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# Liquid-crystalline phases of circular superhelical plasmid DNA and their modification by the action of nuclease enzymes

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# Liquid-crystalline phases of circular superhelical plasmid DNA and their modification by the action of nuclease enzymes

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CD spectra of liquid-crystalline dispersions, X-ray diffraction patterns and optical textures of liquid crystals prepared from native superhelical DNA in poly(ethyleneglycol)-containing water–salt solutions before and after treatment of DNA with micrococcal nuclease have been obtained. It was found that condensation of native superhelical DNA is accompanied by the formation of liquid crystals with a non-specific optical texture. After treatment of the DNA, liquid-crystalline dispersions, with Micrococcal nuclease the DNA is able to form two similar types of liquid crystals with abnormal optical activity which differ in the peculiarities of their textures. The data obtained demonstrate the formation of multiple types of liquid crystals from high molar mass double-stranded optically active DNA molecules.



## 1. Introduction

The existence of multiple lyotropic liquid-crystalline polymorphism of low molar mass ($< 1 \times 10^6$) double-stranded nucleic acid molecules has been described recently [1–3]. The types of liquid crystal phases formed by DNA appear to be very similar to those formed by low molar mass synthetic compounds. The structure of liquid-crystalline DNA solutions is sensitive to changes in the dielectric constant of the solvent, the nature of the DNA molecules as well as the DNA concentration [1–3].

The mode of packing of the DNA molecules of high molar mass is of appreciable biological interest [1]. A study of the packing of linear double-stranded high molar mass ($\sim 25 \times 10^6$) DNA has been undertaken both experimentally as well as theoretically [4–14]. Theoretical considerations suggest two basic postulates, (1) the phase exclusion of high molar mass single DNA molecules under specific conditions [4, 5, 10, 12] leads to their intramolecular condensation and to the formation of globular structures. Segments of a DNA single chain in a globule can be packed in a mode similar to that of low molar mass DNA molecules, giving a liquid-crystalline phase [1]. Comparison of these data demonstrate that an intramolecular liquid crystal can exist [9, 11]; (2) under different conditions there can be an intermolecular aggregation of high molar mass DNA [8, 10]. This aggregation does not result in the formation of highly ordered structures. It should be noted that the number of studies which compare the results of the theoretical analysis with experiment is limited. Therefore it can be assumed that the details of the intramolecular packing of the DNA molecules are not well defined.

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Yevdokimov *et al.* [14, 15] have initiated studies on the peculiarities of packing of other high molecular mass DNA species, namely, homogeneous superhelical, circular, double-stranded DNA (plasmids). These are of interest because they exist in living cells and their structures readily rearrange under the action of different biological factors. From a physico-chemically viewpoint, studies of the packing of homogeneous DNAs throw light on the relationship between the type of spatial packing adopted by biopolymeric molecules upon their condensation and their initial structures.

In the present study, in order to establish the types of the ordered structures formed by plasmid DNA condensation in polymer-containing water–salt solutions the CD spectra of dispersions which are formed by phase exclusion of these plasmids were compared with the results of X-ray scattering and the analyses of optical textures of the phases prepared from such dispersions. A transition between different forms of plasmids was induced by treatment with an enzyme which splits the DNA chain. The results obtained demonstrate the existence of a family of liquid-crystalline states of high molecular mass DNA molecules.

## 2. Materials and methods

The preparations of circular superhelical DNA investigated were pPS-neo (containing 20–30 per cent nicked form, 980 base pairs [16], pBR 322 (10 per cent nicked form, 4363 base pairs) and pGC 20 (15 per cent nicked form, 2704 base pairs). They were isolated by alkaline treatment and additional purification which involved pronase treatment and phenol deproteinization followed by centrifuging in a caesium chloride density gradient.

