Correct equilibrium shape equation of axisymmetric vesicles

Naveen Vaidya[1], Huaxiong Huang[2] and Shu Takagi[3]

[1] Department of Mathematics and Statistics, York University, Toronto, Canada
nvaidya@mathstat.yorku.ca [Corresponding author]
[2] Department of Mathematics and Statistics, York University, Toronto, Canada
hhuang@yorku.ca
[3] Department of Mechanical Engineering, The University of Tokyo, Tokyo, Japan
takagi@mech.t.u-tokyo.ac.jp

1 Introduction

Under favorable conditions, lipid molecules consisting hydrophobic tail and hydrophilic head groups, self assemble to form vesicles in aqueous medium with a lipid bilayer separating the inner and outer solutions [Ino96, Kom96]. Vesicles have been attracting enormous attentions because of their biological significance with numerous applications such as drug delivery and targeting, medical imaging, catalysis, etc. [KR96, Zan96]. It is recognized that the equilibrium shape of the vesicle is determined by minimizing a shape energy given by the spontaneous-curvature model of Helfrich [Hel73, OH89]:

$$F = \frac{1}{2}k_b \oint (c_1 + c_2 - c_0)^2 dA + k_G \oint c_1 c_2 dA + \lambda \oint dA + \Delta P \int dV. \qquad (1)$$

Here dA, dV and k_b are surface area element, volume element and the bending rigidity respectively; c_1 and c_2 denote the two principal curvatures and c_0 denotes the spontaneous curvature which takes the possible asymmetry of the bilayer into account; λ and ΔP are Lagrangian multipliers used to incorporate the constraints of constant area and constant volume respectively. Physically λ and ΔP can be interpreted as the tensile stress and the pressure difference respectively. For vesicles with same topological forms, the Gaussian curvature term $k_G \oint c_1 c_2 dA$ can be dropped from (1).

For vesicles with axisymmetric equilibrium shapes, four different approaches have been used to derive the shape equation in the literature.

A1. In Ou-yang and Helfrich [OH89], a general shape equation was derived by allowing the variation of the functional F only in the normal direction of the membrane surface. The axisymmetric shape equation can be obtained by applying the axisymmetric condition;

A2. This approach is similar to A1, by allowing variation only in the normal direction. The difference is that variation is carried out after the axisymmetric condition is applied [HO93].

A3. Again, functional F is written in the axisymmetric form first. The calculus of variation is performed without the restriction in the normal direction [MFR91, Pet85].

A4. This approach is similar to A3. However, the arc-length is used as the primary variable, instead of the distance to the axis of symmetry [SBL91, Sef66].

Both A1 and A2 generate the same equation. The shape equations produced by A3 and A4, however, are slightly different, as pointed out in [HO93]. In an attempt to clarify the confusion, it was shown in [ZL93] that the shape equations in A1 and A3 are related. However, due to the coordinate singularity, this relationship does not necessarily imply equivalence [BP04, Poz03]. This was confirmed in [NOO93] with the help of an analytical expression of a circular biconcave discoid (the shape of red blood cells). In addition, by considering the 2D limit, it was shown that the equations derived using A3 and A4 are erroneous since they do not recover the correct equation while the equation from A1 and A2 gives the correct limit [BP04, Poz03]. Other special solutions have also been used to validate or invalidate the equivalence of the shape equations [HO93, NOO93]. The most satisfactory discussion about these issues has been presented in [JS94], in which it was shown that the same equation can be obtained by A4 and A1. Their main conclusion is that an additional equation has to be introduced for the Hamiltonian (i.e. constant Hamiltonian) which can be maintained by proper treatment of the boundary conditions. However, this idea of treatment of boundary condition does not work for the fixed integral limits (i.e. constant total contour length) and the validity of the argument was questioned by [BP04, Poz03]. Therefore, it is still not clear whether it is necessary to restrict the variation in the normal direction, as suggested in [OH89].

In this paper we show that the same shape equation in A1 and A2 can be obtained without restricting the variation in the normal direction. We further prove that a slight modification of A3 produces the correct equation. As long as a geometric condition is satisfied (*explicitly* or *implicitly*), the variation does not have to be in the normal direction, contrary to the argument in [HO93]. To show the equivalence of equations by A1 and A4, [JS94] also suggested similar types of geometric conditions. However, they and others following their arguments have not implemented these conditions in their later works [DBS03, JL96] while attempting to get the axi-symmetric shape equations. Our result (correct shape equation by modification of A3) suggests that when A4 is used, apart from extra hamiltonian condition the geometric condition should also be properly imposed to get the correct shape equations.

