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On the Translationally—Invariant Solutions of the Membrane Shape Equation

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• The membrane shape equation describes the equilibrium shapes of a biomembrane, assumed as a bilayer of amphiphilic molecules, in terms of the mean and Gaussian curvatures of its middle-surface.

• At that, the following physical parameters are taken into account:

➢ the bending rigidity and tensile stress of the membrane

➢ the spontaneous curvature of the bilayer

➢ the osmotic pressure difference between both sides of the bilayer.

• A new class of translationally-invariant solutions to the membrane shape equation in elliptic functions is obtained generalizing the solutions presented earlier by the authors.

• With this, all translationally-invariant solutions to the membrane shape equation are determined.

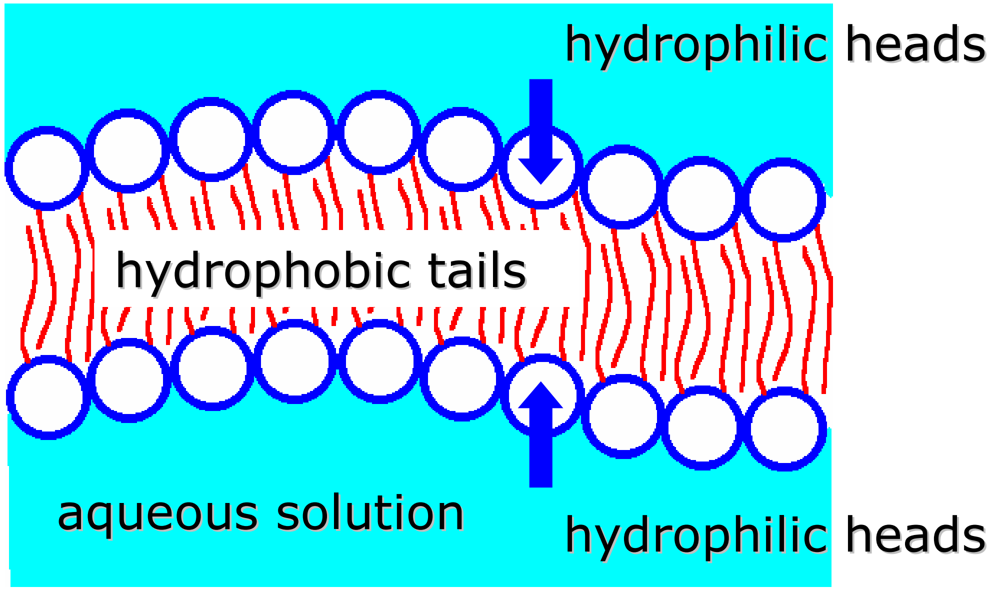
• Special attention is paid to those translationally-invariant solutions of the membrane shape equation that determine cylindrical (tube-like) surfaces (membrane shapes).

• Several examples of such surfaces will be shown.

Biomembranes

• In aqueous solution, amphiphilic molecules (e.g., phospholipids) may form bilayers, the hydrophilic heads of these molecules being located in both outer sides of the bilayer, which are in contact with the liquid, while their hydrophobic tails remain at the interior.

bilayer



• A bilayer may form a closed membrane - vesicle. Vesicles constitute a well-defined and sufficiently simple model system for studying basic physical properties of the more complex cell biomembranes.

Membrane Shapes

• The equilibrium shapes of a lipid vesicle are determined by the extremals of the curvature (shape) energy (*Helfrich*, 1973):

$$F_c = \frac{k_c}{2}\int_S (2H + c_0)^2 dA + \bar{k}\int_S K dA$$

under the constraints of fixed enclosed volume and membrane area.

