Recent progresses in lyotropic chromonic liquid crystal research: elasticity, viscosity, defect structures, and living liquid crystals

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ABSTRACT

Lyotropic chromonic liquid crystals (LCLCs) are formed by linear stacks of disc-shaped molecular in water. Combined by weak, non-covalent forces, these aggregates are reversible, flexible and polydisperse. The self-assembly nature of the basic building units gives nematic LCLCs interesting physical properties, such as very small twist $K_2$ constant as compared with splay $K_1$ and bend $K_3$ constants, very large splay $\eta_s$, and twist $\eta_t$ viscosities, strong temperature dependence of $K_1$, $\eta_s$, and $\eta_t$, diverse responses to different ionic additives, and large and azimuthally asymmetric disclination cores. We discuss our experimental studies on the viscoelastic properties and the fine structure of disclinations of LCLCs and attribute their unusual properties to the fact that LCLC aggregates are not fixed in size, but vary in response to changes of temperature, concentration and ionic content in the system. We further use these properties to explain intriguing phenomena in the ‘living liquid crystals’ composed of chromonic liquid crystal and motile bacteria Bacillus Subtilis.

KEYWORDS

Lyotropic chromonic liquid crystals; elastic constants; viscosities; topological defects; active matter; active nematic; living liquid crystals; Bacillus Subtilis

1. Introduction

Lyotropic chromonic liquid crystals (LCLCs) are a new class of liquid crystal (LC) materials receiving increasing amount of interest in recent years [1–5]. Members of the LCLC family include drugs, dyes [6] and nucleic acids [2,7]. Their molecules typically feature a disc-shaped rigid body, with multiple benzene rings at centre and ionic groups at the periphery (Figure 1a). Once dissolved in water, these disc-shaped molecules stack on top of each other to form slender linear aggregates, while the ionic groups are disassociated, leaving the aggregates’ surface charged (Figure 1b). These linear aggregates can form nematic or columnar phases in an extended range of temperature $T$ and concentration $c$. Unlike classic LCs composed of molecules of fixed size, the length of the LCLC aggregate can vary, since the energy required to break it, the ‘scission energy’ $E$, is on the order of only $10k_BT$. As a result, LCLC phases are sensitive to changes of temperature, concentration [2], ionic contents, pH, and crowding agents in the solution [8,9].

This unique way of forming the basic LC unit challenges both experimentalists and theorists to further understand their physical properties. For example, little was known about the elastic constants and viscosities of LCLCs, and how external parameters, such as temperature and concentration would influence them. In the first section that follows, I will introduce our recent experimental studies on the temperature, concentration and ionic content dependences of the elastic constants and viscosity coefficients of LCLC materials. We explain our findings based on the model for lyotropic LCs composed of thin rods, which connects microscopic length and flexibility of the aggregates to the macroscopic elastic constants and viscosities of the system. We supplement this model with the idea that LCLC aggregates are flexible and can change their length and flexibility in response to external stimuli.

The unusually large difference between splay, bend and twist elastic constants found in the measurements turns out to be the key to understand a peculiar phenomenon in LCLC: the shape of disclinations in LCLC is azimuthally asymmetric, both in the far field, where the scalar order parameter $S$ is a constant, and in the core region, where $S$ decreases to zero, with the overall size of the disclinations over $10\mu m$ in radius. In Section 2, I will discuss our experimental measurements on the fine structure of disclinations. I will further explain our findings using Frank–Oseen model for far field, and Landau–de Gennes (LdG) model for the core region. The measured elastic constants from Section 2 provide us important fitting parameters for the models. The inability of the models to provide a more quantitative explanation lies in the fact that LCLCs have features not captured in existing models, such as the polydispersity of aggregates size, the possible coupling between size distribution and order parameter gradient, etc.
In Section 4, I will discuss our work on an active nematic system, called ‘living liquid crystals’ (LLCs), composed of motile bacteria in LLCs. I will present our results in two scenarios: when the nematic order dominates the dynamics of motile bacteria and when the bacterial activity competes with the nematic order to generate interesting patterns. We again explained the phenomena using the viscoelastic properties of LLCs measured in experiments.

LLCs are important materials for both scientific and applicational reasons. The formation of LLC order helped the discovery of DNA structure [11]. Short DNA and RNA oligomers were shown to form chromonic LC phases [7,12,13] that might have played a role in the prebiotic synthesis of long RNA [14,15]. LLCs have also found applications in real-time biosensors [16,17], polarisers [18,19], controlling nanoparticle self-assembly [20–22] and graphene orientations [23].

2. Elasticity and viscosity of LLCs

2.1. Temperature and concentration dependences of the elastic constants

We studied two representative LLC materials with two different techniques. The first material is the aqueous solutions of disodium salt of 6-hydroxy-5-[(4-sulfophenyl)azo]-2-naphthalenesulfonic acid, also known as sunset yellow (SSY) [24]. The study was performed in the nematic phase with \( T \) changing from 298 K to \( T_{ni} \) for three concentrations \( c = 29.0, 30.0 \) and 31.5 wt% (volume fraction \( \Phi = 0.18, 0.19 \) and 0.20, respectively). To determine the elastic constants, we used a magnetic field to induce director deformation in flat glass cells of thickness \( d = 20 - 25 \mu m \), and optical method to detect the director distortions [24]. The competition between diamagnetic and elastic energy provides information about the elastic constants (Frederiks effects). The glass substrates were rubbed with superfine abrasive paper (001 K Crystal BayTM Crocus Cloth, 3 M) for planar alignment, or unrubbed polyimide SE-7511 (Nissan) for homeotropic alignment.

The second material we studied is the water solution of asthma drug disodium cromoglycate (DSCG) [25]. The study was performed in the temperature range of 294 K to \( T_{ni} \) for four concentrations \( c = 12.5, 14.0, 16.0 \) and 18.0 wt% (volume fraction \( \Phi = 0.089, 0.100, 0.115 \) and 0.129, respectively). We measured the dynamic light scattering (DLS) on the thermal fluctuations of the director field in a planar cell of thickness \( d \approx 19 \mu m \). By evaluating the angular dependence of the depolarised scattering light intensity and its time correlation, we obtained the values of both elastic constants and viscosity coefficients corresponding to splay, bend and twist modes [25].