A Micrococcal nuclease preparation (Sigma, Micrococcal endonuclease, EC-3.1.31.1, from *Staphylococcus aureus*, Foggi strain, Lot 93F-4037, MN) was used. The concentration of the initial MN solution (0·03 M Tris HCl; pH 7·5) was 1 mg/ml. The MN buffer contained 0·015 M Tris HCl; 0·001 M $CaCl_2$; pH 8. Electrophoresis of the superhelical DNA and the preparations which were obtained by treatment with MN was carried out in 1 per cent agarose gel (TAE buffer).

The dispersed phases of superhelical DNA were formed in aqueous solutions containing 0·3 M NaCl; 0·015 M Tris HCl; 0·01 M $CaCl_2$( pH 8 and poly(ethylene glycol) (PEG; mol. mass 4000; Ferak; F.R. Germany) as described in [1]. The enzyme treatment of the original superhelical DNA was carried out by adding MN solutions and stirring. The reaction was stopped by adding EDTA (final concentration 0·015 M) and sodium dodecylsulphate (final concentration 0·5 per cent).

The CD spectra were recorded on a JOBIN–YVON dichrograph, Mark III and the absorption spectra were taken on a SPECORD M-40 (Carl Zeiss, G.D.R.) spectrophotometer.

The samples used for the X-ray investigations were obtained by concentrating particles of the dispersed DNA phase by centrifugation (5000 rev/min; 40 min). The optical textures of thin (20 $\mu$m) layers of these DNA phases were examined as described previously [1, 17].

## 3. Results

### 3.1. *CD spectra of disperse phases prepared from circular superhelical DNA after the action of Micrococcal nuclease*

In figure 1 (A) the CD spectrum of the initial circular superhelical DNA pPS-neo (curve 0) is compared with that of the material after treatment with Micrococcal