• Using Lagrangian multipliers, this yields the functional

$$F = \frac{k_c}{2}\int_S (2H + c_0)^2 dA + \bar{k}\int_S K dA + \lambda\int_S dA + p\int_S dV$$

$k_c, \bar{k}$ – bending and Gaussian rigidities of the membrane
λ – tensile stress of the membrane
c_0 – spontaneous curvature of the bilayer
p – osmotic pressure difference
H, K – mean and Gaussian curvatures of the middle surface S
dA, dV – area and volume elements

Membrane Shape Equation

• The corresponding Euler-Lagrange equation (*Ou-Yang & Helfrich*, 1987, 1989)

$$(1) \qquad 2k_c \Delta H + k_c\left(2H + c_0\right)\left(2H^2 - c_0 H - 2K\right) - 2\lambda H + p = 0$$

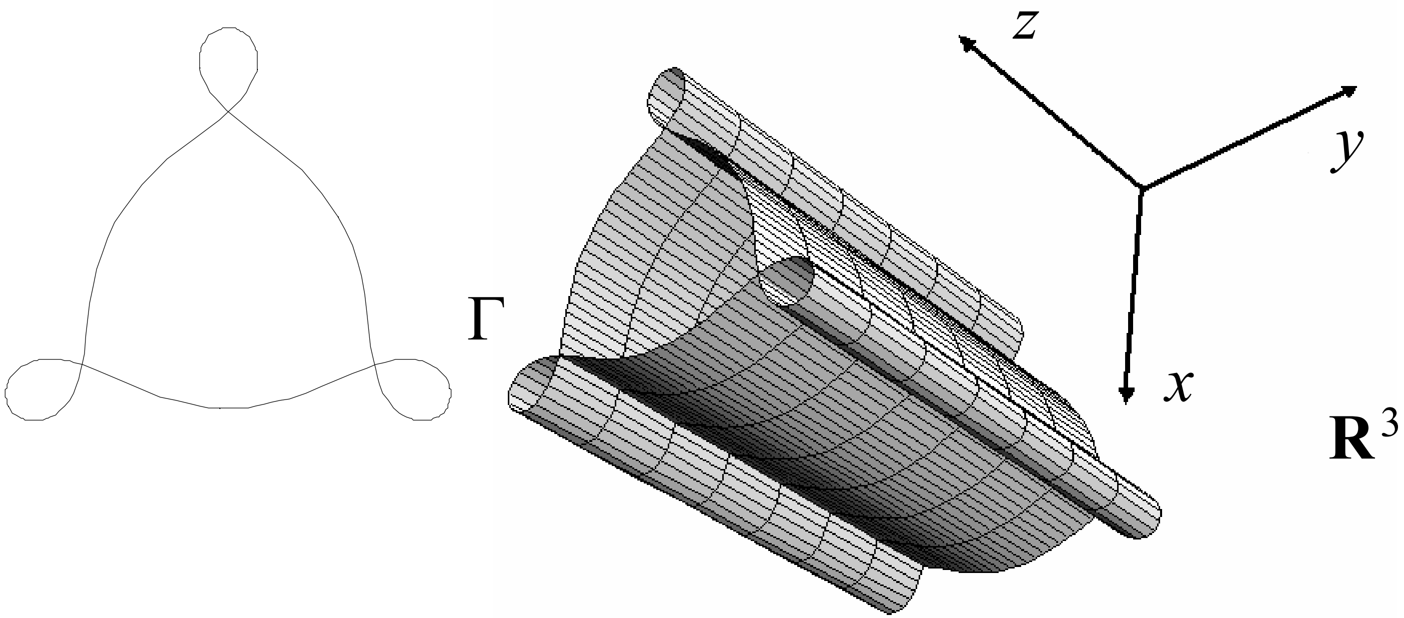
is often referred to as the membrane shape equation. Here Δ is the Laplace-Beltrami operator on the surface S.

• Equation (1) describes the equilibrium shapes of lipid vesicles in terms of the mean H and Gaussian K curvatures of the membrane middle surface S according to the physical parameters:

k_c – bending rigidities of the membrane
λ – tensile stress of the membrane
c_0 – spontaneous curvature of the bilayer
p – osmotic pressure difference between the outer and inner media

Translationally-Invariant Solutions

• The membrane shape equation (1) admits translationally-invariant solutions, which correspond to cylindrical (tube-like) surfaces in the 3-dimensional Euclidean space.



