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INTERNATIONAL ATOMIC ENERGY AGENCY
INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS
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SMR.961 - 17

WORKSHOP ON:
PROTEINS, MEMBRANES and their INTERACTIONS

22 JULY - 2 AUGUST 1996

"Vesicles of non-spherical topology and conformal diffusion"

PART I

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FRANCE

Membranes and Vesicles of non-trivial topology.

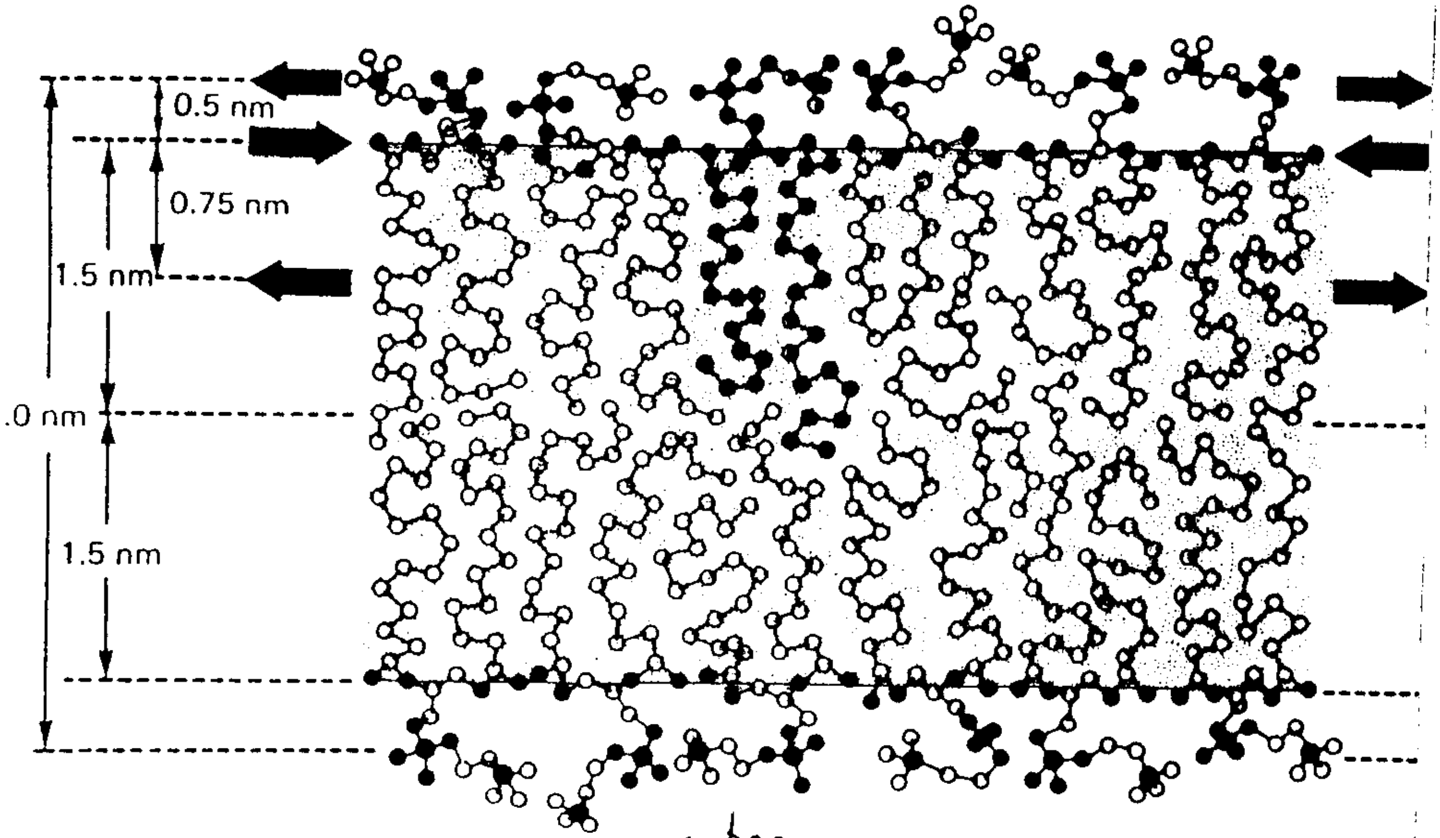
X. Michalet, M. Mutz, B. Fourcade, D.B.

Outline

1) The phospholipid membrane.
2) Elastic theory of fluid membranes.
3) The morphology of closed membranes (vesicles)
    a) Genus zero (sphere)
    b) Genus one (torus)
    c) higher genus
4) Interaction between topological "defects".

The membrane is a bilayer of amphiphiles

water

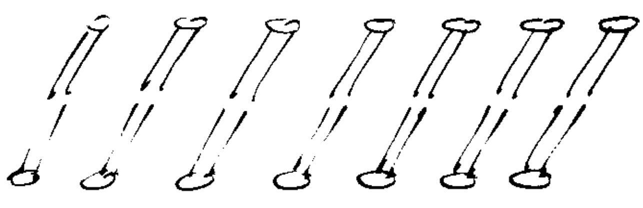


water

bilayer of DPPC (di-palmitoyl phosphatidyl-choline)

When $T > T_m$ (chain melting temperature) the membrane is fluid

when $T < T_m$ the membrane is in the solid (or gel) phase.



$L_{\beta'}$ phase

Elastic theory of fluid membranes (Canham, Helfrich)

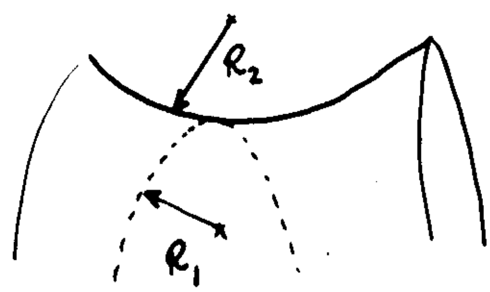
membrane thickness : ~ 50 Å
vesicle size : ~ 10 μm

A membrane is thus a quasi two-dimensional object.

Fluid membrane

$$\mathcal{H} = \frac{\kappa}{2}\int d^2\sigma \left(\frac{1}{R_1}+\frac{1}{R_2}\right)^2$$

$$+ \bar{\kappa} \underbrace{\int d^2\sigma \ \frac{1}{R_1}\cdot\frac{1}{R_2}}_{\text{topological constant by Gauss-Bonnet theorem.}}$$

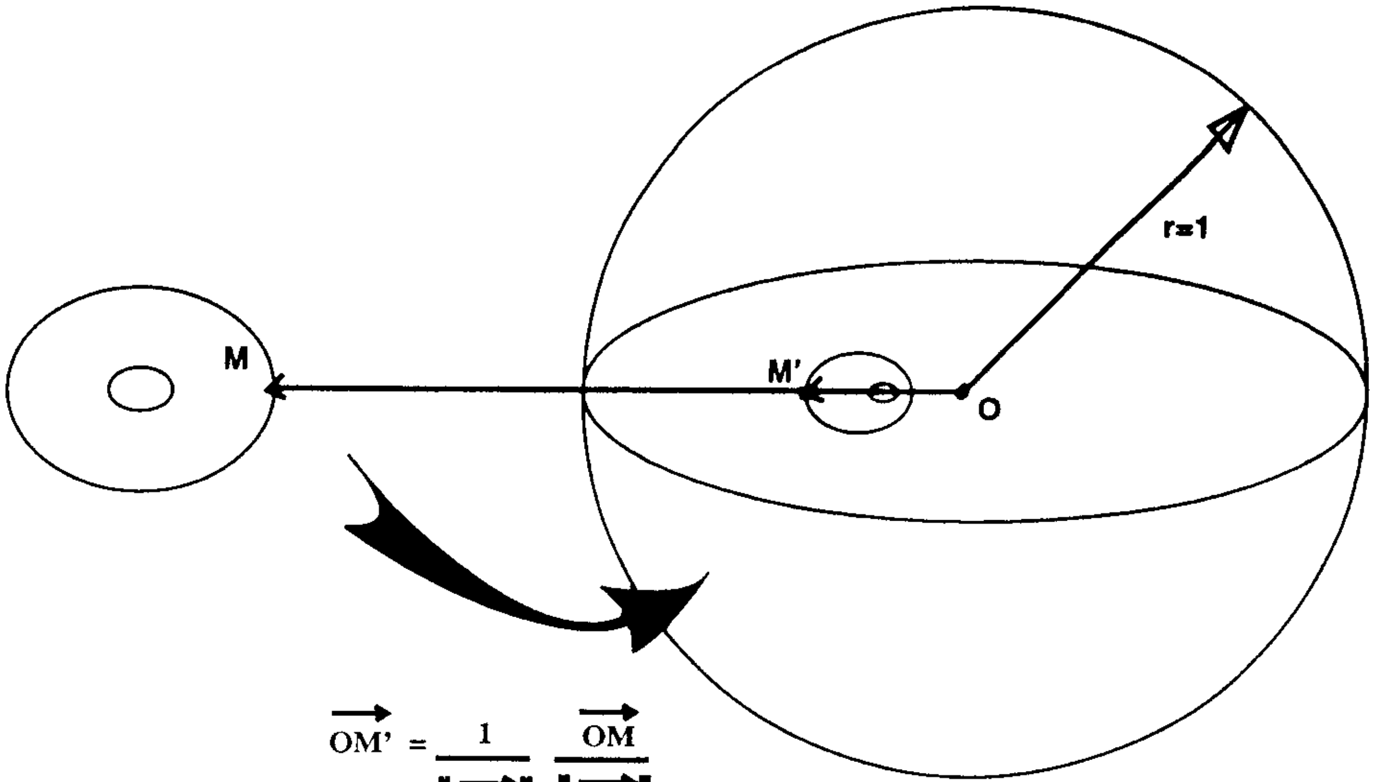


typical values : $\kappa, \bar{\kappa} \sim 10 \div 20 \ k_B T$

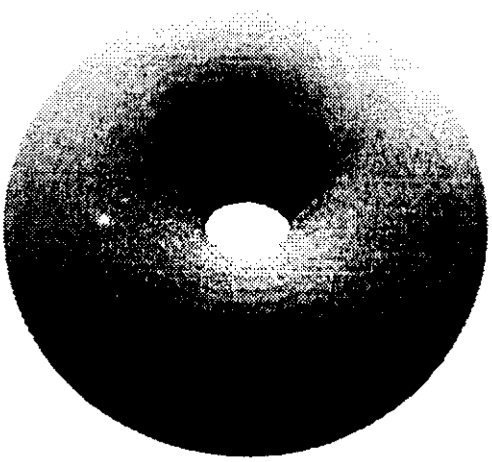
$\mathcal{H}$ is invariant under 3D conformal transformations :

a) translation
b) dilations
c) inversions : $\vec{r}\,'(\sigma') = \dfrac{\vec{r}(\sigma)}{|\vec{r}(\sigma)|^2}$

INVARIANCE DE L'ÉNERGIE DE COURBURE PAR INVERSION

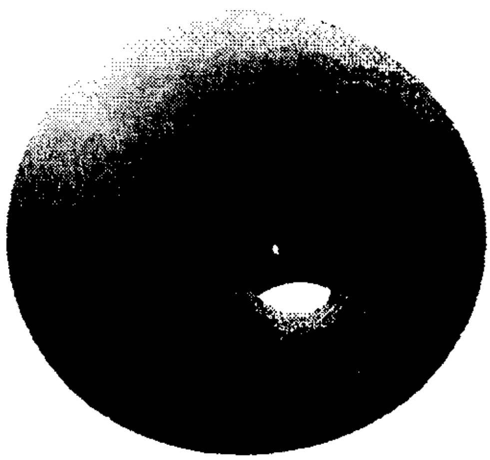


$$\overrightarrow{OM'} = \frac{1}{\|\overrightarrow{OM}\|}\ \frac{\overrightarrow{OM}}{\|\overrightarrow{OM}\|}$$



le tore de Clifford

$v = v_{Clifford} = 0.71$



une cyclide de Dupin

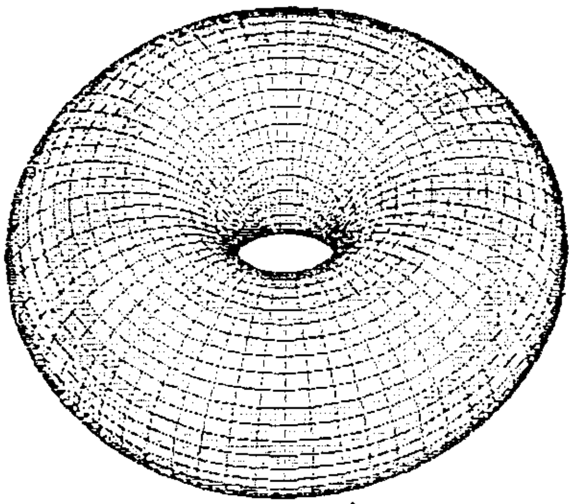
$v = 0.78$

Willmore Surfaces:

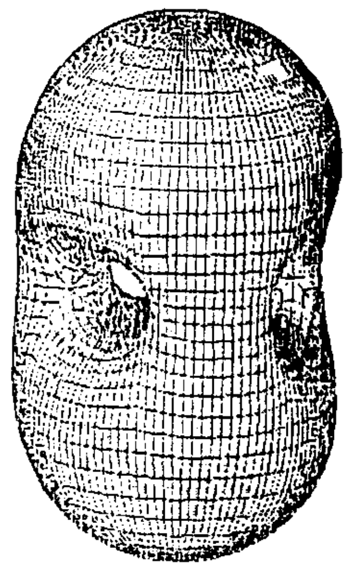
- Surfaces minimizing $\mathcal{H}$.
- Defined modulo a conformal transformation.

Obtained by projecting minimal surfaces from S^3 into $\mathbb{R}^3$. For genus $= 0$, it is the sphere.

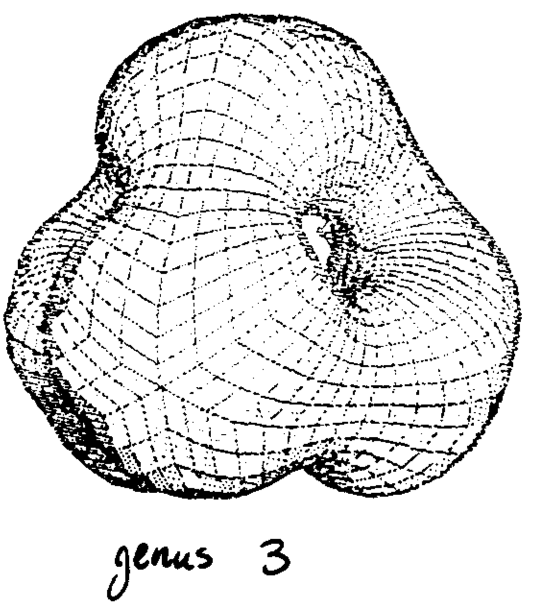
Clifford torus



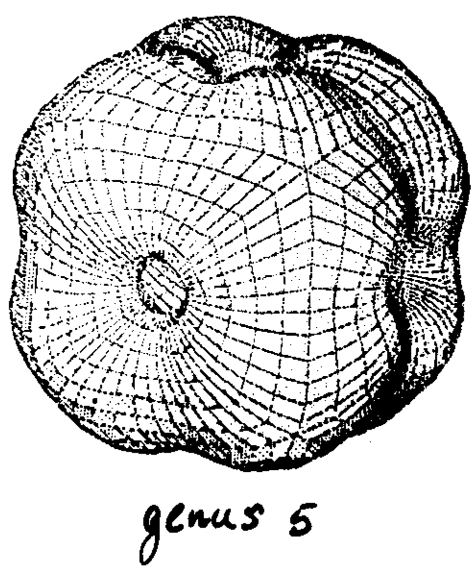
genus 1



genus 2



genus 3



genus 5

The morphology of vesicles

The vesicular morphology is obtained by minimizing $\mathcal{H}$ under constraints:

1) Constant area
2) Constant volume

} constant reduced volume.

