layer of the pollen wall, the medine. In a 1966/67 paper he emphasized that this pectic or callose layer is not soluble in 2-aminoethanol. ROWLEY and ERDTMAN (1967) established that the cellulosic intine form microtubules about 240 Å in diameter near the plasma membrane and generally parallel with it. HORVAT (1969), p. 16: "A cause de sa nature organique, cellulosique (ROWLEY et ERDTMAN, 1967), pectocellulosique (ROLAND, 1967), cellulosique et de composés pectiques, ainsi que d'autres constituants de la paroi cellulaire (SKVARLA et LARSON, 1966), l'intine peut être entièrement détruite par l'acétolyse suivant la méthode de ERDTMAN (1960)." P. 17: "L'intine montre parfois une lamellation faiblement ou délicatement concentrique (SCHWANITZ, 1967) ou une lamellation anastomosée et orientée de la couche interne d'une part, et fibreuse d'orientation quelconque, de la couche externe d'autre part (GULLVAG, 1964)." P. 30: "La réaction phosphatasique est mise en évidence pendant le développement de l'intine." Interesting establishments were published by SKVARLA and ROWLEY (1970), p. 525: "The wall between the channeled region and the cytoplasm, where we find sporopollenin, is without doubt an intine or part of the intine. It is formed at about the time of microspore mitosis, has a fibrillar texture and stained for polysaccharides, including cellulose." MASCARENHAS (1975), p. 264: "The intine contains microfibrils of cellulose which are held together by a matrix of pectic material and hemicelluloses. Proteins are also present." On the basis of a paper by HESLOP-HARRISON (1975) the following may be stressed: p. 277: "The intine forms a continuous layer investing the vegetative cell of the mature pollen grain. Unlike the exine it is unsculptured, although it follows the inner surface topography of the outer layer, and the substances of the two are often interbedded. In gross chemical composition the intine is similar to the primary walls of somatic angiosperm cells, with a microfibrillar cellulose component and matrix material of pectic substances and hemicellulose (SITTE 1953, BROOKS, and SHAW, 1971)." P. 279: "In many earlier descriptions of the intine radially disposed tubules traversing the layer, particularly in the vicinity of the apertures, were reported." "The intine is characterized by its low density to electrons, fibrillar structure, and location between the plasma membrane and nexine"; ROWLEY and DAHL, 1977, p. 214. NILSSON (1978a, b): intine (pollen) – endospore (*Pteridophyta* spores). THANIKAIMONI (1978), p. 235: "Intine is that part of the pollen wall located between the sporopollenin exine and the cytoplasmatic surface. It is often interbedded with the exine but is not itself composed of sporopollenin. In appearance and composition the intine is comparable with the primary plant cell wall and has been characterized by ROLAND (1971) as an amorphous matrix of pectin with infrequent microfibrils (ROWLEY and SKVARLA, 1974)". COUSIN (1979), p. 124: "The intine is thick and perforated with numerous polysaccharides containing cytoplasmatic channels in the interapertural areas where the exine is thick and granular." THANIKAIMONI and ROLAND-HEYDACKER (1979), p. 542: "..intine (inner unit of the sporoderm: essentially a mixture of a pectic amorphous matrix and infrequent microfibrils, cf. ROLAND, 1971)." HESLOP-HARRISON, Y. and HESLOP-HARRISON, J. (1982), p. 831: „The early work of SITTE

