Boundary behaviour of open vesicles in axisymmetric case

Xiaohua Zhou

Shaanxi Engineering Research Center of Controllable Neutron Source, Xijing University, Xi’an 710123, People’s Republic of China

E-mail: zhouxiaohua@xijing.edu.cn

Received 8 January 2019, revised 1 April 2019
Accepted for publication 15 April 2019
Published 17 May 2019

Abstract
A continuous transformation from a closed vesicle to an open vesicle requires that the area of open hole enlarges from zero. Since the shape equation and boundary conditions of lipid open vesicles with free edges have been obtained, we want to know whether this process can be achieved with valid parameters. By studying the boundary conditions in the axisymmetric case, the analytic expression of the boundary edges is obtained generally. It reveals that the radius and line tension of boundary edges are confined strongly by bending moduli. In some cases, there is the minimal nonzero boundary radius and the line tension needs to surmount the maxim following the increase of boundary radius. Without the spontaneous curvature, the line tension will tend to infinite when the boundary radius shrinks to zero. The continuous opening up process requires that the spontaneous curvature is nonzero and the ratio between the bending moduli of Gauss curvature and mean curvature satisfies $k \leq -4$, which is smaller than the value $k \simeq -1$ from experiments and simulations. This result indicates that the opening up process is discontinuous.

Keywords: open vesicle, boundary condition, solution

(Some figures may appear in colour only in the online journal)
equilibrium shape equations and some numeric solutions were studied [18, 23, 24].

Talin is a ubiquitous mechanosensitive protein and plays an important role in cell actin and adhesion [25]. Experiments have found that closed vesicles will change to open vesicles when increasing the talin concentration [5, 6]. In this process, talin assembles on the boundary edges and results in the deformation. Based on the Helfrich’s elastic free energy theory, many researchers discussed the equilibrium shapes of open vesicles with free edges [26–29]. It has been found that the shape equation for open vesicles are similar to closed vesicles with zero osmotic pressure. Besides, the edges should satisfy the boundary conditions [26, 28] which nearly eliminates the possibility to find a suitable boundary line on the known solutions of the shape equation of closed vesicles in the axisymmetric case [28]. Up to now, only an integral case for the shape equation and boundary conditions have been found when the line tension of the free edges can be negative [30, 31]. Finding new analytical solutions for open vesicles is still a challenge [32].

Since the shape equation and boundary conditions of open vesicles with free edges have been obtained, we want to know whether this process can be achieved continuously. For instance, at the beginning of the opening process of a vesicle with an infinite small hole, whether the line tension of the free edge is finite? If it is not, we think the opening process is discontinuous or cannot be achieved physically. In other words, we want to know whether it needs infinite forces to open a closed cell. Further, experiments and simulations have obtained the physical parameters of typical bilayer membranes, such as the bending moduli of mean curvature and Gauss curvature: \( k_c \) and \( k_g \) [33–35], respectively. But we do not know whether they can lead a continuous opening up transition in present open vesicle model. Moreover, in the axisymmetric case the boundary conditions are reduced to ordinary differential equations. In previous works, researcher tried to find solutions of the shape equation of open vesicle with these boundary conditions. Although this method provides some special shapes, revealing the insights of the general behaviour of open vesicles is still difficult. However, if these boundary equations can be solved generally, we can obtain the general characteristics of the boundary edges.

In this work we will study the above questions by investigating the differential equations of boundary conditions in the axisymmetric case. The general solution is obtained and it reveals some of the boundary behaviour of open vesicles. The theoretic conditions for continuous opening up process that we obtained are not in accordance the experiments, which indicates that the opening up transitions are discontinuous. In section 2, the boundary equations are simplified and the general solution is derived analytically. In section 3, general boundary behaviour of open vesicles are discussed and the results are compared with experiments. Finally, these results are recapped in a short discussion in section 4.

2. Analytical solutions for axisymmetrical boundary conditions

The Helfrich free energy for a vesicle is [7]

\[
E = \frac{k_c}{2} \int \int (2H - C_0)^2 \, dA + k_g \int \Lambda \, dA, \tag{1}
\]

where \( H \) and \( \Lambda \) are the mean curvature and Gauss curvature, respectively. \( C_0 \) is the spontaneous curvature and \( dA \) is the area element. For an open vesicle with a free edge, the total energy is

\[
E_i = E + \lambda \int \int dA + \gamma L, \tag{2}
\]

where \( \lambda \) is the area tension and \( \gamma \) is the line tension of the boundary edge with the length \( L \).