3) Bilayer asymmetry (spontaneous curvature, ...)

" - Surfaces

<u>Genus = 0</u>:

Berndl, Käs, Lipowsky, Sackmann & Seifert
Europhys. Lett. <u>13</u>, 659 (1990)

Miao, Fourcade, Rao, Wortis and Zia
Phys. Rev. <u>A43</u>, 6843 (1991)

<u>Genus = 1</u>:

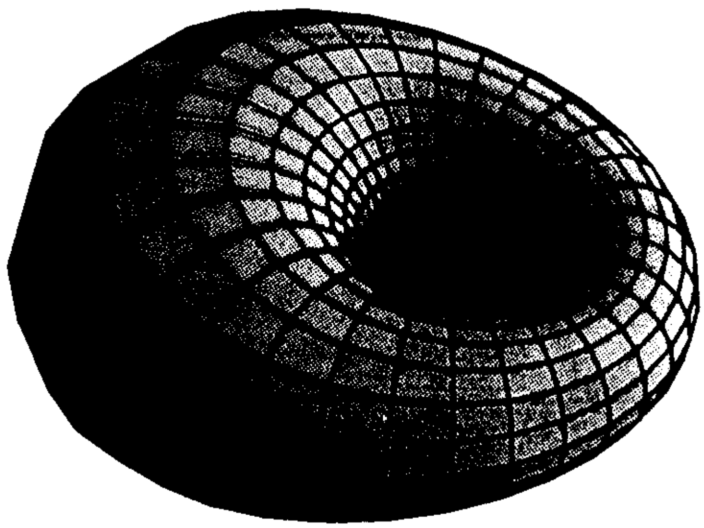
Ou-Yang Zhong-can, Phys. Rev. <u>A41</u>, 4517 (1990)

U. Seifert, Phys. Rev. Lett. <u>66</u>, 2404 (1991)

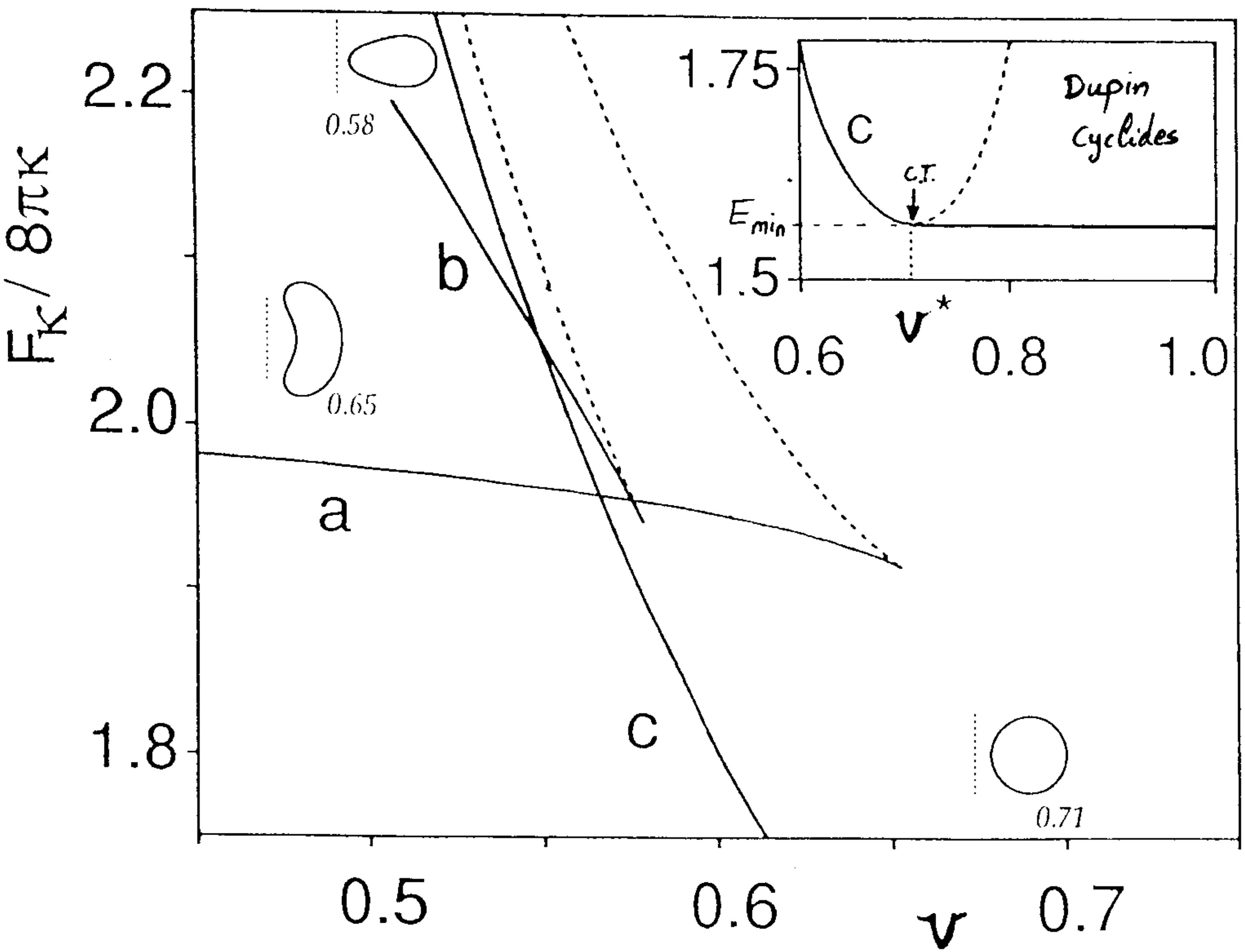
<u>Genus = 2</u>:

F. Jülicher, U. Seifert, R. Lipowsky

torus1



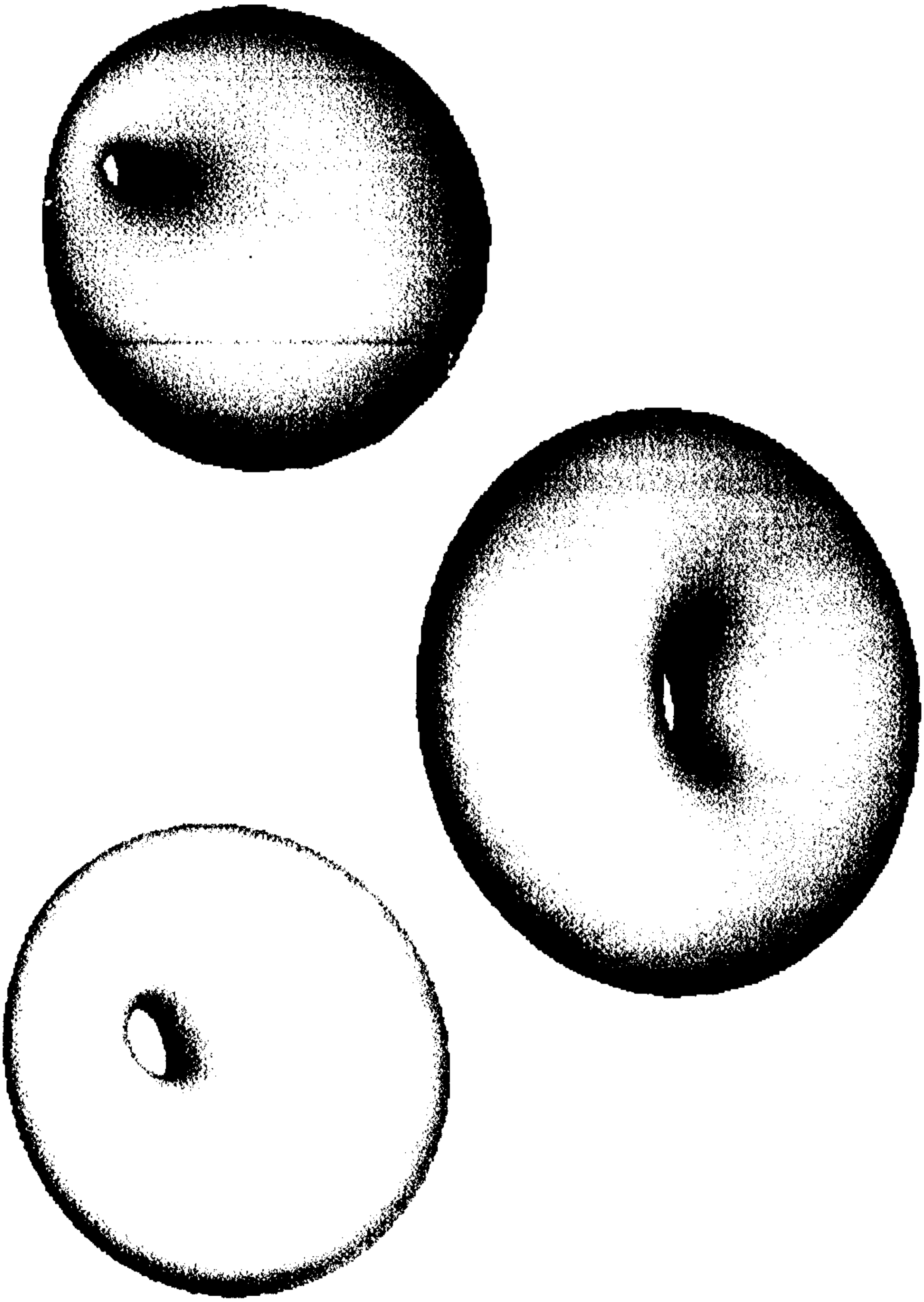
Genus = 1 ($R_0 = 0$.) : U. Seifert. PRL 66, 2404 (1991)

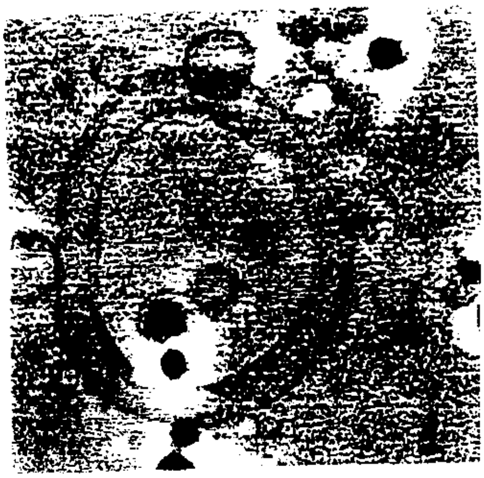


C.T. ≡ Clifford Torus

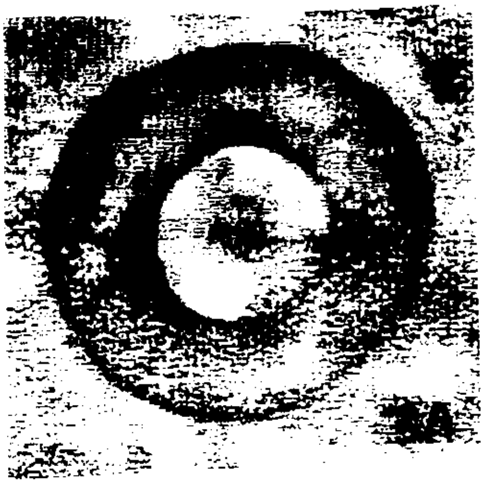
Reduced Volume: $v = \ldots V / S^{3/2}$

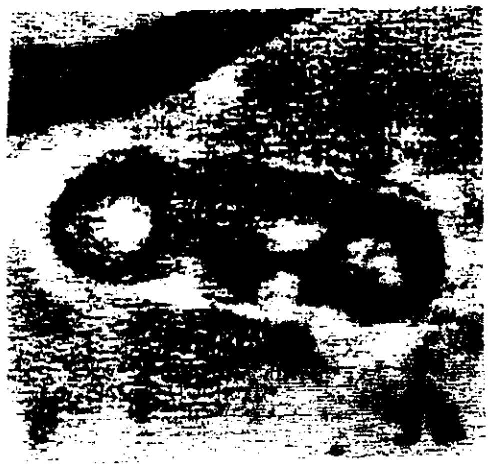
F. Jülicher

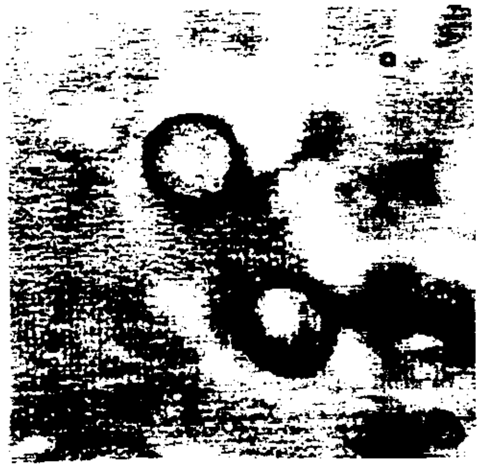


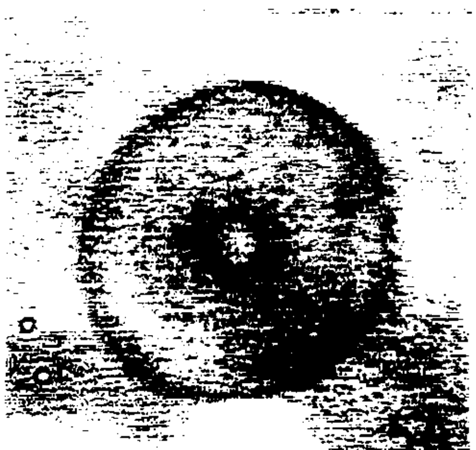

0.21

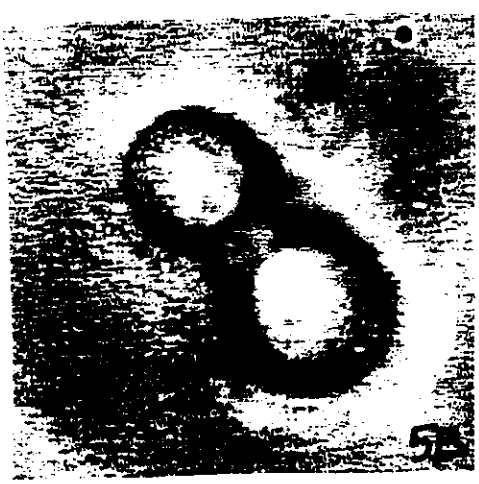

0.34



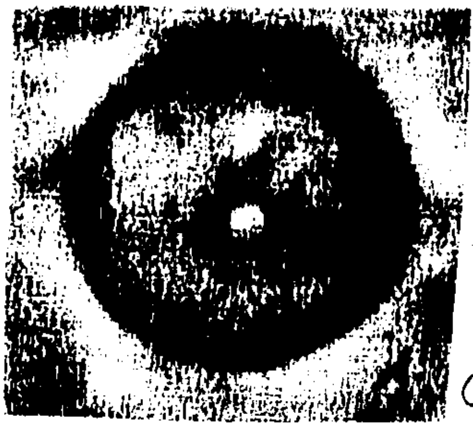

0.51


0.58





0.71



0.76

0.78

3A

3B 0.87

4A

T= 34,5

4B 0.85

T = 24,7 → ?

