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Fluctuation-induced forces between inclusions in a fluid membrane under tension

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We develop an exact method to calculate thermal Casimir forces between inclusions of arbitrary shapes and separation, embedded in a fluid membrane whose fluctuations are governed by the combined action of surface tension, bending modulus, and Gaussian rigidity. Each object's shape and mechanical properties enter only through a characteristic matrix, a static analog of the scattering matrix. We calculate the Casimir interaction between two elastic disks embedded in a membrane. In particular, we find that at short separations the interaction is strong and independent of surface tension.

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Biological membranes are formed by bilayers of amphiphilic lipid molecules with embedded macromolecules such as proteins [1]. While inclusion can dramatically modify the flexibility, surface tension, and spontaneous curvature of biomembranes [2], the interactions between embedded proteins mediated by the membrane, in turn, depend on its mechanical properties [3–7]. Generally, these interactions depend on the separation between the inclusions and can be categorized as elastic and fluctuation-induced [4]. The former is due to static elastic deformations induced in the membrane, while the latter, the Casimir-like force, is due to the modified entropy of the membrane fluctuations.

Despite being the subject of intense research for almost two decades [4, 5, 8, 9], fluctuation-induced forces are just beginning to be understood. Previous theoretical research only considered fluctuations in the separate presence of either surface tension or the bending rigidities, but not the two combined [10], as occurs in reality. While surface tension is negligible for free-floating membranes [4], it is finite for a membrane enclosing a cell with excess osmotic pressure, or for membranes under tension in general [11]. In such cases, the surface tension σ_0 , as well as the bending (κ_0) and Gaussian ($\bar{\kappa}_0 \equiv \mu_0 \kappa_0$) rigidities of the membrane are all non-zero. For such membranes, the static elastic interaction between inclusions is exponentially cut-off at distances larger than the characteristic length [6, 12]

$$\ell_0 \equiv \alpha_0^{-1} = (\kappa_0/\sigma_0)^{1/2}. \quad (1)$$

In this letter, we present an exact method that allows calculations of membrane-mediated fluctuation-induced forces between any number of arbitrarily placed elastic inclusions of any shape for finite ℓ_0 . It is based on the technique previously employed to calculate the Casimir forces in antiferromagnets [13]. It can also be regarded as a version of the scattering-matrix approach [14], generalized to entropic forces for Hamiltonians with quartic in derivatives terms representing bending energy. We find that the Casimir energy between objects embedded in membrane could be expressed in terms of the response of individual objects to the fluctuating field. An object's

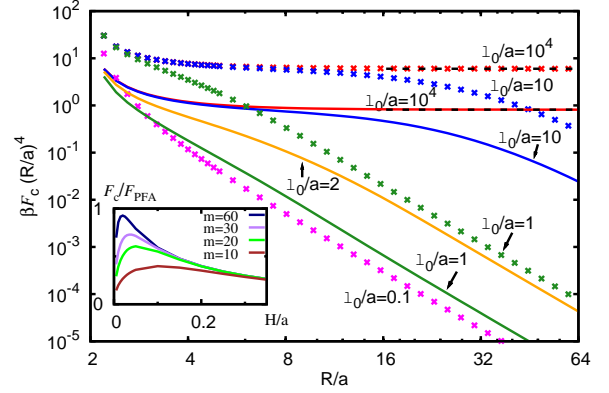


FIG. 1. (color online) The Casimir free-energy (12) scaled with fourth power of the distance as a function of R/a for $\kappa/\kappa_0 = 10^4$ (symbols) and $\kappa/\kappa_0 = 10^{-1}$ (solid lines), with $\alpha_0 a \equiv a/\ell_0$ as indicated. We set $\bar{\kappa}_0 = -\kappa_0$, $\bar{\kappa} = -\kappa$. Dashed black lines indicate asymptotic large- R dependences evaluated with Eq. (16). Plots are horizontal ($\Delta\mathcal{F} \propto R^{-4}$) only for $R \lesssim \ell_0 \equiv \alpha_0^{-1}$; for larger R/ℓ_0 the Casimir energy decays as $\Delta\mathcal{F} \propto R^{-8}$, see Eq. (2). Inset: The Casimir energy of two disks in the regime dominated by the bending energy ($\ell_0/a = 10^4$, $\kappa/\kappa_0 = 10^4$) divided by the PFA estimate (15). The quantity m indicates the multipole order of truncation.

shape and material properties enter only through the coefficient matrix representing the object's response, which is a static analog of the scattering matrix.

