J. Phys. II FYance 3 (1993) 1681-1705 NOVEMBER1993, PAGE 1681

Classification

Physics Abstracts

82.70

Phase diagrams and shape transformations of toroidal vesicles

Frank Jiilicher, Udo Seifert and Reinhard Lipowsky

Institut fur Festk6rperforschung, Forschungszentrum Jiifich, 52425 Jiifich, Germany

(Received 10 May 1993, accepted in final form 21 July 1993)

Abstract. Shapes of vesicles with toroidal topology are studied in the context of curvature
models for the membrane. For two simplified curvature models, the spontaneous-curvature
(SC) model and the bilayer-couple (BC) model, the structure of energy diagrams, sheets of
stationary shapes and phase diagrams are obtained by solving shape equations for axisymmetric
shapes. Three different sheets of axisymmetric shapes are investigated systematically: I) discoid
tori; it) sickle-shaped tori and iii) toroidal stomatocytes. A stability analysis of axisymmetric
shapes with respect to symmetry breaking conformal transformations reveals that large regions
of the phase diagrams of toroidal vesicles are non-axisymmetric. Non-axisymmetric shapes
are determined approxim~tely using conformal transformations. To compare the theory with
experiments, a generalization of the SC and BC model, the area-difference-elasticity-model
(ADlGmodel), which is a more realistic curvature model for lipid bilayers, is discussed. Shapes
of toroidal vesicles which have been observed recently can be located in the phase diagram of
the ADlGmodel. We predict the effect oftemperature changes on the observed shapes-The new
class of shapes, the toroidal stomatocytes, have not yet been observed.

1. Introduction.

Vesicles are closed surfaces, formed by lipid bilayers in aqueous solution [1-3]. The most general
classification of such closed surfaces is by their topology. The different topological classes are
distinguished by their genus, that is by the number of handles (or holes). Vesicles of spherical
topology have been studied intensively, e-g- in experiments, where a change in temperature or
osmotic conditions induces shape transformations between a variety of different shapes [4-6].
Recently, toroidal vesicles have been observed experimentally. The first examples were vesi-
cles made of a partially polymerized bilayer [7]. Typically, these vesicles were close to one
special axisymmetric circular shape, the sc-called Clifford torus. Subsequently, toroidal vesi-
cles consisting of fluid membranes have been found [8, 9]. They exhibit a variety of different
types of shapes of genus one, two and even higher genus. Among the genus-1 surfaces observed
so far, axisymmetric and non-axisymmetric shapes occur. The genus-2 surfaces which are

1682 JOURNAL DE PHYSIQUE II N°11

necessarily non-axisymmetric can crudly be classified into two classes: I) discoid shapes with
two holes and11) shape3 consisting of two spherical parts connected by three necks [8, 9].

Theoretical models for vesicles are based on the idea that the shape of a vesicle is determined
by bending elasticity which can be expressed by the curvature of the surface. For spherical
vesicles, the phase diagrwas of two curvature models [lo, 11], the spontaneous-curvature (SC)
model and the bilayer-couple (BC) model have been studied systematically [12-14]. These
phase diagrams are obtained by minimizing the bending energy for axisymmetric shapes with
a given surface area and enclosed volume. Recently, a more realistic model, the area~difference-
elasticity-model (ADE-model) has been proposed which takes into account that a bilayer is
composed of two compressible monolayers which can glide over each other [15-18]. The SC and
the BC model turn out to be mathematical limits of this more general model.

The systematic theoretical study of toroidal vesicles of genus-I started with a minimal model
for symmetric bilayers (without spontaneous curvature) with the volume to area ratio, I-e- the
reduced volume, as the only parameter. Similar to the spherical topology, several branches of
axisymmetric shapes were found and a one-dimensional phase diagram was determined [19, 20].
According to a

famous conjecture the axisymmetric shape of lowest energy irrespective of the
reduced volume, the Clifford torus, is an absolute energy minimum [21]. Since the bending

energy is a

conformal invariant, this ground state is degenerate, I-e- a one-parameter family
of non-axisymmetric shapes with the same energy can be generated from the Clifford torus
by applying conformal transformations [22]. The physical constraint of a

fixed volume to area

ratio breaks this degeneracy. Consequently, the ground state at fixed reduced volume is unique
but non-axisymmetric over a

large range in the reduced volume [20, 23]. In the vicinity of the
Clifford torus, the eigenmodes of the bending energy which lead to axisymmetry breaking have
been calculated analytically [24, 25].

In this paper, we aim for a

thorough theoretical analysis of toroidal vesicle shapes from
which statements about recent experimental observations as well as predictions for future
experiments can be infered. We start in section 2 by analysing the two curvature models,
the SC and the BC model, which both have been studied intensively for vesicles of spherical
topology. We classify the sheets [26] of stationary shapes and determine the phase diagrams
for both models. Even though, as outlined in section 3, there are good reasons to believe that
neither of the two models gives a

faithful description of the bilayer membrane, a detailed study
of these (from our present perspective) "simplified" or "mathematical" curvature models, is
justified. First of all, important insight into the structure of the possible shapes can already
be obtained in these models. Secondly, the phase diagram for a more realistic model, the
area-difference-elasticity (ADE) model as discussed in section 3.1, can easily be derived by a
general Legendre transformation from the phase diagram of the BC model. The phase diagrwa
of the ADE-model, then provides the basis for a comparison with recent experiments in section
3.2. Moreover, we can make predictions for future experiments in section 3.3.

To facilitate a

coherent reading of the paper, we give in section 2 only results while relegating
all important technicalities to the appendices. The shape equations for toroidal topology are
derived in appendix A. In appendix B, we discuss in detail the energy diagrams for stationary
shapes in the SC and the BC model as well as the different types of limit shapes. In appendix
C, the stability criterion of axisymmetric shapes with respect to symmetry breaking conformal
transformations is derived.

N°11 SHAPE TRANSFORMATIONS OF TOROmAL VESICLES 1683

2. Simplified curvature models.

2.I SPONTANEOUS-CURVATURE MODEL. In the SC model of Helfrich, the energy of the
bilayer is given by [10]

F

e

f /

dA(Ci + C2 Co)~ +

~cg /

dACiC2 (1)
2

Here, Ci and C2 denote the principal curvatures on the surface, while ~c and ~cg are the ordinary
and the Gaussian bending rigidity. The spontaneous curvature Co is a model parameter that
arises if the symmetry between the two monolayers is broken. Physical examples for this case
are: I) a membrane with two different monolayers forming a bilayer or it) a bilayer facing two
different solvents. The Gaufl-Bonnet theorem states that the second term is invariant under

transformations which do not change the topology of the surface. As long as the topology is
fixed, this term can and will be obmitted.
The phase diagram is determined by minimizing the energy F for fixed area A of the surface
and fixed enclosed volume V. Since F is invariant under scale-transformations, there are only
two independent parametdrs. These are the reduced volume

