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Fluctuation-induced interactions between rods on a membrane

Ramin Golestanian
Institute for Advanced Studies in Basic Sciences, Zanjan 45195-159, Iran

Mark Goulian[*]
Exxon Research and Engineering, Annandale, New Jersey 08801

Mehran Kardar
Department of Physics, Massachusetts Institute of Technology, Cambridge, Massachusetts 02139

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We consider the interaction between two rods embedded in a fluctuating surface. The modification of fluctuations by the rods leads to an attractive long-range interaction between them. We consider fluctuations governed by either surface tension (films) or bending rigidity (membranes). In both cases the interaction falls off with the separation of the rods as $1/R^4$. The orientational part of the interaction is proportional to $\cos^2[\theta_1+\theta_2]$ in the former case and to $\cos^2[2(\theta_1+\theta_2)]$ in the latter, where θ_1 and θ_2 are angles between the rods and the line joining them. These interactions are somewhat reminiscent of dipolar forces and will tend to align collections of such rods into chains. [S1063-651X(96)07012-2]

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I. INTRODUCTION

In addition to their structural role of forming the exterior frames of the cell and its interior organelles and vesicles, lipid bilayers act as the host and regulator of many biophysical and biochemical reactions [1,2]. Inter- and intracellular recognition and transport, adhesion, regulation of ion concentrations, and energy conversion are but a few of the processes taking place at the membrane. These tasks are carried out by a variety of proteins, glycolipids, and other macromolecules that move through the many different lipids that make up the bilayer. The resulting membrane is thus far from uniform; there are even examples in which inhomogeneities occur on a larger scale, e.g., domains of phase separated lipids or two-dimensional protein assemblies. In modeling the physical properties of the cell, it is thus essential to have a good understanding of the interactions between inclusions in fluid membranes.

The pursuit of ‘‘biologically inspired’’ materials, which do not possess the full complexity of their natural counterparts, yet retain some of their useful features, is quite active. Artificial protein assemblies within lipid membranes are now routinely produced in the laboratory [3–5]. Such model-membrane systems have potential applications for targeted drug delivery and may also lead to applications such as nanoscale pumps, templates, functionalized interfaces, and chemical reactors. The appropriate design of such artificial membranes again requires an understanding of how inclusions modify the physical properties of the bilayer and how the membrane in turn contributes to the interactions between inclusions. The forces between the inclusions can be broadly subdivided into two categories [6]. The first category includes interactions that are present in the bulk of the solvent. They include the van der Waals interaction, which falls off with separation R as $1/R^6$ at long distances. The Coulomb interaction is strongly screened under physiological conditions. (Typical ion concentrations are a few hundred millimolar, which give a screening length of less than 10 Å .) Hydration and structural forces are also short ranged. The second category includes interactions that are mediated by the membrane itself: the inclusion disturbs the lipid bilayer and this disturbance propagates to neighboring inclusions (cf. [2,7,8,10] and references therein). When macroscopic thermal fluctuations are unimportant (we refer to this case as $T=0$), the resulting interactions tend to be short ranged. For example, if in the region around an inclusion the membrane is forced to deviate from its preferred thickness (∼40 Å), the resulting disturbance in the bilayer decays (heals) over a length of order this thickness [10]. Two nearby inclusions then experience an interaction that falls off exponentially with this characteristic length.

There are also long-range interactions that are mediated by the membrane. To describe such interactions, it should be possible to neglect the microscopic properties of the membrane and its molecular lipid bilayer structure and focus on its macroscopic properties. In the long-distance limit, the membrane is well described by the elastic Hamiltonian [11,12]

$$\mathcal{H}=\int dS\left[\sigma+\frac{\kappa}{2}H^2+\overline{\kappa}K\right], \tag{1}$$

where dS is the surface area element and H and K are the mean and Gaussian curvatures, respectively. The elastic properties of the surface are then described by the tension σ and the bending rigidities κ and $\overline{\kappa}.$ A finite surface tension is in general the strongest coupling in Eq. (1) and dominates the bending terms at long wavelengths. This term is present for films on a frame, interfaces at short distances, and possibly membranes subject to osmotic pressure differences be-

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[*] Present address: Center for Studies in Physics and Biology, The Rockefeller University, 1230 York Avenue, New York, NY 10021.

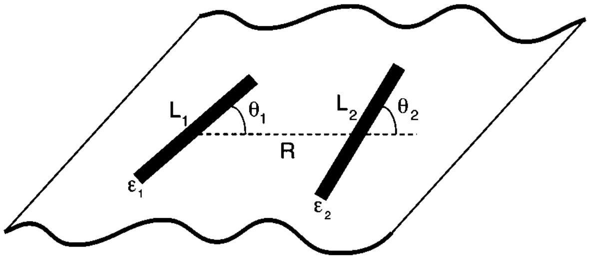

FIG. 1. Two rod-shaped inclusions embedded in a membrane. The rods are separated by a distance R. The ith rod has length L_i, width ϵ_i, and makes an angle θ_i with the line joining the centers of the two rods.

tween their interior and exterior. On the other hand, for unstressed vesicles, the surface tension is quite small and may be neglected at wavelengths well below the size of the vesicle [13–16]. In this case, the energy cost of fluctuations is controlled by the rigidity terms. For simplicity we shall refer to surface-tension-dominated surfaces as films and to rigidity controlled ones as membranes.

The long-range interactions between inclusions in a membrane that result from Eq. (1) were examined in Ref. [8]. If the inclusions are asymmetric across the bilayer and impose a local curvature, even at $T=0$, there is a long-ranged repulsive interaction that falls off with distance as $1/R^4$. The energy scale of this interaction is set by κ and $\bar{\kappa}$. On the other hand, if thermal fluctuations of the membrane are included $(T\neq 0)$, there is a $1/R^4$ interaction for *generic* inclusions. The only requirement is that the rigidity of the inclusion differs from that of the ambient membrane [8]. In particular, the interaction is attractive if the inclusions are stiffer than the membrane. The magnitude of this fluctuation-induced interaction is set by k_BT and is totally independent of the rigidities κ and $\bar{\kappa}$ [8,9].

