The Many Faces of Elastica

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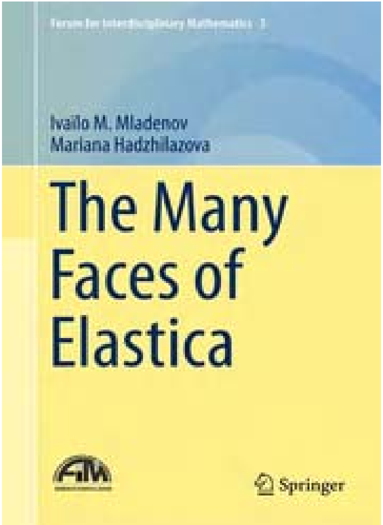
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Chapter 6
Exact Solutions and Applications

Unduloids and Nerve Fibers. Model

The stretching force applied to the membrane edge generates tension in the membrane, which in turn creates hydrostatic pressure in the cytoplasm. Since a fluid surface with surface tension is unstable, it will change its shape, according to the Laplace-Young law. According to the Laplace-Young equation (??) we can write

$$\Delta p = \sigma(\kappa_\pi + \kappa_\mu) \tag{1}$$

where Δp is the transmembrane pressure differential, σ is the surface tension, and κ_π and κ_μ are the so-called parallel, respectively meridional principal curvatures (see (??)) of the axially symmetric surface presenting the beaded shape. The cylindrical part of the transformed nerve has a larger mean curvature than the beaded region. According to equation (1), the membrane over the cylindrical region produces a higher pressure, counteracted by an opposing pressure created by the compressed cytoskeleton core.From a geometrical viewpoint, two beads are generally separated by a compacted neck, but the limit situation of directly connected beds is also possible.

Unduloids and Nerve Fibers. Parametrization

In Markin *et al* [1999], the nerve fibre is modelled as a cylindrical fluid membrane having the ability to change easily its shape at constant membrane area and fibre volume. Since further the ratio of Δp to σ is also a constant, the Laplace-Young equation can be written as

$$\kappa_\pi + \kappa_\mu = \mathrm{const} \tag{2}$$

revealing the fact that we are dealing here with the class of the so-called Delaunay surfaces described in Section **??**, and for more details see Eells [1987] and Oprea [2007]. Kenmotsu [1980] had shown that rotational surfaces of a given mean curvature in $\mathbb{R}^3$ are defined essentially by their Gauss map.

Unduloids and Nerve Fibers. Parametrization

Later on Eells [1987] pointed out that the Gauss map for the Delaunay surfaces is given by the general formula

$$\sin\psi(\rho) = m\rho + \frac{n}{\rho}, \qquad \rho \neq 0, \qquad m, n \in \mathbb{R} \tag{3}$$

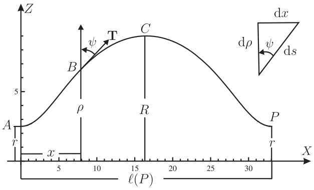
in which ρ is the distance from the symmetry axis, m and n are real parameters, and $\psi(\rho)$ is the angle between the tangent $\mathbf{T}$ to the profile curve at the current point B and the Z axis (cf. Fig. 1). Introducing $\rho_{\max} = R$ and $\rho_{\min} = r$ we easily find that in our case m and n are given by the formulas

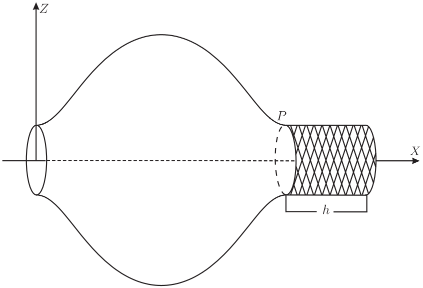
$$m = \frac{1}{R+r}, \qquad n = \frac{Rr}{R+r} \tag{4}$$

and that the meridional curve is determined by the equation

$$\frac{\mathrm{d}x}{\mathrm{d}\rho} = \tan\psi(\rho) = \frac{\rho^2 + Rr}{\sqrt{(R^2-\rho^2)(\rho^2-r^2)}}. \tag{5}$$

Unduloids and Nerve Fibers. Parametrization





Фигура: Geometry of the profile curve of Delaunay's unduloid (left) and that of a full segment of the periodic beaded shape (right).

