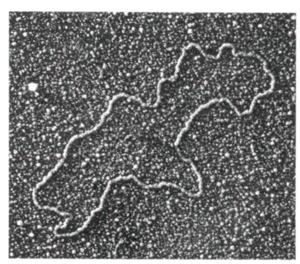
Polymer physics meets cell biology

- Polymers (filamentous proteins) in the cell?
- Outline of topics and problems
- Properties and phase behavior in bulk
  - Model polymers, biomaterials, …novel *rheology*
- Single filament properties
  - dynamics & response --- a toy problem
- Active gels & force propagation

Biopolymers

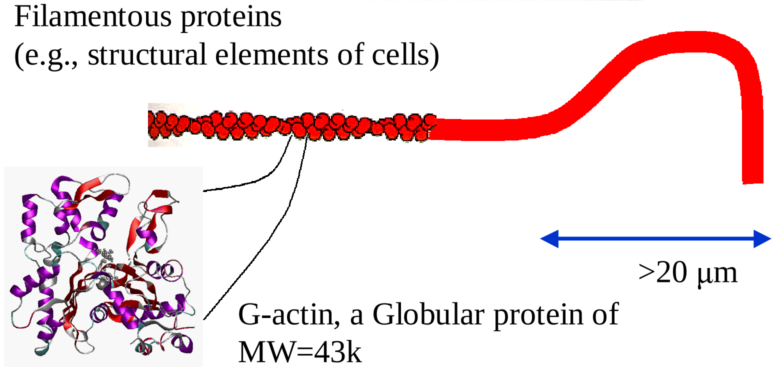
DNA



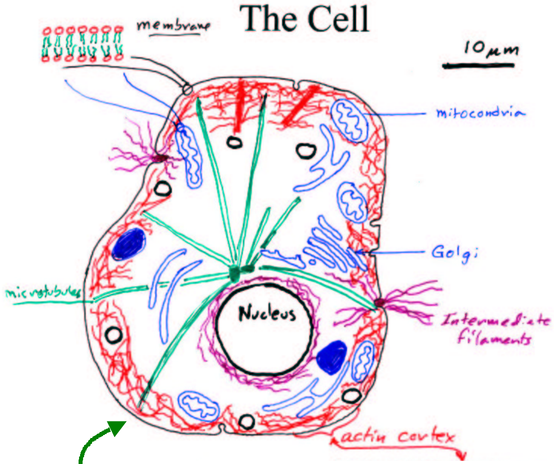
Stryer, 1995

200 nm

Filamentous proteins
(e.g., structural elements of cells)



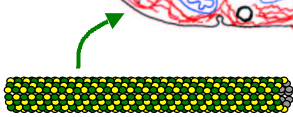
The Cell



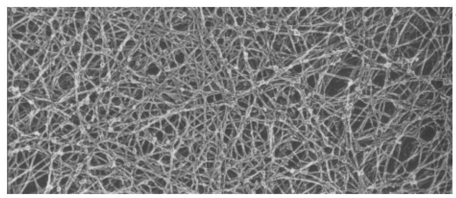
Plant and animal cells have a *cytoskeleton*, consisting largely of polymer, for structure, organization, and transport