For an axisymmetric surface, let the generating line be around the \( z \)-axis and \( \rho \) be the turning radius, we have

\[
x = \rho \cos \phi, y = \rho \sin \phi, z = \int \tan \psi(\rho) \, d\rho, \tag{3}
\]

where \( \phi \) is the azimuthal angle and \( \psi \) is the tangent angle of the profile curve. The surface can be expressed as

\[
r = \{\rho \cos \phi, \rho \sin \phi, z\}. \tag{4}
\]

Defining \( J' = \frac{dJ}{d\rho} \), we have

\[
K_1 = \frac{\sin \psi}{\rho}, K_2 = (\sin \psi)', \tag{5}
\]

\[
H = (K_1 + K_2)/2, \quad \Lambda = K_1 K_2, \tag{6}
\]

where \( K_1 \) and \( K_2 \) are two main curvatures. Hu et al obtained the general shape equation, which is a third-order ordinary differential equation [36]. Zheng et al provided the first integral of the shape equation as follow [37].

\[
\lambda = (2H - C_0) \psi' \cos \psi + 2H \cos^2 \psi \sin \psi - \frac{1}{2} (2H - C_0)^2, \tag{7}
\]

where \( \eta \) is a constant of integration, \( \lambda = \lambda/k_c \) and \( \rho = \rho/k_c \). The above is a second-order ordinary differential equation with the variable \( \rho \). Although it is very difficult to solve generally, several analytical solutions have been found [17].

Besides, the edges should satisfy the following boundary conditions [27, 38]

\[
k = -\frac{2H_c - C_0}{\sin \psi_c} \rho_c, \tag{8}
\]

\[
\frac{1}{2} (2H_c - C_0)^2 + k \Lambda_c + \lambda - \sigma \gamma \frac{\cos \psi_c}{\rho_c} = 0, \tag{9}
\]

where \( k = k_g/k_c \) and \( \gamma = \gamma/k_c \). \( \sigma = 1 \) or \( \sigma = -1 \) if the tangent or the boundary curve is parallel of antiparallel to the rotation direction, respectively. The subscript \( _c \) means that the corresponding value on the boundary line and we name \( \psi_c \) the opening angle. Substituting equations (6)–(8) into equation (9) and choosing \( \sigma = -1 \), we get

\[
\gamma = -2 \rho_c H'_c \cot \psi_c. \tag{10}
\]

Making use of equation (6), equation (8) is changed to

\[
(\sin \psi_c)' + \frac{k + 1}{\rho_c} \sin \psi_c - C_0 = 0. \tag{11}
\]
This equation has the following general solution
\[ \psi_c = \arcsin \left( C \rho_c^{-k-1} + \frac{C_0}{k+2} \rho_c \right) \]  
(12)
where \( C \) is a constant of integration.

Defining the scale factor \( \rho_0 = |C|^{\frac{1}{k+2}} \), the reduced boundary radius \( \bar{\rho}_c = \rho_c / \rho_0 \) and the reduced spontaneous curvature \( c_0 = C_0 \rho_0 \), we have
\[ \psi_c = \psi_{c1} \equiv \arcsin \left[ \delta \bar{\rho}_c^{-k-1} + \frac{c_0}{k+2} \bar{\rho}_c \right] \]  
(13)
where \( \delta = 1 \) for \( C > 0 \) and \( \delta = -1 \) for \( C < 0 \). Here we should note that the function \( \arcsin \) confines \(-\frac{\pi}{2} \leq \psi_c \leq \frac{\pi}{2}\). Actually, besides equation (13), the opening angle can be
\[ \psi_c = \psi_{c2} \equiv \pi - \arcsin \left[ \delta \bar{\rho}_c^{-k-1} + \frac{c_0}{k+2} \bar{\rho}_c \right] \]  
(14)

