7. THREE DIMENSIONAL MODELLING OF THE BIOPOLYMER STRUCTURE OF THE PLANT CELL WALL I.

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Motto: This is not the end. It is not even the beginning of the end. But it is perhaps, the end of the beginning.
(Sir Winston CHURCHILL, 1942)

Abstract

The three dimensional modelling of the biopolymer structure of the plant cell wall starts with this paper. The basic biopolymer unit was prepared from cardboard in a dodecahedron space arrangement. This is the basic element of the PENROSE-like biopolymer structure. One single basic element is suitable to interpret several methodical problems, such as the modified MARKHAM rotation method, and the further symmetry operations. But the quasi-crystalloid skeleton of the highly organized biopolymer structures can also be built from this basic dodecahedron skeleton. Larger PENROSE units, and a single helical structure were prepared as the first step and presented in this paper.
Key words: Plant cell, biopolymer organization, three dimensional modelling.

Introduction

It is a long time ago when the researches of the fine structure and the chemistry of the plant cell wall began. As regards the sporomorphs, a very characteristic survey was published by HESSE (1985), p. 93: "some recent observations suggest that exines are not uniform but are composed of units and subunits (ROWLEY 1981, ROWLEY et al. 1981a,b, ROWLEY and DAHL 1982). ROWLEY et al. (1981a) have used the term tuft for the exinous unit, based on glycocalyx tufts. These (helical) tuft units have an average diameter of less than 40 nm during the early stages of exine development and increase up to 100 nm, presumably by the addition of sporopollenin, during the later stages." In a previous paper (KEDVES 1989) it was emphasized that on the basis of our up-to-date knowledge four organization levels are to be distinguished:

1. Molecular structures, which can be investigated with methods of laboratory chemistry.
2. The basic biopolymer units, e.g.: the regular pentagonal polygons in angstroem dimension. These structures can be observed on the ultrathin sections or fragments

of the partially degraded plant cell walls. Symmetry and further organization can be investigated with the modified MARKHAM rotation method.
3. The so-called sub-units of the sporoderm, helical, globular units, irregular polygons, etc., in nanometer dimension.
4. Finally the higher structures of homogeneous wall substance, which can be investigated with the usual TEM method.

A three dimensional model in nanometer dimension was first published by ROWLEY et al. (1981a,b) this is the famous wire model of the helical structure. Further important establishments were published by ABADIE et. al. (1986—87). From this paper the following may be pointed out; p. 3: "For the exine types studied, a glycocalyx is differentiated by the plasma membrane (1) (glycolemma = plasma membrane and its glycocalyx) in sporal periplasm at an early tetrad stage. The nature of the glycocalyx is visualized as a fine microfilamentous structure having a helicoidal macromolecular arrangement and glycoproteinic and glycolipidic composition." "...two fundamental concepts which are:
1. the tubular skeleton of exine and
2. the relationships between the glycolemma and cytoskeleton..."

Three dimensional modelisation in nm dimension of the exine, model of a tubular subunit, and models of unit structure of the exine were published. A synthetic two dimensional scheme was published by the writer (KEDVES 1989). An attempt to the three dimensional or better say structural modelling in angstroem dimensional elements was published by GÉVAY and KEDVES (1989).

It seems to be important to emphasize that there are essential differences in consequence of the dimension of the elements of the plant cell wall: in angstroem respectively in nanometer dimension. Till this time the limit between these two province is about 20—25 Å. The quasi-crystalloid biopolymer structure is composed of pentagons of diameter below of the above mentioned "limit values". Secondary biopolymer points after rotation appeared only in angstroem dimension, and never in the so-called nm province.

