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Worm-Like Chain Under An External Force: A Classical Mechanical Approach

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Biomolecules, such as DNA, are often modelled by the inextensible Worm-Like Chain (WLC) model when pulled by an external force. We examine the classical mechanical solution of a WLC arbitrarily grafted at one end while stretched with an external force acting on the other end. Shape equations governing the configurations of the WLC can be derived. Detail chain configurations can be solved numerically for arbitrary contour lengths and grafting conditions. Analytic results for the case of low force (linear regime) limit as well as near the fully stretched limit (strong force) and long chain limit are also derived.

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I. Introduction

Current experimental techniques such as optical/magnetic tweezers and micro pipette with fluorescence microscopy, enable the direct manipulation and observation of the behavior of a single macromolecule of size scale at the micrometer level. Because of their appropriate sizes, biomolecules such as DNA, actin and microtubules have been quite intensely investigated by single-molecule force experiments in recent years. The most fundamental physical properties are concerned with the force-extension behavior of such a chain stretched under an external force. The macromolecule is usually grafted with one end on some substrate or a large sphere held by a tweezer and the other end is also attached to another large sphere and pulled by an external force. These force experiments can often be used to test the models for macromolecules in polymer physics. In particular, the elastic properties of a single double-stranded DNA(dsDNA) molecule has drawn most of the research interest in this area due to its possible relations to biological functions [1-8]. In contrast to a flexible polymer in solution, dsDNA has a relatively large bending persistence length, and often is modelled by the worm-like chain (WLC) model [9-15] at the most coarse-grained level. Although more sophisticated models [16-22] can describe the novel elastic behavior of dsDNA better, especially in the large force regime in which the dsDNA takes an S-form, the WLC model provides a rather accurate description for the elastic behavior for the dsDNA that still remains in the B-form. On the other hand, many other frequently encountered biomolecules, such as actin and microtubule also exhibit large bending stiffness and the WLC model can also be used as the simplest theoretical model to account for their elastic behavior.

The statistical mechanical treatment of the WLC model under an external force has been studied several times by various authors [9-15, 23-25]. Standard techniques such as the Green function/path integral approach in polymer physics can be applied to the model. Many useful quantities such as the mean chain extension and correlation functions [15, 24, 25] can be calculated analytically, which also compare favorably with the force experiments in some force regime. However, in such approaches, only the averaged quantities can be calculated and detailed information such as configurations of the chain or the explicit functional form of the chain curve under given grafting conditions cannot be obtained. On the other hand, there was little study on the WLC using classical mechanical approaches [26]. The classical mechanical solution of the same system can provide further insight into the physical behavior of the WLC. Such a treatment is physically valid if thermal fluctuations of the chain can be neglected, such a case can be realized when the external force is large or the persistence length of the chain is large. In this paper, we develop the classical mechanical solution of the WLC under an external pulling force, under arbitrary grafting angles and contour lengths. Detail chain configurations can be explicitly calculated. Analytic results for the low and high force regimes can be obtained.

II. Worm-like chain under a pulling force

The WLC model, also known as the Kratky-Porod chain [9] regards a chain molecule as a slender cylindrical elastic rod with a fixed contour length L and the polymer is represented by the differentiable curve $\mathbf{r}(s)$ parametrized by the arc length s. The unit tangent vector is given by $\mathbf{t}(s) = d\mathbf{r}/ds$. The constraint $|\mathbf{t}| = 1$ imposes the inextensibility condition of the chain and often leads to difficulties in an analytical treatment of the model. Suppose the chain is fixed at the $s = 0$ end by grafting a small portion of its segment at some fixed angle to the substrate (see Fig. 1), and an external force $\mathbf{f}$ is pulling the chain at the other end at $s = L$, then the energy of the system is given by

$$E_{WLC} = \int_0^L \left[\frac{\kappa}{2} \left(\frac{d\mathbf{t}}{ds} \right)^2 - \mathbf{f} \cdot \mathbf{t} \right] ds \tag{1}$$