(1953) showed that the inner wall of the pollen grain, the intine, possesses a microfibrillar component. Since SITTE's observation it has been widely accepted that the microfibrils are cellulosic (see review by LINSKENS, 1967), and thus comparable with those of the primary wall of a somatic cell." SEETHARAM (1985), p. 2: "intine: part of the pollen wall between the exine and the cytoplasm. It lacks sporopollenin and does not resist acetolysis." SOHMA (1985) discussed the nomenclatural problems of the exintine and endintine. HESLOP-HARRISON, Y. et al. (1986), p. 282: "Proteins incorporated in the intine during its deposition are the products of the gametophyte (KNOX and J. HESLOP-HARRISON 1970), but PACINI et al. (1981) have shown that proteins of sporophytic origin may also accumulate at, or actually within, the apertures in many angiosperm pollen." SKVARLA and ROWLEY (1986), p. 397: "The intine is characterized by many narrow and long microvillae-like vaginations which make contact with a manifold-like layer at the base of the channelled zone. Dictyosomes are numerous in the peripheral cytoplasm at this time. Late in development the intine becomes distinctly fibrillar." In resumé the intine is chemically complex: cellulose, hemicellulose, pectin, proteins, sporopollenin. The aim of this paper: To publish the first biopolymer structures in angstroem dimension from the intine, and discuss some methodical and other problems.

Materials and Methods

The material of our investigations, the pollen grains of *Encephalartos ferox* BERTOL, was received from the Botanical Garden of Coimbra, Portugal, in 1972. For the first experimental studies air dried material was used, with the aim to investigate the biopolymer organization of the partially degraded exine. Between several experiments No 181 resulted biopolymer structures in the intine, the above mentioned experiment was as follows:
20 mg air dried pollen grains + 1 ml 2-aminoethanol, temperature 30 °C, length of time: 24^h, + 10 ml $KMnO_4$ aq. dil., temperature 30 °C, length of time 24^h. The washed material was fixed with OsO_4 aq. dil., embedded in Araldite. The ultra-thin section was made in the EM Laboratory of the Biological Centre of the Hungarian Academy of Sciences, on a Porter Blum ultramicrotome. The TEM pictures were taken in the EM Laboratory of the Faculty of Science of the A.J. University, Szeged, on a Tesla BS—500 transmission electron microscope, resolution 6Å. The rotation pictures were made in the Department of Botany of the A.J. University, Szeged.

Results

The experiment moderately degraded the ectexine (Plate 2. 1., fig. 1, 4). Fig. 4 well represents the ultrastructure of the inter-apertural ectexine. The tectum (T), the alveolar infratectal layer (I), and the foot layer (F) are distinctly shown. Near the sulcus (Plate 2. 1., fig. 1), the ectexine was sectioned in tangential plane. Elements of the infratectal layer well shown. The approximatively radially oriented lamellar elements surround in cross-section polygonal spaces. The intine, near the apertural area is well shown, and protruding form the germinal aperture. The granular ultrastructure of the intine is characteristic below the foot layer, but particularly in the protruding apertural intine. The division into two parts of the apertural intine is perceptible only at one part of the apertural intine. In the high magnified pictures characteristic globular biopolymer units were observed (Plate 2. 1., figs. 2, 3, and plate 2.3.). The diameter of these globular elements is 6—7—8 Å.