In particular, we compute fluctuation-induced interactions between two elastic disks. We specifically examine the unexplored parameter range where ℓ_0 is between the disk radius a and the center-to-center separation distance R , $a \lesssim \ell_0 \lesssim R$, so that both the surface tension and bending energies are relevant [Fig. 1]. In the limit of very short separations, we find a very good match between our results and those obtained through Derjaguin [15] or proximity force approximation (PFA) [see the inset in Fig. 1]. In the large separation limit, $R \gg a$, we derive explicit asymptotics for the Casimir interaction, and check them against the known results [4, 5, 8, 9] for cases dominated by either surface tension or bending rigidities.

For a non-zero surface tension, we find that the Casimir energy becomes strongly suppressed at distances R larger

than the characteristic length ℓ_0 , Eq. (1). Note that the Casimir energy retains the power-law asymptotic form

$$\beta \mathcal{F}_C = -A a^n / R^n, \quad \beta \equiv 1/k_B T, \quad R \gg a, \quad (2)$$

with the exponent increasing from $n = 4$ at $R \lesssim \ell_0$ (bending-energy-dominated regime) to $n = 8$ at $R \gtrsim \ell_0$ (tension-dominated regime). This is illustrated in Fig. 1 for two inclusion stiffnesses, with a number of different surface tensions. Depending on the parameters, the Casimir free energy scaled with the fourth power of the distance has either constant or $\propto 1/R^4$ asymptotics.

As seen in the figure, all curves with the same ratio of κ/κ_0 merge at short separations, while at larger separations the value of $l_0/a \propto \sigma_0^{-1/2}$ plays an important role. We also find a surprising effect corresponding to the difference between the Gaussian rigidities of the membrane and the inclusions. In the absence of line tension[16] for the inclusion boundaries [$\sigma = \sigma_0$ in Eq. (3)], the Casimir force at large distances becomes exponentially small when the Gaussian rigidities of the inclusions and the membrane coincide, $\bar{\kappa} = \bar{\kappa}_0$, regardless of κ .

We write the energy of a given configuration as a combination of that of the inclusions (thin isotropic elastic solids characterized by in-plane Lamé coefficients and bending rigidities) and the fluid membrane outside the inclusions (defined by the sum of the surface tension and bending energies). The energy is expanded to quadratic order in the displacements with respect to the equilibrium membrane configuration assumed to be planar in the $z = 0$ plane. The result for the membrane with inclusions has the standard Helfrich form [17],

$$U \equiv \int_{\mathcal{A}} d^2 \mathbf{r} \left[\frac{\sigma}{2} (\nabla u)^2 + \frac{\kappa}{2} (\nabla^2 u)^2 + \bar{\kappa} [u''_{xx} u''_{yy} - (u''_{xy})^2] \right], \quad (3)$$

where primes (') denote the partial derivatives with respect to x or y as indicated, and the integration is done over the total projected area \mathcal{A} . The coefficients κ and $\bar{\kappa}$ in Eq. (3) are position-dependent, e.g., $\kappa \equiv \kappa(\mathbf{r})$, $\mathbf{r} \equiv (x, y)$. Thermodynamical stability requires that $\sigma, \kappa \geq 0$ and $-2\kappa \leq \bar{\kappa} \leq 0$ in Eq. (3).

The first term in Eq. (3) has the standard form of a surface-tension contribution. However, inside inclusions, it represents the elastic energy associated with the in-plane stress induced by the membrane surface tension. In the absence of line tension at the inclusion boundaries, the diagonal components of the equilibrium stress tensor in the inclusions coincide with the surface tension of the membrane, which gives $\sigma = \sigma_0$ in Eq. (3).

The terms with κ and $\bar{\kappa}$ in Eq. (3) represent the bending energy contributions associated with the mean ($\kappa \equiv \kappa_0 + \lambda \kappa_1(\mathbf{r})$) and Gaussian ($\bar{\kappa} \equiv \bar{\kappa}_0 + \lambda \bar{\kappa}_1(\mathbf{r})$) curvatures respectively. While κ_0 and $\bar{\kappa}_0$ correspond to an unperturbed membrane, $\kappa_1(\mathbf{r})$ and $\bar{\kappa}_1(\mathbf{r})$ are position-independent inside, and vanish outside of the inclusions.

