Shape equations of the axisymmetric vesicles

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Based on the same bending energy of the spontaneous curvature model, three shape equations for axisymmetric vesicles are derived from different variational methods. They are degenerate for the spherical vesicle, while for the cylindrical vesicle, two of them are the same. They all have a special toroidal solution, Clifford tori, but the constraints on the Lagrange multipliers ΔP and λ and the spontaneous curvature c_0 are different. We consider the physical mode of variation and introduce an arbitrary parameter for the axisymmetric action; we get the shape equation in terms of this parameter from it. When this parameter is identified as the parameter ρ, it reduces to the same equation that is from the general shape equation.

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Because of the repulsive interactions between the hydrocarbon chains of the lipid and the water molecules, lipids often assemble into bilayers that typically form vesicles. It is believed that these almost two-dimensional objects are dominated by the bending energy [1,2]:

$$F_b=\frac{1}{2}k_c\oint(c_1+c_2-c_0)^2dA+\bar{K}\oint c_1c_2dA\ , \qquad (1)$$

where k_c, $\bar{K}$, c_1, c_2, and c_0 are the bending rigidity, Gaussian curvature modulus, two principal curvatures, and the spontaneous curvature, respectively. As we only consider the vesicles with definite topology, we will neglect the last term, which is a topological contribution.

It is the incompressibility of the fluid in the vesicles and the fluidity of the vesicles that make the volume and area of the vesicles fixed. The shape equation of the vesicle is determined by minimizing F_b for constant volume V and total area A. In practice, we may incorporate these constraints by Lagrange multipliers ΔP and λ. The shape equations are obtained from

$$\delta(F_b+\lambda A+\Delta PV)=0\ , \qquad (2)$$

where δ denotes the variant with respect to the shape of the vesicle. We will see that the different interpretations of this variation result in three different shape equations for the axisymmtric vesicles.

For the sake of simplicity, we only consider the case of the axisymmetric vesicles. So far, there are three ways to get the shape equation of the axisymmetric vesicle.

(i) The most straightforward method is using the general shape equation derived by Ou-Yang and Helfrich [3]; substituting the mean and Gaussian curvatures in it, we get the required equation.

(ii) The second way of deriving the shape equation consists of writing $F_b+\lambda A+\Delta PV$ of the axisymmetric vesicles in the action form (using the arclength of the contour s as a parameter), writing down the Euler-Lagrange equation of this action, and identifying it as the shape equation [4].

(iii) The third way [5] is similar to the second one, except here we use the distance between the symmetric axis and the contour ρ as the parameter, instead for the arclength s.

We find that these equations are different, except for the spherical vesicles, while two of them [(i) and (ii)] are the same in the cylinderical case. These equations all have a sole perfect toroidal solution whose generating radii are in the ratio $1/\sqrt{2}$ (i.e., Clifford tori), but the constraints on ΔP and λ of different equations are different for this solution.

We analyze the physical mode of variations and report an alternative method in deriving the shape equation for the axisymmetric vesicles from the axisymmetric energy functional. By introducing an arbitrary parameter for the axisymmetric action, we get the shape equation in

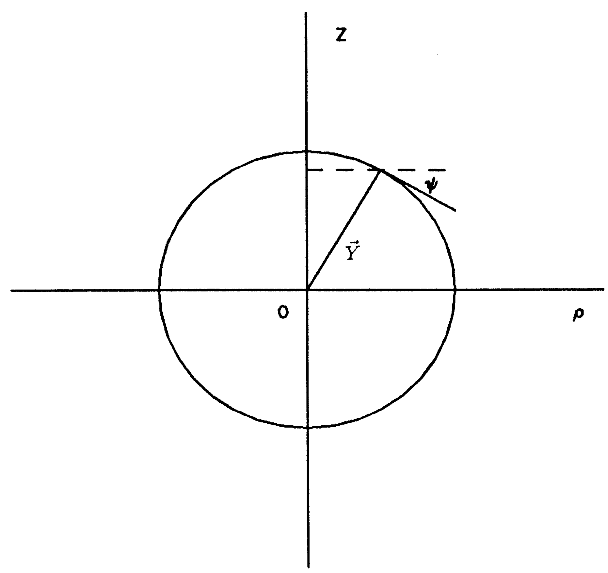

FIG. 1. Schematic graph of an axisymmetric vesicle. The surface is given by the vector **Y**, the axis of symmetry is along the Z axis, the arclength of the contour is denoted by s, ρ is the distance to the symmetric axis, ϕ is the azimuthal angle, and ψ is the angle between the tangent to the contour and the ρ axis.

terms of this parameter. When this parameter is identified as the parameter ρ, it reduces to the same equation from the general shape equation.

