PHYSICAL REVIEW E **71**, 052801 (2005)

Elasticity and stability of a helical filament

Zicong Zhou*
Department of Physics and Graduate Institute of Life Sciences, Tamkang University, Tamsui, Taiwan 251, Republic of China

Pik-Yin Lai†
Department of Physics and Center for Complex Systems, National Central University, Chung-li, Taiwan 320, Republic of China

Béla Joós‡
Ottawa Carleton Institute for Physics, University of Ottawa Campus, Ottawa, Ontario, Canada, K1N-6N5
(Received 3 September 2004; revised manuscript received 14 January 2005; published 20 May 2005)

We derive the general shape equations in terms of Euler angles for a uniform elastic rod with spontaneous torsion and curvatures and subjected to external force and torque. Our results based on an analytic formalism show that the extension of a helical rod may undergo a one-step discontinuous transition with increasing stretching force. This agrees quantitatively with experimental observations for a helix in a chemically defined lipid concentrate. The larger the twisting rigidity, the larger the jump in the extension. The effect of torque on the jump is, however, dependent on the value of the spontaneous torsion. In contrast, increasing the spontaneous torsion encourages the continuous variation of the extension. An "over-collapse" behavior is observed for the rod with asymmetric bending rigidity, and an intrinsic asymmetric elasticity under twisting force is found.

DOI: 10.1103/PhysRevE.71.052801 PACS number(s): 46.32.+x, 46.25.Cc, 62.20.Fe

The shape and elasticity of a long thin rod (i.e., a filament) is a significant issue, not only because of its wide application in engineering and science [1], but also for recent experiments and theories which revealed that it may account for some elastic properties of microscopic objects, from carbon nanotubes [2–5] to biomaterials [6–26]. The conditions to form a helix from a rod and its relevant stability and elasticity are, in particular, interesting topics since the helix is one of the simplest filamentary structures found in nature. It has been reported that a rod under stretching may undergo a sharp multistep extension transition, from a free-standing helix to a distorted helix [22]. On the other hand, recent experiments for a helix in a chemically defined lipid concentrate (CDLC) observed a one-step reversible sharp transition of extension from an almost perfect helix, to an almost straight line [9]. Whether the elastic model can describe such observations is therefore an intriguing question.

In this paper we derive the shape equations for a uniform rod with spontaneous torsion and curvatures in terms of the Euler angles θ, ϕ, and ψ. We find analytically that a helical rod may undergo a one-step discontinuous transition under a stretching force, which quantitatively agrees with the experimental observations for a helix in a CDLC [9]. We find that the larger the twisting rigidity, the larger the jump in the extension. On the other hand, the effect of torque is dependent on the value of the spontaneous torsion. In contrast, increasing spontaneous torsion encourages the continuous variation of the extension. For the rod with asymmetric bending rigidity we observe an "over-collapse" behavior and an intrinsic asymmetric elasticity under twisting.

*Electronic address: zzhou@mail.tku.edu.tw
†Electronic address: pylai@phy.ncu.edu.tw
‡Electronic address: bjoos@uottawa.ca