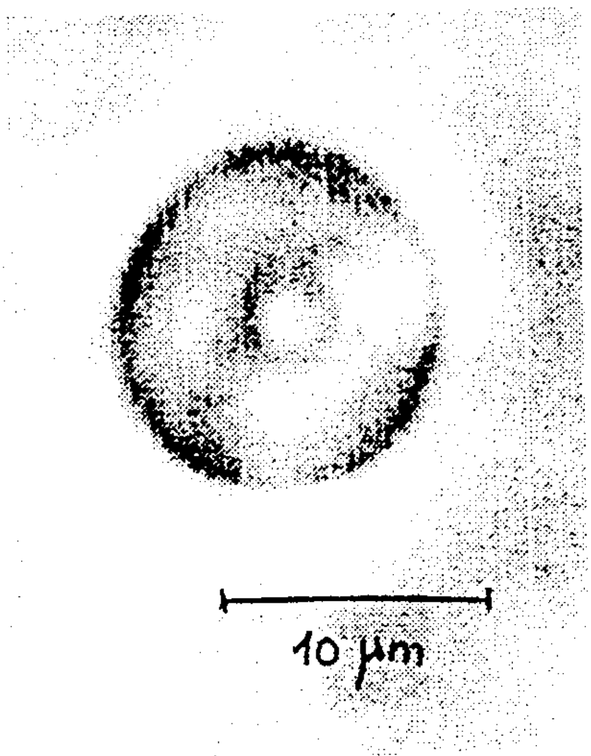
0.92

SHAPES CAN BE CHANGED BY TEMPERATURE VARIATIONS

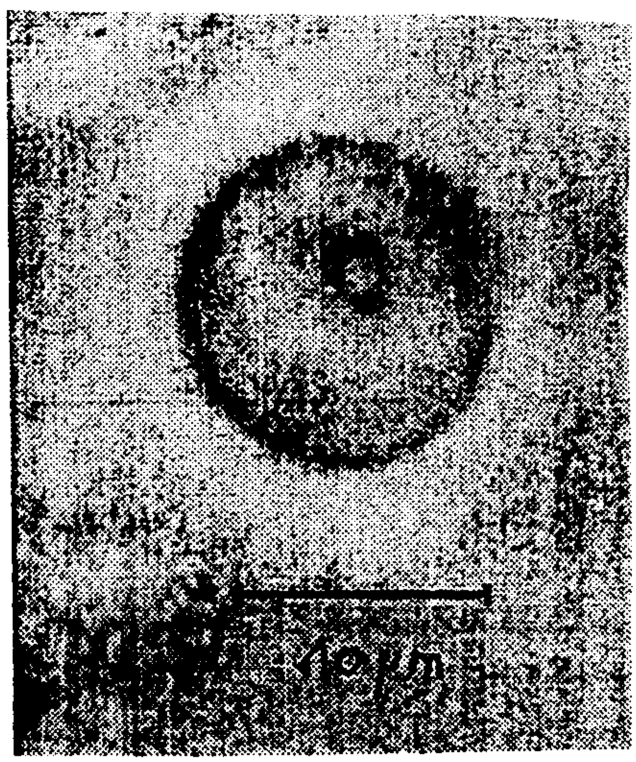
$$v \propto \frac{V}{S^{3/2}} \quad \begin{cases} V = c^{te} \\ \alpha_{lipid} = \dfrac{1}{S}\dfrac{dS}{dT} > 0 \end{cases}$$

v increases when T decreases

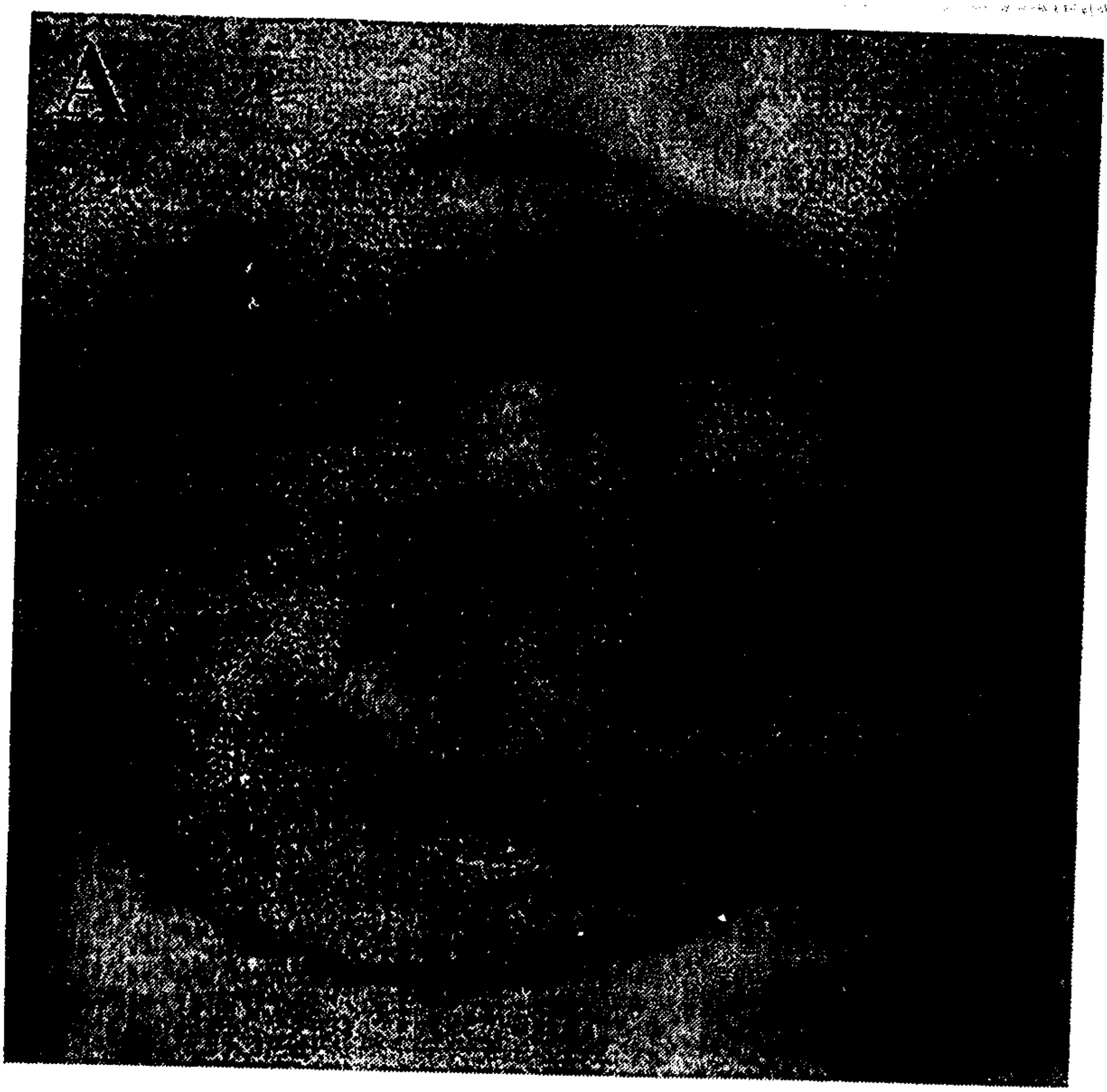
$T = 51.0\ °C \quad \rightleftarrows \quad T = 29.8\ °C$