U ~

~rji13

~~~

and the reduced spontaneous curvature

co + co1G,

(3)

"'~~~~

jio + (A/4ir)~/~ ~~~

is the radius of a sphere with surface area A. Then, the energy F

= F(u,co) and the phase
diagram depend on v and co only.

2.2 BILAYER-couPLE MODEL. In the BC model (14] the bending energy reads

G e
f /

dA(Ci + C2)~ (5)
2

As a

third constraint, the area difference

AA w A~~ A"" m 2DM (6)

between the outer and the inner monolayer is kept fixed, which can be calculated from the

total mean curvature
M +
/

dA(Ci + C2) (7)
2

and the distance D between the neutral surfaces of the monolayers. Physically, the constraint
on AA would describe incompressible monolayers which do not exchange lipid molecules. In

this case the energy G

= G(u,m) can be expressed by the reduced volume v

and the reduced
total mean curvature

m e M/1~ (8)

As derived in reference [12], the stationary shapes are the same in both models. The phase
diagrams are, however, completely different.

1684 JOURNAL DE PHYSIQUE II N°11

2.3 STATIONARY SHAPES OF AXIAL SYMMETRY: SHEETS OF SOLUTIONS. Stationary shapes
of axial symmetry are determined by solving the shape equations (A4-A9) derived in appendix
A. The solutions to these coupled nonlinear differential equations are a discrete set of sheets
with different energies F

or G. Stationary shapes forming such a sheet can be either saddle
points or local minima, I-e- equilibrium shapes, of the curvature energy. The distinction
between both cases requires a complete stability analysis. However, stability with respect to
deformations preserving axisymmetry can be checked by close inspection of the energy diagrams
as discussed in appendix B. In order to study stability with respect to non-axisymmetric
deformations, we use an approximation based on conformal transformations as described in

the next section.

Three different sheets of stationary shapes can be distinguished, see figure 1: I) the sheet
of sickle-shaped tori; it) the sheet of discoide tori and iii) the sheet of toroidal stomatocytes
which do not have a symmetry plane perpendicular to the symmetry axis.
Both, the discoide tori and the sickle-shaped tori have reflection symmetry with respect to
the plane perpendicular to the axis of symmetry. They can be distinguished as different sheets
since they are separated from each other except for one shape which is the Clifford torus.
Therefore, starting with the Clifford torus which has an exactly circular cross section, the two
different ellipsoidal deformations of the contour lead to the sheets of discoide and sickle-shaped
tori [27]. The sheet of toroidal stomatocytes bifurcates from the sheet of sickle-shaped tori and
from the sheet of discoide tori, thus connecting these two sheets. As an illustrative example,
we show in figure la the energy G of the sheets of stationary shapes versus the reduced total
mean curvature m

for shapes with fixed reduced volume u =

0.55. The detailed discussion

of this diagram is given in appendix B. In figure 16, we show the corresponding calculated
contours of shapes of lowest energy G.
Various types of limit shapes, where the sheets end and the shape becomes singular, can be
distinguished. For all three sheets, one class of limit shapes occurs, where the hole diameter
vanishes. Formally, these shapes represent a connection to the spherical topology and are
denoted by Ls;~k, Ld;« and Lsto. Other classes of limit shapes include tori with exactly circular
cross section L~;rc and shapes with diverging hole diameter. A detailed discussion of the limit
shapes is given in appendix B.

2.4 AXIAL-SYMMETRY-BREAKING CONFORMAL TRANSFORMATIONS. The stationary shapes
with axial symmetry can be obtained by solving shape equations for the contour. Non-
axisymmetric shapes become accessible through conformal transformations applied to axisym-
metric shapes. The usefulness of this approximate nlethod to determine the full phase diagram
is first shown using the Clifford torus.

2.4.1 The Clil&ord torus and its conformal transformations. The Clifford torus is an ax-

isymmetric shape with a circular cross section and a

fixed ratio of v5 of its generating radii
with reduced volume v = uci e 3/(25/~irl/~) ci 0.71 and the reduced total mean curvature

m = mcj e

ir~/~25R ci 13.24. The Clifford torus is a stationary shape of the energy F for any
value of Co [28].
An important property of this shape was conjectured by Willmore [21] for genus-I surfaces,
the Clifford torus is the absolute minimum of the bending energy

G e

f

/dA(Ci + C2)~ (9)

2

with G

= Gci % 4ir~~c.

N°11 SHAPE TRANSFORMATIONS OF TOROmAL VESICLES 1685

2.5 Ls,ck

sweshaoed

ton

~(2)
~'~~

CD

i§ ,'
~/
~sto '~ ~d'SC

dscc,d

~.° SZ©xrpes ~d,sc
~°~ II c* ~
l~)

~

Lanc

0.5 1.0 m/41r

~s,ck

~~~k
~d,sc ~D~

,

' '

' ' ~fl~j

' '

~'~ ~
j

l~

(b) 0.29 0.50 0.63 0.52 1.05 1.36

Fig-I- a) Energy G of the axisymrnetric stationary shapes in the BC model versus the total mean
curvature m
for fixed reduced volume v = 0.55. Three different branches can be distinguished: I) a
branch of discoid tori; it) a

branch of sickle-shaped tori and iii) a branch of toroidal stomatocytes.
The toroidal stomatocytes bifdrcate from the other branches at the points C))/~, C)))~ and Cd;sc.
All three branches end at different types of limit shapes: Ls;ck, Lsto and Ld;sc are limit shapes with
a vanishing hole diameter. At Lc;rc, a

limit shape with perfectly circular cross section is reached.
Some parts of these axisymmetric branches are unstable with respect to symmetry breaking conformal
transformations. These instabilities occur at the points C*. b) Sequence of axisymmetric shapes of
minimal energy G for fixed reduced volume u =

0.55 and several values of m/4jr. The first and the
last shape are unstable with respect to non-axisymmetric deformations.

Since the bending energy G is an invariant under conformal transformations in the three-
dimensional embedding space, every shape that is a conformal transformation of the Clifford
torus also has the same energy G. Consequently, the energy minimum for tori is degenerate as
first observed by Duplantier [22] if no further constraints are imposed.
The nontrivial conformal transformations in three dimensions are the special conformal
transformations which can be parametrized by a vector a. This transformation consists of
an inversion R

- R/R~, a

translation by a vector a

and another inversion. Every point R is
thus transformed to R', with

~ l~~~~~ ~~~~

Note, that two successive special conformal transformations (10) with translation vectors al

1686 JOURNAL DE PHYSIQUE II N°11

Fig.2. The Clifford torus and a

shape generated by a special conformal transformation as in (10)
with translation vector ax = 0.3/Ro, and ay = az = 0.

and a2 are equivalent to one special conformal transformation with a = ai + a2, I-e-, the special
conformal transformations form a commutative subgroup.
Conformal transformations of the Clifford torus generate a one-parameter family of non-
axisymmetric shapes. This can be seen by applying a conformal transformation (10) to the
Clifford torus with the Z-axis as the axis of rotational symmetry and the X-Y-plane as the
symmetry plane, see figure 2

as an example. First, choose a vector a =

(lcos#, I sin #, 0).
Varying its length I generates a one-parameter family of non-axisymmetric shapes with vary-
ing reduced volume uci < u(1) < 1. This family of shapes can be described in a closed analytical
form [25]. For 1

=

2~Rir~/~ /(Ro(2~/~ +1)), it ends up at a

limit shape with v = 1. This limit
shape consists of a sphere with an infinitesimal handle. All these shapes have the same bending

energy G~t "

4ir~~c. Therefore, the handle gives a

finite contribution 4ir~~ 8ir~c to the bending
energy, since G

= 8ir~c for a sphere. On the other hand, if a special conformal transformation
with a =

(0, 0, az) is applied to the Clifford torus, this leads only to scale-transformations and
no new shapes are generated. The latter property depends crucially on the circular cross sec-
tion of the Clifford torus. In contrast, for a general toroidal shape with X-Y symmetry plane
(e.g. sickle-shaped tori), a

conformal transformation (10) with a =

(0, 0, az) does generate a
shape with broken up-down symmetry. Thus, even though the special conformal transforma-
tions involve the three parameters (ax, ay, az), there is only a one-parameter family of special
conformal transformations which produces new shapes when applied to the Clifford torus due
to its special symmetry properties. Therefore, for fixed u, there is no conformal degeneracy
that would lead to conformal modes (or "massless Goldstone modes" [23].

2.4.2 Axial symmetry-breaking: approximate phase boundaries. The non-axisymmetric
toroidal shapes of lowest bending energy, as obtained via conformal transformations of the
Clifford torus, represent the ground-state: I) for co "

0 and u > u~t in the SC model and it)
along a

line v = v~(m) in the BC model. This indicates, that regions of non-axisymmetric
shapes exist in the phase diagrams of both models [29].
We now apply the hypothesis that conformal transformations of the various sheets of axisym-
metric shapes provide a

reasonable estimate for the variational solution for all regions of the
phase diagram. Specifically, we analyse the infinitesimal stability of the axisymmetric sheets
with respect to special conformal transformations which can be calculated from the contour
line of this shape [30]. This method gives a

lower bound on that region of the phase diagram

N°11 SHAPE TRANSFORMATIONS OF TOROIDAL VESICLES 1687

Fig.3. An axisymrnetric sickle+haped torus with v =

0.55 and m/4jr =

o-S and a non-

axisymmetric sickle-shaped torus. The non-axisyrnmetric shape was generated by applying the special
conformal transformation (lo) with aX " 0.3/Ro, and ay = az " 0 to the axisymrnetric shape.

in which the ground state is non-axisymmetric. The idea behind this method is to start with
a shape Si on the sheet of lowest energy shapes and apply a special conformal transformation
to Si with aX # 0, see figure 3 for an example. This transformation generates a new non-
axisymmetric shape, Sl', with the same bending energy as Si which is located on a different
point in the phase diagram. The stability of the original shape now depends on the difference
of the energy of Sl' and the energy of the axisymmetric shape S~~~ which is located at the
same point in the phase diagram. The complete derivation of this stability criterion is given
in appendix C.