• The generatrix of such a solution surface is parallel to the z-axis while its directrix is a curve Γ in xy-plane whose curvature k is given by the following equation.

Reduced membrane shape equation

$$(2)\qquad 2\frac{d^2\mathrm{k}}{ds^2}+\mathrm{k}^3-\mu\mathrm{k}-\sigma=0 \qquad\qquad \mu=\frac{1}{4}c_0+\frac{\lambda}{2k_c},\quad \sigma=-\frac{\lambda}{4k_c}$$

for the curvature $\mathrm{k}=\mathrm{k}(s)$ of the curves Γ determining the foregoing translationally-invariant solutions of the membrane shape equation as a function of the arc length s.

• Once a solution of equation (2) is known, it is possible to recover the corresponding curve Γ solving the system

$$(3)\qquad \begin{aligned} &\frac{dx(s)}{ds}\frac{d^2y(s)}{ds^2}-\frac{dy(s)}{ds}\frac{d^2x(s)}{ds^2}=\mathrm{k}(s)\\ &\left(\frac{dx(s)}{ds}\right)^2+\left(\frac{dy(s)}{ds}\right)^2=1 \end{aligned}$$

• Thus, the main problem is to find the solutions to equation (2).

• Equation (2) is studied in (*Arreaga et al*., 2001) with the aim to determine the equilibria of an elastic loop in the plane subject to the constraints of fixed length and fixed enclosed area.

• In the three dimensional case considered here, each such loop will determine a directrix Γ generating a cylindrical surface whose mean and Gaussian curvatures are $H = 2\mathrm{k}$ and $K = 0$, respectively, that is a solution of the membrane shape equation.

• In (*Arreaga et al*., 2001) the determination of the curvature k at equilibrium is reduced to the study of the motion of a fictitious particle in a quartic potential.

• Indeed, equation (2) is the Euler-Lagrange equation associated with the functional

$$(4) \qquad \int (T - U)\,ds, \quad T = \frac{1}{2}\left(\frac{d\,\mathrm{k}}{ds}\right)^2, \quad U = \frac{1}{8}\mathrm{k}^4 - \frac{1}{4}\mu\,\mathrm{k}^2\,\frac{1}{2}\sigma\,\mathrm{k}$$

in which T and U can be thought of as the kinetic and potential energies of the fictitious particle, k gets an interpretation of its displacement and s plays the role of the time.

• Using this analogy, *Arreaga et al*. succeeded to obtain a geometric construction for determination of the embedding without involving explicit expressions for the solutions of equation (2). Nevertheless, in our opinion the knowledge of the solutions of equation (2) in an explicit form is an important and powerful tool in determination of the surfaces corresponding to the translationally-invariant solutions of the membrane shape equation.

• In (*Vassilev, Djondjorov and Mladenov*, 2006) several classes of explicit solutions to equation (2) in elliptic or elementary functions are found. These solutions will be presented below together with a new class of solutions in elliptic functions obtained recently, but first the invariance properties of equation (2) will be discussed.

✓ Equation (2) admits the one-parameter group of translations of the independent variable s as a variational symmetry group and hence, there is a conservation law (first integral).

✓ Equation (2) admits the equivalence transformation

$$\boldsymbol{\tau} : (s, \mathrm{k}) \mapsto (\pm s/\tau, \tau\,\mathrm{k}), \quad \mu \mapsto \mu/\tau^2, \quad \sigma \mapsto \sigma/\tau^3$$

i.e. a special kind of scaling, τ being an arbitrary real number.

Conservation of energy

• The invariance of equation (2) and functional (4) under the one-parameter group of translations of the variable s implies, in virtue of Noether's theorem, the conservation of the “total energy” E:

$$\frac{dE}{ds} = 0, \quad E = T + U$$

• Therefore, each solution of equation (2), which is not identically equal to a constant and corresponds to a certain value of the real constant E, is also solution of the equation

$$(5) \qquad \frac{d\mathrm{k}}{ds} = \pm\sqrt{P(\mathrm{k})}, \quad P(\mathrm{k}) = 2E - \frac{1}{4}\mathrm{k}^4 + \frac{1}{2}\mu\,\mathrm{k}^2 + \sigma\,\mathrm{k}$$

with the appropriate sign, and vice versa. Integrating equation (5) one gets the first integral

$$(6) \qquad s = \pm\int \frac{2}{\sqrt{8E - \mathrm{k}^4 + 2\mu\,\mathrm{k}^2 + 4\sigma\,\mathrm{k}}}\,d\mathrm{k} - A,$$

where A is a real constant, which w. l. g. can be taken equal to zero.