Some selected non-biological basic establishments on the three dimensional modelling of the quasi-crystalloid skeleton

SACHDEV and NELSON (1985) on page 4602, Fig. 6c represents the fivefold axes of an icosahedron. This pattern corresponds to our C.P.5.A.5.10. points of symmetries. The work of HEILBRONNER (1986) is extremely important from the point of view of the symmetry in Chemistry. HARTMANN (1988); p. 467: "in stable equilibrum the symmetry elements of freely interacting systems coincide with each other as far as possible, can be regarded as one phrasing of the CURIE principle." Very important in our respect are the establishments of SCHNEER (1988), p. 395, fig. 4/a/"An icosahedron of 12 equal spheres. The radius ratio of the enclosing sphere to the largest sphere which may fit at the core is f (f is the FIBONACCI ratio 1.6180...)." MCHENRY et al. (1988) published as follows; p. 4257: "Rapidly quenched $Al_{74}Mn_{20}Si_6$ alloys are found to be either of the icosahedral structure or of the β-AlMnSi phase or a combination of these two." MADDOX's (1989) paper is also

fundamental concerning the stability of the quasi-crystalline systems, which is the large entropy. From the submitted paper of JARIC and NELSON the following may be pointed out; p. 9: "A quasiperiodic crystal is a crystal whose three dimensional FOURIER transform (or diffraction pattern) vanishes except on a discrete, but dense set of wavevectors generated by a finite set of basis vectors. This set can be called reciprocal quasilattice."

Finally some interesting statements: JEAN (1989), p. 258: "In the plant kingdom, a and m are generally two consecutive terms of the FIBONACCI series..", p. 259: "Then one comes to realize that other fields of research (e.g. the study of micro-organisms, proteins (1985), medusae and even quasi-crystals) show the same kind of symmetries." KOPTSIK and PETUKHOV (1989), p. 273: "V. I. VERNARSKY suggested that to the drastic difference between living and non-living matter there correspond the non-EUCLIDEAN space or to be more precise the space-time of the living matter."

Highly organized biological structures of the plant cell

GLOBULAR ELEMENTS

Cf. KEDVES et al. (1974) and HESSE (1985, 1986) for the fossil respectively recent exines.

FILAMENTS

KOBAYASHI et al. (1987), p. 69: "...filaments are essential components of the cytoskeleton." "We have been able to demonstrate, for the first time, a dynamic change in the arrangement of actin filaments during the differentiation of tracheary elements, and we have also found an orderly array of foci for the organization of actin filaments." P. 71: "The organization of actin filaments changes dynamically with the progression of the differentiation of tracheary elements. It should be emphasized that the disposition of the actin filaments presages the location and orientation of the secondary wall bands. It appears that actin filaments play an important role in the spatial control of deposition of the cell walls in developing tracheary elements."

HESLOP-HARRISON and HESLOP-HARRISON (1982), p. 831: "The microfibrillar polysaccharide component of the pollen intine can be isolated by progressive chemical digestion of the exine and the cellular contents and the extraction of the matrix material."

KOBAYASHI et al. (1988), p. 29: "Before thickening of the secondary wall began to occur, the actin filaments and microtubules were oriented paralell to the long axis of the cell. Reticulate bundles of microtubules and aggregates of actin filaments emerged beneath the plasma membrane almost simultaneously, immediately before the start of the deposition of the secondary wall."

Following the paper of BEVERIDGE (1988) I would like emphasize the following establishments. P. 363: "a mitochondrion is responsible for aerobic respiration...",

p. 367: "The electron-dense granules which cover the inner and outer surfaces of the wall are polycationic ferritin particles which are adhering to electronegative sites of the wall". Usually walls carry an overall net electronegative charge (Fig. 8), which makes them reactive against electropositive counter ions such as metallic cations (BEVERIDGE 1981), p. 368: "...it is reasonable to suspect that the seiving threshold would be limited to only those molecules which could fit through the polymeric interspaces." P. 369: "*Escherischia coli* walls, for example, consists of a phospholipid-lipopolysaccharide-protein bilayer..."
ROWLEY (1990) as "fundamental" structure of the exine pointed out the following. P. 25:
(1) A network of filaments is a common remnant of partly degraded exines.
(2) Spaces about 40 nm wide are usual in this "fundamental" 3—D network.
(3) Variable amounts of structure remain in these spaces (greatest perhaps in Fig. 3).
(4) Microchannels 20—25 nm wide can be tunneled out to more than twice their original diameter."

