Long-time anomalous swimmer diffusion in smectic liquid crystals

Claudia Ferreiro-Córdova,1 John Toner,2 Hartmut Löwen,3 and Henricus H. Wensink1

1Laboratoire de Physique des Solides, Université Paris-Sud & CNRS, UMR 8502, 91405 Orsay, France
2Department of Physics and Institute of Theoretical Science, University of Oregon, Eugene, OR 97403, USA
3Institut für Theoretische Physik II: Weiche Materie, Heinrich-Heine-Universität Düsseldorf, Universitätsstraße 1, 40225 Düsseldorf, Germany

(Dated: May 21, 2018)

The dynamics of self-locomotion of active particles in aligned or liquid crystalline fluids strongly deviates from that in simple isotropic media. We explore the long-time dynamics of a swimmer moving in a three-dimensional smectic liquid crystal and find that the mean-square displacement (MSD) transverse to the director exhibits a distinct logarithmic tail at long times. The scaling is distinctly different from that in an isotropic or nematic fluid and hints at the subtle but important role of the director fluctuation spectrum in governing the long-time motility of active particles. Our findings are based on a generic hydrodynamic theory and Brownian dynamics computer simulation of a three-dimensional soft mesogen model.

I. INTRODUCTION

The main focus of research in the active matter physics community has recently shifted towards studying microswimming through complex media that can no longer be re-presented by a simple isotropic Newtonian continuum [1]. The main motivation stems from the fact that many microorganisms operate in crowded environments with a non-uniform positional and/or orientational microstructure that may generate liquid crystalline or viscoelastic properties. Examples encompass the dynamics of cilia and spermatozoa in mucus [6,7], of bacteria migrating through tissue [8], or through complex extracellular matrices such as in biofilms and the motion of nematodes residing in soil [9].

These real-life situations call for more sophisticated models for microswimming that aim at a better understanding of the complexity of the medium, such as in the case of viscoelastic fluids [10–20], or liquid crystalline fluids [18, 21–30]. A similar increase in medium complexity is attained by considering active locomotion around random or patterned obstacles [31–33], and by studying the role of active dopants in crystalline host systems [34–36].

With most approaches thus far focussing on collective properties or on short-term swimmer motility, we wish to address the impact of liquid crystalline order on the long-time diffusive behavior of such a swimmer. In a previous paper [23], we have undertaken such a study by focussing on active diffusion through a simple Lebwohl-Lasher lattice nematic. Here, we wish to build upon these findings on active diffusion through tissue [8], or through complex extracellular matrices such as in biofilms and the motion of nematodes residing in soil [9].

Since the typical scaling exponent for a smectic fluid differs from that of a nematic system, measurement of the swimmer MSD transverse to the main director of the host could be used to probe structural features of the medium, in particular the presence of local lamellar order. Of course, to observe this difference, experiments must probe times $t > t_a$, since the scaling for shorter times is the same in both the smectic and nematic phases. In many experimental systems, this will be quite difficult: because of the exponential dependence of the crossover time $t_a$ [23] on material parameters and swimming speed, this time will be literally astronomical in many cases (see the estimates after equation (58) below). The best hope of seeing the $t > t_a$ limit of (1) is for very fast swimmers ($v \sim 50 \mu\text{m sec}^{-1}$) in very high dilution lyotropic smectics (see the estimate below for such smectics).
In our simulations, we circumvent this difficulty by simulating non-momentum conserving dynamics, which, although unphysical for real experiments, reduce the crossover time to extremely small values. The asymptotic form of (1) for \( t \gg t_o \) is unchanged by this change in the dynamics; it is simply reached at much shorter times. And, indeed, these simulations agree with our theoretical predictions which underscores the fundamental impact of director fluctuations in steering swimmers through liquid crystalline backgrounds.

The rest of this paper is structured as follows. In Section II we briefly recapitulate our hydrodynamic theory of swimmer motility in anisotropic media and provide new results for the long-time swimmer dynamics in a three-dimensional smectic phase. These predictions are generic and are valid for swimmers in both thermotropic and lyotropic smectic hosts. The predictions are tested against Brownian dynamics computer simulations based on a soft-nematic model which is described in detail in Section III. In the last Section, we formulate the main conclusions of our study.

II. MODEL FOR LONG-TIME SWIMMER MOTILITY

In very close analogy with earlier treatments of swimmers in nematics [23], we will consider a self-propelled swimmer moving through an otherwise equilibrium, ordered smectic A. This swimmer has no memory, or, at best, only a short term memory, of its past direction of motion. Furthermore, the dynamics of the entire system (nematic plus swimmer) are rotation invariant: that is, the swimmer carries no internal “compass”; any preference it exhibits for one direction of motion over any other must arise from the local layer normal \( \hat{n}(r, t) \) at the current location \( r_s(t) \) of the swimmer. This requirement of locality arises from the physically reasonable assumption that the interactions of the swimmer with the surrounding nematic are short-ranged in space.

The average value of the instantaneous velocity \( dr_s(t)/dt \) of such a swimmer must be along \( \hat{n}(r_s(t)) \); rotation invariance plus locality allow no other direction (except \( -\hat{n}(r_s(t)) \); we will discuss this option below). Hence, the instantaneous velocity \( dr_s(t)/dt \) must be given by

\[
\frac{dr_s(t)}{dt} = v_s \hat{n}(r_s(t), t) + f(t),
\]

where \( f(t) \) is a zero mean random fluctuation in the velocity, and \( v_s \) is the mean speed of the swimmer. Note that in general \( v_s \neq v_s^0 \), where \( v_s^0 \) is the “bare”, or instantaneous, speed of the swimmer, due to the effects of fluctuations. Indeed, in general, we expect \( v_s < v_s^0 \). In practice, \( v_s \) can only be determined by measuring the mean motion of the swimmer over long times; this will be discussed in more detail below.

The statistics of the fluctuations \( f \) are also almost completely determined by the requirements of rotation invariance and locality in space and time. In a “coarse-grained” theory, in which we imagine having averaged our dynamics over time scales long compared to the time of individual molecular “kicks” experienced by the swimmer, but short compared to the time scales we wish to investigate, \( f \) can be thought of as a sum of a large number of random molecular kicks at different microscopic times, which are therefore statistically independent. The central limit theorem then tells us that the statistics of \( f \) should be Gaussian. Its statistics are then completely specified by its two point correlations with the local layer normal \( \hat{n}(r, t) \) and itself; rotation invariance and spatiotemporal locality imply that these are given by:

\[
\langle f_\alpha(t) f_\beta(t') \rangle = 2\Delta_I \delta_\alpha\beta \delta(t - t') + 2\Delta_A n_\alpha(r_s(t), t) n_\beta(r_s(t), t) \delta(t - t'),
\]

and

\[
\langle f_\alpha(t) n_\beta(r_s(t'), t') \rangle = 2\Delta_f \delta_\alpha\beta \delta(t - t'),
\]

where \( \alpha \) and \( \beta \) are Cartesian indices, and \( \Delta_I \), \( \Delta_A \), and \( \Delta_f \) are phenomenological parameters which set the size of the fluctuations of the swimmer. Because the swimmer is a non-equilibrium agent, these parameters do not, in general, satisfy any kind of Einstein relation; that is, they are independent parameters.

The model just described neglects “hairpin turns”: fluctuations in which the swimmer reverses its direction of motion relative to the layer normal (that is, where it makes an angle of more than 90° with the director). As discussed in [23], such turns are strongly suppressed if the “energy barrier” \( \Delta E \) against a reversal of the swimmer direction of motion (that is, the energy cost of the swimmer making an angle of 90° with the layer normal) is large compared to the thermal energy; i.e., if \( \Delta E \gg k_B T \). We have chosen our parameters to ensure this condition in our simulations. Indeed, we have never observed a hairpin turn in our simulations. More importantly, we also expect that in many real experiments, deep within the smectic phase and for a strongly aligned swimmer, \( \Delta E \gg k_B T \), so hairpins should be rare, if not non-existent, as well.

