**Final Honour School of Mathematics Part C**

---

# C5.9: Mathematical Mechanical Biology
# Alain Goriely

---

**dd/mm/yyyy**

**Do not turn this page until you are told that you may do so**

# SOLUTIONS

**Solution 1.**

(a).[BS] Definition: $\mathbf{d}_i$: director basis, $\mathbf{n}$: resultant force, $\mathbf{u}$: Darboux or curvature vector, $\mathbf{m}$: resultant moment, $\mathbf{d}_3$: the tangent vector, $\Gamma$ is the ratio of the torsional stiffness to the bending stiffness, and $K$ the intrinsic curvature. $(\,)'$ denotes the derivative with respect to arc-length.
We have $(\mathbf{n}.\mathbf{n})' = 2\mathbf{n}.\mathbf{n}' = \mathbf{0}$, that is $\mathbf{n}.\mathbf{n} = I_1$. Similarly, $(\mathbf{n}.\mathbf{m})' = (\mathbf{m}'.\mathbf{n})+(\mathbf{m}.\mathbf{n}') = (\mathbf{d}_3\times\mathbf{n}).\mathbf{n} = \mathbf{0}$ and $\mathbf{n}.\mathbf{m} = I_2$.
We have

$$\begin{aligned}\frac{d\boldsymbol{n}}{ds} &= \frac{d}{ds}\left(\mathsf{n}_1\mathbf{d}_1 + \mathsf{n}_2\mathbf{d}_2 + \mathsf{n}_3\mathbf{d}_3\right)\\ &= \frac{d\mathsf{n}_1}{ds}\mathbf{d}_1 + \mathsf{n}_1\frac{\partial\mathbf{d}_1}{\partial s} + \frac{d\mathsf{n}_2}{ds}\mathbf{d}_2 + \mathsf{n}_2\frac{\partial\mathbf{d}_2}{\partial s} + \frac{d\mathsf{n}_3}{ds}\mathbf{d}_3 + \mathsf{n}_3\frac{\partial\mathbf{d}_3}{\partial s}\\ &= \left(\frac{d\mathsf{n}_1}{ds} - \mathsf{n}_2\mathsf{u}_3 + \mathsf{n}_3\mathsf{u}_2\right)\mathbf{d}_1 +\\ &\quad \left(\frac{d\mathsf{n}_2}{ds} + \mathsf{n}_1\mathsf{u}_3 - \mathsf{n}_3\mathsf{u}_1\right)\mathbf{d}_2 +\\ &\quad \left(\frac{d\mathsf{n}_3}{ds} - \mathsf{n}_1\mathsf{u}_2 + \mathsf{n}_2\mathsf{u}_1\right)\mathbf{d}_3,\end{aligned}$$

That is,

$$\frac{d\mathsf{n}_1}{ds} - \mathsf{n}_2\mathsf{u}_3 + \mathsf{n}_3\mathsf{u}_2 = 0, \tag{1}$$

$$\frac{d\mathsf{n}_2}{ds} + \mathsf{n}_1\mathsf{u}_3 - \mathsf{n}_3\mathsf{u}_1 = 0, \tag{2}$$

$$\frac{d\mathsf{n}_3}{ds} - \mathsf{n}_1\mathsf{u}_2 + \mathsf{n}_2\mathsf{u}_1 = 0. \tag{3}$$

A similar computation for $\mathbf{m}$ gives

$$\begin{aligned}&\frac{d\mathsf{m}_1}{ds} - \mathsf{m}_2\mathsf{u}_3 + \mathsf{m}_3\mathsf{u}_2 - \mathsf{n}_2 = 0,\\ &\frac{d\mathsf{m}_2}{ds} + \mathsf{m}_1\mathsf{u}_3 - \mathsf{m}_3\mathsf{u}_1 + \mathsf{n}_1 = 0,\\ &\frac{d\mathsf{m}_3}{ds} - \mathsf{m}_1\mathsf{u}_2 + \mathsf{m}_2\mathsf{u}_1 = 0.\end{aligned}$$