Solutions in elementary functions

(A) The functions

$$\mathrm{k}(s) = -\nu \frac{3-\nu^2 s^2}{1+\nu^2 s^2}$$

where ν is a real number satisfies equation (2) with

$$\mu = 3\nu^2, \quad \sigma = -2\nu^3, \quad E = \frac{3}{8}\nu^4$$

(B) The functions

$$\mathrm{k}(s) = \frac{\sqrt{2}\kappa^3 + \sigma}{\kappa^2} - \frac{2\sqrt{2}\kappa\left(\sqrt{2}\sigma + \kappa^3\right)}{\sqrt{2}\sigma + \kappa^3 + \left(\sqrt{2}\sigma - \kappa^3\right)\tan^2\left(\frac{s\sqrt{2\sigma^2 - \kappa^6}}{2\sqrt{2}\kappa^2}\right)}$$

where κ is a real number satisfies equation (2) with

$$\mu = \frac{\sigma^2 + \kappa^6}{\kappa^4}, \quad E = \frac{\sigma^2\left(2\kappa^6 - \sigma^2\right)}{8\kappa^8}$$

Solutions in elliptic functions

(C) The functions

$$\mathrm{k}(s) = -\frac{2\sigma\,\mathrm{sn}(us,k)}{\mu\left(c+\mathrm{sn}(us,k)\right)}$$

where

$$\mu > 0, \quad k = \sqrt{\frac{\mu\sqrt{\mu} - 2\sqrt{2}\sigma}{\mu\sqrt{\mu} + 2\sqrt{2}\sigma}}, \quad c = \sqrt{1 + \frac{2\sqrt{2}\sigma}{\mu\sqrt{\mu}}}, \quad u = \pm\frac{1}{4}c\sqrt{2\mu}$$

satisfies equation (2). They correspond to the following total energy

$$E = \frac{\sigma^2}{2\mu}$$

The aforementioned three classes of solution to equations of form (2) are presented in (*Vassilev, Djondjorov and Mladenov*, 2006). The next class is new.

(D) Let $\alpha = -(\beta + \gamma + \delta) \neq \beta \neq \gamma \neq \delta$ are the roots of the polynomial $P(\mathrm{k})$. Then the function

$$\mathrm{k}(s) = \frac{\alpha(\beta - \gamma) + \gamma(\beta + 2\gamma + \delta)\mathrm{sn}(us,k)^2}{(\gamma - \beta) + (\beta + 2\gamma + \delta)\mathrm{sn}(us,k)^2}$$

$$u = \frac{1}{4}\sqrt{(2\beta + \gamma + \delta)(\gamma - \beta)}, \quad k = \sqrt{\frac{(\beta + 2\gamma + \delta)(\gamma - \delta)}{(2\beta + \gamma + \delta)(\gamma - \beta)}}$$