MICROTUBULES AND HELICAL STRUCTURES

HESLOP-HARRISON (1975), p. 278: "Microtubules are present at the plasmalemma during intine growth, but generally only in small numbers..." P. 282: "The lipidic fraction are accompanied by tapetal proteins and glycoproteins, which are indeed usually sealed in by the lipidic overlay." BAKHUZIEN et al. (1985); P. 43: "The microtubule distribution during the transition from interphase to the mitotic phase was examined at ultrastructural level in large highly vacuolated cells of *Nautilocalyx lynchii* and in small non-vacuolated cells of *Pisum sativum*. Both cell types contain, besides preprophase bands and perinuclear microtubules, also microtubules radiating from the nucleus into the transvacuolar cytoplasmatic strands and cytoplasm respectively." CYR et al. (1987), p. 365: "The number of cortical microtubules (MTs) increases considerably as cultured carrot (*Daucus carota* L.) cells initiate and progress through somatic embryogenesis." ROWLEY (1986—1988) pointed out as follows. P. 29: "The substructure within the endexine consists of units arranged as short tufts; these are connected to either side of white line-centered lamellations. White lines are junction planes between groups of tufts units..." Extremely intersecting are the following. P. 32: "The function of the endexine can be expected to include recognition, uptake, and other aspects of communication between a heterotrophic organism and its immediate nutritive source, the tapetum." P. 35: "My suggestion is that the channels in a bulged region work like a peristaltic pump." "I suggest that we explore a peristaltic pump-like transport role for endexines."

Following ADLER (1989), p. 17: "A phyllotactic pattern is like a living crystal." "...a helix known as the genetic spiral."
ROWLEY and DUNBAR (1990) published three dimensional diagrammatic models of the exine substructure. Five substructures (the core zone) encircled by a binding substructure.

SOUTHWORTH (1986a), p. 983: "Three types of unstained openings were associated with the granules: (i) single polygons with inner diameter up to 10 nm. (ii) compound polygons with both concave and convex sides and diameters from 15 to 25 nm and irregularly larger; and (iii) open polygons similar to either single or compound polygons in size but with one side missing." Later (SOUTHWORTH, 1986b) she wrote the following, p. 67: "Although the micrographs here show some circular profiles, several considerations argue against a helical model..."

Finally some important establishments:

HESLOP-HARRISON (1978) published a schema to the possible routes of chemical communication between walled cells. RISUENO et al. (1969) reports the first results of their investigations of the first beginnings of sporopollenin granules in the cells of the tapetum. They established as follows. P. 361: "The endoplasmatic reticulum was observed to be the system responsible for their production."
TAYLOR and TAYLOR (1987) proposed a model for the basic subunit construction of the Cretaceous megaspore wall of the genus *Selaginella* from Argentina.

Taking into consideration the previously mentioned and cited statements for the first modelling I have chosen as follows.

1. The basic PENROSE-like biopolymer unit,
2. the first and second steps of a highly organized PENROSE-like biopolymer system,
3. the basic helical or microtubular element.

Firstly the skeleton was modelled and interpreted. Further modelling is in progress, including the stabilizing biopolymer systems.