Using Euler angles to relate the fixed coordinate system to the frame rigidly embedded in the rod [1,15,17–20], the tangent vector $\mathbf{t}_3 \equiv d\mathbf{r}/ds$ of the center line position vector $\mathbf{r}$ of a rod can be written as $\mathbf{t}_3=\{\sin\phi\sin\theta, -\cos\phi\sin\theta, \cos\theta\}$, where s is the arclength. The general configuration of an elastic rod can be described by a triad of unit vectors $\{\mathbf{t}_i(s)\}_{i=1,2,3}$, where $\mathbf{t}_1$ and $\mathbf{t}_2$ are oriented along the principal axes of the cross section. $\mathbf{t}_i(s)$ satisfy the generalized Frenet equations [1,20–22], $d\mathbf{t}_i(s)/ds = -\Sigma_{j,k}\epsilon_{ijk}\omega_j(s)\mathbf{t}_k(s)$, where ϵ_{ijk} is the antisymmetric tensor and $\{\omega_j(s)\}$ are the curvature and torsion parameters. The normal $\mathbf{n}$ of the rod can be expressed as $\mathbf{n}=\{\cos\phi\cos\psi - \cos\theta\sin\phi\sin\psi, \sin\phi\cos\psi + \cos\theta\cos\phi\sin\psi, \sin\theta\sin\psi\}$. It follows (with $\dot{X}\equiv dX/ds$) that $\omega_1 = \sin\theta\sin\psi\dot{\phi}+\cos\psi\dot{\theta}$, $\omega_2=\sin\theta\cos\psi\dot{\phi}-\sin\psi\dot{\theta}$, $\omega_3 = \cos\theta\dot{\phi}+\dot{\psi}$. The linking number (Lk) and the supercoiling degree (σ) of a rod can be expressed as [18]

$$\mathrm{Lk} = \frac{1}{2\pi}\int_0^L (\dot{\psi}+\dot{\phi})ds, \quad \sigma = \frac{\mathrm{Lk}-\mathrm{Lk}_0}{\mathrm{Lk}_0}, \tag{1}$$

where Lk_0 is the Lk in the undeformed state ($f=0$ and $\Gamma=0$), and L is the contour length of the rod.

Under an external torque Γ and a force f ($f>0$ for a stretching force) along the z direction, the energy of a uniform rod can be written as [20–22]

$$E = \int_0^L \mathcal{E} ds, \tag{2}$$

$$\mathcal{E} = \tfrac{1}{2}[a_1(\omega_1-\omega_{10})^2 + a_2(\omega_2-\omega_{20})^2 + a_3(\omega_3-\omega_0)^2] - f\cos\theta - \Gamma(\dot{\phi}+\dot{\psi}), \tag{3}$$

where a_1, a_2 are the bending rigidities, a_3 is the twisting rigidity, and ω_{10}, ω_{20}, and ω_0 are spontaneous curvatures and twist rate, respectively. Note that if the force has all three components (similar to the case of fixing both ends of the rod), the term $f\cos\theta$ must be replaced by $\mathbf{f}\cdot\mathbf{t}$. We do not consider this much more complicated case because the force used in a force experiment is always uniaxial.

The undeformed shape of a rod is given by $\omega_1=\omega_{10}$, $\omega_2=\omega_{20}$, and $\omega_3=\omega_0$. These equations determine a free-standing helix with constant curvature $(=\sqrt{\omega_{10}^2+\omega_{20}^2})$ and constant torsion $(=\omega_0)$.

Extremizing E, we obtain the shape equations

$$-f\sin\theta+\tfrac{1}{4}[2a_3-a_1-a_2+(a_1-a_2)\cos 2\psi]\sin 2\theta\dot{\phi}^2 + [a_2\omega_{20}\cos\psi+a_1\omega_{10}\sin\psi-(a_1-a_2)\sin 2\psi\dot{\theta}]\dot{\psi} + \dot{\phi}[-a_3\omega_0\sin\theta+\cos\theta(a_2\omega_{20}\cos\psi+a_1\omega_{10}\sin\psi) + (a_3+(a_1-a_2)\cos 2\psi)\sin\theta\dot{\psi}]+(a_1\cos^2\psi + a_2\sin^2\psi)\ddot{\theta}+(a_1-a_2)\cos\psi\sin\theta\sin\psi\ddot{\phi}=0, \quad (4)$$

$$-\Gamma+\sin\theta[-a_2\omega_{20}\cos\psi-a_1\omega_{10}\sin\psi+(a_1-a_2)\cos\psi\sin\psi\dot{\theta}+\sin\theta(a_2\cos^2\psi+a_1\sin^2\psi)\dot{\phi}] + a_3\cos\theta(\cos\theta\dot{\phi}+\dot{\psi}-\omega_0)=C, \quad (5)$$

