Mechanics of the Cell

Second edition

Exploring the mechanical features of biological cells, including their architecture and stability, this textbook is a pedagogical introduction to the interdisciplinary fields of cell mechanics and soft matter physics from both experimental and theoretical perspectives.

This second edition has been greatly updated and expanded, with new chapters on complex filaments, the cell division cycle, the mechanisms of control and organization in the cell, and fluctuation phenomena. The textbook is now in full color which enhances the diagrams and allows the inclusion of new microscopy images.

With more than 300 end-of-chapter exercises exploring further applications, this textbook is ideal for advanced undergraduate and graduate students in physics and biomedical engineering. A website hosted by the author contains extra support material, diagrams and lecture notes, and is available at www.cambridge.org/Boal.

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Contents

Preface

The cells of our bodies represent a very large class of systems whose structural components often are both complex and soft. A system may be *complex* in the sense that it may comprise several components having quite different mechanical characteristics, with the result that the behavior of the system as a whole reflects an interplay between the characteristics of the components in isolation. The mechanical components themselves tend to be *soft*: for example, the compression resistance of a protein network may be more than an order of magnitude lower than that of the air we breathe. Cells have fluid interiors and often exist in a fluid environment, with the result that the motion of the cell and its components is strongly damped and very unlike ideal projectile motion as described in introductory physics courses. While some of the physics relevant to such soft biomaterials has been established for more than a century, there are other aspects, for example the thermal undulations of fluid and polymerized sheets, that have been investigated only in the past few decades.

The general strategy of this text is first to identify common structural features of the cell, then to investigate these mechanical components in isolation, and lastly to assemble the components into simple cells. The initial two chapters introduce metaphors for the cell, describe its architecture and develop some concepts needed for describing the properties of soft materials. The remaining chapters are grouped into three sections. Parts I and II are devoted to biopolymers and membranes, respectively, treating each system in isolation. Part III combines these soft systems into complete, albeit mechanically simple, cells; this section of the text covers the cell cycle, various aspects of cell dynamics, and some molecular-level biophysics important for understanding cell function.

Each chapter begins with an experimental view of the phenomena to be addressed, and a statement of the principal concepts to be developed. Those chapters with a fair amount of mathematical formalism are written such that a reader may skip to the last section of the chapter, without going through traditional physics-style derivations, to see the results applied in a biological context. The approach is to keep the mathematical detail manageable without losing rigor. Care has been taken to choose topics that can be approached within a common theoretical framework; this has forced the omission of some phenomena where a disproportionate effort would be required to assemble the related theoretical machinery. Some of the longer

proofs and other support material can be found through the Cambridge University Press website for this book.

Reflecting the multidisciplinary nature of biophysics, four appendices provide quick reviews of introductory material related to the text. For the physicist, Appendices A and B focus on animal cell types and the molecular composition of the cell's mechanical components, respectively. For the biologist, Appendices C and D introduce some core results from statistical mechanics and elasticity theory. The end-of-chapter problems are grouped according to (i) applications to biological systems, and (ii) formal extensions and supplementary derivations. The text is suitable for a one-semester course delivered to senior undergraduate and beginning graduate students with an interest in biophysics. Some formal results from the problem sets may provide additional lecture material for a more mathematical course aimed at graduate students in physics.

Compared to the first edition of this text, the second edition is 50% longer and the number of homework problems per chapter has been doubled. All of the original chapters have been reviewed, updated and reworked as needed. Four new chapters have been added, expanding the treatment of fluids and dynamical processes such as cell growth and division, as well as placing more emphasis on single-molecule aspects of cell mechanics. The mathematical description of soft, fluctuating systems is now part of the text and presented in a dedicated introductory chapter.

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The staff at Cambridge Press, particularly Rufus Neal, Simon Capelin and John Fowler, have helped immensely in bringing focus to the book and placing its content in the larger context. However, the lingering errors, omissions and obfuscations are my responsibility, and I am always appreciative of suggestions for ways to improve the quality of the text.

Dave Boal

List of symbols

A, A_v	area, area per vertex of a network
$\mathbf{a}$	area element of a surface
a, a_o	interface area per molecule (a_o at equilibrium)
$\mathbf{b}_i$, b	monomer bond vector and length
B_{eff}	effective bond length
$b_{\alpha\beta}$	second fundamental form
$\mathscr{C}$	capacitance per unit area
C, C_o	curvature; spontaneous curvature
C_1, C_2	principal curvatures to a surface
C_m, C_p	curvature along, or perpendicular, to a meridian
C_{ijkl}	elastic moduli
C_V	specific heat at constant volume
C_{vdw}	van der Waals interaction parameter
$C(i,j)$	binomial coefficient
c	concentration, units of [*moles*/*volume*] or [*mass*/*volume*]
D	diffusion coefficient
D_f	filament diameter for rods or chains
D_s	distance between two membranes or plates
d	dimensionality of a system
d_{bl}, d_p, d_{sh}	thickness of a bilayer, plate or shell
E	energy
$\mathcal{E}$	energy density
$\mathbf{E}$	electric field
E_{bind}	energy to separate an amphiphile from an aggregate
E_{sphere}, E_{disk}	energy of a spherical shell or flat disk
e	elementary unit of charge
$\mathbf{F}$, F	force
F_{buckle}	buckling force of a rod
F, $\mathcal{F}$	free energy; free energy density
$\mathcal{F}_{sol}$	free energy of a solution phase
G	Gibb's free energy; electrical conductance
$G_{channel}$	conductance of an open channel
$G(t)$	time-dependent relaxation modulus

