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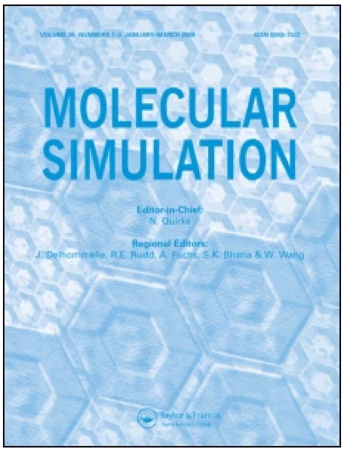

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Simulations of Flexible Manifolds

J. -S. Ho[a][b]; A. Baumgärtner[a]
[a] Höchstleistungsrechenzentrum and Institut für Festkörperforschung, Jülich, Germany [b] IBM Kingston, New York, USA

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SIMULATIONS OF FLEXIBLE MANIFOLDS

J.-S. HO* and A. BAUMGÄRTNER

Höchstleistungsrechenzentrum and Institut für Festkörperforschung, Forschungszentrun Jülich, D-W-5170 Jülich, Germany

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Monte Carlo simulations of flexible two-dimensional model membranes embedded in three space dimensions are reported. We explain in detail the techniques how to simulate fluid open membranes and fluid closed membranes (vesicles). It is shown that *polymerized* open membranes are rough and flat. Accordingly, the two larger components of the inertia tensor are proportional to the number of monomers of the surface, $\lambda_3 \approx \lambda_2 \sim N$, whereas the smallest $\lambda_1 \sim N^{0.65}$. Polymerized vesicles are isotropic and their mean square radius of gyration is $R^2 \sim \lambda_k \sim N$. In contrast, fluid membranes and vesicles exhibit crumpled shapes with $\lambda_k \sim N^{0.8}$ for $k = 1,2,3$. A monomer on a fluid surface exhibits a time-dependent mean squared displacement of $r^2(t) \sim t^{0.8}$.

KEY WORDS: Fluids, membranes, Monte Carlo

1 INTRODUCTION

Fluid isotropic membranes [1,2] and polymerized membranes [3,4] have been predicted to exhibit a high temperature crumpled phase. In fact, for *polymerized* self-avoiding membranes renormalization-group arguments [5,6,7] and the first pioneering Monte Carlo simulations [8] seemed to be supporting evidence for a high temperature crumpled phase, whereas subsequent extensive molecular dynamics [9] and Monte Carlo simulations [10,11,12] have questioned the "crumpling" idea. Simulations of molecular models of *fluid* membranes have not yet been undertaken.

In the present work we report on Monte carlo studies of a novel model membrane which has properties like *fluid* membranes. There the configurational arrangement of the constituents of the membrane, called monomers, represent a distorted two dimensional surface in three space dimensions on which the monomers should be able to diffuse freely among each other. Most of the membranes known in life sciences are fluid and hence investigations on their configurational properties are of great importance. In addition, the present investigations are the first which deal with a molecular model of fluid self-avoiding vesicles, i.e. closed membranes.

Our intention is to demonstrate the suitability of the fluid membrane model by its high temperature configurational and dynamical properties in order to provide a sound basic model for future investigations on the thermodynamics of open membranes and vesicles. As one of the main results, we are able to show that fluid surfaces exhibit a crumpled phase in contrast to polymerized surfaces.

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*Present address: IBM Kingston, New York, USA

2 MODELS AND SIMULATION TECHNIQUES

In this paragraph we describe the models of polymerized and fluid surfaces and the related Monte Carlo techniques. A triangular mesh is used as the simplest approximation of a 2-D membrane in 3-D space. Each grid point on the mesh is connected by bounds with its neighboring points. The length of the bond is confined within a certain range by a square-well potential and the self- avoidance of the membrane is implemented by introducing a hard sphere on each grid point: the diameter of the hard sphere is chosen such that the ratio of the diameter and the maximum bond length disallows the self-penetrating of the membrane, any displacement attempt is rejected if it causes overlaps of hard spheres, thus the model prevents the membrane from self-penetrating. The basic steps of the Monte Carlo simulation of a membrane are the following;

1. Select a grid point randomly or sequentially, displace it to a nearby location which is chosen randomly.
2. Calculate the energy changes δE from the attempt, where δE = energy of the trial configuration - energy of the old configuration.
3. Accept the new location for the grid point with the probability $p = \min(1, \exp(-\delta E/kT))$ then go to step 1. If δE is negative or zero, accept the new location, otherwise, compare the Boltzmann factor with an uniform random number in the interval of (0,1), accept the new location if the latter is smaller, otherwise reject the attempt and keep the old location.