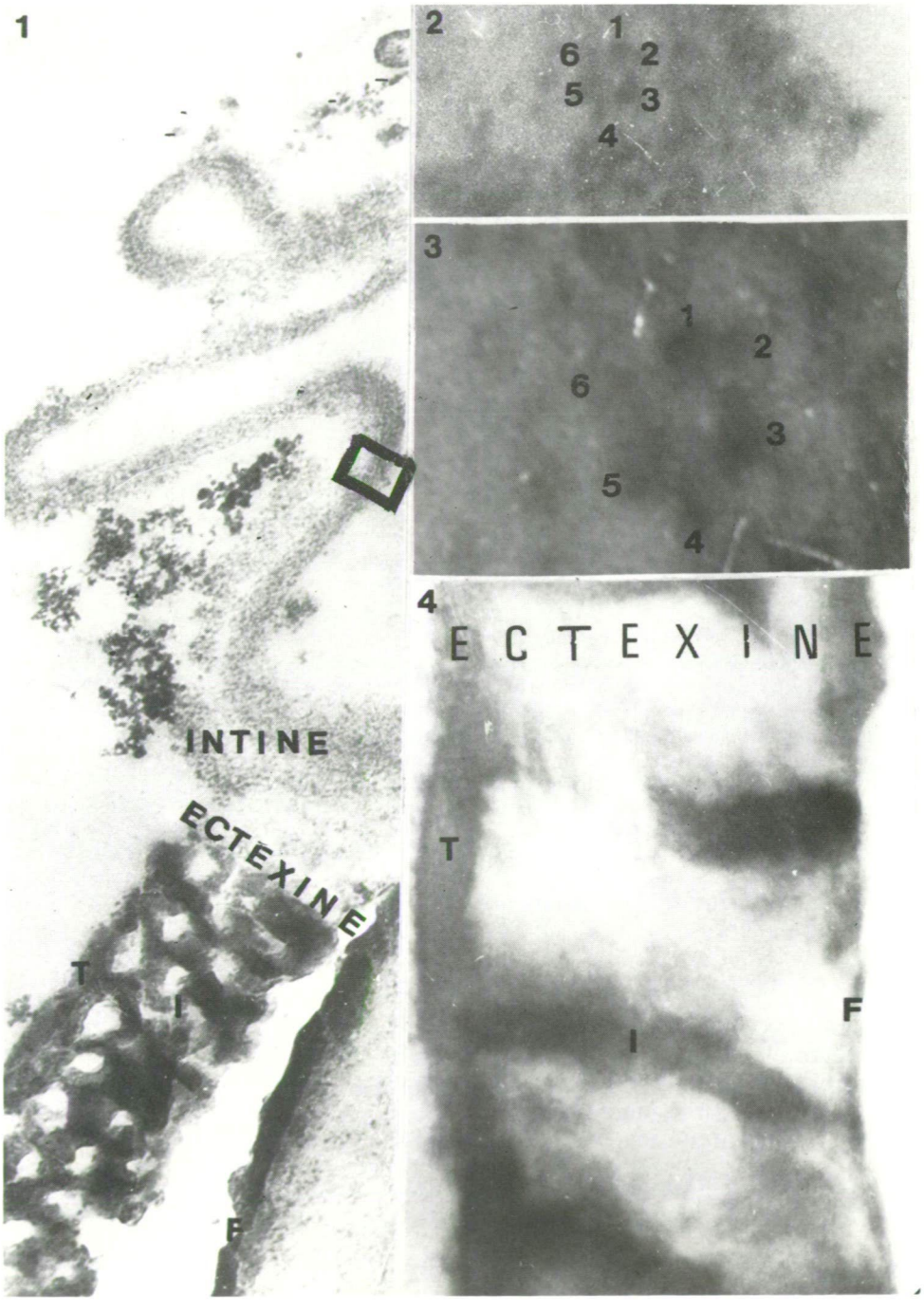
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Plate 2.1.

1—4. *Encephalartos ferox* BERTOL. Ultrastructure of the pollen wall after partial degradation with experiment No 181.

1. TEM picture from the apertural area of the pollen grain. Different layers of the inter-apertural ectexine are well shown: tectum (T), alveolar infratectal layer, in this picture in tangential section (I), and the foot layer (F). The germinal intine is protruding. The intine part, which was investigated in the point of view of the biopolymer units is marked with a frame. Negative no: 7964, x50000.

2, 3. Magnified details from the part of the intine investigated in detail. The globular biopolymer units are marked with numbers. Negative no: 7966.

2. x500000.

3. x1250000.

4. Ultrastructure of the inter-apertural ectexine. Negative no: 7977, x200000.

T = tectum, I = infratectum, F = foot layer.

The arrangement of these biopolymer structures into polygonal units was established. In the non-rotated picture of Plate 2. 3., five to six angular biopolymer structures were observed.

To investigate closely the biopolymer organization of the intine, one so-called etalon basic biopolymer unit was chosen. This is situated in the inner part of the intine. This part is framed in fig. 1, in Plate 2.1. This, probably sixangular biopolymer unit is represented in higher magnified pictures in figs. 2 and 3, Plate 2.1.

