unknowns.

$$W(u,v,w) \to \min \qquad \delta W(u,v,w) = \delta W^{\text{int}} + \delta W^{\text{ext}} \doteq 0 \tag{4.2.10}$$

The internal and external virtual work δW^{int} and δW^{ext} can then be specified as follows.

$$\begin{aligned} \delta W^{\text{int}} &= \int_A \int_{-h/2}^{+h/2} \sigma_{xx}\,\delta\varepsilon_{xx} + 2\sigma_{xy}\,\delta\varepsilon_{xy} + \sigma_{yy}\,\delta\varepsilon_{yy} \quad \mathrm{d}A \\ &= \int_A n_{xx}\,\delta\varepsilon^{\text{con}}_{xx} + 2n_{xy}\,\delta\varepsilon^{\text{con}}_{xy} + n_{yy}\,\delta\varepsilon^{\text{con}}_{yy} \;\; \mathrm{d}z\,\mathrm{d}A \\ \delta W^{\text{ext}} &= \int_A p\,\delta w \quad \mathrm{d}A \end{aligned} \tag{4.2.11}$$

Energy considerations can sometimes be very illustrative. They immediately provide information about the so called energy conjugate pairs. For example, from the above expression, you can easily see that the shear stresses σ_{xy} are energetically conjugate to the shear strains ε_{xy} or that the normal stress resultants n_{xx} are conjugate to the corresponding strains $\varepsilon^{\text{con}}_{xx}$ which are constant over the thickness.

Equibiaxial tension

Let us assume a state for which the in plane normal stresses are the similar for both directions, i.e. $\sigma_{xx} = \sigma_{yy} = \sigma$, while the shear stress vanishes $\sigma_{xy} = 0$. Moreover, we shall assume a uniform extension such that σ takes the same values all over the membrane and is thus independent from the position in space, i.e., $\sigma \neq \sigma(x,y,z)$. In structural mechanics, this loading situation is called homogeneous equilibiaxial tension. For this special case, we have $n_{xx} = n_{yy} = n$ and $n_{xy} = 0$. Accordingly, the force equilibrium in x- and y-direction $(4.2.9)_1$ and $(4.2.9)_2$ is trivially satified. The equilibrium of forces in the transverse direction $(4.2.9)_3$ then reduces to the classical Laplace equation for membranes,

$$n\,[\,w_{,xx} + w_{,yy}\,] + p_z = 0 \tag{4.2.12}$$

which relates the pressure p_z to the second gradient of the transverse displacements w in terms of the surface tension n. Mathematicians would typically express this equation in a somewhat more compact notation through the Laplace differential operator $\Delta = \nabla^2 = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}$ such that $w_{,xx} + w_{,yy} = \Delta w$.

$$p_z = -n\,\Delta\,w \tag{4.2.13}$$

Recall that the negative second derivative of the transverse displacement w takes the interpretation of the curvature κ. Accordingly $-w_{,xx} = \kappa_{xx} = 1\,/\,r_y$ and $-w_{,yy} = \kappa_{yy} = 1\,/\,r_x$ are the radii of curvature of the membrane about the y- and x-axis, respectively.

$$p_z = n\,\left[\,\frac{1}{r_x} + \frac{1}{r_y}\,\right] \tag{4.2.14}$$

For equal radii $r_x = r_y = r$, equation (4.2.14) reduces to the classical membrane equation for spheres $p_z = -n\,\Delta w = n\,[\,1/r_x + 1/r_y\,] = 2\,n\,/\,r$ similar to the one derived for soap bubbles $\Delta p = 2\,\gamma\,/\,r$ in the motivation (4.1.3). Recall that γ was introduced as the surface tension, which is of the unit force per length. The stress resultant n, the force per cross section length, obviously has the same unit and takes a similar interpretation.
To this point, we have only looked into changes of geometry in each direction independently. Sometimes it is interesting to know the response of a two-dimensional element, say in terms of the membrane area A. What is the relation between the applied pressure and the change of an area element of the shell mid-surface? Let us first define a measure for this change in area. By increasing the pressure p_z, or rather by blowing up the soap bubble in section 4.1.2, a small square shell element of initial area $A = L^2$ will increase its area to $a = l^2 = [1+\varepsilon]^2 L^2$. Accordingly, the dimensionless change is defined as the ratio between the deformed and the initial area, $\Delta A = a\,/\,A$. Similar to the one dimensional strain $\Delta L/L = [\,l - L\,]/L = \varepsilon$ which is nothing but the length change ΔL scaled by the original length L, we could thus introduce a two dimensional area strain as the area change ΔA scaled by the original area A.