In a recent report, we considered the dependence of the fluctuation-induced $(T\neq 0)$ interaction between rodlike inclusions on their orientations [17]. The rods are assumed to be sufficiently rigid so that they do not deform coherently with the underlying membrane. They can thus only perform rigid translations and rotations while remaining attached to the surface. As a result, the fluctuations of the membrane are constrained, having to vanish at the boundaries of the rods. Consider the situation depicted in Fig. 1, with two rods of lengths L_1 and L_2 at a separation $R\gg L_i$. For fluctuating films $(\sigma\neq 0)$, there is an attractive fluctuation-induced interaction given by

$$V_F^T(R,\theta_1,\theta_2)=-\frac{k_BT}{128}\frac{L_1^2L_2^2}{R^4}\cos^2[\theta_1+\theta_2]+O(1/R^6), \tag{2}$$

where θ_1 and θ_2 are the angles between the rods and the line adjoining their centers, as indicated in Fig. 1. This angular dependence is actually the *square* of that of a dipole-dipole interaction in two dimensions, with L_1 and L_2 as the dipole strengths. The fluctuation-induced interaction on a membrane $(\sigma=0)$ is very similar and given by

$$V_M^T(R,\theta_1,\theta_2)=-\frac{k_BT}{128}\frac{L_1^2L_2^2}{R^4}\cos^2[2(\theta_1+\theta_2)]+O(1/R^6). \tag{3}$$

The orientational dependence is the *square* of a quadrupole-quadrupole interaction, with the unusual property of being minimized for both parallel and perpendicular orientations of the rods. Note that the strength of the interaction is the same in both cases. The above fluctuation-induced interactions decay less rapidly at large distances than van der Waals forces and may play an important role in aligning asymmetric inclusions in biomembranes. Since orientational correlations are often easier to measure than forces, this result may also be useful as a probe of the fluctuation-induced interaction. Finally, this interaction could give rise to new two-dimensional structures for collections of rodlike molecules. In particular, the resemblance of the orientational part of the interaction to dipolar forces suggests that a suitable way to minimize the energy of a collection of rods is to form them into chains. (If the rods are not collinear, the interactions cannot be minimized simultaneously.) Such chainlike structures are observed for ferromagnetic particles controlled by similar forces [18].

In both [8] and [17], the calculational details are only briefly sketched. In this article we provide a detailed derivation of the fluctuation-induced interaction and justify the approximation of only working to leading order in the inclusion tilt. Asymmetric inclusions have also been recently considered in [19], where results similar to ours are reported.

II. MEMBRANES

We start with a thermally fluctuating planar membrane subject to the Hamiltonian in Eq. (1). We assume that the size of the membrane d is well below the persistence length ξ [13]. In this limit, the membrane undergoes only small fluctuations about a flat state. We may then parametrize the membrane surface with a height function $u(r)$ and approximate the full coordinate-invariant Hamiltonian of Eq. (1) by the quadratic form

$$\mathcal{H}_0=\frac{\kappa}{2}\int_{\mathbb{R}^2}d^2r[\nabla^2u(r)]^2. \tag{4}$$

Since we assume d is large (compared to R and L_i), we denote the (finite but large) reference plane by $\mathbb{R}^2$.

Now consider the situation depicted in Fig. 1, where two rigid, rodlike objects are attached to the membrane. We shall represent the rods by narrow rectangles of lengths L_1 and L_2 and widths ϵ_1 and ϵ_2, ultimately taking the limit of $\epsilon_i\to 0$. We assume that the rods are infinitely rigid and therefore must each lie in a plane. However, each rod is still free to rigidly translate up and down and rotate. We can parametrize all possible configurations of the rods by

$$u(r)|_{r\in L_i}=a_i+\mathbf{b}_i\cdot\mathbf{r} \quad \text{for } i=1,2, \tag{5}$$

where we have also used L_i to denote the ith rod. The constants a_i and $\mathbf{b}_i$ parametrize the planes that the rigid rods are constrained to lie in; variations in a_i and $\mathbf{b}_i$ correspond to rigid translations and rotations, respectively.

To calculate the partition function, we follow a procedure similar to Ref. [8] and sum over all possible configurations of the membrane, weighted by the corresponding Boltzmann factor and subject to the constraints imposed by the rods via Eq. (5). The constraints may be implemented with the aid of δ functions as in Ref. [20], leading to

$$\mathcal{Z}=\int \mathcal{D}u(r)\prod_{i=1}^{2}\int da_i d^2 b_i \times\prod_{r'\in L_i}\delta(u(r')-a_i-\mathbf{b}_i\cdot\mathbf{r}')\exp\left[-\frac{\mathcal{H}_0}{k_BT}\right]. \tag{6}$$

In Eq. (6) we have included only the leading term in an expansion in powers of $\mathbf{b}_i$. As described in Appendix A, higher-order terms come from the projection of L_i onto the x-y plane, as well as from the integration measure for $\mathbf{b}_i$, which is on the sphere of unit normals. Since $\mathbf{b}_i$ controls the gradient of $u(r)$ at the boundary of L_i, the expansion in $\mathbf{b}_i$ is in the same spirit as the gradient expansion for the Hamiltonian in Eq. (4). In Appendix A we further demonstrate that, just as in the case of anharmonic terms that have been neglected in Eq. (4), the higher-order terms in $\mathbf{b}_i$ left out from Eq. (6) are suppressed in the limit $d\ll\xi$. Expressing the δ functions as functional integrals over auxiliary fields $k_i(r)$ defined on the rods, we obtain

$$\mathcal{Z}=\int \mathcal{D}u(r)\prod_{i=1}^{2}\int da_i \mathrm{d}^2 b_i\int \mathcal{D}k_i(r) \times\exp\left[-\frac{\kappa}{2k_BT}\int_{\mathbb{R}^2}d^2r[\nabla^2u(r)]^2 +i\sum_{i=1}^{2}\int_{L_i}d^2r_i k_i(r_i)[u(r_i)-a_i-\mathbf{b}_i\cdot\mathbf{r}_i]\right]. \tag{7}$$

Integrating out $u(r)$, a_i, and $\mathbf{b}_i$, then gives

$$\mathcal{Z}=\prod_i\int \mathcal{D}k_i(r)\,\delta\left(\int_{L_i}d^2r_ik_i(r_i)\right)\delta^2\left(\int_{L_i}d^2r_i\mathbf{r}k_i(r_i)\right) \times\exp\left[-\frac{k_BT}{2\kappa}\sum_{i,j=1}^{2}\int_{L_i}d^2r_i\int_{L_j}d^2r_jk_i(r_i) \times G(\mathbf{r}_i-\mathbf{r}_j)k_j(r_j)\right], \tag{8}$$

where

$$G(\mathbf{r}-\mathbf{r}')=\left(\frac{1}{\nabla^4}\right)_{\mathbf{rr}'}=\frac{1}{8\pi}|\mathbf{r}-\mathbf{r}'|^2\ln|\mathbf{r}-\mathbf{r}'|. \tag{9}$$

Equation (8) is analogous to the partition function for a pair of plasmas confined to the interior of rods L_1 and L_2. The δ functions impose the constraints that the net charge and dipole moments vanish within each rod. When the distance R between rods is much bigger than their size (i.e., $L_i\ll R$), we may approximate $G(\mathbf{r}_1-\mathbf{r}_2)$ in Eq. (8) by a multipole expansion and keep only the leading term, which comes from the quadrupole moments

$$Q_{ab}^{(i)}\equiv\int_{L_i}d^2rr_ar_bk_i(r). \tag{10}$$

After inserting

$$1=\prod_{i=1}^{2}\int d\mathbf{Q}^{(i)}d\mathbf{g}^{(i)}\exp\left[i\sum_{a,b}g_{ab}^{(i)}\left(Q_{ab}^{(i)}-\int_{L_i}d^2rr_ar_bk_i(r)\right)\right] \tag{11}$$