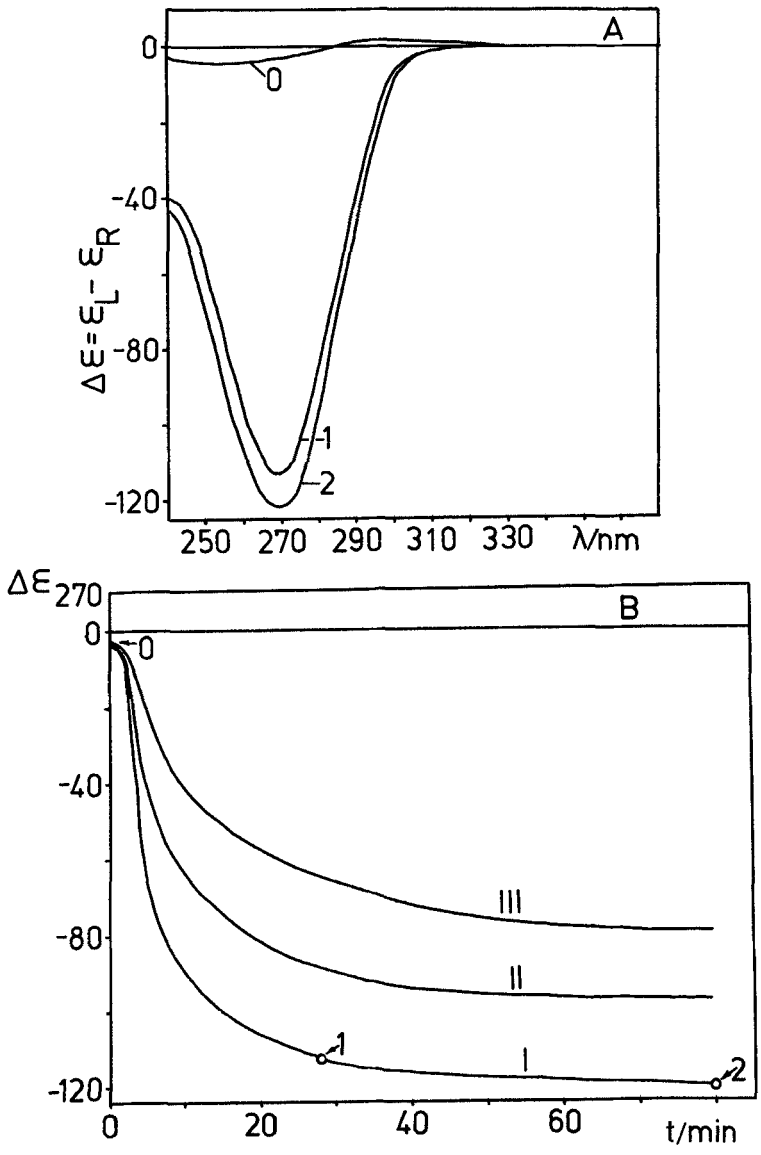


Figure 1. (A) The CD spectra of the pPS-neo DNA disperse phase ($C_{DNA}$ = 15·5 m kg/ml) for different times of treatment with nuclease. Curve 0, CD spectrum without nuclease treatment; curves 1 and 2, CD spectra after 28 and 80 min treatment, respectively. ($\Delta A = A_L - A_R$ in centimetres, 1 cm = $10^{-4}$ optical units). Solvent: 0·265 M NaCl; 0·015 M Tris HCl; 0·001 M $CaCl_2$; pH 8; $C_{PEG}$ = 170 mg/ml. (B) Dependence of the amplitude of the band ($\lambda_{max}$ = 270 nm) in the CD spectra of DNA dispersions versus treatment time of dispersions with Micrococcal nuclease. Curve I, pPS-neo DNA ($C_{DNA}$ = 15·5 m kg/ml; $C_{nuclease}$ = 0·03 m kg/ml; $C_{PEG}$ 170 mg/ml). Curve II, pBR 322 DNA ($C_{DNA}$ = 9·84 m kg/ml; $C_{nuclease}$ = 0·011 m kg/ml; $C_{PEG}$ = 151 mg/ml). Curve III, pGC 20 DNA ($C_{DNA}$ = 14·6 m kg/ml; $C_{nuclease}$ = 0·03 m kg/ml; $C_{PEG}$ = 151 mg/ml). Solvent: 0·265 M NaCl; 0·015 M Tris HCl; 0·001 M $CaCl_2$; pH 8; $C_{PEG}$ = 170 mg/ml.

nuclease (curves 1 and 2). The initial dispersed phase has a characteristic low optical activity ($\Delta\varepsilon_{max}$ = 3–5 units). Upon treatment with MN the optical activity increases and after a specific time $\Delta\varepsilon$ reaches its maximum value of about 120 units (see curve 1, figure 1 (B)). Points 0, 1 and 2 in curve I (see figure 1 (B)) correspond to CD spectra 0, 1, 2 in figure 1 (A). Similar results were obtained from the pBR 322 and pGC 20 materials (see curves II and III respectively, in figure 1 (B)) which differ in their molar masses. The rate of increase of the amplitude of the negative band in the CD spectrum depends only on the ratio of the DNA and nuclease concentrations. It does not depend on the molar masses of the original DNA sample.

### 3.2. *Electrophoregrams of DNA samples resulting from the action of MN on superhelical DNA*

In figure 2 electrophoregrams of pPS-neo preparations before (track 0) and after (tracks 1 and 2) MN treatment are shown. The original superhelical and the nicked forms of pPS-neo DNA are mainly converted after the MN treatment into a linear form (molar mass $\sim 6{\cdot}5 \times 10^6$). Longer treatments with MN gives DNA fragments with relatively low molar mass (molar mass $\sim 8 \times 10^5$ average) (track 2).