Unduloids and Nerve Fibers. Parametrization

The integration of (5) amounts to evaluating the integral

$$\int \frac{(\rho^2 + Rr)\mathrm{d}\rho}{\sqrt{(R^2 - \rho^2)(\rho^2 - r^2)}} \tag{6}$$

which can be performed via the Jacobian elliptic function $\mathrm{dn}(u, k)$, i.e.,

$$\rho = \frac{r}{\mathrm{dn}(u, k)}, \qquad k = \frac{\sqrt{R^2 - r^2}}{R} \tag{7}$$

where u is its argument, and k is the so called elliptic modulus. The above substitution produces immediately

$$\frac{\mathrm{d}\rho}{\sqrt{(R^2 - \rho^2)(\rho^2 - r^2)}} = \frac{\mathrm{d}u}{R} \tag{8}$$

and therefore

$$x(u) = \frac{1}{R} \int \rho^2(u)\mathrm{d}u + ru. \tag{9}$$

Unduloids and Nerve Fibers. Parametrization

The first integral can be evaluated by taking into account the formula (cf formula 315.02 in Byrd & Friedman [1971])

$$\int \frac{\mathrm{d}u}{\mathrm{dn}^2(u,k)} = \frac{1}{\tilde{k}^2}\left(E(\mathrm{am}(u,k),k) - k^2\frac{\mathrm{sn}(u,k)\,\mathrm{cn}(u,k)}{\mathrm{dn}(u,k)}\right) \tag{10}$$

in which $\tilde{k}$ is the so-called complementary elliptic modulus

$$\tilde{k}^2 = 1 - k^2 = \frac{r^2}{R^2} \tag{11}$$

while the second one is trivial. Taken together they give

$$x(u) = RE(\mathrm{am}(u,k),k) + rF(\mathrm{am}(u,k),u) - Rk^2\frac{\mathrm{sn}(u,k)\mathrm{cn}(u,k)}{\mathrm{dn}(u,k)}. \tag{12}$$

Unduloids and Nerve Fibers. Parameters of the Nerve Fibers

The length $\ell(P)$ of a single bead (Fig. 1) can be found by noticing that the real period of $\mathrm{dn}(u,k)$ is $2K(k)$ along with the equality $\mathrm{am}(K(k),k) = \pi/2$ and (12), which combined lead to the result

$$\ell(P) = 2(RE(k) + rK(k)). \tag{13}$$

The area of the striped part of the undulated surface see (Fig. 2) is given by the application of the slice formula

$$\mathcal{A}(B) = 2\pi \int \rho \mathrm{d}s \tag{14}$$

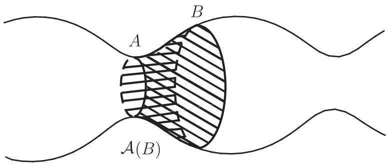
where

$$\mathrm{d}s = \sqrt{1 + \left(\frac{\mathrm{d}x}{\mathrm{d}\rho}\right)^2}\mathrm{d}\rho = \frac{(R+r)\rho\mathrm{d}\rho}{\sqrt{R^2-\rho^2)(\rho^2-r^2)}} \tag{15}$$

and therefore

$$\mathcal{A}(B) = 2\pi(R+r)\int \frac{\rho^2\mathrm{d}\rho}{\sqrt{(R^2-\rho^2)(\rho^2-r^2)}}. \tag{16}$$

Unduloids and Nerve Fibers. Parameters of the Nerve Fibers



Фигура: The area of the striped part of the unduloid surface is given by formula (17). The dotted domain presents the volume enclosed by the unduloid surface and the two disks through the points A and B.