into Eq. (8) and performing the multipole expansion, we obtain

$$\mathcal{Z}=\prod_i\int \mathcal{D}k_i(r)\int d\mathbf{Q}^{(i)}d\mathbf{g}^{(i)}da_id^2b_i \times\exp\left\{-\frac{k_BT}{2\kappa}\sum_i\int_{L_i}d^2rd^2r'k_i(r)G(\mathbf{r}-\mathbf{r}')k_i(r') -i\sum_i\int_{L_i}d^2rk_i(r)[a_i+\mathbf{b}_i\cdot\mathbf{r}+\mathbf{r}\cdot\mathbf{g}^{(i)}\cdot\mathbf{r}] +i\sum_i g_{ab}^{(i)}Q_{ab}^{(i)}-\frac{k_BT}{2\kappa}v[\mathbf{Q}^{(1)},\mathbf{Q}^{(2)}]\right\}, \tag{12}$$

where we have recast the δ functions in Eq. (8) in terms of integrals over a_i and $\mathbf{b}_i$. The quadrupole-quadrupole interaction is given by

$$v[\mathbf{Q}^{(1)},\mathbf{Q}^{(2)}]=\frac{1}{8\pi R^2}[Q_{aa}^{(1)}Q_{bb}^{(2)}+2Q_{ab}^{(1)}Q_{ab}^{(2)} -2Q_{aa}^{(1)}\hat{\mathbf{R}}\cdot\mathbf{Q}^{(2)}\cdot\hat{\mathbf{R}}-2Q_{aa}^{(2)}\hat{\mathbf{R}}\cdot\mathbf{Q}^{(1)}\cdot\hat{\mathbf{R}} -8\hat{\mathbf{R}}\cdot\mathbf{Q}^{(1)}\cdot\mathbf{Q}^{(2)}\cdot\hat{\mathbf{R}} +8\hat{\mathbf{R}}\cdot\mathbf{Q}^{(1)}\cdot\hat{\mathbf{R}}\hat{\mathbf{R}}\cdot\mathbf{Q}^{(2)}\cdot\hat{\mathbf{R}}]+O(1/R^3) \tag{13}$$

(with implicit summation over repeated a and b). Note that the Green's function in Eq. (9) should also contain homogeneous terms, which reflect the boundary conditions at the outer edge of the membrane $r=d$. However, we have only used the explicit form of the Green's function in computing the leading terms in the multipole expansion. As long as L_1 and L_2 are sufficiently far (compared to R) from the edge, the particular choice of boundary conditions at $r=d$ does not modify the leading terms in this expansion. The homogeneous terms can therefore be safely suppressed in Eq. (9).

We first isolate the integration over $k_1(r)$ in Eq. (12),

$$I_1\equiv\int \mathcal{D}k_1(r)\exp\left\{-\frac{k_BT}{2\kappa}\int_{L_1}d^2rd^2r'k_1(r)G(\mathbf{r}-\mathbf{r}')k_1(r') -i\int_{L_1}d^2rk_1(r)[a_1+\mathbf{b}_1\cdot\mathbf{r}+\mathbf{r}\cdot\mathbf{g}^{(1)}\cdot\mathbf{r}]\right\}. \tag{14}$$

To perform the above integration, the Green's function in Eq. (9) has to be inverted in the finite region L_1. In order to do this, we introduce an auxiliary field $h(\mathbf{r})$ and write

$$I_1=\int \mathcal{D}h(r)\exp\left[-\frac{\kappa}{2k_BT}\int_{\mathbb{R}^2}d^2r[\nabla^2 h(r)]^2\right]\times\prod_{r'\in L_1}\delta(h(r')-a_1-\mathbf{b}_1\cdot\mathbf{r}-\mathbf{r}\cdot\mathbf{g}^{(1)}\cdot\mathbf{r}). \tag{15}$$

This is just the partition of a membrane constrained by a single rod. After evaluating the contribution on L_1 (via the δ function), we are left with

$$I_1=\exp\left[-\frac{2\kappa}{k_BT}\epsilon_1 L_1(g^{(1)}_{aa})^2\right]\times\int{}'\mathcal{D}h(r)\exp\left[-\frac{\kappa}{2k_BT}\int_{\mathbb{R}^2-L_1}d^2r[\nabla^2h(r)]^2\right], \tag{16}$$

where the prime indicates that the function $h(r)$ and its normal gradient are constrained to satisfy the following conditions on the boundary ∂L_1 of L_1:

$$h(r)|_{r\in\partial L_1}=a_1+\mathbf{b}_1\cdot\mathbf{r}+\mathbf{r}\cdot\mathbf{g}^{(1)}\cdot\mathbf{r},$$

$$\frac{\partial h(r)}{\partial\mathbf{n}}\Big|_{r\in\partial L_1}=\frac{\partial}{\partial\mathbf{n}}(a_1+\mathbf{b}_1\cdot\mathbf{r}+\mathbf{r}\cdot\mathbf{g}^{(1)}\cdot\mathbf{r}). \tag{17}$$

Now let $h_0(r)$ denote a solution to the biharmonic equation

$$\nabla^4 h_0=0 \tag{18}$$

on $\mathbb{R}^2-L_1$ with the boundary conditions of Eqs. (17). We then set

$$h(r)=h_0(r)+\delta h(r),$$

where both $\delta h(r)$ and its normal gradient are zero on the boundary of L_1. Following this change of variables,

$$I_1=A\exp\left[-\frac{2\kappa}{k_BT}\epsilon_1L_1(g^{(1)}_{aa})^2\right]\times\exp\left[-\frac{\kappa}{2k_BT}\int_{\mathbb{R}^2-L_1}d^2r[\nabla^2h_0(r)]^2\right], \tag{19}$$

where

$$A=\int\mathcal{D}\delta h(r)\exp\left[-\frac{\kappa}{2k_BT}\int_{\mathbb{R}^2-L_1}d^2r[\nabla^2\delta h(r)]^2\right]$$

is a normalization constant, independent of a, $\mathbf{b}$, and $\mathbf{g}$, which does not affect the remaining computations. In order to solve Eq. (18) we must specify the boundary conditions at $r=d$, which are the same as those for $u(r)$. As discussed earlier, the results should be independent of this choice, and it is convenient to select

$$h|_{r=d}=\frac{\partial h}{\partial r}\Big|_{r=d}=0. \tag{20}$$

As shown in Appendix B, the solution for the case when the rod is along the y axis, in the limit $d\gg L_1$, gives

$$\int_{\mathbb{R}^2-L_1}d^2r[\nabla^2h_0(r)]^2=2\pi(L_1g^{(1)}_{xy})^2+\frac{1}{\ln(4d/L_1)}[s_1b^2_{1x}+s_2b^2_{1y}]+O(L_1/d), \tag{21}$$

where s_i are numerical constants. The second term on the right-hand side of Eq. (21) is examined in Appendix A, where the irrelevance of higher-order terms in $\mathbf{b}$ is demonstrated. In the limit $d\gg L_1$, it suffices to keep only the first term on the right-hand side of Eq. (21), which gives

$$I_1=A\ \exp\left\{-\frac{\kappa}{k_BT}[2\epsilon_1L_1(g^{(1)}_{aa})^2+\pi(L_1g^{(1)}_{xy})^2]\right\}. \tag{22}$$