The modified Markham rotation (cf. KEDVES 1989c), was used in the following mode of action:

Rotation: C.P.6.A.6.6. (Plate 2.2. fig. 1).

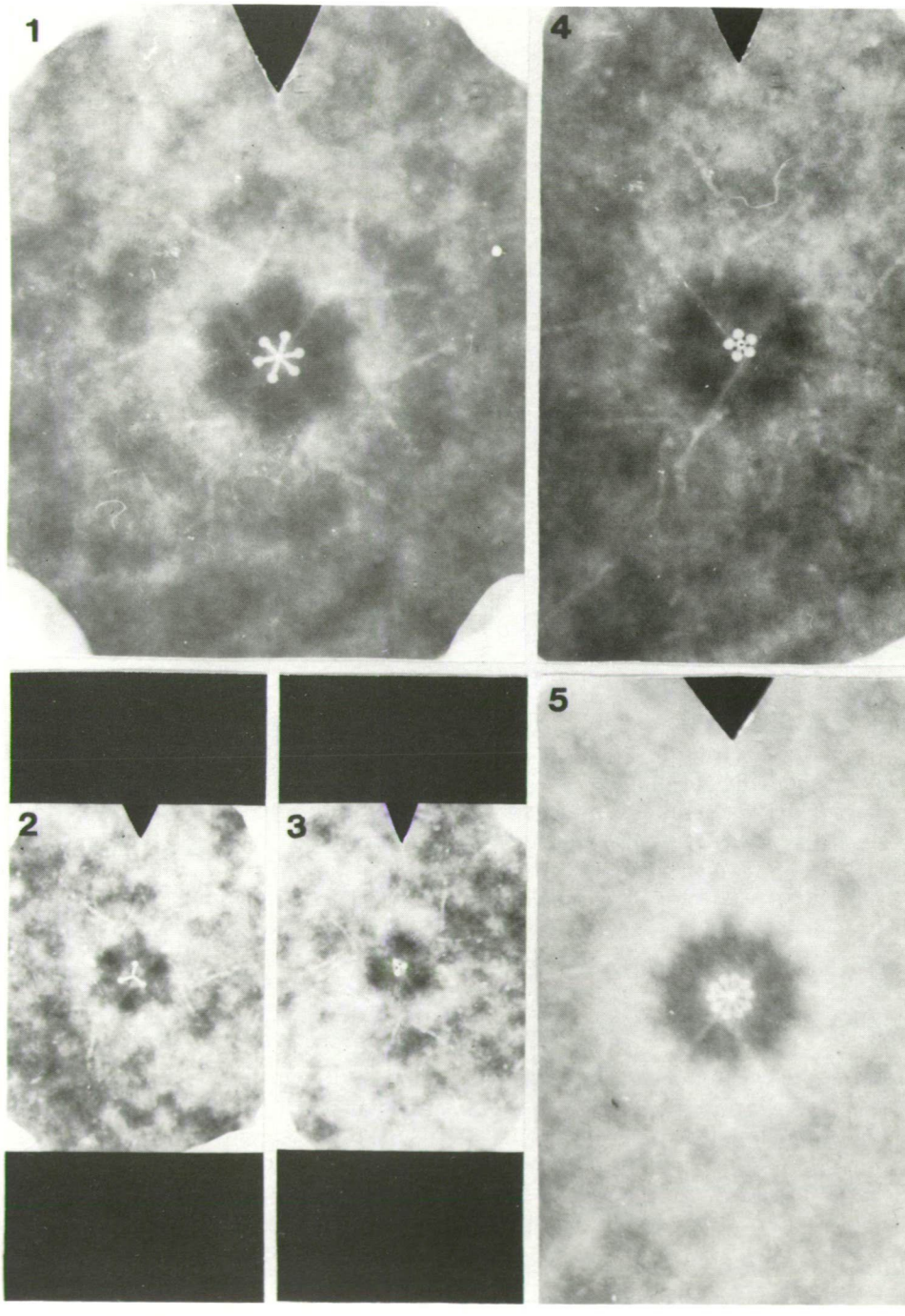
This kind of rotation well reinforced the six globular biopolymer units. These globular elements are much more nearer to one another than at the regular basic pentagonal polygon units of the sporopollenin of the ectexine. Moreover the connectives between the globular elements are not perceptible against the above mentioned biopolymer units of the ectexine. The diameter of the hexangular polygon after rotation: 22 Å. Around the hexangular biopolymer unit, there is a 6—8 Å wide light-coloured zone. This is followed by a darker zone composed from six not so characteristic points of symmetry are not definite.