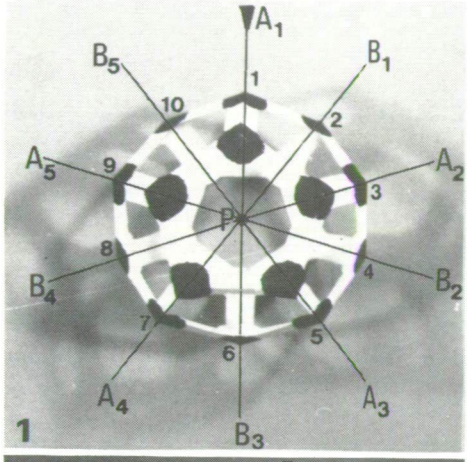
Results

The basic model of the dodecahedrane (PENROSE-like) biopolymer unit was prepared from cardboard in such a manner. The size follows the relation of the first observed regular pentagonal polygon unit on the partially degraded exine of *Pinus griffithii* MCCLELL (about 14 Å; the diameter of the model-unit is 7 cm.). The whole diameter of the basic PENROSE-like model indicates 20—25 Å, which corresponds approximatively to the measured values on the TEM pictures of the recent and fossil partially degraded exines, e.g.: KEDVES et al. (1974).

1. THE BASIC PENROSE-LIKE BIOPOLYMER UNIT
(Plate 7.1., fig. 1,2)

The investigation from different angles of this basic dodecahedron biopolymer model results extremely interesting configurations regarding the points of symmetries. At right angles to one plane which has a form of pentagonal polygon, all kinds of basic rotation points of symmetry and axes can be observed (Plate 7.1., fig. 1):

C.P.5.A.5.5.
C.P.5.B.5.5.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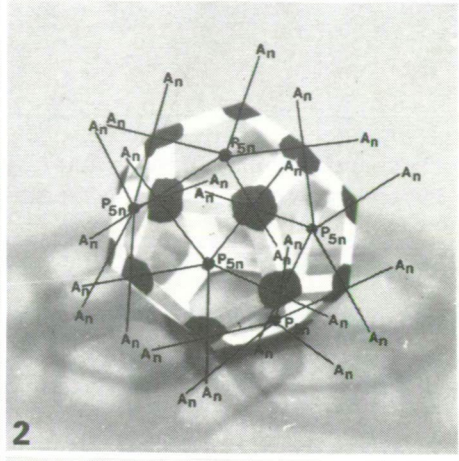
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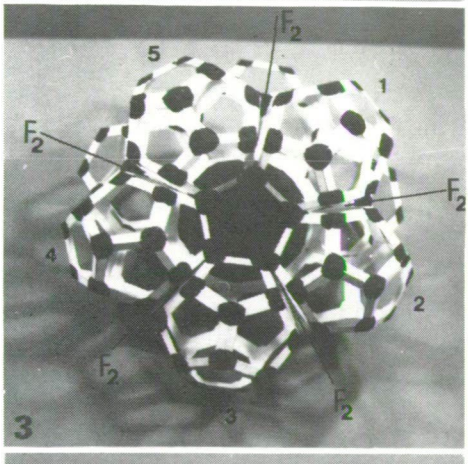
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5
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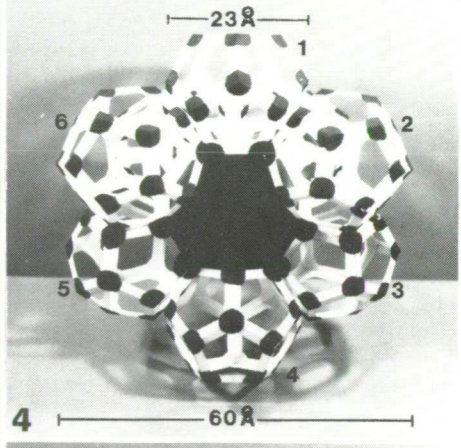
23 Å
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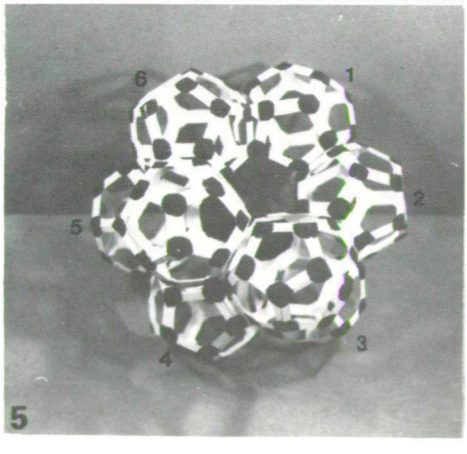
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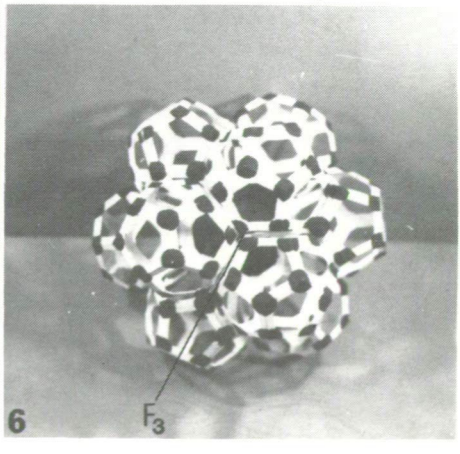