The result of the $k_2(r)$ integration in Eq. (12) is similar, with the index 2 replacing 1 and with the coordinate axis appropriately rotated to align with the second rod. The overall expression for the partition function now reads (dropping unimportant multiplicative constants)

$$\mathcal{Z}=\prod_{i=1}^{2}\int d\mathbf{Q}^{(i)}d\mathbf{g}^{(i)}\exp\left\{-\frac{\pi\kappa}{k_BT}[(L_1g^{(1)}_{x'y'})^2+(L_2g^{(2)}_{x''y''})^2]\right\}\exp\left\{-i\sum_i g^{(i)}_{ab}Q^{(i)}_{ab}-\frac{k_BT}{2\kappa}v[\mathbf{Q}^{(1)},\mathbf{Q}^{(2)}]\right\}, \tag{23}$$

where we have set the widths of the rods to zero (i.e., taken the $\epsilon_i\to0$ limit). The primed indices x',y',x'',y'' indicate that the corresponding components are with respect to the coordinate frames where $L_1\|y'$ and $L_2\|y''$. We define an unprimed coordinate system such that the x axis is parallel to $\hat{R}$ and the two rods make angles of θ_1 and θ_2 with respect to the x axis as in Fig. 1. Integration over $\mathbf{g}$ yields

$$\begin{aligned}\mathcal{Z}=\prod_{i=1}^{2}\int d\mathbf{Q}^{(i)}\,&\delta(Q^{(i)}_{xx}\cos^2\theta_i+Q^{(i)}_{xy}\sin2\theta_i+Q^{(i)}_{yy}\sin^2\theta_i)\,\delta(Q^{(i)}_{xx}\sin^2\theta_i-Q^{(i)}_{xy}\sin2\theta_i\\&+Q^{(i)}_{yy}\cos^2\theta_i)\exp\left\{-\frac{k_BT}{2\kappa}\left[\sum_i\frac{1}{2\pi L_i^2}\times\left(\frac{1}{2}(Q^{(i)}_{yy}-Q^{(i)}_{xx})\sin2\theta_i+Q^{(i)}_{xy}\cos2\theta_i\right)^2\right]\right\}\\&\times\exp\left\{-\frac{k_BT}{2\kappa}v[\mathbf{Q}^{(1)},\mathbf{Q}^{(2)}]\right\}.\end{aligned} \tag{24}$$

Since we are working in the large-R limit, the $\mathbf{Q}$ integrations are most easily performed by expanding Eq. (24) to second order in v. After expanding $-k_BT\ \ln\mathcal{Z}$, we find the (R,θ_1,θ_2)-dependent part of the free energy given in Eq. (3). We can rewrite this interaction in a coordinate invariant form, in terms of the vector $\hat{\mathbf{R}}$ and the directors $\hat{\mathbf{L}}_1$ and $\hat{\mathbf{L}}_2$ along the rods, as

$$V_M^T = -\frac{k_BT}{128}\frac{L_1^2L_2^2}{R^4}\{2[2(\hat{\mathbf{L}}_1\cdot\hat{\mathbf{R}})(\hat{\mathbf{L}}_2\cdot\hat{\mathbf{R}})-\hat{\mathbf{L}}_1\cdot\hat{\mathbf{L}}_2]^2-1\}^2$$
$$+O(1/R^6). \tag{25}$$

III. FILMS

We now turn to the analogous calculation for films. Again we use a Gaussian approximation for the Hamiltonian in Eq. (1), but keep only the surface tension this time,

$$\mathcal{H}_0 = \frac{\sigma}{2}\int d^2r[\nabla u(r)]^2. \tag{26}$$

All anharmonic corrections to the above expression are unimportant in the limit $\sigma a^2 \gg k_BT$, where a is a microscopic length. We follow a procedure similar to that described in Sec. II, but with the differences noted below. The expression for the partition function is similar to Eq. (6), with $\mathcal{H}_0$ now given by Eq. (26). For films, however, we cannot justify keeping only the leading terms in an expansion in $\mathbf{b}_i$. Thus the full rotationally invariant measure of integration on the sphere of slopes $\mathbf{b}_i$ should be employed (see Appendix A). Also, the appropriate domain replacing L_i is the projected length $\overline{L}_i \equiv L_i/\sqrt{1+b_{iy}^2}$. After introducing auxiliary fields $k_i(r)$ as in Sec. II, the analog of Eq. (8) may be written as

$$\mathcal{Z} = \prod_i \int \frac{d^2b_i}{(1+\mathbf{b}_i^2)^{3/2}}\int \mathcal{D}k_i(r)\,\delta\left(\int_{\overline{L}_i} d^2r_ik_i(r_i)\right)$$
$$\times\exp\left[-\frac{k_BT}{2\sigma}\sum_{i,j=1}^{2}\int_{\overline{L}_i}d^2r_i\int_{\overline{L}_j}d^2r_jk_i(r_i)\right.$$
$$\left.\times\mathcal{G}(\mathbf{r}_i-\mathbf{r}_j)k_j(r_j)-i\sum_i\mathbf{b}_i\cdot\int_{\overline{L}_i}d^2r_i\mathbf{r}_ik_i(r_i)\right], \tag{27}$$

where

$$\mathcal{G}(\mathbf{r}-\mathbf{r}') = \left(\frac{1}{-\nabla^2}\right)_{\mathbf{rr}'} = \frac{1}{2\pi}\ln|\mathbf{r}-\mathbf{r}'|. \tag{28}$$

Note that for films, the dipole moment of $k_i(r)$ does not vanish. Expanding $\mathcal{G}(\mathbf{r}-\mathbf{r}')$ in a multipole expansion and keeping only the leading term, which now comes from the dipole moments $\mathbf{p}_i \equiv \int \mathbf{r}k_i(r)$, we find

$$\mathcal{Z} = \prod_i \int \mathcal{D}k_i(r)\int d\mathbf{p}^{(i)}d\mathbf{g}_ida_i\frac{d^2b_i}{(1+\mathbf{b}_i^2)^{3/2}}$$
$$\times\exp\left\{-\frac{k_BT}{2\sigma}\sum_i\int_{\overline{L}_i}d^2rd^2r'k_i(r)\mathcal{G}(\mathbf{r}-\mathbf{r}')k_i(r')\right.$$
$$-i\sum_i\int_{\overline{L}_i}d^2rk_i(r)[a_i+(\mathbf{b}_i+\mathbf{g}_i)\cdot\mathbf{r}]+i\sum_i\mathbf{g}_i\cdot\mathbf{p}^{(i)}$$
$$\left.-\frac{k_BT}{2\sigma}u[\mathbf{p}^{(1)},\mathbf{p}^{(2)}]\right\}, \tag{29}$$

where

$$u[\mathbf{p}^{(1)},\mathbf{p}^{(2)}] = -\frac{1}{\pi R^2}[\mathbf{p}^{(1)}\cdot\mathbf{p}^{(2)}-2(\mathbf{p}^{(1)}\cdot\hat{\mathbf{R}})(\mathbf{p}^{(2)}\cdot\hat{\mathbf{R}})] \tag{30}$$

is the effective dipole-dipole interaction, analogous to Eq. (13), and $\mathbf{g}_i$ is the variable conjugate to $\mathbf{p}^{(i)}$. We integrate out $k_i(r)$ as in Sec. II by introducing an auxiliary field $h(r)$. In this case we must solve a harmonic equation on $\mathbb{R}^2-\overline{L}_i$, instead of the biharmonic Eq. (18), with the boundary condition on $\overline{L}_i$,

$$h_0(r)|_{r\in\partial\overline{L}_i} = a_i+(\mathbf{b}_i+\mathbf{g}_i)\cdot\mathbf{r}. \tag{31}$$