where κ is the bending stiffness. To proceed with our analytical calculations, the coordinate system with $\mathbf{f} = f\hat{\mathbf{z}}$ and $\mathbf{t} \equiv (\sin\theta\cos\phi, \sin\theta\sin\phi, \cos\theta)$ is taken such that the $|\mathbf{t}| = 1$ constraint will always be fulfilled. Minimizing E_{WLC} for given initial grafting orientation $\mathbf{t}(0) = (\sin\theta_0 \cos\phi_0, \sin\theta_0 \sin\phi_0, \cos\theta_0)$, one arrives at the Euler-Lagrange equations

$$\ddot{\theta} - \sin\theta\cos\theta\dot{\phi}^2 - (f/\kappa)\sin\theta = 0; \tag{2}$$

$$\sin^2\theta\dot{\phi} = \text{constant}; \tag{3}$$

with boundary conditions $\theta(0) = \theta_0$, $\phi(0) = \phi_0$ and $\dot{\theta}(L) = \dot{\phi}(L) = 0$. These shape equations can also be derived from the equation of equilibrium of the chain [27] such that the total moment acting on an element ds must be zero:

$$\frac{d\mathbf{M}}{ds} = \mathbf{f} \times \mathbf{t}. \tag{4}$$

FIGURES

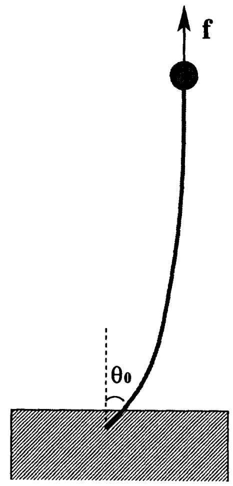

FIG. 1. Schematic picture of a chain grafted at one end and pulled at the other end by a force **f**. The angle between the grafted segment and **f** is θ_o.

The bending moment $\mathbf{M}$ of a rod with bending rigidity κ (but without twist rigidity) is

$$\mathbf{M} = \kappa\, \mathbf{t} \times \frac{d\mathbf{t}}{ds}. \tag{5}$$

Direct calculation gives

$$d\mathbf{t}/ds = (\dot\theta \cos\theta \cos\phi - \dot\phi \sin\theta \sin\phi, \dot\theta \cos\theta \sin\phi + \dot\phi \sin\theta \cos\phi, -\dot\theta \sin\theta)$$

and hence

$$\mathbf{M} = \kappa(-\dot\theta \sin\phi - \dot\phi \sin\theta \cos\theta \cos\phi, \dot\theta \cos\phi - \dot\phi \sin\theta \cos\theta \sin\phi, \dot\phi \sin^2\theta). \tag{6}$$

Therefore the B.C.s at the $s = L$ end, $\dot\theta(L) = \dot\phi(L) = 0$ are equivalent to the vanishing moment at the free end: $\mathbf{M}(L) = 0$. Using $\mathbf{f} \times \mathbf{t} = f \sin\theta(-\sin\phi, \cos\phi, 0)$ and directly differentiating $\mathbf{M}$, one gets from Eqn. (4)

$$-\ddot\theta \sin\phi - \dot\theta\dot\phi \cos\phi + \dot\phi^2 \sin\theta \cos\theta \sin\phi - \cos\phi\, d[\dot\phi \sin\theta \cos\theta]/ds = -(f/\kappa) \sin\theta \sin\phi, \tag{7}$$

$$\ddot\theta \cos\phi - \dot\theta\dot\phi \sin\phi - \dot\phi^2 \sin\theta \cos\theta \cos\phi - \sin\phi\, d[\dot\phi \sin\theta \cos\theta]/ds = (f/\kappa) \sin\theta \cos\phi, \tag{8}$$

$$d(\dot\phi \sin^2\theta)/ds = 0. \tag{9}$$

Eqn. (9) is the same as Eqn. (3). Eliminating the fourth terms on the LHS of (7) and (8) gives $\ddot\theta - \dot\phi^2 \sin\theta \cos\theta = (f/\kappa) \sin\theta$, which is the same as Eqn. (2).