Figures 2 and 3 summarise the results from these experimental studies. The two materials show some common features of the elastic constants:

a. The values of \( K_1 \) and \( K_3 \) constants are both on the order of 10pN, similar to those of thermotropic LCs such as 4-n-pentyl-4’-cyanobiphenyl (5CB). The \( K_2 \) constants are typically 10 times smaller, \( K_2 \approx 1 \) pN, much smaller than that of 5CB.

b. All three constants \( K_1, K_2 \) and \( K_3 \) decreases as \( T \) increases, or as \( c \) decreases.

c. \( K_1 \) constant has the strongest temperature dependences as compared with \( K_2 \) and \( K_3 \). For example, in DSCG, \( K_1 \) decreases exponentially as \( T \) increases, following a universal law for all concentrations,

\[
K_1(T) \propto \exp(-\beta K T)
\]

where \( \beta K = 0.20 \pm 0.01 K^{-1} \) (Figure 3a inset). \( K_2 \) and \( K_3 \) change only linearly with \( T \) (Figure 3b and 3c).

d. The ratio \( K_1/K_3, K_1/K_2 \) both decreases with the increase of \( T \). \( K_3/K_2 \) for DSCG remains practically

![Figure 1. Chromonic molecules form linear stacks and nematic phase. LCLC molecules, represented here by (a, up) disodium cromoglycate and (a, middle) sunset yellow (SSY), are modelled as (a, down) rigid discs with charged group at the periphery. (b) The linear molecular stacks form nematic phase. Reprint from [10].](image-url)
constant over a wide range of temperature and concentrations. For SSY, \( K_3/K_2 \) also changes over a smaller magnitude as compared with \( K_1/K_2 \) in the tested \( T \) and \( c \) range.

To understand these features of the elastic constant, we first compare the experimental results with the predictions of the phenomenological LdG model [26]. Within the LdG model, the temperature dependences of Frank constants are determined by that of the scalar order parameter \( S \), namely, \( K_{1,2,3} \propto S^2 \) [26], implying \( K_1/K_3 \) and \( K_1/K_2 \) should be temperature independent. In experiment, especially for the case of DSCG, \( K_1 \) shows an obviously different temperature behaviour from \( K_2 \) and \( K_3 \). \( K_1/K_3 \) and \( K_1/K_2 \) for both SSY and DSCG strongly decrease with \( T \) at all concentrations.

We then turned to the Onsager type models developed for lyotropic LCs, based on the idea of excluded volume. In the simplest version, the building units are uniform rigid rods with the length-to-width ratio \( L/D \gg 1 \). The nematic order is caused by the increase of volume fraction \( \Phi \) over a critical value \( \Phi_c = 4.5D/L \): the rods sacrifice orientational freedom for translational freedom. The excluded volume theory [27] predicts the elastic constants of a system of rigid long rods as follows:

\[
K_1 = \frac{7}{8} \pi k_B T D \Phi \frac{L}{D}, \quad K_2 = K_1/3, \quad K_3 = \frac{4}{3\pi^2} \pi k_B T \Phi^3 \left( \frac{L}{D} \right)^3.
\]

Clearly, this model does not describe our experimental findings for LCLCs as well. First, in DSCG the measured \( K_2/K_1 \) can be as small as \(~0.03\) (\( c=18 \text{ wt}\%\), \( T \approx 294 \text{ K} \)), much smaller than the predicted constant value of 1/3. To explain the smallness of \( K_2 \), one may consider the electrostatic repulsion between surface-charged LCLC aggregates that tend to align them perpendicular to each other [28]. However, quantitative analysis showed that this ‘twisting effect’ only modifies \( K_2 \) by a few percent [25,29], and thus does not explain the small value of \( K_2 \) in experiments. Second, this model predicts

\[
\frac{K_3}{K_1} \approx \frac{1}{3} \Phi^2 \left( \frac{L}{D} \right)^2.
\]

Considering the volume fraction

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**Figure 2.** Temperature and concentration dependences of SSY elastic constants and their ratios. (a) \( K_1 \) and \( K_3 \), (b) \( K_2 \), (c) \( K_1/K_3 \) and (d) \( K_1/K_2 \) all decrease as \( T \) increases or \( c \) decreases. Reprint from [10].
corresponding to nematic phase, $\Phi / C_2^1 \Phi_c = 4.5D/L$, this infers $K_3/K_1 > 10$. In contrast, experiments show $K_3/K_1 \sim (1-3)$ for both DSCG and SSY (Figures 2 and 3).

This simple Onsager type model does not take into account that the aggregates are not rigid but rather flexible [27,30,31], which is characterised by a finite persistence length $\lambda_p$. Flexibility of LCLC aggregates is evident in recent numerical simulations [32,33] and is suggested by nuclear magnetic resonance measurements, where column undulation within the molecular stack involving 4–8 molecules was observed [34]. With flexible aggregates, the bend deformation is no longer inhibited by the contour length of the rods but followed by bending each rod in the system (Figure 4a). The bending energy of a single rod is $F_3 = \frac{1}{2} \kappa L \rho^2$, where $\kappa$ is the bending stiffness and $\rho$ the curvature [35,36]. For a rod suspension of volume fraction $\Phi$, the volumetric elastic energy density is then $f_3 = F_3 \Phi (4D^2L)^{-1}$. Using the relationship [35] $\lambda_p = \kappa / k_B T$ and $f_3 = \frac{1}{2} K_3 \rho^2$, one arrives at

$$K_3 = \frac{4 k_B T}{\pi D} \Phi \frac{\lambda_p}{D}$$  \hspace{1cm} (2)

With the typical experimental value of $K_3 = 10 \text{pN}$, $\Phi = 0.1$ and $D = 1.6 \text{nm}$ for DSCG [29], Equation (2) yields an estimate of $\lambda_p = 50 \text{nm}$. This value is close to the persistence length of double-stranded DNA (dsDNA) [7], which has structural parameters similar to the aggregate of DSCG (diameter ~2 nm, 6 ionisable groups per nanometre of length).

The splay constant $K_1$ is not affected by the flexibility of the rods but constrained by the contour length $L$. As pointed out by de Gennes [37] and explained by Meyer [38], splay deformation in a system of long rods creates local compressions and dilations that tend to change the density of the system. The constant-density constraint limits the freedom of rod ends in a splay deformation, which decreases the entropy (Figure 4b). A large $L$ implies a smaller number of free ends available to accommodate for splay, therefore a larger value of $K_1$. Following [39]:

$$K_1 = \frac{4 k_B T}{\pi D} \Phi \frac{L}{D}$$  \hspace{1cm} (3)

Using the experimental results of $K_1 = 5 \text{pN}$, $\Phi \approx 0.1$, $D = 1.6 \text{nm}$ for $c = 14 \text{wt} \%$ DSCG at $T = 297 \text{K}$ (3 K below $T_{ni}$), we find $L \approx 25 \text{nm}$, which compares well with previous estimate [40] of $L = 18 \text{nm}$ for the isotropic phase of the same concentration at 305 K, 5 K above $T_{ni}$.