$$(a_1-a_2)\cos\psi\sin\psi\dot{\theta}^2+\sin\theta(a_1\omega_{10}\cos\psi-a_2\omega_{20}\sin\psi)\dot{\phi} - (a_1-a_2)\cos\psi\sin^2\theta\sin\psi\dot{\phi}^2+a_3(\cos\theta\ddot{\phi}+\ddot{\psi}) - \dot{\theta}\{a_2\omega_{20}\cos\psi+a_1\omega_{10}\sin\psi + [a_3+(a_1-a_2)\cos 2\psi]\sin\theta\dot{\phi}\}=0, \quad (6)$$

where C is an integral constant. A helix requires $\theta(s)=\theta=\text{const}$ (we choose θ as a constant henceforth for convenience) and $\phi(s)=\dot{\phi}_h s$ with $\dot{\phi}_h$ also being a constant. Therefore, for a helix, Eqs. (4)–(6) can be simplified to

$$\dot{\psi}=\frac{f\sin\theta-(\dot{\phi}_h^2/4)[2a_3-a_1-a_2+(a_1-a_2)\cos 2\psi]\sin 2\theta-\dot{\phi}_h[\cos\theta(a_2\omega_{20}\cos\psi+a_1\omega_{10}\sin\psi)-a_3\omega_0\sin\theta]}{a_2\omega_{20}\cos\psi+a_1\omega_{10}\sin\psi+\dot{\phi}_h[a_3+(a_1-a_2)\cos 2\psi]\sin\theta}, \quad (7)$$

$$\dot{\psi}=\frac{C+\Gamma-\sin\theta[-a_2\omega_{20}\cos\psi-a_1\omega_{10}\sin\psi+\dot{\phi}_h\sin\theta(a_2\cos^2\psi+a_1\sin^2\psi)]-a_3\cos\theta(\dot{\phi}_h\cos\theta-\omega_0)}{a_3\cos\theta}, \quad (8)$$

$$\ddot{\psi}=\frac{-\dot{\phi}_h\sin\theta(a_1\omega_{10}\cos\psi-a_2\omega_{20}\sin\psi)+\dot{\phi}_h^2(a_1-a_2)\cos\psi\sin^2\theta\sin\psi}{a_3}. \quad (9)$$

Since on the right-hand sides of Eqs. (7) and (8), all quantities except for ψ are constants, ψ must also be a constant, except for the previously solved case $a_1=a_2$, and $\omega_{10}=\omega_{20}=0$ [1]. We recover the result reported in Ref. [27]. The conditions to form a helix is then determined by the vanishing of the numerators in Eqs. (7)–(9).

Let us now suppose that the chain is fixed at $s=0$. An extremum in the energy requires the following additional boundary conditions (BCs) at $s=L$: $[(\partial\mathcal{E}/\partial\dot{\theta})\cdot\delta\theta]_{s=L}=0$, $[(\partial\mathcal{E}/\partial\dot{\phi})\cdot\delta\phi]_{s=L}=0$, and $[(\partial\mathcal{E}/\partial\dot{\psi})\cdot\delta\psi]_{s=L}=0$. For a helix, the first BC is equivalent to the vanishing of the numerator in Eq. (9) so it is automatically satisfied. And note that for a helix, we have only one undetermined constant C in the numerator of Eq. (8); one cannot require that both $(\partial\mathcal{E}/\partial\dot{\phi})_{s=L}=0$ and $(\partial\mathcal{E}/\partial\dot{\psi})_{s=L}=0$, since it gives overdetermined equations. The remaining BCs are

$$\delta\phi(L)=0 \text{ and } \delta\psi(L)=0; \quad (10)$$

$$\text{or } (\partial\mathcal{E}/\partial\dot{\phi})_{s=L}=0 \text{ and } \delta\psi(L)=0; \quad (11)$$

$$\text{or } (\partial\mathcal{E}/\partial\dot{\psi})_{s=L}=0 \text{ and } \delta\phi(L)=0. \quad (12)$$