$$\frac{\Delta A}{A} = \frac{a - A}{A} = \frac{[1+\varepsilon]^2 L^2 - L^2}{L^2} = 2\,\varepsilon + \varepsilon^2 \approx 2\,\varepsilon \tag{4.2.15}$$

Here, we have made use of the assumption of small strains and therefore neglected the quadratic term $\mathcal{O}(\varepsilon^2)$. In the case of equibiaxial tension with $n_{xx} = n_{yy} = n$, the in plane force equilibrium $(4.2.7)_1$, and similarly $(4.2.7)_2$, can obviously be further simplified. With the help of $\varepsilon_{xx} = \varepsilon_{yy} = \varepsilon$ with $\varepsilon = [\Delta A\,/\,A]\,/\,2$, equation $(4.2.7)_1$ can then be rewritten in the following form.

$$n = \frac{E\,h}{1-\nu^2}\,[\,\varepsilon_{xx} + \nu\,\varepsilon_{yy}\,] = \frac{E\,h}{1-\nu^2}\,[1+\nu]\,\varepsilon = \frac{E\,h}{2\,[\,1-\nu\,]}\,\frac{\Delta A}{A} \tag{4.2.16}$$

The proportionality factor of Young's modulus E devided by $[1-\nu]$ scaled by the thickness h is often referred to as area expansion modulus $K_A = \frac{E\,h}{2\,[\,1-\nu\,]}$. You can easily check that it has the dimensions of force per length similar to the stress resultant n. Accordingly, we obtain the remarkably simple constitutive relation

$$n = K_A\,\tfrac{\Delta A}{A} \tag{4.2.17}$$

between the forces n and the area strain $\Delta A\,/\,A$ in terms of the area expansion modulus K_A. Typical values of the area expansion modulus for lipid bilayers are in the range of $K_A = 0.1 - 1.0$ N/m. The cell membrane of red blood cells, for example, has an area expansion modulus of approximately $K_A = 0.45$ N/m. This value is incredibly huge as compared to the other moduli which indicates that cell membranes can be treated as nearly incompressible. The large resistance to area change can be attributed to the changes in energy associated with exposing the hydrophobic core of the lipid bilayer to water as the spacing between the individual molecules is increased.

Shear

Until now, we have assumed that the in plane normal stresses are the similar for both directions and that the shear term vanishes. A typical loading scenario that would involve shear though is the application of tension in one direction, say σ_{xx} such that the membrane stretches in x direction while it contracts under smaller tension σ_{yy} in the y direction. Although we only apply normal stresses of different magnitude and we do not apply shear stress in the original coordinate system where $\sigma_{xy} = 0$, surfaces oriented under an angle of 45^o exhibit pure shear stress which is of the magnitude $\sigma_{xy} = [\,\sigma_{xx} - \sigma_{yy}\,] \,/\, 2$. Biological membranes, in particular the lipid bilayer that forms the cell membrane, hardly display any resistance to shear. In that sense, they behave like fluids and are therefore often treated as a two-dimensional liquids. You can simply check the lack of shear resistance by putting a flat plate on the surface of water. The force you need to apply to move the plate around is relatively small as compared to, for instance, the force you would need in order to press it down. This characteristic behavior is reflected through a relatively small shear modulus $G = E \,/\, [\,2\,[1+\nu]]$ and a relatively large bulk or rather volume expansion modulus $K = E \,/\, [\,3\,[1-2\nu]]$. From the constitutive equation introduced in chapter 2, we can extract the stress strain relation for the shear component $\sigma_{xy} = 2\,E \,/\, [\,2\,[1+\nu]]\,\varepsilon_{xy} = 2\,G\,\varepsilon_{xy}$. It introduces the following constitutive relation between the shear stress resultant $n_{xy} = \sigma_{xy}\,h$ and the shear strain ε_{xy}.

$$n_{xy} = K_S\,\varepsilon_{xy} \tag{4.2.18}$$

Here, we have introduced the membrane shear modulus $K_S = 2\,G\,h = 2\,E\,h \,/\, [\,2\,[1+\nu]]$, which has the unit force per length. The cell membrane of a red blood cell would have a typical value of $K_S = 6 - 9 \cdot 10^{-6}$ N/m. This value is extremely small, especically when compared to the area expansion modulus of red blood cell membranes $K_A = 0.45$ N/m. This indicates that the effect of shear can usually be neglected under static loading. However, it might play a significant role under dynamic loading conditions. Fluids typically display a significant strain rate sensitivity, an effect which is referred to as viscosity.