satisfies equation (2) with

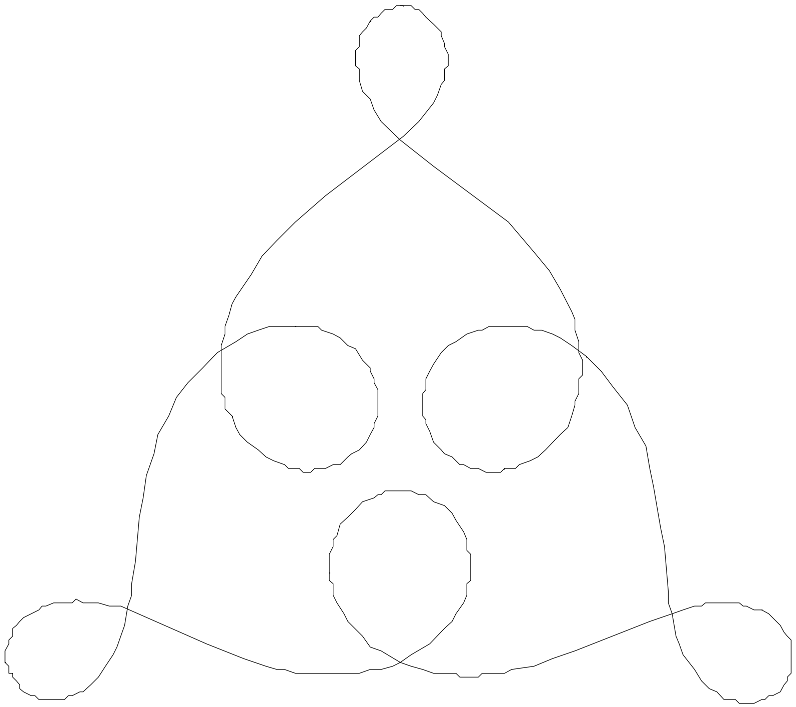
$$\mu = \frac{1}{2}\left(\beta^2 + \gamma^2 + \delta^2 + \beta\gamma + \beta\delta + \gamma\delta\right)$$

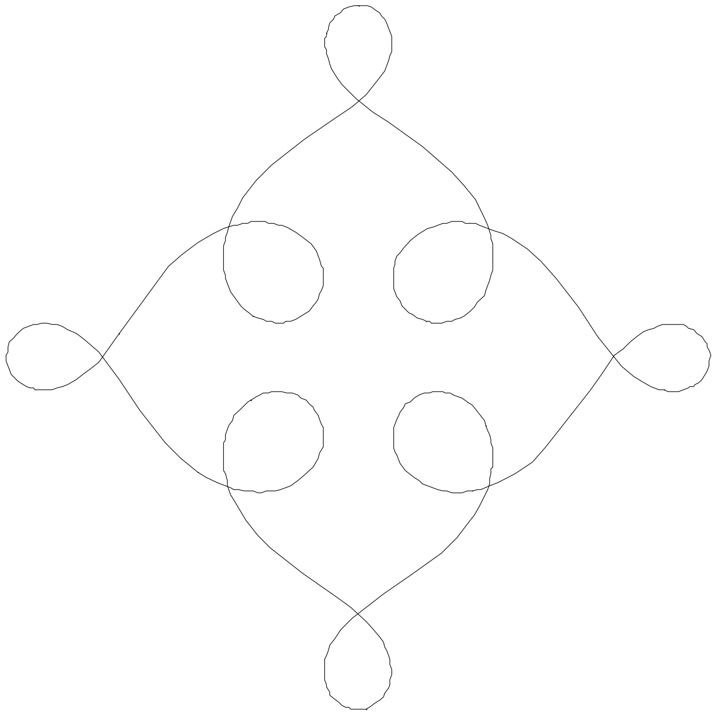
$$\sigma = -\frac{1}{4}(\beta + \gamma)(\beta + \delta)(\gamma + \delta)$$