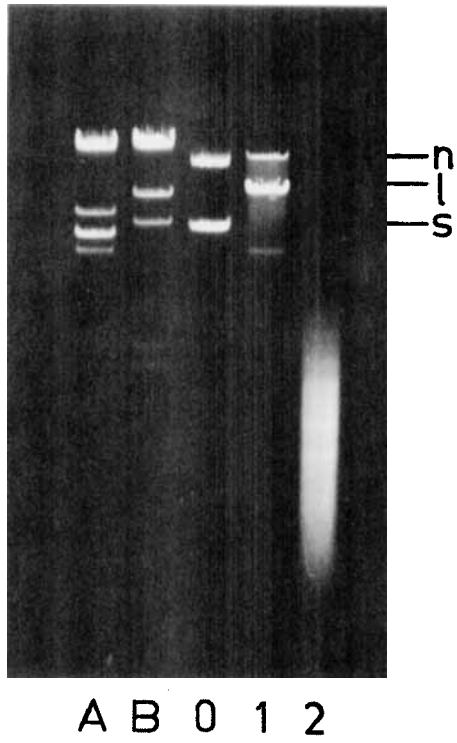


Figure 2. Electrophoregrams of pPS-neo DNA after Micrococcal nuclease treatment of liquid-crystalline dispersions. Track A, DNA molecular weight marker ($\lambda$ DNA EcoR I); track B, DNA molecular weight marker ($\lambda$ DNA Hind III); track 0, native superhelical DNA pPS-neo containing about 30 per cent of the nicked form; track 1, treatment time 28 min. Track 2, treatment time 80 min. n, l and s denote nicked, linear and superhelical forms of DNA, respectively.

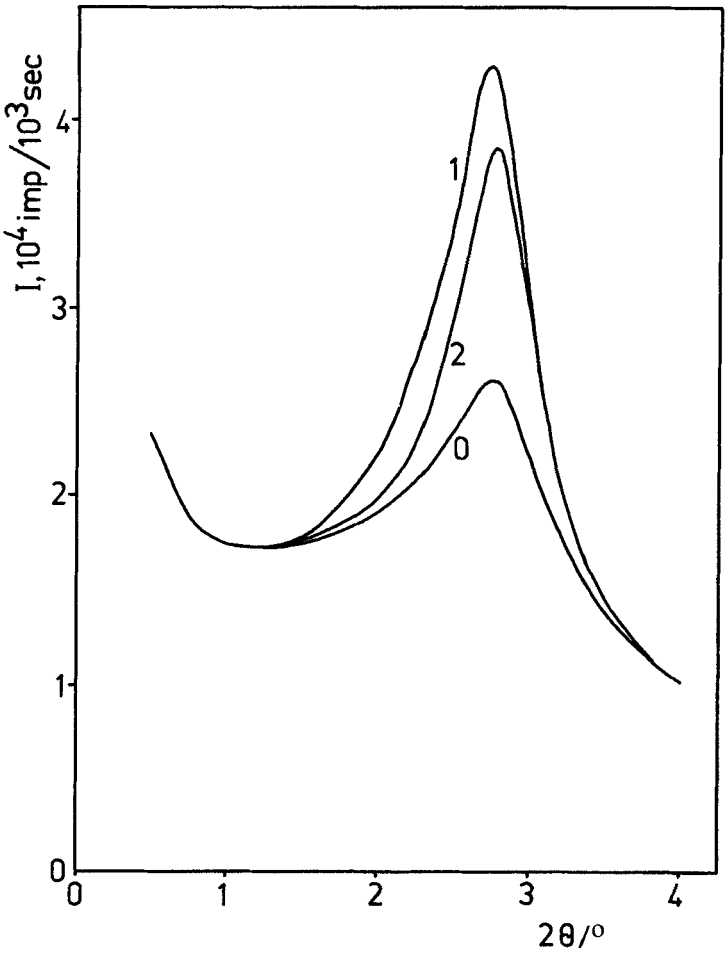


Figure 3. Small-angle X-ray diffraction patterns for liquid crystals formed from pPS-neo DNA. Curve 0, without nuclease treatment. Curves 1 and 2, time of treatment of the DNA with Micrococcal nuclease in the composition of the dispersions was 28 and 80 min, respectively. Solvent: 0·265 M NaCl; 0·015 M Tris HCl; 0·001 M $CaCl_2$; pH 8; $C_{PEG}$ = 170 mg/ml.