The partition function \mathcal{Z} of an inhomogeneous membrane can be found as a Boltzmann sum over all membrane configurations $u(\mathbf{r})$. With quadratic Eq. (3), the

free energy, $\mathcal{F} \equiv -\beta^{-1} \ln \mathcal{Z} = (2\beta)^{-1} \sum_n \ln(\beta E_n) + \text{const}$, is expressed in terms of the eigenvalues E_n of the hermitian “Hamiltonian” operator $\hat{\mathcal{H}} \equiv \hat{\mathcal{H}}_{\mathbf{r}}$ obtained as the second functional derivative of Eq. (3) over $u(\mathbf{r})$. The corresponding set of orthonormal eigenfunctions $u_n \equiv u_n(\mathbf{r})$, $\hat{\mathcal{H}} u_n = E_n u_n$, is complete in the space of the functions with continuous second derivatives on \mathcal{A} . We define the Green’s function (GF) of the operator $\hat{\mathcal{H}}$,

$$\hat{G} \equiv G(\mathbf{r}, \mathbf{r}') = \sum_n \frac{u_n(\mathbf{r}) u_n(\mathbf{r}')}{E_n}, \quad (4)$$

which obeys the usual equation $\hat{\mathcal{H}}_{\mathbf{r}} G(\mathbf{r}, \mathbf{r}') = \delta(\mathbf{r} - \mathbf{r}')$. For a uniform membrane, the term with $\bar{\kappa}$ in the integrand of Eq. (3) is a total derivative; the corresponding energy operator is $\hat{\mathcal{H}}_0 = \kappa_0(\nabla^4 - \alpha_0^2 \nabla^2)$, with $\alpha_0^2 \equiv \sigma_0/\kappa_0$. The uniform-membrane GF is a combination of GFs for the Laplace and the Helmholtz equations [12],

$$G_0(r) = -\frac{1}{2\pi\sigma_0} [K_0(\alpha_0 r) + \ln(\alpha_0 r)], \quad r \equiv |\mathbf{r} - \mathbf{r}'|. \quad (5)$$

Note that the operator $\hat{\mathcal{H}} \equiv \hat{\mathcal{H}}_0 + \lambda \hat{\mathcal{V}}$, the eigenfunctions $u_n \equiv u_n^\lambda$, the energies $E_n \equiv E_n^\lambda$, and the free energy $\mathcal{F} \equiv \mathcal{F}_\lambda$ depend on the coupling parameter λ , with $\lambda = 0$, corresponding to a non-perturbed (uniform) membrane. We use the Hellmann-Feynman theorem [18] to write the part of the free energy associated with the inclusions, $\Delta \mathcal{F}_\lambda \equiv \mathcal{F}_\lambda - \mathcal{F}_0$, as an integral over the parameter λ ,

$$\beta \Delta \mathcal{F}_\lambda = \frac{1}{2} \int_0^\lambda d\lambda' \text{Tr}(\hat{\mathcal{V}} \hat{G}_{\lambda'}). \quad (6)$$

For $k > 1$ membrane inclusions, we further decompose the free energy into the part associated with individual inclusions, $\sum_{l=1}^k \Delta \mathcal{F}_\lambda^{(l)}$, and the Casimir energy proper,

$$\mathcal{F}_C \equiv \Delta \mathcal{F}_\lambda - \sum_{l=1}^k \Delta \mathcal{F}_\lambda^{(l)}. \quad (7)$$

To this end we write $\hat{\mathcal{V}} = \sum_{l=1}^k \hat{\mathcal{V}}_l$, where the operator $\hat{\mathcal{V}}_l$, $l = 1, 2, \dots, k$, is only non-zero inside the corresponding inclusion. Then, if we expand the GF in the integrand of Eq. (6) in the perturbation series over λ' , the n -th term is a loop with the unperturbed \hat{G}_0 connecting exactly n operators $\hat{\mathcal{V}}_l$. We group together subsequent terms corresponding to the same inclusion l by introducing the exact GF for a single inclusion,

$$\hat{G}_\lambda^{(l)} \equiv \hat{G}_0 - \lambda \hat{G}_0 \hat{\mathcal{V}}_l \hat{G}_0 + \lambda^2 \hat{G}_0 \hat{\mathcal{V}}_l \hat{G}_0 \hat{\mathcal{V}}_l \hat{G}_0 - \dots \quad (8)$$