$\delta\psi(L)=0$ or $\delta\phi(L)=0$ mean that we need to fix $\psi(L)$ or $\phi(L)$, respectively. But since $\psi=\text{const}$, fixing $\psi(L)$ does not provide an extra equation. To realize this condition one simply does not stick the cross section of the end tightly on a nondeformable surface, which allows the relaxation of ψ to the required value. This is also the BC used in most force experiments. In contrast, fixing $\phi(L)$ leads to the constraint $\dot{\phi}_h=[\phi(L)-\phi(0)]/L$ to determine the unknown constant. This condition is, however, difficult to realize since it requires to fix both $\phi(0)$ and $\phi(L)$ and may require complicate applied torque on both ends. But note that by replacing Γ by $\Gamma+C$, the BCs (10) and (11) give exactly the same results so they are in fact equivalent. In the same way, fixing θ and ϕ at $s=0$ is in fact unnecessary for a helix.

From the shape equations and BCs we can find relations between f, Γ (or σ), $\mathcal{E}$, and $\cos\theta$. The final equations are essentially quartic equations of $\cos\theta$ and $\sin\psi$, and so can be solved to arbitrary accuracy. BCs (11) and (12) lead to different solutions. But in general, under the same f and Γ, the solutions obtained from BCs (12) always have higher energies than the solutions found from BCs (11). It means that the latter should be more stable or easier to realize, so we shall focus on those solutions. Note that for a helix, $z\equiv\cos\theta$ is equal to the relative extension and this is also an advantage of the use of Euler angles.

The solutions obtained from the shape equations may be unstable since they may correspond to a maximum in energy. The stable (or metastable) rod requires

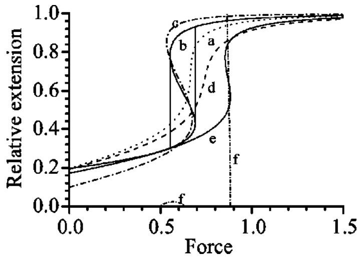

FIG. 1. Relative extension (cos θ) vs force for a helix. The values of the parameters in the figure are: (a) (dotted line) $\omega_0=0.2$, $\omega_{10}=1.0$, $\omega_{20}=0.05$, $a_1=1$, $a_2=5$, $a_3=4$, $\Gamma=0$; (b) (solid line) the same as in (a) except for $a_3=10$. The solid vertical lines indicate the jump points for decreasing and increasing f, respectively; (c) (dash-dotted line) the same as in (a) except for $\omega_0=0.1$; (d) (dashed line) the same as in (a) except for $\omega_{20}=0.2$; (e) (solid line) the same as in (a) except for $\Gamma=0.2$; (f) (short dash-dotted line) positive part of S for the case (e), $S>0$ for $f>0.8817$. The same units are used for f and $a_1\omega_{10}^2$.

$$\delta^2 E = \int_0^L \left(\sum_{i,j=1,5} \frac{\partial^2 \mathcal{E}}{\partial \eta_i \partial \eta_j} \delta\eta_i \delta\eta_j \right) ds > 0, \qquad (13)$$

with $\eta_1=\theta$, $\eta_2=\psi$, $\eta_3=\dot{\theta}$, $\eta_4=\dot{\phi}$, $\eta_5=\dot{\psi}$. The stability criterion can be obtained from the positive definiteness of $S \equiv \det|\partial^2\mathcal{E}/\partial\eta_i\partial\eta_j|$. For a helix, S is a constant and can be evaluated easily.