We now proceed to analyze the implications of this theory for the motion of the swimmer. We will start with the mean position. Taking the average of Eq. (3), and recalling that \( \langle f \rangle = 0 \), we immediately obtain an expression for the mean position of the swimmer:

\[
\langle r_s(t) \rangle = v_s t \hat{n},
\]

where we have taken the mean direction of the layer normal \( \hat{n} \) to be along \( \hat{z} \), and the mean swimmer speed in the \( z \) direction is given by \( v_z = v_s |\hat{n}| \). Thus, the mean motion of the swimmer is purely ballistic. Note that the speed \( v_z \) of this motion is not \( v_s \), due to the fact that fluctuations reduce \( \langle \hat{n} \rangle \) below 1. Indeed, the speed \( v_z \) can not even be predicted by the continuum theory developed below, since the fluctuations which dominate this reduction are predominantly short wavelength, and therefore not
accurately described by the continuum, long-wavelength hydrodynamic theory of smectics. Nonetheless, we have still made a universal scaling prediction: the mean motion of the swimmer is ballistic, as shown by Eq. (6).

We now turn to the fluctuations about this mean. Consider first the mean squared lateral displacement of the swimmer:

\[ \langle (\Delta r_s^\perp(t))^2 \rangle \equiv \langle |r_s^\perp(t) - r_s^\perp(0)|^2 \rangle , \]  

(7)

perpendicular to the mean director of the smectic. Here and throughout this paper, \( \perp \) and \( \parallel \) denote directions perpendicular to, and along, the layer normal, respectively.

Using the projection of our equation of motion Eq. (3) perpendicular to the mean layer normal direction \( \hat{z} \), which reads

\[ \frac{d r^\perp_s(t)}{dt} = v_s n_\perp(r_s,t) + f_\perp , \]

(8)

and integrating over time gives

\[ \Delta r^\perp_s(t) \equiv r^\perp_s(t) - r^\perp_s(0) = \int_0^t dt' (v_s n_\perp(r_s,t') + f_\perp(t')) . \]

(9)

Squaring this, and averaging, we find that \( \langle (\Delta r^\perp_s(t))^2 \rangle \) is given by

\[ \langle (\Delta r^\perp_s(t))^2 \rangle = \int_0^t dt' \int_0^t dt'' [v_s^2 (n_\perp(r_s(t'),t') \cdot n_\perp(r_s(t'',t''))) + 2v_s (n_\perp(r_s(t'),t') \cdot f_\perp(t'')) + (f_\perp(t') \cdot f_\perp(t''))] \]

(10)

Using the expressions Eq. (4) and Eq. (5) for the two-point correlations of the Gaussian random velocity, we can immediately evaluate the last two terms, denoted by \( I_2 \) and \( I_3 \), respectively. The first of them is

\[ I_2 = \int_0^t dt' \int_0^t dt'' 2v_s (n_\perp(r_s(t'),t') \cdot f_\perp(t'')) = 6 \Delta f n t \]

(11)

while the second is

\[ I_3 = \int_0^t dt' \int_0^t dt'' (f_\perp(t') \cdot f_\perp(t'')) = [6 \Delta f + 2 \Delta s] t , \]

(12)

Both of these terms are extremely boring: their contribution to the mean squared lateral wandering \( \langle (\Delta r^\perp_s(t))^2 \rangle \) is simply conventionally diffusive: that is, proportional to time \( t \). The anomalous diffusion that we predict comes entirely from the first term in Eq. (10):

\[ I_1 = v_s^2 \int_0^t dt' \int_0^t dt'' (n_\perp(r_s(t'),t') \cdot n_\perp(r_s(t'',t'))) \]

(13)

Because the smectic dynamics are invariant under space and time translations, the general director two point correlation function depends only on the differences of the space and time coordinates; that is

\[ C_\perp \equiv \langle n_\perp(r',t') \cdot n_\perp(r'',t'') \rangle = C_\perp (r' - r'',t' - t'') . \]

(14)

Now in Eq. (13), we need this correlation function evaluated when \( r' = r_s(t') \) and \( r'' = r_s(t'') \). These vectors are given by:

\[ r_s(t) = r_s(0) + v_s t \hat{z} + \Delta r_s^\perp(t) . \]

(15)

To proceed further, we need to calculate this director correlation, which is independent of the dynamics of the swimmer, but clearly does depend on the dynamics of the smectic. However, we will show, in the final subsection of this theoretical section, that in fact the motion of the swimmer is, at sufficiently long times, independent of the smectic dynamics, provided only that those dynamics do relax back to thermal equilibrium.

However, that phrase "sufficiently long times" is highly loaded: for many real experimental systems, the time that must be reached before the asymptotic law for the lateral superdiffusion of the swimmer that we find below holds is astronomical. Fortunately, for shorter time scales, the behavior is still superdiffusive, but with a different scaling law. All of this will be discussed in the final subsection of this theoretical section.

In the next subsection, we will obtain the asymptotic superdiffusive scaling law that applies for all dynamical models.

### A. Universal asymptotic superdiffusion

We will show in the next subsection that at very long times, the correlation function \( C_\perp (r' - r'',t' - t'') \), when evaluated at typical values of \( r' = r_s(t') \) and \( r'' = r_s(t'') \), is well approximated by its equal time value; that is,

\[ C_\perp (r_s(t') - r_s(t''),t' - t'') \approx C_\perp (r_s(t') - r_s(t''),0) . \]

(16)

However, we will also show in the next subsection that for many realistic experimental systems, this "equal-time" approximation only holds for astronomically long time scales. For shorter time scales, we still predict superdiffusive behavior, but with a different scaling law. Our simulations, however, are done for a model and in a regime in which this asymptotic behavior is reached at quite short times. For this section, we will simply assume that this equal time approximation holds, and investigate its
consequences for the lateral diffusion of the swimmer.

The simplification provided by the equal time approximation is that equal time correlations can be calculated from equilibrium Boltzmann statistics. Indeed, many different dynamical models will relax back to the same equilibrium Boltzmann distribution, and, therefore, the same equal time correlation functions. This is particularly relevant for the simulations we perform here, since we simulated a model without momentum conservation, whereas any real bulk three dimensional smectic will, of course, have momentum conservation \[37\]. We will not consider the motion of a swimmer in such systems here. Fortunately, since our model (by construction) relaxes back to the equilibrium state of a smectic A, it is guaranteed to have the same equal time correlation functions as the more realistic momentum conserving models that describe the experimentally relevant momentum conserving case.

Having reduced our problem to the calculation of equilibrium, equal-time correlations of the layer normal in a smectic A, we now proceed to calculate those correlations. This quite standard calculation starts with the observation that, in a smectic A, the layer normal \(\hat{n}(r,t)\) is determined entirely by the smectic layer displacement field \(u(r,t)\) through the simple geometrical relation \[38\]:

\[
\hat{n}(r,t) \approx \hat{z} - \nabla_\perp u(r,t),
\]

where the approximate equality holds to linear order in \(\nabla_\perp u(r,t)\). Fourier transforming this relation in space then implies

\[
\langle |\mathbf{n}_\perp(q,t)|^2 \rangle = q_\perp^2 \langle |u(q,t)|^2 \rangle.
\]

The calculation of the \(u-u\) correlation function in this expression from equilibrium Boltzmann statistics requires only a knowledge of the equilibrium elastic Hamiltonian for layer positional fluctuations \(u(r)\). This is well known to be \[38\] \[39\):

\[
H = \frac{1}{2} \int d^3r \left[ B (\partial_\perp u)^2 + K (\nabla_\perp^2 u)^2 \right].
\]

From this model, it is straightforward to derive the required \(u-u\) correlation function in \[18\] by Fourier transforming and applying equipartition. This gives the standard result \[38\]

\[
\langle |u(q,t)|^2 \rangle = \frac{k_B T}{G_q},
\]

where we have defined

\[
G_q \equiv K q_\perp^4 + B q_\perp^2.
\]