2.5 PHASE DIAGRAM oF THE SPONTANEOUS-CURVATURE MODEL. The analysis of the
stationary axisymmetric shapes together with the stability analysis with respect to conformal
transformations leads to phase diagrams. Quite generally, a phase diagram consists of several
regions where the shapes have different symmetry properties. Transformations between shapes
of different regions are called shape transitions.
The phase diagram for the SC model is shown in figure 4. It contains three regions: I) a
region of axisymmetric sickle-shaped tori; it) a region of tori with nearly circular cross section
"circular tori" [31] and iii) a

large region of non-axisymmetric shapes. The two axisymmetric
regions are separated by the discontinuous phase boundary Dax. The axisymmetry of the sickle
shaped tori and the circular tori is broken continuously at the lines C];~~ and C(~~~, respectively.
These lines end up at two different critical endpoints Di and D2 on the discontinuous transition
line Dax. The line Dax extends into the non-axisymmetric region until it ends up in the critical
point D~p. The Clifford torus is located along a

line CL with v = u~i which connects the lines
C(;~~ and Dax.
The lines C]~~~ and C(;~~ give the instabilities with respect to axisymmetry breaking if
deformations are restricted to conformal transformations. Thus, they represent bounds for the
instabilities which would have been obtained by a

full stability analysis of the axisymmetric
sheets: the non-axisymmetric regions extend at least to the lines C]~~~ and C]~~~. For the
Clifford torus, the conformal mode is the unstable eigenmode. To get an idea of the shapes
in the non-axisymmetric region close to C(;~~, a conformally unstable axisymmetric stationary
shape can be used. By applying a

conformal transformation to such a shape, non-axisymmetric
shapes are generated which should be good approximations for shapes of minimal energy in

1688 JOURNAL DE PHYSIQUE II N°11

2

'

~/ ',

Co / ~~~

IQ '