$G'(\omega), G''(\omega)$	shear storage and loss moduli
g, $g_{\alpha\beta}$	metric; metric tensor
H, H_v	enthalpy; enthalpy per vertex
h	Planck's constant
$h(x, y)$	height of a surface in Monge representation
h_x, h_{xx}	first and second derivatives of $h(x, y)$ in the x-direction
$\mathcal{I}$	moment of inertia of cross section
j	flux
K_A, K_V	compression modulus for area, volume
k_B	Boltzmann's constant
k_{on}, k_{off}	capture and release rates in polymerization
k_{sp}	spring constant
L	length of a rod
$\mathcal{L}(y)$	Langevin function
L_c	contour length of a filament
$\mathcal{L}_K$	Kuhn length of a polymer
Lk	linking number
ℓ_B	Bjerrum length
ℓ_{cc}	C–C distance projected on the axis of hydrocarbon chain
ℓ_D	Debye length
ℓ_{hc}	length of hydrocarbon chain along its axis
$\mathcal{M}$	bending moment
$[M]$	monomer concentration
$[M]_c$, $[M]_{ss}$	minimum $[M]$ for filament growth; $[M]$ at treadmilling
m	molecular mass
m_j	mRNA concentration
N, n	number of monomers in a polymer chain
N_A	Avogadro's number
N_K	number of Kuhn lengths in a polymer
n_c	number of carbon atoms in a hydrocarbon chain
$\mathbf{n}$	unit normal vector to a curve or surface
$\mathbf{n}_x$, $\mathbf{n}_y$	derivative of $\mathbf{n}$ in the x or y direction
P	pressure
$\mathcal{P}$, $\mathcal{P}(x)$, $\mathcal{P}_r$	probabilities and probability densities
P_L, P_R, P_{net}	probabilities of motion for thermal ratchets
$\mathbf{p}$	momentum
p	bond or site occupation probability on a lattice; pitch of a helix
p_{bound}	probability of receptor–ligand binding
p_C, p_R	connectivity and rigidity percolation thresholds

p_j	repressor protein concentration
Q, q	electric charge
R, R_p	radius; electrical resistance; pipette radius
R	Reynolds number
R_{hc}	effective radius of a hydrocarbon chain
R_v, R_v*	vesicle radius, minimum vesicle radius
R_1, R_2	principal radii of curvature
r	position vector with Cartesian components (x, y, z)
S	entropy
S	structure factor
S_{gas}	entropy of an ideal gas
S_{ijkl}	elastic constants
s	arc length
s, s_o	spring length (s_o at equilibrium)
T	temperature
$\mathcal{T}$	torque
t	unit tangent vector to a curve
Tw	twist
U^α	eigenvalues of strain tensor
u	displacement vector in a deformation
u, u_{ij}	strain tensor
V	volume, electrical potential difference
$V(x)$	potential energy function
V_{mol}, V_{slab}	van der Waals potentials
V_o	volume of undeformed object
V_{qss}	quasi-steady-state potential across a membrane
v_{ex}	excluded volume parameter of a polymer
v_{hc}	volume of a hydrocarbon chain
v_{red}	reduced volume parameter
$\mathcal{W}_{ad}$	adhesion energy per unit area
w	width parameter of triangular probability distribution
Wr	writhe
Y	Young's modulus
Z	partition function
α	twist angle per unit length
β	inverse temperature $(k_B T)^{-1}$
γ	surface tension
γ_K, γ_{Na}	membrane conductivities (2D) for Na and K ions
ΔG_{conc}	change in free energy per ion from concentration gradient
ΔG_{coul}	change in free energy per ion from electrical potential

ε, ε_o	permittivity; permittivity of vacuum
ε_h	hydrophobic contact energy
η	viscosity
κ_{ax}	conductivity (3D) of an axon
κ_f	flexural rigidity of filament
κ_b, κ_G	bending rigidity or Gaussian bending rigidity of a membrane
κ_{nl}	non-local bending resistance
κ_{tor}	torsional rigidity of a filament
λ	edge tension of bilayer; protein degradation rate
λ^*	minimum edge tension for membrane stability
λ_p	mass per unit length of polymer
Λ, Λ_x, Λ_y, Λ_z	deformation scaling parameter
μ	mean value of a Gaussian distribution
μ_p, μ_s	pure, simple shear moduli
ν, ν_{Fl}	scaling exponent; Flory exponent for self-avoiding polymers
ξ_p	persistence length
ρ	number density (for chains or molecules)
ρ^*	transition density between dilute and semi-dilute solutions
ρ^{**}	transition density between semi-dilute and concentrated solutions
ρ_{agg}	critical aggregation density
ρ_{ch}	charge per unit volume
ρ_m	mass per unit volume
ρ_L	contour length of polymer per unit volume
ρ_N	transition density between isotropic and nematic phases
ρ_+, ρ_-, ρ_s	number densities of ions in solution
σ	width parameter of a Gaussian distribution
σ_{ij}, σ_θ, σ_z	stress tensor; hoop and axial stress of a cylinder
σ_p	Poisson ratio
σ_s	charge per unit area
τ	two-dimensional tension; decay time in RC circuit
τ_θ, τ_z	hoop and axial tension of a cylinder
Ψ, ψ	electric potential
χ	rotational drag parameter
ζ	roughness exponent for membranes