Each Monte Carlo step consists of N such attempts, where N is the total number of the grid points on the mesh. As mentioned above, in the simple model the connectivity or the integrity of the mesh is maintained by imposing a square-well potential on the bonds and the topological character of the membrane is preserved by introducing hard spheres of proper size at the grid points. Any displacement attempt resulting bond breaking or sphere overlaps is rejected at step 3, and the action can be taken at step 2 once any violation on the connectivity or excludedness is detected. In a more elaborate model, one can include several energy contributions into the system Hamiltonian: bending energy associated with the local curvature, stretching energy associated with the surface area, and in the closed membrane case the volume energy associated with the interior-exterior pressure difference. In addition, one can also include some electric charges on the grid points to emulate membrane and vesicle systems occurring in nature.

The Monte Carlo steps described above are sufficient to simulate polymerized membranes and vesicles. However, most membranes and vesicles in biological system are fluid-like, i.e., the constituent molecules can diffuse on the surface of the structure. In order to account for this character of the membrane without going into the detailed relization of surface diffusion mechanism on the molecular level, one must adopt a much simpler and more abstract model suitable for numerical simulation.

With this idea in mind and based on the experience with the model of the polymerized membrane, we have developed a simple model for the fluid-like membranes. A similar model has been developed for studying flexible phantom surfaces (i.e. without self-avoidance) in the context with problems in high energy physics (see e.g. [13]).

One of many important features of a fluid-like structure is that within a reasonable amount of observation time, the fluid particles diffuse significant distances against their background, both the relative distances and the neighboring relations of the

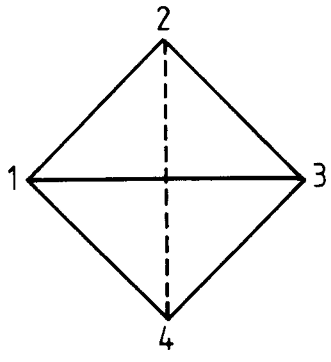

Figure 1 Scheme of triangulation procedure for fluid two-dimensional manifolds in three space dimensions.

particles are changing. In the mesh model for the polymerized membrane, one can view the grid points as the crosslink junctions of a real polymer network and the bonds as polymer segments between them. However from a more abstract point of view, we can just use the mesh to emulate the shape of the membrane and all the detailed structures are absorbed into some effective potentials like hard sphere size, bond length and all other energy parameters. In this picture, all the chemical details are hidden in the model and the grid points and their connections are just used for locating the positions of the membrane and preserving its integrity and topology.

In a polymerized membrane, the connectivity of each grid point is fixed. The diffusion of each point is severly restricted by all its connected neighbors. If we want to use the mesh model to study the fluid membrane, we must relax the restriction on fixed connectivity, thus allow the grid points to exchange their neighbors, and at the same time, preserve the topology and the integrity of the structure. In a triangular mesh, this can be accomplished by following mechanism ("triangulation"):

Select a pair of grid points randomly or sequentially such that they are the respective vertices of two triangles which share the same edge, then perform a bond-exchange step if the following conditions are satisfied (Figure 1):

1. These two points are not directly connected yet.
2. The numbers of direct-connected neighbors of these two points are both less than the maximum allowed number (say, 8).
3. The numbers of direct-connected neighbors of the two vertices of the common edge are both greater than the minimum allowed number (say, 3).
4. The distance between these two points are within the interval of the acceptable bond length.
5. The energy difference caused by the bond-exchange procedure are put into the Boltzmann factor and is in favor of the exchange.