~j

~~~~~~

~' '
~ '

i~ '

"

~

'
,

nonaxisymmetnc
sickle-shaped for,

-2
0 0.5 v

Fig.4. Phase diagram for toroidal vesicles in the SC model. The two model parameters are the

reduced volume u

and the reduced spontaneous curvature co- The line Dax which ends in the critical

point Dcp, represents the line of discontinuous shape transformations. It separates a

region of circular

tori from a

region of sickle-shaped tori. At the dotted line SIS;ck, the sickle-shaped tori selfintersect.
The two dashed lines C];~k and C(;~~ represent lines ofinstabiliy of axisymmetric shapes with respect to
symmetry breaking conformal transformations. They serve as approximations for the exact continuous
shape transformations of axisymmetry breaking. Two different types of non-axisymmetric shapes can
be distinguished: I) non-axisymmetric sickle-shaped tori and it) non-axisymmetric circular tori. For
co " 0, the Clifford torus (CL) appears in the phase diagram on the line C],~~. The Clifford torus is
the minimal energy shape along the dotted line with v = u~j.

this region. An example for a shape generated in this way is the conformally transformed
Clifford torus shown in figure 2. Likewise, a conformally unstable axisymmetric sickle-shaped
torus can be used to approximate non-axisymmetric sickle-shaped tori below C]~~~, see figure
3.

The lines Mi and M2 represent borders of metastability related to the discontinuous transi-
tions along the line Dax. Starting, for example, from the region of sickle-shaped tori, crossing
the line Dax, the sickle-shaped tori become metastable while the circular tori are shapes of min-
imal energy. At Mi, the metastable sickle-shaped tori become unstable. Similarly, metastable
circular tori become unstable at M2. Along the line SIsj~k the contour of the sickle-shaped tori
selfintersects in the symmetry plane of these shapes. For a

calculation of shapes beyond this
line, one would have to include selfinteractions of the vesicle membrane.

2.6 PHASE DIAGRAM oF THE BILAYER-couPLE MODEL. Figure 5 shows the phase diagram
of the BC model which depends on the reduced volume v

and the reduced total mean curvature
m. For a

closed surface, the surface average of the mean curvature is positive and therefore
m > 0. Four different regions can be distinguished: I) a region of discoid tori; it) a region
of sickle-shaped tori; iii) a region of toroidal stomatocytes and iv) a

large region of non-
axisymmetric tori.

N°11 SHAPE TRANSFORMATIONS OF TOROIDAL VESICLES 1689

2

,

~ l
@

~

j
,

' ~

0

ig. 5. -

eparated by shape transformation fines Csick and Cd;sc

can be distinguished: I) discoid
tori; it) sickle-shaped tori and iii) toroidal tomatocytes. The line C* indicates the instability
respect to axisymmetry breaking conformal On the right hand side of this line, non-
axisymmetric shapes have nfinimal energy. The lines Ldisc> Lsto and Ls,ck represent limit shapes with
vanishing hole diameter. Above the line of circular limit shapes Lcirc, no axisymmetric stationary
shapes exist. The contour of discoid tori begins to selfintersect at the line SIdisc.

The mirror symmetry planes of the discoid tori and of the sickle-shaped tori are broken con-
tinuously at the lines Cdi« and Csj~k, respectively, leading to the region of toroidal stomatocytes
without a

reflection symmetry plane.

Continuous axisymmetry breaking occurs along the line C* which separates a region of non-
axisymmetric shapes for relatively large v

in the phase diagram from the region of axisymmetric
shapes for relatively small v [32]. This line begins at large m with discoid tori with a nearly
circular cross section. It continues with sickle-shaped tori until it ends in the point iv, m) =
(0,0). A special shape on this line is the Clifford torus, again denoted by CL. In this phase
diagram, the Clifford torus is a multicritical point where the continuous shape transformation
lines Cdi«, C~i~k and C* meet.

The line C* was obtained by analyzing the conformal instability of axisymmetric shapes. This
conformal instability which occurs in the BC model for the same shapes as in the SC model, is
again a

lower bound for the extension of the region of non-axisymmetric shapes. It becomes the
correct phase boundary at the Clifford torus CL. The examples of non-axisymmetric shapes
as shown in figures 2 and 3 hold for the BC model too.

The dotted lines in the phase diagram represent lines of limit shapes and selfintersection, as
described in appendix B. A general property of the phase diagram of the BC model is, that all
shape transformations are continuous as it has previously been observed for spherical shapes
[12]. However, we are not aware of any reason for the absence of first order transitions in the
BC model for all topologies.

1690 JOURNAL DE PHYSIQUE II N°11

3. Relation to experiments: The ADE-model.

3.1 THE ADE-MODEL. The two curvature models described so far seem to contain essential

features of the bilayer membrane. Reflection on the physical assumptions underlying these
models, however, reveals that both of them give only a crude representation of one important
aspect of the physical properties of the bilayer system. The two monolayers forming a

fluid

lipid bilayer are able to slide with respect to each other with relative ease. When such a
bilayer forms a closed vesicle and experiences changes in local curvatures, there will be a net
expansion or compression of the surface area of the individual monolayers of the order D/Ro.
Since relative movement can take place between the leaves, such expansion or compression
will be homogeneous over the whole surface or "non-local" rather than location dependent
[11]. Neither the SC model nor the BC model has incorporated this effect. The SC model
neglects this non-local factor, since it implicitly assumes that the two monolayers are rigidly
connected and have no relative movement, thus being essentially a model for interdigitated
monolayers. On the other hand, the BC model recognizes the specific way of coupling between
the two monolayers but does not allow any deviation of the monolayer surface area from its
equilibrium value, assuming a zero area-compressibility for the individual monolayers.
We will now consider a model where this non-local bending energy is incorporated. In
addition, it will be assumed that the number of lipid molecules remains constant within each
monolayer, I-e-, that no exchange of lipid molecules occurs between the two adjacent monolayers
even though their density is now different. This is the area-difference-elasticity (ADE) model.
Its energy reads in scaled variables [15, 16, 18]

W e

~

/(Ci + C2)~dA + aim mo)~l" G +

~"

(m mo)~ Ill)
2 2

The second term explicitly attributes an elastic energy to deviations of the area difference
AA e 2DRom from an equilibrium value AAO + 2DRomo. The area difference AAO of
the relaxed bilayer depends on the preparation of each individual vesicle. The dimensionless
parameter a

is the ratio of area difference elastic energies to the usual bending energies and is
for realistic bilayers close to one. For the calculation of the phase diagram, we choose a = 1
which is supported by the so far only measurement of this quantity [18]. In the limits of large
a and small a, the BC model and the SC model are recovered, respectively.
The phase diagram of the ADE-model can be derived from that of the BC model as follows:
the energy W has to be minimized for fixed enclosed volume V, surface area A and mo.
Stationary shapes of the energy W of the ADE-model can be determined by first varying W
with respect to the subspace of shapes with fixed reduced total mean curvature m. This leads

to the energy

W(u, m, mo) " G(u, m) + ~ca(m mo)~/2 (12)

The final variation of W(v, m, mo) with respect to m for fixed mo leads to

~~jj>

~~
=

-J~aim mo) i13)

This relation determines the value of m as a

function of mo. Inserting this value of m in
equation (12) leads to the energy W(mo>u) of stationary shapes of the ADE-model. The
curves of conformal instability in the BC model can be transformed by the same generalized
Legendre transformation to the ADE-model since the conformal stability of axisymmetric
shapes with mirror symmetry plane does not depend on a [33].
In figure 6, we show the phase diagram of toroidal vesicles in the ADE-model. It depends
on two parameters, the reduced volume u and mo. This phase diagram is qualitatively sim-

N°11 SHAPE TRANSFORMATIONS OF TOROmAL VESICLES 1691

2

0

0.5 v

Fig.6. Phase diagram for toroidal vesicles in the ADE-model with a =

1. The phase diagram
is very similar to that of the BC model elplained in figure 5. Three axisymmetric regions which are
separated by continuous shape transformation lines Csick and Cdisc can be distinguished: I) discoid tori;
it) sickle-shaped tori and iii) toroidal stomatocytes. The line Ldisc represent limit shapes with vanishing
hole diameter. The instability with respect to axisymmetry breaking conformal transformations is
denoted by C*. Within the region of axisymmetric shapes with reflection plane, discontinuous shape
transformations from circular tori to discoid tori occur along the line D. This line ends up in a

critical

point Dcp. The Clifford torus is the shape of minimal energy along the dotted line CL. A temperature
change corresponds to a

temperature trajectory as indicated by the dashed line (tt). This trajectory
crosses the line C* which implies that axisymmetry breaking shape transformations of toroidal vesicles
can be induced by temperature changes.

ilar to the phase diagram of the BC model, compare figure 5. There is a

large region of
non-axisymmetric shapes which are separated from the axisymmetric shapes by the phase
boundary C*. All sheets of axisymmetric shapes appear within the ADE-model as shapes of
minimal energy: I) discoid tori; it) sickle-shaped tori and iii) toroidal stomatocytes. Symmetry
breaking shape transformations occur at the lines C*, Cdi« and Csi~k. These transitions are all
continuous. A discontinuous transition line D which ends in the critical point D~p separates
discoid tori from tori with a circular cross section within the region of mirror symmetric ax-
isymmetric shapes. While in the BC model the Clifford torus is a multicritical point where all
symmetry breaking phase boundaries meet, a whole line CL of Clifford tori exists in the phase
diagram of the ADE-model, as it does in the SC model.

3.2 EXPERIMENTALLY OBSERVED SHAPES: LOCATION IN THE PHASE DIAGRAM. The obser-

vations by Fourcade, Mutz and Bensimon include shapes of genus one and genus two. Vesicles
of genus one can be immediately located in the phase diagram for toroidal vesicles in the
ADE-model. As a

first example, consider the axisymmetric circular torus shown in reference
[8] for which the authors estimate u ci 0.5. The value of mo cannot be measured directly. In
principle, it could be obtained by carefully comparing the contour of the observed torus with

1692 JOURNAL DE PHYSIQUE II N°11

the solutions of the shape equations. Inspection of the phase diagram shows, that circular
shapes with u = 0.5 exist within a

large range of mo, indeed. Second, consider the observed
non-axisymmetric torus with u ci 0.77. This shape resembles the non-axisymmetric shape
shown in figure 2. The phase diagram of the ADE-model shows that shapes with u > 0.77 are
definitely non-axisymmetric for all mo.

'~

Let us now discuss the genus-2 shapes seen by Fourcade et al.. Even without an explicit
calculation of minimal energy shapes with g > I, which are necessarily non-axisymmetric,
the observed genus-2 shapes can be related to calculated genus-I shapes which occur in the
phase diagram. This can be seen by starting e-g- with a discoid torus in the limit where
the hole diameter vanishes ii-e- with a

limit shape Ldi« as discussed in appendix B). In this
case, the hole gives no contribution to the bending energy and the shape is identical to a
spherical discocyte. If now a second infinitesimal hole is inserted, the energy will only change
infinitesimally. This indicates that mirror-symmetric discoid shapes, with two holes in this
symmetry plane, occur in the phase diagram of genus-2 vesicles [34]. They are related to
discoid tori of genus one. An example of such a discoid shape of genus 2 has been reported in
reference [8].
By a

similar argument sickle-shaped tori can be related to the second type of genus-2 shapes
observed so far. In the limit of zero u, the sickle-shaped tori consist of two concentric spheres
of equal radii connected by two infinitesimal necks. Inserting a

third infinitesimal neck to a

sickle-shaped torus with infinitesimal u does not change the energy. This indicates that shapes
consisting of two spherical parts connected by three necks are genus-2 shapes with minimal
energy for small u

and small m. A third neck breaks the axisymmetry of the original sickle-
shaped tori, but can be arranged in such a way that the positions of the necks obey a

threefold

symmetry. Conformal transformations applied to such a shape will induce a

shift of the neck

positions comparable to the one shown in figure 3 for the genus-I torus. In fact, a shape with
fluctuating neck positions has recently been observed [9].

3.3 PREDICTIONS FOR FUTURE EXPERIMENTS. So far, in the experiments by Bensimon
and co-workers shapes with non-trivial topology are recorded without changing external pa-
rameters. For a crucial test of the theory presented here, one should vary one parameter sys-
tematically. Temperature changes have successfully been used for vesicles of spherical topology
to induce shape transitions [4, 5]. We recall that a change in temperature affects both u

and

mo because of the thermal expansivities of the monolayers of the membrane and the enclosed
water. These temperature trajectories in the phase diagram, and the corresponding sequence
of shape transformations, are significantly affected by any small asymmetry of the order of
10~~ in the thermal expansion coefficients of the two monolayers [4, 12]. So far, there are
no independent measurements or estimates for such a possible asymmetry. In this paper, we
therefore discuss the ideal case of symmetric thermal expansion of the monolayers. If the total
bilayer volume is constant, temperature trajectories can be described by [12]

mo "

(mo@)/u,

(14)

where if, mo) denotes a starting point in the phase diagram. Figure 6 shows such a tem-
perature trajectory (tt). For decreasing temperature the reduced volume u

increases while

mo decreases. Starting in the axisymmetric region of discoid tori, the trajectory crosses the
continuous shape transformation C* where the axisymmetry is broken. Thus, the model pre-
dicts that for any circular torus a decrease in temperature will lead to a non-axisymmetric

torus via a

continuous shape transformation (provided the bilayer remains in the fluid state).
Since this transformation is reversible, increasing the temperature, I-e- reducing u, renders

N°11 SHAPE TRANSFORMATIONS OF TOROIDAL VESICLES 1693

the vesicle axisymmetric again. This prediction can be extended to all axisymmetric shapes
which include the sickle-shaped tori and the toroidal stomatocytes described below: starting
with any axisymmetric shape, a decrease in temperature leads to a non-axisymmetric shape
via a continuous shape transition which breaks the axisymmetry. In the phase diagram of
the ADE-model with a = 1, metastable shapes exist only within a very small stripe along
the discontinuous line D. Therefore, almost all shape changes are reversible in this case. This
differs significantly from the situation in the SC model, which exhibits a

large region between
the lines Mi and M2, where the vesicle would stay in a metastable state because of the large

activation barrier for the first order transition.

Finally, a new type of toroidal shapes which has not been observed yet is predicted by our
phase diagram: two continuous shape transformations, Cdi« and Cs;~k, separate the toroidal
stomatocytes without reflection plane from the shapes with reflection plane. At these phase
boundaries, the mirror symmetry is broken continuously. The phase diagram shows that the
region of toroidal stomatocytes can not be reached via a temperature trajectory from the
circular or non-axisymmetric shapes described so far. However, if it was possible to decrease mo
at fixed v, a circular torus should loose its reflection plane and become a

toroidal stomatocyte.
For even smaller mo, the reflection symmetry is restored at C~i~k. The area difference mo of the
monolayers can be changed without changing the reduced volume by redistributing the lipids
through the bilayer. For vesicles of spherical topology, such a

redistribution has been induced

by Farge and Devaux with a mixture of lipids and a pH gradient across the membrane [6].

4. Summary.

We systematically analysed vesicle shapes of minimal bending energy for toroidal topology in
two steps. First, we followed the established technique of solving the Euler Lagrange equations
for axisymmetric shapes numerically as in the case of spherical topology. These axisymmetric
solutions can be classified into sheets. We find sheets of discoid, sickle-shaped and, for the
first time, up/down asymmetric toroidal stomatocytes, see figure I. In a

second step, we
analysed the stability of these shapes with respect to conformal transformations which break
the axisymmetry. Even though this cannot replace a

full stability analysis, this method provides
a
lower bound on the extension of non-axisymmetric shapes within a phase diagram. However,
it is even exact for a special shape, the Clifford torus, and should, by continuity, give a good
approximation to the phase boundaries in a certain neighborhood of this shape.
The phase diagrams which are obtained by this two-step procedure have been determined
for three different curvature models, the spontaneous-curvature (SC) model, the bilayer-couple
(BC) model and the area-difference-elasticity-model (ADE-model), see figures 4, 5 and 6.
The phase diagrams in the two simplified models (SC and BC model) are two-dimensional and
are both characterized by a

large region of non-axisymmetic shapes. In the BC model, all
phase transitions are continuous and all sheets of shapes show up as shapes of minimal energy
somewhere in the phase diagram. In contrast, the phase diagram of the SC model contains a
discontinuous transition and the toroidal stomatocytes do not represent states of lowest energy
in this model.

For a comparison with experiments we discussed the more realistic ADE-model which takes
into account that the bilayer consists of two compressible monolayers. Its phase diagram, figure
6, which constitutes our main result, has been obtained from the phase diagram of the BC
model by a generalized Legendre transformation. It contains a

large region of non-axisymmetric
shapes. All transitions but one are continuous. All observations of toroidal vesicles available
so far are consistent with this phase diagram. While the observed genus-I tori can be located
explicity therein, the two types of genus-2 vesicles reported in experimental work can be closely

1694 JOURNAL DE PHYSIQUE II N°11

z

v

R

Fig.?. Parametrization of an axisymmetric toroidal contour. Z is the coordinate along the sym-
metry axis, R is the distance from the axis and 1~ is the tilt angle of the contour.

related to genus-I vesicles appearing in our phase diagram.
We then used this phase diagram for predictions of future experiments. Any axisymmetric
torus should become non-axisymmetric when the temperature is decreased. A subsequent
increase should render this shape axisymmetric again without any hysteresis effects since the
axisymmetry breaking transition is predicted to be continuous. The predicted new type of
axisymmetric shapes without reflection plane cannot easily be reached from known shapes by
a change in temperature. One rather has to change the relative amount of lipid molecules in
the two monolayers at fixed reduced volume.
In conclusion, we gave a

fairly detailed analysis of toroidal shapes which minimize curvature
energies. The phase diagram for a

realistic curvature model provides the basis for a discussion
of available experiments and should, as we hope, stimulate and guide the search for as yet
unobserved but theoretically predicted shapes. For a quantitative comparison of theory and
experiment, we also stress the relevance of systematic experiments where a parameter such as
temperature is changed in a controlled fashion.

Acknowledgments.

We are grateful to X. Michalet, D. Bensimon and B. Fourcade for sending us video snapshots
of genus-2 surfaces and reference [9] prior to publication.

Appendix A.

Derivation of the shape equations for toroidal vesicles.

Shapes with axial symmetry can be parametrized by three functions R(S), Z(S) and 1~(S), see
figure 7. R is the distance from the axis of symmetry, Z the coordinate along the axis and ifi
the tilt angle of the contour, while S is the arclength along the contour. The three functions
R, Z and ifi are related by

R

= cos ifi and Z

=

sin ifi (A.1)

The principal curvatures on the surface are Ci " ifi and C2 "

sin ifi/R.
The functional F augmented with a term LA + PV for the area and volume constraint has
to be minimized with respect to R, Z and ifi. Introducing two further Lagrange multiplier

N°11 SHAPE TRANSFORMATIONS OF TOROmAL VESICLES 1695

functions 'f(S) and q(S) to ensure (A.1), the functional F' to be minimized can be written as

F' + 2ir~c /~~ dS L (A.2)

o

Here,

L =

I

II +

~i'~ Co

~

+ £R + lR~ Sin1fi +

7(R cos ifi) +

iii + sin ifi) (A.3)
plays the role of a Lagrange function. The parameters £

= L/~c and fl = P/~c are the rescaled
Lagrange multipliers for the volume and area constraints. From the condition 6F' = 0, the
Euler-Lagrange equations follow:
ij = U (AA)

~