Respectively, the Casimir free energy (7) comprises the terms with at least two unequal inclusion indices[19],

$$\beta \mathcal{F}_C = -\sum_{n>1} \frac{(-\lambda)^n}{2n} \sum_{\{l_i\}} \text{Tr} \hat{\mathcal{V}}_{l_1} \hat{G}_\lambda^{(l_1)} \hat{\mathcal{V}}_{l_2} \hat{G}_\lambda^{(l_2)} \dots \hat{\mathcal{V}}_{l_n} \hat{G}_\lambda^{(l_n)}, \quad (9)$$

where the n -th term involves the summation over n inclusion indices $1 \leq l_i \leq k$, with the neighboring indices

different, $l_{i+1} \neq l_i$, $l_n \neq l_1$. Physically, this can be interpreted as fluctuations' back-and-forth "hopping" between the inclusions. To evaluate the resulting series, we introduce the $k \times k$ operator-valued matrix $\hat{\Sigma}$ with elements $\Sigma_{ll'} \equiv (1 - \delta_{ll'}) \hat{\mathcal{V}}_l \hat{G}_\lambda^{(l)}$ (no summation), and write the inner sum in the n th term of Eq. (9) as

$$\text{Tr } \hat{\Sigma}^n \equiv \sum_{\{l_i\}} \text{Tr } \Sigma_{l_1 l_2} \Sigma_{l_2 l_3} \dots \Sigma_{l_{n-1} l_n} \Sigma_{l_n l_1}, \quad n > 1, \quad (10)$$

where neighboring indices are automatically different. Now, the Casimir free energy becomes

$$\beta \mathcal{F}_C \equiv \frac{1}{2} \text{Tr } \log(\mathbb{1} + \lambda \hat{\Sigma}). \quad (11)$$

This equation is our main general result: it is exact, remains finite in the limit $\lambda \rightarrow \infty$, and can be applied to calculate the Casimir forces between a finite number of compact objects of arbitrary shape and separation. The result can also be recast[19] in a form similar to that of the scattering matrix approach employed to calculate the electromagnetic (EM) Casimir interaction[14].

We now focus on the case of two uniform circular disks embedded in a membrane. The corresponding matrix $\hat{\Sigma}$ is 2×2 , with no diagonal elements, and, therefore, the terms with odd powers of λ in the expansion of Eq. (11) disappear. The matrices $\hat{\Sigma}^n$, with even powers $n = 2s$, are diagonal, since $\hat{\Sigma}^2 = \text{diag}(\hat{\mathcal{V}}_1 \hat{G}_\lambda^{(1)} \hat{\mathcal{V}}_2 \hat{G}_\lambda^{(2)}, \hat{\mathcal{V}}_2 \hat{G}_\lambda^{(2)} \hat{\mathcal{V}}_1 \hat{G}_\lambda^{(1)})$. The two matrix elements give equal contributions to the trace,

$$\begin{aligned} \beta \mathcal{F}_C &= -\frac{1}{2} \sum_s \frac{\text{Tr}[\lambda^2 \hat{\mathcal{V}}_1 \hat{G}_\lambda^{(1)} \hat{\mathcal{V}}_2 \hat{G}_\lambda^{(2)}]^s}{s} \\ &= \frac{1}{2} \text{Tr } \log(\mathbb{1} - \lambda^2 \hat{\mathcal{V}}_1 \hat{G}_\lambda^{(1)} \hat{\mathcal{V}}_2 \hat{G}_\lambda^{(2)}). \end{aligned} \quad (12)$$

For actual calculations, we construct the exact single-disk GFs $\hat{G}_\lambda^{(l)}$, $l = 1, 2$, as a series in polar coordinates, including the terms corresponding to both the Laplace ($\propto r^{\pm m}$) and the Helmholtz ($\propto K_m(\alpha r)$, $I_m(\alpha r)$) equations [cf. Eq. (5)], with the azimuthal quantum number $m < m_{\max}$. This requires four boundary conditions on the circumference: continuity of the function, normal derivative, as well as of the following two quantities,

$$Q_3 \equiv \sigma \partial_r u - \kappa \partial_r (\nabla^2 u) + \frac{\bar{\kappa}}{r} \partial_r \left(\frac{1}{r} u''_{\theta\theta} \right), \quad (13)$$

$$Q_4 \equiv \kappa \nabla^2 u + \frac{\bar{\kappa}}{r} \left(\frac{1}{r} u''_{\theta\theta} + \partial_r u \right). \quad (14)$$

Here $u''_{\theta\theta}$ is the second derivative over the polar angle with respect to the center of the disk. The same boundary conditions are used to evaluate the matrix elements of the operators $\hat{\mathcal{V}}_l$ in Eq. (12). This gives the argument of the logarithm in Eq. (12) as a $2m_{\max} \times 2m_{\max}$ matrix (mode doubling corresponds to Helmholtz/Laplace components), which is non-diagonal since the GFs are expanded with respect to two different centers.