Compared with splay and bend deformation, twist is the easiest, as it conserves density and requires no deformation of the aggregates. In an ideal case, flexible rods can be closely arranged in ‘pseudo layers’ with $\mathbf{n}$ uniform in each layer. As one goes along the surface normal to the adjacent layer, $\mathbf{n}$ changes by a
small angle (Figure 4c). Thermal fluctuation and non-ideal packing may put the flexible rods across pseudo layers to hinder the twist deformation, but the flexibility of the rods can relieve such interference by bending along local \( \hat{n} \). Therefore, \( K_2 \) is expected to be independent of \( \hat{L} \) and only weakly dependent on \( \lambda_p \) (as compared with \( K_3 \)). A more detailed model by Odijk [27] is as follows:

\[
K_2 = \frac{K_0 T}{D} \Phi^{1/3} \left( \frac{\lambda_p D}{D} \right)^{1/3} \tag{4}
\]

According to Equations (2) and (4), for typical values \( \Phi = 0.1 \), \( \lambda_p = 50 \text{ nm} \), \( D = 1.6 \text{ nm} \), we deduce \( \frac{K_0}{K_3} = \frac{A}{D} \left( \Phi \frac{D}{D} \right)^{-2/3} \approx 0.37 \), which qualitatively explains the small values of \( K_2 \), but is still far away from the experimentally observed \( \frac{K_0}{K_3} \approx 0.025 - 0.04 \) for DSCG, and \( \frac{K_0}{K_3} \approx 0.1 \) for SSY. A more accurate theory of \( K_2 \) is needed.

The Onsager type theory is essentially athermal as the behaviours are controlled exclusively by entropy. To explain the temperature dependences of \( K \) constants and their ratios, we need to further find the temperature dependences of \( \hat{L} \) and \( \lambda_p \) of the LCLC aggregates. Following the work of van der Shoot and Cates [41] on wormlike surfactant micelles, we estimated the average contour length \( \hat{L} \) as follows [24]:

\[
\hat{L} = L_0 \Phi^{5/6} \left( \frac{\lambda_p D}{D} \right)^{1/3} \exp \left( \frac{E + \varepsilon \Phi}{2k_B T} \right) \tag{5}
\]

where \( L_0 = 2\pi^{-2/3} \sqrt{a_s D} \) is a length characterising the size of a monomer, \( a_s \approx 0.34 \text{ nm} \) is the period of molecular stacking along the aggregate for both SSY and DSCG, and \( \varepsilon \approx 4k_B T \) is a constant describing the enhancement of aggregation by the excluded volume effect [41]. Comparing experimental data with Equations (3) and (5), we estimate that for DSCG, \( \hat{L} \) is in the range of (20–270) nm, and \( E_\alpha(\Phi, T) \approx (8 - 14)k_B T \) [25]; for SSY, the results are similar [24]. These results agree well with the estimates for SSY by Collings et al. [42], \( E_\alpha \approx 7k_B T \), and by Day et al. [43], \( E_\alpha \approx 11k_B T \), and for DNA oligomers [7] by Clark et al., \( E_\alpha \approx (4 - 8)k_B T \). Numerical simulations [33] showed that the persistence length \( \lambda_p \) of chromonic aggregates follows a linear relation:

\[
\lambda_p \propto 5 + 2.14E/k_B T \tag{6}
\]

In both SSY and DSCG measurements, \( K_1/K_3 = \hat{L}/\lambda_p \approx (0.25 - 1.2) \), implying \( \lambda_p \) on the same order of magnitude with \( \hat{L} \), which agrees well with the simulation results [33] \( L/\lambda_p \approx 1 \). Further, the exponential dependence of \( K_1 \) on \( \hat{L} \), linear dependence of \( K_3 \) on \( E \), and an even weaker dependence of \( K_2 \) on \( E \) explain the temperature dependences of the ratios between \( K \) constants:

\[
\frac{K_1}{K_3} \propto \Phi^{5/6} \exp \left( \frac{E + \varepsilon \Phi}{2k_B T} \right) \left( \frac{E}{k_B T} \right)^{-2/3} \tag{7}
\]

\[
\frac{K_1}{K_2} \propto \Phi^{3/2} \exp \left( \frac{E + \varepsilon \Phi}{2k_B T} \right) \tag{8}
\]
These equations imply that both $K_1/K_3$ and $K_1/K_2$ decreases when $T$ increases or $\Phi$ decreases, consistent with our measurements. The theory also indicates:

$$\frac{K_3}{K_2} \propto \Phi^{2/3} \left(\frac{h_0}{D}\right)^{2/3} \propto \Phi^{2/3} \left(\frac{E}{k_B T}\right)^{2/3}$$

(9)

implying that $K_3/K_2$ also decreases when $T$ increases or $\Phi$ decreases. However, for DSCG, $K_3/K_2$ remain practically constant for a wide range of $T$ and $\Phi$, and even decreases for $\Phi = 0.129$ (c = 18 wt%) at low $T$ (Figure 3f). Apparently, an improved theory is needed.

### 2.2. Viscosities

In the DLS experiments on DSCG, the viscosities of each deformation mode were measured from the time autocorrelation of the scattered light intensity [25]. Figure 5 summarises the results. The splay mode viscosity $\eta_{\text{splay}}$ is comparable with $\eta_{\text{twist}}$ and are both in the range of $(1 - 500)$ kgm$^{-1}$s$^{-1}$, while $\eta_{\text{bend}}$ is only $(0.007 - 0.03)$ kgm$^{-1}$s$^{-1}$. $\eta_{\text{splay}}$ and $\eta_{\text{twist}}$ show very strong temperature dependences, changing over 100 times when $T$ changes only 10 K, while $\eta_{\text{bend}}$ only weakly depends on $T$ and $\Phi$. Fitting the data with $\eta_{\text{splay}}(T) \propto \exp(-\beta_s T)$ and $\eta_{\text{twist}}(T) \propto \exp(\beta_t T)$ results in $\beta_s = 0.41 \pm 0.02 K^{-1}$, $\beta_t = 0.37 \pm 0.01 K^{-1}$. Note that $\beta_s \approx \beta_t \approx 2\beta_0$ (Equation 1). The ratio $\eta_{\text{splay}}/\eta_{\text{twist}}$ slowly increases from about 1 near the nematic to nematic-isotropic biphasic transition $T_{\text{NI}}$ to about 2 as $T$ decreases by 12 K.