4.2.3 Transverse deformation - Bending

In the previous subsection, we have elaborated the contributions to the strains which are constant over the thickness and could be related to in plane tension and shear. Let us now examine the contributions which vary linearly over the thickness. These contributions are related to the transverse displacement w or rather its second derivative. From a structural mechanics point of view they introduce a phenomenon which is referred to as bending, as illustrated in figure 4.10.

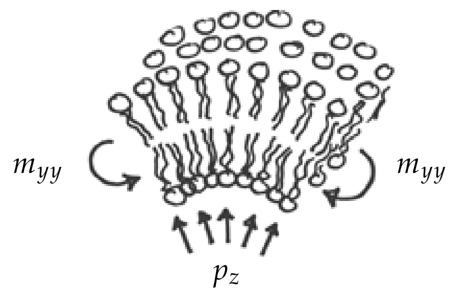

Figure 4.10: Infinitesimal element of the cell membrane with transverse pressure p_z and bending moment m_{yy}

In this section, we derive the classical Kirchhoff plate equation, a fourth order differential equation that essentially governs the transverse displacement or rather out of plane deflection w in response to a given pressure p_z acting in the out-of-plane direction z. The plate equation is a result of four sets of governing equations, the kinematics, the constitutive equations, the definition of the stres resultants and the equilibrium equations which are illustrated in detail in the sequel. Similar to the previous subsection, we begin by taking a look at equation (4.2.4). This time, we extract all non constant terms that involve the z-coordinate. The resulting kinematic equations relate the in in plane normal strains ε_{xx} and ε_{yy} and the in plane shear strain ε_{xy} to the second derivatives of the membrane deflection $w_{,xx}$, $w_{,yy}$ and $w_{,xy}$.

$$
\begin{aligned}
\varepsilon_{xx} &= -w_{,xx}\ z = \kappa_{xx}\ z \\
\varepsilon_{yy} &= -w_{,yy}\ z = \kappa_{yy}\ z \\
\varepsilon_{xy} &= -w_{,xy}\ z = \kappa_{xy}\ z
\end{aligned}
\tag{4.2.19}
$$

Recall that, from a kinematical point of view, the second derivatives of the deflection represent the curvatures $-w_{,xx} = \kappa_{xx}$, $-w_{,yy} = \kappa_{yy}$ and $-w_{,xy} = \kappa_{xy}$. From chapter 2, we can extract the relevant constitutive equations, i.e. the equations relating stress and strain. In particular they relate the in plane normal stresses σ_{xx} and σ_{yy} and the in plane shear stress σ_{xy} to the corresponding strains ε or curvatures κ

$$\begin{aligned}
\sigma_{xx} &= \tfrac{E}{1-\nu^2}\;[\,\varepsilon_{xx} + \nu\,\varepsilon_{yy}\,] = \tfrac{E}{1-\nu^2}\;[\,\kappa_{xx} + \nu\,\kappa_{yy}\,]\;z \\
\sigma_{yy} &= \tfrac{E}{1-\nu^2}\;[\,\varepsilon_{yy} + \nu\,\varepsilon_{xx}\,] = \tfrac{E}{1-\nu^2}\;[\,\kappa_{yy} + \nu\,\kappa_{xx}\,]\;z \\
\sigma_{xy} &= \tfrac{E}{1+\nu}\qquad \varepsilon_{xy} \qquad = \tfrac{E}{1+\nu}\qquad \kappa_{xy}\qquad z
\end{aligned} \tag{4.2.20}$$

Similar to the previous section, we could rewrite the last equation of this set as $\sigma_{xy} = G\,\varepsilon_{xy}$ where $G = \frac{E}{2\,[1+\nu]}$ is the shear modulus. Equation (4.2.20) tells us something about the stresses in a particular cross section. Stresses, however, cannot be directly used to evaluate equilibrium. To state the equilibrium equations, we therefore derive the stress resultants m_{xx}, m_{yy} and m_{xy} in terms of corresponding stresses integrated over the surface thickness h. These resultants are the moments per cross section length which unlike the forces introduced in the previous section are not continuous across the cross section. Therefore, as indicated before, we really have to evaluate them through an integration across the thickness.