7 nm

F-actin



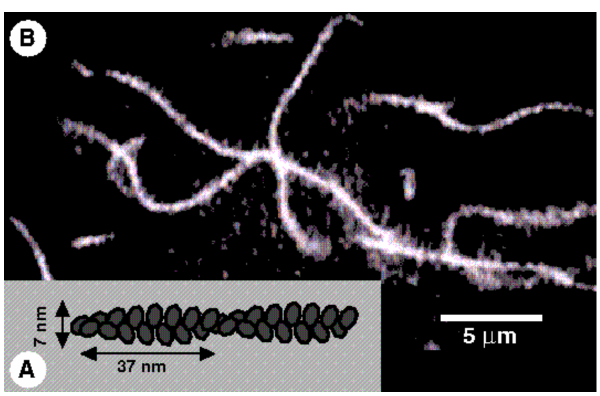
microtubule



Alberts,… 1994

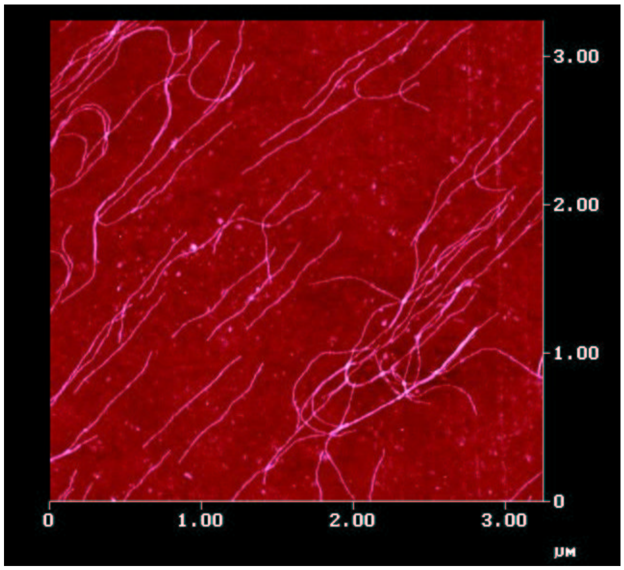
Why biopolymers?

- SIZE: can visualize basic polymer physics in an optical microscope!



J Kas, P Janmey, 1995

Viruses (fd, tmv, …)

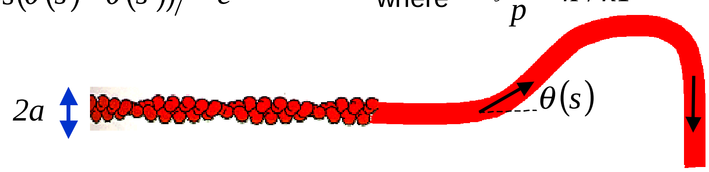


(J Tang)

Elasticity of *semiflexible* polymers

$$E_{\text{bend}} = \frac{1}{2}\kappa \int \left(\frac{\partial \theta}{\partial s}\right)^2 ds$$

$$\langle \cos(\theta(s) - \theta(s')) \rangle = e^{-|s-s'|/\ell_p}$$ where $\ell_p = \kappa / kT$



Expect: $\kappa \cong E a^4$

For $E \cong 10^9$ Pa and $a \cong 3$ nm, $\ell_p \cong 10\ \mu$m — Actin

$a \cong 10$ nm, $\ell_p \cong 1$ mm — Microtubules

$a \cong 0.2$ nm, $\ell_p \cong 100$ nm — DNA

Topics

- Phase behavior (liquid crystalline phases)
  order from entropy
- Rheology (flow properties, viscoelastic response)
  in Bulk
  microrheology (theory and experiment)
  composites of biopolymer + membrane
- Dynamics & response of single filaments
- Geometry of *twist* and *writhe*
- Collapse and condensation of biopolymers
- Active gels! (with molecular motors)
- Force generation, transmission *in vivo*

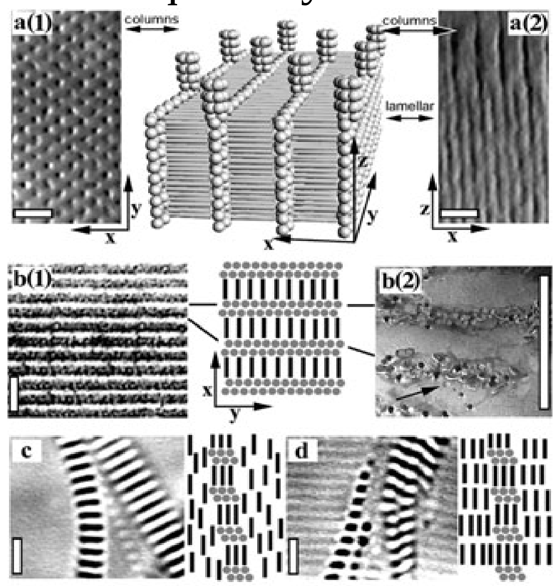
When should we have a nematic?

Onsager:

excluded volume of one rod $v \cong L^2 a$

concentration for nematic $\phi \cong a / L \cong a / \ell_p$ (Khokhlov,Semenov)

Some Liquid Crystalline Phases



(Fraden group)

When should we have a nematic?

