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DISTRIBUTION OF PORE-SIZE IN AN EXACTLY SOLVABLE TWO-DIMENSIONAL BIOMEMBRANE MODEL

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A model for a two-dimensional lipid bilayer in which both short range repulsive forces and long range attractive forces play a role, and which can be solved exactly, is discussed. It is shown that the bilayer consists of long stretches of relatively densely packed lipids separated by small pores. The statistical distributions of number and size of the pores are calculated from first principles.

1. Introduction

Because of their crucial role in the regulation of most of the physical-chemical processes in the living cell biomembranes continue to attract much attention. A variety of structures has been suggested to account for the variety of experimental facts concerning the composition and function of biomembranes; most of these structures are somehow built up from: (1) a lipid bilayer; (2) structural proteins; (3) functional proteins. In the present paper we shall disregard the membrane proteins entirely and focus attention on the lipid bilayer.

A theoretical description of a lipid bilayer from first principles would take the form of a statistical mechanical analysis in which the macroscopic properties (thermodynamic functions, pore dimensions, relaxation times etc.) would be expressed directly in terms of the constitution of the solvent and the interactions between the lipids. It is, therefore, of interest to find a model for a lipid bilayer for which such an analysis can be performed explicitly. Whereas the statistical mechanics of a three-dimensional lipid bilayer structure can only be developed using certain ad hoc approximation techniques, the particular two-dimensional biomembrane model which forms the subject of this and a previous paper[1]) can be analyzed rigorously.

The macroscopic behavior of the lipid bilayer is the outcome of a process of competition between the long range attractive forces and the short range repulsive forces which act between the lipids. To be more specific: if the bilayer is in a configuration in which the lipids are packed very closely then the energy is very low. However, closely packed hydrocarbon tails do not have many available configurations, due to steric hindrance, so that the corresponding entropy is small. On the other hand, the bilayer can gain entropy by assuming a configuration in which each lipid has more space available; this leads to an increase in the energy. Because of the very large

number of degrees of freedom of the membrane the outcome of this competitive process is very hard to forecast unless one can calculate the partition function exactly. The exact results of the following sections show that even very small changes in density, temperature or lipid–lipid interaction can drastically alter the macroscopic properties of the membrane.

The contents of this paper are as follows: In section 2 the model for the lipid bilayer is discussed and the results of reference 1 are summarized. In section 3 the probability distributions for the number and the size of the pores in the bilayer are given; in this section only results are quoted. The explicit calculation of the pore-size distribution is relegated to the appendix. It will be found that under certain conditions the average number and diameter of the pores are very sensitive to small changes in the parameters of the bilayer. Some concluding remarks are collected in section 4. A summary of the contents of this paper has been published in the form of a letter[2]).

2. Exactly solvable two-dimensional biomembrane model

Let the head groups and the hydrocarbon tails of the lipids be constrained to the vertices and the edges of a square lattice, as indicated in fig. 1. As we

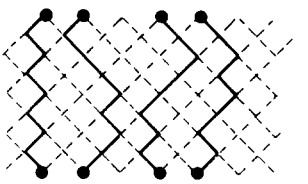

Fig. 1. A two-dimensional model for a lipid bilayer. The dashed lines indicate the underlying square lattice; the dots, the head groups of the lipids; the heavy lines, the lipid hydrocarbon chains.

shall be interested in the combinatorics of the chains, the energy difference between a trans- and a gauche conformation of a C–C bond will be neglected. The strong, short-range repulsive forces between the chains will be represented by the constraint that a lattice vertex can be occupied by at most one C atom in a chain. Thus the chain configurations are represented by sequences of lattice edges which do not intersect each other or themselves. The chains are not supposed to fold back, i.e. a chain has only one point in common with any line parallel to the surface of the membrane.

Most of the lipids which occur in nature, like the abundant phosphoglycerides phosphatidyl ethanolamine and phosphatidyl choline, have two hydrocarbon chains attached to one polar head group. This fact will be disregarded in the present model. Finally, the lipids belonging to different halves of the bilayer are merged in pairs by making their tails continuous (see fig. 1).