$$\begin{aligned}
m_{xx} &= \int_{-h/2}^{+h/2} \sigma_{xx}\,z\,\mathrm{d}z = \tfrac{E\,h^3}{12\,[1-\nu^2]}\;[\,\kappa_{xx} + \nu\,\kappa_{yy}\,] \\
m_{yy} &= \int_{-h/2}^{+h/2} \sigma_{yy}\,z\,\mathrm{d}z = \tfrac{E\,h^3}{12\,[1-\nu^2]}\;[\,\kappa_{yy} + \nu\,\kappa_{xx}\,] \\
m_{xy} &= \int_{-h/2}^{+h/2} \sigma_{xy}\,z\,\mathrm{d}z = \tfrac{E\,h^3}{12\,[1+\nu]}\qquad \kappa_{xy}
\end{aligned} \tag{4.2.21}$$

Unlike in the previous section, where the stress resultants had the charcter of forces per length we have now introduced resultants which are of the unit force times length per length which is characteristic for distributed moments. By assuming a uniform thickness and homogeneous material properties across the thickness, we can introduce the bending stiffness $K_B = \int_{-h/2}^{+h/2} \frac{E}{1-\nu^2}\,z^2\,\mathrm{d}z = \frac{E\,h^3}{12\,[\,1-\nu^2\,]}$. The equilibrium equations for bending which can be motivated from figure **??** consist of the force equilibrium in z-direction and the equilibrium of momentum around the x- and y-axis.

$$\begin{aligned}
\textstyle\sum f_x \doteq 0: \quad & -n_{xx}\mathrm{d}y + [n_{xx} + n_{xx,x}\mathrm{d}x]\mathrm{d}y - n_{yx}\mathrm{d}x + [n_{yx} + n_{yx,x}\mathrm{d}y]\mathrm{d}x = 0 \\
\textstyle\sum f_y \doteq 0: \quad & -n_{yy}\mathrm{d}x + [n_{yy} + n_{yy,y}\mathrm{d}y]\mathrm{d}x - n_{xy}\mathrm{d}y + [n_{xy} + n_{xy,y}\mathrm{d}x]\mathrm{d}y = 0 \\
\textstyle\sum f_z \doteq 0: \quad & -n_{xx}\mathrm{d}y\,w_{,x} + [n_{xx} + n_{xx,x}\mathrm{d}x]\mathrm{d}y[w_{,x} + w_{,xx}\mathrm{d}x] \\
& -n_{xy}\mathrm{d}y\,w_{,y} + [n_{xy} + n_{yx,x}\mathrm{d}x]\mathrm{d}y[w_{,y} + w_{,yx}\mathrm{d}x] \\
& -n_{yx}\mathrm{d}x\,w_{,x} + [n_{yx} + n_{xy,y}\mathrm{d}y]\mathrm{d}x[w_{,x} + w_{,xy}\mathrm{d}y] \\
& -n_{yy}\mathrm{d}x\,w_{,y} + [n_{yy} + n_{yy,y}\mathrm{d}y]\mathrm{d}x[w_{,y} + w_{,yy}\mathrm{d}y] + p_z\,\mathrm{d}x\mathrm{d}y = 0
\end{aligned} \tag{4.2.22}$$

Just like for the in plane deformation equilibrium, we divide each equation by $\mathrm{d}x\mathrm{d}y$ and cancel the remaining terms with $\mathrm{d}x$ or $\mathrm{d}y$ which are small when compared to the remaining terms. The remaining terms then yield the following simplified set of equations.

$$\begin{aligned} \sum f_z &\doteq 0 & q_{x,x} &+ q_{y,y} + p_z = 0 \\ \sum m_y &\doteq 0 & m_{xx,x} &+ m_{yx,y} - q_x = 0 \\ \sum m_x &\doteq 0 & m_{yy,y} &+ m_{xy,x} - q_y = 0 \end{aligned} \tag{4.2.23}$$