At large separations, it is sufficient to keep the terms up to quadrupole ($m_{\max} = 2$). As the distance R between the disks decreases, higher order multipoles become relevant. Generally, when the distance between the edges of the disks, $H \equiv R - 2a$, is small, a large number of multipoles, $m_{\max} \gtrsim a/H$, is required for convergence. In this regime the Casimir energy becomes large, and independent of the surface tension (see Fig. 1).

The short separation asymptotic form of the Casimir energy can also be evaluated within PFA[15]. Here, the interaction between curved edges is expressed as a sum over infinitesimal straight line segments approximated as parallel. We found that the Casimir energy per unit length for two half-planes is $\beta \mathcal{F}_C/L = f/H$, with $f = \pi/24$ in the limit dominated by the surface tension, and $f \approx 0.46$ in the limit dominated by the bending energy (it is the latter limit that is relevant at very small H for finite ℓ_0). Then, for two hard disks, PFA gives

$$\beta \mathcal{F}_{\text{PFA}} = -\pi f \left[x^{-1/2} + \frac{1}{2} - \frac{3}{8} x^{1/2} + \mathcal{O}(x) \right], \quad x \equiv \frac{H}{a}. \quad (15)$$

We plot the ratio of the Casimir energy, \mathcal{F}_C [Eq. (12)] calculated for different cutoff m in the regime dominated by the bending energy, and \mathcal{F}_{PFA} [Eq. (15)] in the inset of Fig. 1, and find that the ratio $\mathcal{F}_C/\mathcal{F}_{\text{PFA}}$ approaches one only at short separations. As the figure shows the higher order multipoles are necessary at shorter separations.

Analytical results for the Casimir free energy (12) can also be obtained in the weak coupling regime (small λ), regardless of the separation distance R , or for any λ if $R \gg a$. These regimes correspond to keeping the first term in the expansion of the logarithm in Eq. (12). For the weak coupling regime (small λ), we can further simplify the calculations by replacing $G_\lambda^{(l)}$ with the bare GF, G_0 . The full analytical expressions[19] are too cumbersome to quote here, and we only present simplified results for three important parameter ranges.

(a) $\ell_0 \gg R$, regime dominated by the bending rigidities of the membrane. The Casimir energy (12) has the asymptotic form (2) with $n = 4$ and the coefficient

$$\begin{aligned} A &= (4B_2^g + A_0^f)B_2^g, \\ B_2^g &= \frac{\bar{\kappa}_0 - \bar{\kappa}}{4\kappa_0 + \bar{\kappa}_0 - \bar{\kappa}}, \quad A_0^f = \frac{4(\kappa - \kappa_0) + 2(\bar{\kappa} - \bar{\kappa}_0)}{2\kappa + \bar{\kappa} - \bar{\kappa}_0}. \end{aligned} \quad (16)$$

It is remarkable how the Casimir energy depends on the flexibility of disks in this regime. For inclusions with finite rigidities, Eq. (16) is proportional to $\bar{\kappa} - \bar{\kappa}_0 \equiv \lambda \bar{\kappa}_1$, i.e., a discontinuity in $\bar{\kappa}$ is required for a non-zero Casimir force. The general expression (16) reproduces the results obtained previously in two limiting cases. In the rigid-disk limit[4, 5], where both κ and $-\bar{\kappa}$ are infinite, Eq. (16) gives $A = 6$ (horizontal portion of the line shown with red symbols in Fig. 1). In the weak-coupling limit[4, 5], it gives $A = -\lambda^2 \kappa_1 \bar{\kappa}_1 / 2\kappa_0^2$.