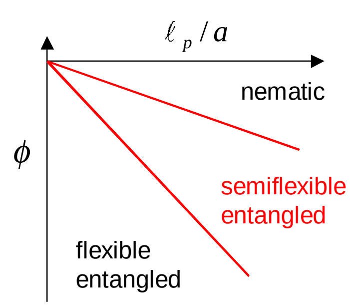
Onsager:

excluded volume of one rod $v \cong L^2 a$

concentration for nematic $\phi \cong a/L \cong a/\ell_p$ (Khokhlov,Semenov)

Isotropic, *flexible* solution?

$$\phi \leq (a/\ell_p)^2$$

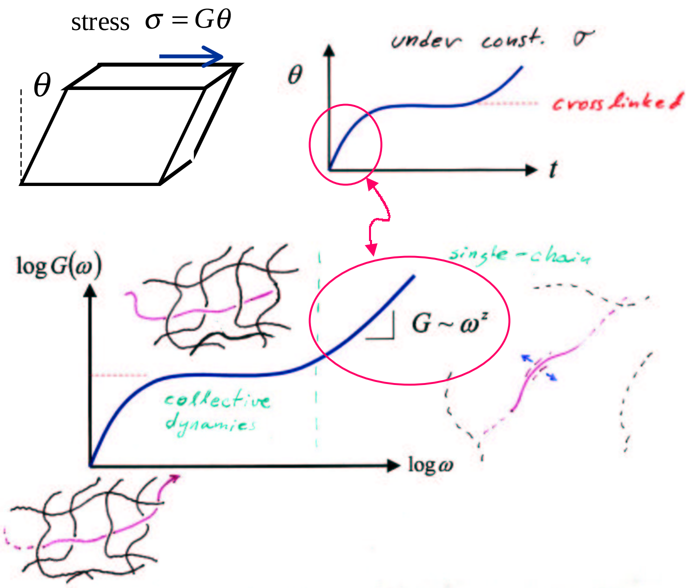


e.g.,

DNA c = 1-10 mg/ml

F-actin c = (0.01) - 2 mg/ml

Viscoelasticity of (bio)polymers

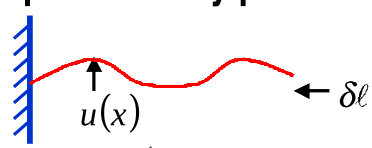


The Shear Modulus depends on frequency and time

$G \approx \omega^{3/4}$

Experiments (actin): Gittes, ...; Schnurr, … ’97; Xu, … ’98; Gisler, Weitz ’99
Theory: Morse ’98; Gittes, FCM ’98; Pasquali … ‘01)

Single-filament dynamics/response: a toy problem



$$\delta\ell = \frac{1}{2}\int_0^{\ell} (\nabla u)^2\, dx = \frac{1}{2}\sum_q \ell^2 q^2 \left\langle u_q^{\,2} \right\rangle$$

fluctuations

$$E_{\text{bend}} = \frac{kT}{2}\ell_p \int \left(\nabla^2 u\right)^2 dx \Rightarrow \left\langle u_q^{\,2} \right\rangle = \frac{1}{\ell \ell_p q^4}$$

dynamics

$$\kappa \nabla^4 u + \zeta \dot{u} = \text{noise}\,; \quad \zeta = 4\pi\eta / \log(0.6\lambda / a)$$

$$\Rightarrow \left\langle u_q(t) u_{-q}(0) \right\rangle = \left\langle u_q^{\,2} \right\rangle e^{-\omega_q t}\,; \quad \boxed{\omega_q = \kappa q^4 / \zeta}$$

projected length fluctuations

$$\left\langle \left[\delta\ell(t) - \delta\ell(0)\right]^2 \right\rangle = \frac{1}{2}\sum_{q,q'} \ell^2 \left\langle q^2 q'^2 \left(u_q^{\,2} u_{q'}^{\,2} - u_q(t)^2 u_{q'}(t)^2 \right) \right\rangle$$

$$= \ell^2 \sum_q q^4 \left\langle u_q^{\,2} \right\rangle^2 \left(1 - e^{-2\omega_q t}\right) \approx \boxed{\frac{\ell}{\ell_p^2} \left(\frac{\kappa t}{\zeta} \right)^{3/4}}$$