We start by parametrizing the vesicle, as in Fig. 1. An easy calculation gives the mean curvature and Gaussian curvature as (using the parameter s)

$$H=-\frac{1}{2}\left[\frac{d\psi(s)}{ds}+\frac{\sin\psi}{\rho(s)}\right], \quad K=\frac{\sin\psi}{\rho(s)}\frac{d\psi(s)}{ds}, \tag{3}$$

which can be rewritten in parameter ρ as

$$H=-\frac{1}{2}\left[\cos\psi(\rho)\frac{d\psi(\rho)}{d\rho}+\frac{\sin\psi}{\rho}\right], \quad K=\cos\psi(\rho)\frac{\sin\psi}{\rho}\frac{d\psi(\rho)}{d\rho}. \tag{4}$$

Ou-Yang and Helfrich [3] have derived a general shape equation by the shape variation of the kind $\delta\mathbf{Y}=\psi\mathbf{n}$:

$$\Delta P-2\lambda H+k_c(2H+c_0)(2H^2+2K-c_0H)+2k_c\nabla^2H=0; \tag{5}$$

here $\mathbf{Y}$ is the position vector of the vesicle, and $\mathbf{n}$ is the normal vector of the surface, defined as

$$\mathbf{n}\equiv\frac{\frac{\partial\mathbf{Y}}{\partial s}\times\frac{\partial\mathbf{Y}}{\partial\phi}}{\left|\frac{\partial\mathbf{Y}}{\partial s}\times\frac{\partial\mathbf{Y}}{\partial\phi}\right|}. \tag{6}$$

Inserting the H and K of the axisymmetric vesicle [i.e., Eq. (4)] into Eq. (5), we have

$$\cos^3\psi\left[\frac{d^3\psi}{d\rho^3}\right]=4\sin\psi\cos^2\psi\left[\frac{d^2\psi}{d\rho^2}\right]\left[\frac{d\psi}{d\rho}\right]-\cos\psi(\sin^2\psi-\tfrac{1}{2}\cos^2\psi)\left[\frac{d\psi}{d\rho}\right]^3+\frac{7\sin\psi\cos^2\psi}{2\rho}\left[\frac{d\psi}{d\rho}\right]^2$$
$$-\frac{2\cos^3\psi}{\rho}\left[\frac{d^2\psi}{d\rho^2}\right]+\left[\frac{c_0^2}{2}-\frac{2c_0\sin\psi}{\rho}+\frac{\sin^2\psi}{2\rho^2}+\frac{\lambda}{k_c}-\frac{\sin^2\psi-\cos^2\psi}{\rho^2}\right]\cos\psi\left[\frac{d\psi}{d\rho}\right]$$
$$+\left[\frac{\Delta P}{k_c}+\frac{\lambda\sin\psi}{k_c\rho}-\frac{\sin^2\psi}{2\rho^3}+\frac{c_0^2\sin\psi}{2\rho}-\frac{\sin\psi\cos^2\psi}{\rho^3}\right]. \tag{7}$$

The second means of getting the shape equation of the axisymmetric vesicle is to change Eq. (2) to an action form [4]

$$F_b+\lambda A+\Delta PV=2\pi k_c\int L\left[\rho(s),\frac{d\rho(s)}{ds},\psi,\frac{d\psi(s)}{ds},\gamma\right]ds. \tag{8}$$

Here we use the arclength s as the parameter, and the Lagrangian is

$$L\left[\rho(s),\frac{d\rho(s)}{ds},\psi,\frac{d\psi(s)}{ds},\gamma\right]=\frac{\rho}{2}\left[\frac{d\psi}{ds}+\frac{\sin\psi}{\rho(s)}-c_0\right]^2+\frac{\lambda\rho}{k_c}+\frac{\Delta P}{k_c}\rho^2\sin\psi+\gamma\left[\frac{\rho}{ds}-\cos\psi\right]. \tag{9}$$