Using this in \[18\] gives the director correlations in Fourier space

\[
\langle |\mathbf{n}_\perp(q,t)|^2 \rangle = \frac{k_B T q_\perp^2}{G_q},
\]

which in turn implies that real space director fluctuations are given by

\[
C_\perp(r,0) = \langle \mathbf{n}_\perp(\mathbf{r} + \mathbf{R},t) \cdot \mathbf{n}_\perp(\mathbf{R},t) \rangle = k_B T \int \frac{d^3q}{8\pi^3} \frac{q^2 e^{i\mathbf{q} \cdot \mathbf{r}}}{G_q}.
\]

Using this expression in our equal time approximation \[10\], and using that in turn in expression \[14\] for the nematic correlations and \[13\] for the superdiffusive integral \(I_1\), we obtain

\[
I_1 = v_s^2 \int_0^t dt' \int_0^t dt'' C(t' - t'').
\]

where we have defined

\[
C(\delta t) \equiv C_\perp(r_s(t + \delta t) - r_s(t),0),
\]

with \(r_s(t)\) given by \[15\]. Using \[23\] in this expression, and performing the integral over \(q_\perp\) by complex contour techniques gives

\[
C(\delta t) = \langle \mathbf{n}_\perp(\Delta \mathbf{r}_s^\perp(\delta t) + v_s \delta t \hat{z},0) \cdot \mathbf{n}_\perp(0,0) \rangle = k_B T \int \frac{d^3q}{8\pi^2 \sqrt{BK}} e^{i\mathbf{q} \cdot \Delta \mathbf{r}_s^\perp(\delta t) - v_s \lambda q_\perp |\delta t|}.
\]

where \(\lambda \equiv \sqrt{K/B}\) is the familiar smectic penetration length \[38\], and we have defined \(\Delta \mathbf{r}_s^\perp(\delta t) \equiv \mathbf{r}_s(t + \delta t) - \mathbf{r}_s(t)\). Doing the simple Gaussian integrals over the two components of \(\mathbf{q}_\perp\) gives:

\[
C(\delta t) = \frac{k_B T}{8\pi v_s K |\delta t|} \exp \left\{ -\frac{(\Delta \mathbf{r}_s^\perp(\delta t))^2}{4v_s |\delta t|} \right\}.
\]

Noting that each of the two components \(\Delta x, \Delta y\) of \(\Delta \mathbf{r}_s^\perp(\delta t)\) is a zero-mean Gaussian random variable (since it is the sum of Gaussian random variables, as it is linearly related to the noise, which is Gaussian, and the director \(\hat{n}\), whose fluctuations are also Gaussian), and using the result for a zero mean Gaussian random variable \(x\) that \(\exp(-kx^2) = 1/\sqrt{1 + 2kx^2}\), we get

\[
C(\delta t) \approx \frac{k_B T}{2\pi \sqrt{BK}} \left\langle (\Delta \mathbf{r}_s^\perp(\delta t))^2 \right\rangle \frac{1}{\lambda^2}
\]

where in the last, approximate, equality, we have assumed (as we will verify a posteriori) is true in the limit \(\delta t \to 0\) that \(\left\langle (\Delta \mathbf{r}_s^\perp(\delta t))^2 \right\rangle \gg \lambda v_s K |\delta t|\). This assumption amounts to assuming that there is anomalous diffusion in this case, as we will now show.

Using the approximate equality of \[28\] in \[10\] leads to a self-consistent equation for \(\left\langle (\Delta \mathbf{r}_s^\perp(t))^2 \right\rangle\):

\[
\left\langle (\Delta \mathbf{r}_s^\perp(t))^2 \right\rangle = \frac{k_B T}{2\pi \sqrt{BK}} \int_0^t dt' \int_0^t dt'' \frac{1}{t''} \left\langle (\Delta \mathbf{r}_s^\perp(t' - t''))^2 \right\rangle.
\]
We will seek a self-consistent solution to this equation of the form
\[
\left\langle \left( \Delta r_s^+ (t) \right)^2 \right\rangle = \mathcal{D} t \left[ \ln \left( \frac{t}{t_0} \right) \right]^{\alpha}, \tag{30}
\]
where in the second step the integrals over \( t' \) and \( t'' \) exclude the region in which \( |t' - t''| < t_0 \). This expression is clearly satisfied if \( \alpha = 1 - \alpha \), so \( \alpha = \frac{1}{2} \), and
\[
\mathcal{D} = \frac{v_s}{(BK)^{1/4}} \sqrt{\frac{k_B T}{\pi}}. \tag{32}
\]
Inserting these results into our ansatz (30) leads to our final prediction for asymptotic lateral diffusion of the swimmer at asymptotically large times:
\[
\left\langle \left( \Delta r_s^+ (t) \right)^2 \right\rangle = \mathcal{D} t \left[ \ln \left( \frac{t}{t_0} \right) \right], \tag{33}
\]
with the anomalous diffusion constant \( \mathcal{D} \) given by (32).

Recall that these results were derived on the assumption that the explicit dependence on \( t' - t'' \) of \( C_\perp \) in (14) could be neglected for sufficiently large times. In the next subsection, we will demonstrate that this is true both for the non-momentum conserving model that we simulate, and for real smectics, in which momentum is conserved. We will also estimate how large the time has to be before the asymptotic law (33) applies. This asymptotic time \( t_a \) proves to be quite short for the non-momentum conserving model, but depends exponentially on parameters for momentum conserving models. As a result, for many momentum conserving models, \( t_a \) is astronomically large, and a different, but still anomalous, scaling law, which we also derive below, applies.

**B. Asymptotic time for different dynamical models**

There are a number of different dynamical models for \( u(r, t) \) that will relax to the equilibrium distribution for a smectic A. We simulate a simple, purely relaxational model, which reduces at long wavelengths to:
\[
\frac{\partial u(r, t)}{\partial t} = -\Gamma \frac{\delta H}{\delta u} + f(r, t), \tag{34}
\]
where the Hamiltonian \( H \) is given by (19), and the noise \( f \) in Eq. (34) must obey the fluctuation-dissipation theorem, which implies:
\[
\langle f(r, t) f(r', t') \rangle = 2 \Gamma k_B T \delta^3(\mathbf{r} - \mathbf{r}') \delta(t - t'). \tag{35}
\]
where \( t_0 \) is a short-time cutoff, and \( \alpha \) and \( \overline{D} \) are, respectively, an exponent and a “superdiffusion” constant, both of which we will determine self-consistently. This leads to the condition:
\[
\mathcal{D} t \left[ \ln \left( \frac{t}{t_0} \right) \right]^{\alpha} = \frac{k_B T}{2\pi \overline{D} \sqrt{BK}} \int_0^t dt' \int_0^t dt'' \frac{1}{|t' - t''|} \left[ \ln \left( \frac{|t' - t''|}{t_0} \right) \right]^{\alpha}. \tag{31}
\]

These dynamics differ from those of real bulk smectics which are complicated by the coupling of the layer displacement field \( u(r, t) \) to background fluid flow. In the important range of wavevectors \( q \lesssim \lambda q_z^{-1}, |\mathbf{q}| \ll a^{-1} \) (where \( a \) is the smectic layer spacing), these equations reduce to (40)
\[
\frac{\partial u(r, t)}{\partial t} = \frac{q_z}{\rho_0} \nabla^2 u, \tag{36}
\]
\[
\frac{\partial g_z(r, t)}{\partial t} = -\frac{\delta H}{\delta u} + \frac{\eta_z}{\rho_0} \nabla^2 g_z + f_z(r, t), \tag{37}
\]
where \( g_z \) is the local \( z \)-component of the momentum density of the smectic, \( \rho_0 \) is the mean density of the smectic, \( \eta_z \) is one of the five viscosities characterizing the viscous response of uniaxial systems like smectics A, the elastic Hamiltonian \( H \) is still given by (19), and the noise \( f_z \) is constrained by the fluctuation-dissipation theorem to satisfy
\[
\langle f(r, t) f(r', t') \rangle = 2 \eta_z k_B T \nabla^2 z \delta^3(\mathbf{r} - \mathbf{r}') \delta(t - t'), \tag{38}
\]
again in the wavevector regime of interest.