The model can be studied both with or without attractive interactions between the lipids. We summarize the results of ref. 1. In the absence of attractive interactions the pressure and the density in the grand canonical ensemble can be shown to be, for $z \geqslant \frac{1}{2}$:

$$\beta p_0(z,\beta) = \frac{1}{8\pi^2}\int_0^{2\pi} d\theta \int_0^{2\pi} d\phi \ln[1 + 2z^2 + 2z(\cos\theta + \cos\phi) + 2z^2\cos(\theta - \phi)], \tag{1}$$

$$\rho_0(z) = \frac{1}{\pi}\arcsin\left(1 - \frac{1}{4z^2}\right)^{1/2} + \frac{1}{2\pi}\arcsin\frac{1}{2z^2}(4z^2 - 1)^{1/2}. \tag{2}$$

Here $\beta = (k_B T^{-1})$ with k_B denoting Boltzmann's constant and T the absolute temperature, and ρ_0 is identical to both the fraction of lattice vertices occupied by hydrocarbon chains and to the fraction of lattice points at the outer or inner surface of the membrane occupied by head groups of the lipids. The asymptotic behavior of pressure and density for z near to $\frac{1}{2}$ and for $z \to \infty$ can be found from (1) and (2):

$$\beta p_0(z,\beta) = \frac{16}{3\pi}(z - \tfrac{1}{2})^{3/2} + \cdots, \quad (z \downarrow \tfrac{1}{2}), \tag{3a}$$

$$\beta p_0(z,\beta) = \ln z + \frac{1}{\pi z} + \cdots, \quad (z \to \infty), \tag{3b}$$

$$\rho_0(z) = \frac{4}{\pi}(z - \tfrac{1}{2})^{1/2} + \cdots, \quad (z \downarrow \tfrac{1}{2}), \tag{4a}$$

$$\rho_0(z) = 1 - \frac{1}{\pi z} + \cdots. \quad (z \to \infty). \tag{4b}$$

The isotherm is found upon elimination of z between (1) and (2); its low and high density behavior is found upon elimination of z between (3) and (4). Denoting the density by ρ one finds:

$$\beta p_0(\rho) = \frac{\pi^2}{12}\rho^3 + \cdots, \quad (\rho \downarrow 0), \tag{5a}$$

$$\beta p_0(\rho) = (1 - \rho) + \ln\frac{1}{\pi(1-\rho)} + \cdots, \quad (\rho \uparrow 1). \tag{5b}$$

In a similar way, the entropy per lattice point (S_0) is found as a function of the density:

$$\frac{S_0(\rho)}{k_B} = \rho \ln 2 - \frac{\pi^2}{24}\rho^3 + \cdots, \quad (\rho \downarrow 0), \tag{6a}$$

$$\frac{S_0(\rho)}{k_B} = (1 - \rho) + (1 - \rho)\ln\frac{1}{\pi(1-\rho)} + \cdots, \quad (\rho \uparrow 1). \tag{6b}$$

In fig. 2 the pressure and entropy of the model without attractive interactions have been drawn qualitatively.

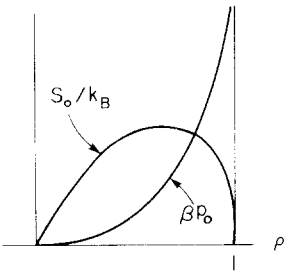

Fig. 2. Qualitative representation of the entropy per lattice vertex (S_0/k_B) and of the isotherm (βp_0) of the model without attractive forces.

When attractive interactions between the lipids are taken into account the partition function can still be calculated explicitly provided the potential of the total attractive force between two lipids the head groups of which are separated by a distance $|x - x'|$ is of the form:

$$V(x - x') = \tfrac{1}{2} m\gamma w_0 \, e^{-\gamma|x-x'|}. \tag{7}$$

Here w_0 denotes a positive constant and γ^{-1} is the range of the attractive force. A rigorous analysis of this model is possible only if $\gamma l \ll 1$, where $l\sqrt{2}$ denotes the C–C distance in a hydrocarbon chain. In the same way, the membrane thickness ml has to be large compared to l in order to make an exact treatment possible.

In the limit $m \to \infty$ the isotherm of this model with attractive interactions is found to have the form:

$$p(\rho, \beta) = 0 \qquad (\rho \leq \rho_s(T)), \tag{8a}$$

$$p(\rho, \beta) = p_0(\rho, \beta) - \frac{w_0}{4l}\rho^2 \qquad (\rho > \rho_s(T)). \tag{8b}$$

Here the density $\rho_s(T)$ is the solution of the equation

$$\frac{w_0}{4l}\rho_s^2 = p_0(\rho_s, \beta) \tag{9}$$

and increases from 0 to 1 if w_0 increases (for fixed T) from 0 to ∞; $\rho_s(T)$ decreases from 1 to 0 if T increases (for fixed w_0) from 0 to ∞. In ref. 1 it has been argued that $\rho_s(T)$ must be identified with the density of a membrane which is formed through a process of self-assemblage.