~~~

~i~~

~

~)

~ ~ ~~ ~" ~ ~
i

"~ ~ ~

~i ~" ~ ~~'~~

i

=

(U Co)~

"~ /

+ f

+ flR sin ifi (A.6)
2 2R
I

= 0 (A.7)
h

=

cosifi (A.8)
2

=

sin ifi (A.9)
These are the shape equations for stationary shapes with axial symmetry. Note, that q turns
out to be constant while 7 = 7(S) is a

function along the contour. The boundary conditions
for R, Z and ifi are chosen to ensure a closed contour corresponding to a

toroidal shape:
R(o) = Rjsi) = Ri jA.io)
zjo) =

zjsi) =

o (A.ii)
~(o) =

- ~r/2 (A.12)
~jsi) = 3~r/2 jA.13)

The boundary conditions for 7 and U are
~jsi) = ~jo) and ujsi) = ujo) jA.14)

The variation of F' with respect to the total contour length Si leads to the condition H(Si " 0,
where

H +

-L + ifi

~~

+

li ~~

+ 2 ~f
3ifi 3R 32

=

~

ifi~ (~ o) ~

~R~ sin ifi £R

2 R 2

+'f cos ifi q sin ifi (A.15)
is the Hamiltonian function which is conserved along the contour. Thus,

q =

~~ U(0)~ Co

+
)) ~R(+

fRi (A.16)
2

1

~

2

is determined by the other boundary values to ensure H(Si) " o.

1696 JOURNAL DE PHYSIQUE II N°11

Appendix B.

Stationary shapes and limit shapes.

B-I SHEETS AND BRANCHES. Stationary shapes of the energy functionals F and G can be
parametrized by two independent parameters, e-g- u and co, and, thus, form two-dimensional
manifolds, or sheets [13]. Three different sheets of solutions of the shape equations (A4 A9) for
toroidal vesicles can be distinguished: I) the sheet of discoid tori; it) the sheet of sickle-shaped
tori and iii) the sheet of toroidal stomatocytes. The classification and the topology of these
sheets is unique and does not depend on a special model. Phase diagrams are determined by the
energies F and G of the sheets as functions of iv, co) and iv, m), respectively. These functions
are plotted in energy diagrams, which are cuts across the sheets along a one-dimensional line
in the parameter space. Thus, the two~dimensional sheets are reduced to one~dimensional
branches. One sheet can lead to more than one branch in an energy diagram, provided the

sheet has one or several cusps. For a

sheet with a cusp, two different cases can be distinguished:
I) the cut cuts across the cusp, leading to an energy diagram which shows one branch with a
cusp or it) the cut does not cut across the cusp which leads to two separate branches in the
energy diagram. Thus, the number of branches depends on I) how often the corresponding
energy sheets are folded and it) the precise location of the cut. As an example, figure 8 shows

the energy F

as a

function of u

for the cut co " 1. This diagram exhibits four branches. Three
of them can be uniquely related to three different sheets of stationary shapes. The fourth
branch belongs to the sheet of discoid tori for u < v~i> and to the sheet of sickle-shaped tori
for v > u~i At u = u~j ci 0.71 this branch contains the Clifford torus CL where the two sheets
are connected. Both sheets have wedges at co < 0. This generates the fourth branch as a
combination of two parts which meet at the Clifford torus. All shapes along this branch have
an approximately circular cross section. Therefore, we call them circular tori.