The rest of the paper is organized as follows. In Section 2 we present the equations obtained using A1-A3 in the literature. In Section 3, we show that the correct equation can be obtained by taking the variation in the direction perpendicular to the axis of symmetry. Furthermore, by imposing the geometric condition implicitly in the action form of the energy functional, we show that A3 can produce exactly the same equation as A1 (and A2). Various topological shapes of vesicles are discussed in Section 3.4 and we conclude the paper in Section 4.

2 Shape Equation

We consider vesicles of axisymmetric shape with the axis of symmetry along the z-axis. We denote the arc-length of the contour, the distance to the symmetric axis and the angle made by the tangent to the contour with the plane perpendicular to the axis of symmetry by s, ρ and ψ respectively (See Fig. 1a).

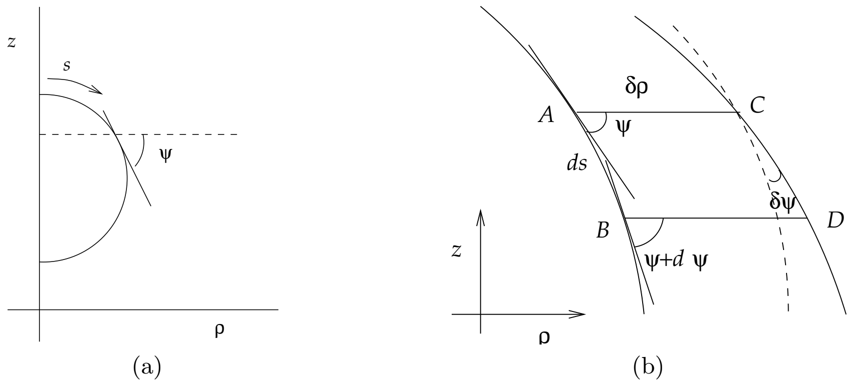

Fig. 1. (a) Schematic diagram of the axisymmetric vesicle. (b) The variation in the direction perpendicular to the axis of symmetry (i.e in ρ-direction). $AB = ds$ is the segment in the original generating curve, CD is the corresponding segment in the curve deduced by the variation $\delta\rho$ in ρ-direction and dashed curve is the curve deduced by moving the original curve from A to C.

Using A1 (i.e. substituting the mean curvature $H = -(c_1 + c_2)/2 = -(1/2)[\cos\psi(d\psi/d\rho) + \sin\psi/\rho]$ and the Gaussian curvature $K = c_1 c_2 = \cos\psi\sin\psi(1/\rho)(d\psi/d\rho)$ in the general shape equation derived by Ou-Yang and Helfrich [OH89]), the shape equation can be obtained as [BP04, HO93, NOO93, Poz03, ZL93]:

$$\cos^3\psi\frac{d^3\psi}{d\rho^3} = 4\sin\psi\cos^2\psi\frac{d^2\psi}{d\rho^2}\frac{d\psi}{d\rho} - \cos\psi(\sin^2\psi - \frac{1}{2}\cos^2\psi)\left(\frac{d\psi}{d\rho}\right)^3 + \frac{7\sin\psi\cos^2\psi}{2\rho}\left(\frac{d\psi}{d\rho}\right)^2 - \frac{2\cos^3\psi}{\rho}\frac{d^2\psi}{d\rho^2}$$

$$+\left(\frac{c_0^2}{2}-\frac{2c_0\sin\psi}{\rho}+\frac{\sin^2\psi}{2\rho^2}+\frac{\lambda}{k_b}-\frac{\sin^2\psi-\cos^2\psi}{\rho^2}\right)\cos\psi\frac{d\psi}{d\rho}$$
$$+\frac{\Delta P}{k_b}+\frac{\lambda\sin\psi}{k_b\rho}-\frac{\sin^3\psi}{2\rho^3}+\frac{c_0^2\sin\psi}{2\rho}-\frac{\sin\psi\cos^2\psi}{\rho^3}. \tag{2}$$

The axisymmetric shape equation using A3, in which axisymmetric expressions for curvatures are used in (1) and Euler-Lagrange equation is obtained, is [MFR91, Pet85]

$$\mathcal{H}=0, \tag{3}$$

where

$$\mathcal{H}=\cos^2\psi\frac{d^2\psi}{d\rho^2}-\frac{\sin\psi\cos\psi}{2}\left(\frac{d\psi}{d\rho}\right)^2-\frac{\sin\psi}{2\rho^2\cos\psi}-\frac{\sin\psi\cos\psi}{2\rho^2}-\frac{c_0^2\sin\psi}{2\cos\psi}$$
$$+\frac{\cos^2\psi}{\rho}\frac{d\psi}{d\rho}-\frac{c_0\sin^2\psi}{\rho\cos\psi}-\frac{\Delta P\rho}{2k_b\cos\psi}-\frac{\lambda\sin\psi}{k_b\cos\psi}. \tag{4}$$

The shape equation using A4 is obtained in the same way [JS94, SBL91, Sef66].