Rotation: I.P.6.A.6.3.

This kind of rotation may be achieved in different ways. Firstly, the first exposition was made to reinforce the globular biopolymer unit intersected by the P.A. axis. Thereafter the photographic paper was turned in the axis of P and the 3rd globular unit. Finally the last exposition was made in the axis of point P and 5th globular unit. This kind of rotation was designated as follows:

Rotation: I.P.6.A.6.3a (Plate 2.2., fig. 2, text-fig. 2.1.).

It is interesting that in this case of rotation the 2nd, 4th and 6th globular units were reinforced. Two triangles appeared in cross position. Further zones around the partially rotated bipolymer unit appeared approximatively as at the previously discussed rotation C.P.6.A.6.6.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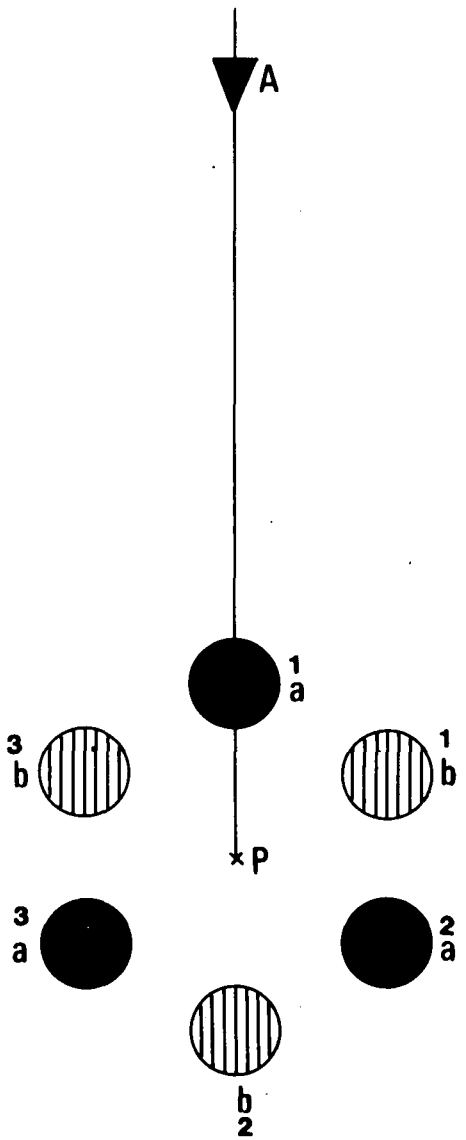
◀ Plate 2.2.

Encephalartos ferox BERTOL., biopolymer unit of the intine after partial degradation with experiment No 181, and different kinds of rotation.

1. Rotation: C.P.6.A.6.6., x1000000.
2. Rotation: I.P.6.A.6.3a., x500000.
3. Rotation: I.P.6.A.6.3b., x500000.
4. Rotation: C.P.6.A.5.5., x1000000.
5. Rotation: C.P.6.A.5.10., x1000000.



Text-fig. 2.1. Scheme of the incomplete three-fold rotation.