The harmonic problem can be solved either by a method similar to that described in Appendix B or by conformal mapping. The resulting expression for the partition function reads

$$\mathcal{Z} = \prod_i \int d\mathbf{p}^{(i)}d\mathbf{g}_i\frac{d^2b_i}{(1+\mathbf{b}_i^2)^{3/2}}\exp\left[-\frac{\sigma}{2k_BT}\right.$$
$$\times\left(\frac{\pi}{4}\overline{L_1}^2(b_{1y'}+g_{1y'})^2+\frac{\pi}{4}\overline{L_2}^2(b_{2y''}+g_{2y''})^2\right)$$
$$\left.+i\sum_i\mathbf{g}_i\cdot\mathbf{p}^{(i)}-\frac{k_BT}{2\sigma}u[\mathbf{p}^{(1)},\mathbf{p}^{(2)}]\right], \tag{32}$$

where the meaning of the primes is the same as in Sec. II. One can now see explicitly that the higher-order terms in the expansion in $\mathbf{b}_i$ are important in this case. The remaining integrations, except those of $b_{1y'}$ and $b_{2y''}$, can be performed in a straightforward manner. The latter two integrals are rather complicated and in order to get a simple result, we restrict ourselves to the case $\sigma L^2(L^2/R^2) \ll k_BT$. In this limit, the integrals can be approximated by Gaussian forms. After expanding $-k_BT\ln\mathcal{Z}$, we find Eq. (2), which can be expressed in a coordinate invariant form, in terms of the vector $\hat{\mathbf{R}}$ and the directors $\hat{\mathbf{L}}_1$ and $\hat{\mathbf{L}}_2$ along the rods, as

$$V_F^T = -\frac{k_BT}{128}\frac{L_1^2L_2^2}{R^4}[2(\hat{\mathbf{L}}_1\cdot\hat{\mathbf{R}})(\hat{\mathbf{L}}_2\cdot\hat{\mathbf{R}})-\hat{\mathbf{L}}_1\cdot\hat{\mathbf{L}}_2]^2+O(1/R^6). \tag{33}$$

IV. DISCUSSION

We shall now discuss some general aspects of the fluctuation-induced interactions Eqs. (2) and (3). The magnitudes are solely determined by k_BT and are independent of the tension and rigidity coefficients σ and κ. This is a signature of the entropic nature of the interactions. The number of allowed modes in the membrane is independent of the membrane elastic constants; however, it does depend on the position and orientation of the rods. Note that, although the total entropy of the membrane modes diverges, the contribution that depends on the rods' orientations and separation is finite. (A similar effect is seen in the Casimir effect and other fluctuation-induced interactions; cf. [20] and references therein.) In the above calculations we have taken the rods to be infinitely rigid. This approximation holds in the limit that the rod elastic constants are much larger than those of the membrane; for sufficiently large values of the membrane

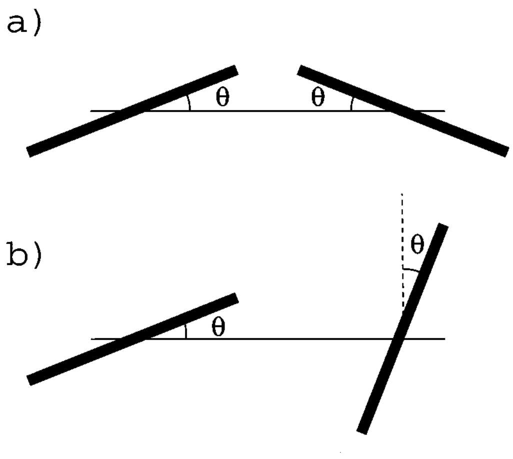

FIG. 2. Minimal-energy orientations for two rods in a membrane [(a) and (b)] and a film [(a) only]. The energy is minimal for all values of θ.

bending energy, the above results will break down. Thus if we denote the bending rigidity of the rods by κ_r, we expect the leading correction to Eq. (3) to be of order κ/κ_r; similar considerations apply for films. An explicit calculation of the fluctuation-induced interaction for disks in the limit in which the inclusion and membrane elastic constants are comparable is described in [8].

For both membranes and films, the interaction falls off with distance as $1/R^4$. Since the direct van der Waals interactions between inclusions still fall off as $1/R^6$, the forces mediated through the two-dimensional surface will always asymptotically dominate. Of course, the dimensional dependence of R^4 is canceled by a product of lengths in the numerator. For spherical inclusions, this is given by the product of two inclusion areas (see Ref. [8]) and for rods by the product of the squares of their lengths. Presumably, for general shapes, there is a formula that interpolates between these two limits. Another potential extension is to a polymer floating on a membrane. The interplay between the elasticity and shapes of a polymer and membrane, neglecting membrane fluctuations, has been examined in [21]; an extension to the case of a fluctuating membrane has also recently appeared [22]. There is also interesting behavior in the opposite limit of $R \ll L$ for the interaction between two parallel semiflexible polymers [23].

Finally, the most interesting aspect of our calculation is the orientational dependence of the force. This is most easily discussed for the film, where an intermediate stage involves calculating the angular dependence of a dipole-dipole interaction, which is subsequently squared. The final angular dependence is thus that of *squared dipolar interactions*. Similarly, the result for the membrane corresponds to *squared quadrupolar interactions*. The minimal-energy orientations are shown in Fig. 2; note that there is a large degeneracy. We also note that these interactions cannot be obtained by adding two-body potentials on the rods: To find the orientational dependence of additive forces, let us consider an interaction $U(|r_1 - r_2|) du_1 du_2$ between any two infinitesimal segments of two rods of length L at a distance $R \gg L$. Expanding $|r_1 - r_2|$ and integrating over the two rods leads to the interaction

$$V(R,\theta_1,\theta_2) = L^2 U(R) + \frac{L^4}{6}\left(\frac{U'(R)}{R} + U''(R)\right) - \frac{L^4}{12}\left(\frac{U'(R)}{R} - U''(R)\right)(\cos 2\theta_1 + \cos 2\theta_2). \tag{34}$$

Note that the angular dependence is now completely different and minimized when the two rods are parallel to their axis of separation. Presumably both interactions are present for rods of finite thickness; the additive interaction is proportional to $L^2(L\epsilon/R)^2$, where ϵ is the thickness. The previously calculated interactions are thus larger by a factor proportional to $(R/\epsilon)^2$ and should dominate at large separations.