B.2 SPONTANEOUS-CURVATURE MODEL. In the SC model only two sheets of stationary
shapes are relevant for the phase diagram. These are: I) the sheet of discoid tori and it)
the sheet of sickle-shaped tori. The shapes on both sheets have a

reflection symmetry plane.
The sheets of toroidal stomatocytes bifurcate from both sheets and connect them, but for
-2 < co < 2, which is the range we investigated, their energy F is always larger than the
energy of the shapes with reflection symmetry.
First, consider the energy F for fixed spontaneous curvature co As an example, figures 8a,

b show the energy F of four branches as a function of u

for fixed co "

1: I) a branch of discoid
tori; it) a branch of sickle-shaped tori; iii) a branch of toroidal stomatocytes which bifurcates
at the point Csj~k from the branch of sickle-shaped tori and iv) a branch of circular tori which
contains at u = u~i Cf 0.71 the Clifford torus CL. Shapes with lowest energy are sickle-shaped
tori for u < uD t 0.41 and circular tori for u > uD. At v = uD where the two branches cross,
a discontinuous shape transformation Dax occurs. The branches of toroidal stomatocytes and
the discoid tori end up in limit shapes L~to and Ldim where the hole diameter vanishes. A
different limit occurs for sickle-shaped tori which selfintersect at SIsi~k with u ci 0.03. At C*
with u ci 0.68, the circular shapes become unstable with respect to axisymmetry breaking

conformal transformations.
The energy F

versus co is plotted for fixed u =

0.55 in figures 9a, b. Three different branches
occur for this cut. Figure 9a shows the two branches with up~down reflection symmetry while
figure 9b shows the branches of toroidal stomatocytes only. The discoid branch exhibits a Gibbs
loop which separates discoid tori from circular shapes on this branch. The sickle-shaped branch
crosses the discoid branch for co t 0.1 at the point Dax. At C))/~, C))/~ and Cdi«, branches

N°11 SHAPE TRANSFORMATIONS OF TOROIDAL VESICLES 1697

~ ~
~ ~

~ ~

d,sco,de ton
U- U-

3
3

~~~'~~ ~'~~

loroidal

~

slomaiocfles

~

s,ckle-shaped
t~~, ~ s,ckle-shaped ~
ax

~

tar, ax

l ~~ i

~d'SC

(a) c,rculartor, (b) c,rculartor,

0 0.25 0.5 Vci v
o 3 0.4 0.5 V

Fig.8. Energy F

versus u
for co " 1.0: a) shows the complete branches and b) gives some details
near u ci 0.5. Four branches are displayed. Three of them correspond to the different sheets of
stationary shapes: one branch of discoid tori, one branch of sickle-shaped tori and one branch of
toroidal stomatocytes. The branch of circular tori is for u < uci # 0.71 part of the discoid sheet
and for u > uci part of the sickle-shaped sheet. For u = ucj it contains the Clifford torus (CL) which
connects the two sheets. At the point Cs;ck> the toroidal stomatocytes bifurcate from the sickle-shaped
branch. This branch ends up in a

limit shape Lsto with vanishing hole diameter. A similar limit shape
Ld;sc also exists for the branch of discoid tori.

~ ~
~ ~
~ ~
~ ~-

tore,dal siomatocyies

3 ~
~disc ~~~k
~(2)
s,ck ",, ",
,, ',,
Q,,,

S'ckle.shaPed (1) ~ ~

~ ton

~

~ ~~~

"'~~',~~

(a)

,sco,d~~

~sick ~~~ "~~'~

-l 0 ~ -l 0 co

Fig.9. Energy F

versus co for u = 0.55. In la) the branches of discoid tori and sickle-shaped
tori with reflection symmetry are displayed. The branches of toroidal stomatocytes are plotted in
16). The toroidal stomatocytes bifurcate from the other branches in the points C)))~, C)()~ and Cdisc.
Lsto is a

limit shape of these stomatocytes. The sickle-shaped branch and the branch of discoide tori
cross in the point Dax. In the phase diagram, this leads to a discontinuous shape tranformation from
sickle-shaped tori to circular tori.

of toroidal stomatocytes bifurcate from the branches of sickle-shaped tori and discoid tori,
respectively, and connect them. One branch of toroidal stomatocytes ends up in a

limit shape
L~to with infinitesimal hole diameter. For u > v~j ci 0.71, the topology of the branches changes.
In figure 10, we show F

versus co for u =

0.73. In the co-interval chosen, only the sickle-shaped
branch exists. This branch exhibits a Gibbs loop corresponding to the discontinuous transition

1698 JOURNAL DE PHYSIQUE II N°11

~

~-

4
3

hi

~

c*

2

~

I

cularton

la) 2

- 2 0 1

Co _1.5 -1 1

.5 Cc

Fig.10. - nergy F versus co for u = 0.73. The circular tori on

Dax from sickle-shaped tori to shapes with a

circular contour. These circular shapes become
unstable with respect to axisymmetry breaking at C* with co ci -0.5. Using these and further
energy diagrams, we obtained the phase diagram for the SC model as shown in figure 4.

B.3 BILAYER-couPLE MODEL. In the BC model, the energy G as a function of v and m de-
termines the phase diagram. Figure la shows G versus m for the branches of stationary shapes
with u =

0.55. Three different branches, corresponding to the three sheets, are displayed. The
branch of sickle-shaped tori starts for small m at a

limit shape L~i~k. However, these shapes
are unstable with respect to symmetry breaking conformal transformations. They become
stable at the point C* with v ci 0.45. Beyond the point C))/~ where the branch of toroidal
stomatocytes bifurcates from the branch of sickle-shaped tori, the branch of sickle-shaped tori
corresponds to saddle points, I.e. it is locally unstable. For larger values of m, there is another
bifurcation C))/~ where a branch of toroidal stomatocytes meets the sickle-shaped branch. The
branch of discoid tori starts from a

limit shape L~ir~ with perfectly circular cross section. The
point C* close to L~ir~ indicates that L~ir~ is unstable with respect to perturbations which break
the axisymmetry. The toroidal stomatocytes bifurcate from the discoide branch at Cdim. The
discoid branch ends up at a second limit shape Ldim which is identical to a selfintersecting
spherical oblate. Likewise, the toroidal stomatocytes reach a

limit shape L~to with infinites-
imal hole. The energy diagram therefore leads to a sequence of shapes of minimal energy as
shown in figure 16. This scenario holds for 0.55 < v < v~i Cf 0.71. For u = u~i the branches
of sickle-shaped and discoid tori meet in a cusp at the Clifford torus where the derivative
3G/3m is singular. For v > u~i> the energy of the discoid branch is larger than the energy of
the sickle-shaped branch and the toroidal stomatocytes disappear. Figures 11a, b show the
two branches for u =

0.73. Here, the sickle-shaped branch begins at a

limit shape L~jr~. Two
points C* of conformal instability occur on this branch. Between these points, axisymmetric
shapes are stable.

Again, the information extracted from these and similar energy diagrams lead to the phase
diagram for the BC model as shown in figure 5.

N°11 SHAPE TRANSFORMATIONS OF TOROIDAL VESICLES 1699

~'~
d@We ~

m ~

~ CQ

CQ ~f d

~

d,scoidton

scmeshaoedton 7

si~kle-shajj~ L~i~

1.6

~$

.0 m/41r .025

Fig.11. Energy G as a

function of m for fixed u = o.73. In tl~is case, the sickle-shaped branch
has always lowest energy. At Lc;rc, it ends up in a

limit shape with exactly circular cross section. C*
denotes the points of conformal instability.

B.4 LIMIT SHAPES AND NECK CONDITION. In this section, we discuss limit shapes, which
are singularities on the sheets of stationary shapes. Different types of limit shapes occur for
toroidal topology.
In the limit of large co limit shapes L~jr~ with exactly circular cross section appear. In the
iv, m) plane these shapes fall on the hyperbola m = 3ir/u.
Another type of limit shapes are tori with a hole of vanishing diameter, Ri "

o. They are
denoted: I) Ldi« on the branch of discoid tori; it) L~j~k on the branch of sickle-shaped tori and
iii) Lsto on the branch of toroidal stomatocytes, respectively, see figure 1.
Toroidal shapes with an infinitesimal neck should be closely related to shapes of spherical
topology which start to selfintersect. The numerical analysis shows, in fact, that the shapes
with reflection plane Ld;« and Lsi~k bifurcate from branches of selfintersecting shapes of spher-
ical topology. The limit shapes Ld;« form exactly the line of selfintersecting spherical oblates,
denoted SIab in reference [12]. At the point of selfintersection, an infinitesimal hole does not
change the bending energy and, thus, the toroidal shape of minimal energy is identical to the
spherical shape with the same u and m.
The shapes Ls;~k can also be understood in terms of spherical shapes as follows. A spherical
prolate A is located within a perfect sphere B touching the prolate at two points where the
shapes are connected by infinitesimal necks. Both shapes have the same tension L(~) =

L(~)
but opposite pressures P(~) =

-P(~) and spontaneous curvatures Cj~~ =

-Cj~~ These
conditions are necessary to get a stationary toroidal combination of the two shapes of spherical
topology. The sphere and the prolate can be connected by an infinitesimal neck provided the
distance between the two poles of the prolate is equal to the diameter of the enclosed sphere.
All these conditions can indeed be fulfilled simultaneously since for any fixed P and Co IL is

used to choose a

length scale) there exists a spherical prolate and a sphere which coexist. One
of the two parameters, P and Co, can now be used to change the sphere diameter in such a
way that the prolate fits into the sphere. The second parameter is still free and therefore a
whole line of limit shapes Ls;~k exists [35].
The limit shapes of vesicles of spherical topology which consist of one or more spherical
shapes, have been found to be connected by ideal necks [12, 13]. Ideal necks of such spherical

1700 JOURNAL DE PHYSIQUE II N°11

~
~

Co i

/§ ~
i d'S~
/

2.1 L ,/
StO j

«
,,,

toroidal
,, stomatocfles

," c

,,' d,s~
,~

sph

2 ~~sto

~s,ck

0.5 m/41r 1_o

Fig.12. Energy G versus m for u = 0.55 which represents a part of figure 1. There are two branches
of toroidal stomatocytes which seem to intersect with a common tangent. The lower branch connects
the branch of sickle-shaped tori with the branch of discoid tori. The energies of shapes of spherical
stomatocytes which selfintersect SI][$, are shown for comparison. They have a

larger energy G than
toroidal stomatocytes.

shapes fulfill the neck condition
C~ + C~ = Co (B.1)

where C~ and C~ are the values of the curvatures of the two shapes adjacent to the neck
[12, 13]. The neck condition, thus, selects sets of spherical shapes which remain stationary
shapes when connected by infinitesimal necks.
For the limit shapes Ldi« and Lsi~k the numerical findings that these shapes occur along
one-dimensional curves in the space of shapes shows that a neck condition similar to (81) does
not apply here. For any further condition would select only a discrete number of shapes along
these curves.

Therefore, we conclude that the ideal neck condition (81) is special to vesiculated shapes
but does not apply to infinitesimal necks under all circumstances. Obviously, more work would
be needed to understand this phenomenon mathematically.
Toroidal stomatocytes with vanishing hole diameter Lsto can not easily be reduced to spher-
ical shapes. Even though they look very similar to spherical stomatocytes that begin to self-
intersect SI]($, denoted SI~to in reference [12], the numerical analysis reveals, that they are
different. This is demonstrated in figure 12 where the branches of toroidal stomatocytes and
the shapes SI]($ are shown to be separated. Thus, there is no obvious connection between the
branches of spherical and toroidal stomatocytes and any further analysis of the shapes L~to is
difficult. In particular, their location in the phase diagram is hard to obtain accurately.

B,5 RELATION To Two-DIMENSIONAL vEsIcLEs. For diverging hole diameter Ri with
fixed contour length Si " 2irR2, an axisymmetric torus reaches the limit of a

long cylinder
with reduced volume u +~ 1/Ri and area A m 4ir~RiR2. This limit occurs for the unstable
branches of both, the discoid shapes and the sickle-shaped tori, where for infinitesimal u

the

N°11 SHAPE TRANSFORMATIONS OF TOROIDAL VESICLES 1701

energies F and G diverge. In this limit, the shape equations reduce to those of two-dimensional
vesicles.

With the parametrization R(S) = RI + R2r(S) of the contour, the functional F' as in (A2)
expanded in lowest order in R2/Ri reads

F' =
2ir~c~~ /~~ ds(ifi CoR2)~ + 2irfR(+ flR~ ~(~ + O(R2/Ri j

(B.2)
R2 2

o R~

with the dimensionless integration variable s = S/R2. A2d denotes the area of the cross-

section which is the area of a

two-dimensional vesicle. Variation of (82) for fixed Ri and R2
with respect to the shape leads to the shape equations of two-dimensional vesicles [36] which
describe stationary solutions of the functional

f(d + f2d + P2d ~((B.3)
~~~~