F3
6

◀ Plate 7.1.

1, 2. The model of the basic pentagon dodecahedron biopolymer unit.
Fig. 1 represents this unit in front, with the rotation axes of the modified MARKHAM rotation.
Fig. 2 is a lateral view picture of this unit with several rotation axes.
3, 6. The first step of the highly organized PENROSE-like biopolymer skeleton. This is approximatively the model of a larger globular unit.
Figs. 3—5 illustrate the not competely closed biopolymer model from different views.
Fig. 6, the complete or closed biopolymer skeleton. F_2 = frustration, the distance between two globular biopolymer elements at the edges of the pentagonal side.

C.P.5.A.5.10.
C.P.5.B.5.10.

It is interesting that the scanning electron micrograph of young flower of *Aquilegia vulgaris (Ranunculaceae)* published by ENDRESS (1987) is extremely similar to our basic three dimensional biopolymer unit.

In the case of an oblique-angled view of this unit, when approximatively three planes of the dodecahedron unit may be seen, several P values may be indicated with five AP axes by each plane (Plate 7.1., fig. 2).

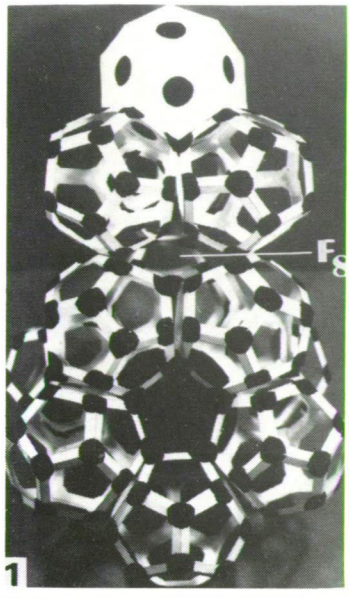
2. HIGHLY ORGANIZED PENROSE-LIKE BIOPOLYMER SKELETONS (Plate 7.1., fig. 3—6)

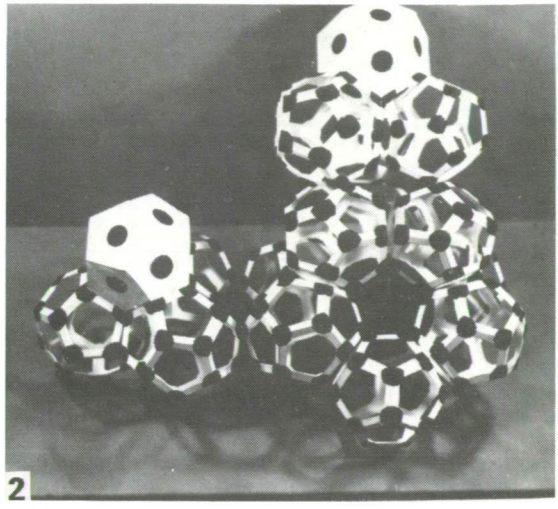
2.1. The first step of this modelling is when one so-called central dodecahedron biopolymer unit is surrounded with twelve same dodecahedron biopolymer units. We have prepared this kind of model as follows. The model of the "central unit" is a black and compact pentagon dodecahedron. The "building" was made as follows.