Furthermore, we define the following reduced parameters:
\[ \bar{K}_{1c} = \bar{\rho}_0 K_{1c}, \quad \bar{K}_{2c} = \rho_0 K_{2c}, \quad \bar{H}_c = H_c / \rho_0, \quad \bar{\Lambda}_c = \Lambda_c / \rho_0, \quad \bar{\gamma} = \gamma / \rho_0 \]  
and \( \bar{\lambda} = \lambda / \rho_0 \). Substituting equations (13) and (14) into equations (5)–(7) and (10), we obtain
\[ \bar{K}_{1c} = \frac{c_0}{k+2} + \delta \bar{\rho}_c^{-2-k}, \]  
(15)
\[ \bar{K}_{2c} = \frac{c_0}{k+2} - \delta (1+k) \bar{\rho}_c^{-2-k}, \]  
(16)
\[ \bar{H}_c = \frac{c_0}{k+2} - \frac{\delta}{2} \bar{\rho}_c^{-2-k}, \]  
(17)
\[ \bar{\Lambda}_c = \frac{\lambda}{(2+k)^2} - (1+k) \bar{\rho}_c^{-2(2+k)} - \frac{\delta c_0 k}{2+k} \bar{\rho}_c^{-2-k}, \]  
(18)
\[ \bar{\gamma} = \epsilon \frac{\delta k (k+2)^2 \sqrt{1 - [c_0 \bar{\rho}_c / (k+2) + \delta \bar{\rho}_c^{-k-1} ]^2}}{\delta (k+2) \bar{\rho}_c + c_0 \bar{\rho}_c^{3+k}}. \]  
(19)
\[ \bar{\lambda} = \frac{\delta k (2+k)^2 \bar{\rho}_c^{-2} - k [\delta (2+k) + c_0 \bar{\rho}_c^{2+k}]^2}{\delta (2+k) + c_0 \bar{\rho}_c^{2+k} - 2 (2+k) \bar{\rho}_c^{2(2+k)}}. \]  
(20)
Where \( \epsilon = -1 \) for \( \psi_c = \psi_{c1} \) and \( \epsilon = 1 \) for \( \psi_c = \psi_{c2} \). Particularly, equations (15) and (16) yield
\[ \bar{K}_{1c} (1+k) + \bar{K}_{2c} = c_0. \]  
(21)
This condition gives a general structure characteristic of the boundary edges.

The shape of open vesicles can be changed by adjusting the concentration of talin [5]. A reasonable interpretation is that talin assembled boundary edges changes the line tension \( \gamma \). But we do not know whether a closed vesicle can be opened by choosing suitable \( \gamma \). In other words, \( \gamma \) must be finite at the beginning of the opening process. For an open vesicle, if \( \gamma \rightarrow \pm \infty \) or \( \lambda \rightarrow \pm \infty \) when the area of open hole shrinks...
to zero, the deformation between the closed vesicle and open vesicle cannot be achieved physically.

In the axisymmetrical case, on the north pole of a closed vesicle, there are \( \gamma = \pi \) and \( \rho = 0 \). Supposing that the opening process begins at this pole and the closed vesicle changes to an open vesicle continuously, we need

\[
\gamma \text{ and } \rho \text{ are finite, } \psi_c \to \pi, \text{ when } \tilde{\rho}_c \to 0. \tag{22}
\]

In the following text, we discuss whether the above conditions can be satisfied in equations (19) and (20) by choosing suitable parameters.

### 3. Transformations between a closed shape and an open shape

#### 3.1. Without the spontaneous curvature

First, let us consider the state \( c_0 = 0 \). Then, equations (12), (19) and (20) are reduced to

\[
\psi_c = \arcsin(\delta \tilde{\rho}_c^{-k-1}) \text{ or } \psi_c = \pi - \arcsin(\delta \tilde{\rho}_c^{-k-1}), \tag{23}
\]

\[
\tilde{\gamma} = \epsilon k (k + 2) \tilde{\rho}_c^{-1} \sqrt{1 - \tilde{\rho}_c^{-2k-2}}, \tag{24}
\]

\[
\tilde{\lambda} = \frac{1}{2} k (k + 2) (2 \tilde{\rho}_c^{-2} - \tilde{\rho}_c^{-2(k+2)}). \tag{25}
\]

In equation (24) we need \( 1 - \tilde{\rho}_c^{-2k-2} \geq 0 \) and it yields

\[
\tilde{\rho}_c \geq 1, \quad k > -1, \quad \tilde{\rho}_c \leq 1, \quad k < -1. \tag{26}
\]

We can also obtain

\[
\tilde{\gamma} = 0, \quad \psi_c = \pm \pi/2, \quad \text{when } \tilde{\rho}_c = 1 \text{ and } k > -1, \tag{28}
\]

\[
\tilde{\gamma} \to \pm \infty, \quad \psi_c = 0 \text{ or } \pi, \quad \text{when } \tilde{\rho}_c = 0 \text{ and } k < -1. \tag{29}
\]

Moreover, we can find that \( \tilde{\lambda} \to \pm \infty \) when \( \tilde{\rho}_c = 0 \). Since \( \tilde{\gamma} \to \pm \infty \) has no physical meaning, the above results indicates that a closed vesicle cannot change to an open vesicle continuously when \( c_0 = 0 \). We show several examples of the relationships between the \( \tilde{\rho}, \tilde{\gamma} \) and \( \tilde{\rho}_c \) in figure 1.