We will now consider each of these models in turn, and show that the long-time limit of the superdiffusive behavior is given by (33) for both of them. We will also calculate the asymptotic time \( t_a \) for both models, and derive the alternative superdiffusive law for \( t \ll t_a \) in the momentum conserving case, for which \( t_a \) can be astronomically large.

1. Non-momentum conserving model

We seek the space and time dependent correlation function \( C_\perp(r, t) \) in equation (14) of the director. As before, we will obtain this from the correlations of the displacement field \( u(r, t) \). These can readily be obtained from the equation of motion (34) by Fourier transforming in space, solving the resultant ordinary differential equation for \( u(\mathbf{q}, t) \) in terms of \( f_z(\mathbf{q}, t) \), and autocorrelating the result at two different times. This gives
\[
\langle u(\mathbf{q}, t + \tau) u(-\mathbf{q}, \tau) \rangle = \frac{k_B T e^{-\Gamma q_z^4 t}}{G_{\mathbf{q}}}. \tag{39}
\]
where we have defined
\[
G_{\mathbf{q}} = k_q^4 + B q_z^2. \tag{40}
\]
This implies that director correlations in Fourier space are given by

\[
\langle \mathbf{n}_\perp (\mathbf{q}, t + \tau) \cdot \mathbf{n}_\perp (-\mathbf{q}, \tau) \rangle = \frac{k_B T q^2 e^{-\Gamma G q t}}{G_q},
\]

which in turn implies that real space director fluctuations are given by

\[
C(r, t) = \langle \mathbf{n}_\perp (r + \mathbf{R}, \tau + \tau) \cdot \mathbf{n}_\perp (\mathbf{R}, \tau) \rangle = k_B T \int \frac{d^3 q}{8\pi^3} \frac{q^2 e^{i\mathbf{q} \cdot \mathbf{r} - \Gamma G q t}}{G_q}.
\]

Changing variables of integration in this multiple integral from \( \mathbf{q} \) to \( \mathbf{q}_\perp \equiv |\mathbf{r}| \mathbf{q} \) and from \( q_z \) to \( Q_z \equiv |r_z| q_z / \lambda \) enables us to rewrite this in a scaling form:

\[
C(r, t) = \frac{k_B T}{\sqrt{BK} |r_\perp|^2} \Upsilon_N \left( \frac{\lambda z}{|r_\perp|^2}, \frac{\Gamma K t}{|r_\perp|^4} \right),
\]

where we have defined the scaling function

\[
\Upsilon_N (\psi, \zeta) = \int \frac{d^3 Q Q^4}{8\pi^3} \exp \left[ i(Q_z + Q_\perp \psi) - \zeta (Q_z^2 + Q_\perp^2) \right] \frac{Q_z^2 + Q_\perp^2}{Q_z^4 + Q_\perp^4}.
\]

To justify the equal-time approximation made in the preceding section, we need to show that the explicit time dependence of this correlation function can be neglected. From the scaling form, we see that this will be a good approximation whenever the dimensionless scaling variable \( \zeta = \frac{\Gamma K t}{|r_\perp|^4} \) associated with time is small; that is, \( \zeta \ll 1 \). Using our result (43) from the previous section for \( \langle |r_\perp|^2 \rangle \), and estimating the typical value of \( |r_\perp|^4 \sim \langle |r_\perp|^2 \rangle^2 \) leads to the condition for the validity of our asymptotic result (43):

\[
\frac{\Gamma K}{D^2 t \ln \left( \frac{t}{t_a} \right)} \ll 1
\]

which is clearly always satisfied at long times. Indeed, it is satisfied whenever

\[
t \gg t_a = \frac{\Gamma K}{D^2} = \frac{\Gamma K \sqrt{BK}}{k_B T v_s^3}.
\]

Since \( t_a \) is a fairly weak function (i.e., algebraic, rather than exponential, as in the momentum conserving case) of the parameters of our model, we expect it to be fairly easy to reach the asymptotic regime \( t \gg t_a \), in which our asymptotic result (43) applies. And indeed, we find in our simulations that (43) holds from very early times out to the longest times we can simulate, as we have just predicted.

### 2. Momentum conserving model

In Fourier space, our momentum conserving model becomes

\[
\frac{\partial u(\mathbf{q}, t)}{\partial t} = g_z(\mathbf{q}, t) / \rho_0,
\]

\[
\frac{\partial g_z(\mathbf{q}, t)}{\partial t} = -G_q u - \frac{\eta_2}{\rho_0} g_z^2(\mathbf{q}, t) + f_z(\mathbf{q}, t),
\]

where \( G_q \) was defined in (40). If we assume we are in the Stokesian limit, in which the viscous (\( \eta_2 \)) term dominates the inertial \( 2g_z^2(\mathbf{q}, t) \) term in (48), then we can solve that equation directly for \( g_z(\mathbf{q}, t) \), obtaining

\[
g_z(\mathbf{q}, t) = -\rho_0 \left( G_q u(\mathbf{q}, t) - f_z(\mathbf{q}, t) \right) / \eta_2 g^2_q .
\]

Inserting this into the equation of motion (48) for \( u(\mathbf{q}, t) \) gives

\[
\frac{\partial u(\mathbf{q}, t)}{\partial t} = - \frac{G_q u(\mathbf{q}, t) - f_z(\mathbf{q}, t)}{\eta_2 q^2} .
\]

We can now check a posteriori our assumption that we are in the Stokesian limit by using this expression to compute \( \frac{\partial g_z(\mathbf{q}, t)}{\partial t} \), and taking into account the reduction of \( \chi \) just used, we still get

\[
\frac{\partial u(\mathbf{q}, t)}{\partial t} \sim \frac{\rho_0 G_q}{\eta_2 q^2}.
\]

This ratio is clearly a monotonically increasing function of \( q^2 \), so it is biggest when \( q = 0 \), at which point it is given by \( K_{\mathbf{q}_0} / \eta_2 \equiv \chi \). The smaller this ratio, the better our Stokesian approximation. For typical thermotropic smectics, \( K \sim 5 \times 10^{-7} \text{dynes} \), \( \rho_0 \sim 1 \text{gram cm}^{-2} \text{sec}^{-1} \), and \( \eta_2 \sim 1 \text{Poise} \), which gives \( \chi \sim 5 \times 10^{-7} \). Even in lyotropic smectics, for which \( \eta_2 \) approaches the viscosity of water, which is two orders of magnitude smaller than the value of \( \eta_2 \) we have just used, we still get \( \chi \sim 5 \times 10^{-3} \), and this is before taking into account the reduction of \( K \) due to dilution. So our Stokesian approximation is clearly a very good one in all cases.