With the use of the x-derivative of the balance of momentum $(4.2.23)_2$ $q_{,xx} = m_{xx,xx} + m_{yx,yx}$, the y-derivative of the balance of momentum $(4.2.23)_3$ $q_{,yy} = m_{yy,yy} + m_{xy,xy}$ and the fact that $m_{xy,xy} = m_{yx,yx}$, we can rewrite the balance of forces in thickness direction $(4.2.23)_1$. The equilibrium equations (4.2.23) can thus be summarized in just one simple equation.

$$m_{xx,xx} + 2\, m_{xy,xy} + m_{yy,yy} + p_z = 0 \tag{4.2.24}$$

The above equation can be reformulated by inserting the definition of the stress resultants, by making use of the constitutive equations and the kinematic assuptions to finally yield the classical fourth order differential equation for thin plates, the Kirchhoff plate equation.

$$p_z = K_B \left[w_{,xxxx} + 2\, w_{,xxyy} + w_{,yyyy} \right] \tag{4.2.25}$$

It relates the pressure p_z to the fourth gradient of the transverse displacements w in terms of the bending stiffness K_B. Mathematicians would typically rewrite the plate equation in compact notation in terms of the Laplace differential operator $\Delta = \nabla^2 = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}$.

$$p_z = K_B\, \Delta^2 w \tag{4.2.26}$$

Typical values for the bending stiffness K_B are in the order of 10^{-19} Nm for lipid bilayers such as the cell membrane of the red blood cell. This is a really low value as compared to the area expansion modulus K_A. It is even low when compared to the membrane shear modulus K_S! This indicates that the effect of bending is of minor order in biomembranes. This is not surprising though since membrane structures are, by their very definition, structures that try to achieve an optimal stiffness to weight ratio by carrying loads exclusively through in plane normal forces and avoiding out of plane bending as much as possible!
Again, we can write derive the equilibrium equations through an energy principle. To this end, we would minimize the overall energy with respect to the

transvere displacement w, or, equivalently, evaluate its vanishing first variation δW with respect to w.

$$W(w) \rightarrow \min \qquad \delta W(w) = \delta W^{\rm int} + \delta W^{\rm ext} \doteq 0 \tag{4.2.27}$$

The internal and external energy expression could then be expressed as follows.

$$\begin{aligned} \delta W^{\rm int} &= \int_A \int_{-h/2}^{+h/2} \quad \sigma_{xx}\,\delta\varepsilon_{xx} + 2\sigma_{xy}\,\delta\varepsilon_{xy} + \sigma_{yy}\,\delta\varepsilon_{yy} \quad \mathrm{d}z\,\mathrm{d}A \\ &= \int_A \qquad m_{xx}\,\delta\kappa_{xx} + 2m_{xy}\,\delta\kappa_{xy} + m_{yy}\,\delta\kappa_{yy} \qquad \mathrm{d}A \\ \delta W^{\rm ext} &= \int_A \qquad\qquad p\,\delta w \qquad\qquad \mathrm{d}A \end{aligned} \tag{4.2.28}$$

We can immediately see that the stress resultants m are energetically conjugate to the curvature κ. Again, by carrying out an intergration by parts, energy minimization would yield the equilibrium equations (4.2.23) which in that context, would be referred to as the Euler-Lagrange equations.

4.2.4 In plane and transverse deformation - Tension and bending

For the sake of clarity, we have treated the load cases of tension and bending as individual phenomena so far. Of course, in reality, both usually occur simultaneously, however, most of the times one really dominates the other. An overall description that captures both phenomena and is thus representative for biomembranes in general summarizes both transverse force equilibrium equations $(4.2.9)_3$ and $(4.2.23)_1$ or rather equations (4.2.12) and (4.2.25) in one single equation.

$$n\,[\,w_{,xx} + w_{,yy}\,] + K_B\,[\,w_{,xxxx} + 2\,w_{,xxyy} + w_{,yyyy}\,] + p_z = 0 \tag{4.2.29}$$

The ratio between the two constants n and K_B would then immediately tell us which of the two phenomena is dominant. Let w be the transverse displacement and λ be a characteristic length over which these transverse displacements may vary. The membrane term would thus scale with $n\,w\,/\,\lambda^2$ while the bending term scales with $K_B\,w\,/\,\lambda^4$. The ratio of these scaling factors $K_B\,/\,[n\,\lambda^2]$ could give us an indication of whether tension or bending is relevant under the given conditons.

$$\begin{aligned} \frac{K_B}{n\,\lambda^2} &\ll 1 \qquad \text{tension dominated} \\ \frac{K_B}{n\,\lambda^2} &\gg 1 \qquad \text{bending dominated} \end{aligned} \tag{4.2.30}$$

A typical value for cells at $K_B = 10^{-18}$Nm, $n = 5 \cdot 10^5$N/m and $\lambda = 1\mu$m would be $\frac{K_B}{n\,\lambda^2} = 0.02$ which would indicate that in biological cells, membrane effects are typically dominant over bending.