#### 3.2. With nonzero spontaneous curvature

When \( c_0 \neq 0 \), the relationship between \( \tilde{\gamma} \) and \( \tilde{\rho} \) is intricate. Besides the behaviour in figure 1, we can find (\( \epsilon = 1 \))

\[
\tilde{\gamma} = 0, \quad \psi_c = \pi, \quad \text{when } \tilde{\rho}_c = 0 \text{ and } k < -3, \tag{30}
\]

\[
\tilde{\gamma} = 3\delta/c_0, \quad \psi_c = \pi, \quad \text{when } \tilde{\rho}_c = 0 \text{ and } k < -3. \tag{31}
\]

The above results satisfy the conditions in equation (22). When \( k > -3 \) and \( \tilde{\rho}_c = 0 \), we find that there always is \( \gamma \to \pm \infty \). Moreover, if \( k > -4 \), we find \( \tilde{\lambda} \to \pm \infty \) when \( \tilde{\rho}_c = 0 \) in equation (20). The valid states for finite \( \tilde{\lambda} \) are

\[
\tilde{\lambda} = \frac{-kc_0^2}{2(2+k)} \text{, when } \tilde{\rho}_c = 0 \text{ and } k < -4, \tag{32}
\]

\[
\tilde{\lambda} = -16\delta/c_0 - \frac{c_0^2}{k}, \quad \text{when } \tilde{\rho}_c = 0 \text{ and } k = -4. \tag{33}
\]

Moreover, if \( k \leq -4 \), it is easy to get

\[
\tilde{H}_c = \frac{c_0}{2+k}, \quad \tilde{\lambda}_c = \frac{c_0^2}{(2+k)^2}, \quad \text{when } \tilde{\rho}_c = 0. \tag{34}
\]
A closed spherical solution with the radius $R$ and zero pressure satisfies [10]

$$2\tilde{\lambda}R - c_0(2 - c_0R) = 0.$$  \hspace{1cm} (35)

Supposing that this sphere begins to open up with $\tilde{\rho}_c = 0$, equation (34) gives $R = 1/\tilde{H}_c = (2 + k)/c_0$. This result and $\tilde{\lambda}$ in equation (32) satisfy equation (35). Therefore, the open process can begin with a sphere.

In equation (12), we define

$$f = \delta \tilde{\rho}_c^{-k-1} + \frac{c_0}{k + 2} \tilde{\rho}_c.$$  \hspace{1cm} (36)

If $f = 0$, we have $\psi_c = 0$ or $\psi_c = \pi$. Also, it yields $\rho_c = 0$ and $\rho_c = (\frac{k+2}{4c_0})^{\frac{1}{k+1}}$. But if $\rho_c = (\frac{k+2}{4c_0})^{\frac{1}{k+1}}$, we have $\gamma \to \pm \infty$. Therefore, this result gives two kinds of impossible shapes as shown in figure 2. Moreover, $f = \pm 1$ yields $\psi_c = \pm \pi/2$ and $\gamma_c = 0$.

Based on the above analysis, we can conclude that the continuous deformation between closed vesicles and open vesicles can only occur when $c_0 \neq 0$ and $k \leq -4$. Figure 3 shows an example by choosing $k = -6$, $c_0 = -4$, $\psi_c = \psi_c2$ and $\delta = 1$. In figure 3(a), the open process begins at the point $a$. With the increase of the reduced line tension $\tilde{\gamma}$, the reduced bounder radius $\tilde{\rho}_c$ will increase until it reaches the point $c$. On which, the open hole reaches the biggest state. Accordingly, figure 3(b) shows that the opening angle decrease from $\psi_c = 180^\circ$ on point $a$ to $\psi_c = 162.3^\circ$ on point $c$. But if we keep on increasing $\tilde{\gamma}$ on point $c$, there is no evolving pathway for the shape. Considering that our model is in the axisymmetric case, we think the shape will change to be non-axisymmetric in this case. Moreover, if we decrease $\gamma_c$ on point $c$, there are two deformation paths. One changes back to the initial closed shape on point $a$. The other changes to point $d$ with a nonzero $\tilde{\rho}_c$. Figure 4 shows the evolving paths in the 3D case. The (a)–(d) shapes correspond to the $a$–$d$ points in figure 3.