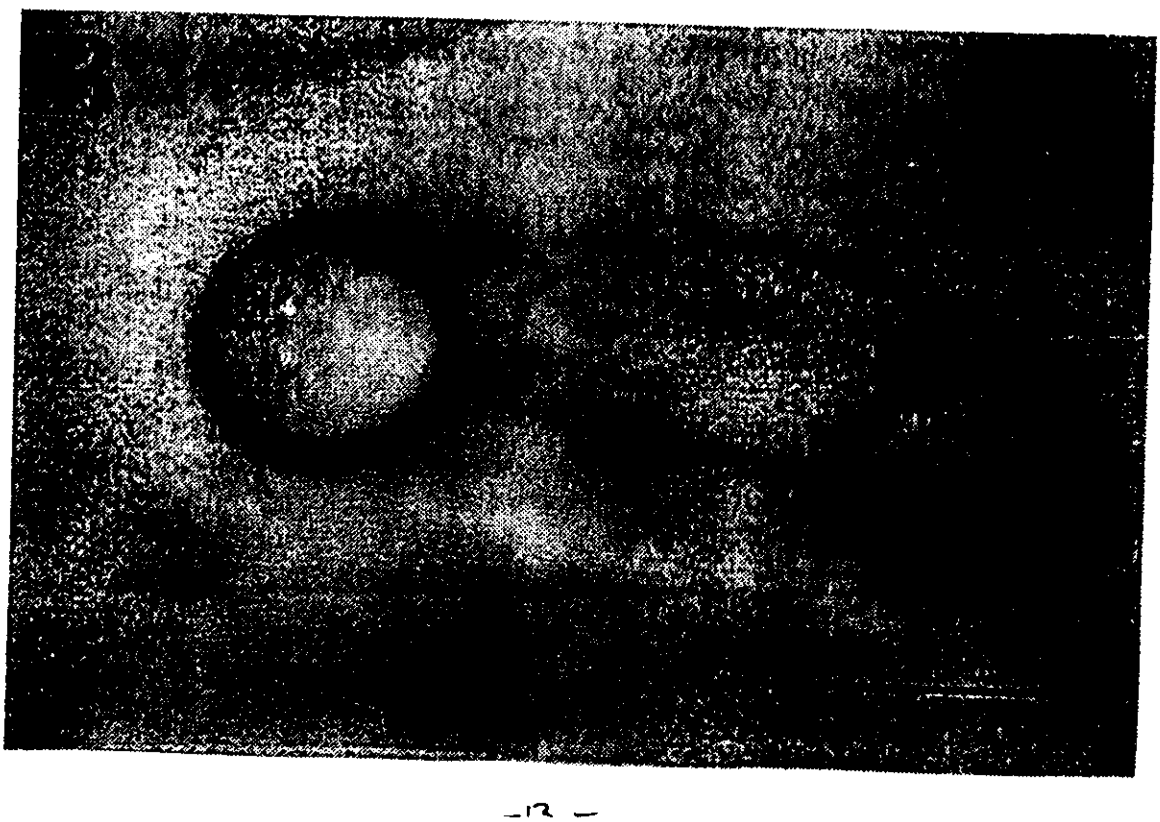


$v = 0.71$

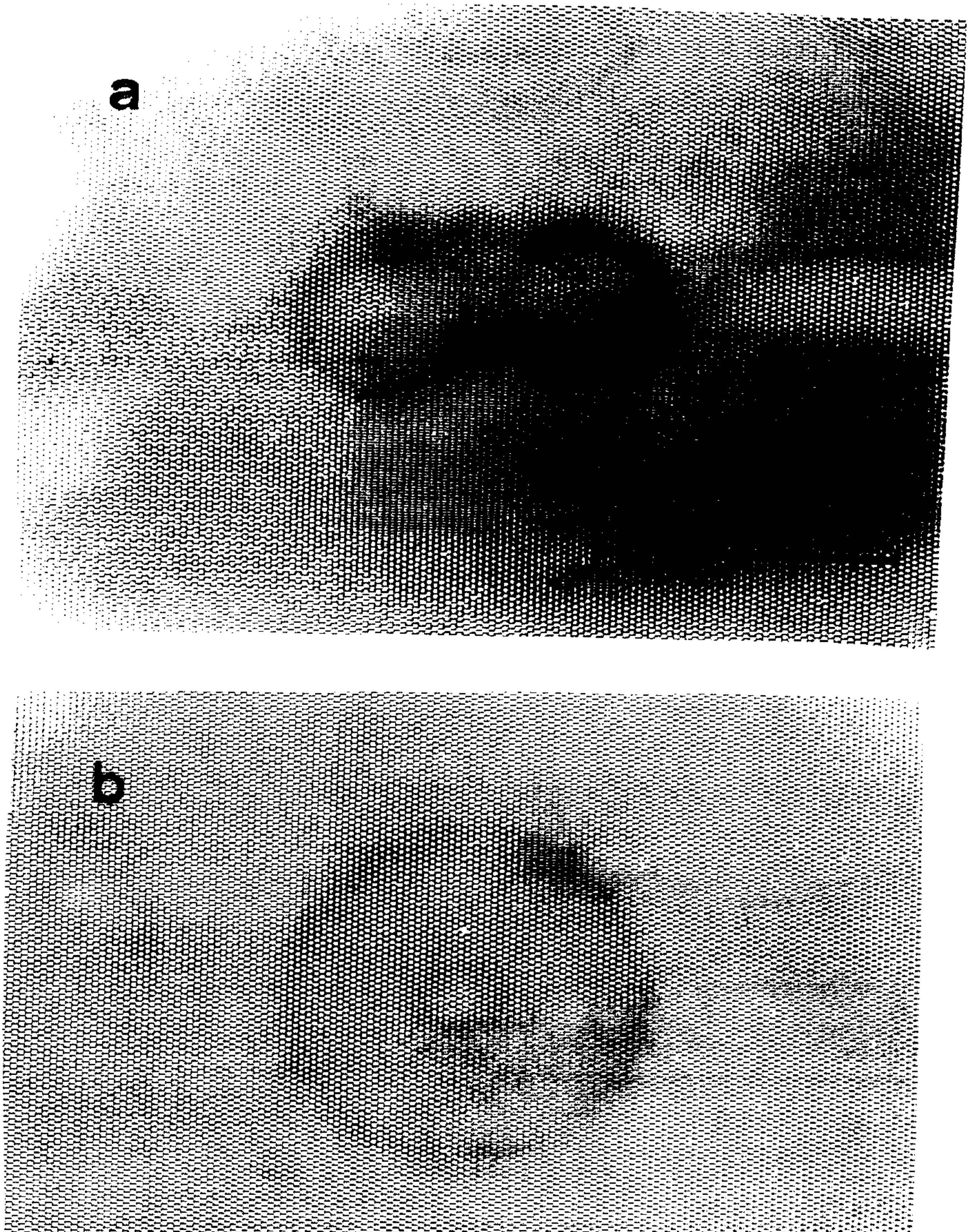


$v = 0.74$

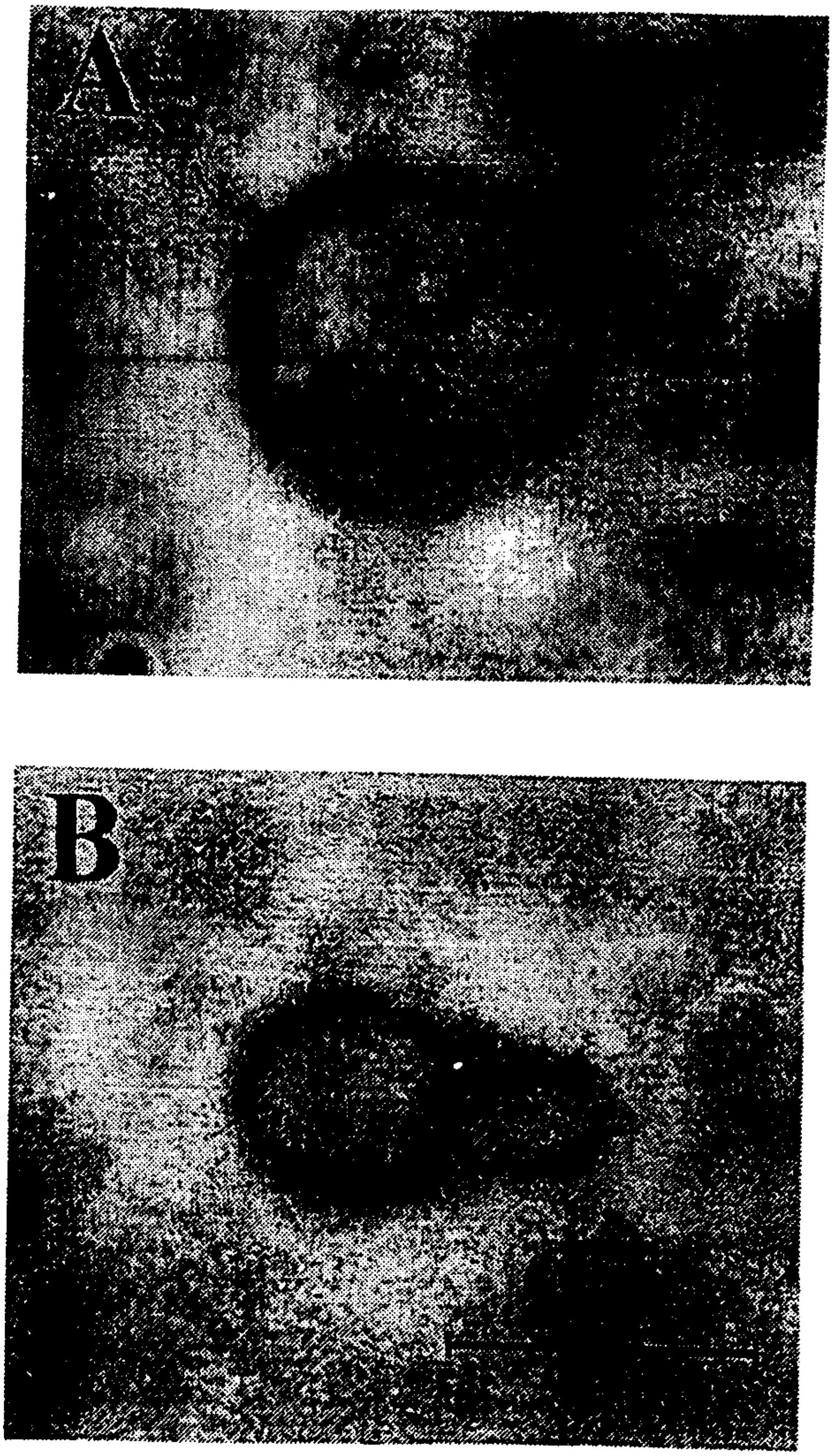

A



Genus = 1. No volume constraint.
⇒ Clifford Torus

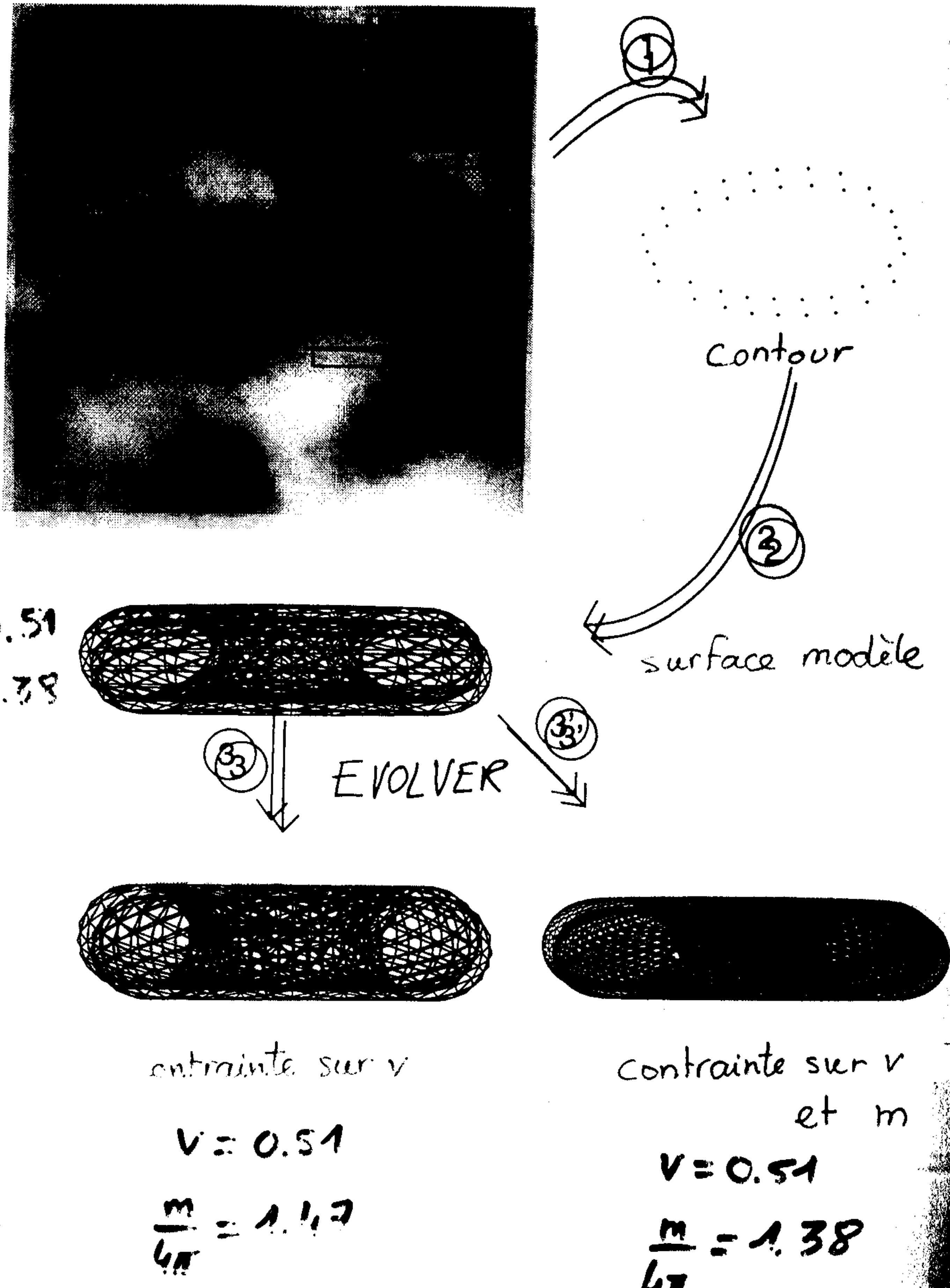


$v = 0.71$

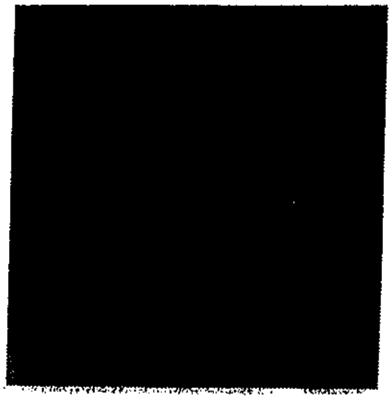


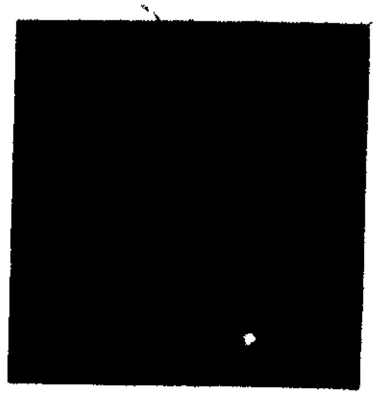
$v = 0.77$

Fig. 2

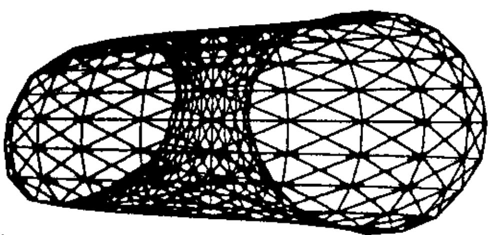

1
contour
2
surface modèle
V = 0.51
$\frac{m}{4\pi}$ = 1.38
3
EVOLVER
3'
contrainte sur v
V = 0.51
$\frac{m}{4\pi}$ = 1.47
contrainte sur v et m
V = 0.51
$\frac{m}{4\pi}$ = 1.38

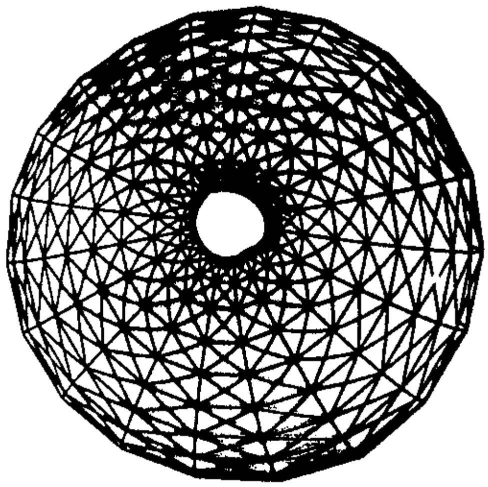
EXEMPLE NON PRÉDIT ...





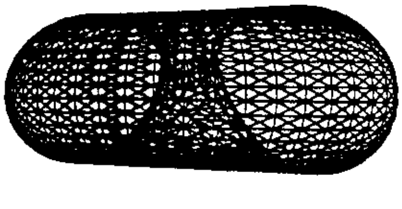
observation

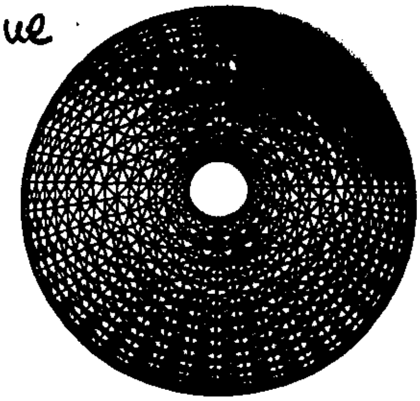




approximation

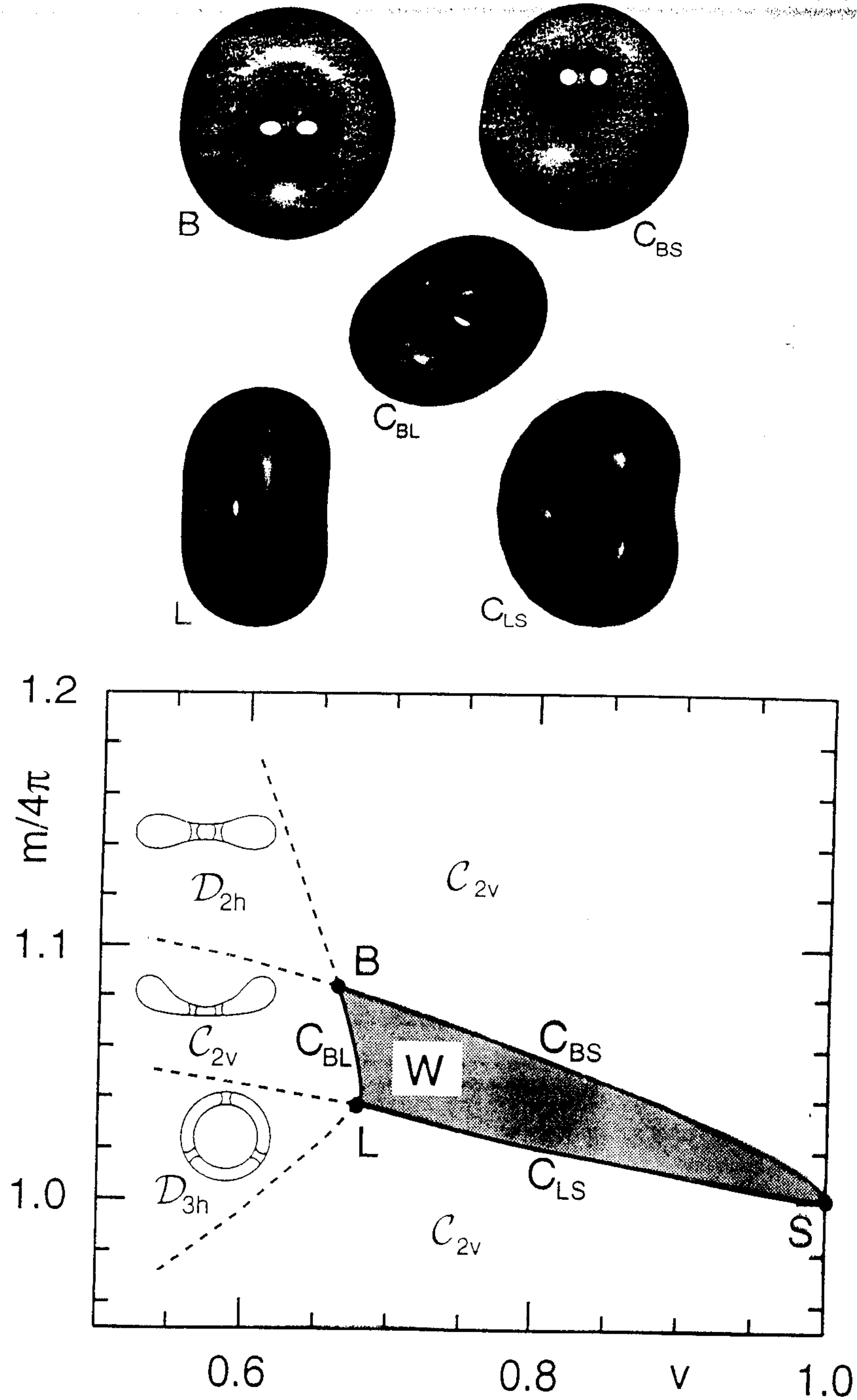
Évolution Numérique





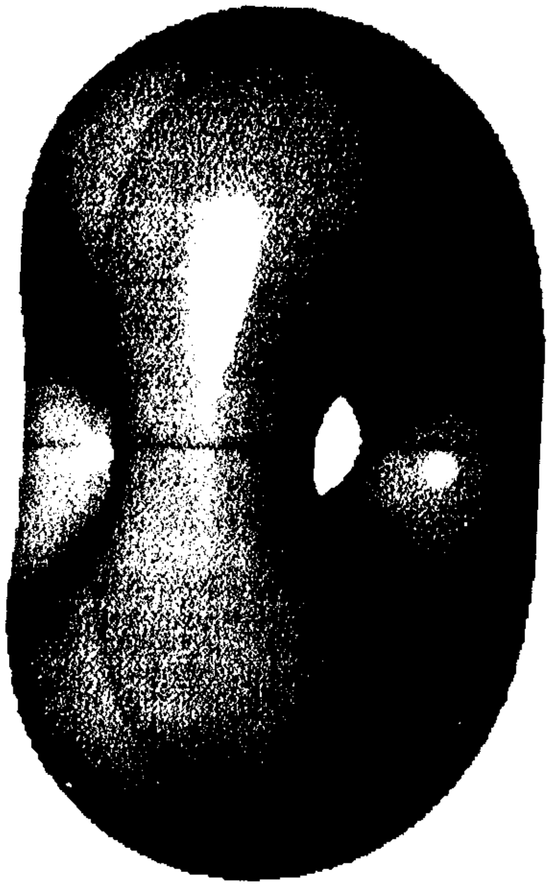
surface équilibrée numériquement

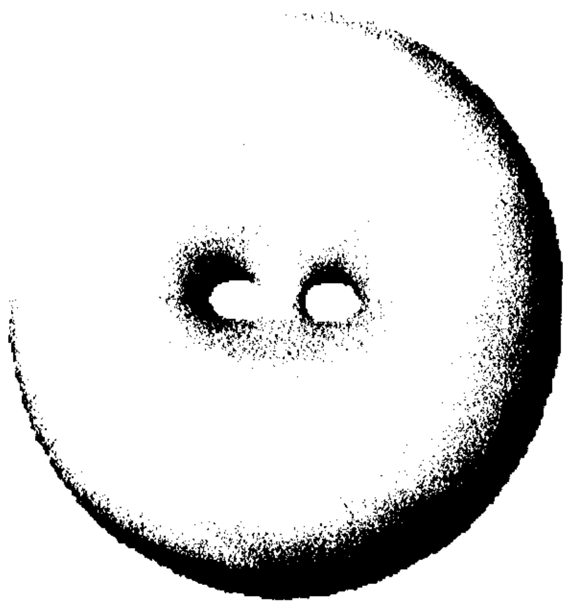
... MAIS COMPATIBLE !