The correlation functions of \( u \) can now be obtained from (50), as in the nonconserving case, by Fourier transforming in space, solving the resultant ordinary differential equation for \( u(\mathbf{q}, t) \) in terms of \( f_z(\mathbf{q}, t) \), and autocorrelating the result at two different times. This gives

\[
\langle u(\mathbf{q}, t + \tau) u(-\mathbf{q}, \tau) \rangle = \frac{k_B T e^{-\Gamma G q t}}{G_q} .
\]

This implies that director correlations in Fourier space are given by

\[
\langle \mathbf{n}_\perp (\mathbf{q}, t + \tau) \cdot \mathbf{n}_\perp (-\mathbf{q}, \tau) \rangle = \frac{k_B T q^2 e^{-\Gamma G q t}}{G_q} .
\]
which in turn implies that real space director fluctuations are given by
\[
C(\mathbf{r},t) = \langle \mathbf{n}_\perp (\mathbf{r} + \mathbf{R}, \tau + t) \cdot \mathbf{n}_\perp (\mathbf{R}, \tau) \rangle = k_B T \int \frac{d^3q}{8\pi^3} \frac{q^2 e^{-\frac{\mathbf{q} \cdot \mathbf{r}}{\eta_2 r_\perp^2}}}{G_q} .
\] (53)

Changing variables of integration in this multiple integral from \( q_z \) to \( q_\perp \equiv q_{\perp} q_z \) and from \( q_z \) to \( Q_z \equiv |q_\perp|^2 q_z / \lambda \) enables us to rewrite this in a scaling form:
\[
C(\mathbf{r},t) = \frac{k_B T}{\sqrt{\alpha K} r_\perp^2} \Upsilon_C \left( \frac{\lambda z}{|r_\perp|^2}, \frac{Kt}{\eta_2 |r_\perp|^2} \right) ,
\] (54)

where we have defined the scaling function
\[
\Upsilon_C (\psi, \zeta) = \int \frac{d^3Q}{8\pi^3} Q^2 \exp \left[ i (Q_z + Q_\perp \psi) \zeta - \zeta \left( \frac{Q^2_\perp}{Q^2_z} + \frac{Q^4_\perp}{Q^4_z} \right) \right] \frac{Q^2_\perp + Q^4_\perp}{Q^4_z + Q^4_\perp} .
\] (55)

To justify the equal-time approximation made in the preceding section, we need to show that the explicit time dependence of this correlation function \( \Upsilon_C \) can be neglected. From the scaling form, we see that this will be a good approximation whenever the dimensionless scaling variable \( \zeta = \frac{Kt}{\eta_2 r_\perp^2} \) associated with time is small; that is, \( \zeta \ll 1 \). Using our result \( \Upsilon_C (\psi, 1) \) from the previous section for \( \langle |r_\perp|^2 \rangle \), and estimating the typical value of \( |r_\perp|^2 \ll \langle |r_\perp|^2 \rangle \) leads to the condition for the validity of our asymptotic result \( \Upsilon_C \):
\[
\frac{Kt}{\eta_2 \sqrt{D} t \ln \left( \frac{1}{t_0} \right)} \ll 1
\] (56)

which is clearly always satisfied at long times. Indeed, it is satisfied whenever
\[
t \gg t_a \equiv t_0 \exp \left[ \left( \frac{K}{\eta_2 D} \right)^2 \right] \equiv t_0 \exp \left[ \left( \frac{v_c}{v_s} \right)^2 \right] ,
\] (57)

where we have defined a characteristic velocity
\[
v_c \equiv B^{1/4} K^{5/4} \lambda \sqrt{\frac{\pi}{k_B T}} .
\] (58)

In deriving this expression, we have used equation \[ \ref{B} \] for \( D \).

We see from equation \[ \ref{asymp_time} \] that, in contrast to the non-momentum conserving case, when momentum is conserved, the asymptotic time \( t_a \) is extremely sensitive (indeed, exponentially so) to material parameters, and to the speed of the swimmer. It can also become astronomically large. Taking typical numbers for a thermotropic smectic, such as \( B \sim 5 \times 10^7 \text{ dynes} / \text{cm}^2 \), \( K \sim 5 \times 10^{-7} \text{ dynes} \), and \( \eta_2 \sim 1 \text{ Poise} \) gives \( v_c \sim 5 \text{ cm/sec} \). Putting a bacterium with a swimming speed of \( v_s \sim 50 \text{ µm/sec} \) in such a smectic, we see that equation \[ \ref{asymp_time} \] implies an asymptotic time of \( t_a = t_0 \exp(10^4) \), which, for any reasonable \( t_0 \), is far longer than the age of the universe!

However, the extreme exponential sensitivity of the asymptotic time \( t_a \) means that it should be achievable in other systems. Lyotropic smectics are a good candidate. In a highly dilute lyotropic smectic, the elastic constants obey \[ \ref{elastic_const} \] \( B \sim \left( \frac{K_T}{\alpha \mu} \right)^2 \), and \( K \sim \frac{\mu}{\ell^2} \), where \( \ell \) is the lamellar spacing and \( \kappa \) is the bend rigidity per unit area of a single lamella. Inserting these expressions into our expression \[ \ref{asymp_time} \] gives
\[
v_c \sim \frac{\kappa}{\eta_2 \ell^2} .
\] (59)

Thus, for very dilute systems, in which \( \ell \) is large, we can make the characteristic speed \( v_c \) very small. Taking a typical lamellar bend stiffness \( \kappa \sim 5 \times 10^{-14} \text{ ergs} \) and noting that for a highly dilute lamellar phase, we expect \( \eta_2 \sim \eta_{\text{H2O}} \sim 10^{-2} \text{ Poise} \), we obtain from \[ \ref{asymp_time} \]
\[
v_c \sim 5 \frac{\mu_{\text{sec}}}{\ell} \left( \frac{1}{\mu_{\text{sec}}} \right)^2 ,
\] (60)

which implies from \[ \ref{asymp_time} \] that for a lamellar phase with a layer spacing of \( \ell = 0.3 \text{ micron} \), and a bacteria swimming at \( v_s = 50 \text{ µm/sec} \), the asymptotic time would be
\[
t_a \sim t_0 \exp(10/9) \approx 3.44 t_0 ,
\] (61)

which should be quite experimentally accessible.

What about those cases in which \( t_a \) is astronomically large? We can show that in those cases, there is also anomalous diffusion, but with a different scaling law. To see this, we note that \( t \ll t_a \), the time variable is now the dominant one in the scaling law \[ \ref{asymp_time} \] for the correlation function. Hence, we can evaluate that correlation function setting \( r_\perp \) and \( z \) to zero in our general expression \[ \ref{asymp_time} \] for \( C_{\perp} \). This gives
\[
C(\mathbf{r} = 0, t) = \langle \mathbf{n}_\perp (\mathbf{r} + \mathbf{R}, \tau + t) \cdot \mathbf{n}_\perp (\mathbf{R}, \tau) \rangle = k_B T \int \frac{d^3q}{8\pi^3} \frac{q^2 e^{-\frac{\mathbf{q} \cdot \mathbf{r}}{\eta_2 q^2}}}{G_q} .
\] (62)

With the change of variables \( q_z \) to \( Q_z \equiv \sqrt{q_z / q^2} q_\perp \) and from \( q_z \) to \( Q_z \equiv q_z \frac{Kt}{\eta_2} \), we can pull the time dependence out of this expression, obtaining
\[
C(\mathbf{r} = 0, t) = \left( \frac{k_B T \eta_2}{8\pi^3 \sqrt{K \alpha K^3}} \right) f(\frac{1}{t}) ,
\] (63)

where we have defined
\[
f(x) \equiv \int d^3Q_\perp Q^2_\perp e^{-x \left( \frac{Q^2_\perp + Q^4_\perp}{Q^2_z + Q^4_\perp} \right)} .
\] (64)

This function can easily be evaluated by differentiating it with respect to \( x \); this gives
\[
f'(x) = \int d^3Q e^{-x \left( \frac{Q^2_\perp + Q^4_\perp}{Q^2_z + Q^4_\perp} \right)} .
\] (65)
Performing the Gaussian integral over $Q_z$ gives
\[
f'(x) = \int d^2Q_\perp e^{-xQ_\perp^2}Q_\perp \sqrt{\frac{\pi}{x}}.
\] (66)

The integral $d^2Q_\perp$ is also elementary; we thereby obtain
\[
f'(x) = -\frac{\pi^2}{2x^2}.
\] (67)

Integrating this, and determining the unknown constant of integration by noting, from inspection of (65), that $f(x \to \infty) \to 0$, we obtain
\[
f(x) = \frac{\pi^2}{2x}.
\] (68)

Using this in (63) gives
\[
C(r = 0, t) = \left( \frac{k_B T \eta_2}{16\pi \sqrt{B K^3}} \right) \frac{1}{t}.
\] (69)

Now replacing $(\mathbf{u}_1(r_s(t')), t') \cdot \mathbf{u}_1(r(t', t''))$ in equation [10] with $C(r = 0, t' - t'')$ from this expression, and doing the $t'$ and $t''$ integrals in (10) gives, again, anomalous diffusion, but with a different scaling law:
\[
\langle (\Delta \mathbf{r}_s^i(t))^2 \rangle = \left( \frac{k_B T \eta_2}{16\pi \sqrt{B K^3}} \right) t \ln \left( \frac{t}{t_0} \right).
\] (70)

This is the expression that is most experimentally relevant to thermotropic smectics, or to lyotropics at lower dilutions (i.e., lamellar spacings $\ell \ll 1\mu$).