In fig. 3 of Plate 7.1. it is well shown that one plane of the "central" pentagon dodecahedron is not connected with its "corresponding" pentagon dodecahedron. The regular pentagon in the centrum and the five surrounding basic PENROSE-like units are well illustrated. The frustrations (sensu NELSON 1986) between the two edges (there are two globular biopolymer units also well illustrated, and indicated with F_2. F = frustration, the index indicates the numbers of the globular biopolymer units.) The values of the F_2 frustrations based on the measurements of these model indicate the following in angstroem dimension, for the "biological polymers": 2.2—3.0 Å.

The opposite face (Plate 7.1., fig. 4) of the above discussed plane is an apex bordered with three pentagons. The number of the surrounding dodecahedron biopolymer is six. In this way, sexangular, globular biopolymer arrangement may also appear. In fig. 4 (Plate 7.1.), the approximative sizes (diameters) in Å are also indicated. It is also necessary to point out, that the diameter of the biopolymer skeleton composed from 13 basic pentagon dodecahedron in 6 nm only. It seems to be important to emphasize this fact for the comparison of the published data in literature. We have observed several times that the same morphological unit may appear in different dimensions with different functional, phylogenetical importance.

Fig. 5 of Plate 7.1., is a semi-lateral view of the position illustrated in fig. 3, Plate 7.1.


F_8
1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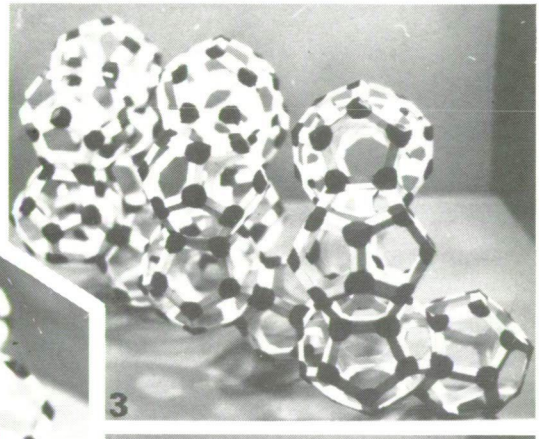
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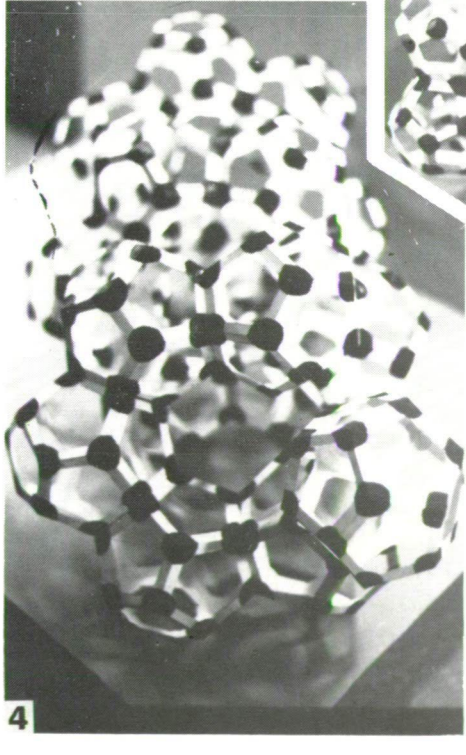
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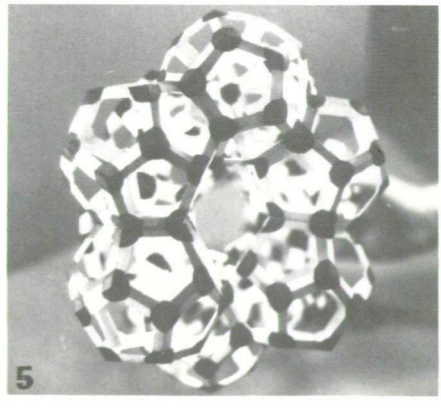
5

◀ Plate 7.2.