### 3.3. *X-ray characteristics of condensed phases formed from MN treated superhelical DNA molecules*

Figure 3 compares the small angle X-ray scattering curves of the original condensed pPS-neo DNA phase (curve 0) and of the MN-treated DNA (curves 1 and 2). Curve 0–2 in figure 3 correspond to curves 0–2, in figure 1 (A) and to curves 0–2 in figure 2. The X-ray diffraction patterns of DNA phases formed under different conditions (see the table) do not change significantly upon (circular superhelical—linear low molar mass DNA) transition which occurs upon MN treatment of DNA in the composition of particles of the dispersed phase.

### 3.4. *Optical textures of condensed phases formed from MN-treated circular superhelical DNA molecules*

Figures 4 (A) and (B) show the optical textures observed at 22°C of the initial superhelical circular pPS-neo phase. The textures in figure 4 (C), (D) are typical of

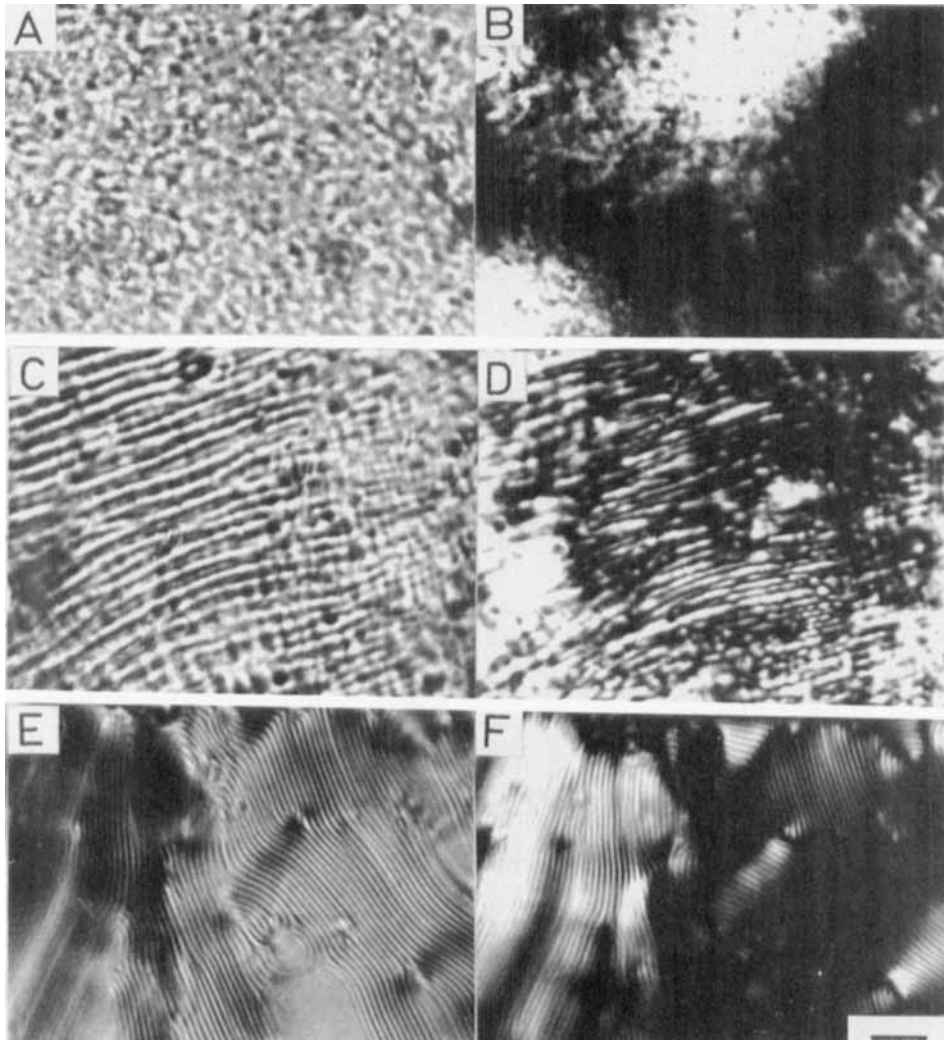


Figure 4. Optical textures of pPS-neo DNA liquid crystals. A and B, without nuclease treatment; C and D, nuclease treatment time 28 min. E and F, nuclease treatment time 80 min. (Textures A, C, E were taken with parallel polars; textures B, D, F, with crossed polars. The bar shown in the texture F is equal to 10 $\mu$m.)

those shown by high molar mass linear pPS-neo DNA samples obtained by treatment with MN for 28 min of circular superhelical pPS-neo DNA (cf. curve 1 in figure 1 (A) and curve 1 in figure 3; track 1 in figure 2). The textures shown in figures 4 (E), (F) are of samples of low molar mass linear DNA fragments (molar mass $8 \times 10^5$) obtained after longer MN treatment (80 min) of superhelical pPS-neo DNA indicate that cholesteric liquid crystals are formed.

## 4. Discussion

The data presented show that dispersed phases formed from native optically active double-stranded circular superhelical DNA of different molar masses do possess low

X-ray parameters for pPS-neo DNA liquid crystals formed under different conditions.