The solution of the shape equations is easily obtained to be $\phi(s) = \phi_0$, i.e. the chain lies in the same plane. And by a simple integration, the solution of θ is given by

$$\sqrt{\frac{2f}{\kappa}}\, s = \int_{\theta}^{\theta_0} \frac{du}{\sqrt{\cos\theta_L - \cos u}}, \tag{10}$$

where $\theta_L \equiv \theta(L)$ is obtained by solving for it from the following relation involving an improper integral,

$$\sqrt{\frac{2f}{\kappa}}\, L = \int_{\theta_L}^{\theta_0} \frac{du}{\sqrt{\cos\theta_L - \cos u}}. \tag{11}$$

Once the solution $\theta(s)$ is obtained, the locus of the chain can be obtained easily from

$$\mathbf{r}(s) = \left(\int_0^s \sin\theta(u)\,du,\, 0,\, \int_0^s \cos\theta(u)\,du \right), \tag{12}$$

with $\mathbf{r}(0)$ at the origin. In the following, the dimensionless quantities $\lambda \equiv \sqrt{\frac{2f}{\kappa}}\, L$ and $\bar{s} \equiv \sqrt{\frac{2f}{\kappa}}\, s$ will be used for convenience.

III. Validity in force experiments

The WLC model has been used for various stiff chain like molecules in different experimental systems such as DNA, actin and microtubule. The typical values of the parameters in the WLC model in typical experimental situations are analyzed in the following. For most experiments at room temperatures ($kT \approx 4 \times 10^{-21}$J), the bending rigidity κ in the WLC model is related to the persistence length of the chain, ℓ_p, as $\kappa = \ell_p kT$. Therefore, in terms of ℓ_p, the dimensionless λ is given by

$$\lambda = \sqrt{\frac{2f\ell_p}{kT}} \left(\frac{L}{\ell_p} \right).$$

The typical persistence lengths for dsDNA, actin and microtubules under ordinary conditions are 50 nm, 17 μm and 5.2 mm respectively. For current force experiments on DNA molecules, the external stretching forces are around the order of pN. Let $f = \alpha$ pN, then one can easily estimate the values of the dimensionless length λ for these biomolecules, $\lambda_{DNA} \approx 5\sqrt{\alpha}(L/\ell_p)$, $\lambda_{actin} \approx 30\sqrt{\alpha}(L/\ell_p)$, $\lambda_{microtubule} \approx 1600\sqrt{\alpha}(L/\ell_p)$. Therefore, in most experimental situations, $\lambda >> 1$ holds for microtubules and actin filaments. For DNA molecules in most experiments, $L \sim 10$ - $100\,\mu$m, and hence $\lambda_{DNA} >> 1$ also holds, unless f is as small as in the fN range [28], in which case λ_{DNA} can be of $O(1)$.

IV. General solution of $\theta(s)$

For general given values of λ, $\theta(s)$ is obtained by numerical integration in Eqn. (10), but the value of θ_L has to be solved from Eqn. (11) first. The numerical evaluation of the improper integral in Eqn. (11) is given in the Appendix. Fig. 2 displays the values of θ_L as solved from Eqn. (11) as a function of λ for different initial grafting directions. It clearly shows that $\theta_L \to 0$

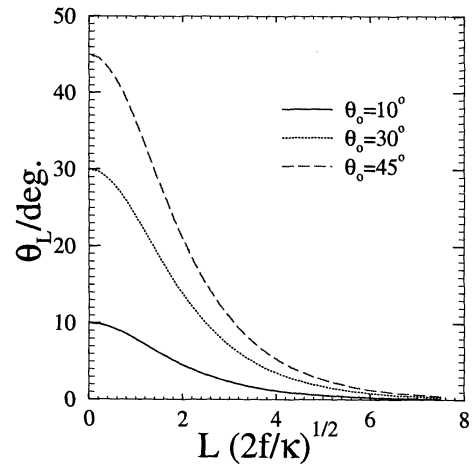

FIG. 2. Solution of μ_L as a function of L solved from Eqn. (11) for different initial grafting orientations.