1, 2. First steps of the modelling of the second stage of the highly organized globular (PENROSE-like) biopolymer skeleton. The frustrations between 8 biopolymer units are extremely characteristic.
3, 5. Quasi-crystalloid biopolymer skeleton of the singlest helical (or microtubular) organization. Fig. 5 represents well the narrow central channel inside the helix.

Fig. 6, Plate 7.1. represents the completed biopolymer system of the apical view. F_3 frustration is well shown; the space between three apical globular biopolymer units. The measured values indicate 1.4—2.6 in angstroem dimension for the "biological biopolymer" unit.

2.2. To continue this kind of quasi-crystalloid biopolymer skeleton, additional elements were built (Plate 7.2., fig. 1, 2). To distinguish the central dodecahedron unit, the sides are white, with one point in the centrum. Fig. 1, of Plate 7.2., represents well the connection between two connecting sides, F_8 is relatively large. Fig. 2 of Plate 7.2., represents further connecting units. This kind of quasi-crystalloid biopolymer skeleton needs further modelling investigations.

3. HELICAL (MICROTUBULAR) QUASI-CRYSTALLOID SKELETON (Plate 7.2., figs. 3—5, plate 7.3., figs. 1—5)

The first problem to solve in this respect, is whether the basic dodecahedron model unit is suitable to be a "building" element of the helical biopolymer system? As the first step, the most single form was built and photographed from different views. These pictures represents well that from the point of view of the methods of the modified MARKHAM rotation there are a lot of opportunities. There seems in the up-to-date stage of our knowledge no reason to start the investigation of the symmetry axes of these pentagon planes. Their number is so high, but in all probability this question will be emerged secondly later with supplementary documents. Taking into consideration the size of our model this helical unit corresponds to one helical unit of the "tuft unit of the exine" published by ROWLEY, e.g. in 1981. The building of the biopolymer skeleton of the complete "wire-wound model" of ROWLEY seems to be possible but seems to be a hard job.

Discussion and conclusions

1. The first modelling of the highly organized quasi-crystalloid biopolymer skeleton justified that the basic pentagon dodecahedron biopolymer unit is really an elementary biological unit. Not only globular, but helical/tubular system was modelled in this way.

2. As it was pointed out in the published data of the different research fields in the literature, the helical/microtubular structures are extremely important in the cell biological systems. But the fibrillar and lamellar structures, in particular on the surfaces are also extremely important in cell biology. Modelling of these biopolymer structures is also in progress.