3 Equivalence of the Shape Equations

Equation (4) has been obtained without any reference to coordinate z. Therefore, $\psi(\rho)$ varies over a larger class of functions and the extreme function which minimizes the energy functional may not be admissible. In fact, the coordinates $z(s)$ and $\rho(s)$ have to satisfy the geometrical relations: $d\rho/ds=\cos\psi$ and $dz/ds=-\sin\psi$, which gives the geometric relation in the parameter ρ as

$$\frac{dz}{d\rho}\cos\psi+\sin\psi=0. \tag{5}$$

In the following we show that the correct shape equation can be obtained if this geometric condition is imposed explicitly or implicitly. We will demonstrate this fact by using two different approaches.

3.1 Variation in the ρ-direction

We now derive the shape equation for axisymmetric vesicles by taking the variation of the axisymmetric energy functional. The method used here is similar to A2 [HO93] but the variation is performed along the direction perpendicular to the axis of symmetry (i.e. ρ-direction) and the corresponding induced variations in ψ and s are obtained by using the geometric relations $d\rho/ds=\cos\psi$ and $dz/ds=-\sin\psi$. The method used here is similar to the method used to find the equation of geodesics in Riemannian geometry by means of the variational method [HO93, Spi79].

We start with the following axisymmetric shape energy functional with parameter s

$$F_s = \pi \int \left[k_b \rho \left(\frac{d\psi}{ds} + \frac{\sin\psi}{\rho} - c_0 \right)^2 + \Delta P \rho^2 \sin\psi + 2\lambda\rho \right] ds \tag{6}$$

and introduce an arbitrary parameter t to get

$$F_s = \pi \int \bar{L} \left(\rho(t), \psi(t), \dot{\psi}(t), \dot{s}(t) \right) dt, \tag{7}$$

where

$$\bar{L} \left(\rho(t), \psi(t), \dot{\psi}(t), \dot{s}(t) \right) = \frac{k_b \rho (\dot{\psi})^2}{\dot{s}} + \frac{k_b \dot{s} \sin^2\psi}{\rho} + k_b \rho c_0^2 \dot{s} - 2k_b c_0 \rho \dot{\psi} + 2\lambda\rho\dot{s} + \Delta P \rho^2 \sin\psi \dot{s}. \tag{8}$$

Note that the terms $2k_b\dot{\psi}\sin\psi$ and $-2k_b c_0 \dot{s}\sin\psi$ have been neglected in (8) as they do not contribute to the shape equation [HO93].

Let $\delta\rho$ be the infinitesimal variation along the ρ-direction so that the variation along the z-direction is $\delta z = 0$ (See Fig. 1b). The geometric relation $d\rho = \cos\psi ds$ gives

$$-\sin\psi ds(\delta\psi) + \cos\psi \delta ds = \delta d\rho. \tag{9}$$

Similarly, the geometric relation $dz = -\sin\psi ds$, using $d\delta z = \delta dz$ due to independence between operators d and δ, gives

$$\cos\psi ds(\delta\psi) + \sin\psi \delta(ds) = 0. \tag{10}$$

Solving Equations (9) and (10) for $\delta\psi$ and $\delta(ds)$, we get

$$\delta\psi = -\frac{\sin\psi\delta d\rho}{ds}, \delta(ds) = \cos\psi\delta d\rho, \delta\dot{\psi} = -\frac{d}{dt}\left(\frac{\sin\psi\delta d\rho}{ds} \right), \delta\dot{s} = \frac{\cos\psi\delta d\rho}{dt}.$$

The shape equation is determined by the variational equation $\delta F_s = 0$, which gives

$$\int \left[\frac{\partial\bar{L}}{\partial\rho}\delta\rho + \frac{\partial\bar{L}}{\partial\psi}\delta\psi + \frac{\partial\bar{L}}{\partial\dot{\psi}}\delta\dot{\psi} + \frac{\partial\bar{L}}{\partial\dot{s}}\delta\dot{s} \right] dt = 0. \tag{11}$$