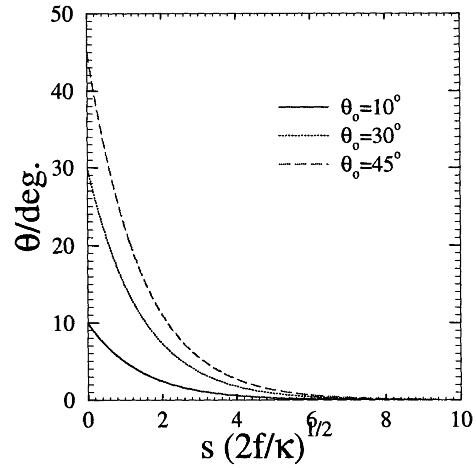

FIG. 3. Solution of $\mu(s)$ for the WLC under different initial grafting directions. L = 10.

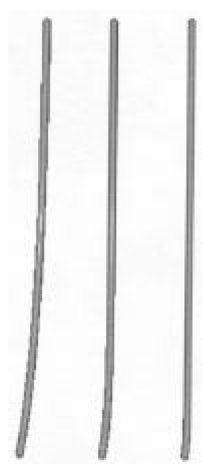

FIG. 4. Configurations of a L = 10 WLC under various stretching forces. The initial grafting angle $\mu_o = 10^{\pm}$. From left to right: $f = \cdot$ = 0.1, 1 and 10 respectively.

as L becomes large which agrees with the analysis in the next section. In fact μ_L is practically zero for L » 10 regardless the values of μ_o. Fig. 3 shows the variation of μ as a function of s from numerical integrating Eqn. (10) with different initial conditions for L = 10. Once the solution of $\mu(s)$ is obtained, the full configuration information of the WLC can be computed via Eqn. (12). Fig. 4 shows the chain configurations of a WLC of L = 10 under different pulling forces showing that the chain is bent by the external force. The correlation between the initial grafting direction rapidly decays along the contour and the decay is faster for stronger forces.

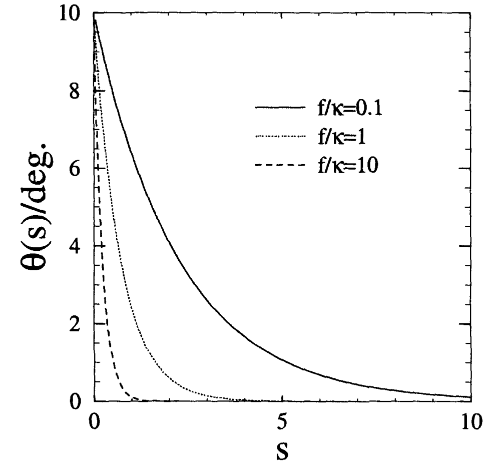

FIG. 5. Solution of $\theta(s)$ for the WLC under different reduced pulling forces in the long chain limit with $\theta_0 = 10^{\circ}$.

V. Long chain/strong force regime

In the case of a strong pulling force and/or long chain limit, $\bar{L} \to \infty$ (i.e. $f \to \infty$ or $L \to \infty$), one expects $\theta_L \to 0$ since the end of the chain will be aligned by the external force f. This has also been verified in the numerical result of θ_L in Fig. 2. In this limit, one easily gets from Eqn. (10) that

$$\theta(s) \simeq 4\tan^{-1}\left[\exp(-\bar{s})\tan\frac{\theta_0}{4}\right]. \tag{13}$$

The initial grafting orientation decays exponentially fast along the contour length. Also $\bar{L}$ diverges as $\bar{L} \simeq -\lim_{\theta_L\to 0}\ln(\tan\theta_L/\tan\theta_0)$. Fig. 5 displays $\theta(s)$ for various reduced stretching forces in the long L limit as given by Eqn. (13).

The relative end-to-end extension of the chain projected along the direction of the force, Z/L, which is the most common quantity measured in force experiments, is given by

$$\frac{Z}{L} = \frac{1}{L}\int_0^L \cos\theta(s)ds. \tag{14}$$

In the strong force limit, one expects $Z/L \to 1$ and, from Eqn. (10), that $\theta_L \to 0$ and $\kappa\dot{\theta}^2 = 2f(\cos\theta_L - \cos\theta) \simeq 2f(1-\cos\theta)$. Thus one has

$$1 - \frac{Z}{L} = \frac{1}{L}\int_0^L (1-\cos\theta(s))\, ds \simeq \frac{1}{\bar{L}}\int_0^{\theta_0} \sqrt{1-\cos\theta}\, d\theta. \tag{15}$$

Thus the approach to the fully extended limit behaves as

$$1 - \frac{Z}{L} \simeq \frac{2}{L}\sqrt{\frac{\kappa}{f}}\left(1-\cos\frac{\theta_0}{2}\right). \tag{16}$$

The $\sqrt{f}$ approach to the fully stretched limit is in agreement with the results dotained by statistical mechanical approaches using standard polymer physics techniques [15, 25]. This is expected since, near the fully stretched limit, the possible chain configurations are greatly reduced and are dominated by the classical trajectory, which validates the use of classical mechanics.