i

2w

f2d %

/

dsqj2

~~~ ~~~~~~~ ~~ ~' ~~~ ~~~~ ~~ ~~~~~"~~

Y
~he minimal energy f[~(p~~) ~~~~

~~

jj~ j

F' = 2ir~c) f[~(flR() 2irCoR2 + irC(R(+ 2ir£R(+ O(R2/Ri)) (B.5)

2

Variation of (85) with respect to Ri leads to

f[~(flR() 2irCoR2 + irC(R(+ 2ir£llj = 0 (B.6)

A second condition results from varying (85) with respect to R21

Using 3f(~/3p2d " A2d/ill and combining (86) and (87) leads to an additional condition on
a
two-dimensional vesicle contour being a

solution in the limit of infinitesimal v

for toroiodal

topology:

~~d

1~2d j~ ~~0~2 (~.8)

With equation (83), this can be rewritten as

~2d

fl2d
~~ ~ ~~°~2 ~~'~~

The limit of large Ri with R2 fixed is now taken for fixed reduced spontaneous curvature co,
which implies that Co is rescaled according to Co " Co/(RiR2)~f~ Since Co becomes zero for
diverging Ri, equation (89) has to be solved for Co "

0. Solutions can be found by plotting
the energy f2d of two-dimensional stationary shapes together with)p2dA2d/ll~ versus p2d
[36]. Two solutions exist: I) a circular contour which fulfills the cylinder equations for three-
dimensional vesicles [12], and it) an ellipsoidal contour with p2d " P* which is part of the line
of non-circular shapes of two-dimensional vesicles. This two-dimensional ellipsoidal contour

taken as a cross-section of a

toroidal vesicle with the long axis parallel to the axis of symmetry
corresponds to the limit shape of the unstable sickle-shaped branch for small u. Likewise, the
same cross-section with the long axis perpendicular to the axis of symmetry corresponds to
the limit shape of discoid tori. Finally, the circular cross-section corresponds to the limit of

circular tori for small u.

1702 JOURNAL DE PHYSIQUE II N°11

Appendix C.

Stability with respect to special conformal transformations.

We restrict the stability analysis to axisymmetric shapes with an additional reflection plane.
The origin of the coordinate system is chosen where the symmetry axis crosses the reflection
plane. Under a special conformal transformation, parametrized by the vector a, the trans-
formed area A expanded to second order in a

is

A' = A 2a~ /

dAR~ + 12 /

dA(a R)~ + O(a~) (C.1)

The special conformal transformation is followed by a

scale transformation R" = AR with
I

=

(A'/A)~/~ which restores the surface area A. The transformed volume V and total mean
curvature M expanded in a

read

V" =
l~V' = Vii + a~B$~ap) + O(a~) (C.2)

and

M" = AM' = M(I + a~B$~ap) + O(a~) (C.3)

For axisymmetric shapes, B$~ and B$~ can be expressed by integrals along the contour
functions R(S), Z(S) and ifi(S). The stability analysis with respect to modes with az " 0,
which break the axisymmetry, require the calculation of

B(j = B10 =

~) /~ dS(RZ~ 2R~) +

) /~ dS(9R~Z RZ~) cos ifi (C.4)

o o

and

B(§ = Bi~$~ =

$

+ ~
/~~ dS(R~ RZ~)(U + @)

o

+

j~~
/~~ dSR~ sin ifi +

j I' dS(RZ~ 2R~) (C.5)

o o

For a derivation of the stability criterion, first consider the SC model. Choose a branch of
stationary shapes for fixed Co and A but varying volume V. Let F(V) denote the energy of
these shapes. Choose a stationary shape Si along this branch with volume Vi, energy F(Vi)
and total mean curvature Mi A special conformal transformation with subsequent rescaling
applied to this shape Si, generates a non-axisymmetric shape Sl' with energy

FscT la) = FjW) 2~cCo(Mj'ja) Mi

,
(C.6)

volume I~"(a) and total mean curvature Ml'(a).
To lowest order in VI'- Vi and Ml'- Mi, the energy FscT defined in equation (C6) changes
linearly as a

function of l~':

FscTlvl') = FIB) 21GCo)~(fit It" H) + Ollvl' H)~) lC.7)

1

~~

On the other hand, along the branch F(V), there exists a shape S~~~ with volume l~" which
has an energy F(Vl'), compare figure 13. This energy F(Vl') expanded to lowest order in

N°11 SHAPE TRANSFORMATIONS OF TOROIDAL VESICLES 1703

F

Flv)

Ii F jv")
~j~/")

~~~ ~

i'n I

~cT~~~~~

y y" v~ j' v

Fig.13. Stability analysis with respect to special conformal transformations for shapes on an ax-
isymrnetric branch of stationary shapes with energy F(V). Starting with a

shape Si with volume l§
and energy F(Vi)> an infinitesimal special conformal transformation generates a new shape Sl' with
volume Vi' and energy FscT (Vi'). This energy has to be compared to Fin (Vi' of a shape S~~ on the
branch. The figure shows two cases: I) on the left hand side of C*, FscT(Vi') > Fin(V(~) shows that
the branch is locally stable; it) on the right hand side of C* FscT(V(~) < Rin(V(~) indicates, that the
branch is unstable with respect to special conformal transformations.