| Time of nuclease action on superhelical DNA liquid-crystalline dispersions, t/min | $2\theta_{max}$/° | $d$/Å | $\Delta/d$ | $r_m$/Å |
|---|---|---|---|---|
| 0 | 2·75 | 32·1 | 0·166 | 186 |
| 28 | 2·72 | 32·5 | 0·162 | 199 |
| 80 | 2·77 | 31·9 | 0·177 | 162 |

$d = \lambda/(2\sin\theta)$ denotes the average distance between axes of adjacent DNA segments in the liquid-crystalline phase, $\lambda$ is the X-ray wavelength (in our case $\lambda = 1{\cdot}54$ Å), $\theta$ is half of the angle for the scattered X-ray; $\Delta/d = (1/\pi)(\beta_s d/\lambda)^{-1/2}$ denotes the disorder parameter, $\Delta$ is the semiquadratic deviation from $d$, $\beta_s$ is the integral half-width of the maximum; $r_m = (\pi/2{\cdot}5)^2(\lambda/\beta_s)$ denotes the interaction radius.

optical activity (see for example, figure 1 (A), curve 0). The only small-angle reflection ($d \sim 32$ Å) in the X-ray diffraction patterns of phases formed from dispersions of superhelical circular DNA (see figure 3 and the table) demonstrates the close packing of DNA molecules (or segments) in the composition of condensed phases, i.e. the existence of one dimensional ordering of DNA molecules. The non-specific textures of the initial materials (see figures 4 (A), (B)) indicate the optical anisotropy of these phases despite their low birefringence. This together with the one dimensional ordering of DNA molecules proves the liquid-crystalline nature of native circular superhelical DNAs phases. The non-specific optical texture is observed under all experimental conditions for the liquid-crystalline phases prepared from native circular superhelical DNA. It should be added that thin layers of the liquid-crystalline phases formed from native superhelical DNA are characterized by a low optical activity in contrast to the abnormally high optical activity for thin layers of cholesteric liquid crystals formed by linear DNA molecules [1, 18]. These data suggest that solutions of native superhelical DNA are not cholesteric.