4.3 Problems

1. We have seen that surface tension is important to give the cell membrane its spherial shape. A way to visualize surface tension is to float a paper clip on the surface of water. Think of other ways to illustrate surface tension! (other examples: If you fill a glass with water, you will be able to add water above the rim of the glass because of surface tension! Small insects such as the water strider can walk on water because their weight is not enough to penetrate the surface.)

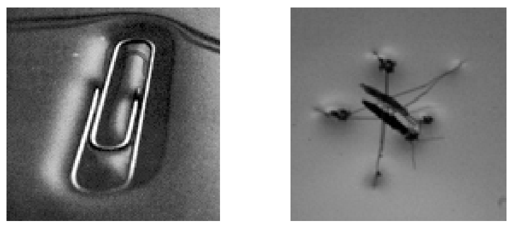

Figure 4.11: Phenomenon of surface tension

2. Look up the number of sides and the surface to volume ratio for the five platonic solids. Show that the surface to volume ratio decreases with increasing number of sides. Compare your results against the surface to volume ratio of a sphere with infinely many sides.

solid	no of sides	volume	surface
tetrahedron	4	1 cubic inch	
cube	6	1 cubic inch	
octahedron	8	1 cubic inch	
dodecahedron	12	1 cubic inch	
icosahedron	20	1 cubic inch	
sphere	∞	1 cubic inch	

Table 4.1: Surface to volume ratio of platonic solids

3. In the text, we have described the derivation of the von Kármán strains

$$
\begin{aligned}
\varepsilon_{xx} &= u_{,x} + \tfrac{1}{2}\, w_{,x}^2 - z\, w_{,xx} & \qquad \varepsilon_{xy} &= \tfrac{1}{2}\,[u_{,y} + v_{,x}] + w_{,x} w_{,y} - z\, w_{,xy} \\
\varepsilon_{yy} &= v_{,y} + \tfrac{1}{2}\, w_{,y}^2 - z\, w_{,yy} & \qquad \varepsilon_{yz} &= 0 \\
\varepsilon_{zz} &= 0 & \qquad \varepsilon_{zx} &= 0
\end{aligned}
$$

in words. Verify these equations by following what is described in the text in going from the nonlinear Green Lagrange strains E to the small strains ε by neglecting higher order terms. Make sure you understand which terms can be neglected and why! Then, insert the definitions of the total displacments u^{tot}, v^{tot} and w^{tot} to end up with the Kármán strains.

4. You have seen that the force equilibrium in transverse direction $n_{xx}\,w_{,xx} + 2\,n_{xy}\,w_{,xy} + n_{yy}\,w_{,yy} + p_z = 0$ is really important. In the text we have described how this simplified form can be obtained from the more general format $[n_{xx}\,w_{,x} + n_{xy}\,w_{,y}]_{,x} + [n_{xy}\,w_{,x} + n_{yy}\,w_{,y}]_{,y} + p_z = 0$ by making use of equations $(4.2.9)_1$ and $(4.2.9)_2$. Verify that the two expressions above are identical!

Bibliography

[1] ALBERTS, B., A. JOHNSON, J. LEWIS, M. RAFF, K. ROBERTS & P. WALTER [2002]. *Molecular biology of the cell*. Garland Science, Taylor & Francis Group, New York.

[2] BOAL, D. [2002]. *Mechanics of the Cell*. Cambridge University Press, Cambridge.

[3] BOYS, C. V. [1890]. *Soap-Bubbles: Their Colours and the Forces Which Mold Them*. Dover Publications (reprint from 1959).

[4] BUSTAMANTE, C., Z. BRYANT & S. B. SMITH [2003]. 'Ten years of tension: single-molecule DNA mechanics.' *Nature*, **421**, pp. 423–427.