### III. SIMULATION MODEL

We will now attempt to corroborate the theoretical predictions for the long-time swimmer dynamics in the smectic fluid using a particle-based simulation model. The model potential employed in our simulations is designed to generate stable nematic and smectic (A) phases at low temperature while producing trivial isotropic fluids at high temperature. It corresponds to a simple soft-core potential proposed in Ref. [42] and models the interaction energy $U_{SC}$ between two soft spherocylinders at centre-of-mass displacement $\Delta \mathbf{r}$ with orientation unit vectors $\hat{\mathbf{u}}$ and $\hat{\mathbf{u}}'$:

\[
U_{sc} = \begin{cases} 
    u_m(1 - \sigma)^2 + \epsilon, & \sigma < 1 \\
    u_m(1 - \sigma)^2 - U_a(1 - \sigma)^4 + \epsilon, & 1 \leq \sigma < \sigma_c \\
    0, & \sigma \geq \sigma_c
\end{cases}
\] (71)

where $\sigma(\Delta \mathbf{r}, \hat{\mathbf{u}}, \hat{\mathbf{u}}')$ denotes the shortest distance between two short spherocylinders of length $L$ and diameter $\sigma_0$ at fixed mutual orientation. The attractive part of the potential takes the form

\[
U_a = u_a - 5\epsilon_1 P_2(\hat{\mathbf{u}} \cdot \hat{\mathbf{u}}') - 5\epsilon_2[\hat{\mathbf{P}}_2(\Delta \hat{\mathbf{r}} \cdot \hat{\mathbf{u}}) + \hat{\mathbf{P}}_2(\Delta \hat{\mathbf{r}} \cdot \hat{\mathbf{u}}')] 
\] (72)

in terms of a second-order Legendre polynomial $\mathcal{P}_2$ and centre-of-mass distance unit vector $\Delta \hat{\mathbf{r}}$. Furthermore, $\epsilon(\Delta \hat{\mathbf{r}}, \hat{\mathbf{u}}, \hat{\mathbf{u}}') = -u_m^2/4U_a(\Delta \hat{\mathbf{r}} \cdot \hat{\mathbf{u}}')$ is the maximum well depth for the configuration chosen such as to guarantee the potential and its first derivative to reach zero at the cut-off distance $\sigma_c(\Delta \hat{\mathbf{r}}, \hat{\mathbf{u}}, \hat{\mathbf{u}}') = 1 + \sqrt{u_m/2U_a(\Delta \hat{\mathbf{r}} \cdot \hat{\mathbf{u}}')}$. The shape of the core-potential can be judiciously tuned through the four-parameter combination $(u_m, u_a, \epsilon_1, \epsilon_2)$ enabling facile simulation of a range of liquid crystalline mesophases [42].

The swimmer is described as a point particle with position $\mathbf{r}$, and orientation unit vector $\hat{\mathbf{u}}$. It interacts with the surrounding soft rods by means of a coupling potential [23] of strength $\epsilon_s$:

\[
U_s = \epsilon_s \sum_i \mathcal{P}_2(\hat{\mathbf{u}}_i \cdot \hat{\mathbf{u}})g(r_{i,s})
\] (73)

The coupling potential decays with increasing distance $r_{i,s} = ||\mathbf{r}_{i,s}||$ between the swimmer and the soft rods through a Gaussian $g(r_{i,s}) = \exp[-(r_{i,s}/\sigma_s)^2]$ with $\sigma_s$ a characteristic length scale setting the coupling range.

The microscopic equations of motion for the positional coordinates describe overdamped Brownian motion of each rod $i$:

\[
\xi_i \partial_t \mathbf{r}_i = -\nabla_{\mathbf{r}_i} U(\{\mathbf{r}_i, \hat{\mathbf{u}}_i\}) + \tilde{f}_i
\] (74)

where $\xi_i = \xi_{||} \hat{\mathbf{u}} + \xi_\perp (\mathbf{1} - \hat{\mathbf{u}} \hat{\mathbf{u}})$ denotes the translational friction tensor of a uniaxial rod. The first term on the rhs is a direct force on rod $i$ due to presence of neighboring liquid crystal particles via the total potential energy $U = \frac{1}{2} \sum_i \mathcal{U}_{sc}$ assumed pairwise additive. Furthermore, $\tilde{f}_i = \sqrt{2\sigma_{\alpha} k_B T} R_{\alpha}(t)$ is a Gaussian random force acting on each rod with zero mean $\langle R_{\alpha}(t) \rangle = 0$ and variance $\langle R_{\alpha}(t) R_{\alpha}(t') \rangle = \delta_{\alpha,\gamma} \delta(t - t')$ with $\alpha, \gamma$ indicating the components of a rod-based orthonormal frame $\mathbf{f} = \tilde{f}^2 + \tilde{f}^1 \hat{\mathbf{e}}_1 + \tilde{f}^0 \hat{\mathbf{e}}_2$. The equation of motion for the orientation of the soft-particle follows from a similar balance of torques, via

\[
\xi_R \partial_t \hat{\mathbf{u}}_i = (\mathbf{w}_i + \mathbf{w}_{i,s} + \tilde{\mathbf{w}}) \times \hat{\mathbf{u}}_i
\] (75)

with $\xi_R$ the rotational friction factor, $\mathbf{w}_i = \lambda_i \hat{\mathbf{u}}_i - \partial U/\partial \hat{\mathbf{u}}_i$ the torque on particle $i$ due to the surrounding rods (with $\lambda_i$ a Lagrange multiplier ensuring normalization of $\hat{\mathbf{u}}_i$), and $\mathbf{w}_{i,s} = \lambda_i \hat{\mathbf{u}}_i - \partial U_s/\partial \hat{\mathbf{u}}_i$ the contribution imparted by the presence of the swimmer, and $\tilde{\mathbf{w}}_s = \sqrt{2\sigma_{\alpha} k_B T} R_{\alpha}(t)$ a random Gaussian torque within the orthonormal particle frame so that $\alpha = \{1,1,\perp\}$. The geometric factors $\{\xi_{||}, \xi_{\perp}, \xi_R\}$ depend solely on the rod aspect ratio $p = (L + \sigma_0)/\sigma_0 > 0$, and we adopt the standard expressions for rod-like macromolecules, as given in [43]:

\[
\begin{align*}
    \xi_{||} &= \frac{1}{4\pi} \left( \ln p + 0.839 + 0.185/p + 0.233/p^2 \right), \\
    \xi_{\perp} &= \frac{1}{2\pi} \left( \ln p - 0.207 + 0.980/p - 0.133/p^2 \right), \\
    \xi_R &= \frac{3}{2\pi p^2} \left( \ln p - 0.207 + 0.980/p - 0.133/p^2 \right)
\end{align*}
\] (76)
with $\xi_0$ and $\xi_R 0$ the friction factors of a reference sphere with radius $\sigma_0$. Defining $D_0 = k_B T/\xi_0$ as the translational diffusion coefficient of a reference sphere.