![Figure 4](image-url)

**Figure 4.** Deformation paths depend on the change of line tension. The (a)–(d) shapes correspond to the $a$–$d$ points in figure 3. There is $\psi_c = \pi$ for (d) and shape (e) is a non-axisymmetric shape.

![Figure 5](image-url)

**Figure 5.** Relationships between the reduced bounder radius $\tilde{\rho}_c$ and spontaneous curvature $c_0$ and between $\tilde{\rho}_c$ and opening angle $\psi_c$. We fixed $\gamma = 0.1$, $k = -5$ and $\delta = 1$.

### 3.3. Opening process induced by spontaneous curvature

In the up sections we take $c_0$ and $k$ as constants and show that one can open a closed shape through increasing the line tension. But we do not known whether it is possible to open...
a closed shape by changing other parameters, such as \( c_0 \). If \( \tilde{\gamma} \) in equation (19) is fixed and taking \( c_0 \) as variable, we obtain the relationships between \( c_0 \) and \( \psi_c \) and between \( c_0 \) and \( \tilde{\rho}_c \). Figure 5 shows an example by choosing \( \tilde{\gamma} = 0.1 \). From figure 5(a) we can see that the closed shape with \( c_0 = 0 \) is opened up through changing \( c_0 \). Increasing or decreasing \( c_0 \) from zero seems has similar effect. But there is also deference. Following the increase of \( \tilde{\rho}_c \), there are the maximal and minimal points for \( c_0 \). Figure 5(b) indicates that increasing \( c_0 \) will enlarge the opening angle, which means that the hole is opened outward. Inversely, decreasing \( c_0 \) will reduce the opening angle and make a hole opened inward. This deference is shown in figure 6 in the 3D case. Figure 5(a) also indicates that, before \( c_0 \) reaches the maximal or minimal value, changing back \( c_0 \) to zero will close the open hole.

4. Discussions

When neglecting the in-plane deformations, the energy of an elastic shell is similar to equation (1) and there is \( k = \nu - 1 \) [39], where \( \nu \) is the Poisson ratio. Considering \(-1 \leq \nu \leq 0.5 \), we have \(-2 \leq k \leq -0.5 \). If we just uses elasticity theory to estimate the vesicle, the condition \( k \leq -4 \) cannot be satisfied and a closed vesicle cannot be opened up continuously. Of course, applying elasticity theory for molecular membranes is questionable. For bilayer membranes, the values of \( k \) and \( \gamma \) have been obtained by experiments and simulations [33–35]. Scarce as they are, the value of \( k \) is in a range around \(-1 \) [35], which also indicates that is a discontinuous transition. Also, we should note that these works didn’t consider the effect of talins assembled on the edge. Although a small quantity of talin proteins on the edge probably cannot influence \( k \), the line tension \( \gamma \) will be changed. So, the value of \( \gamma \) needs to be measured in this case. But if a large number of talins assemble on the edge, the last term on the right side of equation (2) is insufficient to describe the aggregation energy of talins and the model in equation (2) is suspectable. Therefore, it needs new methods to investigate the opening up transitions of vesicles induced by proteins. From a topological point of view, the transition from a closed membrane to a pore with an edge is clearly discontinuous.

5. Conclusions

In this work, based on the Helfrich free energy model, we obtain the general solution of the boundary equations of open vesicles in the axisymmetric case. Some general behaviour of the boundary edges are revealed and the results indicate that the radius and line tension of boundary edges are confined strongly by bending moduli. Without the spontaneous curvature, the line tension will trend to infinite when the boundary radius shrinks to zero. This implies that a closed vesicle cannot be opened by using finite forces in this case, or that there is discontinuous transformation between a closed and an open vesicle. With finite physical parameters, opening and closing processes need that the spontaneous curvature is nonzero and that the ratio between the bending moduli of Gauss curvature and mean curvature satisfies \( k \leq -4 \). Considering the experimental value \( k \simeq -1 \), this result indicates that closed vesicles cannot change to open vesicles continuously.

Acknowledgments

This work is funded by the National Natural Science Foundation of China Grants (No. 11304383), the Natural Science Foundation of Shaanxi Province of China (No. 2018JM1019), and the scientific research plan projects of education department of Shaanxi provincial government (No. 18JK1202).