There do not appear to be any systematic studies of the textures of liquid crystals formed from polymers with a molar mass exceeding $1 \times 10^6$. Therefore we can only compare our observations with those textures of liquid crystals with relatively low molar mass compounds. The non-specific optical textures of the initial superhelical materials resemble those of hexagonal chromonic phases of drugs and dyes [19]. Torbet and Langowski [20] who studied the properties of the concentrated phase of superhelical pHC 624 DNA also point out (without presenting conclusive evidence) the possibility that DNA can form a hexagonal phase. The fact that only one small-angle reflection is observed in our X-ray diffraction patterns makes it improbable that superhelical DNA molecules have an ideal hexagonal packing. Indeed, the presence of supertwists in the DNA structure may not noticeably effect the local packing of adjacent segments of DNA but it would be expected to hinder any long range ordering. We conclude that the presence of only one reflection in the small-angle X-ray diffraction pattern, the absence of abnormal optical activity and the non-specific texture of the liquid crystals indicate a local pseudohexagonal nematic packing of adjacent DNA segments.

Short term exposure to MN results in the cleavage of both strands of the initial circular superhelical DNA and so creates linear DNA molecules with the same molar mass (see figure 4). The condensation of superhelical DNA molecules does not inhibit

the nuclease action. After nuclease treatment there is a sharp increase in the amplitude of the negative band in the CD spectrum at 270 nm (see figure 1 (A), curve 1). This suggests the development of a long range helicoidal ordering previously prevented by the circular plasmid structure. In contrast, the short range ordering (as indicated by the X-ray diffraction patterns) is relatively unchanged (see the table). This means that the structural rearrangement of DNA molecules can include just minor changes in the mutual orientation of adjacent molecules (or that of their segments) in the liquid-crystalline dispersions. We would add that the optical texture of the liquid-crystalline phase formed from the dispersion of linear pPS-neo DNA molecules (molar mass $\sim 6 \times 10^6$) which were obtained from native circular DNAs after MN splitting is presented as a system of black and white lines (the average distance ($S$) between them being 3 $\mu$m (see figure 4 (C), (D)). Despite this fact such a texture does not resemble exactly the ideal finger-print texture characteristic of cholesteric liquid crystals [21].

Prolonged enzyme treatment of high molar mass linear pPS-neo DNA gave relatively low molar mass DNA fragments (molar mass $\sim 8 \times 10^5$, corresponding to an average length of about $4 \times 10^3$ Å). Liquid-crytalline dispersions of this material have an enhanced band at 270 nm in the CD spectrum (cf. curves 0 and 2 in figure 1) and show a finger-print texture typical of cholesteric liquid crystals (see figures 4 (E), (F)). The cholesteric pitch, $P$, which is calculated from these textures as twice the band spacing, $S$, is about 2·5 $\mu$m which is close to values previously observed [22–24] for cholesteric liquid crystals formed from low molar mass DNA under rather different conditions. Since

$$P = 2\pi d/\theta_0,$$

where $P$ is the pitch of the cholesteric superstructure; and $d$ is the distance between DNA molecules in the liquid crystal, which can be obtained from X-ray scattering studies and $\theta_0$ is the twist angle which the DNA molecules make with respect to one another, we can determine that for the DNA cholesteric liquid crystals the angle $\theta_0$ is about 0·7°. This value differs from that of the mutual twist angle between polypeptide molecules forming cholesteric liquid crystals ($P \approx 31\,\mu$m, $\theta_0 \approx 0{\cdot}03°$ [25]) as well as from the angle of the DNA helix axis oriented in the liquid-crystalline state [17] obtained by $^3$H NMR measurements for liquid crystals prepared in water–salt (0·06 M NaCl) solution from DNA (the average molecular length was $\sim 3{\cdot}4 \times 10^2$ Å, $C_{DNA}$ 100 mg/ml) [26]. The reasons for the differences between the $\theta_0$ values for the DNA liquid crystals are not known.

The optical texture of the liquid-crystalline phase which is formed from dispersions of pBR 322 linear DNA molecules having a lower molar mass ($M_w = 2{\cdot}88 \times 10^6$) is similar to the classic finger-print texture. The presence of this texture together with the large intensity of the negative band in the CD spectrum of a thin layer of the phase formed demonstrates that the linear pBR 322 DNA molecules are able to form a liquid-crystalline phase of the classic cholesteric type in spite of the relatively high molar mass. This fact allows us to suggest that for the formation of cholesteric liquid crystals (or liquid-crystalline dispersions) the DNA molecules must have molar masses which are comparable with $3 \times 10^6$.