If all these conditions are satistified, the new bond between these two points is created and the bond of the common edge of the two triangles is removed. In this bond-exchange procedure, the total numbers of bonds and triangles are preserved, so is the 2-D topology of the membrane which is the essential of the structure. The advantage of this simple procedure is its locality, only the local connections are rearranged and the cumulative effects of the bond-exchange and grid point displacement allow the grid points to have more freedom to more in space, not just a restricted diffusion in 3-D as in the case of fixed-connected mesh but also in the 2-D surface itself. In fact, within certain number of steps, each grid point would have the opportunity of being connected with any other point and this resembles the fluidity of the system.

The detailed implementation of this procedure has some influence on its effectiveness and should be studied thoroughly before launching a series of simulations. One can go through all grid points to check the candidates for bond-exchange, or go through some of them only, either at random or sequentially. Each point during one sweep is allowed to have one bond-exchange or many, the displacement attempt and the bond-exchange attempt are performed alternatively or to have separate phases during each Monte Carlo step, ..., etc..

The efficiency of the simulation program can be enhanced by using a proper data structure. In our study, we use a simple two dimensional array $NV1$ (I,J) to store the labels of points which are connected to point J, I is from 1 to NA (J), where NA (J) is the number of conneced neighbors of J. The point labels in array $NV1$ are stored counterclockwise so that the sequence in index I reflects the spatial relations of the points connected to point J. This array facilitates the bond-exchange procedure considerably: the procedure corresponds to one insertion or deletion of one entry on each of the four lists involved. In addition, array $NV1$ is needed to check the connectivity of the membrane and the order of the list also makes the area and volume (in 3-D vesicle case) calculation a easy task.

The procedures described above can be used to study both open and closed, polymerized and fluid-like membrane. The dfference between the open and closed membranes is the connectivity of the mesh, and this is determined at the construction of the initial configuration. Since three points in 3-D space uniquely define a plane, a triangular mesh is the natural choice to approximate the shape of a membrane. For an open membrane, one can use a triangular mesh of hexagonal shape as the initial configuration. If m is the number of points on each side of the hexagon, the total number of grid points on the mesh is $3m\,(m\,-\,1)+\,1$. For a closed membrane, the construction of the initial configuration is a little more complicated. In our study, we use a triangular mesh on a sphere which resembles a geodesic sphere: begin with a icosahedron which has 12 points, 20 triangles, we construct a larger structure by including the triangle centers in the mesh. After n iterations of the same procedure, we obtained a closed triangular mesh of size $10 \times 3^n + 2$ (if one uses the middle points of bonds intead of the triangles' centers, one get a mesh of size $10 \times 4^n + 2$). In this mesh, all points except the original 12 of them have 6 connected neighbors and the length of the bonds are within a narrow interval. Once the coordinates of the grid points are determined, the connectivity of the mesh is calculated by applying a Delaunay triangulation procedure on the sphere. This procedure is a modified method proposed by Tanemura *et al.* [14]. After the connection is established, we rescale the size of the mesh such that the minimum bond length is one unit.

In any simulation on systems of interacting particles, the most time consuming part of the simulations is the calculation of the interactions. If the interactions are of short-ranged, a proper neighbor table can reduce the computation considerably. In this study, we adopted a Verlet-type neighbor table method [15] with the help of a cubic lattice. The construction of the neighbor table consists of two steps: first sort the mesh points into the cells of the cubic lattic, then for each mesh point J, collect the labels of all other mesh points in the same cell and those in 26 neighboring cells and store them in array $NV2$ $(I,J,)$. The side length of the cell is one unit of the maximum bond length and the number of cells in the x, y and z directions are adjusted dynamically according to the shape of the membrane such that the center of mass of the membrane is always near the center of the cubic lattic between two updating of the neighbor table. The advantage of this method is that it avoids the $N \times N$ distance checking and the difficulties arise at the lattice boundaries. The array $NV2\ (I,J)$ is used in the excluded volume checking.

The traditional single-move Monte Carlo method is used to performed simulations of polymerized membranes of small size (say, < 272) and of fluid membranes. For polymerized membrane of larger size, a vectorized multimove Monte Carlo method is developed to achieve high efficiency of the simulation. The latter method is borrowed from sublattice techniques used in simulations of lattice models in statistical mechanics. This method consists essentially in labeling the monomers according to several subclasses such that the monomers of the same subclass are not direct-connected neighbors among themselves.