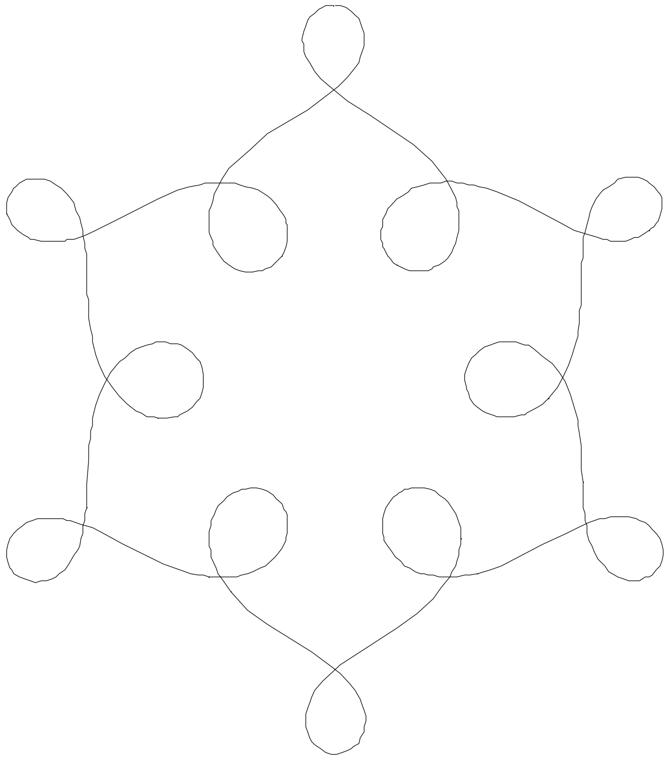
$$E = -\frac{1}{8}\beta\gamma\delta(\beta + \gamma + \delta)$$

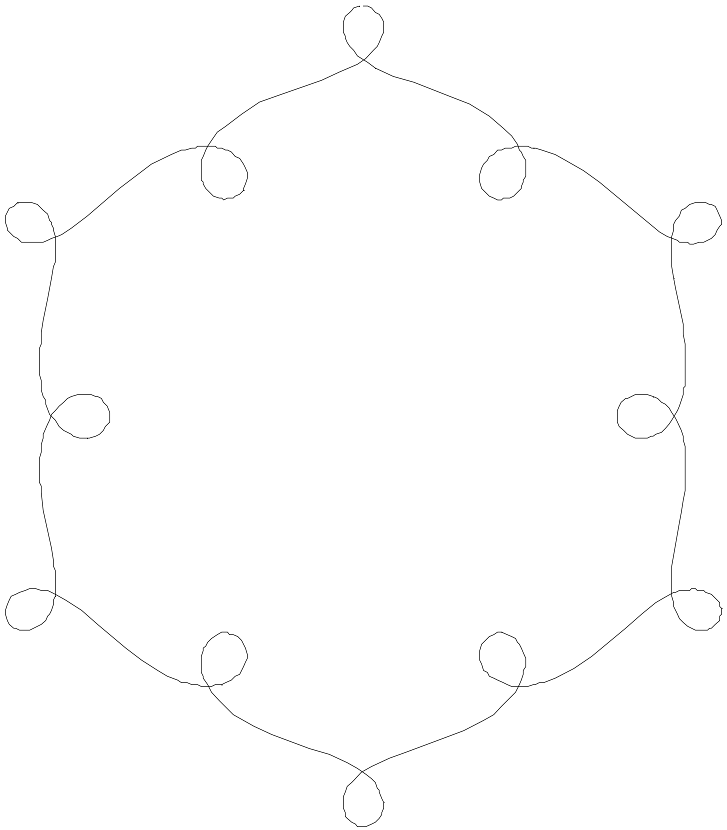
Examples

Curves corresponding to solutions of type (**D**)