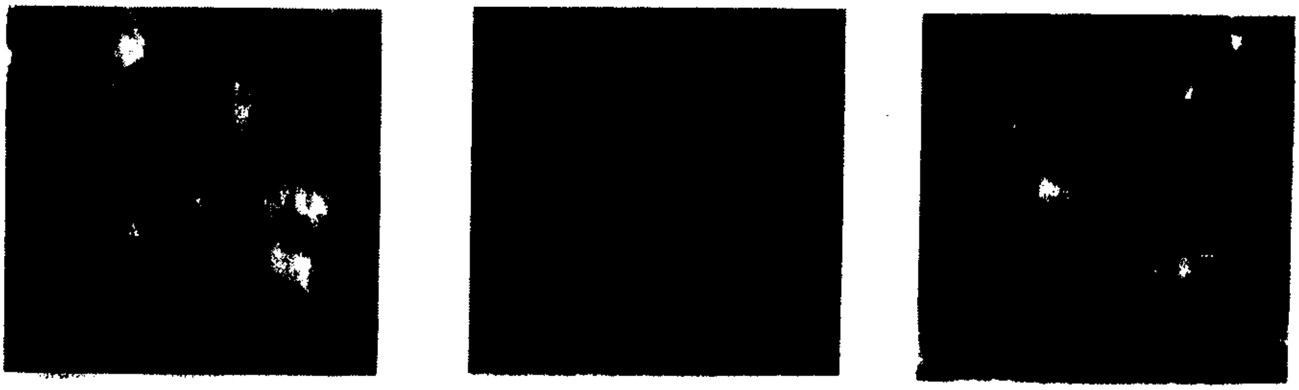


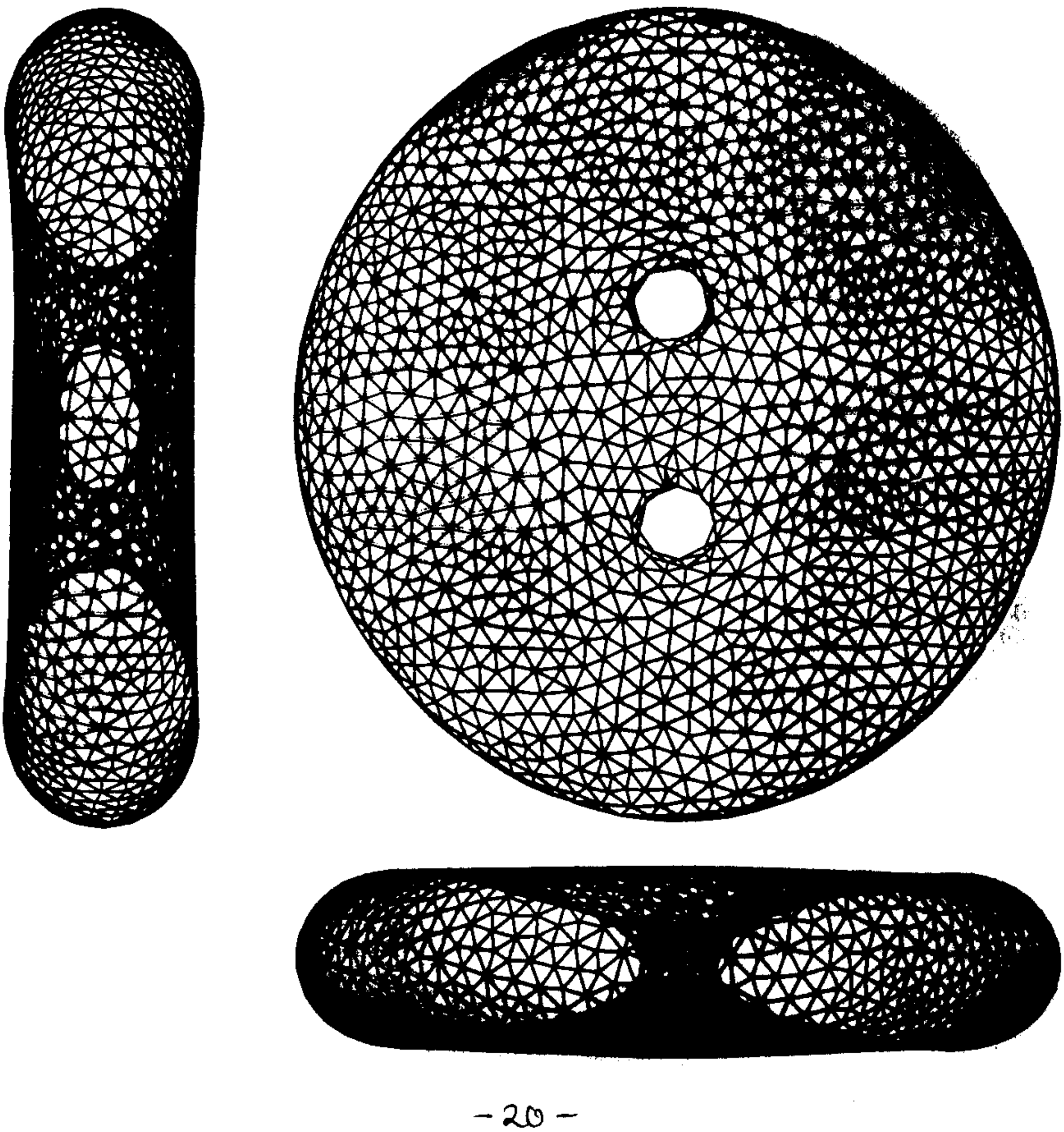
LIPONSKY'S GROUP IN JÜLICH

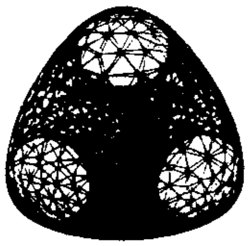
F. Julicher, U. Seifert & R. Lipowsky

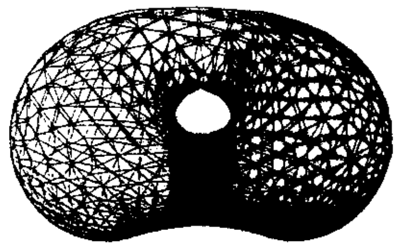


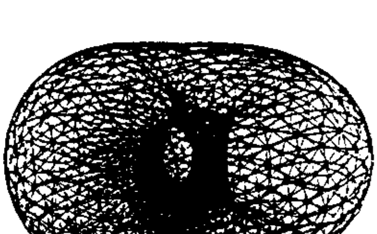


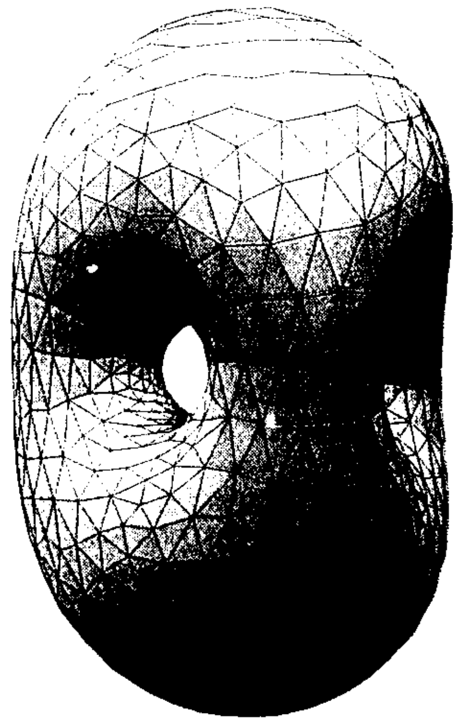




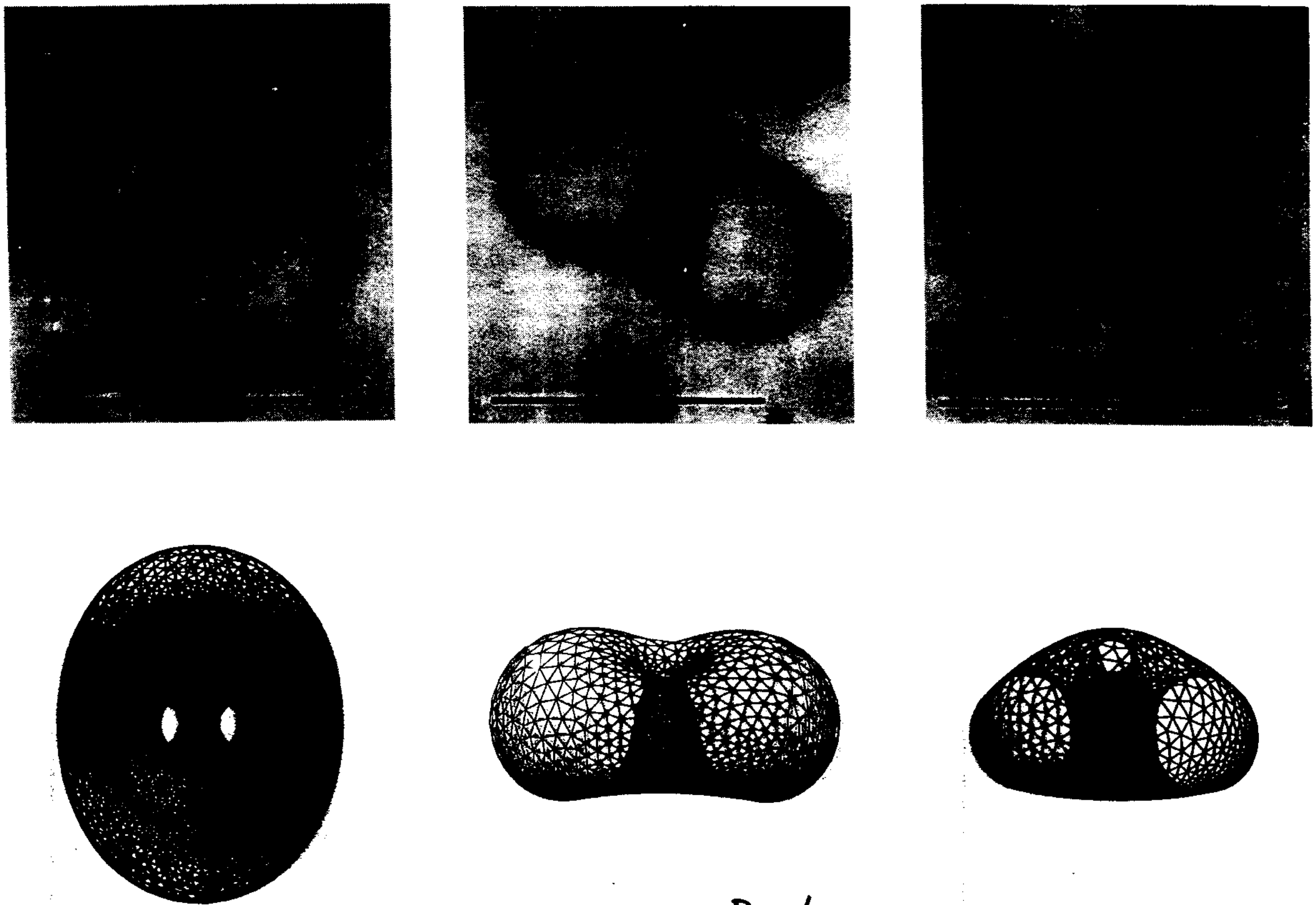






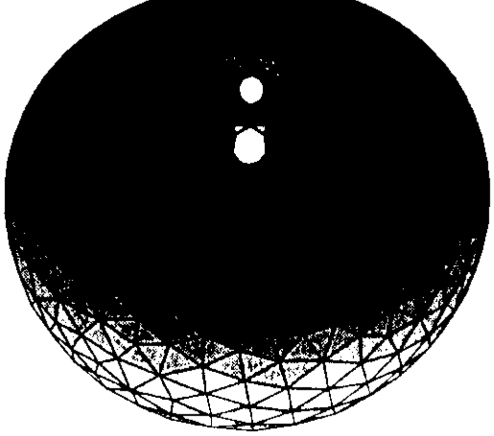


L



Type B-L

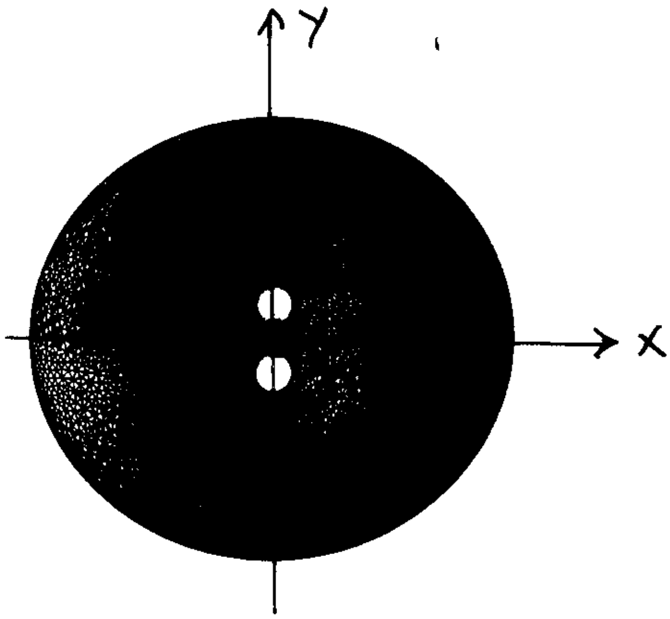
INVERSION d'une surface de genre 2 :