Using expressions for $\delta\psi$, $\delta\dot{\psi}$ and $\delta\dot{s}$ in (11) and performing integration by parts and simplification, we obtain the following shape equation

$$\frac{\partial\bar{L}}{\partial\rho} + \frac{d}{dt}\left(\frac{\sin\psi}{\dot{s}} \frac{\partial\bar{L}}{\partial\psi} \right) - \frac{d}{dt}\left(\frac{\sin\psi}{\dot{s}} \frac{d}{dt} \frac{\partial\bar{L}}{\partial\dot{\psi}} \right) - \frac{d}{dt}\left(\cos\psi \frac{\partial\bar{L}}{\partial\dot{s}} \right) = 0. \tag{12}$$

We use Equation (8) in (12) and consider ρ as a parameter by taking $t = \rho$. Then using $\dot{\psi} = d\psi/d\rho$, $\dot{s} = ds/d\rho = 1/\cos\psi$, $\dot{\rho} = 1$ along with their higher derivatives in the resulting equation, we obtain (2), which is also the shape equation obtained in the literature using A2. Therefore, we have shown that the variation does not have to be in the normal direction, the variation in other directions can also produce the same shape equation if the induced variations in other variables are obtained by using the geometric relations $d\rho/ds = \cos\psi$ and $dz/ds = -\sin\psi$. We note that the approach outlined here breaks down when the surface is perpendicular to the axis of symmetry. We now move on to a more general approach.

3.2 The method of Lagrange multiplier

We include the geometric condition (5) in the action form of shape energy functional via an additional Lagrange multiplier η as follows:

$$F = \pi \int \tilde{L}\left(\rho, \psi(\rho), z(\rho), \eta(\rho), \frac{d\psi}{d\rho}, \frac{dz}{d\rho}\right) d\rho, \tag{13}$$

where the Lagrangian $\tilde{L}$ is

$$\begin{aligned}\tilde{L} = &\frac{k_b\rho}{\cos\psi}\left(\frac{d\psi}{d\rho}\cos\psi + \frac{\sin\psi}{\rho} - c_0\right)^2 + \frac{\Delta P\rho^2\sin\psi}{\cos\psi} + \frac{2\lambda\rho}{\cos\psi}\\ &+\eta\left(\frac{dz}{d\rho}\cos\psi + \sin\psi\right).\end{aligned} \tag{14}$$

This gives the following Euler-Lagrange equations

$$\mathcal{H} = \frac{\eta}{2k_b\rho}, \tag{15}$$

$$\frac{dz}{d\rho} = -\frac{\sin\psi}{\cos\psi}, \tag{16}$$

$$\cos\psi\frac{d\eta}{d\rho} = \eta\sin\psi\frac{d\psi}{d\rho}. \tag{17}$$

We rewrite (15) as $\eta = \eta\left(\rho, \psi, d\psi/d\rho, d^2\psi/d\rho^2\right)$ and find the expression for $d\eta/d\rho$. Then we substitute the expressions for η and $d\eta/d\rho$ in (17). After lengthy mathematical manipulations, we obtain (2), which is the equation obtained using A1 (and A2).

This suggests that the discrepancy in the shape equations obtained by different approaches in the literature occurs when the geometric relation (5) is not imposed. A3 can produce the same equation as A1 (and A2) as long as the geometric relation (5) is preserved when the variation is performed. In the situation when ψ can vary independently without taking z into consideration, the geometric condition is not necessary. Furthermore, if the variation is with respect to the normal displacement as in A1 and A2, ρ and z are proportionately varied so that the geometric relation is implicitly preserved.

3.3 Relationship between the shape equations

Equation (17) can be expressed as $d(\eta\cos\psi)/d\rho = 0$, which by using (15) leads to $d(\rho\mathcal{H}\cos\psi)/d\rho = 0$. We note that this relation differs from the equation in [ZL93] i.e. $(1/\rho)[d(\rho\mathcal{H}\cos\psi)/d\rho] = 0$, which has an extra factor $1/\rho$. Not having $1/\rho$ avoids the singularity at $\rho = 0$, which removes the doubt on the validity of the conclusion in [ZL93], as pointed out in [BP04, Poz03]. Integrating it once yields $\eta\cos\psi = 2k_b\rho\mathcal{H}\cos\psi = \mathcal{C}$, where $\mathcal{C}$ is an integrating constant. Obviously $\mathcal{C} = 0$ does not necessarily lead to $\mathcal{H} = 0$ unless $\rho\cos\psi \neq 0$. Therefore, (2) and (4) are equivalent if and only if $\eta = 0$, which is relatively easy to verify.