Figure 1 shows typical results of the force-extension relation for a helix. Curve (a), with $\omega_0=0.2$, $\omega_{10}=1.0$, $\omega_{20}=0.05$, $a_1=1$, $a_2=5$, $a_3=4$, $\Gamma=0$, gives a critical case, in which z varies smoothly with increasing force, but changes rapidly around $f=0.65$. Curve (b) shows that increasing a_3 causes a first-order transition of z from 0.4375 to 0.9311 at $f=0.6900$. In contrast, if we decrease f from the full length ($z=1$), the same rod should collapse at $f=0.5528$, and z would drop from 0.7830 to 0.3025, which means that a hysteresis occurs. Decreasing ω_0 also favors the transition, as shown in curve (c). But increasing ω_{20} discourages the jump, as shown in curve (d). In contrast, increasing ω_{10} favors the jump. The effect of Γ is more complex than expected. In general, a larger Γ leads to a larger critical f, and the helix can exist only in a finite range of f for a strong negative Γ. We find that if ω_0 is large enough, increasing Γ tends to cause a jump, as shown in curve (e). However, for a small ω_0, a small $|\Gamma|$ disfavors the jump but a large positive Γ favors the jump. Moreover, we do not observe multiple-steps transition as reported for a distorted helix (under nonvanishing tensile force) in Ref. [22]. We also find that z just after the jump is always very close to 1 for different choices of parameters.

Multiple local minima in the energy function $\mathcal{E}$ can be observed for the rods near the critical point, as shown in Fig. 2. The bifurcating behavior of $\mathcal{E}$ is responsible for the sharp transition and the hysteresis loop. The energy-force curve is self-crossed when the rod undergoes a transition, as shown in curves (b) and (e). Moreover, we find that the crossover point always gives the lowest energy under a given force. Therefore, in principle, the jump in z should occur at the crossover

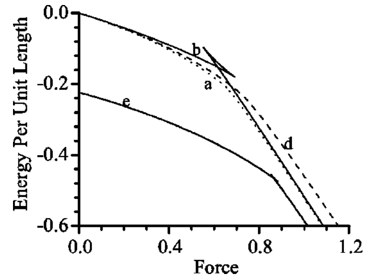

FIG. 2. Energy-force relation for a helix. The values of the parameters in this figure are the same as in Fig. 1, but for clarity, we do not display the data corresponding to curve (c) in Fig. 1. The same units are used for the force and the energy per unit length as for $a_1\omega_{10}^2$.

point so the hysteresis may not be observable. However, in practice, the jump is more likely to occur at the tip of the sharp edge of the energy-force curve (which corresponds to the tip of the sharp edge of the extension-force curve), since to jump at the crossover point requires a careful equilibrium at that point. Therefore, in fact, the jump can occur at any point between the crossover point and the tip of the sharp edge so these two points define a metastable regime. If $\mathcal{E}$ varies monotonously, as in curves (a) and (d), there is no sharp transition in z.

It has been reported that a helix in a CDLC can undergo a one-step reversible sharp transition in the relative extension z from an almost perfect helix to an almost straight line ($z=1$) [9], and there is a metastable regime, $z=0.28$ to $z=0.41$ (note that the pitch angle ψ in Ref. [9] is the same as $\pi/2-\theta$ in this work), in which upon nucleation, the helix separates into two domains, one straight and the other helical ($z=0.28$). A free-energy model was constructed in Ref. [9] to account for the phenomena. However, we find that our elasticity model can predict these observations. We use the radius R_0, z ($=z_0=0.19$) of the free-standing helix, and the elastic constant reported to remove three parameters in our model and fit the other parameters to the observed data. For an isotropic helix, where there is a total of four parameters to fit, we can get perfect agreement with experimental observations with the choice $a_1=a_2=1.7797\times10^{-19}$ N m^2, $a_3=18.686\times10^{-19}$ N m^2, $\omega_0=0.098\,18\times10^5$ m^{-1}, $\sqrt{\omega_{10}^2+\omega_{20}^2}=0.507\,32\times10^5$ m^{-1} (this is the form in which ω_{10} and ω_{20} appear in the expressions for the isotropic case). In particular, we can predict a metastable regime from $z=0.278$ to 0.413. However, it is known that there is anisotropy in the studied helix. This gives additional degrees of freedom in the choice of parameters, namely $a_1\neq a_2$ and ω_{10} and ω_{20} appear separately. Using for instance $a_1=3.4690\times10^{-19}$ N m^2, $a_2=1.0407\times10^{-19}$ N m^2, $a_3=22.718\times10^{-19}$ N m^2, $\omega_0=0.098\,18\times10^5$ m^{-1}, $\omega_{10}=0.235\,90\times10^5$ m^{-1}, $\omega_{20}=0.449\,13\times10^5$ m^{-1}. This choice of parameters fits well the data and predicts a metastable regime between $z=0.31$ and 0.41.