The integration is immediate due to formula (10) and gives

$$\mathcal{A}(B) = 2\pi(R+r)R\left(E(\mathrm{am}(u,k),k) - k^2\frac{\mathrm{sn}(u,k)\mathrm{cn}(u,k)}{\mathrm{dn}(u,k)}\right). \quad (17)$$

Obviously, the surface area of the whole bead is

$$\mathcal{A}(P) = 2\mathcal{A}(C) = 4\pi R(R+r)E(k). \quad (18)$$

The volume enclosed by the unduloid surface and the two disks through the points A and B can be found in a similar way. Together the slice formula (5) and (7) lead to the following result

$$\begin{aligned}\mathcal{V}(B) &= \pi\int_0^u \rho^2 \mathrm{d}x = \pi\int_0^u \frac{\rho^2(\rho^2+Rr)\mathrm{d}\rho}{\sqrt{(R^2-\rho^2)(\rho^2-r^2)}} \\ &= \pi\left(\frac{r^4}{R}\int_0^u \frac{\mathrm{d}u}{\mathrm{dn}^4(u,k)} + r^3\int_0^u \frac{\mathrm{d}u}{\mathrm{dn}^2(u,k)}\right).\end{aligned} \quad (19)$$

The formula for the first of the integrals above is also available, namely (see Byrd & Friedman [1971] formula 315.04)

$$\int \frac{\mathrm{d}u}{\mathrm{dn}^4(u,k)} = \frac{1}{3\tilde{k}^4}\left[2(2-k^2)\left(E(\mathrm{am}(u,k),k) - k^2\frac{\mathrm{sn}(u,k)\mathrm{cn}(u,k)}{\mathrm{dn}(u,k)}\right)\right.$$

$$\left. -\tilde{k}^2F(\mathrm{am}(u,k),k) - k^2\tilde{k}^2\frac{\mathrm{sn}(u,k)\mathrm{cn}(u,k)}{\mathrm{dn}^3(u,k)}\right]$$

and having (10) in mind, we end up with the expression

$$\begin{aligned}\mathcal{V}(B) &= \frac{\pi R}{3}[(2R^2+3Rr+2r^2)E(\mathrm{am}(u,k),k)-r^2F(\mathrm{am}(u,k),k) \\ &\quad -(2R^2+3Rr+3r^2)k^2\frac{\mathrm{sn}(u,k)\mathrm{cn}(u,k)}{\mathrm{dn}(u,k)}].\end{aligned} \tag{20}$$

The formula for the volume of the entire bead follows immediately

$$\mathcal{V}(P) = \frac{2\pi R}{3}[(2R^2+3Rr+2r^2)E(k)-r^2K(k)]. \tag{21}$$

The surface and volume enclosed by the membrane are assumed to remain unchanged during the transformation of the nerve fibre caused by the action of hydrostatic pressure and axial tension. As the initial configuration is a cylinder of radius $\mathring{r}$ and length ℓ_0 we have

$$\mathcal{A} = 2\pi\mathring{r}\ell_0, \qquad \mathcal{V} = \pi\mathring{r}^2\ell_0, \qquad \frac{\mathcal{V}}{\mathcal{A}} = \frac{\mathring{r}}{2} = \frac{\mathcal{V}(P)}{\mathcal{A}(P)}$$

and therefore

$$\mathring{r} = 2\frac{\mathcal{V}(P)}{\mathcal{A}(P)}. \tag{22}$$

By definition, the average radius $\bar{r}$ of the bead is

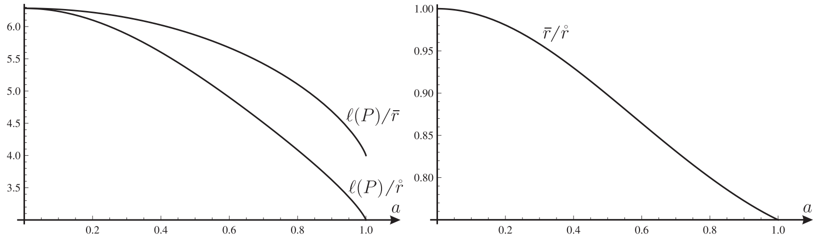
$$\bar{r} = \frac{R+r}{2} \tag{23}$$

which allows us to write down the following relations

$$\begin{aligned} \frac{\ell(P)}{\bar{r}} &= \frac{4(RE(k)+rK(k))}{R+r}, \qquad \frac{\ell(P)}{\mathring{r}} = \frac{(RE(k)+rK(k))\mathcal{A}(P)}{\mathcal{V}(P)} \\ \frac{\bar{r}}{\mathring{r}} &= \frac{R+r}{4}\,\frac{\mathcal{A}(P)}{\mathcal{V}(P)}. \end{aligned} \tag{24}$$