In a many-move Monte Carlo step, each subclass performs sequentially displacement attempts. In these attempts, all monomers of this subclass are moved to nearby random positions, monomers belonging to different subclasses remain at their old positions. Each of the new positions are rejected if either one of the following conditions occurs:

1. One of the bonds connecting the moved monomer and its neighbors is outside the allowed range. Obviously, this vectorizable procedure is the main reason for classifying monomers according to subclasses.
2. Two monomers overlap with each other and therefore violate the excluded volume condition. There are two possibilities: one of the two overlapping monomers is a moved one, or both of them perform trial moves.

For condition (1), the single-move Monte Carlo method would produce the same results in a statistical sense, because the displacements are random and the sequence of the attempts doesn't affect the final outcome. For condition (2), the single-move Monte Carlo method would reject the attempt immediately if any overlapping occurs. If the moved monomer overlaps monomers of different subclasses, the attempt is rejected and hence the many-move Monte Carlo method would produce the same results as the single-move Monte Carlo method does. If the moved monomer overlaps monomers of the sam subclass, the single-move Monte Carlo method guarantees that one monomer of the overlapping pair monomers may still at the old position. In order to make the many-move Monte Carlo method produce the same results, it is necessary to check if the moved monomers overlap the monomers of the same subclass at their both previous and attempted positions. The attempts are rejected individually according to the condition of each moved monomer. In other words, the co-operative displacement is not implemented, and the old positions are always reserved for the moved monomers in that attempt.

The vectorization of many-move Monte Carlo method uses an integer array to mask the rejected attempts and uses indirect addressing to move data into proper places in arrays.

There must be enough mesh points which can be moved at a time in order to compensate the overhead of the vector processing. For a vesicle of 812 mesh points, it is possible to classify them into 11 sublattices, 9 of them have at least 80 points and are processed in vector mode and the rest of points are processed in scalar mode. For larger systems and more regular meshs, the vector length is longer, and the many-move Monte Carlo method is more efficient than the single-move version. The vectorization of the many-move Monte Carlo method uses an integer array to mask the rejected attempts and uses indirect addressing to move data into proper places in arrays. In fluid membrane cases, the advantage of many-move Monte Carlo method is reduced since the bond-exchange procedure cannot be vectorized efficiently.

One extension of the bond-exchange mechanism is to relax the restriction on the conservation of the numbers of edges and triangles. In this case, the edges and the triangles are allowed to be created or removed as long as the topology of the 2-D network is preserved. This means no hole is allowed and the integrity of the membrane is maintained. One of the possibilities is to allow the removal of the edges on the membrane boundary, or to allow the formation of a new edge by connecting two boundary points which are next-nearest neighbors of each other. If only the bond creation and bond exchange procedures are implemented, the open membrane will eventually become a 3-D vesicle. The topology of the open and the closed surface are certainly different, but this procedure can be used to generate the initial vesicle configuration without triangulation a sphere, and provides more number of different sizes of the system. Since in a fluid membrane the local connectivity is not fixed, each point has a chance to connect any other point, thus the anisotropy of the initial configuration has a minimum impact on the outcome of the simulation.

To facilitate the bond removal and creation procedure, an auxiliary array $NC\ (I,J)$ is needed. For monomer J, $NC\ (I,J)$ is 1 if the Ith and the $I + 1$ th neighbors of J are connected, is 0 otherwise. In case of $I + 1 > NA\ (J)$, $I + 1$ is replaced by 1, where $NA\ (J)$ is the number of neighbors of monomer J. Only the points on the boundary of an open membrane have zero $NC\ (I,J)$ values. To avoid creating dangling triangles, any monomer can have at most one $NC\ (I,J)$ equals to zero. For two boundary monomers, both are connected to the third boundary monomer, a new bond can be created to connect them, if the following conditions are met:

a. These two monomers are not connected yet,

b. They are within the bond length distance.

c. The number of neighbors of these three monomers are within the allowed number (between 3 and 8, say)

Once the new bond is formed, the third monomer is no longer on the boundary and all its $NC\ (I,J)$ are equal to 1.

To eliminate a bond between two boundary monomers, the following conditions are needed:

a. The third monomer which connects both monomers is not on the boundary, i.e., all its $NC\ (I,J)$ are equal to 1.

b. The number of neighbors of both monomers must be larger than the minimum allowed number (say, 3).