We use the constitutive law for $\mathbf{m}$ to obtain

$$\frac{d\mathsf{u}_1}{ds} - \mathsf{u}_2\mathsf{u}_3 + \Gamma\mathsf{u}_3\mathsf{u}_2 - \mathsf{n}_2 = 0 \tag{4}$$

$$\frac{d\mathsf{u}_2}{ds} + (\mathsf{u}_1 - K)\mathsf{u}_3 - \Gamma\mathsf{u}_3\mathsf{u}_1 + \mathsf{n}_1 = 0 \tag{5}$$

$$\Gamma\frac{d\mathsf{u}_3}{ds} + K\mathsf{u}_2 = 0. \tag{6}$$

(b). [S] First, we have the trivial solution $\kappa = \tau = 0$ that exists for all applied force $N$. Second, If $\mathbf{n} = \alpha\mathbf{u}$, then (6),(7),(8) are automatically satisfied. Taking $\mathsf{u}_i$ to be constant and $\mathsf{u}_2 = 0$ in Equations (9), (10), (11) leads to $\mathsf{n}_1 = \Gamma\tau\kappa - (\kappa - K)\tau$ which implies $\alpha = \Gamma\tau - (1 - K/\kappa)\tau$. The solutions are either helices ($\kappa \neq 0 \neq \tau$), rings ($\kappa \neq 0 = \tau$), or straight rods ($\kappa = 0\tau$).

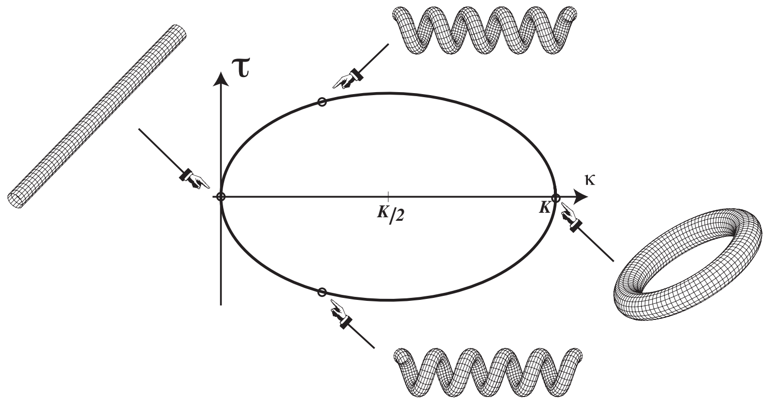
(c). [N] Since $M = \mathbf{m}.\mathbf{e}_z$ and $\mathbf{e}_z$ is along $\mathbf{n}$, we have that $M = 0$ implies $I_2 = 0$, that is $\mathbf{m}.\mathbf{u} = 0$. That is

$$\kappa(\kappa - K) + \Gamma\tau^2 = 0 \tag{7}$$

which can be written as

$$(\kappa - K/2)^2 + \Gamma\tau^2 = K^2/4, \tag{8}$$

an ellipse in the $\kappa - \tau$ plane. We have $N^2 = \alpha^2\mathbf{u}^2 = \alpha^2(\kappa^2 + \tau^2)$. Therefore, for a given $N$, if $\kappa \neq 0 \neq \tau$, there exist two solutions with $\pm\tau$ corresponding to helices with equal radii and pitch but opposite chirality. If $\tau = 0$ then $\kappa = K$ and $N = 0$ and the solution is a multi-covered ring. If $\kappa = 0 = \tau$, then the solution is a straight rod which exists for all values of $N$ (see Figure)




(d). [N] We solve $\kappa(\kappa - K) + \Gamma\tau^2 = 0$ with respect to $\tau^2 = \Gamma^{-1}\kappa(K - \kappa)$ and substitute the result in $N^2 = \tau^2\left(\Gamma^2 - (1 - K/\kappa)\right)^2(\kappa^2 + \tau^2)$ to find

$$N^2 = \Gamma^{-1}\kappa(K - \kappa)\kappa^{-2}\left(\kappa\Gamma^2 - (\kappa - K)\right)^2(\kappa^2 + \Gamma^{-1}\kappa(K - \kappa)\right) \tag{9}$$

In the limit $\kappa \to 0$, we find $N_{\text{crit}} = K^2/\Gamma$.