It is interesting to note that we always have $S=0$ for a free-standing helix. This is simply because the axis of a free-standing helix can point in an arbitrary direction. For small $|f|$, S is negative (except for $\omega_{10}=\omega_{20}=0$, when S is always positive). This is a consequence of our assumption that θ

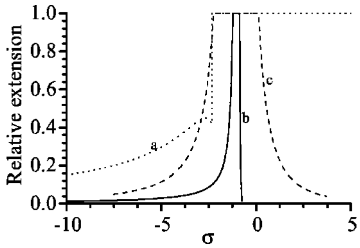

FIG. 3. Relative extension ($\cos\theta$) vs supercoiling degree for a helical rod. The values of the parameters in the figure are: (a) (dotted line) $\omega_0=0.2$, $\omega_{10}=\omega_{20}=0$, $a_1=1$, $a_2=5$, $a_3=3$, $f=0.1$; (b) (solid line) $\omega_0=0.2$, $\omega_{10}=\omega_{20}=0$, $a_1=1$, $a_2=100$, $a_3=10$, $f=-0.1$; (c) (dashed line) the same as in (b) except for $f=-5$.

=const, and means that a perfect helix is generally unstable under a small force; in other words, it can adopt a different shape, such as a helix slightly distorted at the ends (as seen in Ref. [9] for a helix in a CDLC). Under a larger stretching force $S>0$. These results are consistent with the conclusion that when $a_1=a_2$, the effect of pulling a helix is to stabilize it, whereas pushing the helix will create unstable modes [28]. In contrast, increasing Γ tends to destabilize a helix. $S>0$ usually appears just before the critical point in the force-extension curve, as can be seen in curve (f) of Fig. 1.

When $\omega_{10}=\omega_{20}=0$, we have $\sin\psi=0$ or $\cos\psi=0$, and the simplest solution for the shape equations is $z=1$, representing a twisted vertical rod. However, $z=1$ does not always give the lowest-energy solution. We find that in general, under a fixed stretching force and with sufficiently large $|\sigma|$ ($\sigma<0$ in such a case), and $a_3<a_2$, the rod may "over collapse," from $z=1$ to a helix with finite $z<1$, as shown in curve (a) of Fig. 3. It recovers slightly to a local maximum of z with a further increase in $|\sigma|$, and then z decreases again; $S>0$ in this regime so that the helix is at least in a metastable state. In contrast, if $a_3>a_2$, no over-collapse occurs. Some more interesting phenomena occur when the rod is subjected to a fixed compressive force. It reveals a continuous but asymmetric elasticity when $|f|$ is small, but tends to have a symmetric and continuous behavior when $|f|$ is large, though the symmetric center is not at $\sigma=0$. The stronger the asymmetry of the bending rigidities, the more obvious the phenomena is. The results with $a_2 \gg a_3 \gg a_1$ are displayed in curves (b) and (c) of Fig. 3. This result shows that the asymmetric bending rigidities of a rod lead to intrinsic asymmetric elasticity, agreeing with that obtained using the statistical mechanics approach for the same model [21]. It also resembles the behavior of a double-stranded DNA molecule at room temperature and subjected to a moderate stretching force [11,12].