The last term should be added when we variate L with respect to $\rho(s)$ and $\psi(s)$ independently. The Euler-Lagrange equations for ψ, ρ, and γ are, respectively,

$$\frac{d^2\psi}{ds^2}=-\frac{\cos\psi}{\rho}\left[\frac{d\psi}{ds}\right]+\frac{\sin2\psi}{2\rho^2}+\frac{\gamma\sin\psi}{\rho}+\frac{\Delta P\rho\cos\psi}{2k_c}, \tag{10}$$

$$\frac{d\gamma}{ds}=\left[\frac{d\psi}{ds}-c_0\right]^2\Big/2-\frac{\sin^2\psi}{2\rho^2}+\frac{\Delta P\rho\sin\psi}{k_c}+\frac{\lambda}{k_c}, \tag{11}$$

$$\frac{d\rho}{ds}=\cos\psi. \tag{12}$$

These differential equations have been used to calculate the phase diagrams for axisymmetric vesicles in spherical and toroidal topologies [4]. For the sake of comparison, we change the parameter s to ρ and reduce them to a single differential equation

$$\cos^3\psi\left[\frac{d^3\psi}{d\rho^3}\right]=\left[3\sin\psi\cos^2\psi+\frac{\cos^2\psi}{\sin\psi}\right]\left[\frac{d^2\psi}{d\rho^2}\right]\left[\frac{d\psi}{d\rho}\right]-\cos\psi\sin^2\psi\left[\frac{d\psi}{d\rho}\right]^3$$
$$+\frac{(2+5\sin^2\psi)\cos^2\psi}{2\rho\sin\psi}\left[\frac{d\psi}{d\rho}\right]^2-\frac{2\cos^3\psi}{\rho}\left[\frac{d^2\psi}{d\rho^2}\right]-\left[\frac{c_0\sin\psi}{\rho}+\frac{\sin^2\psi}{\rho^2}+\frac{\Delta P\rho}{2k_c\sin\psi}\right]\cos\psi\left[\frac{d\psi}{d\rho}\right]$$
$$+\left[\frac{\Delta P}{k_c}+\frac{\lambda\sin\psi}{k_c\rho}+\frac{c_0^2\sin\psi}{2\rho}-\frac{\sin\psi(1+\cos^2\psi)}{2\rho^3}\right]. \tag{13}$$

The third method is similar to the second, but here the parameter ρ is used. The action is

$$F_b+\lambda A+\Delta PV=2\pi k_c\int L\left[\psi(\rho),\frac{d\psi}{d\rho},\rho\right]d\rho\ ,$$

where

$$L\left[\psi(\rho),\frac{d\psi}{d\rho},\rho\right]=\frac{\rho}{2\cos\psi}\left[\cos\psi\left[\frac{d\psi}{d\rho}\right]+\frac{\sin\psi}{\rho}-c_0\right]^2+\frac{\lambda\rho}{k_c\cos\psi}+\frac{\Delta P\rho^2\sin\psi}{2k_c\cos\psi}\ . \tag{14}$$

The Euler-Lagrange equation corresponding to this Lagrangian is [5]

$$\cos^2\psi\left[\frac{d^2\psi}{d\rho^2}\right]=\frac{\sin\psi\cos\psi}{2}\left[\frac{d\psi}{d\rho}\right]^2-\frac{\cos^2\psi}{\rho}\left[\frac{d\psi}{d\rho}\right]+\frac{\sin 2\psi}{2\rho^2}+\frac{\Delta P\rho}{2k_c\cos\psi}+\frac{\lambda\sin\psi}{k_c\cos\psi}+\frac{\sin\psi}{2\cos\psi}\left[\frac{\sin\psi}{\rho}-c_0\right]^2\ . \tag{15}$$

Obviously, these shape equations [i.e,. (7), (13), and (15)] are different in general. These differences are due to the different interpretations of the variation δ in (2): Eq. (5) [and thus (7)] is the extreme of the general action (2), with respect to positional variation $\delta\mathbf{Y}=\psi\mathbf{n}$, which has simple geometrical meaning; while Eqs. (13) and (15) are extreme in the variation $\delta\psi$ of the axisymmetric action (8) and (14), with different parameters. This kind of variation $\delta\psi$ cannot assure the induced variation in $\mathbf{Y}$ along the direction of the normal vector $\mathbf{n}$, so it is different from $\mathbf{Y}=\psi\mathbf{n}$.