(b) $\ell_0 \ll a \ll R$, regime dominated by the surface tension of the membrane. We find that the leading-order

power law term in a/R (resulting from dipole-like fluctuations around the inclusions) is zero, and the next-order terms give the Casimir energy (12) falling off much faster, $\mathcal{F}_C \propto 1/R^8$, with the coefficient proportional to $\bar{\kappa}_1^2$. The full result being too bulky, we only present the strong-coupling limit, $\beta\Delta\mathcal{F}_C = -9(a/R)^8$ (in agreement with Refs. 8 and 9), and the leading-order contribution in λ at weak-coupling,

$$\beta\mathcal{F}_C^{(2)} = -\frac{36\lambda^2\bar{\kappa}_1^2a^4}{\sigma_0^2R^8} = -\frac{36(\bar{\kappa} - \bar{\kappa}_0)^2a^4}{\sigma_0^2R^8}. \quad (17)$$

Note that we also obtain the same power law in the presence of line tension energy on the inclusions boundary, in which case Eq. (3) has $\sigma \neq \sigma_0$ inside inclusions[19]. While a power law $\propto 1/R^8$ has been previously obtained [8, 9] for hard inclusions in soap films ($\kappa_0 = \bar{\kappa}_0 = 0$), we find it remarkable that the Casimir energy (17) depends on the difference between the Gaussian rigidity of inclusions and that of the membrane.

(c) $a \lesssim \ell_0 \lesssim R$, with both surface tension and bending rigidities of the membrane relevant. The full analytical expression [19] for the Casimir energy between two disk-like inclusions contains terms decaying like an inverse power of the distance R , and exponentially decaying terms $\propto K_m(\alpha_0 R)$. In particular, for $\ell_0 \ll R$, the terms $\propto K_m(\alpha_0 R)$ are exponentially small. In this case the Casimir interaction energy scales $\propto 1/R^8$, with the coefficient which is a complicated function of parameters, especially in the region $\ell_0 \sim a$. The exponentially small terms become relevant when $\ell_0 \sim R$, where Casimir energy crosses over to the small- σ regime (a) with $\mathcal{F}_C \propto 1/R^4$. This crossover can be seen in Fig. 1. A representative case corresponds to $\ell_0 = 10a$, where $A \equiv -(R/a)^4\mathcal{F}_C$ is nearly constant for $R \lesssim \ell_0$, is strongly reduced for larger R , and eventually crosses over to $\propto 1/R^4$ ($\mathcal{F}_C \propto 1/R^8$) for $R \gg \ell_0$. At smaller R , the same asymptotic power law is also seen, e.g., for $\ell_0/a = 1$.

Note that the distance dependence of the Casimir energy is the same, $\propto 1/R^8$, as long as $\ell_0 \ll R$, which includes regimes (b) and (c). In the regime (b), dominated by the surface tension, this power law can be obtained by treating the inclusions as point-like objects in the effective field theory (EFT)[9]. For inclusions that are free to tilt with the membrane, the expansion starts with the quadrupole terms[9]. In the regime (c) the higher-order multipole terms in the EFT expansion diverge as increasing powers of $\ell_0/a \gg 1$. However, the contributions to the Casimir energy coming from higher-order multipole terms also get suppressed as increasing powers of $1/R$. As a result, the leading-order quadrupole terms dominate, which again gives $\mathcal{F}_C \propto 1/R^8$ for $\ell_0 \ll R$. For $\ell_0 \sim R$, where we recover the exponentially small terms $\propto K_m(R/\ell_0)$, all multipoles contribute equally and the EFT approach cannot be used.

In conclusion, we have developed an exact method for computing the Casimir energy between elastic inclu-

sions of arbitrary shapes embedded in a biological membrane under tension, characterized by the surface tension σ_0 and bending and Gaussian rigidities, κ_0 and $\bar{\kappa}_0$. The method allows to calculate the Casimir forces in all ranges of parameters and for all separations. The Casimir energies are fully characterized by the objects' "scattering" matrices, which encode the shapes and mechanical properties. In particular, for two elastic disks, the Casimir energy scales as $\propto 1/R^4$ for $R \lesssim \ell_0$, and crosses over to $\propto 1/R^8$ for $R \gtrsim \ell_0$. At short distances, the Casimir energy is large; for hard disks our findings agree with the corresponding PFA results, $\mathcal{F}_C \propto H^{-1/2}$. One interesting result is that the Casimir energy is strongly suppressed for inclusions whose Gaussian rigidity $\bar{\kappa}$ equals that of the membrane.

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