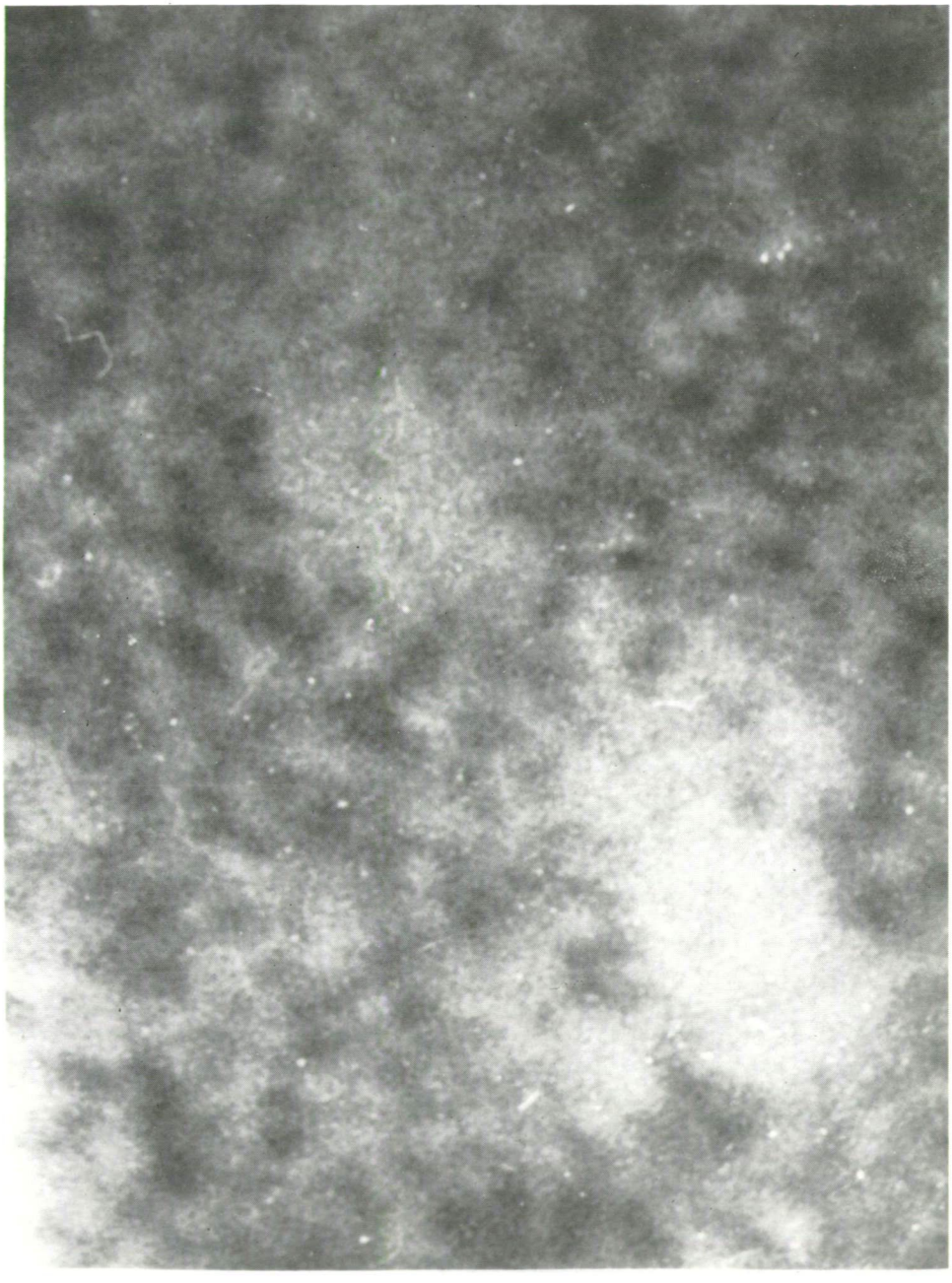


Plate 2.3.

Encephalartos ferox BERTOL., biopolymer units of the intine after partial degradation with experiment No 181. Well shown are the globular biopolymer units and its arrangements in hexagonal and/or pentagonal units. Negative no: 7968, x1250000.