3.4 Vesicles with distinct topological shapes

It has been pointed out in the literature that the shape equations obtained using different approaches are equivalent only for spherical vesicles. We now demonstrate this by observing the value of Lagrangian multiplier η used in our approach.

Spherical Vesicles

For spherical vesicles, $\rho = r_0 \sin\psi$, (2) leads to $\Delta P r_0^3 + 2\lambda r_0^2 + k_b c_0^2 r_0^2 - 2k_b c_0 r_0 = 0$ and (15)-(17) yields $\Delta P r_0^3 + 2\lambda r_0^2 + k_b c_0^2 r_0^2 - 2k_b c_0 r_0 + \eta \cot\psi \csc\psi r_0 = 0$. Since these two conditions are identical, we have $\eta = 0$. Thus (4) is equivalent to (2) for spherical vesicles. This is due to the fact that we do not need to impose any constraint on z and its derivatives, which allows ψ to vary freely.

Cylindrical Vesicles

We now assume that the vesicle is of cylindrical shape, which is given by the equations $\rho = r_0, \psi = \pi/2$. Substituting this in (2) and in (15)-(17), we can verify that for this cylindrical vesicle equation to be solution of both (2) and (15)-(17), we require

$$\mathcal{C} = \Delta P r_0 \left(2 - r_0\right) + 2\lambda r_0 \left(\frac{1}{r_0} - 1\right) + c_0^2 k_b r_0 \left(\frac{1}{r_0} - 1\right) + 2k_b c_0 - \frac{k_b}{r_0} \left(\frac{1}{r_0} + 1\right).$$

Since $\mathcal{C} \neq 0$ and $\cos\psi = 0$, η cannot be zero. To obtain the cylindrical vesicle we need to have infinite slope $dz/d\rho$ $(= -\sin\psi / \cos\psi)$, which must be maintained when the variation is performed. Hence, (4) and (2) are not equivalent for cylindrical vesicles.

Toroidal Vesicles

Similarly, a vesicle of perfect torus shape given by $\rho = x + \sin\psi$, where $1/x$ is the ratio of its generating radii, can be solution of both (2) and (15)-(17) only if $\mathcal{C} = 2k_b(1 + 2c_0)$. Thus $\eta = 0$ only if $c_0 = -1/2$. However, based on experiments performed in [FMB92, MBB91, MB91] and theoretical result in [Wil82], in general [HO93] $c_0 \neq -1/2$. Therefore, $\eta \neq 0$ and (4) is not equivalent to (2) for toroidal vesicles.

As a simple observation, we offer the following explanation. To have a vesicle of perfect torus shape, we need to have vanishing slope of the curve $z = z(\rho)$ at the point $\rho = x$ (i.e. $(dz/d\rho)|_{\rho=x} = 0$). Because of this condition, ψ can not vary without taking z into consideration.

Circular biconcave discoids

In [NOO93] the authors showed that $\psi = \arcsin[\rho(c_0 \ln \rho + b)]$ with a constant b, is a solution of (2) under the condition $\Delta P = \lambda = 0$. This solution with $c_0 < 0$ represents a circular biconcave discoid, the shape of the red blood cell (RBC). For this vesicle to be a solution of (15)-(17) under the condition $\Delta P = \lambda = 0$, we require $\eta = 4k_b c_0/(\sqrt{1 - \rho^2(c_0 \ln \rho + b)^2})$. The nonzero η indicates that (4) is not equivalent to (2), unless $c_0 = 0$.

When $c_0 \neq 0$, the biconcave vesicles $z = z(\rho)$ has the local extreme value i.e., $dz/d\rho = 0$ at $\rho = \exp(-b/c_0)$. Thus, ψ can not vary independently. When $c_0 = 0$, the biconcave vesicle becomes spherical with $b = 1/r_0$, thus $\eta = 0$ and (4) and (2) become equivalent.

4 Conclusion

We have introduced two new approaches for deriving the equilibrium shape equation for axisymmetric vesicles. We have shown that as long as the geometric relation $dz/d\rho = -\tan \psi$ is maintained in performing the calculus of variation, both approaches produce the correct shape equation. We have also shown that the variation does not have to be in the normal direction. Furthermore, by imposing the geometric condition as a Lagrange multiplier, we established a simple relationship between the two distinct shape equations derived previously in the literature. Using this relationship, it becomes a straightforward exercise to verify the equivalence of the shape equation using explicit shape solutions.

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