VI. Low force regime

For $f = 0$, one clearly has the trivial straight chain solution of $\theta(s) = \theta_L = \theta_0$. For low values of f, one can expand around the trivial solution systematically. First, θ_L can be expanded in powers of ϵ as (see Appendix)

$$\theta_L = \theta_0 - \frac{A_0}{4}\epsilon^2 + \frac{B_0}{16}\epsilon^4 - \frac{C_0}{64}\epsilon^6 + O(\epsilon^4); \tag{17}$$

where A_0, B_0 and C_0 are given by Eqn. (25) in the Appendix. In a similar way, $\theta(\bar{s})$ and hence $\cos\theta(\bar{s})$ can be expanded in a power series of ϵ and $\bar{s}$ (see Appendix). Finally the relative extension can be expanded in powers of ϵ, or explicitly in f as follows

$$\frac{Z}{L} = \cos\theta_0 + \frac{A_0 \sin\theta_0}{3}\frac{fL^2}{\kappa} - \left(\frac{1}{5}B_0\sin\theta_0 + \frac{1}{3}A_0\cos\theta_0\right)\frac{f^2L^4}{\kappa^2} + \cdots; \tag{18}$$

The extension projected in the pulling direction is given by $Z - L\cos\theta_0$ and hence the linear extension is given by

$$\delta R_L = \frac{fL^3}{3\kappa}\sin^2\theta_0. \tag{19}$$

Obviously, for $\theta_0 = 0$, $\delta R_L = 0$ since the WLC is inextensible. The linear extension coefficient is $\propto \sin^2\theta_0 L^3/\kappa$.

VII. Conclusion

In this paper, we developed the classical mechanical treatment of the semi-flexible WLC under an external force and calculated systematically the solution of the classical path of the WLC for any given contour length and initial grating direction. Analytic expressions for the solution $\theta(s)$ and the relative extension in the low force and long chain limits can be derived. This method can be employed to tackle more realistic and sophisticated chain models in dsDNA [29] and the WLC model that includes torsional rigidity [16] to obtain valuable insights into these complicated models. Furthermore, the classical mechanical approach could allow one to compute many detailed dynamical properties of the chain that would otherwise be impossible by the path integral formalism in standard polymer physics.

However, one should always bear in mind that the present approach makes physical sense based on the grounds that the chain is highly stretched such that the classical path dominates. Thus our results should be physically valid in the high force regime, but one should be very cautious in attempting to apply the result in the low force regime. Only in the case of very stiff chain with $\kappa/(kT) \gg L$ (i.e. l_p is comparable to the chain length) that our low force result will also be physically applicable. In this sense, our low-force classical mechanical results would be practically more useful for actin and microtubule, that are not very long, or for DNA at unusually low temperatures. Otherwise the entropic nature of the elasticity of the chain would have important contributions.

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Appendix

To evaluate numerically the improper integral in Eqn. (11), the integrand is decomposed into two parts as

$$\tilde{L} = \int_{\theta_L}^{\theta_o} P(u)du + \int_{\theta_L}^{\theta_o} G(u)\, du; \tag{20}$$

where $G(u) \equiv \frac{1}{\sqrt{\cos\theta_L - \cos u}} - P(u)$ for $u \neq \theta_L$ and $G(\theta_L) = 0$. $P(u)$ gives the dominant contribution of $\tilde{L}$ and is obtained by expanding the original integrand up to fourth order:

$$\begin{aligned} P(u) = \frac{1}{\sqrt{\sin\theta_L (u-\theta_L)}} \Bigg\{ 1 &- \frac{\cot\theta_L}{4}(u-\theta_L) + \frac{1}{4}\left(\frac{1}{3} + \frac{3}{8}\cot^2\theta_L\right)(u-\theta_L)^2 \\ &- \frac{\cot\theta_L}{8}\left(\frac{1}{3} + \frac{5}{16}\cot^2\theta_L\right)(u-\theta_L)^3 \\ &+ \frac{1}{32}\left(\frac{1}{5} + \frac{3}{4}\cot^2\theta_L + \frac{35}{64}\cot^4\theta_L\right)(u-\theta_L)^4 \Bigg\}. \end{aligned} \tag{21}$$