VI'- % is given by

Rinlt'l = FlHl +

iii" H) + Ollvl' H)~) lC.8)

If the slope of FscT(l£') is smaller than the slope of F(l~"), I-e- if F(l~'(a)) < FscT(a)
in the limit of small a, a special conformal transformation will generate a non-axisymmetric
shape Sl' with volume l£' which has a

lower energy than the stationary shape S"I with the
same volume. The axisymmetric shape S~~ with volume l~" is therefore not a shape of lowest
energy. The perturbation is marginal when both slopes are equal. The stability criterion
obtained by these arguments for the SC model thus reads [30]

$VB(j + 2~CCOMB(§ 5 0 (C.9)

Note, that 3F/3V =

- ~CP, where P is known from solving the shape equations.
For the BC model, the energy G(l§ M) of a branch of axisymmetric shapes is invariant under
a special conformal transformation. A non-axisymmetric shape Sl', generated from a shape
Si with energy G(l§,Mi) by a special conformal transformation has the energy GscT(a) =
G(l§, Mi), volume l~"(a) and total mean curvature Ml'(a). Comparison of the energy of shape
Sl' with the energy G(l£', Ml') of a shape S~* along the branch of axisymmetric stationary
shapes leads to the stability criterion

GscTl<'la), Ml'la)) 5 Glvi, Mi lC. lo)

1704 JOURNAL DE PHYSIQUE II N°11

Expanding

together with

$

= 2~cCo,

(C.13)

again leads to the criterion (C9) as it was obtained for the SC model.
For shapes without reflection plane, generalized stability criteria can be obtained which differ
for the BC model and the SC model. We have not checked the toroidal stomatocytes for their

conformal stability. However, we believe that they are conformally stable in all regions of the
phase diagram where they have lower energy than the shapes with a

reflection plane for the
following reason. We find that the axisymmetric shapes from which the toroidal stomatocytes
bifurcate are conformally stable. By continuity, this will hold at least in the vicinity of the
bifurcation for the toroidal stomatocytes too.

References

[1] Lipowsky R., Nature 349 (1991) 475.
[2] Wortis M., Seifert U., Berndl K., Fourcade B., Miac L., Rao M., Zia R-K-P-, Proceedings of
the workshop on Dynamical Phenomena at Interfaces, Surfaces and Membranes, D. Beysens, N.
Boccara, G. Forgacs Eds. (Nova Science).
[3] The Structure and Conformation of Amphiphilic Membranes, R. Lipowsky, D. Richter, K. Kremer
Eds. (Springer, Berlin, 1992).
[4] Berndl K., K£s J., Lipowsky R., Sackmann E., Seifert U., Europhys. Lett. 13 (1990) 659.
[5] Kis J., Sackmann E., Biophys. J. 60 (1991) 825.
[6] Farg6 E., Devaux P-F-, Biophys. J. 61 (1992) 347.
[7] Mutz M., Bensimon D., Phys. Rev. A 43 (1991) 4525.
[8] Fourcade B., Mutz M., Bensimon D., Phys. Rev. Lett. 68 (1992) 2551.
[9] Michalet X., Bensimon D., Fourcade B., Proceedings of the workshop on Soft order in physical
systems (Les Houches, Feb. 16 Feb. 25, 1993).
[10] Helfrich W., Z. Naturforsch., C28 (1973) 693.
[11] Evans E., Biophys. J. 14 (1974) 923.
[12] Seifert U., Berndl K., Lipowsky R., Phys. Rev. A 44 (1991) l182.
[13] Miac L., Fourcade B., Rao M., Wortis M., Zia R-K-P-, Phys. Rev. A 43 (1991) 6843.
[14] Svetina S., iek§ B., Eur. Biophys. J. 17 (1989) 101.
[15] Seifert U., Miac L., D6bereiner H.-G., Wortis M., p. 93 in reference [3];
Miao L., Ph.D. thesis, Simon Fraser University (1992);
Miao L., Seifert U., Wortis M., D6bereiner H.-G., submitted to Phys. Rev. E.
[16] Wiese W., Harbich W., Helfrich W., J. Phys. condensed matter 4 (1992) 1647.
[17] Evans E., Yeung A., Waugh R., Song J., p. 148 in reference [3].
[18] Waugh R-E-, Song J., Svetina S., iek§ B., Biophys. J. 61 (1992) 974.
[19] Seifert U., J. Phys. Cofloq. FYance 41 (1990) C7-339.
[20] Seifert U., Phys. Rev. Lett. 66 (1991) 2404.

N°11 SHAPE TRANSFORMATIONS OF TOROIDAL VESICLES 1705

[21] Willmore T-J-, Total Curvature in Riemannian Geometry (Ellis Horwood Ltd., Chichesteri 1982).
[22] Duplantier B., Physica A 168 (1990) 179;
Duplantier B., Goldstein R-E-, Rcmero-Rcchin V., Pesci A.I., Phys. Rev. Lett. 65 (1990) 508.
[23] This corrects an erroneous statement in reference [20], where a

two-fold degeneracy of the ground
state was claimed even if the constraint on the area to volume ratio is taken into account.

[24] Mosseri R., Sadoc J-F-, Charvolin J., p. 97 in reference [3].
[25] Fourcade B., J. Phys. II FYance 2 (1992) 1705.
[26] The difference between branches and sheets is discussed in appendix B-1.
[27] For the long axis of the ellipse perpendicular to the axis of symmetry, the tori become discoid,
while for the long axis parallel to the axis of symmetry, the tori become sickle-shaped.
[28] Zhong-can Ou-Yang, Phys. Rev. A 41 (1990) 4517.
[29] In fact, for u m I toroidal shapes of lowest energy cannot be axisymmetric, since a axisymmetric
shape with u m I has to look like a sphere with a hole along the axis of rotational symmetry.
For vanishing hole diameter, the bending energy of such a shape diverges. Thus, the shape with

lowest energy is a

sphere with an infinitesimal handle, which is necessarily non-axisymmetric.
[30] Seifert U., J. Phys. A Math. Gen. 24 (1991) L573.
[31] Technically speaking, these shapes are for u < uct part of the discoid sheet and for u > uci part of
the sheet of sickle-shaped tori, see appendix B-1.
[32] In the phase diagram of the SC model, we have distinguished two lines C]j~~ and C];~~ of axisym-
metry breaking. They originate from the same instability C* but appear separated into two parts
by the line of discontinuous transitions Dax.
[33] In appendix C, the criterion of conformal stability of axisymmetric shapes with a

reflection plane
is shown to be the same in the SC and the BC model. The generalization of this analysis for
arbitrary values of a

shows that the criterium is, in fact, independent of o.
[34] Jiilicher F., Seifert U., Lipowsky R., Phys. Rev. Lett. 71 (1993) 452.
[35] Another type of limit of sickle-shaped tori exists for u - 0 and co < 0. These shapes consist of
two identical spheres of radius Ro which are connected by two infinitesimal necks. The two spheres
can coexist in a

toroidal shape if fl = 2Co/Rl> f

=

-C(/2. From these shapes, the line Ls;ck
bifurcates at co Ci -4.24. This bifurcation corresponds to the bifurcation of the prolate branch
from the branch of spheres in the case of spherical shapes.
[36] Seifert U., Phys. Rev. A 43 (1991) 6803.