Nevertheless, if the vesicle is a sphere, (i.e., $\rho=r_0\sin\psi$), these equation are the same:

$$\Delta Pr_0^3+2\lambda r_0^2+k_cc_0^2r_0^2-2k_cc_0r_0=0\ , \tag{16}$$

where r_0 is the radius of the vesicle. This equation can be viewed as a constraint on the two Lagrange multipliers ΔP and λ for given c_0, k_c, and r_0, so one of them can be freely chosen.

In the case of the cylindrical vesicle, $\rho=r_0$, $\psi=\pi/2$, and (6) and (12) are degenerate:

$$\Delta Pr_0^3+\lambda r_0^2+\frac{k_c}{2}(c_0^2r_0^2-1)=0\ , \tag{17}$$

while Eq. (14) is

$$\Delta Pr_0^3+2\lambda r_0^2+k_c(c_0r_0-1)^2=0\ , \tag{18}$$

which is different from the former two, but is also a balance equation for the cylinder [3].

Now let us discuss the vesicle whose shape is a perfect torus. In Fig. 2, we define the parameters of the torus:

$$\rho=R+r\sin\psi\equiv r(x+\sin\psi)\ , \tag{19}$$

where $0\le\psi\le 2\pi$. Because we are only interested in the ratio of the generating radii of the torus, it is convenient to put $r=1$; then $\rho=x+\sin\psi$, and $1/x$ is called the ratio of the generating radii.

Substituting $\rho=x+\sin\psi$ and its derivates into Eq. (7), we have

$$\begin{aligned}&\left[\left[\frac{2\lambda+2\Delta P}{k_c}+c_0^2-1\right]x^3+2x\right]+\left[3x^2\left[\frac{2\lambda+2\Delta P}{k_c}+c_0^2-1\right]+x^2\left[\frac{2\lambda}{k_c}+c_0^2-4c_0+3\right]\right]\sin\psi\\&+\left[3x\left[\frac{2\lambda+2\Delta P}{k_c}+c_0^2-1\right]-3x+2x\left[\frac{2\lambda}{k_c}+c_0^2-4c_0+3\right]\right]\sin^2\psi\\&+\left[\left[\frac{2\lambda+2\Delta P}{k_c}+c_0^2-1\right]-2+\left[\frac{2\lambda}{k_c}+c_0^2-4c_0+3\right]\right]\sin^3\psi=0\ ;\end{aligned} \tag{20}$$

so when

$$x=\sqrt{2}\ ,\quad \lambda=k_c(2c_0-c_0^2/2)\ ,\quad \Delta P=-2k_cc_0\ , \tag{21}$$

Eq. (20) satisfies identically. [If we change the direction of the normal vector (i.e., $\mathbf{n}\to-\mathbf{n}$), then the λ of Eq. (21) will be the same as that in [6].] From Eq. (21), we see that, concerning the perfect-torus solution, Eq. (7) has one and only one class of solution whose ratio of generating radii is $1/\sqrt{2}$ (i.e., Clifford tori), and now ΔP and λ are fixed by k_c and c_0, as shown in Eq. (21). Note that $\Delta P=\lambda=0$ when $c_0=0$.

Similarly, for Eq. (13) (i.e., the second method), we get

$$x=\sqrt{2}\ ,\quad \lambda=k_c(c_0-2-c_0^2/2)\ ,\quad \Delta P=k_c\ ; \tag{22}$$

for Eq. (15) (i.e., the third method), we get

$$x=\sqrt{2}\ ,\quad \lambda=-\tfrac{9}{8}k_c\ ,\quad \Delta P=k_c\ ,\quad c_0=-\tfrac{1}{2}\ . \tag{23}$$

So Eqs. (13) and (15) both admit the Clifford tori as their solution, and that solution is also the sole solution of torus shape. For Eq. (13), the $\Delta P=k_c$ is independent of