These together with the bond exchange procedure can be used to model open fluid membranes without fixed boundary. In this case, only the number of monomers is conserved, both the numbers of edges and triangles are allowed to fluctuate.

3 RESULTS

In Figure 2a and Figure 2b, the time-dependent mean squared displacement $r^2\ (t)$ of a labeled monomer relative to the motion of the center of mass is depicted, for vesicles and open membranes, respectively,

$$r^2\ (t) = < [\mathbf{r}_k\ (0) - \mathbf{r}_{cm}\ (0) - \mathbf{r}_k\ (t) + \mathbf{r}_{cm}\ (t)]^2 > \qquad (1)$$

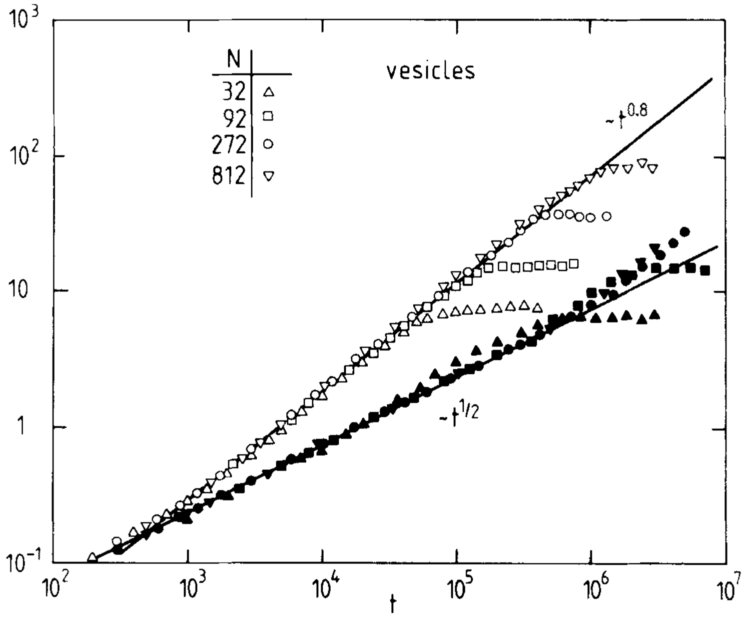

Figure 2a Log-log plot of the time-dependent mean square displacements r^2 (t) of a labeled monomer relative to the center-of-mass displacements of fluid vesicles (open symbols) and of *polymerized* vesicles (full symbols) consisting of N monomers.

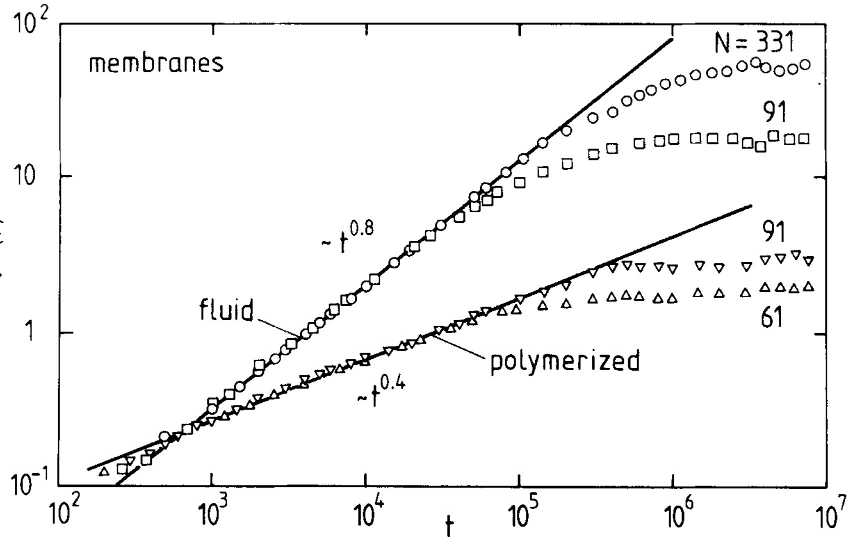

Figure 2b Log-log plot of the time-dependent mean square displacements r^2 (t) of a labeled monomer relative to the center-of-mass displacements of fluid open membranes (circles, squares) and of *polymerized* open membranes (triangles) consisting of N monomers.