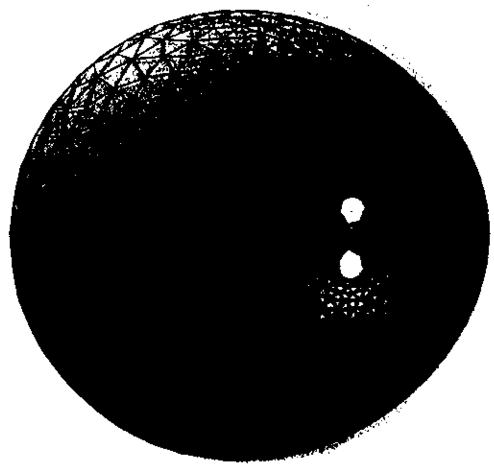


y

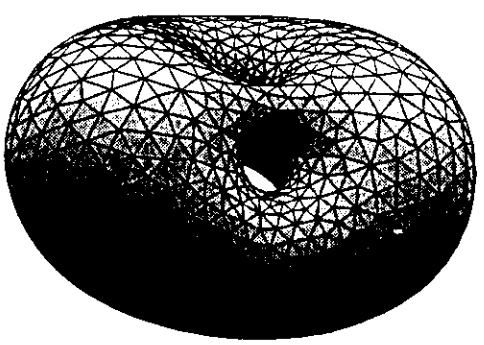
$\boxed{\text{3 paramètres}}$

pour obtenir une surface de même énergie de courbure



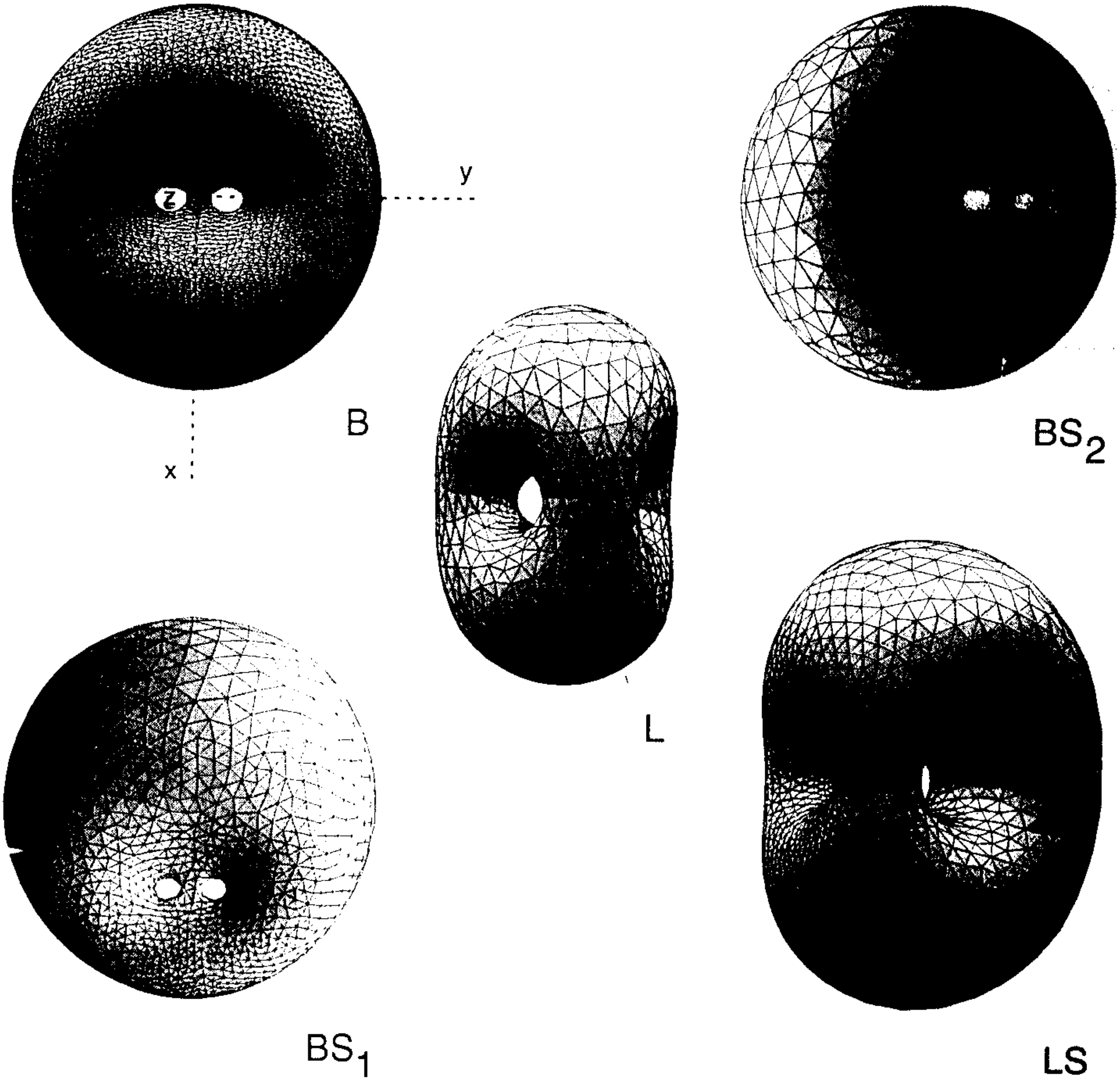


x

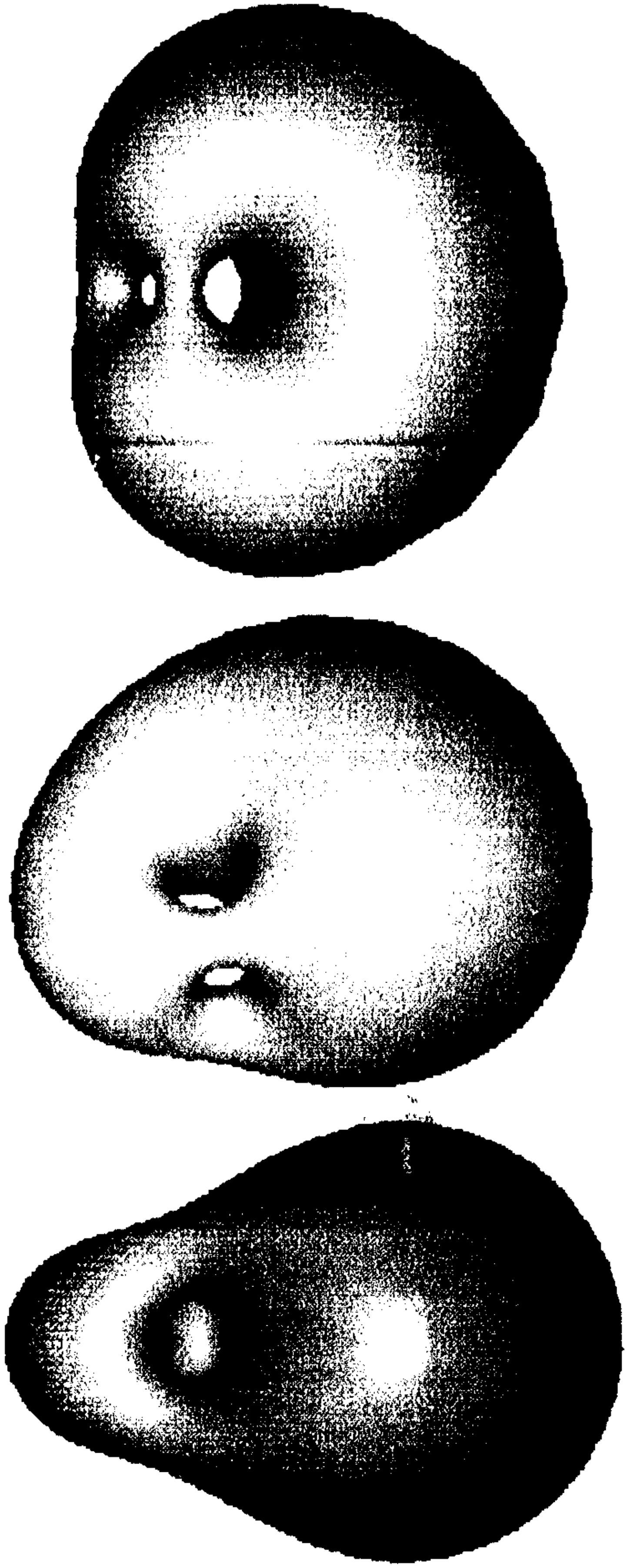


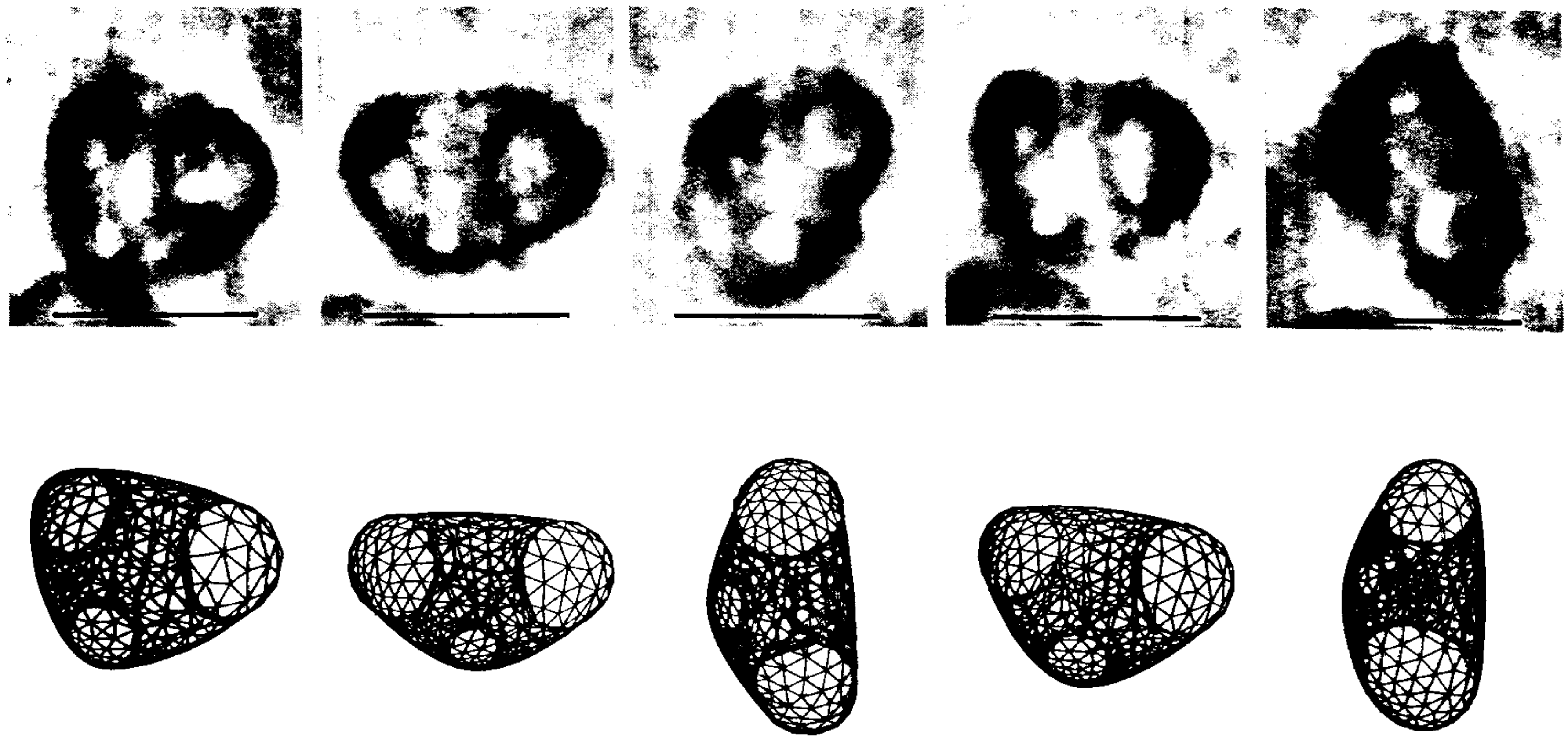
z

$\boxed{v + m = 2 \text{ contraintes}}$


y
z
x
B
BS_2
L
BS_1
LS

F. Jülicher





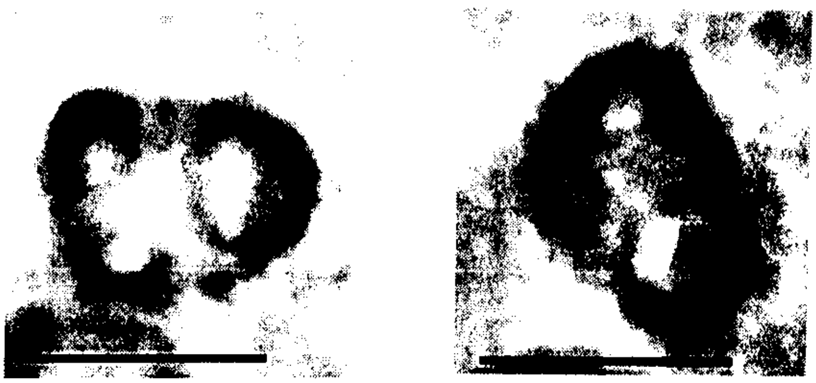
diffusion conforme $\quad (\Delta t \sim 20$ secondes$)$

= état d'équilibre dégénéré

Diffusion conforme
(temps caractéristique)

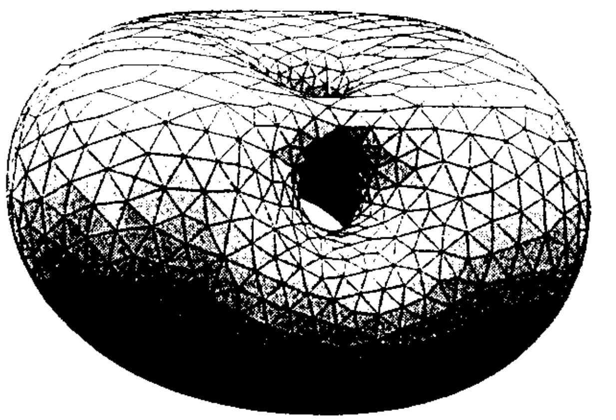
B A

10 μm

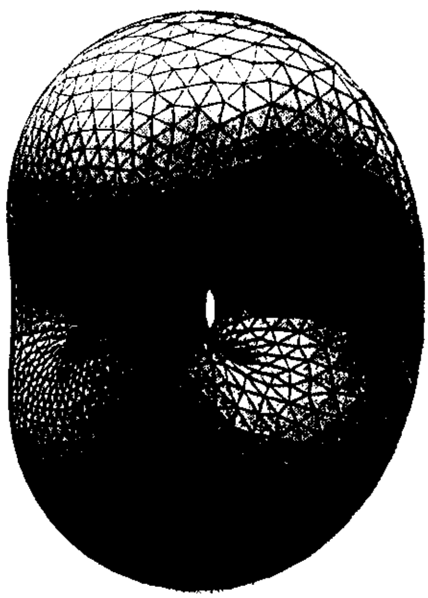


B

$\Delta t \sim 20\,s$



A

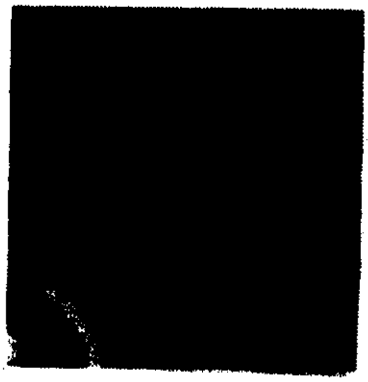


B

$\Delta t \sim 15\text{-}30$ sec

(a)