As a result of stretching, the length of the fibre in principal should increase and it is an interesting problem to analyze how this deformation actually depends on the oscillating amplitude a defined by the formula

$$a = \frac{R-r}{R+r}. \tag{25}$$



Фигура: The plots of $\ell(P)/\bar{r}$ and $\ell(P)/\mathring{r}$ (left), and that of the average radius normalized by $\mathring{r}$ (right).

Corresponding plots of the dependencies of (24) on a are presented in Fig. 3.
It is immediate to prove also that we have

$$r = \frac{1-a}{1+a}R = (1-a)\bar{r}, \qquad k = \frac{2\sqrt{a}}{1+a}$$

which makes clear that the shape of the bead depends exclusively on the amplitude while R specifies its bulk size

$$\ell = \mathcal{A}\frac{L_{\rm tot}}{A_{\rm tot}} = 2\pi\mathring{r}\ell_0\frac{L_{\rm tot}}{A_{\rm tot}}.$$

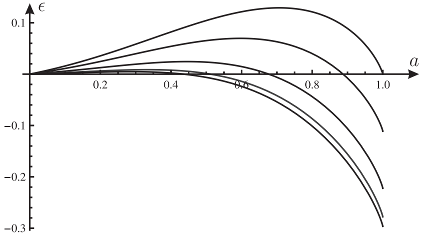
The latter means that we can find the ratio

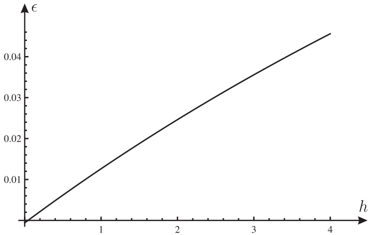
$$\frac{\ell}{\ell_0} = 4\pi\frac{\mathcal{V}(P)}{\mathcal{A}(P)}\frac{L_{\rm tot}}{A_{\rm tot}} = 4\pi\frac{\mathcal{V}(P)}{\mathcal{A}(P)}\frac{\ell(P)+h}{\mathcal{A}(P)+2\pi rh}$$

and respectively the elongation

$$\epsilon = \frac{\ell}{\ell_0} - 1.$$

Its variations as a function of a and h are depicted in Fig. 4.
The evolution recorded in Fig. 4 shows that the elongation is limited to values less than 15% in tension, but can reach values up to 30% in compression (when $R \geq h$). A maximum in ϵ is observed for values of the parameter h higher than a certain critical value a.
The closed form expressions for the beaded shape of neurons under stretch which have been obtained represent a significant improvement compared to the Markin *et al* [1999] approach based entirely on numerical solution of the determining equations. These results allow a sensitivity analysis of the dependence of the equilibrium shapes on the model parameters and visualization of morphological transformations.





Фигура: The plots of elongation ϵ as a function of the amplitude oscillation a and different values of h (left), and that of the length h of the cylindrical neck (right) for the fixed value of $a = 0.2$.

Mathematical Model of the Cole Experiment

The main aim in this section is to study in some detail the strongly nonlinear behavior of the vesicle deformations. The lipid membrane is treated as a thin elastic shell that possesses four modes of deformation – dilation, bending, shearing and torsion. From the geometrical viewpoint, the bending and torsion are related to the variations of the two principal curvatures of the interface.