The unusual dependence on orientation in Eqs. (2) and (3) could lead to new types of orientational ordering in ensembles of rod-shaped particles. Of course, due to the nonadditive nature of the forces, the fluctuation-induced interaction should be calculated separately for each arrangement. However, a cursory examination suggests that three-body and higher-order interactions fall off with separation as $1/R^6$. Thus, for $R \gg L$, a collection of rods can be treated as if they interact through additive pair potentials. It is amusing to examine the minimum of such an interaction for three rods placed on the vertices of an equilateral triangle. One possible equilibrium configuration is a three arm star with the relative angles of $2\pi/3$ between the rods. Interestingly, this so-called ''triskelion'' structure is indeed formed by three rodlike ''clathrin'' proteins [1]. (Another stable configuration has each rod parallel to the corresponding side of the equilateral triangle.) Of course, given the relative proximity of the three proteins, it is not clear that the asymptotic interactions of Eq. (3) are applicable to this case. Another generic aspect of dipole and quadrupolar interactions is that they are frustrated (i.e., cannot be simultaneously minimized with respect to the orientations) if the rod centers are not aligned. There may thus be an overall tendency to arrange rod-shaped molecules into chains. (Naturally this effect competes with the tendency to aggregate the inclusions together.) We hope that the orientational-dependent interactions calculated in this paper will provide a fresh perspective on the behavior of inclusions in biological membranes.

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APPENDIX A: INTEGRATION OVER TILT ANGLES

In this appendix we examine the higher-order terms in the tilts of the rods $\mathbf{b}_i$ and show that they may be neglected. For simplicity we shall focus on $\mathbf{b}_1$; similar arguments apply to $\mathbf{b}_2$. Whenever possible we drop the index and use $\mathbf{b} \equiv \mathbf{b}_1$ and $L \equiv L_1$. The integration for $\mathbf{b}$ must be performed over all possible orientations of the rod L in the three-dimensional embedding space. The manifold of orientations is the unit sphere. In terms of the vector $\mathbf{b}$, defined in Eq. (5), the rotation invariant measure on the unit sphere is given by

$$d\Omega=\frac{d^2b}{(1+\mathbf{b}^2)^{3/2}}. \tag{A1}$$

The leading term of the expansion of Eq. (A1) in $\mathbf{b}$, d^2b, was used as the integration measure in Eq. (6). Additional $\mathbf{b}$ dependence comes from the projection of the tilted rods onto the x-y reference plane. For example, the conditions imposed in Eq. (5) do not really apply for $r\in L$ but rather for r in the projected image of L, which is a rod of length $L/(1+b_y^2)^{1/2}$. Again, in Eq. (6) we have taken the leading order in an expansion in $\mathbf{b}$ by setting $1/(1+b_y^2)^{1/2}\approx 1$.

We shall now demonstrate that the higher-order terms in $\mathbf{b}$ can be neglected [as discussed after Eq. (6)]. The argument is presented explicitly for terms of order $\mathbf{b}^2$, but is easily extended to higher orders. Including the first corrections to Eq. (7) results in

$$\mathcal{Z}\equiv\int \mathcal{D}u(r)\prod_{i=1}^{2}\mathcal{D}k_i(r)\,da_i\,d^2b_i(1+\Gamma_x b_x^2+\Gamma_y b_y^2)\times\exp\left[-\frac{\kappa}{2k_BT}\int d^2r[\nabla^2u(r)]^2+i\sum_i\int_{L_i}d^2r_i k_i(r_i)[u(r_i)-a_i-\mathbf{b}_i\cdot\mathbf{r}_i]\right], \tag{A2}$$

where Γ_x and Γ_y are independent of $\mathbf{b}$. If, as in Sec. II, only the leading term is retained, the integration over $\mathbf{b}$ leads to the constraint that the dipole moment $k_1(r)$ must be zero [see Eqs. (7) and (8)]. Due to the higher-order terms in $\mathbf{b}$, this constraint is modified and we have to take into account the dipole moment

$$\mathbf{p}\equiv\int_{L_1}d^2r\,\mathbf{r}\,k_1(r). \tag{A3}$$

Following the same procedure used for the quadrupole moment in Sec. II, we introduce an auxiliary variable $\mathbf{f}$, via

$$1=\int d\mathbf{p}\,d\mathbf{f}\,\exp\left[i\mathbf{f}\cdot\left(\mathbf{p}-\int_{L_1}d^2r\,\mathbf{r}\,k_1(r)\right)\right]. \tag{A4}$$

Inserting Eqs. (A4) and (11) into Eq. (A2) and performing the multipole expansion gives

$$\mathcal{Z}=\int\prod_i \mathcal{D}k_i(r)\,d\mathbf{Q}^{(i)}da_i\,d\mathbf{g}^{(i)}d\mathbf{b}_2\,d\mathbf{b}\,d\mathbf{f}\,d\mathbf{p}\times(1+\Gamma_x b_x^2+\Gamma_y b_y^2)\times\exp\left\{-\frac{k_BT}{2\kappa}\int_{L_1}d^2r\,d^2r'\,k_1(r)G(\mathbf{r}-\mathbf{r}')k_1(r')-i(\mathbf{b}-\mathbf{f})\cdot\mathbf{p}-i\int_{L_1}d^2r\,k_1(r)[a_1+\mathbf{f}\cdot\mathbf{r}+\mathbf{r}\cdot\mathbf{g}^{(1)}\cdot\mathbf{r}]\right\}\times\cdots. \tag{A5}$$

In the above equation, the ellipsis denotes factors that are independent of $k_1(r)$, $\mathbf{b}$, and $\mathbf{f}$ and identical to the corresponding terms in Eq. (12) with the exception that $v[\mathbf{Q}^{(1)},\mathbf{Q}^{(2)}]$ is replaced by $v[\mathbf{p},\mathbf{Q}^{(1)},\mathbf{Q}^{(2)}]$, i.e., the multipole energy now also depends on $\mathbf{p}$. The integration over $k_1(r)$ is the same as in Eq. (14), except that $\mathbf{b}_1$ is replaced by $\mathbf{f}$. Thus, after substituting $\mathbf{f}$ for $\mathbf{b}_1$ in Eq. (21), we are left with the modified integrals

$$\mathcal{Z}=\int d\mathbf{b}\,d\mathbf{f}\,d\mathbf{p}\,\exp\left[-\frac{\kappa}{2k_BT\,\ln(4d/L)}(s_1f_x^2+s_2f_y^2)-i(\mathbf{b}-\mathbf{f})\cdot\mathbf{p}\right](1+\Gamma_x{b_x}^2+\Gamma_y{b_y}^2)\times(W_0+W_{1x}p_x^2+W_{1y}p_y^2+\cdots). \tag{A6}$$

In the above equation, $\{W_0,W_{1x},W_{1y},\ldots\}$ refer to the results of the remaining integrations, which are performed after expanding $\exp[-k_BTv(\mathbf{p},\mathbf{Q}^{(1)},\mathbf{Q}^{(2)})/2\kappa]$ in powers of $\mathbf{p}$ and are independent of $\mathbf{p}$, $\mathbf{b}$, and $\mathbf{f}$. After integrating over $\mathbf{f}$ and dropping an unimportant constant, we obtain

$$\mathcal{Z}=\int d\mathbf{b}\,d\mathbf{p}\,\exp[-i\mathbf{b}\cdot\mathbf{p}](1+\Gamma_x{b_x}^2+\Gamma_y{b_y}^2)\times\left[W_0-W_0\frac{k_BT\,\ln(4d/L)}{2\kappa}\left(\frac{p_x^2}{s_1}+\frac{p_y^2}{s_2}\right)+\cdots\right]. \tag{A7}$$

