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To cite this version:
Y. Bouligand. DEFECTS AND TEXTURES IN CHOLESTERIC ANALOGUES GIVEN BY SOME BIOLOGICAL SYSTEMS. Journal de Physique Colloques, 1975, 36 (C1), pp.C1-331-C1-336. <10.1051/jphyscol:1975156>. <jpa-00216235>

HAL Id: jpa-00216235
https://hal.archives-ouvertes.fr/jpa-00216235
Submitted on 1 Jan 1975

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DEFECTS AND TEXTURES IN CHOLESTERIC ANALOGUES GIVEN BY SOME BIOLOGICAL SYSTEMS (*)

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1. Introduction. — In a previous work [1], a comparison was made between certain fibrous and regularly twisted biological materials and cholesteric liquid crystals. The twisted fibrous systems are found in varied cytoplasmic inclusions, in the organic matrix of numerous skeletal structures, in the connective tissue of certain Invertebrates, in the nucleus of many Bacteria and in the Dinoflagellate chromosomes. Very long polymer chains occur in such materials (chitin, collagen, different proteins, D. N. A., etc...). These systems are more or less solid, but they nevertheless show the optical and geometrical properties of cholesterics. Such biological materials contain defects very similar to those appearing in true cholesteric liquids. The distribution of these defects is often different in cholesteric phases and in their biological analogues. The growth mechanisms of the twisted fibrous arrangements in biological tissues or cells provide interpretations for these differences.

2. Defects in cholesteric liquid crystals and their biological analogues. — The cholesteric layering is often altered by many defects and these have been seen very clearly by the first observers; see, for example, Lehmann [2]. The focal conics have been described by Friedel and Grandjean [3] primarily for smectics but these authors also mentioned their occurrence in cholesterics [3, 4]. More recently, de Gennes [5], Friedel and Kléman [6] have proposed models of edge-dislocations and disclinations in the cholesteric systems. We have proved the existence of several of these arrangements [7]. Punctual singularities have been supposed to occur in nematic droplets [8] and they have been shown to exist in certain geometrical situations [6, 9]. Many defects are located on different interfaces (as the limit with the isotropic liquid). These singularities are lines or points due to certain angular conditions imposed on the molecular orientation in the vicinity of the limiting surface [10, 11]. The main lines visible in the bulk have been represented in several papers [6, 12]. They have been found in synthetic polymerized cholesterics [13]. Figure 1 shows that they exist in different polymerized biological systems. In the latter, we have not studied the possible occurrence of punctual singularities and surface defects.

2.1 Translation dislocations. — We have described screw-dislocations in the crab-cuticle [1]. Our model was planar, the cholesteric axis and the dislocation line being vertical. The director trajectories are drawn in horizontal planes and may give either confocal parabolae (+ π disclinations) or the complementary arrangement (−π disclinations). Electron micrographs are in good agreement with this model. Recently, Smith, Telfer and Neville [14] have obtained electron micrographs of such patterns in the chori– of a moth: Hyalophora cecropia. The thin sections are exactly horizontal and one sees the filaments running near the core, in the plane of the preparation with a very weak vertical component (Fig. 1a). Screw-dislocations may occur along the axis of certain Dinoflagellate chromosomes (Fig. 1b). There is no great difference between the aspects given by a screw and an edge-dislocation seen in oblique section. However, the distinction is made easier with serial
sections. One recognizes that a screw-dislocation changes rapidly its position with respect to the cholesteric layering and lies along the axis [15].

Edge-dislocations have been proved to exist in the Locust tibia [1] but this defect is probably very frequent in many materials.

2.2 Focal curves or lines of flare. — The focal lines have been discovered by Friedel and Grandjean [3] in smectics and in cholesterics. The smectic parallel layers form Dupin’s cyclides showing conical singular points, located along two conics (ellipse and hyperbola) in focal position. In cholesterics, the layering is conical around such lines but without any singular points: the apexes of the cones are replaced by narrow areas of strong curvature [12]. Such a situation occurs very probably in smectics but has never been proved.

Such lines of conical distortion are not always conics. They show varied shapes in cholesterics. In certain cases, the focal curves are conics, but are not in focal position. The terminology focal curve is confusing and we prefer to use line of flare, an expression which seems to be more appropriate and refers to the trumpet-shape of the stacked laminae around these lines. The lines of flare show a polarity defined by the orientation of the apexes of the cones. In the case of focal conics, the polarity is inverted when the curves meet their plane of symmetry.

The lines of flare are very common in the Arthropod cuticle (crabs, beetles, etc...) and they have been observed in synthetic polymerized liquid crystals [1, 13].