The curvature dependence of the interfacial tension was investigated for the first time by Young and Laplace. The variational problem is connected with the minimization of the functional

$$\sigma \int \mathrm{d}\mathcal{A} + \Delta p \int \mathrm{d}V \tag{26}$$

and leads to the Laplace-Young equation

$$\Delta p = 2\sigma H \tag{27}$$

which can be easily established by relying on the results about the variations of the surface area and the volume, i.e.,

$$\delta \oint \mathrm{d}\mathcal{A} = -2 \oint \psi H \mathrm{d}\mathcal{A}, \qquad \delta \int \mathrm{d}V = \int \psi \mathrm{d}\mathcal{A}. \tag{28}$$

Mathematical Model of the Cole Experiment

Having in mind (28) the variation of (26) results in

$$-2\sigma \oint \psi H \mathrm{d}\mathcal{A} + \Delta p \int \psi \mathrm{d}\mathcal{A} \tag{29}$$

which is zero at a minimizer, i.e.,

$$\oint \psi(\Delta p - 2\sigma H)\mathrm{d}\mathcal{A} = 0. \tag{30}$$

As the latter has to be satisfied for any smooth function ψ this equality is equivalent with equation (27).

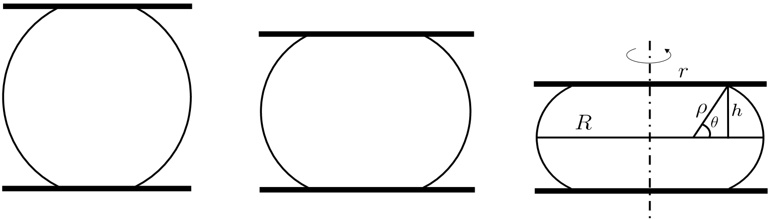
In the above proof we have not considered any specific shape of the membrane (for example with some symmetry) and consequently the equation (27) is valid for an arbitrary membrane.

Mathematical Model of the Cole Experiment. Cole Model

It seems appropriate to recall here the essential points of Cole's method of calculations. Cole compressed a spherical egg of initial radius a between two parallel plates with a fixed force F. The surface tension was then evaluated by the measurement of flattening (the half-thickness h), the radius r of the contact area A and the equatorial radius R (see Fig. 5). The values of the parameters h and R can be measured with high enough accuracy, but this is not the case with r, particularly when the contact angle is very close to 180°. The other two parameters which enter into the model are the inner radius ρ of the torus-like outer part of the membrane and the contact angle θ. Relying again on geometry, one can easily find that the above parameters are given by the expressions

$$\rho = \frac{h^2 + (R-r)^2}{2(R-r)}, \qquad \theta = \arcsin \frac{h}{\rho}. \tag{31}$$

Mathematical Model of the Cole Experiment. Cole Model



Фигура: Geometry of the Cole's experiment.

Mathematical Model of the Cole Experiment. Cole Model

The profile curve of the torus-like part of the egg is parameterized explicitly by the formulas

$$x = R - \rho + \rho \cos u, \qquad z = \rho \sin u, \qquad u \in [-\arcsin\frac{h}{\rho}, \arcsin\frac{h}{\rho}]$$

and this is enough for finding the volume, respectively the surface area in the form (cf. Hadzhilazova & Mladenov [2004])

$$V = 2\pi[h(R^2 + 2\rho^2 - 2R\rho + (R-\rho)\sqrt{\rho^2 - h^2}) + \rho^2(R-\rho)\theta - \frac{h^3}{3}] \quad (32)$$

$$S = 4\pi\rho[(R-\rho)\theta + h] + 2\pi r^2. \quad (33)$$

Mathematical Model of the Cole Experiment. Cole Model

By photographically obtained values for R, ρ and h, the first two are plotted against the third and, after that, analytically fitted by explicit functions of $h \equiv z$. The remaining parameter r can be found by solving equation (31) with respect to this variable and this gives

$$r(z) = R - \rho - \sqrt{\rho^2 - z^2}.$$

Having $\rho(z)$, $R(z)$ and $r(z)$ one can put them back into (32) in order to check practically the constancy of the volume $V = (4/3)\pi a^3$. Besides, one can find the values of $1/R + 1/\rho$ for the points at the equator and using

$$\Delta p = F/A = \sigma(1/R + 1/\rho) \tag{34}$$

determine the surface tension σ, which was the main purpose of the Cole [1932] experiment.