The very large values of $\eta_{\text{splay}}$ and $\eta_{\text{twist}}$, their strong temperature dependences, and the big difference between $\eta_{\text{splay}} \approx \eta_{\text{twist}}$ and $\eta_{\text{bend}}$ are features not seen in thermotropic LCs, or lyotropic polymer LCs with length-fixed molecules. To understand these features, we follow the arguments put forward by de Gennes [44] and Meyer [31,38,45,46] for lyotropic nematic systems of flexible rods of ‘infinite’ length, $L / D \rightarrow \infty$. In this limit, twist deformation produces flow perpendicular to the director with the gradient along the director (Figure 4d). Energy dissipation rate in such flow field is estimated as $\dot{P} = \mu \frac{L^2}{12} \left(\frac{h_0}{D}\right)^2$, implying the effective viscosity for twist deformation as $\eta_{\text{twist}} \propto \frac{L^2}{D}$. Same analysis applies to splay deformation, resulting in $\eta_{\text{splay}} \propto L^2$. Compared with the theory of $K_1 \propto L$, $\eta_{\text{splay}} \propto \eta_{\text{twist}} \propto K_1^2$ is expected. Experimental results indeed show a scaling relation $\beta_s \approx \beta_t \approx 2\beta_0$ that matches this prediction. $\eta_{\text{bend}}$ is small, comparable to values of thermotropic LCs such as 5CB, and is insensitive to the change of $T$ and $\Phi$. This is because bend deformation only requires the aggregate to ‘slide’ parallel to each other [38,39,45,46], and therefore is not inhibited by the growth of $L$ as $T$ decreases or $\Phi$ increases.

### 2.3. Effect of ionic additives

The microscopic properties of LCLC aggregates, such as their contour length and persistence length, are the results of subtle balances of dispersive, hydrophobic and hydrophilic, depletion, and electrostatic forces. The main effects are the van der Waals attractions between the aromatic centres of the chromonic molecules, characterised by energy $E_a$, and the electrostatic repulsions between the charged groups at the surface of the aggregates, $E_e$. The difference between the two gives rise to the scission energy $E = E_a - E_e$, which determines the average length $L \propto \exp\left(\frac{E_a}{k_B T}\right)$ and persistence length $\lambda_p \propto \left(\frac{E_a}{k_B T}\right)$ of the aggregates. The ionic nature of the LCLC aggregates make them sensitive to the ionic environment in the solution. Previous studies have shown that the phase diagrams of LCLCs can be significantly shifted by ionic additives [8,9,48,49] (Figure 6a). Similar sensitivity is also expected on the viscoelastic properties of LCLCs.

We studied the elastic constants and viscosities of SSY as a function of various ionic contents. The SSY concentration is fixed at $c_{\text{SSY}} = 0.98$ mol/kg, corresponding to a volume fraction of $\Phi \approx 0.2$ [24], while the concentration of additives vary: monovalent salt sodium chloride (NaCl) changes from 0 to 0.9 m, divalent salt magnesium sulphate (MgSO$_4$) 0 to 1.2 m, and pH agent sodium hydroxide (NaOH) 0 to 0.2 m. The elastic constants show diverse responses to different additives. The splay constant $K_1$ increases when MgSO$_4$ is added but shows no response to the addition of NaCl (Figure 6b). The bend constant $K_2$ at a given temperature decreases when NaCl concentration increases, but increases when MgSO$_4$ concentration increases (Figure 6d). At a fixed relative temperature $\Delta T = T - T_{\text{NI}}$, both NaCl and MgSO$_4$ reduces $K_3$ (Figure 6e). $K_2$ behaves similarly to $K_3$ (Figure 6c). The rotation viscosity $\gamma_1$ increases only by a small factor as 0.9 m NaCl is added, but by up to 10 times when 1.2 m MgSO$_4$ is added (Figure 7). With and without additional additives, the scaling relation of $\gamma_1 \propto K_1^2$ holds (Figure 7 inset). Adding pH agent NaOH, even at small amount (0.01 mol/kg), causes all three elastic constants and the rotational viscosity to decrease dramatically. To explain these experimental results, we again resort to the theory of lyotropic nematic composed of flexible rods.

The chromonic aggregates are charged. With each LCLC molecule carrying two ionic groups on it edge (sulphonate for SSY, carbonate for DSCG) and stacking along the aggregate axis with a repeating distance $\alpha_z \approx 0.34$ nm, the maximum linear charge density reaches $\tau_{\text{max}}e \approx 6e/\text{nm}$ in a fully ionised state. The repulsion between like-charges gives rise to $E_e \propto \tau^2$. However, condensation of counterions reduces effective linear charge density from $\tau_{\text{max}}e \approx$
6e/nm to a level of \( e_i \approx Z/e_0 \), where \( Z \) is the valence of counter ions, and \( l_B = e^2/(4\pi\varepsilon_0 k_B T) \approx 0.7 \) nm is the Bjerrum length in water at 300 K \([50\text{–52}]\). Debye screening further reduces \( E_e \). Following MacKintosh et al. \([53]\), we estimate that \( E_e \) scales as

\[
E_e \propto \tau^2 \lambda_D^2
\]

where \( \lambda_D = \sqrt{\frac{e^2 \sum n_i q_i^2}{4\pi\varepsilon_0 k_B T}} \) is the Debye screening length, \( n_i, q_i \) are the number density and strength of the \( i \)th ions in solution, respectively. Comparing \( E_e \) in the original, 0.9 m NaCl added, and 1.2 m MgSO\(_4\) added SSY solutions, we have \( E_e^{NaCl} : E_e^{MgSO_4} = 1:0.72:0.10 \). Therefore, the total scission energy \( E \), assuming \( E_a \) not affected by the ionic environment, has the relation \( E^o < E^{NaCl} < E^{MgSO_4} \). This qualitatively explained the most significant increase of \( K_1 \) and \( \gamma_1 \) when MgSO\(_4\) is added into the system, since \( \sqrt{\gamma_1} \propto K_1 \propto L \propto \exp\left(\frac{E}{2k_B T}\right) \). Interestingly, \( \tau_{\text{max}} \approx 6e/nm \) is also found in the structure of ds-DNA. Even though ds-DNA cannot change their length due to the covalent bonded side chain, end-to-end attraction of short DNA strands has been observed in presence of divalent ion

\[\text{Figure 5. Temperature and concentration dependences of DSCG viscosities and their ratios. (a) } \eta_{\text{splay}}, \text{ (b) } \eta_{\text{twist}} \text{ (c) } \eta_{\text{bend}} \text{ and (d) } \eta_{\text{splay}}/\eta_{\text{twist}} \text{ decrease as } T \text{ increases and as } c \text{ decreases. Dashed lines in the horizontal axis indicate } T_n. \text{ Reprint from [25].}\]
Mg$^{2+}$ but not in presence of Na$^+$ [54]. Ionic additives are also known to change the aggregation length in self-assembled polyelectrolytes such as worm-like micelles [53,55,56].