2.3 Disclinations. — These lines have been first observed by Lehmann [2] in cholesterics showing an helicoidal pitch of several microns. Disclinations are of the $+\pi$ or $-\pi$ types and belong to the $\lambda$ category, in the terminology of Friedel and Kléman [6]. The director distribution of such systems is continuous. Disclinations $-\pi$ are frequent in Dinoflagellate chromosomes (Fig. 1c), but the $\lambda$ or $\tau$ nature of such defects is not easy to establish. Their functional significance is not clear. These disclinations have been supposed to be involved in the splitting and the segregation of chromosomes during the cell-division [16]. In fact, figures of coalescence and disclinations are frequent between several different chromosomes in the cell nucleus [17].

Examples of $\lambda^-$ disclinations have been found in the collagen distribution in the connective tissue of certain marine sponges [18]. This cholesteric pseudomorphosis envelops very young buds of the sponge. Gourret [19] has observed $\lambda^+$ disclinations (Fig. 1d) in twisted bodies floating in vacuoles of certain plant cells (root nodules of Vicia). These twisted bodies nucleate from the $\lambda^+$ axis. Such disclinations are rare in the true liquid crystals.

3. Textures. — The distribution of defects can be considered as the texture frame. The cholesteric liquids show three main textures [20], which can be called:

1) Fan-shaped textures (with disclinations, focal curves and translation dislocations);
2) Polygonal fields (with focal curves and dislocations);
3) Planar texture (with dislocations only).

Disclinations are defects of high energy and occur mainly in the vicinity of the isotropic transition. Accordingly, the periphery of a cholesteric phase is mostly a fan-shaped texture. The cholesteric layering is less distorted in the polygons and in the planar texture.

In several cases, the twisted plywood of the Arthropod cuticle is more or less related to the polygonal fields or to the planar texture. However, some strong differences can be evidenced by comparing the density of the focal curves of distinct polarities and their spatial arrangement. In the crab-cuticle (dorsal cephalothorax of Carcinus maenas and Cancer pagurus), all the focal curves lying vertical (normal to the cuticle) have the same polarity; there are very few exceptions.

In the exocuticle of the beetle Plusiotis gloriosa [21], it clearly appears (after a document communicated by Dr. A. Pace) that the ratio is $\frac{1}{4}$ for the two opposite polarities; 44 lines of flare are oriented in one sense
and 86 in the opposite sense (Fig. 2). This ratio corresponds to a statistically hexagonal array in horizontal projection. Lines of flare belonging to one orientation are the centres of hexagons formed by the opposite series; this system shows many defects and some polygons have five or seven sides instead of six.

Fig. 2. — Distribution of the vertical lines of flare (vl) in the cuticle of the beetle: Pluotis gloriosa. The black points and the circles represent lines of opposite concavities. The solid lines are probably horizontal lines of flare.

Extremely varied patterns are found in the beetle cuticle. The lines of flare may be ordered along longitudinal lines. Certain axes correspond to strong deformations, whereas other curves of flare are the centres of minor deviations of the laminae, and show in certain cases the opposite orientation. A polygonal

Fig. 3. — Electron micrographs of thin sections of the integu-ment of the Crab: Carcinus maenas, at the limit between the epidermal cytoplasm and the freshly deposited cuticle. The organic matrix of the body-wall is made of fibrils (chitin and proteins) and will be later mineralized (calcite). The fibrous framework (f) is penetrated by pore-canals (pc) projecting vertically from the cytoplasm (cyt). These micrographs correspond to a period of strong secretion. At a higher magnification (b), one distinguishes four main steps leading to the fibril differentiation.
field given by a true liquid crystal (M. B. B. A. to which has been added cholesterol benzoate), observed between slide and coverslip shows an equal number of vertical lines of flare, with the two opposite orientations [12]. The situation of the mesomorphic slab between the glass plates is symmetrical. The cuticle, on the contrary, is asymmetrical with an inner side and an outer one. These differences are related to the mechanisms involved in the growth of such fibrous systems. In the Crustacean cuticle, electron micrographs show the successive steps of the fibril differentiation, starting from small subunits, as can be shown from figure 3. It seems likely that the secretion passes through a very dense and brief colloidal state. Very thin and short filaments (or segments) are first deposited in the vicinity of the cytoplasmic membrane of the epidermal cells. The subunits appear from small thickened and electron dense areas of this membrane. They are progressively gathered into larger units and form a fibrous network. Each fibril is a bundle of filaments and numerous exchanges occur here and there. Such a situation is sketched in figure 4. This colloidal system, which seems to be a gel is transformed into a fibrous network and could allow a self-assembly, without passing through a genuine mesomorphic state. The organic matrix of a Crustacean cuticle has never been a liquid crystal in the bulk and does not seem to pass any brief liquid state at the secretion time. The first secreted deposit is more probably an oriented gel.