## Solution 2.

**(a).**[B] The elastic energy of a fluid biomembrane with surface $\Sigma$ is given by

$$\mathcal{E} = \int_{\Sigma} \mathrm{d}S \left[\sigma + 2\kappa(H - H_0)^2 + \bar{\kappa}K_G\right] \tag{10}$$

where

- $H$ and $K_G$ are the mean and Gaussian curvatures,
- $\sigma$ is the surface tension,
- $\kappa$ is the bending modulus,
- $\bar{\kappa}$ is the saddle-splay modulus,
- $H_0$ is the intrinsic mean curvature of the biomembrane.

We can ignore the contribution of $K_G$, the Gaussian curvature, since according to the Gauss-Bonnet theorem the contribution of the Gaussian curvature to the elastic energy for a closed surface is a topological constant.

**(b)**[SN] The surface $\Sigma$ can be represented by a height function $h = h(x)$ of class $C^2$. Define $r_x = (1, 0, h_x)$, $r_y = (0, 1, 0)$. The metric is

$$G = \begin{pmatrix} 1 + h_x^2 & 0 \\ 0 & 1 \end{pmatrix} \tag{11}$$

with determinant $g = 1 + h_x^2$. The unit normal is $\mathbf{n} = (-h_x, 0, 1)/\sqrt{g}$ and the extrinsic curvature matrix is

$$K = \begin{pmatrix} h_{xx}/\sqrt{g} & 0 \\ 0 & 0 \end{pmatrix}, \tag{12}$$

so that the principal curvature matrix is

$$L = G^{-1}K = \begin{pmatrix} g^{-3/2}h_{xx} & 0 \\ 0 & 0 \end{pmatrix}, \tag{13}$$

from which we obtain the Gaussian curvature $\det(L) = 0$ and mean curvature $H = g^{-3/2}h_{xx}/2$. The area element is $\mathrm{d}S = g\mathrm{d}x\mathrm{d}y$.
In the small-gradient approximation, we have $H = h_{xx}/2$ so that

$$\mathcal{E} = \frac{1}{2}w \int_0^L \mathrm{d}x \left[\sigma h_x^2 + \kappa h_{xx}^2\right]. \tag{14}$$

**(c).**[SN] The first variation $h \to h + \tau$ is carried out by repeated integrations by part to obtain

$$\begin{aligned} \frac{1}{w}\delta E &= \int_0^L \left[\kappa h_{xxxx} - \sigma h_{xx}\right]\tau \mathrm{d}x \\ &\quad + (\sigma h_x - \kappa h_{xxx})\tau]_0^L + \kappa h_{xx}\tau_x]_0^L. \end{aligned} \tag{15}$$

The shape equation is

$$\lambda^2 h_{xxxx} - h_{xx} = 0 \tag{16}$$

with $\lambda^2 = \kappa/\sigma$. Both terms in the boundary conditions must be satisfied so that we must have at each boundary ($h_{xx} = 0$ or $h_x$ fixed (so that $\tau_x = 0$)) AND ($h_x = \lambda^2 h_{xxx}$ or $h$ fixed (so that $\tau = 0$)).

**(d).**[N] The general solution of the shape equation is

$$h(x) = C_1 + C_2 x + C_3 \sinh(x/\lambda) + C_4 \cosh(x/\lambda). \tag{17}$$

The boundary conditions are $h(0) = h_0$, $h(L) = 0$, $h_{xx}(0) = h_{xx}(L) = 0$ so that $C_3 = C_4 = 0$ and $C_1 = h_0,\ C_2 = -h_0/L$.

## Solution 3.

**(a)**[B] The growth stretch is defined as

$$\gamma = \frac{\partial s}{\partial S_0}, \tag{18}$$

and its evolution is given by

$$\frac{\partial \gamma}{\partial t} = K\gamma u. \tag{19}$$

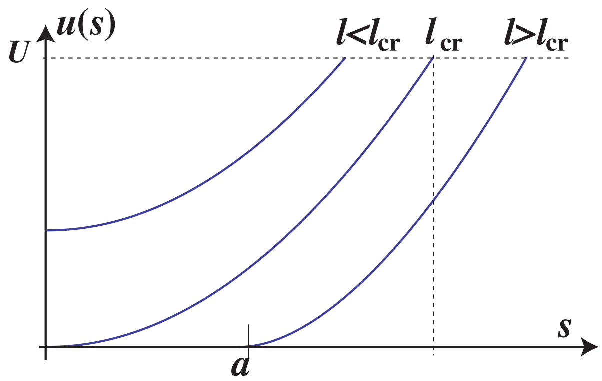
where $K > 0$ is a constant.