Bend $K_3$ and twist $K_2$ constants are determined by the flexibility of the aggregates $\lambda_2$ (Equations (2) and (4)). When a rod undergoes bend deformation, the surface charges become closer, contributing a repulsive force...
against the bend. Increased ionic strength screens such like-charge repulsion, thus increases the flexibility of the rod. Adding NaCl into the system does not reduce $E$, evidenced by unaffected $K_1$ values, but still significantly reduces $K_3$ with this softening effect. Plot of $K_3$ against $\lambda r^2$ (tuned by $c_{\text{NaCl}}$) at each $\Delta T = T - T_n$ shows linear relations (Figure 6f). Similar effect of rigidity reduction has been studied on isolated ds-DNA molecules [57–59]. The Odijk–Skolnick–Fixman (OSF) model [60,61] predicted a reduction of $\lambda_r$ by 10% when $c_{\text{NaCl}}<0.05$M, while Manning’s approach [50–52] predicted a reduction of $\lambda_r$ by up to 45% for 0.1M $< c_{\text{NaCl}} < 1$M. Our experimental results fall in between the two predictions. Both models predict $\lambda_r \propto \lambda^2$, consistent with our experimental $K_3$ values and Equation (2). The effect of MgSO$_4$ on $K_3$ is more complex, since the increase of $E$ works against the softening effect of ionic screening. At a fixed temperature, the increase of $K_3$ is dominated by the increase of $E$, according to Ref. [33] and Equation (6) (Figure 6d). When evaluated at relative temperature $\Delta T = T - T_n$, the effect of added MgSO$_4$ is evidently in the reduction of $K_3$, Figure 6(e), in agreement with the idea of salt-induced screening of the surface charges that make the aggregates more flexible.

Adding NaOH into the solution significantly increases the pH and destabilises the nematic phase. High pH increases the degree of ionisation $\tau$ of the sulfonate groups [9,62], thus enhancing electrostatic repulsions of the molecules and reduces $E$. As a result, all $K$-constants and rotation viscosity $\gamma_1$ decreases.

As a summary of Section 2, LCLCs have shown unique viscoelastic properties as compared with other LCs. The pronounced differences between elastic constants and viscosity coefficients, their strong temperature dependences, and diverse responses to ionic contents can be attributed to the fact that LCLCs are composed of reversible aggregates, whose length and flexibility are sensitive to external stimuli.

3. Fine structures of topological defects: a study of disclinations in DSCG

One of the most challenging tasks in condensed matter physics is to measure and understand the fine structures in the core region of defects, where the deformations of order parameters are so strong that phenomenological models valid in far-field fails. For example, in the case of topological defects in hard and soft matters, such as dislocations and disclinations, the gradient energy becomes comparable with the condensation energy only at atomic/molecular length scale. Small size made it practically impossible to experimentally examine the defects with optical or even electronic microscopy [63–65]. Theoretical models [66–68] often treat the cores with several simplifying assumptions, such as angular and radial independence of the order parameters inside and outside of the core region. For disclinations in nematic, the cores are usually treated as an isotropic melt of cylindrical shape, with a constant amplitude of order parameters outside of the isotropic melt.

LCLCs provide us unique opportunities to explore the fine structures of disclinations in the nematic phase. Disclinations in LCLCs extends over tens of micrometres in size, large enough for optically exploring their spatial variation. In the experiments, we confine 15wt% DSCG between glass substrates that impose degenerate tangential orientation of the director $\bar{n}$. By quenching the $\sim 5$μm thick sample from isotropic phase to nematic, we create a network of 1/2 and $-1/2$ topological defects, with their axis orientated perpendicular to the substrates. We studied well-separated disclinations using LC-PolScope microscopy [69] that maps $\bar{n}$ and optical retardation $\Gamma$ in 2D. To describe the shape of the disclination core, we setup polar coordinates $(r, \theta)$ centred at the isotropic melt; the azimuthal angle $\theta$ is measured from the radial director $\bar{n} \parallel \hat{r}$. The director field around each disclination reorients by $\pi$ (defects of strength $m = 1/2$) or by $-\pi$ ($m = -1/2$), when one circumnavigates the core once. The spatial variation of $\bar{n} = (\cos \phi^{(m)}, \sin \phi^{(m)}, 0)$ is described by its azimuthal orientation $\phi^{(m)}(r, \theta)$, where $\phi^{(m)}(r, \theta) = m\theta + \phi^{(m)}(r, \theta)$ is a combination of linear term $m\theta$ and a periodic anisotropic function $\tilde{\phi}^{(m)}(r, \theta)$. It is convenient to further examine $\tilde{\phi}^{(m)}(r, \theta)$ by its Fourier harmonics $\tilde{\phi}^{(m)}(r, \theta) = \tilde{\phi}_1^{(m)}(r) \sin \theta + \tilde{\phi}_3^{(m)}(r) \sin 3\theta$. Similarly, we examine spatial distribution of optical retardation $\Gamma \propto \Delta n \propto S$ by its Fourier harmonics: $\Gamma^{(m)}(r, \theta) = \Gamma_0^{(m)}(r) + \Gamma_3^{(m)}(r) \cos 3\theta$. Here the lowest order harmonic $\Gamma_0^{(m)}(r)$ describes the size of the disclination, and higher order terms $\Gamma_1^{(m)}(r)$ and $\Gamma_3^{(m)}(r)$ characterised the shape.

The following features of the disclination core are found in the experiments [70], Figure 8:

1. In the far field from the core, $r>20$μm, $\Gamma_0^{(1/2)}(r, \theta) = \Gamma_1^{(1/2)}(r, \theta) = \Delta nd$ are constant. $\tilde{\phi}_1^{(1/2)}(r, \theta) = \tilde{\phi}_3^{(1/2)}(\infty) \sin \theta$ and $\tilde{\phi}_3^{(1/2)}(r, \theta) = \tilde{\phi}_3^{(1/2)}(\infty) \sin 3\theta$, where $\phi_1^{(1/2)}(\infty) \approx 14^{\circ}$ and $\phi_3^{(1/2)}(\infty) \approx -3.5^\circ$ are $r$-independent constants for 1/2 and $-1/2$ disclinations.