ORCID iDs

Xiaohua Zhou ∗ https://orcid.org/0000-0001-9871-5845

References

[1] Szoka F and Papahadjopoulos D 1980 Ann. Rev. Biophys. Bioeng. 9 467–508
[2] Evans E and Rawicz W 1990 Phys. Rev. Lett. 64 2094–7
[3] Hotani H 1984 J. Mol. Biol. 178 113–20
[4] Jung H, Lee S Y, Kaler E W, Coldren B and Zasadzinski J A 2002 Proc. Natl Acad. Sci. USA 99 15318–22
[5] Saitoh A, Takiguchi K, Tanaka Y and Hotani H 1998 Proc. Natl Acad Sci. USA 95 1026–31
[6] Takeda S, Saitoh A, Furuta M, Satomi N, Ishino A, Nishida G, Sudo H, Hotani H and Takiguchi K 2006 J. Mol. Biol. 362 403–13
[7] Helfrich W 1973 Z. Naturforsch. 28C 693–703
[8] Meyer R B 1968 Phys. Rev. Lett. 22 918
[9] David S C 1998 Toxicol. Lett. 23 431–39
[10] Ou-Yang Z C and Helfrich W 1987 Phys. Rev. Lett. 59 2486–88
[11] Ou-Yang Z C and Helfrich W 1989 Phys. Rev. A 39 5280–88
[12] Ou-Yang Z C 1990 Phys. Rev. A 41 4517–20
[13] Naito H, Okuda M and Ou-Yang Z C 1993 Phys. Rev. E 48 2304–7
[14] Naito H, Okuda M and Ou-Yang Z C 1995 Phys. Rev. Lett. 74 4345–8
[15] Zhang S G and Ou-Yang Z C 1996 Phys. Rev. E 53 4206–8
[16] Zhang S G 1997 Acta Phys. Sin. 6 641–55
[17] Ou-Yang Z C, Liu J X and Xie Y Z 1999 Geometric Methods in the Elastic Theory of Membranes in Liquid Crystal Phases (Singapore: World Scientific)
[18] Seifert U, Berndt K and Lipowsky R 1991 Phys. Rev. A 44 1182–202
[19] Yan J, Liu Q H, Liu J X and Ou-Yang Z C 1998 Phys. Rev. E 58 4730–36
[20] Michalet X 2007 Phys. Rev. E 76 021914
[21] Zhou X H, Zhang S G, Xie L Q and Zheng F 2008 Int. J. Mod. Phys. B 22 2769–79
[22] Evans E 1980 Biophys. J. 30 265–84
[23] Miao L, Seifert U, Wortis M and Döbereiner H 1994 Biophys. J. 49 5389–407
[24] Zherl P and Svetina S 2007 Proc. Natl Acad. Sci. USA 104 761–65
[25] Kumar A, Ouyang M, den Dries K, McGhee E J, Tanaka K, Anderson M D, Grosman A, Goult B T, Anderson K I and Schwartz M A 2016 J. Cell Biol. 213 371–83
[26] Ni D, Shi H J and Yin Y J 2005 Colloid. Surface. B 46 162–68
[27] Tu Z C and Ou-Yang Z C 2003 Phys. Rev. E 68 061915
[28] Tu Z C 2010 J. Chem. Phys. 132 084111
[29] Biria A, Maleki M and Fried E 2013 Adv. Appl. Mech. 46 1–68
[30] Zhang Y H, McDargh Z and Tu Z C 2018 Chin. Phys. B 27 038704
[31] Zhou X H 2018 Int. J. Non-Linear Mech. 106 25–8
[32] Tu Z C 2013 Chin. Phys. B 22 028701
[33] Siegel D P 2008 Biophys. J. 95 5200–15
[34] Semrau S, Iedema T, Holtzer I L, Schmidt T and Storm C 2008 Phys. Rev. Lett. 100 088101
[35] Hu M, Briguglio J J and Deserno M 2012 Biophys. J. 102 1403–10
[36] Hu J G and Ou-Yang Z C 1993 Phys. Rev. E 47 461–67
[37] Zheng W M and Liu J X 1993 Phys. Rev. E 48 2856–60
[38] Capovilla R, Guven J and Santiago J A 2002 Phys. Rev. E 66 21607
[39] Landau L D and Lifshitz E M 1986 Theory of Elasticity (Oxford: Pergamon)