Rotation: I.P.6.A.6.3b (Plate 2.2., fig. 3, text-fig. 2.1.).

This kind of rotation started with the exposition of the 2nd globular biopolymer unit, followed by the 4th and 6th. In this way essentially the lst, 3rd, and 5th biopolymer units were reinforced, but in this case the reinforced units are not so characteristic as in the previous case.

Methodically it is important to control the symmetry. For this reason, the sexangular biopolymer basic unit was rotated by the five-fold symmetry, too.

Rotation: C.P.5.A.5.5. (Plate 2.2., fig. 4.).

It is well shown that this kind of rotation resulted not a characteristic pentagonal polygon biopolymer unit. An extremely indistinct pentagon appeared, but without characteristic secondary points.

Rotation: C.P.5.A.5.10. (Plate 2.2., fig. 5.)

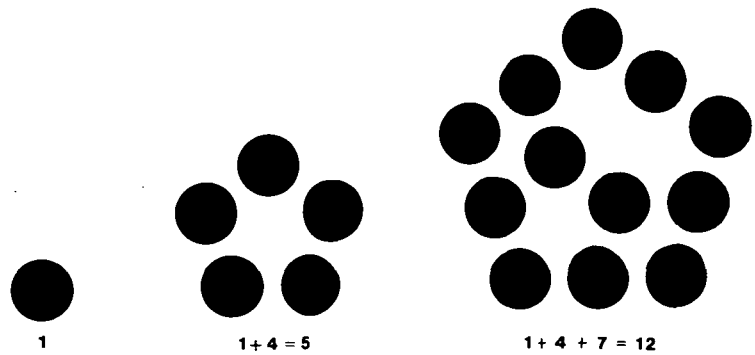
Similarly to the previous rotation this method neither resulted in characteristic points of symmetry.

Discussion

1. As it was emphasized by several authors, cited in the introduction, the researches of the intine were neglected in contrast to the exine. This establishment is valid to the biopolymer organization of this layer. This paper presents the first results in this respect. It seems to be important that the biopolymer unit revealed for the first time is of a hexangular symmetry against the quasi-crystalloid basic biopolymer units of the exine. Naturally, it is necessary to continue further researches in this field. Taking into consideration the up-to-date knowledge of the biopolymer organization of the exine it may be presumed that the intine will also be heterogeneous is this respect. Probably the *Helix* enzyme method will be more successful in the researches of the intine because of its cellulosic content.

2. The Markham rotation method applied to the investigations of the structural organization of the quasi-crystalloid skeleton of the exine was discussed and elaborated in several papers, cf. KEDVES (1989a-d), KEDVES et al. (in print). The basic biopolymer unit, the regular pentagonal polygon in Angstroem dimension needed verification by several ways. Its peculiar characteristics are newly under elaboration. The incomplete rotation and the rotations by 2, 3, 4, 6, 7, 8, and 9-fold symmetry at the basic biopolymer etalon resulted in very characteristic biopolymer points of symmetry. This is also an argument for the peculiar symmetry characteristic of the regular pentagonal polygon as it was established a long time ago. It seems that presence of fivefold symmetry in the structure involves presence of other kinds of rotational symmetries. We are referring here to the old Pythagoreans who gave a polygonal representation of the natural members and showed how the pentagonal numbers do include other ones (cf. text-fig 2, of the book of SAIN 1986; cf. ORE 1977). Of course, our observation still requires closer analysis.

In this way it is not surprising, that the regular pentagonal biopolymer unit has



Text-fig.2.2. Scheme of the Pythagorean pentagon numbers.
After SAIN (1986), modified.

been rotated succesfully corresponding to different symmetries. The statements of HEILBRONNER (1986) concerning the symmetry in the Chemistry is important; p. 112: Wie zu erwarten, ist nun die Zahl der zusätzlichen Symmetrieelemente, die man neben den beiden Translationen einbauen kann, großer als im eindimensionalen Fall. Es läßt sich zeigen, daß es auch hier nur eine endliche Zahl von prinzipiell verschiedenen Typen geben kann, die übrigens mit 17 erstaunlich niedrig ist. Einer der Gründe für diese drastische Beschränkung ist, daß die Zahl der Drehungen, welche ein solches zweidimensionales Muster zuläßt, sich auf die Symmetrieoperätionen C_2, C_3, C_4 und C_6 beschränkt. Insbesondere ist zum Beispiel C_5 verboten.