Note that the W_{1x} and W_{1y} have been dropped since they are subleading in the limit $d\gg L$. Integrating over $\mathbf{b}$ and $\mathbf{p}$ then gives

$$\mathcal{Z}=W_0+W_0\frac{k_BT\,\ln(4d/L)}{\kappa}\left(\frac{\Gamma_x}{s_1}+\frac{\Gamma_y}{s_2}\right)+\cdots. \tag{A8}$$

As discussed in Sec. II, we assume that the size of the membrane is much less than the persistence length ξ. Thus the higher-order terms in the expansion in Eq. (A8) are smaller by powers of

$$\frac{k_BT\,\ln(4d/L)}{\kappa}\approx\frac{\ln(d/L)}{\ln(\xi/a)}\ll 1. \tag{A9}$$

Here we have used the result [13] $\xi\approx a\,\exp(2\pi\kappa/k_BT)$, with a short-distance cutoff a of order molecular size, leading to the hierarchy of length scales $a<L\ll d\ll\xi$. To leading order, then, we have $\mathcal{Z}=W_0$, which is independent of Γ_x and Γ_y and therefore the lowest-order term in the expansion in b. It is interesting to note that the above argument does not hold for films controlled by surface tension, as discussed in Sec. III.

APPENDIX B: SOLUTION OF THE BIHARMONIC EQUATION

The biharmonic equation [Eq. (18)] for a single rod is discussed in detail in this appendix. The problem is to find the solution to

$$\nabla^4h=0 \tag{B1}$$

on a finite disk of radius d from which a line segment of length L along the y axis has been removed. The boundary conditions are

$$h\left(x=0,-\frac{L}{2}\leqslant y\leqslant\frac{L}{2}\right)=a+b_y y+g_{yy}y^2, \tag{B2}$$

$$\frac{\partial}{\partial x}h\left(x=0,-\frac{L}{2}\leqslant y\leqslant\frac{L}{2}\right)=b_x+2g_{xy}y,$$

$$h(d)=0,$$

$$\frac{\partial}{\partial r}h(d)=0.$$

Note that for the boundary conditions, the derivatives are taken before the limit $\epsilon\to 0$. It turns out to be easier to impose a weaker boundary condition at $r=d$, namely,

$$h(d)=O\left(\frac{L}{d}\right),\quad \frac{\partial}{\partial r}h(d)=O\left(\frac{L}{d}\right). \tag{B3}$$

Since we have $d\gg L$, it will suffice to keep the leading terms in the limit $L/d\to 0$. Performing the integration by parts yields

$$\begin{aligned}\int_{\mathbb{R}^2-L}d^2r(\nabla^2 h)^2&=\int_{\partial(\mathbb{R}^2-L)}dl\left(\nabla^2 h\frac{\partial h}{\partial n}-h\frac{\partial\nabla^2 h}{\partial n}\right)\\&=\int_{-L/2}^{L/2}dy\left(h(0,y)f_1(y)-\frac{\partial h}{\partial x}(0,y)f_2(y)\right),\end{aligned} \tag{B4}$$

where

$$f_1(y)=\left.\frac{\partial\nabla^2 h}{\partial x}\right|_{x=0^+}-\left.\frac{\partial\nabla^2 h}{\partial x}\right|_{x=0^-}, \tag{B5}$$

$$f_2(y)=\nabla^2 h|_{x=0^+}-\nabla^2 h|_{x=0^-},$$

and, as in the text, we have denoted the finite disk of radius d by $\mathbb{R}^2$ for simplicity. It is easy to check that the above boundary value problem on $\mathbb{R}^2-L$ is completely equivalent to the problem

$$\nabla^4 h=f_1(y)\,\delta(x)+f_2(y)\frac{\partial}{\partial x}\delta(x) \tag{B6}$$

on $\mathbb{R}^2$, provided that the conditions in Eqs. (B3) at $r=d$ are satisfied. The solution to Eq. (B6) can be given in terms of the unknown functions $f_1(y)$ and $f_2(y)$ as

$$\begin{aligned}h(x,y)=&\int_{-L/2}^{L/2}dy'\,G_1(x,y;x'=0,y')f_1(y')\\&+\int_{-L/2}^{L/2}dy'\,G_2(x,y;x'=0,y')f_2(y').\end{aligned} \tag{B7}$$

The Green's functions G_i, which satisfy

$$\nabla^4 G_1(x,y;x',y')=\delta(x-x')\,\delta(y-y'), \tag{B8}$$

$$\nabla^4 G_2(x,y;x',y')=\frac{\partial}{\partial x}\delta(x-x')\,\delta(y-y')$$

and obey the conditions in Eq. (B12) at $r=d$, are given by

$$\begin{aligned}G_1(x,y,y')=&\frac{1}{16\pi}[x^2+(y-y')^2]\ln\left[\frac{x^2+(y-y')^2}{d^2}\right]\\&+\frac{1}{8\pi}\frac{yy'}{d^2}(r^2+r'^2)+\frac{1}{16\pi}[d^2-r^2-r'^2],\end{aligned} \tag{B9}$$

$$\begin{aligned}G_2(x,y,y')=\frac{x}{8\pi}\Bigg\{&\ln\left[\frac{x^2+(y-y')^2}{d^2}\right]+2\frac{yy'}{d^2}+1\\&-\left(\frac{r^2+r'^2}{d^2}\right)\Bigg\}.\end{aligned}$$

Note that the boundary conditions in Eq. (B3) do not uniquely specify G_1 and G_2, but allow different choices that differ by subleading $O(L/d)$ terms at $r=d$. Indeed the asymmetry in G_1 with respect to the interchange of x and $y-y'$ is a result of this freedom. If we require h and $\partial h/\partial r$ to vanish at $r=d$, then G_1 would be rotationally symmetric. The unknown functions f_i in the above solution can now be obtained self-consistently by matching to the known forms of h and $\partial h/\partial x$ on L, as given by the boundary conditions in Eq. (B2). We thus end up with the integral equations

$$a+b_y y+g_{yy}y^2=\int_{-L/2}^{L/2}dy'\,G_1(x=0,y;x'=0,y')f_1(y'), \tag{B10}$$

$$b_x+2g_{xy}y=\int_{-L/2}^{L/2}dy'\frac{\partial}{\partial x}G_2(x=0,y;x'=0,y')f_2(y'). \tag{B11}$$