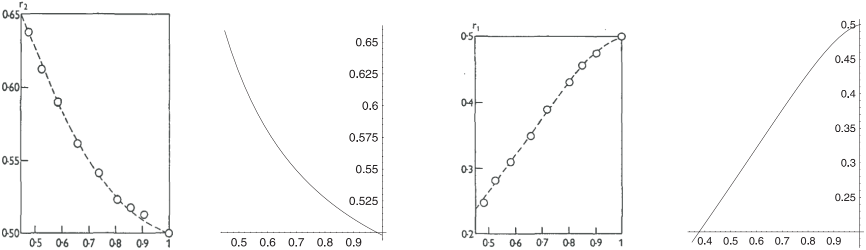
Mathematical Model of the Cole Experiment. Yoneda Method

In order to bypass the ambiguity in the measurement of the radius r of the contact disk area, Yoneda [1964] proposed another method for calculation of the surface tension. It is based on the following arguments. Let us assume that the egg is compressed to the thickness z under the external force F. If under a slightly increasing force the egg is compressed further by the distance $-\mathrm{d}z$, the work required for this additional compression is $-F\mathrm{d}z$, assumed to be expended entirely for stretching of the cortex by neglecting any other effects ((bending, etc.). If $\mathrm{d}S$ is the stretching of the surface produced by the compression, this work is just the surface tension σ (supposing that it is uniform on the entire surface) multiplied by $\mathrm{d}S$, i.e.,

$$-F\mathrm{d}z = \sigma\mathrm{d}S \qquad \text{or} \qquad F = -\sigma\frac{\mathrm{d}S}{\mathrm{d}z}\cdot \tag{35}$$

If F is plotted against $-\dfrac{\mathrm{d}S}{\mathrm{d}z}$, the last equation implies that σ is given as the slope of the line through the origin and this is confirmed experimentally by Yoneda [1964].

Mathematical Model of the Cole Experiment. Yoneda Method



Фигура: The experimental results and the approximate curves for R are presented on the left, and these ones for ρ on the right.

Mathematical Model of the Cole Experiment. Nodoids and the Compression of Spherical Eggs

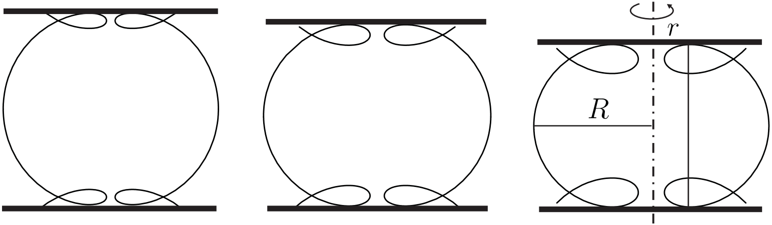
Looking at (34) it is clear that the surface tension will be constant provided we deal with axially symmetric surfaces of constant mean curvature, which according to the Delaunay classification are called nodoids. The profile curve of a such surface is periodic along the symmetry axis and has one local minimum and one local maximum in each period. Its geometry is presented at the outermost right hand side in Fig. 7. We can describe the deformed part of the egg in analytical form using the formulas

$$x(u) = R\sqrt{1 - k^2 \sin^2 u}, \quad z(u) = R\left(E(u,k) - \varepsilon^2 F(u,k)\right) \quad (36)$$

where

$$u \in [-\arcsin\frac{1}{\sqrt{1+\varepsilon^2}}, \arcsin\frac{1}{\sqrt{1+\varepsilon^2}}], \; k^2 = 1 - \varepsilon^4, \; \varepsilon = r/R. \quad (37)$$

Mathematical Model of the Cole Experiment. Nodoids and the Compression of Spherical Eggs



Фигура: Nodoid's geometry.