The integral of $P(u)$ can be easily evaluated analytically while the integral of $G(u)$ is evaluated numerically using the 4th order Simpson's method. One can easily sees that the integral of P is convergent, with

$$\int_{\theta_L}^{\theta_o} P(u)\, du = 2\sqrt{\frac{\theta_o - \theta_L}{\sin\theta_L}}\left[1 - a(\theta_o - \theta_L) + b(\theta_o - \theta_L)^2 - c(\theta_o - \theta_L)^3 + d(\theta_o - \theta_L)^4 + \cdots\right]; \tag{22}$$

and

$$\begin{aligned} a &= \frac{1}{12\tan\theta_L}; \\ b &= \frac{1}{20}\left(\frac{1}{3} + \frac{3}{8\tan^2\theta_L}\right); \\ c &= \frac{1}{56\tan\theta_L}\left(\frac{1}{3} + \frac{5}{16\tan^2\theta_L}\right); \\ d &= \frac{1}{288}\left(\frac{1}{5} + \frac{3}{4\tan^2\theta_L} + \frac{35}{64\tan^4\theta_L}\right). \end{aligned} \tag{23}$$

In fact, one easily sees that, by expanding the integrand of the integral in (11), $\tilde{L}$ is given by the RHS of Eqn. (22) plus higher order terms. For small f (small $\tilde{L}$), $\theta_L - \theta_0$ is small and one can safely truncate the series. a, b, c can also be expanded as $a = a_0 + \tilde{L}^2/\sin\theta_0/48 + \cdots$ and $b = b_0 + O(\tilde{L}^2)$, where the subscript $_0$ denote the quantities defined in Eqn. (23) with θ_L replaced by θ_0. The series representation of (11) can be inverted to give

$$\theta_L = \theta_0 - \frac{A_0}{4}\tilde{L}^2 + \frac{B_0}{16}\tilde{L}^4 - \frac{C_0}{64}\tilde{L}^6 + O(\tilde{L}^8), \tag{24}$$

where

$$\begin{aligned} A_0 &= \sin\theta_0, \\ B_0 &= \frac{11}{24}\sin 2\theta_0, \\ C_0 &= \left(\frac{1}{12} + \frac{31}{60}\sin^2\theta_0 + \frac{1193}{1440}\cos^2\theta_0\right)\sin\theta_0. \end{aligned} \tag{25}$$

Similarly, by expanding the integrand in Eqn. (10) and inverting the series, one arrives at

$$\begin{aligned} \theta(\tilde{s}) = \theta_0 &- \frac{A_0}{4}\left(\tilde{L}^2 - (\tilde{L}-\tilde{s})^2\right) + \frac{B_0}{16}\left(\tilde{L}^4 - (\tilde{L}-\tilde{s})^4\right) \\ &- \frac{C_0}{64}\left(\tilde{L}^6 - (\tilde{L}-\tilde{s})^6\right) + \cdots. \end{aligned} \tag{26}$$

$\cos\theta(\tilde{s})$ can further be expanded and hence the relative extension can be calculated

$$\begin{aligned} \frac{Z}{L} = \frac{1}{\tilde{L}}\int_0^{\tilde{L}} \cos\theta(\tilde{s})d\tilde{s} &= \cos\theta_0 + \frac{1}{6}A_0\sin\theta_0\tilde{L}^2 \\ &- \left(\frac{1}{20}B_0\sin\theta_0 + \frac{1}{60}A_0\cos\theta_0\right)\tilde{L}^4 + \cdots, \end{aligned} \tag{27}$$

then the small f expansion for the relative extension is given in Eqn. (18).

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