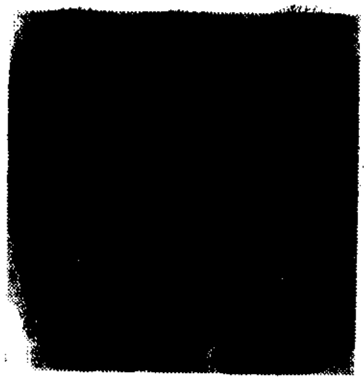
(b)



(c)

(d)

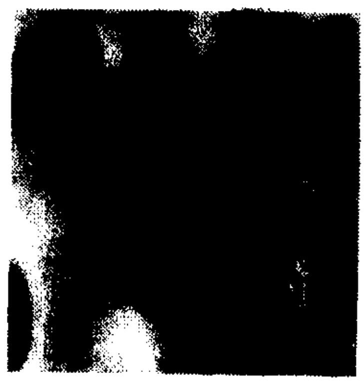
(e)



(f)

(g)

(h)

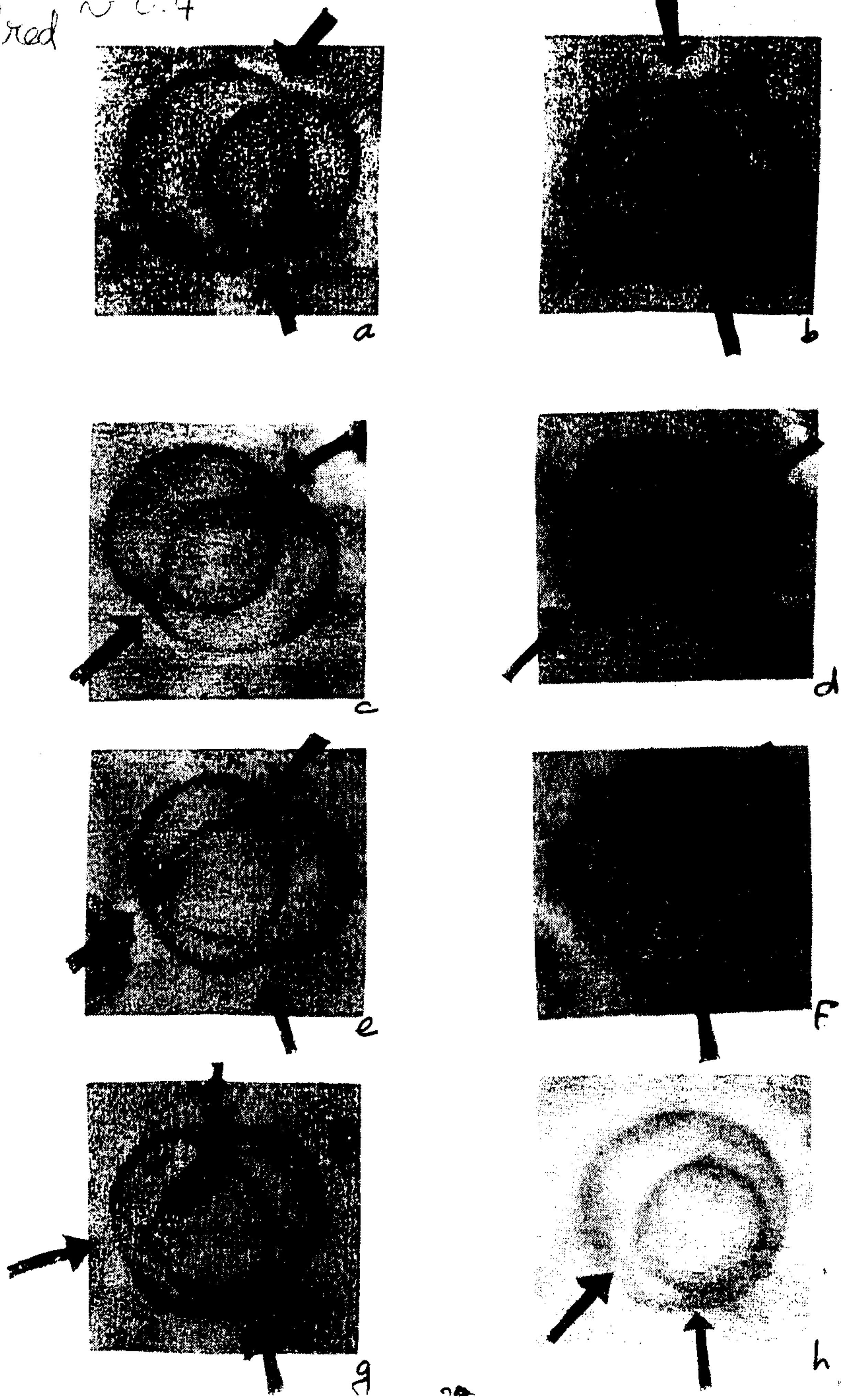


(i)

INTERNAL PINNING ALSO EXISTS

FOR HIGHER GENUS. Here $g = 3$

$\nu_{red} \sim 0.4$



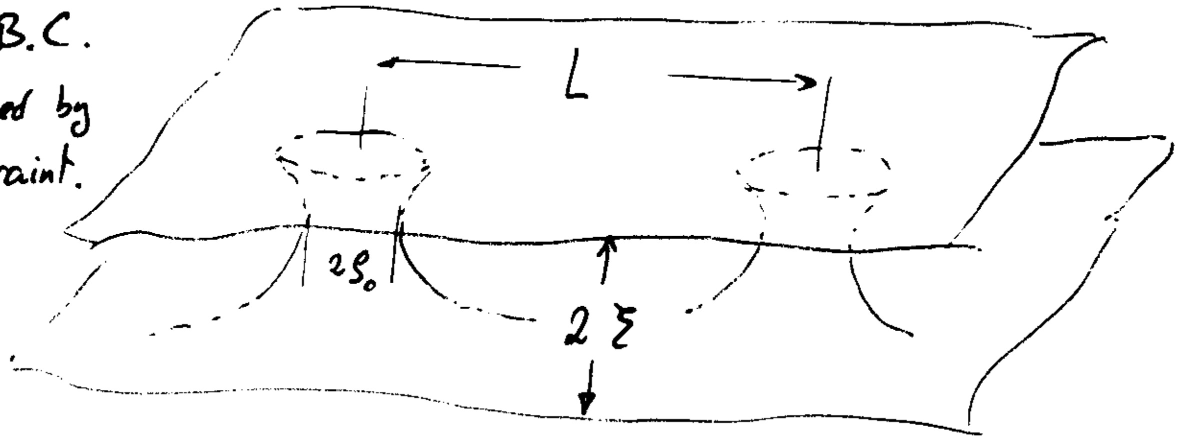
Interaction between topological "defects"

<u>Problem</u>: What is the interaction energy of two necks between membranes?

Periodic B.C.

, determined by

,lume constraint.



Inner region: $\varrho_0 < r \ll L$

Minimization of $\mathcal{H}$ yields: $\quad \xi_{in}(r) = \pm \varrho_0 \cosh^{-1}(r/\varrho_0)$

(catenoid)

$$\xi_{in}(r) = \pm \varrho_0 \cosh^{-1}(r/\varrho_0) \xrightarrow{r \gg \varrho_0} \varrho_0 \ln r$$

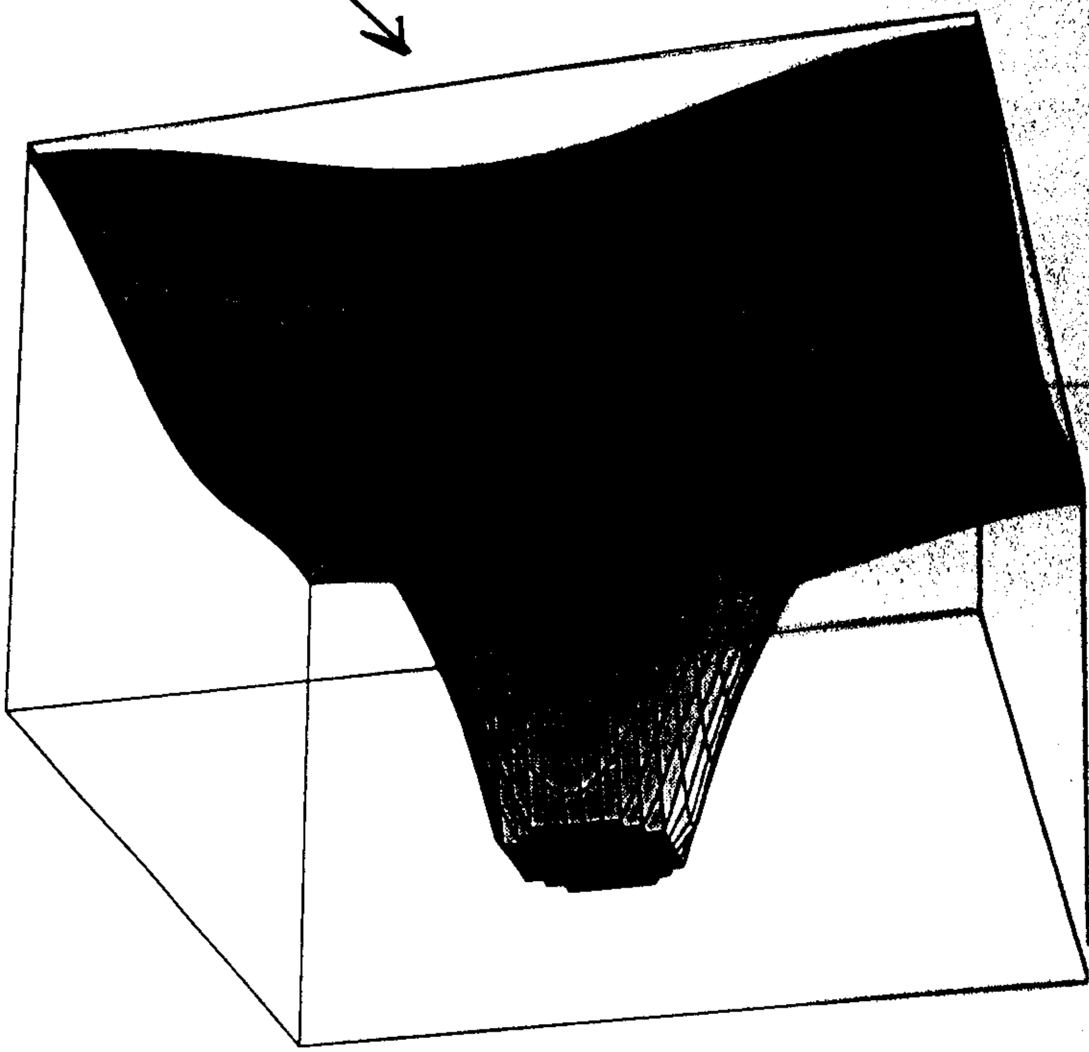
Outer region: $\varrho_0 \ll r < L$

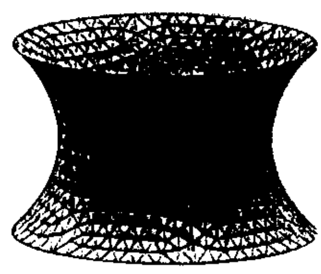
$$\frac{1}{R_1} + \frac{1}{R_2} \approx \nabla^2 \xi_{out}$$

Minimization of $\mathcal{H}$ yields:

$$\nabla^2 \xi_{out} = \text{const.} = 2\pi \varrho_0 / L^2$$

OUTER SOLUTION: ELECTROSTATIC POTENTIAL





INNER SOLUTION: CATENOÏD

$$\xi_{out} = \mathrm{Re}\left[\rho_0 \log \prod_{m=0}^{\infty} \left[1 + \frac{\sin^2 \pi z}{sh^2 \pi (m+1/2)} \right] \right] - \pi \rho_0 y^2$$

with: $z = \dfrac{x+iy}{L}$.

$\big\downarrow \quad |z - \frac{i}{2}| = r \ll 1$

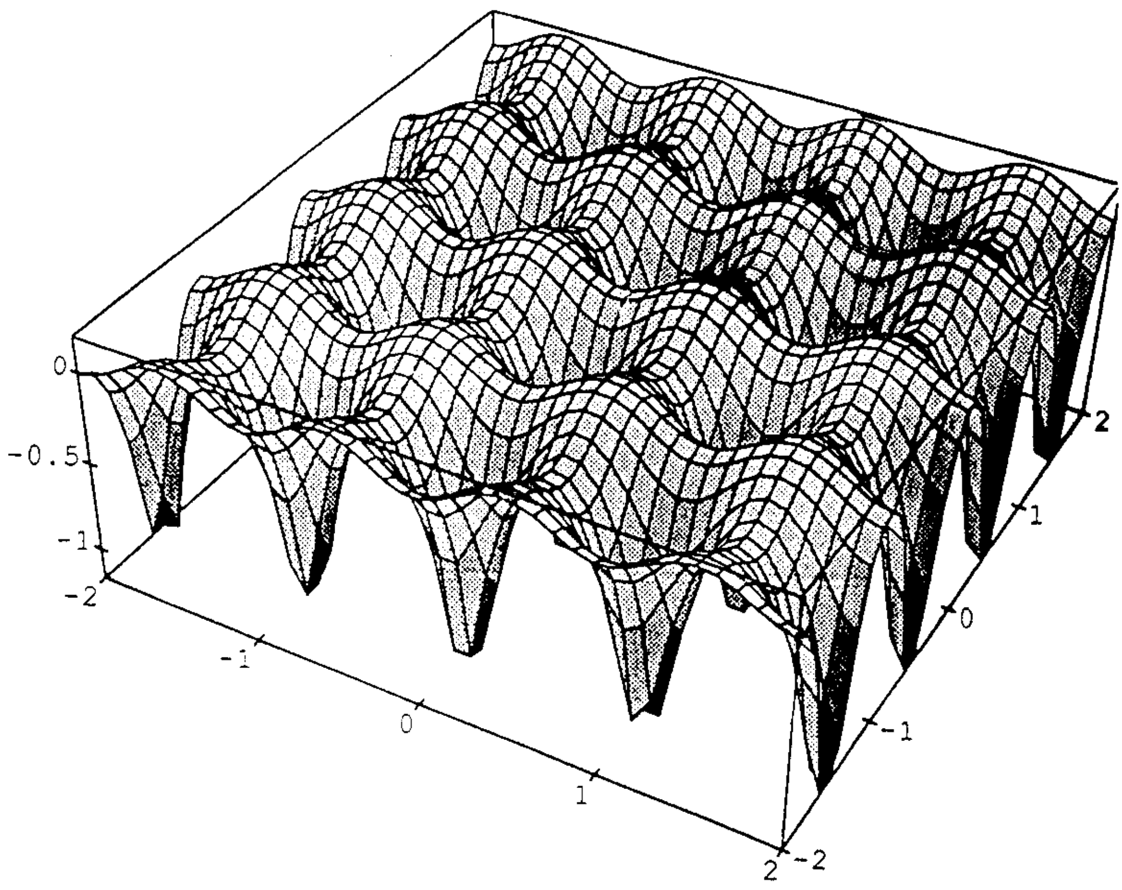
$\rho_0 \ln r \Rightarrow$ matches with $\xi_{in}(r)$.