where $\mathbf{r}_k(t)$ and $\mathbf{r}_{cm}(t)$ are the position vectors of the k-th monomer and the center of mass at time t, respectively. One Monte Carlo "time " step is defined, as usual [16], and N attempted moves of the monomers, i.e., within that time unit all particles of the system perform one trial move. This provides a time scale independent of the number of constituent particles of the system. This convention is applied to both single-move and many-move techniques. According to the data in Figure 2a for fluid vesicles and in Figure 2b for open fluid membranes, the behavior of $r^2(t)$ is close to $\sim t^{0.8}$ and almost independent of the size of the surfaces consisting of N monomers. (averages have been taken over six different monomer trajectories, and their deviations are in the order of the size of the symbols in Figure 2. Averages over more trajectories would decrease the statistical error, of course, but would require more memory storage). This seems to support the idea of a monomer freely draining among others, similar to particles in a fluid, but here confined to a rough surface in three space dimensions, Following similar arguments as for the restricted motion of a polymer chain trapped in a random tube [17] the displacements of monomer trapped on a random surface can be understood [18] as follows: In a surface-fixed coordiante system the monomer performs isotropic linear displacements $L^2 \sim t$, where $L^2 \sim N$. Since the surface is $R^2 \sim L^{2\nu}$, where r is the radius of gyration, the monomer moves in the laboratory system according to

$$r^2(t) \sim t^{\nu}, \ (t < \tau_2) \tag{2}$$

where $\nu \simeq 0.8$ is the correlation length exponent and is discussed below. For very long time, $r^2(t)$ saturates and remains constant,

$$r^2(\infty) \sim R^2 \sim N^{\nu} \ (t > \tau_2) \tag{3}$$

reflecting the fact that the displacements of a monomer are measured relativce to the center-of-mash displacements and are bounded therefore by the finite size of the surface. The corresponding crossover time defines the longest relaxation time τ_2 of the membrane or vesicle.

The radius of gyration of fluid vesicles (Figure 3) and fluid membranes (Figure 4)

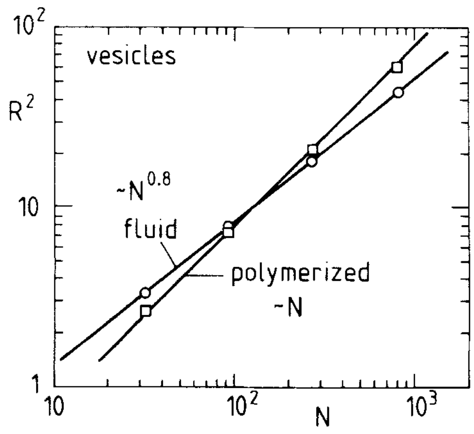

Figure 3 Mean square radius of gyration R^2 for fluid (circles) and *polymerized* vesicles (squares) for various sizes N.

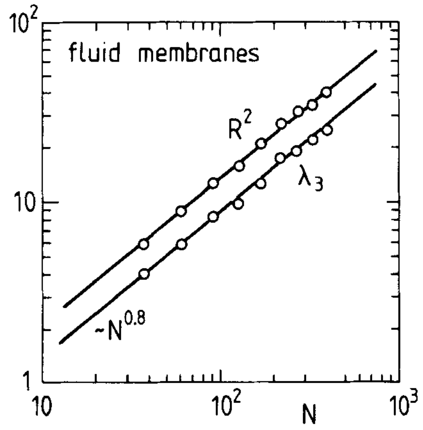

Figure 4 Mean square radius of gyration R^2 and largest eigenvalue of the inertia tensor λ_3 for fluid open membranes for various sizes N.

exhibit $R^2 \sim N^{0.8}$. Estimates of the largest eigenvalue of the inertia tensor of fluid membranes are presented in Figure 4 as well, and exhibit $\lambda_3 \sim N^{0.8}$, which is in agreement with the behavior of the radius of gyration, as expected, because of the well-known relation

$$R^2 = \lambda_1 + \lambda_2 + \lambda_3 \ . \tag{4}$$

The eigenvalues λ_1 and λ_2 exhibit the same N dependence as λ_3, but differ from each other by prefactors, indicating a weak anisotropy.