2. Near the centre of disclinations, $r<20$μm, $\tilde{\phi}_1^{(-1/2)}(r)$ and $\tilde{\phi}_3^{(-1/2)}(r)$ are radius dependent
and decreases to 0 as \( r \to 0 \). Optical retardation field can be described as 

\[
\Gamma^{(1/2)}(r, \theta) = \Gamma_0^{(1/2)}(r) + \Gamma_1^{(1/2)}(r) \cos \theta, \quad \Gamma^{(-1/2)}(r, \theta) = \Gamma_0^{(-1/2)}(r) + \Gamma_3^{(-1/2)}(r) \cos 3\theta,
\]

and show distinct shapes for \( 1/2 \) and \(-1/2\) disclinations, both deviate significantly from the azimuthally symmetric cylindrical shape. \( 1/2 \) disclination has a cusp-like region, quantitatively described by the \( \Gamma_1^{(1/2)}(r) \) term, which can be up to 20% of the zero harmonic \( \Gamma_0^{(1/2)}(r) \). \(-1/2\) disclination has three cusp-like regions, described by the \( \Gamma_3^{(-1/2)}(r) \) term that can be about 7% of \( \Gamma_0^{(-1/2)}(r) \).

**Figure 8.** Experimentally determined fine structure of disclination cores in chromonic nematic. Both \( m = 1/2 \) and \( m = -1/2 \) disclinations show azimuthally asymmetric shapes in (a,b) the director field \( \vec{n} \) and (c,d) optical retardance \( \Gamma \). Fourier analysis of the anisotropic function of the azimuthal orientation of \( \vec{n} \) shows that (e) the first harmonic \( \tilde{\phi}_1^{(1/2)} \) for \( m = 1/2 \) and (f) the third harmonic \( \tilde{\phi}_3^{(-1/2)} \) for \( m = -1/2 \) are both functions of radial distance \( r \) and vanishes as \( r \to 0 \). (g,h) Fourier analysis of \( \Gamma(r, \theta) \) reveals the non-cylindrical shape of the cores with one and three cusp-like regions for \( m = 1/2 \) and \( m = -1/2 \) disclinations, respectively. Experimental data were shown as discrete points with error bar, while theoretical fitting shown with dotted and dashed lines. Reprint from [70].
To understand these features, we resort to various theories that describe the distorted orders parameters in a nematic LC. In the far field, where scalar order parameter \( S \propto I \) is a constant, the director field \( \mathbf{n} \) is characterised by the Frank–Oseen elastic energy density:

\[
f_{\text{FO}} = \frac{1}{2} K_1 (\text{div} \mathbf{n})^2 + \frac{1}{2} K_2 (\mathbf{n} \cdot \text{curl} \mathbf{n})^2 + \frac{1}{2} K_3 (\mathbf{n} \times \text{curl} \mathbf{n})^2
\]

(11)

Dzyaloshinsky [66,71] demonstrated that the behaviour of \( \phi(\theta) \) is governed by the nonlinear differential equation [66,72]:

\[
\frac{\partial^2 \phi}{\partial \theta^2} [1 - \epsilon_k \cos 2(\phi - \theta)] - \left[ 2 \frac{\partial \phi}{\partial \theta} - \left( \frac{\partial \phi}{\partial \theta} \right)^2 \right] \epsilon \sin 2(\phi - \theta) = 0
\]

(12)

where \( \epsilon_k = (K_3 - K_1)/(K_1 + K_3) \) is the splay-bend elastic anisotropy. Solving Equation (12) in the Fourier space of \( \theta \) results in the following relation between \( \epsilon_k \) and the main harmonics \( \tilde{\phi}_1^{(1/2)} \) and \( \tilde{\phi}_3^{(-1/2)} \) of the anisotropy function \( \tilde{\phi}^{(m)} \) [70]:

\[
\epsilon_k = \frac{4\tilde{\phi}_k^{(m)}}{4k^2 - 1}
\]

(13)

where \( k = 2(1 - m) \). From the experimental results of \( \tilde{\phi}_1^{(1/2)}(\infty) \approx 14^\circ \) and \( \tilde{\phi}_3^{(-1/2)}(\infty) \approx -3.5^\circ \), we determined the splay-bend elastic anisotropy as \( \epsilon_k = 0.34 \) and \( \epsilon_k = 0.44 \), when \( m = 1/2 \) and \( m = -1/2 \) were analysed, respectively. These values match well with the independent study of the elastic constants discussed before [25], which yields \( \epsilon_k = (0.33 - 0.52) \).

The Frank–Oseen description of energy density assumes constant scalar order parameter \( S \), which is no longer valid near the core of the disclination, as demonstrated by Lyuksyutov [67] and Schopohl and Sluckin [68]. As \( r \to 0 \), \( S \) gradually decrease to 0 in an azimuthally asymmetric way, accompanied by the vanishing of anisotropic function \( \tilde{\phi}^{(m)}(r, \theta) \). To understand the coupling between the change of \( S \) and \( \mathbf{n} \), we turn to the LdG model that describes uniaxial nematic with a traceless symmetric tensor order parameter [26,73]:

\[
Q_y = S(\hat{n}_i\hat{n}_j - \delta_{ij}/3)
\]

(14)

Energy density associated with the gradient terms of \( Q_y \) writes [74–77]:

\[
f_g = L_1 Q_{g,k}Q_{g,k} + L_4 Q_{g,i}Q_{g,k} + L_2^{(3)} Q_{g,i}Q_{g,k}Q_{g,i} + L_3^{(3)} Q_{g,i}Q_{g,k}Q_{g,i}Q_{g,i}
\]

(15)

where \( L_n \) are the elastic constants, and \( \partial_k = \partial/\partial x_k \) are the spatial derivatives. Comparing \( f_{\text{FO}} \) and \( f_g \) results in the following relations between the elastic constants:

\[
K_1 = 2S^2(2L_1 + L_3) - S^2L^{(3)}/2
\]

(16)

\[
K_2 = 4S^2L_1
\]

(17)

\[
K_3 = 2S^2(2L_1 + L_3) + S^2L^{(3)}/2
\]

(18)

from which we deduce \( K_1K_3 = 2 + \epsilon_k \). Using the experimentally measured values of elastic constant discussed above, we get \( L_4/L_1 \approx 40 \). The Q-tensor field of a disclination is determined by minimising the functional \( F = \int f_g dV \).

Fitting with the experimental data qualitatively explained the azimuthal asymmetry of the disclination core (Figure 8e–h). This result also allowed us to estimate the width of nematic–isotropic interfaces when the core fully melt into an isotropic domain [70]. When \( \mathbf{n} \) aligns perpendicular to the interface, the width \( w_p \propto \sqrt{6L_1 + 4L_3} \), and when tangential \( w_t \propto \sqrt{6L_1 + L_3} \). Difference of the two is caused by the ‘anisotropy’ constant \( L_4 \). Due to the very large difference between \( K_1 \approx K_3 \) and \( K_2 \) constant, \( L_4/L_1 \approx 40 \) exceeds most thermotropic LCs, and leads to \( w_p/w_t \approx 2 \). This indeed is consistent with experimental measurement of the nematic–isotropic interface width, where \( w_t \approx 4.0 \mu \text{m} \) and \( w_p \approx 8.5 \mu \text{m} \) were observed [70,78].