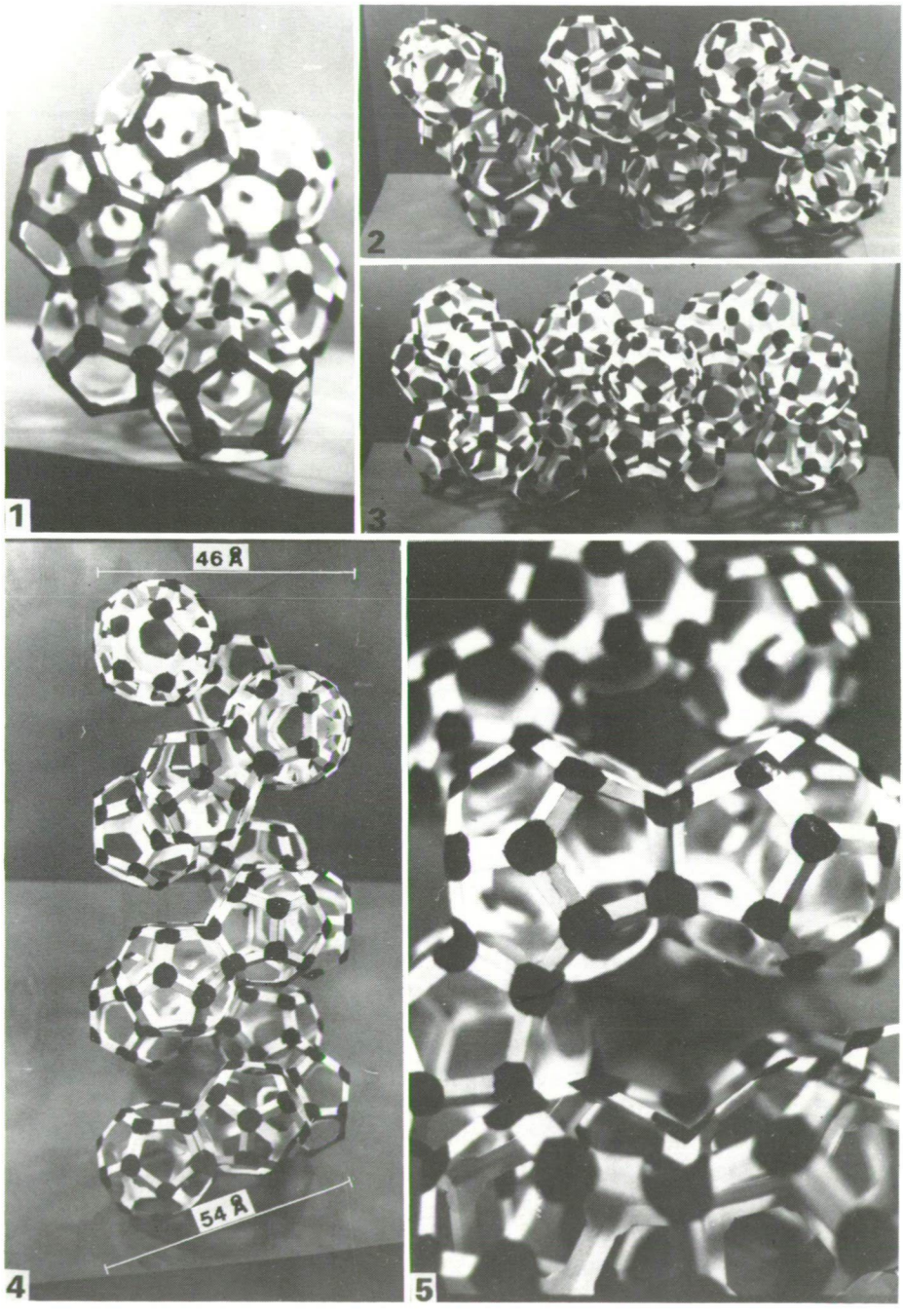

Plate 7.3.

1—5. Different views and enlargements of the helical biopolymer model.

3. Paralell to the modelling of the highly organized quasi-crystalloid biopolymer skeleton we started the modelling of the stabilizing biopolymer systems, too. As it was established in several papers, combined biopolymer structures are present in the holes of the biopolymer skeleton. These biopolymer structures have among other a stabilizing function.

4. In the future the biopolymer model of all important cell organells will be prepared.

5. Finally on the basis of our up-to-date knowledge it seems that at the biopolymer systems in nanometer dimension the rules of the PENROSE tiling are valid. In angstroem dimension, the PENROSE-model (= quasi-crystalloid) structures are present with completely different characteristic features, including biological and/or energetical characteristic features too.

Acknowledgements

This work was supported by the grant OTKA—2, 24/88. The author is deeply indebted to Dr. R. ZÁNTHÓ ass. professor for the linguistic corrections of the text, to Dr. I. BAGI, Mrs. I. BIRÓ — HALÁSZ, E. FARKAS, E. MARKÓ and L. TÓTH for its technical assistance.

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