For finite $m \gg 1$ an exact calculation shows that the isotherm is very near to the isotherm (8) but the singularity in the isotherm at density $\rho_s(T)$ must be replaced by a smooth but rapid transition from the behavior (8a) to the behavior (8b). In this case the pressure for $\rho = \rho_s(T)$ is of the order of magnitude:

$$p(\rho_s, \beta) \sim \frac{\gamma l}{m} \exp\left(-c\frac{m}{\gamma l}\right), \tag{10}$$

where c does not depend on m or γl. Since $m \gg 1$ and $\gamma l \ll 1$ the isotherm of a membrane of finite thickness is very near to the isotherm (8) which holds in the limit of infinite thickness. In fig. 3 the isotherm is drawn for these two cases.

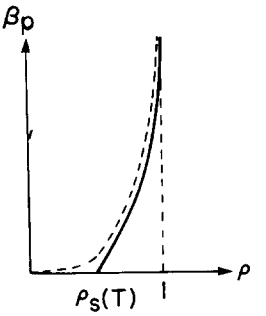

Fig. 3. The solid line represents the isotherm of the bilayer model with attractive interactions, in the limit of an infinitely thick membrane. The isotherm of a bilayer of finite thickness, indicated by the dashed line, approached the solid line very rapidly with increasing $m(\gamma l)^{-1}$, as indicated by eqs. (10) and (A.16).

3. Distribution of pore size

A mathematical analysis which has been relegated to the appendix shows that the membrane consists of long stretches of relatively densely packed lipids separated by pores. The diameter D of a pore is a fluctuating quantity with a probability distribution:

$$p(D) = \frac{1}{\Delta} \exp\left(-\frac{D}{\Delta}\right). \tag{11}$$

The average pore diameter Δ is given in the neighborhood of $\rho_s(T)$ by the expression:

$$\Delta = \frac{d}{2K^2}\{(e^{mdB_s} - 1) + \sqrt{(e^{mdB_s} - 1)^2 + 4K^2}\}. \tag{12}$$

Whereas the various quantities appearing in (12) are defined precisely in the appendix, for the interpretation one only needs to know that $K \ll 1$, that $B_s(\rho) > 0$ for $\rho < \rho_s(T)$ and that $B_s(\rho) < 0$ for $\rho > \rho_s(T)$. The behavior of the average pore size upon slight variations of ρ is given by:

$$\Delta(\rho) \sim \frac{d}{K^2}(e^{mdB_s} - 1) \quad \text{if } K \ll \rho_s - \rho, \tag{13a}$$

$$\Delta(\rho_s) \sim \frac{d}{K}, \tag{13b}$$

$$\Delta(\rho) \sim d(1 - e^{mdB_s})^{-1} \quad \text{if } K \ll \rho - \rho_s. \tag{13c}$$

The average pore size, thus, increases drastically if the density of the bilayer approaches $\rho_s(T)$ from above. The average pore diameter is represented in fig. 4.

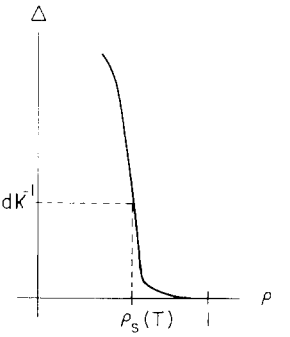

Fig. 4. The average pore size, which increases rapidly when ρ decreases through $\rho_s(T)$.

Another quantity of interest to the statistics of these pores is their average number per unit length in the bilayer. In the appendix this quantity is found to equal:

$$\frac{N_p}{L} = \frac{K^2}{d}\{(e^{mdB_s} - 1)^2 + 4K^2\}^{-1/2}. \tag{14}$$

Thus, the pores not only grow in size when $\rho \downarrow \rho_s(T)$, but they also become more numerous. However, because of the small value of K, the number of pores per unit of length will always be small, even at density $\rho_s(T)$. The result (14) is represented in fig. 5.

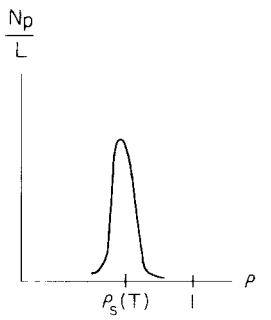

Fig. 5. The number of pores per unit of length in the membrane. Even for $\rho = \rho_s(T)$ this number is small compared to d^{-1}.