LCLCs allowed us to experimentally measure the core structure of the disclinations in nematic phase. As explained earlier, the aggregate nature makes \( K_1 \) and \( K_3 \) one order of magnitude larger than \( K_2 \). This anisotropy of elasticity, equivalent to a large \( L_4/L_1 \) value in the LdG theory, is responsible for the strong coupling between \( S \) and \( \mathbf{n} \) field that causes the azimuthally asymmetric shape of the disclination cores. In a more intuitive picture, one might imagine that strong distortion around the disclination ‘breaks’ the aggregates into smaller pieces, since the scission energy \( E \) between LCLC molecules is only on the order of \( 10k_B T \). Or, the strong distortion creates a gradient of size distribution around the core, since the aggregates length is polydisperse and fluctuating. These degrees of freedom are beyond the current frame work of theoretical description of nematic order. Therefore, it is hard to expect a better agreement between the experimental observation and the LdG model.

## 4. Living liquid crystals

One useful feature of LCLCs compared with other LCs is their intrinsic compatibility with biological systems. Unlike thermotropic LCs that do not mix with water,
or the surfactant-based lyotropic LCs that are typically antiseptic. LCLCs were shown to be harmless to bacteria [79] and have enabled applications such as real-time biosensors [16,17]. Combining DSCG with living bacteria *B. Subtilis*, we create a new active matter system that demonstrated a wealth of interesting phenomena, such as director guided bacteria motion, birefringence-enabled visualisation of bacteria flagella beating, local melting of nematic LC by bacteria induced shear flow, cargo particle transportation, activity triggered two-stage pattern formation [80,81], and new tumbling behaviour of bacteria in nematic environment [82]. We explain these phenomena by the unique viscoelastic features of LCLCs, and by the competition between activity and nematic order in the system.

The mixture of DSCG LCLC and rod-shaped bacteria *B. Subtilis* were injected into a thin cell that provides either unidirectional planar anchoring [80,81], or homeotropic anchoring at the substrates [82]. We used polarising, phase contrast, and LC-PoLoScope microscopy to take images and videos, and particle tracking velocimetry to characterise the bacteria motion. The data were analysed using in-house MATLAB code. The representative results are discussed below.

*Bacillus Subtilis* are known to ‘run-and-tumble’ in isotropic media. This random motion in a 2D confinement was also observed in our experiment when the DSCG LC is heated to isotropic phase. In the nematic phase, however, bacteria swim along the director, and therefore follow prescribed trajectories. In a unidirectional planar cell, they move along straight lines (Figure 9a). When the LC is partially melted into isotropic phase, bacteria follow curved director field tangential to the nematic–isotropic interface (Figure 9e). Later work by Peng et al. shows that one can command the bacteria motion by surface patterning the director field [83].

A closer examination of the motile bacteria in nematic reveals great details of their motion. From the birefringent patterns created by flagella rotation and body counter-rotation, we could characterise the bacteria swimming mechanics (Figure 9c and 9d). We find that the pattern at the wake has a period of ~2 μm, matching the pitch of flagella helix measured in other studies, p = 2.2 μm. The strong shear flow caused by flagella rotation can trigger nematic–isotropic phase transition when the system is slightly overheated above $T_{n_i}$, creating a bacteria version micro- ‘Wilson chamber’ (Figure 9f).

The coupling between flagella motion and local nematic order not only makes the visualisation possible but also the swimming more efficient. The flagella rotate in DSCG at about 16Hz, 10 times slower than in water, but still propel the bacteria at a comparable speed of 15 μm/s, vs. 21 μm/s in water. The swimming efficiency, $df/v \approx 2.5$, is much better in nematic DSCG than in water $df/v \approx 17$. In water, bacteria can propel themselves because the drag coefficient perpendicular to the flagella segment is about two times the drag coefficient along the segment [84]. In DSCG, as discussed earlier, the viscosity is orders of magnitude larger if the shear flow is perpendicular to director, corresponding to $\eta_{\text{bend}}$ than when the shear flow is parallel to director, corresponding to $\eta_{\text{twist}}$. This additional anisotropy contribution is likely to provide more thrust to the bacteria and lead to a more efficient swimming in nematic DSCG. A more detailed analysis and nematodynamic simulation is needed.

To study the flow field of bacteria, we place passive particles on the bacterial trajectories predetermined by $\hat{n}$. We observe that the interaction between particle and bacterium starts at very long distance, about 50–80 μm along $\hat{n}$. The bacterium can keep pushing the particle for tens of seconds to displace it tens of micrometre away from its original location. In contrast, a particle placed 1–2 μm away from the trajectory received little influence (Figure 10a). These observations suggest that flow streamlines are strongly confined along $\hat{n}$, coaxial with the bacterial body. To obtain further insight, we reconstruct the flow filed generated by a localised bacteria from the birefringent pattern, using the nematodynamic theory [26] (Figure 10b). The flow field decays over tens of μm along $\hat{n}$ but very rapidly across $\hat{n}$, in good agreement with the observed particle-bacteria interaction through long-range axial flow. An intuitive understanding again comes from the anisotropy of viscosity in DSCG: since the viscosity perpendicular to $\hat{n}$ is orders of magnitude larger than along $\hat{n}$, the flow generated by a swimming bacterium is stretched along $\hat{n}$ and becomes long ranged.

So far, we discussed phenomena on well separated, individual bacterium, whose behaviour is dominated by the nematic environment. When the concentration of bacteria increases, the director distortion created by each of them starts to couple, resulting in a globally changed director orientation. We saw two transitions starting from the uniform state, $\hat{n} = \text{const}$, when activity is absent, Figure 11a–b. When small amount of activity is introduced (by low bacteria concentration $c_{\text{bac}}$), the director experiences bend modulation of a characteristic length scale $\xi$ (Figure 11c–e). When the cell gap $h$ decreases, or when $c_{\text{bac}}$ (hence activity) increases, $\xi$ decreases (Figure 11h). At higher activity (with increased $c_{\text{bac}}$), a secondary transition, marked by generation of pairs of 1/2 and $-1/2$ disclinations in the tightly bend
Figure 9. Individual bacterium motion in nematic LLC DSCG. (a) A motile bacterium *Bacillus Subtilis* swims along straight line in a shallow cell with unidirectional planar alignment. (b) Flagella motion causes reduction of optical retardance, imaged by LC-PolScope. (c,d) Time evolution of patterns around a swimming bacterium reveals important dynamic parameters, such as rotation frequencies of flagella and body. (e) Bacterium follows curved director filed induced by the nematic–isotropic interface. (f) Bacteria ‘Wilson chamber’: a motile bacterium triggers local nematic–isotropic phase transition and leaves behind a trace of isotropic tactoids. Scale bar 5 μm (a,b), 2 μm (c), 10 μm (e) and 20 μm (f). Reprint from [80].