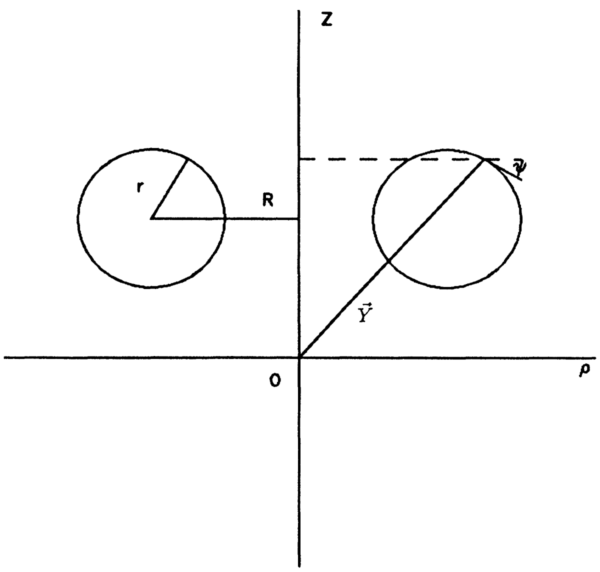

FIG. 2. Parameters of the torus. R and r are two radii of the torus. Here $0 \le \psi \le 2\pi$.

the spontaneous curvature c_0; for Eq. (15), a very stringent condition is imposed, i.e., $c_0 = -\frac{1}{2}$, for having the solution of Clifford tori.

On the experimental side [7], it is argued that the random partial polymerization of membranes contributes to the spontaneous curvature c_0 [8], so it would be very difficult, though not impossible, to tune the c_0 to $-\frac{1}{2}$ to find the vesicles whose shapes are Clifford tori, if the shape equation is given by Eq. (15).

On the theoretical side, it is known that the Clifford tori are a solution of Eq. (2), when $c_0 = \lambda = \Delta P = 0$ [9]. It is easy to see that Eq. (21) is compatible with this result, while Eqs. (22) and (23) are inconsistent with it.

Now let us have a discussion on using different parameters. In the third method, the action is of the form

$$F_b + \lambda A + \Delta P V = 2\pi k_c \int L \left[\psi(\rho), \frac{d\psi}{d\rho}, \rho \right] d\rho \, .$$

Using the parameter s instead, it is

$$F_b + \lambda A + \Delta P V = 2\pi k_c \int L' \left[\psi(s), \frac{d\psi}{ds}, \rho(s) \right] ds \, , \tag{24}$$

where

$$L' \left[\psi(s), \frac{d\psi}{ds}, \rho(s) \right] = L \left[\psi(\rho), \frac{d\psi}{d\rho}, \rho \right] \left[\frac{d\rho}{ds} \right] . \tag{25}$$

The corresponding Euler-Lagrange equation is

$$\frac{d}{ds} \left[\frac{\delta L'}{\delta \left[\frac{d\psi}{ds} \right]} \right] = \frac{\delta L'}{\delta \psi} \, . \tag{26}$$

Insert Eq. (25) into (26); it becomes

$$\frac{d}{ds} \left[\left[\frac{\delta L}{\delta \left[\frac{d\psi}{ds} \right]} \right] \left[\frac{d\rho}{ds} \right] + \left[\frac{\delta \left[\frac{d\rho}{ds} \right]}{\delta \left[\frac{d\psi}{ds} \right]} \right] L \right] = \left[\frac{\delta L}{\delta \psi} \right] \left[\frac{d\rho}{ds} \right] + \frac{\delta \left[\frac{d\rho}{ds} \right]}{\delta \psi} L \, . \tag{27}$$

When $d\rho/ds$ is independent of the variational field ψ, as usual, the Euler-Lagrange equation reduces to

$$\frac{d}{d\rho} \left[\frac{\delta L}{\delta \left[\frac{d\psi}{d\rho} \right]} \right] = \frac{\delta L}{\delta \psi} \, ; \tag{28}$$

this is the Euler-Lagrange equation using the parameter ρ. That is to say, the Euler-Lagrange equations are the same when the transformation matrix $d\rho/ds$ does not depend upon the variational field ψ.

But in our case, $d\rho/ds = \cos\psi$ depends on the variational field ψ, so the Euler-Lagrange equation in the parameter s is different from that in ρ [see (15) and(10) with $\gamma = 0$], so the difference in using different parameters is easy to understand.

It seems natural that any variation of position $\delta \mathbf{Y}$ can be decomposed into three directions: $\mathbf{n}$, $\partial \mathbf{Y}/\partial\theta$, and $\partial \mathbf{Y}/\partial\phi$. But it can be shown that any infinitesimal variations in the tangent planes of the surface can be attributed to the reparametrization of the surface. Infinitesimal variation in the tangent plane can be expressed as

$$\delta \mathbf{Y}(\theta,\phi) = \alpha_i(\theta,\phi) \mathbf{Y}_i(\theta,\phi) \, , \tag{29}$$

or reexpressed as

$$\mathbf{Y}'(\theta,\phi) = \mathbf{Y}(\theta,\phi) + \alpha_1(\theta,\phi) \frac{\partial \mathbf{Y}}{\partial\theta} + \alpha_2(\theta,\phi) \frac{\partial \mathbf{Y}}{\partial\phi} \, , \tag{30}$$

where $\mathbf{Y}$, θ, and ϕ are the position vector, and two parameters of the surface, respectively. $\alpha_i(\theta,\phi)$ are infinitesimal functions of θ,ϕ.