In summary, we derive the shape equations for a uniform elastic rod in terms of Euler angles and find the conditions to form a helix. We provide analytic proof that the extension of a helix under external force and torque may be subject to a one-step sharp transition, which quantitatively agrees with the experimental observations for a helix in CDLC [9]. Though the shape equations we derived are very general, we focus only on the simplest helical solutions in this work. In practice, a stable rod exhibits many other shapes [6,7,27,28]. Under what conditions these shapes will change from one to another is a very interesting issue. This question has been addressed extensively by solving the relevant kinematical equations [6,7,27,28], but our stationary shape equations and stability criterion may provide additional views on the question. In this paper, thermal effects are not considered. Probably the most important, the configurational entropic effect, leads to a contraction of the rod, analogous to a compressive force for a long rod, and may make the transition behavior smoother.

This work has been supported by the National Science Council of the Republic of China under Grants No. NSC 93-2112-M-032-006, and 92-2112-M-008-051, and the Natural Sciences and Engineering Research Council of Canada.

[1] A. E. H. Love, *A Treatise on the Mathematical Theory of Elasticity* (Dover, New York, 1944).
[2] S. Iijima, Nature (London) **354**, 56 (1991); S. Iijima, T. Ichihaschi, and Y. Ando, *ibid.* **356**, 776 (1992).
[3] M. S. Dresselhaus, Nature (London) **3548**, 195 (1992).
[4] X. B. Zhang, Europhys. Lett. **27**, 141 (1994).
[5] M.-F. Yu, *et al.*, Phys. Rev. B **64**, 241403(R) (2001).
[6] A. Goriely and M. Tabor, Phys. Rev. Lett. **80**, 1564 (1998).
[7] R. E. Goldstein *et al.*,Phys. Rev. Lett. **84**, 1631 (2000).
[8] D. Coombs, *et al.*, Phys. Rev. Lett. **89**, 118102 (2002).
[9] B. Smith *et al.*, Phys. Rev. Lett. **87**, 278101 (2001).
[10] Y. Cui and C. Bustamante, Proc. Natl. Acad. Sci. U.S.A. **97**, 127 (2000).
[11] T. R. Strick *et al.*, Science **271**, 1835 (1996).
[12] T. R. Strick *et al.*, Proc. Natl. Acad. Sci. U.S.A. **95**, 10579 (1998).
[13] S. B. Smith *et al.*, Science **271**, 795 (1996).
[14] J. D. Moroz and P. Nelson, Proc. Natl. Acad. Sci. U.S.A. **94**, 14418 (1997).
[15] F. Tanaka and H. Takahashi, J. Chem. Phys. **83**, 6017 (1985).
[16] J. F. Marko and E. D. Siggia, Phys. Rev. E **52**, 2912 (1995).
[17] C. J. Benham, Proc. Natl. Acad. Sci. U.S.A. **74**, 2397 (1977).
[18] B. Fain, *et al.*, Phys. Rev. E **55**, 7364 (1997).
[19] B. Fain and J. Rudnick, Phys. Rev. E **60**, 7239 (1999).
[20] S. Panyukov and Y. Rabin, Phys. Rev. E **64**, 011909 (2001).
[21] S. V. Panyukov and Y. Rabin, Europhys. Lett. **57**, 512 (2002).
[22] D. A. Kessler and Y. Rabin, Phys. Rev. Lett. **90**, 024301 (2003).
[23] S. B. Smith *et al.*, Science **258**, 1122 (1992).
[24] J. F. Marko and E. D. Siggia, Science **265**, 506 (1994).
[25] P. Cluzel, *et al.*, Science **271**, 792 (1996).
[26] J. F. Léger *et al.*, Phys. Rev. Lett. **83**, 1066 (1999).
[27] T. McMillen and A. Goriely, J. Nonlinear Sci. **12**, 241 (2002).
[28] A. Goriely and M. Tabor, Proc. R. Soc. London, Ser. A **453**, 2583 (1997).