**(b)**[S] The problem is symmetric with respect to the origin, so the solution for $u$ is even and we only look at the solution for $s \geqslant 0$ (solutions shown for $s > 0$ or for both $s < 0$ and $s > 0$ are equally accepted as valid). The solution of $u_{ss} = Q/D$ is $u = \frac{Q}{2D}s^2 + C_1 s + C_2$. For $l < l_{\text{crit}}$, the second constant is set by the behaviour at the origin where we have $u_s = 0$, that is $C_1 = 0$, which gives

$$u_1 = \frac{Q}{2D}(s^2 - l^2) + U. \tag{20}$$

The critical length is the value of $l$ such that $u_1(s = 0) = 0$ that is $l_{\text{crit}} = \sqrt{2UD/Q}$, the penetration length.
For $l > l_{\text{crit}}$, the no-flux condition at an arbitrary point $s = a$ leads to

$$u_2 = \begin{cases} 0 & \text{if } s \in [0, a], \\ \frac{Q}{D}(s-a)^2, & \text{if } s \in [a, a + l_{\text{crit}}]. \end{cases} \tag{21}$$



**(c)**[SN] Since $\partial_t \gamma = \partial_t(\partial_{S_0} s) = K\gamma u$, we have

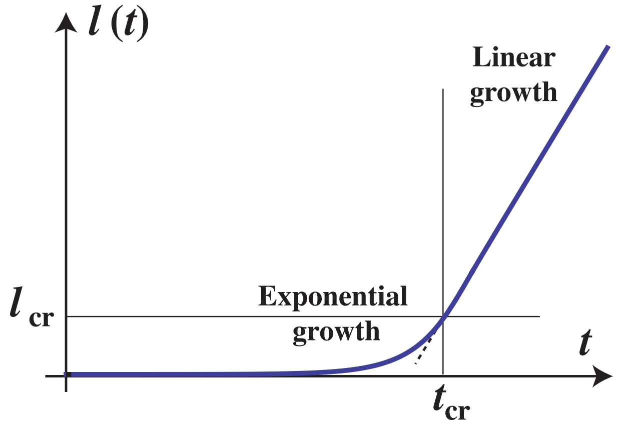
$$\partial_t s(S_0, t) = \int_0^{S_0} K\gamma u(s(\sigma_0, t), t) d\sigma_0 \tag{22}$$

And, by changing variables in the integral and using $ds = \gamma dS_0$, we have

$$\partial_t s(S_0, t) = \int_0^{s} K u(\sigma, t) d\sigma. \tag{23}$$

In particular, the equation for the length is given by

$$\frac{\partial l(t)}{\partial t} = \int_0^{l} K u(\sigma, t) d\sigma. \tag{24}$$




Consider first the solution for $l < l_{\text{crit}}$. In this case, we use $u = u_1$ and we have

$$\frac{\partial l(t)}{\partial t} = K \int_0^l (\frac{Q}{2D}(\sigma^2 - l^{2)} + U) d\sigma, \tag{25}$$

$$= -\frac{KQ}{3D} l^3 + KUl. \tag{26}$$

For $l \ll l_{\text{crit}}$, $\frac{\partial l(t)}{\partial t} \sim KUl$ and

$$l(t) \sim L_0 \exp(KUt) \tag{27}$$

For $l > l_{\text{crit}}$, we use $u = u_2$ and we have now

$$\frac{\partial l(t)}{\partial t} = \frac{KQ}{2D} \int_a^{a + l_{\text{crit}}} (\sigma - a)^2 d\sigma, \tag{28}$$

$$= \frac{2UK}{3} l_{\text{crit}} \tag{29}$$

That is,

$$l(t) = \frac{2UK}{3} l_{\text{crit}} (t - t_{\text{crit}}) + l_{\text{crit}} \tag{30}$$

and we conclude that, for $l \gg l_{\text{crit}}$, growth is linear in time with velocity $\frac{2UK}{3} l_{\text{crit}}$. (Note: students do no need to find the time $t_{\text{crit}}$ as they are only asked about the asymptotic behaviour).