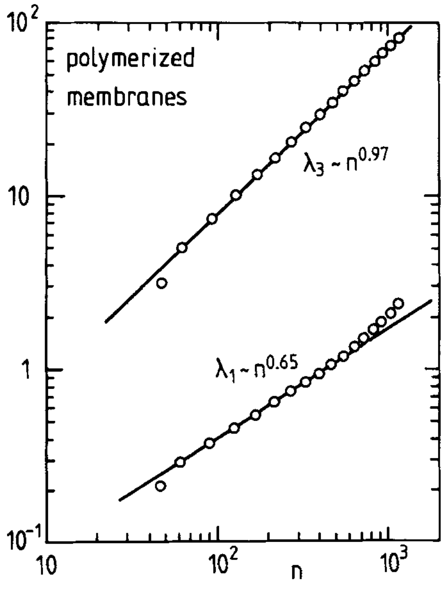

Figure 5 Largest eigenvalue λ_3 and smallest eigenvalue λ_1 of the inertia tensor for *polymerized* open membranes for various sizes n of patches out of a membranes of size N = 1141.

It is of importance to compare the static and the dynamic properties of *fluid* membranes and vesicles with those of their *polymerized* counterparts. This is discussed below.

We found $\nu \simeq 1$ from the radius of gyration of polymerized vesicles (Figure 3), $R^2 \sim N$, and from the largest eigenvalue of the inertia tensor of polymerized open membranes (Figure 5), $\lambda_3 \sim n^{0.97 \pm 0.03}$ (since λ_2 is comparable to λ_3, the former has been omitted in Figure 5). That means that polymerized surfaces are essentially "flat", which is in agreement with previous observations [9,10,11,12]. As a technical remark, it shold be noted that estimates of λ_k as depicted in Figure 5 have been obtained from a single large membrane of size $N = 1141$. There one defines inside the membrane patches consisting of $n < N$ monomers, from which the exponent can be estimated according to $\lambda_k \sim n^{\nu}$. It is interesting to note that the smallest eigenvalue λ_1 of polymerized open membranes is not a constant, but increases approximately as $\lambda_1 \sim N^{0.65 \pm 0.02}$ (Figure 5), which characterizes the roughness of an open membrane [12,19]. The time-dependent displacements of labeled monomer on *polymerized* vesicles (Figure 2a) and on *polymerized* membranes (Figure 2b) are much smaller than those of a monomer on fluid surfaces. This can be understood within the well known framework of polymer dynamics [20] and has been shown [8] to be related to the Rouse model where $r^2\ (t) \sim t^{\nu/\nu+1}$, $\tau_2 \sim N^{\nu+1}$, and $r^2\ (\infty) \sim R^2 \sim N^{\nu}$ for $t \geqslant \tau_2$. Using the correlation length exponent $\nu \simeq 1$ for polymerized vesicles (Figure 3) yields $r^2\ (t) \sim t^{1/2}$, which is in good agreement with the Monte Carlo result depicted in Figure 2a. However, for polymerized membranes the agreement is not satisfactory. Using the correlation length exponent $\nu \simeq 1$ of the largest eigenvalue λ_3 (Figure 5), which yields $r^2\ (t) \sim t^{1/2}$, gives a poor agreement with the observation $r^2\ (t) \sim t^{0.40 \pm 0.05}$ in Figure 2b. Assuming that the smallest eigenvalue with $\lambda_1 \sim N^{0.65}$ dominates the monomer displacements, one has $r^2\ (t) \sim t^{0.4}$, which is in better agreement with the Monte Carlo result. Wether this is just fortuitous or not deserves further investigations.

It should be noted that for fluid as well as for polymerized membranes and vesicles, the center-of-mass diffusion is linear in time and the corresponding diffusion coefficient $\sim N^{-1}$, as expected from the free draining behavior $r^2_{cm}\ (t) \sim l^2\ N^{-1}\ t$. Finally it should be noticed tha the relation of fluid model vesicles as invesigated in the present work to real vesicles as one encounters in biology is probably only superficial, since real vesicles exist generally at constant volume [21]. The effect of this constraint on the equilibrium properties of vesicles will be investigated in the future.

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