Now we choose another set of parameters (θ',ϕ') for the original surface, which are related to the old parameters by

$$\begin{aligned} \theta' &= \theta + \alpha_1(\theta,\phi) \, , \\ \phi' &= \phi + \alpha_2(\theta,\phi) \, . \end{aligned} \tag{31}$$

We expand $\mathbf{Y}(\theta',\phi')$ about $\mathbf{Y}(\theta,\phi)$ up to the linear order of $\alpha_i(\theta,\phi)$ as

$$\begin{aligned} \mathbf{Y}(\theta',\phi') &= \mathbf{Y}(\theta,\phi) + (\theta' - \theta) \frac{\partial \mathbf{Y}(\theta',\phi')}{\partial\theta'} \Bigg|_{\substack{\theta'=\theta \\ \phi'=\phi}} + (\phi' - \phi) \frac{\partial \mathbf{Y}(\theta',\phi')}{\partial\phi'} \Bigg|_{\substack{\theta'=\theta \\ \phi'=\phi}} \\ &= \mathbf{Y}(\theta,\phi) \alpha_1(\theta,\phi) \frac{\partial \mathbf{Y}(\theta,\phi)}{\partial\theta} + \alpha_2(\theta,\phi) \frac{\partial \mathbf{Y}(\theta,\phi)}{\partial\phi} \, . \end{aligned} \tag{32}$$

From (4) and (6), we have

$$\mathbf{Y}'(\theta,\phi)=\mathbf{Y}(\theta',\phi') , \tag{33}$$

that is to say, when a surface is variated infinitesimally in its local tangent planes, the deduced surface is the same surface, but in different parameters.

In its L_α phase, the lipid bilayer has no internal coordinates (i.e., fluidity), which implies it is reparametrization invariant, so there are no physical effects from variating in the tangent plane; only the variations along the normal vector $\mathbf{n}$ are physical. When we derive the shape equations, we only have to consider this kind of variation $\delta\mathbf{Y}=\psi\mathbf{n}$ [10].

As we have shown, the most straightforward method to get the shape equation for the axisymmetric vesicles is (i), in which we apply the variation $\delta\mathbf{Y}=\psi\mathbf{n}$ to the general energy functional to find the general shape equation, substitute the mean and Gaussian curvatures of the axisymmetric vesicles in it, and get the axisymmetric shape equation.

Nevertheless, there is another question left. Can we get the same shape equation for the axisymmetric vesicles by variating the axisymmetric energy functional, instead of the general energy functional? In the following part of this paper, we will answer this question by giving an alternative way of deriving the shape equation for the axisymmetric vesicles.

Substituting (4) into the effective energy,

$$E_{\text{eff}}=2\pi\left[\frac{k_c}{2}\left[\frac{d\psi}{ds}+\frac{\sin\psi}{\rho}-c_0\right]^2+\lambda+\frac{\Delta P}{2}\rho\sin\psi\right]\rho\, ds , \tag{34}$$

where $E_{\text{eff}}\equiv F_b+\lambda A+\Delta PV$. This is the axisymmetric energy functional to which we will apply the variation $\delta\mathbf{Y}=\psi\mathbf{n}$. In addition, there are relations

$$\frac{dz}{ds}=\sin\psi , \qquad \frac{d\rho}{ds}=\cos\psi . \tag{35}$$

The shape equation is determined by the variational equation $\delta E_{\text{eff}}=0$, in which δ means the variation along the normal vector $\mathbf{n}$. Let δf be the infinitesimal variation along this direction; its induced variations in ρ and z are

$$\delta\rho=(\sin\psi)\delta f , \qquad \delta z=-(\cos\psi)\delta f . \tag{36}$$