In connection with the results obtained a question arises as to the mechanism of the transition from the nematic to the cholesteric type of packing for the DNA molecules in the liquid-crystalline dispersions. Our data could be interpreted in terms of two different hypotheses. First, the structure of the high molar mass DNA in

particles of the liquid-crystalline dispersion depends on both structural and kinetic factors. The superhelical circular DNA molecules of high molar mass form a liquid-crystalline dispersion as a result of phase separation in PEG-containing solutions. The kinetic factors during the mixing of DNA and PEG solutions and subsequent phase separation do not permit segregation and orderly packing of double-stranded optically active superhelical DNA molecules to be achieved. When the superhelical DNA is cut by MN giving the linear form the structural limitations preventing favourable packing of adjacent DNA molecules begin to disappear and the molecules are able to pack in the mode typical of all linear optically active molecules, i.e. in a helical array. Taking into account the high molar mass of the DNA we can imagine that adjacent high molar mass DNA molecules tend to form either an irregular cholesteric with a large pitch or a structure having a similarity to twisted smectics (segments of adjacent DNA molecules, for example, can be considered as an element of the smectic structure). Occurrence of helicoidal elements of any type in the structure of the liquid-crystalline dispersion (or phase) is accompanied by the appearance of abnormal optical activity, in particular, the very intense band in the CD spectrum located in the absorption region of the nitrogen bases (see figure 1). However the general space rearrangement of DNA molecules in the liquid-crystalline dispersion is still limited by the high molar mass of DNA. Further cutting of the DNA into shorter lengths leads to the situation where the molecular rearrangement becomes progressively easier. In complete accord with theory [27, 28] short, rigid, double-stranded, optically active DNA molecules form a classic cholesteric phase. In this state the intense band in the CD spectrum reaches its maximum value (see figure 1 (A)).



According to the second hypothesis the abnormal optical activity of the particles of the liquid-crystalline dispersion formed from superhelical DNA molecules depends on the thickness of a hypothetical liquid-crystalline layer inside the particle of the dispersed phase. Because of their superhelical structure the thickness of this hypothetical layer formed from its initial plasmid molecules is very small and a helicoidal arrangement of native superhelical molecules is not possible. The system may be locally ordered but it does not possess the long range order required to give the abnormal optical activity characteristic to the cholesteric phase. The cutting of DNA molecules by enzymes and the disappearance of supertwists in the DNA structure allows, according to this hypothesis, the increase of thickness of the hypothetical layer and a helicoidal arrangement becomes possible. An abnormal optical activity is then obtained. This hypothesis takes into account the results of theoretical studies [29] which show that the probability of a transition from a nematic to a helicoidal arrangement of the molecules forming the liquid-crystalline layer depends on its thickness.

Whichever view is correct there exists a complex relationship between the character of the DNA molecules packing in liquid-crystalline dispersions (phases) and the DNA molar mass. This implies that sometimes the presence of the intense band in the CD spectrum of liquid-crystalline dispersions formed from high molecular mass DNAs is not an unequivocal indication for ideal cholesteric packing.

In conclusion it can be mentioned that the data obtained by us demonstrate that different structural types of high molecular mass double-stranded DNAs are able to form liquid-crystalline dispersions (phases) which differ in the character of their spatial organization. The condensed state of DNA molecules is not an obstacle to the nuclease action. The nuclease action can induce reformation of one type of spatial organization of DNA molecules inside the liquid-crystalline dispersions to the other.

This observation suggests that the character of the spatial organization of lyotropic liquid crystals of DNA can also change under the action of different biological factors, i.e. the result obtained may be of biological importance.

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