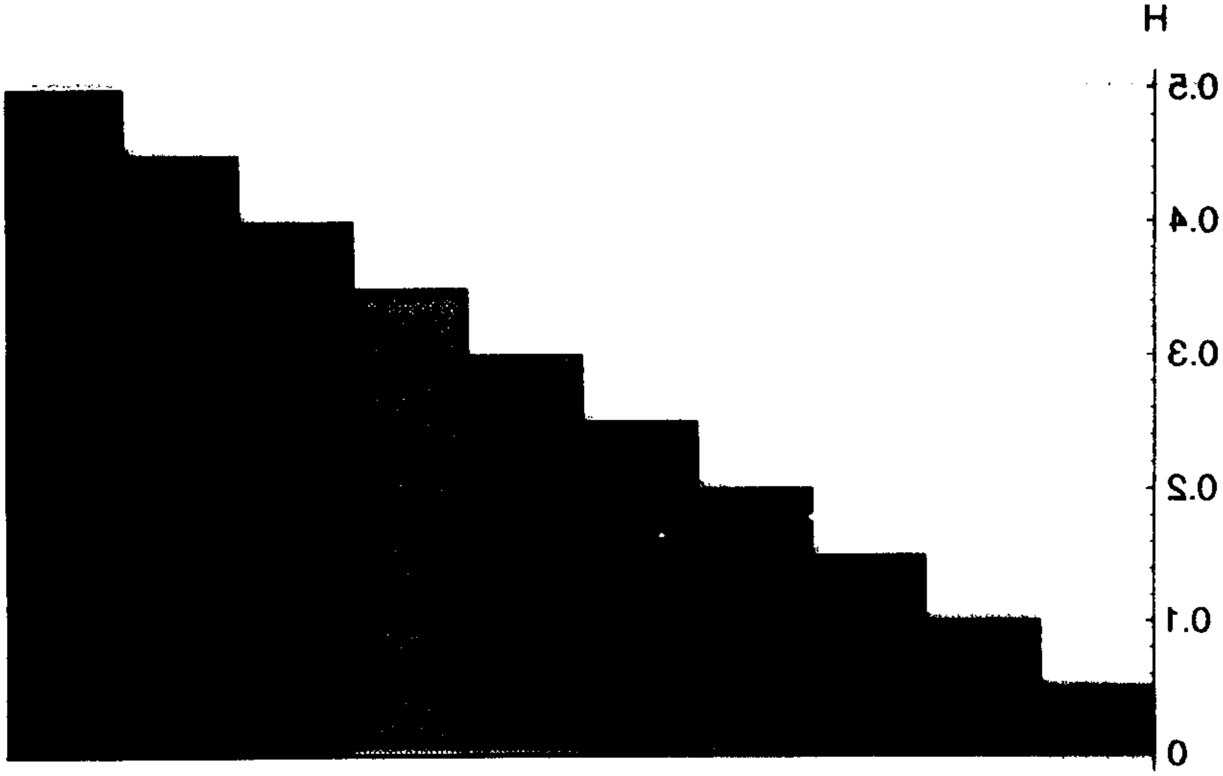
$$\Longrightarrow \quad \mathcal{H} \sim K \left(\frac{\rho_0}{L} \right)^2$$

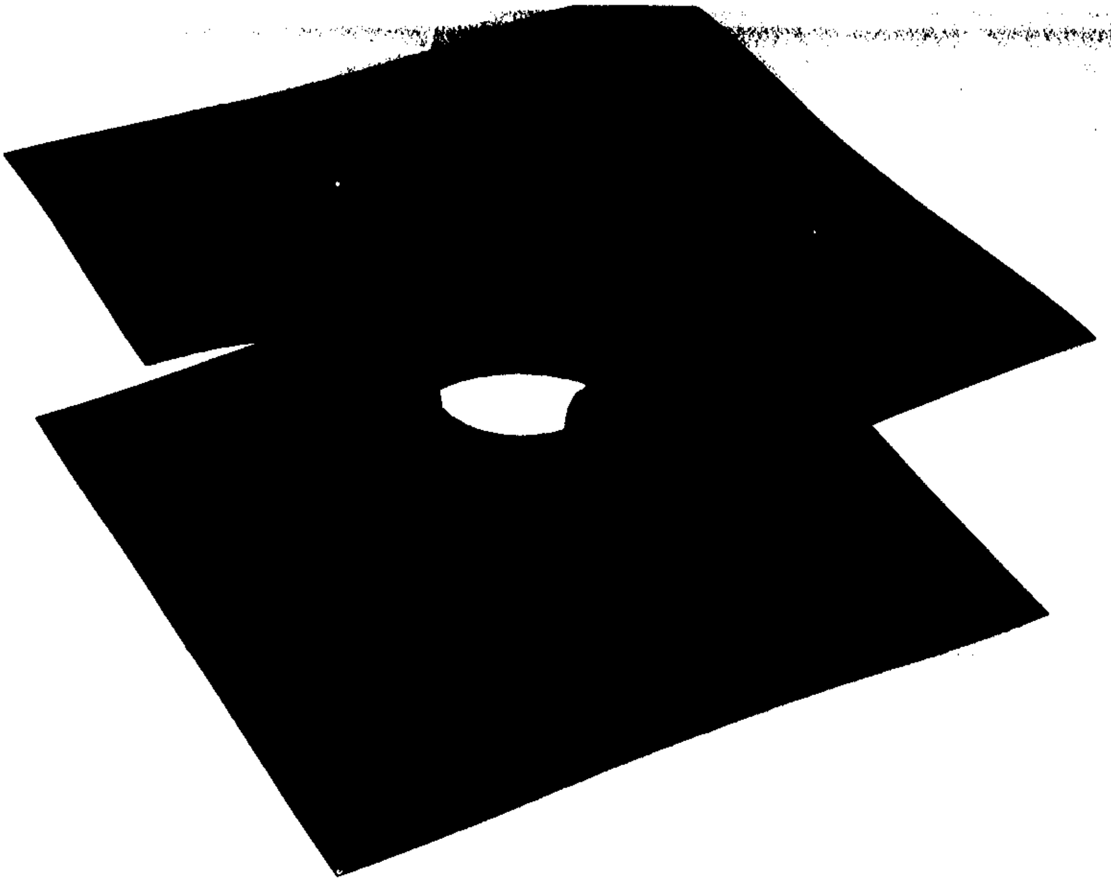
Also from dimensional analysis:

$$\mathcal{H} \sim K \int dx^2 \cdot (\nabla^2 \xi)^2 \sim K \cdot L^2 \cdot \frac{\rho_0^2}{L^4} \sim K \left(\frac{\rho_0}{L} \right)^2$$

Since ρ_0 ... expect big fluctuations.



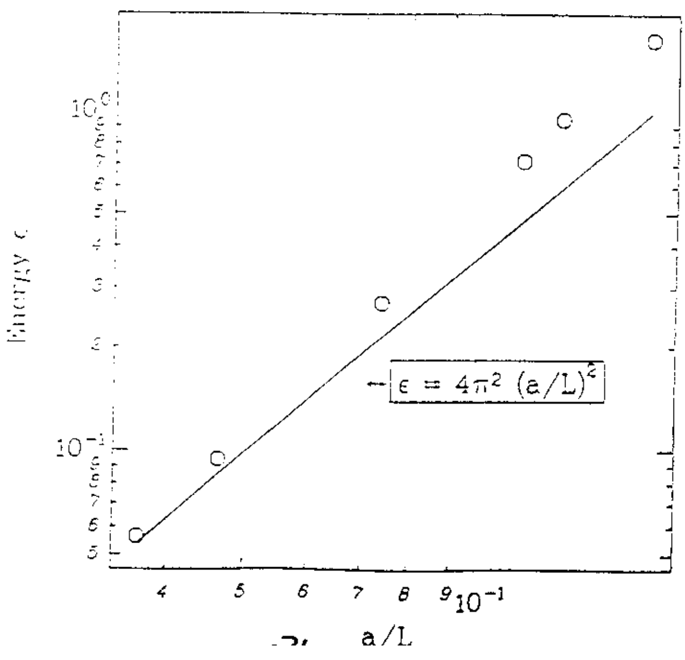

H
0.5
0.4
0.3
0.2
0.1
0



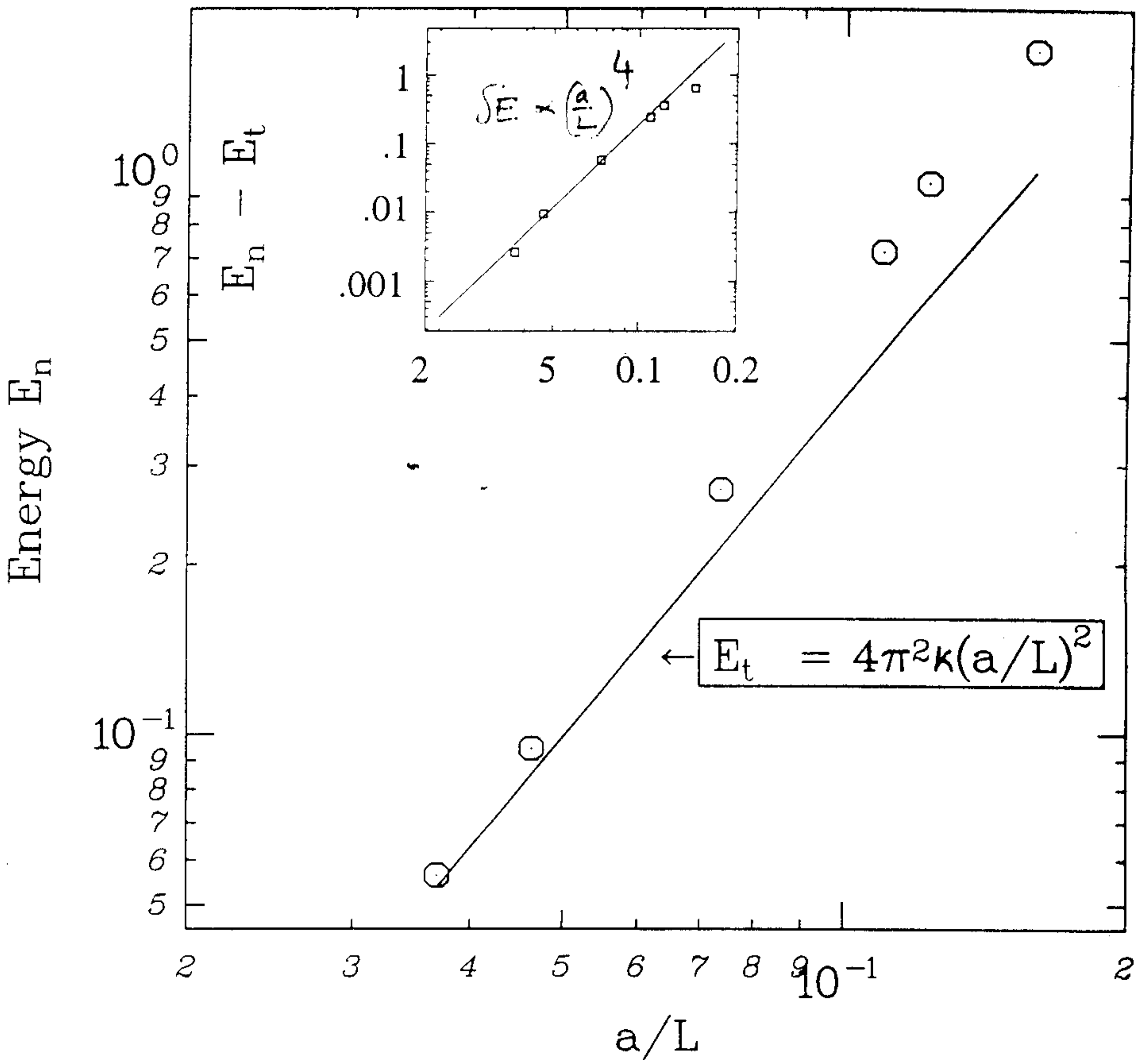
$\frac{a}{L} = 0.11$

$H_{out} = 0.41$

Elastic Energy



a/L



λM, B. FOURCADE (○), D. BENSIMON

For N necks solution is similar as long as their inner regions do not overlap (superposition princ.)

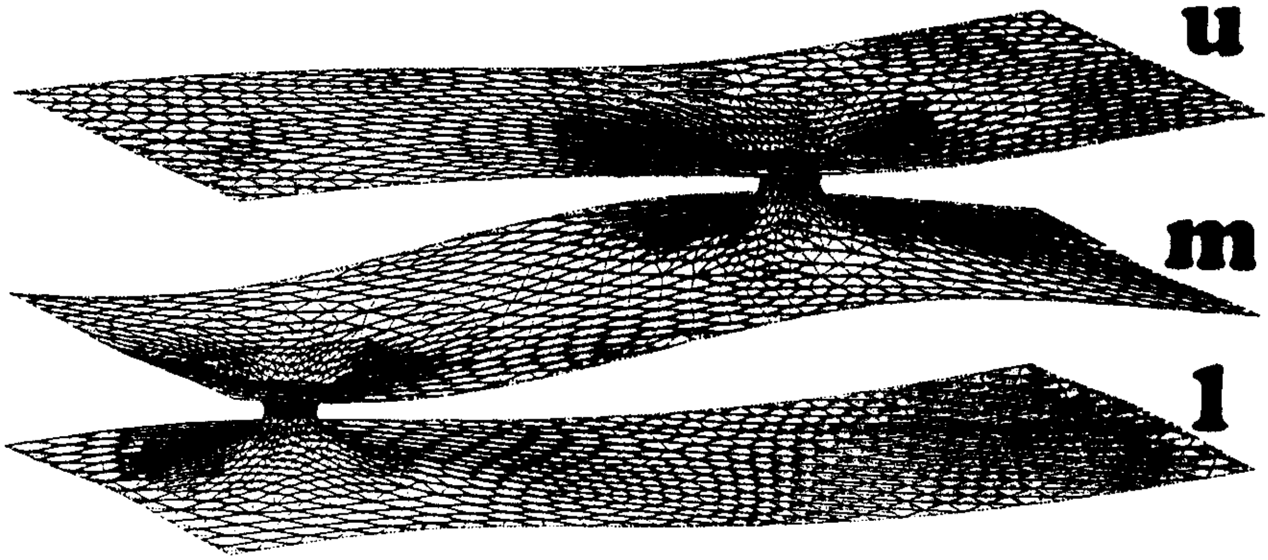
As the inner regions of two necks overlap inner problem is <u>not</u> solved by a minimal surface $\left(\frac{1}{R_1} + \frac{1}{R_2} \neq 0 \right)$.

therefore the energy increases $\longrightarrow$ the necks repell.

The necks behave as a gas of free particles with a hard core repulsion.

There might however exist bound states of three necks (or more) between stacks (of $M \geq 3$) membranes (Costa surfaces).

The necks repell.



"Costa Surface": Bound state of three necks.