Granek ’97; sims: Gittes … ’98; Everaers … ’99; Pasquali … ’01

response function and modulus

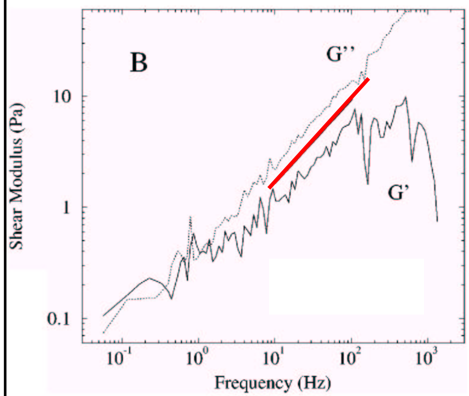
$$\left\langle \delta\ell_\omega^{\,2} \right\rangle = \frac{2kT}{\omega}\,\text{Im}(\alpha_\omega) \Rightarrow G(\omega) = \rho \frac{\ell}{15\alpha_\omega} - i\omega\eta = \boxed{\rho kT \frac{\ell_p^{\,2}}{15} \left(\frac{-2i\zeta\omega}{\kappa} \right)^{3/4} - i\omega\eta}$$

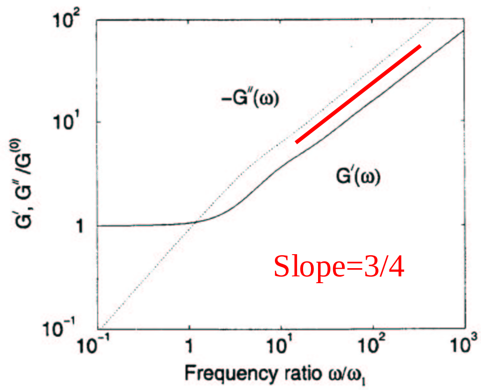
Morse ’98; Gittes … ’98; Pasquali … ‘01

High ω rheology

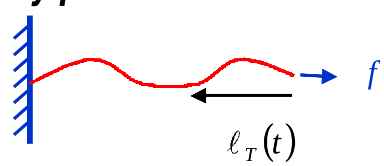
Experiments
Gittes, ...; Schnurr, … ’97
Xu, … ’98;
Gisler, Weitz ‘99

Theory
Morse ‘98; Gittes …‘98;
Pasquali … ‘01





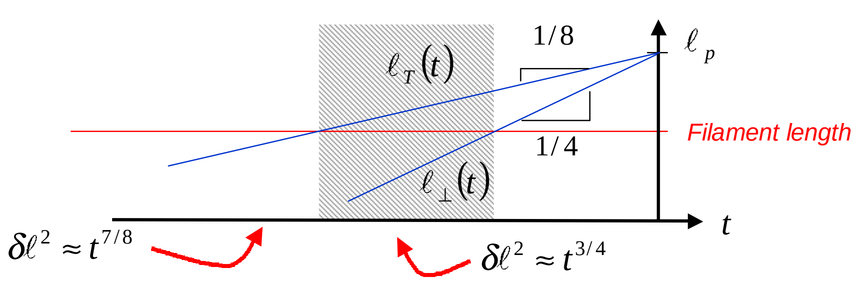
Tension propagation in the *toy problem*?



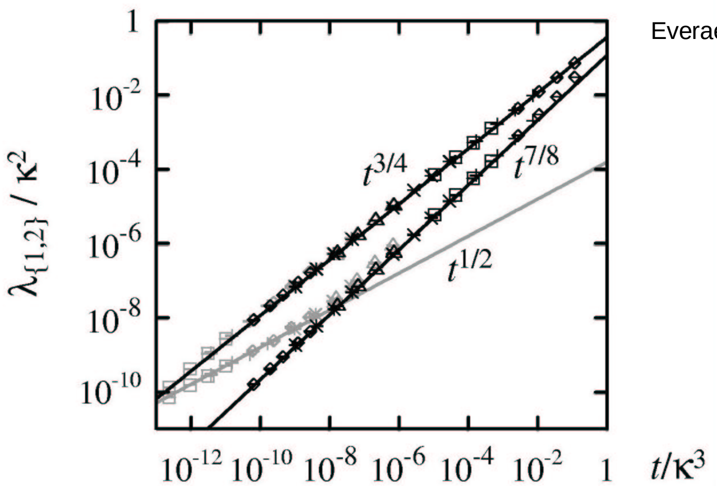
$$\ell_T(t) \approx \sqrt{\ell_p \ell_\perp(t)} \approx t^{1/8},$$

where $\ell_\perp(t) = (t\kappa/\zeta)^{1/4}$

Morse ’98;
Everaers … ’99



Simulations



Everaers … '99

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