The trajectory $\{r_s(t), \hat{n}_s(t)\}$ of the swimmer is governed by the following equations of motion:

$$
\xi_s \partial_t r_s = f_a \hat{u}_s \\
\xi_R s \partial_t \hat{n}_s = (w_{s,i} + w_s) \times \hat{u}_s
$$

(77)

with $\xi_R s$ the rotational friction factor and $\xi_s$ the translational friction tensor of the swimmer, $w_{s,i} = \lambda_s \hat{u}_s - \partial U_s / \partial \hat{u}_s$ the torque acting on the swimmer imparted by neighboring soft rods and $w_s$ a random torque. The geometric factors are identical to Eq. (76) for a given hydrodynamic swimmer aspect ratio $p_s > 1$ which may be different from that of the soft rods $p$. The translational noise on the swimmer is ignored as it is assumed to be negligible compared to the orientational noise (as is the case for motile bacteria [44]). Throughout this study, we use dimensionless expressions for time $\tau = tD_0 / \sigma_0^2$, temperature $T^* = k_B T / u_a$, particle density $\rho^* = N \sigma_0^2 / V$ (with $N$ the number of particles and $V$ the system volume) and active force $f_a^* = f_a \sigma_0 / \epsilon_s$.

The interaction parameters (in units $k_B T$) for the current model are the following: $u_m = 25$, $u_a = 150$, $\epsilon_1 = 10$, $\epsilon_2 = -2$. The rod aspect ratio is fixed at $p = L / \sigma_0 = 3.0$. For these values the system undergoes a transformation from an isotropic, a nematic and a smectic phase upon lowering the temperature and/or increasing particle density. We employ a cubic simulation box with periodic boundary conditions in all three directions. The initial configuration represents $N = 3500$ rods forming a square smectic lattice at a given density $\rho^*$. It is allowed to melt during an equilibration run of at least $\Delta \tau = 2000$. Once the host phase is equilibrated, a swimmer is placed in the centre of the simulation box and the whole system is re-equilibrated during at least $\Delta \tau = 2000$. To avoid numerical artifacts the time step associated with the linear discretization of the equations of motion is kept sufficiently small ($\delta \tau < 0.001$). The parameters defining the interaction between the swimmer and the host rods are: $\epsilon_s = 1k_B T$, $\sigma_s = (L + \sigma_0) / 2$ for the coupling strength and range, respectively, and $p_s = 5$ for the swimmer aspect ratio. Production runs during which observables of interest were recorded span a total time interval of at least $\Delta \tau = 5000$.

Let us define the displacement vectors $\Delta r^i_s (\tau) \equiv (r_s(\tau) - r_s(0)) \cdot \hat{n}$ along, and $\Delta r^\perp_s (\tau) \equiv \Delta r_s (\tau) - \Delta r^i_s (\tau)$ perpendicular to, the layer normal $\hat{n}$, with $\Delta r_s (\tau) = r_s(\tau) - r_s(0)$. We then determined from our simulations the mean squared displacements $\langle (\Delta r^i_s (\tau))^2 \rangle$ and $\langle (\Delta r^\perp_s (\tau))^2 \rangle$, where $\langle \cdot \cdot \cdot \rangle$ denotes a time-average in the steady state. We also monitor the mean-squared rotation of the swimmer via:

$$
\langle P_n (\hat{n}_s(\tau), \hat{n}_s(0)) \rangle, \quad n = 1, 2
$$

(78)

These quantities enable us to gauge the typical rotational relaxation time of the swimmer in relation to the symmetry of the medium and temperature. Since the effective shape of the swimmer is strongly anisotropic, i.e. $p_s > 1$, the rate of hairpin turns is extremely small and no such events are recorded during the course of our simulations except, of course, in the case of an isotropic background medium (at $T^* \gg 1$) where the orientational fluctuations of the swimmer are strong and the long-time dynamics becomes strictly diffusive.

An overview of the transverse MSDs for a swimmer moving is shown in Fig. [1]. In this particular representation, the logarithmic long-time tails clearly show up in a linear fashion with the scaling exponent for the smectic systems differing significantly from those of the nematic.
systems. Note that, in Fig. 1a, time is represented on an extremely compressed \( \ln(\ln \tau) \)-scale and deviations from linear scaling occur at very long times where the statistics is no longer fully reliable. Running systematically longer simulation runs will obviously remedy this. The fitted exponents (\( \alpha = 0.5 \pm 0.1 \) for the smectic and \( \alpha = 1.0 \pm 0.1 \) for the nematic) are in agreement with the ones established from our theoretical model. As expected, the mean-squared displacement parallel to the director remains ballistic throughout the sampled time interval for the nematic and smectic phases (suggesting hairpin turns to be completely absent), but for the isotropic phase it crosses over from ballistic to diffusive \( \propto \tau \) beyond the typical effective rotation time of the swimmer. The periodic boundary conditions employed in the simulation impart a weak bias on the layer normal which usually points along either of the Cartesian axes of the simulation box, but it may also point along the box diagonal as we observe for the smectic phase. The effect of this bias can be systematically weakened by increasing the system size. We find, however, that the latter has no measurable impact on the long-time scaling of the transverse MSD implying that the simulation set-up does not break the rotational invariance of the nematic or smectic fluid.

The distinct lamellar signature of the smectic phase can be probed through the self-part of the van Hove function:

\[
G(z_\parallel, \tau) = \frac{1}{N} \left< \sum_{i=1}^{N} \int d\mathbf{r}_\parallel \delta(z_\parallel - |\Delta \mathbf{r}_i(\tau)|) \right> \tag{79}
\]

representing the average distribution of displacements of the host particles along the layer normal over time. The results, depicted in Fig. 2, enable a clear distinction between the Gaussian patterns of a spatially uniform nematic fluid, whereas the shoulders point to a lamellar microstructure of the smectic host phase.

In our simulations we have also tested an alternative model in which a swimmer is conceived simply by rendering one of the passive host rods active by applying an active force \( f_a \) along its main orientation axis. In this model, the coupling between the swimmer and the host rods proceeds via the short-ranged, direct interaction given by Eq. (71). It turns out that both point-\( \mathcal{P}_2 \)-type swimmer and rod-based swimmer produce the same asymptotic scaling of the transverse (and parallel) MSDs. This illustrates that the long-time scaling of the swimmer superdiffusion does not depend on the details of the swimmer-host coupling provided its propulsion direction is aligned along the local nematic director. A clear advantage of the rod-based swimmer is that enables us to unambiguously recover standard long-time diffusion in an isotropic fluid (see Fig. 1b), while the mean-field \( \mathcal{P}_2 \) coupling interaction Eq. (73) yields spurious results for these dilute environments.

IV. CONCLUSIONS

In this paper we have addressed the long-term motility of a swimmer dispersed in a smectic A (or lamellar) fluid phase. Using hydrodynamic theory for the swimmer dynamics subject to a fluctuating smectic director field, we have derived universal scaling expressions for the mean-squared swimmer displacement perpendicular to the director. The predictions are relevant to a vast range of
smectic phases of both thermotropic and lyotropic origin, and are independent of the dynamical process through which the nematic director field relaxes towards equilibrium. We find that the long-time lateral diffusion of the swimmer across the smectic membranes exhibits a logarithmic $[\ln(t/t_0)]$ scaling with time $t$ which is distinctly different from the anomalous swimmer diffusion $[t \ln(t/t_0)]$ in nematic fluids[23] or the trivial long-time diffusion ($t$) encountered in isotropic media. We corroborate our predictions using particle-based simulation of an active point-particle moving through a smectic A phase composed of soft mesogens. Upon increasing temperature (and reducing particle concentration), the smectic host transforms into a nematic and, subsequently, an isotropic fluid. The concomitant transversal mean-squared swimmer displacement is fundamentally different in each of these phases and the measured long-time scaling laws are in full agreement with theory. Given the universality of our theoretical predictions one could envisage as a possible experimental application measuring the long-time diffusion of swimming micro-organisms or active colloids propelling through liquid-crystalline media as a dynamical probe to identifying the microstructure of the anisotropic host phase. Efforts to relate our theoretical findings to experimental model systems of external field-controlled active colloids moving through thermotropic liquid crystals[27, 45] are currently being undertaken.