In order to have the shape equation, we need more relations. Variating $d\rho=(\cos\psi)ds$ in terms of δ, one has

$$\delta d\rho=-(\sin\psi)ds(\delta\psi)+(\cos\psi)\delta(ds) , \tag{37}$$

while derivating $\delta\rho=(\sin\psi)\delta f$ by d, one gets

$$d\delta\rho=(\cos\psi)d\psi\delta f+(\sin\psi)d(\delta f) . \tag{38}$$

Independence between operators d and δ gives

$$d\delta\rho=\delta d\rho . \tag{39}$$

So the equation

$$-(\sin\psi)ds\delta\psi+(\cos\psi)\delta(ds)=(\sin\psi)d(\delta f)+(\cos\psi)d\psi\delta f \tag{40}$$

is satisfied for any ψ. Then we have

$$\delta\psi=-\frac{d(\delta f)}{ds} , \qquad \delta(ds)=(d\psi)\delta f . \tag{41}$$

These relations can also be read out from the figure (see Fig. 3).

Let us recall what we do to find the equation of geodesics in Riemann geometry by means of the variational method [11]. Our task is to deal with this equation:

$$\delta\int ds=0 . \tag{42}$$

It is convenient to introduce an arbitrary parameter t that is independent of the variation δ, so that our question becomes the form of minimization of action

$$\delta\int\frac{ds}{dt}dt=\int\delta\left[\frac{ds}{dt}\right]dt=0 , \tag{43}$$

where ds/dt is the "Lagrangian." Then the Euler-Lagrange equation is the equation of geodesics.

After we get the equation of geodesics in terms of this arbitrary parameter, we may identify the parameter t as the arclength s; then we have the geodesic equation in terms of the arclength.

In order to get the shape equation of the axisymmetric vesicles, we may use a similar trick, introducing an arbitrary parameter t, which has no special geometric meaning, but only keeps the order of point on the generating curve. In terms of this parameter, the effective energy is

$$E_{\text{eff}}=2\pi\int L(\rho(t),\psi(t),\dot\psi(t),\dot s(t))dt , \tag{44}$$

where $\dot\psi(t)\equiv d\psi/dt$, $\dot s(t)\equiv ds/dt$, and

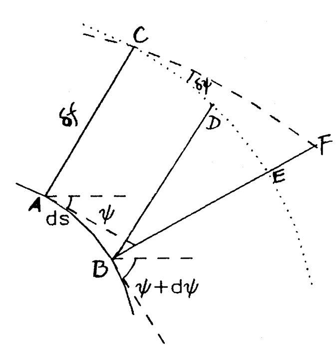

FIG. 3. The solid curve is the original generating curve for the axisymmetric vesicle, the dashed curve is the curve deduced by the variation δf, and the dotted one is the curve deduced by moving the original curve from A to C. Since $|AB|=ds$, $|AC|=\delta f$, $|BD|=\delta f$, $|DE|=\delta(ds)$, $|EF|=d(\delta f)$, $\angle DBE=d\psi$, and $\angle ECF=\delta\psi$, we have $\delta(ds)=(d\psi)\delta f$ and $(ds)\delta\psi=-d(\delta f)$.

$$L(\rho,\psi,\dot\psi,\dot s)$$
$$=\left[\frac{k_c}{2}\left[\frac{\dot\psi}{\dot s}+\frac{\sin\psi}{\rho}-c_0\right]^2+\lambda+\frac{\Delta P}{2}\rho\sin\psi\right]\rho\dot s$$
$$=\frac{k_c\rho(\dot\psi)^2}{2\dot s}+\frac{k_c\dot s\sin^2\psi}{2\rho}+\frac{k_c\rho\dot s c_0^2}{2}-c_0k_c\rho\dot\psi$$
$$+\lambda\rho\dot s+\frac{\Delta P}{2}\rho^2\dot s\sin\psi+k_c\dot\psi\sin\psi-c_0k_c\dot s\sin\psi. \tag{45}$$

Here the last two terms

$$k_c\dot\psi\sin\psi-c_0k_c\dot s\sin\psi=-k_c\frac{d\cos\psi}{dt}+c_0k_c\frac{dz}{dt} \tag{46}$$

are totally derivatives and do not contribute to the shape equation, so we will neglect them.