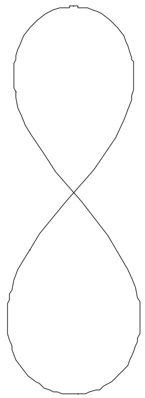


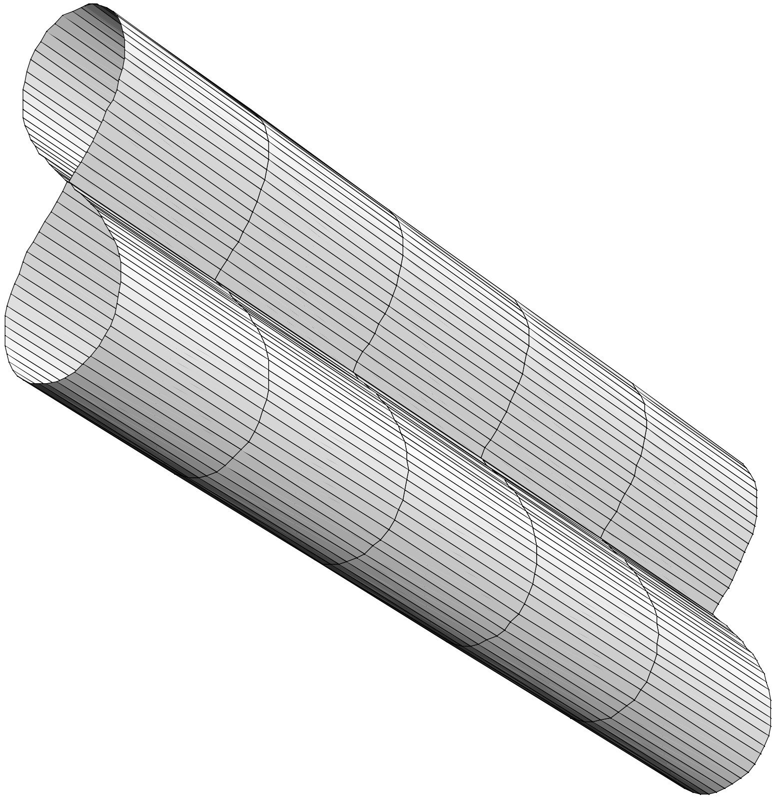






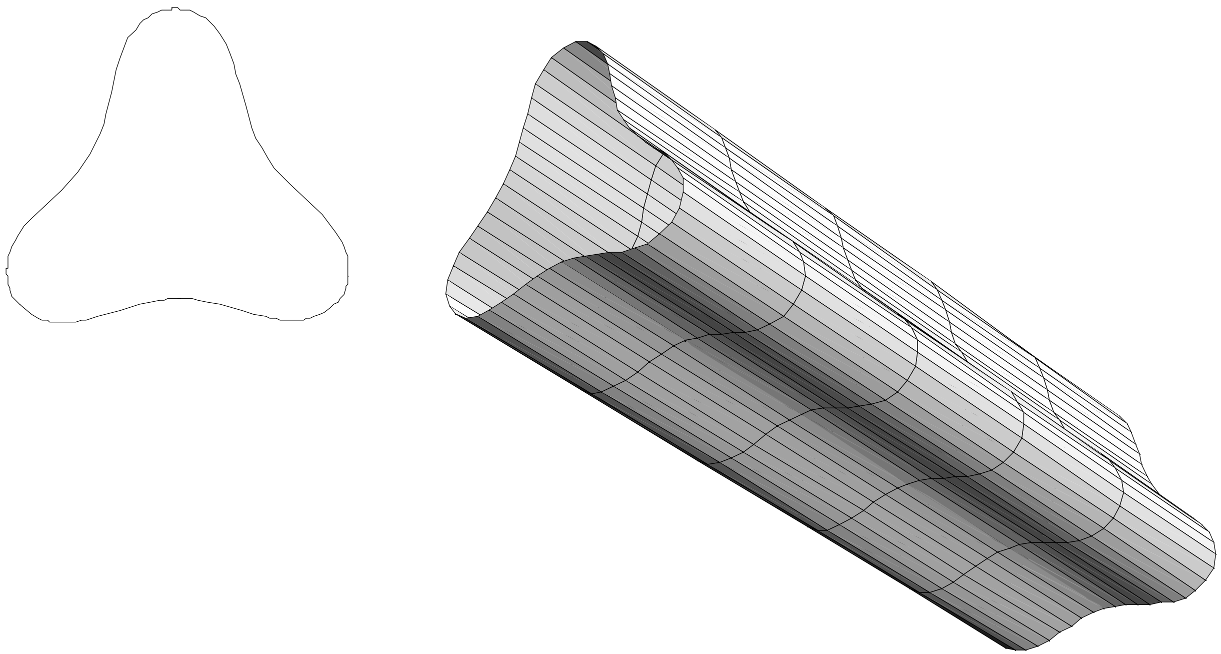
Type **(D)** μ = 1.8862, σ = -0.28762, E = 0.598728





1-fold symmetry

Type **(D)** μ = -7.58, σ = 12.58 , E = 8.31



3-fold symmetry

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