Mathematical Model of the Cole Experiment. Nodoids and the Compression of Spherical Eggs

Here $F(u,k)$ and $E(u,k)$ denote the incomplete elliptic integrals of the first and second kind, and k is the elliptic modulus. Using the explicit parametrization (36) of the compressed egg profile we can prove that the infinitesimal arclength of the profile curve is determined by the formula

$$\mathrm{d}s = \frac{R^2 + r^2}{R}\mathrm{d}u \tag{38}$$

and that the mean curvature of the deformed egg is

$$H = \frac{R}{r^2 - R^2}. \tag{39}$$

According to the second formula in (36) The height of the contact plane is

$$z(\varepsilon) = R\left(E(\arcsin\frac{1}{\sqrt{1+\varepsilon^2}}, k) - \varepsilon^2 F(\arcsin\frac{1}{\sqrt{1+\varepsilon^2}}, k)\right).$$

Mathematical Model of the Cole Experiment. Nodoids and the Compression of Spherical Eggs

By using again the fact that during the compression the volume is conserved one can find the relationship between the geometrical parameters that are needed - the initial radius a and that of the deformed egg R. The realization of this strategy gives us the relationship

$$\frac{R}{a} = \left[\left((1 - \frac{3\varepsilon^2}{2} + \varepsilon^4)\left(1 - \varepsilon^2 + E(k)\right) + \varepsilon^2(1 - \varepsilon^2 - \frac{\varepsilon^2 K(k)}{2})\right)/2\right]^{-\frac{1}{3}} \tag{41}$$

and this means that knowing a, measuring R and using formula (41) one can find ε, and therefore via (36) and (37) the profile curve of the compressed egg.

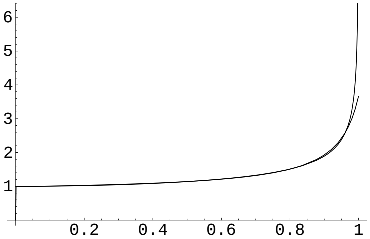
Mathematical Model of the Cole Experiment. Nodoids and the Compression of Spherical Eggs

Taking into account that the right hand side of (41) is a function only of the deformation parameter ε and that its values belong to the interval $0 \leq \varepsilon \leq 1$, we can find a linear fractional function which approximates it very well (see Fig. 8). We find, with accuracy exceeding the experimental accuracy, that we have the relations

$$R = a\frac{0.99098 - 0.77075\varepsilon}{1 - 0.93678\varepsilon}, \qquad \varepsilon = \frac{99098a - 100000R}{77075a - 93678R}, \qquad r = \varepsilon R. \tag{42}$$

The last equation means that it is not necessary to measure the radius of contact area!

Mathematical Model of the Cole Experiment. Nodoids and the Compression of Spherical Eggs



Фигура: The graphics of the function in the right hand side of equation (41) and its linear fractional approximation.

Mathematical Model of the Cole Experiment. Nodoids and the Compression of Spherical Eggs

If one wants to use Yoneda's equation (35), it is necessary to find the area of the surface outside the contact area which is defined by the formula

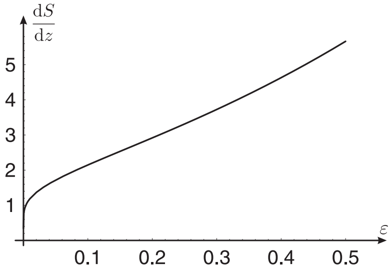
$$\mathcal{A}(\varepsilon) = 2\pi\int_0^{\arcsin \frac{1}{\sqrt{1+\varepsilon^2}}} x(u)\mathrm{d}s = 2\pi R^2(1+\varepsilon^2)E\left(\arcsin \frac{1}{\sqrt{1+\varepsilon^2}}, k\right). \tag{43}$$

By adding the surface of the contact disk $\pi r^2 = \pi R^2\varepsilon^2$ one finds full area (of the upper side) of the egg in the form

$$\mathcal{S}(\varepsilon) = \pi R^2 \left(2(1+\varepsilon^2)E(\arcsin \frac{1}{\sqrt{1+\varepsilon^2}}, k) + \varepsilon^2\right). \tag{44}$$

We note that the expressions for the surface area (44) and the height (40) are analytical functions only of the deformation parameter ε and their differentials in Yoneda's formula (35).

Mathematical Model of the Cole Experiment. Nodoids and the Compression of Spherical Eggs



Фигура: The graphics of the derivative in Yoneda's equation (35).

Thank you for attention!