The variational equation now is

$$\int\delta L(\rho(t),\psi(t),\dot\psi(t),\dot s(t))dt=0\ , \tag{47}$$

which can be changed to

$$\int\left[\frac{\partial L}{\partial\rho}\delta\rho+\frac{\partial L}{\partial\psi}\delta\psi+\frac{\partial L}{\partial\dot\psi}\delta\dot\psi+\frac{\partial L}{\partial\dot s}\delta\dot s\right]dt=0\ . \tag{48}$$

Expressing $\delta\rho$, $\delta\psi$, $\delta\dot\psi$, and $\delta\dot s$ in terms of δf [using (36) and (41)], and after some calculations, we get the shape equation:

$$\left[\frac{\partial L}{\partial\rho}\right]\sin\psi+\frac{d}{dt}\left\{\frac{1}{\dot s}\left[\frac{\partial L}{\partial\psi}-\frac{d}{dt}\left[\frac{\partial L}{\partial\dot\psi}\right]\right]\right\}+\left[\frac{\partial L}{\partial\dot s}\right]\dot\psi=0\ . \tag{49}$$

Written more explicitly, it becomes

$$\frac{k_c\rho}{(\dot s)^2}\dddot\psi=\frac{3k_c\rho\ddot s}{(\dot s)^3}\ddot\psi-\frac{2k_c\dot\rho}{(\dot s)^2}\ddot\psi+\frac{k_c\sin\psi}{2\dot s}(\dot\psi)^2-\frac{k_c\rho}{2(\dot s)^2}(\dot\psi)^3$$
$$+\left[\frac{k_c(2-3\sin^2\psi)}{2\rho}-\frac{k_c\ddot\rho}{(\dot s)^2}+\frac{k_c\rho\dddot s}{(\dot s)^3}-\frac{3k_c\rho(\ddot s)^2}{(\dot s)^4}+\frac{3k_c\dot\rho\ddot s}{(\dot s)^3}-c_0k_c\sin\psi+\frac{c_0^2k_c}{2}\rho+\lambda\rho\right]\dot\psi$$
$$+\left[\Delta P\rho\cos\psi\dot\rho-\frac{k_c\sin 2\psi}{2\rho^2}\dot\rho+c_0k_c\frac{\ddot\rho}{\dot s}-c_0k_c\frac{\dot\rho\ddot s}{(\dot s)^2}\right]+\dot s\left[-\frac{k_c\sin^2\psi}{2\rho^2}+\frac{c_0^2k_c}{2}+\lambda+\Delta P\rho\sin\psi\right]\sin\psi\ . \tag{50}$$

This is the shape equation of the axisymmetric vesicles in terms of an arbitrary parameter t.

For the sake of comparison, we now identify the parameter t as the parameter ρ, the distance between the generating curve and the axis of symmetry. Then

$$\dot\psi=\frac{d\psi}{d\rho}\ ,\quad \dot s=\frac{ds}{d\rho}=\frac{1}{\cos\psi}\ ,\quad \dot\rho=1\ . \tag{51}$$

Substituting Eq. (51) and the higher derivatives into Eq. (50), we get the shape equation in terms of the parameter ρ, which is the same as in (7). This result implies that it does not matter whether we calculate the extreme of the effective energy (2) for general shapes of vesicles first, or impose the axisymmetric condition first.

We would like to make some comments on the derivation of the shape equation by using ρ as the parameter in the axisymmetric energy functional, instead of the arbitrary parameter t. In this case

$$E_{\text{eff}}=2\pi\int L\left[\psi(\rho),\frac{d\psi}{d\rho},\rho\right]d\rho\ . \tag{52}$$

If one erroneously equates

$$\delta E_{\text{eff}}=2\pi\int\delta L\left[\psi(\rho),\frac{d\psi}{d\rho},\rho\right]d\rho \tag{53}$$

and identifies the corresponding Euler-Lagrange equation as the shape equation, one has obviously ignored the change of the parameter $\delta d\rho$. Actually,

$$\delta E_{\text{eff}}=2\pi\int\delta L'\left[\psi(\rho),\frac{d\psi}{d\rho},\rho\right]d\rho$$
$$+2\pi\int L'\left[\psi(\rho),\frac{d\psi}{d\rho},\rho\right]\delta d\rho\ ; \tag{54}$$

expressing $\delta d\rho$ in terms of δf as in (37), one will get the same shape equation as (7).

In summary, we show that the three shape equations of axisymmetric vesicles are actually different. We consider the physical mode of variation and introduce an arbitrary parameter; we get the shape equation in terms of this parameter from the axisymmetric action.

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