4. Concluding remarks

The spontaneous division of the membrane in long stretches of more densely packed lipids separated by pores in which the lipid density vanishes is the direct outcome of the process of competition between the long range attractive forces and the short range repulsive forces. This is an example of spontaneous breaking of symmetry: whereas the model itself is translationally invariant, the statistically favored configurations of the bilayer correspond to alternating regions of high- and vanishing lipid density.

The statistical properties of the pores have been analyzed in section 3. Whereas the pores are small and infrequent for densities larger than $\rho_s(T)$, their size increases rapidly when the density approaches $\rho_s(T)$, from above, and they also become more numerous. It is interesting to note that a variation of the pore size can also be accomplished by keeping density and temperature constant but varying the parameter w_0 which according to (7) is a measure for the strength of the long range lipid–lipid attraction. A slight increase in w_0 will increase $\rho_s(T)$ according to (9), which will cause a rapid increase in the size of the pores.

Some experimental evidence suggests the existence in synthetic lipid membranes of small regions in which the lipid density is low. Cotterill studied the dynamics of a biological membrane by computer simulation and found such low density regions[3]). Experiments on membrane rupture by Krizan and Williams[4]) might point in the same direction. A recent phenomenological theory due to Stoeckly[8]) (which leads to fair agreement with experimental data) also assumes clustering of the molecules in a way similar to the cluster formation found in this paper.

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Appendix

Derivation of the pore-size distribution

The statistical properties of the pores in the lipid bilayer can be obtained from the functional integral representation of the grand canonical partition function, for the derivation of which the reader may again be referred to[1]):

$$\mathcal{Z}(z, \beta, L) = N^{-1} \int \exp\left\{ -\frac{m}{2\beta w_0 \gamma^2} \int_0^L \left(\frac{\mathrm{d}\phi}{\mathrm{d}x}\right)^2 \mathrm{d}x - m \int_0^L B(\phi)\, \mathrm{d}x \right\} \mathrm{d}[\phi(x)]. \tag{A.1}$$

Here $B(\phi)$ denotes the function

$$B(\phi) = \frac{\phi^2}{2\beta w_0} - \frac{1}{2l}\beta p_0(\zeta\, e^{\phi}), \tag{A.2}$$

where ζ is given by:

$$\zeta = z \exp(-\tfrac{1}{4}\beta w_0 \gamma). \tag{A.3}$$

The length of the membrane is denoted by L. The integral symbol in (A.1) denotes a path integral; a discussion of path integration and its applications to statistical mechanics is contained in a recent review[5]). The normalization constant N is defined by:

$$N = \int \exp\left\{-\frac{m}{2\beta w_0 \gamma^2}\int_0^L \left(\frac{d\phi}{dx}\right)^2 dx - \frac{m}{2\beta w_0}\int_0^L \phi^2\, dx\right\} d[\phi(x)] = \sum_{n=0}^{\infty} e^{-(n+1/2)\gamma L}, \tag{A.4}$$

and will not play a role in the rest of this appendix.

In order to evaluate (A.1) we shall follow a method which has been discussed in great detail in ref. 5. To streamline the calculation we follow the slightly simpler version of this method as presented by Jalickee, Wiegel and Vezzetti[6]) and by the author[7]). One first finds all the stationary points (denoted by $\bar{\phi}(x)$) of the integrand of (A.1). These are the solutions of the Euler–Lagrange equation:

$$\frac{1}{\beta w_0 \gamma^2}\frac{d^2\bar{\phi}}{dx^2} = B'(\bar{\phi}), \tag{A.5}$$

which obey appropriate boundary conditions. As we are interested in the thermodynamic limit $L \to \infty$ the precise choice of the boundary conditions will not play a role in the pore-size distribution. Now (A.5) is the equation of motion of a classical particle with mass $1/\beta w_0 \gamma^2$ moving along the $\bar{\phi}$ axis in time x in a potential $-B(\bar{\phi})$. From (A.2) and the explicit expressions (1) and (2) for $\beta p_0(z, \beta)$ and $\rho_0(z)$ it can easily be shown that for densities ρ near to $\rho_s(T)$ the potential $-B(\bar{\phi})$ has two maxima of nearly equal height. One maximum obtains at $\bar{\phi} = 0$ with $-B(0) = 0$; the other maximum obtains at $\bar{\phi} = \bar{\phi}_s$ with $-B(\bar{\phi}_s) \equiv -B_s$. The solutions of (A.5) will, therefore, equal 0 or $\bar{\phi}_s$ in most of the lipid-bilayer, with rapid transitions between. The distance d over which a typical solution $\bar{\phi}(x)$ makes the transition from the value 0 to the value $\bar{\phi}_s$ is of the order of:

$$d = \frac{\bar{\phi}_s}{(d\bar{\phi}/dx)_0}, \tag{A.6}$$

where $(d\bar{\phi}/dx_0)$ is of the order of the velocity of the fictitious particle in a point $\bar{\phi}_0$ halfway between $\bar{\phi} = 0$ and $\bar{\phi} = \bar{\phi}_s$. Using (A.5) one finds explicitly:

$$d = c'/\gamma; \quad c' = \bar{\phi}_s\{2\beta w_0 B(\bar{\phi}_0)\}^{-1/2}. \tag{A.7}$$

Note that c' is a function of z and β, but not of γ and m.

Now divide the lipid bilayer in stretches (cells) of length d. This length, which sets the scale on which the properties of the bilayer vary appreciably, is of the order of the range of the attractive forces between the lipids. Let the successive cells be labelled by an index $i = 1, 2, \ldots, n = L/d$ and attach a spin $\sigma_i = \pm 1$ to cell i. For any solution $\bar{\phi}(x)$ of (A.5) one can determine the space average of $\bar{\phi}(x)$ over cell i; according to the previous remarks, this average will either be very near to $\bar{\phi}_s$ (in which case one defines $\sigma_i = +1$) or it will be very near to 0 (in which case $\sigma_i = -1$). Thus, the collection of stationary points of the integrand of (A.1) is in a one-to-one correspondence with all the sequences $(\sigma_1, \sigma_2, \ldots, \sigma_n)$ of n spins. It is clear that a cell with $\sigma_i = +1$ will contribute a factor $\exp(-mdB_s)$ to the integrand of (A.1); whereas, a cell with $\sigma_i = -1$ contributes a factor 1. However, if a pair of neighbouring cells carries spins with opposite signs it is erroneous to attach weights according to these rules. This error is corrected for by multiplying the integrand of (A.1) with a factor:

$$K = \exp\left[+mdB_s - m\int_{-d}^{+d}\left\{(2\beta w_0\gamma^2)^{-1}\left(\frac{d\bar{\phi}}{dx}\right)^2 + B(\bar{\phi})\right\}dx\right] \tag{A.8}$$

for each pair of opposite spins. Substituting (A.5) one finds for values of ρ very near to $\rho_s(T)$:

$$K \cong \exp\left(-c\frac{m}{\gamma l}\right); \quad c = \int_0^{\bar{\phi}_s}\left\{\frac{2l^2}{\beta w_0}B(\phi)\right\}^{1/2}d\phi. \tag{A.9}$$

Again the constant c is a function of z and β, but not of γ and m.

The grand canonical partition function can now be calculated by summing the integrand of (A.1) over all the solutions of (A.5). In order to obtain a formalism which will permit the calculation of the pore-size distribution we shall introduce the generating function of the grand canonical partition function with respect to the number (n) of cells:

$$\tilde{Z}(z, \beta, t) \equiv \sum_{n=1}^{\infty} Z(z, \beta, nd)t^n. \tag{A.10}$$

The generating function can be expressed in terms of the generating functions $U(t)$ and $V(t)$ for a stretch with length nd of densely packed lipid c.q. for a pore of length nd:

$$U(t) = \sum_{n=1}^{\infty} t^n \exp(-mdB_s n) = t(e^{+mdB_s} - t)^{-1}, \tag{A.11}$$

$$V(t) = K^2 \sum_{n=1}^{\infty} t^n = K^2 t(1-t)^{-1}. \tag{A.12}$$

One easily finds (suppressing the variables z and β):

$$\tilde{Z}(t) = U(t) + U(t)V(t)U(t) + U(t)V(t)U(t)V(t)U(t) + \cdots \tag{A.13a}$$

$$= \frac{U(t)}{1 - V(t)U(t)}. \tag{A.13b}$$

Here it is assumed for convenience that the bilayer starts and ends with uninterrupted stretches of densely packed lipids. Thus, the successive terms on the right side of (A.13a) give the contributions due to configurations of the membrane in which 0, 1, 2, ... pores are present. The partition function itself can be found from (A.10) and (A.13) by integration along a contour which encircles the origin of the complex t-plane once in counterclockwise direction:

$$\begin{aligned} Z(z, \beta, nd) &= (2\pi\,\mathrm{i})^{-1} \oint \tilde{Z}(t) t^{-n-1}\,\mathrm{d}t \\ &= (2\pi\,\mathrm{i})^{-1} \oint \frac{U(t)}{1 - V(t)U(t)}\, t^{-n-1}\,\mathrm{d}t. \end{aligned} \tag{A.14}$$