3. Finally the prospects and the first results of the biopolymer organization of the plant cell wall, and its aspects:

3.1. New energy basis (KEDVES, 1986, 1987). The quasi-crystalloid biopolymer skeleton of the plant cell wall is extremely unstable. Scanning effect may explode the pollen grains. KEDVES (1987, p. 163): .."it may be hoped that with a rentable technology the oil shale can be a new energy basis, by the liberation of the binding energy of the wall biopolymer structure."

3.2. Coal pulver explosion (KEDVES, 1989a, b). The coal pulver of the explosion dangerous coal mines at Komló were investigated experimentally. Fossil quasi-crystalloid biopolymer structures were demonstrated, and different kinds of the modified Markham rotation were also applied. The taphonomical processes of the sedimentation may discover the quasi-crystalloid skeleton of the plant cell wall, and this extremely labile dry coal pulver for an initial energy may explode. It may also be presumed that the unstable coal pulver may be also an energy basis.

3.3. Modeling of the biopolymer structures resulted in new things. Concerning this subject, the following may be pointed out; KEDVES (1988a): "More highly organized globular structures (KEDVES et al., 1974) and helical structures (ROWLEY, 1980) are derived from the basic polygon elements. These, in turn, are similar to the structure of solar and galactic systems, and also to microbial entities such as

Micrococcus, Spirillum and *Treponema.* Viruses are in general crystalloids. An exception is the AIDS virus which is modeled after a pulsar or neutron star cf. Crab Nebula (TUCKER, 1976), MACKAY (1982, p. 517), following KEPLER's concept (1596), stated that "the five regular polyhedra were the 'spherical harmonies' which were the key to the structure of the Solar System". This is mirrored in the biopolymer organization of the sporoderm. Earth expansion (KREMP, 1984) (+) Sun collapsing (−) is part of an equilibrum in the solar system?"

In general it seems that several new ideas published by the K−TEC research program group are very useful for further multidisciplinary researches.

3.4. As a new concept, the cytoskeleton structures and the highly organized biopolymer units may be mentioned. There is an extreme similarity between the two structures. For the cytoskeleton — the gelatinous part of the cytoplasm, — see the review of LISZT and FRIDVALSZKY (1989), for the highly organized biopolymer structures of the sporoderm the paper of the writer (1989d). On the other hand the sporopollenin deposition on unit membranes was established a long time ago, cf. ROWLEY and SOUTHWORTH (1967); synthesis by ABADIE et al. (1986−1987). It may be presumed that in consequence of analogies in nanometer dimension between the cytoskeleton and the highly organized biopolymer units of the sporopollenin, the quasi-crystalloid structure in the cytoskeleton may be present. When the biopolymer structure corresponding to the so-called PENROSE units KEDVES (1989d) may be established in the cytoskeleton, this will be a new aspect to cell biology. *Probably this will bring new ideas to the pathological cell-division, for example to some kinds of cancer.* For the biological quasi-crystalloid structures the new concept of the quasi-crystals is very important namely that entropy stabilizes them. MADDOX (1989), p. 261: .."by different methods to arrive at a convincing demonstration that the stability of real quasicrystalline systems arises not because of some decisive energetic advantages but because of the large entropy of these systems."

If entropy has a certain importance in the biological quasi-crystalloid structures cell biology and cell biophysics will have further perspectives. It is hoped that the results achieved on the biopolymer organization of the spore-pollen wall and other kind of plant cell walls will be useful in further investigations of cell biology.

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