ACKNOWLEDGMENTS

We thank J. Ignés-Mullol and F. Sagués for helpful discussions. C.F.C. and H.H.W. gratefully acknowledge funding from the French National Research Agency (ANR) through the "ANR-JCJC" grant "UPSCALE". H. L. was supported by the DFG within project LO 418/20-1. J.T. thanks the Institut für Theoretische Physik II: Weiche Materie, Heinrich-Heine-Universität, Düsseldorf; the Max Planck Institute for the Physics of Complex Systems Dresden; the Department of Bioengineering at Imperial College, London; The Higgs Centre for Theoretical Physics at the University of Edinburgh; and the Lorentz Center of Leiden University, for their hospitality while this work was underway.

[1] M. C. Marchetti, J. F. Joanny, S. Ramaswamy, T.Liverpool, J. Prost, M. Rao, and R. A. Simha, Rev. Mod. Phys. 85, 1143 (2013).
[2] P. Romanczuk, M. Bär, W. Ebeling, B. Lindner, and L. Schimansky-Geier, Eur. Phys. J. Spec. Top. 202, 1 (2012).
[3] J. Elgeti, R. G. Winkler, and G. Gompper, Rep. Prog. Phys. 78, 056601 (2015).
[4] C. Bechinger, R. Di Leonardo, H. Löwen, C. Reichhardt, G. Volpe, and G. Volpe, Rev. Mod. Phys. 88, 045006 (2016).
[5] M. F. Hagan and A. Baskaran, Curr. Opin. Cell Biol. 38, 74 (2016).
[6] M. A. Sleigh, J. R. Blake, and N. Liron, Am. Rev. Respir. Dis. 137, 726 (1988).
[7] S. S. Suarez and A. A. Pacey, Hum. Reprod. Update 12, 23 (2006).
[8] C. Josenhans and S. Suerbaum, Int. J. Med. Microbiol. 291, 605 (2002).
[9] H. R. Wallace, Ann. Rev. Phytopathol. 6, 91 (1967).
[10] H. C. Fu, T. R. Powers, and C. W. Wolgemuth, Phys. Rev. Lett. 99, 258101 (2007).
[11] X. N. Shen and P. E. Arratia, Phys. Rev. Lett. 106, 208101 (2011).
[12] D. A. Gagnon, N. C. Keim, and P. E. Arratia, J. Fluid. Mech. 758 (2014).
[13] B. Liu, T. R. Powers, and K. S. Breuer, Proc. Nat. Acad. Sci. 108, 19516 (2011).
[14] J. Schwarz-Linek, V. Valeriani, A. Cacciuto, M. E. Cates, D. Marenduzzo, A. N. Morozov, and W. C. K. Poon, Proc. Nat. Acad. Sci. 109, 4052 (2012).
[15] T. Qiu, T. C. Lee, A. G. Mark, K. I. Morozov, R. Muenster, O. Mierka, S. Turek, A. M. Leshansky, and P. Fischer, Nature Comm. 5, 5119 (2014).
[16] L. Zhu, E. Lauga, and L. Brandt, J. Fluid. Mech. 726, 285 (2013).
[17] E. E. Riley and E. Lauga, EPL 108, 34003 (2014).
[18] G. J. Elfring and E. Lauga, in Complex Fluids in Biological Systems, edited by S. E. Spagnolie (Springer, 2015).
[19] J. R. Gomez-Solano, A. Blokhuis, and C. Bechinger, Phys. Rev. Lett. 116, 138301 (2016).
[20] J. Berner, B. Müller, J. R. Gomez-Solano, M. Krüger, and C. Bechinger, Nature Comm. 9, 999 (2018).
[21] L. Shi and T. R. Powers, Phys. Rev. Fluids 2, 123102 (2017).
[22] J. S. Lintuvuori, A. Würgler, and K. Stratford, Phys. Rev. Lett. 119, 068001 (2017).
[23] J. Toner, H. Löwen, and H. H. Wensink, Phys. Rev. E 93, 062610 (2016).
[24] S. Zhou, A. Sokolov, O. D. Lavrentovich, and I. S. Aranson, Proc. Nat. Acad. Sci. 111, 1265 (2014).
[25] O. D. Lavrentovich, Curr. Opin. Colloid Interface Sci. 21, 97 (2016).
[26] P. C. Musherheim, R. R. Trivedi, H. H. Tuson, D. B. Weibel, and N. L. Abbott, Soft Matter 10, 79 (2014).
[27] S. Hernandez-Navarro, P. Tierno, J. Ignés-Mullol, and F. Sagués, IEEE Trans. Nanobiosci. 14, 267 (2015).
[28] M. S. Krieger, M. A. Dias, and T. R. Powers, Eur. Phys. J. E 38, 94 (2015).
[29] M. S. Krieger, S. E. Spagnolie, and T. R. Powers, Soft Matter 11, 9115 (2015).
[30] R. R. Trivedi, R. Maeda, N. L. Abbott, S. E. Spagnolie, and D. B. Weibel, Soft Matter 11, 8404 (2015).
[31] O. Chepizhko and F. Peruani, Phys. Rev. Lett. 111, 160604 (2013).
[32] G. Volpe, I. Buttinoni, D. Vogt, H.-J. Kümerer, and C. Bechinger, Soft Matter 7, 8810 (2011).
[33] A. Morin, N. Desreumaux, J.-B. Caussin, and D. Bartolo, Nature Physics \textbf{13}, 63 (2017).

[34] M. S. Krieger, S. E. Spagnolie, and T. R. Powers, Phys. Rev. E \textbf{90}, 052503 (2014).

[35] B. van der Meer, L. Filion, and M. Dijkstra, Soft Matter \textbf{12}, 5630 (2016).

[36] A. T. Brown, I. D. Vladescu, A. Dawson, T. Vissers, J. Schwarz-Linek, J. S. Lintuvuori, and W. C. K. Poon, Soft Matter \textbf{12}, 131 (2016).

[37] The only exception to this would be smectics in aerogels. In these systems, the smectic can lose momentum to the aerogel mesh. However, in this case the physics is quite different, due to the effects of the disorder of the aerogel on the smectic. See L. Radzihovsky, J. Toner, and N. Clark, Science, \textbf{294}, 1074 (2001), for a discussion of these systems.

[38] P. G. de Gennes and J. Prost, \textit{The Physics of Liquid Crystals} (Clarendon Press, Oxford, 1995).

[39] The full smectic elastic Hamiltonian contains anharmonic terms which are known to significantly change the scaling of the smectic correlations at long distances. However, the length scale at which these effects become important is also astronomically large in most real systems. Hence we will ignore these effects here. The theory of these effects was worked out by G. Grinstein and R. A. Pelcovits, \textit{Phys. Rev. Lett.} \textbf{47}, 856 (1981).

[40] P. C. Martin, O. Parodi, and P. S. Pershan, Phys. Rev. A \textbf{6}, 2401 (1972).

[41] W. Helfrich, Z. Naturforsch. \textbf{33a}, 305 (1978).

[42] J. S. Lintuvuori and M. R. Wilson, J. Chem. Phys. \textbf{128}, 044906 (2008).

[43] M. M. Tirado, J. G. de la Torre, and C. L. Martinez, J. Chem. Phys. \textbf{81}, 2047 (1984).

[44] K. Drescher, J. Dunkel, L. H. Cisneros, S. Ganguly, and R. E. Goldstein, Proc. Natl. Acad. Sci. USA \textbf{108}, 10940 (2011).

[45] S. Hernandez-Navarro, P. Tierno, J. Ignes-Mullol, and F. Sagues, Soft Matter \textbf{9}, 7999 (2013).