Substituting the explicit expressions (A.11) and (A.12) the complex integral can easily be performed and one finds asymptotically for $n \to \infty$:

$$Z(z, \beta, nd) \sim (t^*)^{-n}, \tag{A.15a}$$

$$t^* = \tfrac{1}{2}(1 - K^2)^{-1}\{(1 + \mathrm{e}^{mdB_s}) - \sqrt{(\mathrm{e}^{mdB_s} - 1)^2 + 4K^2\,\mathrm{e}^{mdB_s}}\}. \tag{A.15b}$$

The grand canonical pressure is, thus, found in the vicinity of $\rho_s(T)$:

$$\begin{aligned} \beta p(z, \beta) &= \frac{2l}{d} \lim_{n \to \infty} \frac{1}{mn} \ln Z(z, \beta, nd) \\ &= \frac{2l}{md} \ln|2(1 - K^2)\{(1 + \mathrm{e}^{mdB_s}) - \sqrt{(\mathrm{e}^{mdB_s} - 1)^2 + 4K^2\,\mathrm{e}^{mdB_s}}\}^{-1}|. \end{aligned} \tag{A.16}$$

As $B_s > 0$ for $\rho < \rho_s(T)$ and $B_s < 0$ for $\rho > \rho_s(T)$ one finds that the pressure is an analytic function of z and β unless $(\gamma l) \downarrow 0$ or $m \to \infty$. For the pressure in the transition point $\rho_s(T)$ one easily recovers the result (10). Thus, (A.16) describes how the singularity in the isotherm of the bilayer develops in the limit $(\gamma l) \downarrow 0$ or $m \to \infty$.

The total number of pores (N_p) in the membrane can be calculated from the observation that the successive terms on the right-hand side of (A.13a) give the contributions due to configurations in which the membrane has 0, 1, 2, ... pores. This immediately gives:

$$N_p = \partial \ln Z / \partial \ln(K^2). \tag{A.17}$$

Substituting (A.15) one finds an inelegant expression, the leading part of which has the simple form:

$$N_p \cong nK^2\{(\mathrm{e}^{mdB_s} - 1)^2 + 4K^2\}^{-1/2} \tag{A.18}$$

in the vicinity of $\rho_s(T)$.

The distribution of pore size is also found from (A.13a) in the following way. The total weight of all the membrane configurations in which, for example, the first pore from the left has a diameter νd equals:

$$W_\nu = (2\pi\,\mathrm{i})^{-1} \oint [0 + U(t) \cdot K^2 t^\nu \cdot U(t) + U(t) \cdot K^2 t^\nu \cdot U(t) V(t) U(t) + \cdots] t^{-n-1}\,\mathrm{d}t$$

$$= (2\pi\,\mathrm{i})^{-1} \oint U(t) K^2 t^\nu \frac{U(t)}{1 - V(t)U(t)}\, t^{-n-1}\,\mathrm{d}t. \tag{A.19}$$

Evaluating the contour integral with the explicit expressions (A.11) and (A.12) and normalizing the weights to unity, one finds for the probability p_ν that a pore has a diameter νd:

$$p_\nu = \frac{1}{t^*}(1 - t^*)(t^*)^\nu \quad (\nu = 1, 2, 3, \ldots). \tag{A.20}$$

Now the fact that the diameter D of a pore takes only discrete values νd is an artifact of the present approximation method that can be avoided using the more sophisticated approach in ref. 5. This leads to the continuous form of (A.20):

$$p(D) = \frac{1}{\Delta} \exp\left(-\frac{D}{\Delta}\right), \tag{A.21}$$

where the average pore diameter Δ is given by:

$$\frac{\Delta}{d} = \left(\ln \frac{1}{t^*}\right)^{-1}. \tag{A.22}$$

Substituting (A.15b) one finds in the neighbourhood of $\rho_s(T)$:

$$\frac{\Delta}{d} \cong \frac{1}{2K^2}\{(\mathrm{e}^{mdB_s} - 1) + \sqrt{(\mathrm{e}^{mdB_s} - 1)^2 + 4K^2}\}. \tag{A.23}$$

The interpretation of the results (A.18, 21, 23) forms the subject of section 3.

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