Figure 10. Cargo transportation by swimming bacteria in nematic LC. (a) A motile bacterium (marked by red dashed ellipse) pushes a tracer particle (green dashed circle) from tens of μm away and transport it over extended time and distance. Particles located slightly off the trajectory (solid blue circles) are not affected. (b) Reconstructed flow velocity field near a localised bacterium in nematic DSCG indicates a long-distance extension along bacterial body axis and a tight compression in orthogonal directions. Reprint from [81].
regions. The disclinations start to move and creates a turbulent state, even though the Reynolds number remains low (Figure 11f and 11g). The disclinations are constantly being generated and annihilate with each other, similar to the recent experiments in active nematic composed of microtubule bundles [85].

The emergence of $\xi$ and its dependence on cell thickness and activity can be understood by the balance between reorienting torque of the director caused by bacterial flow, $-\alpha_0 c_{bac} U_0 \vartheta/(h)$, and the restoring torque by nematic elasticity $-K \frac{\partial^2 \vartheta}{\partial x^2}$ (Figure 11i). The balance results in a coherence length $\xi = \sqrt{\frac{kh}{\alpha_0 c_{bac} U_0}}$. Similar theoretical argument of bend instability in active nematic has been put forward by Ramaswamy [86]. This relation fits well with the experimental data on periodicity of stripe pattern as a function of $c_{bac}$ and $h$ (Figure 11h). Note that bacteria collective motion in

---

**Figure 11. Emergence of a characteristic length $\xi$ in LLCs.** (a,b) LLCs adapt uniform director field when activity is absent. Bacteria (highlighted by yellow ellipses) align parallel to director. (c,d) Active bacteria causes periodic bend in the director field. (e) Proliferation of stripe patterns in a sample of thickness $h = 20 \mu m$ and low concentration of bacteria, $c_{bac} \approx 0.9 \times 10^9$ cell/cm$^3$. (f) When $c_{bac}$ increases to $1.6 \times 10^9$ cell/cm$^3$ in a thicker sample $h = 50 \mu m$, LLCs patterns evolve from uniform bend to topological turbulence state at high-$O_2$ area, with generations of $1/2$ and $-1/2$ disclinations, highlighted in (g). The characteristic wavelength $\xi$ of the bend stripes fits well with the theory, $\xi = \sqrt{\frac{kh}{\alpha_0 c_{bac} U_0}}$. Inset shows the collapse of the data onto a universal behaviour following the theoretical model. (i) Bacteria-generated flow field realign the LC director by an angle $\vartheta$. Scale bar 50 $\mu m$ (a–d), 100 $\mu m$ (e–g). Reprint from [80].
isotropic media also creates patterns with similar disclinations, but $\chi_{\text{bac}}$ required there is about 10 times larger than in LLCs. In the nematic environment, their interactions are mediated by nematic elasticity and anisotropic viscosity, therefore becomes long ranged.

The LLCs demonstrates a wealth of phenomena not observed either in suspensions of bacteria in Newtonian fluid, or in passive ordered fluids. On one hand, LLCs show a new way to control active particles for useful tasks by harnessing anisotropy of the media [83, 87]. On the other hand, LLCs establishes a platform where the interaction of activity and orientational order can be explored systematically. The optical birefringence of the LC media can be a useful tool to characterise the swimming mechanism of microorganisms as well.

5. Conclusions

In this review, we discussed some interesting features of LCLCs, including their viscoelastic properties, the fine structures of disclination cores, and intriguing phenomena in the active system based on LCLCs and bacteria. The macroscopic properties of the system, such as elastic constants and viscosities, are controlled by their microscopic features, i.e. the length and flexibility of the molecular aggregates. These basic units responsible for nematic order are not molecules or particles fixed in size and shape by covalent bond, but only assembled by weak interactions on the order of $10k_BT$. This allows their size and flexibility to change easily as external factors, such as temperature, concentration, ionic content, or pH in the solution change. The non-surfactant nature of LCLC systems allows them to host biological entities such as bacteria and become active. The active system demonstrates some unique phenomena due to the interactions between activity and nematic order.

The viscoelastic properties of the LCLCs also help people understand other new phenomena in LCLCs. The smallness of $K_2$ is the key to understand director distortions in droplet and capillaries where a surprisingly large splay-splay $K_{24}$ constant was deduced [88–91]. It is also responsible for the spontaneous chiral symmetry breaking in nematic tactoids [92], based on which ultra-sensitive chiral molecular sensor is made possible [93]. Director distortions around colloidal particles couple orientational fluctuation of nematic LC to the thermal motion of the particle [94–96]. The very long crossover time from sub-diffusive to diffusive particle motion in LCLCs is explained by the slow relaxation of twist mode, due to the small $K_2$ and large $\eta_{\text{twist}}$ values [97].

Living LC systems were also realised in combination of DSCG with other bacteria. Mushenheim et al. use DSCG to guide *Proteus mirabilis* motion in confinement [98], and to assemble them by nematic elasticity [99] and by nematic–isotropic interfaces [100]. Trivedi et al. demonstrated bacterial transport of non-motile eukaryotic cells and polymer microparticles in the same system [101]. The contact time between *Proteus mirabilis* and particle is over 2500 times greater than in water, resulting in over 2000 body length delivery distance in a programmed fashion.

Despite many recent progresses in understanding LCLCs and using them for new scientific exploration and applications, much remains to be explored. Theoretical models so far only consider the average aggregates length, leaving the role of polydispersity unclear in controlling their phase behaviour, in their viscoelastic properties, and in defect structures. The microscopic origin of elastic constants, especially for unusually large $K_{24}$ modulus, remains unclear. Experimentally, aligning LCLCs remains a challenging task [102] as compared with aligning thermotropic LCs. Complex processes, such as photo patterning [103] and graphene deposition [104], are often required, hindering a more comprehensive use of LCLCs for scientific and application purposes. A greater potential of LCLCs as feature-rich multifunctional materials, and as hosts of biological active matter system can be expected.

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