There is a great difference between the cuticular cholesteric pseudomorphosis and the polymerized liquid crystals carried out by organic chemists [21]. In the biological systems, the process of polymerization occurs during the secretion itself and the fibrous arrangement is forming in the vicinity of the front of secretion. On the contrary, in the polymerizing liquid crystals synthetized by Strzlecki and Liébert, cross-bridges appear in the bulk, and the geometry of the mesophase is fixed in the resulting solid. The main textures known in liquid crystals can be fossilized by this method. Fans, polygons and planes have been observed in such pseudomorphosis.

The texture in an Arthropod cuticle depends mainly on the morphology of the first deposited layer or epicuticle. In the case of the crab, small convex areas are uniformly dispersed on the back of this animal. Such swellings may present a revolution symmetry and the successive layers form lines of flare along each axe of deformation [1].

The helicoidal pitch often keeps a constant value in the cuticle at a definite depth, but shows strong variations during the secretion cycle, between two successive molts [23]. In Locusts, a nematic pseudomorphosis is forming during the day, whereas, during the night, a cholesteric plywood is normally deposited. A thin section of the elongated tibia of the hind-legs of a Locust allows to observe in alternance twisted lamellated zones and layers of preferred microfibrillar orientation [24]. It seems that a twisting substance is secreted by the epidermis with a varying concentration during the cuticle cycle. The brief polymerization and the hardening of the cuticle stabilizes the helical pitch. Its abrupt variations could not occur if the cuticle was mesomorphic in the bulk at the time of secretion.

Another point concerning the textures is the orientation of the cholesteric layering with respect to the limiting surface of the fibrous system. It seems that, for certain Dinoflagellate species such as *Prorocentrum micans* or *Amphidinium elegans*, there is no definite angular condition imposed on the D. N. A. filaments in the vicinity of the limiting surface of the chromosome. This can be seen from figure 5b-d; but there are probably many exceptions. In the bacterial cell, the nucleus dimensions are small and do not allow much more than two or three half helicoidal pitches for the D. N. A. arrangement [26] but there is however good evidence for a twist of constant orientation (Fig. 5e-g). The Dinoflagellate chromosome has the texture of a M. B. B. A. droplet twisted by a cholesterol derivative. The bacterial nucleus can show this geometry, but is often distorted (cell division,
FIG. 5. - Twisted arrangement of the D. N. A. filaments in the chromosomes of Dinoflagellates and Bacterias. The fibrous appearance is due to the lack of histones (basic proteins which exist in the chromatin and the chromosomes of Eucaryotic organisms; in these latter, the D. N. A. filaments are not visible in thin section). a) Model of a Dinoflagellate chromosome. The geometry is identical to that of a cholesteric rodlet floating in the isotropic phase. The successive planes with D. N. A. filaments of parallel orientation are convenient for the understanding of the structure, but this latter is continuous. It leads, in oblique section, to a series of bow-shaped lines [1]. a') Helicoidal arrangement of the average orientation of D. N. A. filaments along the chromosome axis. b) Oblique sections of a chromosome of *Prorocentrum micans* (replica from a freeze-etched sample). The limiting surface of the chromosome does not modify the D. N. A. orientation in its vicinity (this drawing is made after a micrograph published by P. Giesbrecht, see ref. [25]). c, d) Oblique sections in chromosomes of *Amphidinium elegans* (after de Haller and coworkers, see ref. [25]). The D. N. A. orientation does not depend on the limiting surface. e, f, g) Thin sections of *Bacillus subtilis* (after Rytzer [26]). The chromosomic network (ch) shows a twisted arrangement seen in cross-section (e) and in oblique section, with the bow-shaped patterns (f, g); w: cell-wall; m: cell-membrane; cyt: cytoplasm; p: growing partition between two daughter-cells.
cytoplasm motion) and seems to be very sensitive to the limiting surface conditions. When Trypanosomes are treated by certain drugs, the D. N. A. network of their kinetoplast is transformed into a cholesteric gel [27] showing varying textures, possibly related to the surface conditions and to some inner topological constraints (Fig. 6a, b).

Simple planar textures have been observed in plastids of certain plant cells infected by Viruses [28].

4. Conclusions. — From this brief review, it can be concluded that the fibrous biological analogues of cholesteric liquid crystals show defects which are those observed in the normal mesophases: dislocations, curves of flare and disclinations. However, the distribution of these defects and therefore the textures, may differ. For example, the unusual textures of certain Arthropod cuticle seem to originate from the epip- iccular morphology and the growth mechanisms of the underlying cuticle, involving a brief passage through an oriented gel allowing certain twisting forces to exert. The D. N. A. in chromosomes or in certain inclusions gives rise to very varied textures.

References


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