[5] FLORY, P. J. [1969]. *Statistical Mechanics of Chain Molecules*. John Wiley & Sons, Chichester – New York.

[6] FLORY, P. J. [1976]. 'Statistical thermodynamics of random networks.' *Proceedings of the Royal Society of London A*, **351**, pp. 351–378.

[7] FLÜGGE, W. [1973]. *Stresses in Shells*. Springer Verlag, New York.

[8] GOETZ, R., G. GOMPPER & R. LIPOWSKY [1999]. 'Mobility and elasticity of self-assembled membranes.' *Phys. Rev. Lett.*, **82(1)**, pp. 221–224.

[9] HOWARD, J. [2001]. *Mechanics of Motor Proteins and the Cytoskeleton*. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts.

[10] INGBER, D. E. [2003]. 'Tensegrity I. Cell structure and hierarchical systems in biology.' *J. Cell Sciences*, **116(7)**, pp. 1157–1173.

[11] INGBER, D. E. [2003]. 'Tensegrity II. How structural networks influence cellular information processing networks.' *J. Cell Sciences*, **116(8)**, pp. 1397–1408.

[12] ISRAELACHVILI, J. N. [1991]. *Intermolecular and Surface Forces With Applications to Colloidal and Biological Systems*. Academic Press, London.

[13] KUHN, W. [1934]. 'Über die Gestalt fadenförmiger Moleküle in Lösungen.' *Kolloid-Zeitschrift*, **52**, pp. 2–15.

[14] KUHN, W. & F. GRÜN [1942]. 'Beziehungen zwischen elastischen Konstanten und Dehnungsdoppelbrechung hochelastischer Stoffe.' *Kolloid-Zeitschrift*, **101**, pp. 248–271.

[15] KWON, R. Y. & C. R. JACOBS [2007]. 'Time-dependent deformations in bone cells exposed to fluid flow in vitro: Investigating the role of cellular deformation in fluid flow-induced signaling.' *J. Biomechanics (in press)*.

[16] DE LAPLACE, P. S. [1996]. *Traité de Mécanique Célèste. Suppl. 10th book: Sur l'Action Capillaire*. Coureier, Paris.

[17] MALONE, A. M. D., N. N. BATRA, G. SHIVARAM, R. Y. KWON, L. D. YOU, C. H. KIM, J. RODRIGUEZ, K. JAIR & C. R. JACOBS [2007]. 'The role of actin cytoskeleton in oscillatory fluid flow-induced signaling in MC3T3-E1 osteoblasts.' *Amer. J. Physiology – Cell Physiology*, **292(5)**, pp. C1830–C1836.

[18] MARKO, J. F. & E. D. SIGGIA [1995]. 'Stretching DNA.' *Macromolecules*, **28**, pp. 8759–8770.

[19] MOFRAD, M. R. K. & R. D. KAMM [2006]. *Cytoskeletal Mechanics*. Cambridge University Press, Cambridge.

[20] MÜLLER, I. & P. STREHLOW [2004]. *Rubber and Rubber Balloons – Paradigms of Thermodynamics*. Springer Verlag, Berlin.

[21] MÜLLER, I. & W. WEISS [2005]. *Energy and Entropy - A Universal Competition*. Springer Verlag, Berlin.

[22] PASTOR, R. W. [1994]. 'Molecular dynamics and Monte Carlo simulations of lipid bilayers.' *Curr. Opin. Struct. Biol.*, **42**, pp. 486–492.

[23] REDDY, J. N. [2004]. *An Introduction to Nonlinear Finite Element Analysis*. Oxford University Press, Oxford.

[24] SACKMANN, E. [1990]. 'Molecular and global structure and dynamics of membranes and lipid bilayers.' *Can. J. Phys.*, **68**, pp. 99–1012.

[25] SINGER, S. J. & G. L. NICOLSON [1972]. 'The fluid mosaic model of the structure of cell membranes.' *Science*, **175**, pp. 720–731.

[26] TRELOAR, L. R. G. [1975]. *The Physics of Rubber Elasticity*. Clarendon Press, Oxford.

[27] TRELOAR, L. R. G. [1976]. 'The mechanics of rubber elasticity.' *Proceedings of the Royal Society of London A*, **351**, pp. 301–330.

[28] YOUNG, T. [1804]. *Phil. Trans. Roy. Soc.*, **95**, pp. 65.