(Note that at $x=0$, G_2 and $\partial G_1/\partial x$ are both identically zero.) We start with Eq. (B11) for $f_2(y)$, which is somewhat easier to solve. After changing variables to $y=(L\cos\phi)/2$ and $y'=(L\cos\phi')/2$, this equation reads

$$b_x+Lg_{xy}\cos\phi=\frac{L}{2}\int_0^{\pi}d\phi'\sin\phi' f_2\left(\frac{L}{2}\cos\phi'\right)G'(\phi,\phi'), \tag{B12}$$

where

$$G'(\phi,\phi')=\frac{1}{8\pi}\left[2\ln(2|\cos\phi-\cos\phi'|)-2\ln\left(\frac{4d}{L}\right)+1\right]. \tag{B13}$$

We now use the expansion [24]

$$\ln(2|\cos\phi-\cos\phi'|)=-\sum_{n=1}^{\infty}\frac{2}{n}\cos n\phi\,\cos n\phi' \tag{B14}$$

and define a series

$$\sin\phi' f_2\left(\frac{L}{2}\cos\phi'\right)=\sum_{m=0}^{\infty} a_m \cos m\phi' . \tag{B15}$$

Solving Eq. (B12) for the a_m's gives, to leading order in $d \gg L$,

$$f_2\left(\frac{L}{2}\cos\phi'\right)=\frac{1}{\sin\phi'}\left[\frac{-8b_x}{L\ln\left(\frac{4d}{L}\right)}-8g_{xy}\cos\phi'\right]. \tag{B16}$$

The integral equation for f_1 requires more care. First, note that the choice of G_1 in Eq. (B9) does not lead to a vanishing normal derivative at $r=d$ unless the condition

$$\int_{-L/2}^{L/2} dy' y'^2 f_1(y')=0 \tag{B17}$$

is satisfied. Setting up the expansion

$$\sin\phi' f_1\left(\frac{L}{2}\cos\phi'\right)=\sum_{m=0}^{\infty} b_m \cos m\phi' \tag{B18}$$

for f_1, this requirement implies

$$2b_0+b_2=0. \tag{B19}$$

The integral equation (B10) can now be written as

$$a+\frac{L^2}{8}g_{yy}+\frac{L}{2}b_y\cos\phi+\frac{L^2}{8}g_{yy}\cos 2\phi$$
$$=\frac{L}{2}\int_0^{\pi} d\phi' \sin\phi' f_1\left(\frac{L}{2}\cos\phi'\right)G(\phi,\phi'), \tag{B20}$$

where

$$G(\phi,\phi')=\frac{L^2}{32\pi}\left[(\cos\phi-\cos\phi')^2\ln(2|\cos\phi-\cos\phi'|)-(\cos\phi-\cos\phi')^2\ln\left(\frac{4d}{L}\right)+2\frac{d^2}{L^2}-\frac{1}{2}\cos^2\phi\right]$$
$$=-\frac{L^2}{32\pi}\Bigg(-2\frac{d^2}{L^2}+\ln\left(\frac{4d}{L}\right)-\frac{3}{4}+\left[-\frac{3}{4}+\frac{1}{2}\ln\left(\frac{4d}{L}\right)\right]\cos 2\phi'$$
$$+\cos\phi\left\{\left[\frac{5}{2}-2\ln\left(\frac{4d}{L}\right)\right]\cos\phi'+\frac{1}{6}\cos 3\phi'\right\}+\cos 2\phi\left[-\frac{1}{2}+\frac{1}{2}\ln\left(\frac{4d}{L}\right)-\frac{1}{3}\cos 2\phi'+\frac{1}{24}\cos 4\phi'\right]$$
$$+\sum_{n=3}^{\infty}\cos n\phi\Bigg[\left(\frac{2}{n}-\frac{1}{n-1}-\frac{1}{n+1}\right)\cos n\phi'+\frac{1}{2}\left(\frac{1}{n+2}+\frac{1}{n}-\frac{2}{n+1}\right)\cos(n+2)\phi'+\frac{1}{2}\Bigg(\frac{1}{n-2}+\frac{1}{n}$$
$$-\frac{2}{n-1}\Bigg)\cos(n-2)\phi'\Bigg]\Bigg). \tag{B21}$$

In going to the second form of $G(\phi,\phi')$ in Eq. (B21), we have used the expansion in Eq. (B14) and rearranged the resulting expression as a series expansion so that it resembles the left-hand side of the integral equation. Substituting the expansion of Eq. (B18) in the integral equation (B20) and equating the coefficients of $\cos n\phi$ on both sides, we obtain the following set of linear equations for the b_n:

$$\left(\frac{2}{n}-\frac{1}{n-1}-\frac{1}{n+1}\right)b_n+\frac{1}{2}\left(\frac{1}{n+2}+\frac{1}{n}-\frac{2}{n+1}\right)b_{n+2}$$
$$+\frac{1}{2}\left(\frac{1}{n-2}+\frac{1}{n}-\frac{2}{n-1}\right)b_{n-2}=0 \quad (n>2), \tag{B22a}$$

$$\left[\frac{5}{2}-2\ln\left(\frac{4d}{L}\right)\right]b_1+\frac{1}{6}b_3=-\frac{64}{L^2}b_y , \tag{B22b}$$

$$2\left[-2\frac{d^2}{L^2}+\ln\left(\frac{4d}{L}\right)-\frac{3}{4}\right]b_0+\left[-\frac{3}{4}+\frac{1}{2}\ln\left(\frac{4d}{L}\right)\right]b_2$$
$$=-\frac{128}{L^3}a-\frac{16}{L}g_{yy} , \tag{B22c}$$

$$2\left[-\frac{1}{2}+\frac{1}{2}\ln\left(\frac{4d}{L}\right)\right]b_0-\frac{1}{3}b_2+\frac{1}{24}b_4=-\frac{16}{L}g_{yy} . \tag{B22d}$$

The solution to the above equations is (to leading order in $d \gg L$)

$$b_0=\left(\frac{L^2}{d^2}\right)\left[\frac{4}{L}g_{yy}+\frac{32}{L^3}a\right], \tag{B23}$$

$$b_1=\frac{32}{L^2\ln\left(\frac{4d}{L}\right)}b_y,$$

$$b_2=-2\left(\frac{L^2}{d^2}\right)\left[\frac{4}{L}g_{yy}+\frac{32}{L^3}a\right],$$

$$b_3=0,$$

$$b_4=-\frac{384}{L}g_{yy}$$

and all other b_n are determined by the recursion relation (B22a). Putting the results for f_1 and f_2 into Eq. (B4), we find Eq. (21), with $s_1=s_2=4\pi$.

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[9] The expression for $\mathcal{H}$ below Eq. (8) in Ref. [8] should read

$$\mathcal{H}=\frac{(k_BT)^2}{64\kappa_0 A}\left(Q^{(1)}_{ij}Q^{(1)}_{ji}+2Q^{(1)}_{ii}+Q^{(2)}_{ij}Q^{(2)}_{ji}+2Q^{(2)}_{ii}\right)-\frac{(k_BT)^2}{2\kappa_0}V_1(\mathbf{Q}^{(1)},\mathbf{Q}^{(2)}).$$

This changes the final answer by a factor of 1/2. Thus Eq. (10) of Ref. [8] for the interaction between two inclusions of area A, separated by a distance R, becomes $V^T(R)=-k_BT6A^2/(\pi^2R^4)$.

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