Analytic theory of DNA condensation

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We introduce a novel model for DNA condensation (whip-toroid transition) using the path integral method in the framework of the non-linear sigma model on a line segment. We show that some of its classical configurations exhibit toroidal forms, and the system has phase transitions from a whip to toroidal phases with a parameter \( c = \frac{2g}{N} \left( \frac{L}{R} \right)^2 \). We also discuss stability and finite size effect on these states.

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Since in living cells DNA is often packaged tightly, for instance, inside phage capsids, DNA condensation has drawn much attention \cite{1, 2, 3, 4, 5, 6} as well as its biochemical/medical importance in the emerging field of gene therapy. In fact, when we put condensing agents as multivalent cations into DNA solution, it can cause DNA to undergo the condensation from a worm-like chain (whip) to toroidal states \cite{1, 2, 3, 4}.

A double stranded DNA chain can be modelled, for example, by a semiflexible homopolymer chain \cite{7, 8, 9}. To increase our understanding of “whip-toroid transition”, semiflexible homopolymers in a poor solvent condition (i.e. effective interactions between polymer segments are attractive) have been investigated as simple models \cite{10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24}. Simulations using Monte Carlo, Langevin approaches or Gaussian variational method, calculated phase diagram for the semiflexible chain in a poor solvent \cite{10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24}. In theoretical works, existing phenomenological models balance the bending and surface free energies to estimate toroidal properties \cite{17, 18, 19, 20, 21, 22, 23, 24}. It becomes increasingly probable that toroid is the stable lowest energy state — the ground state. We note, however, that the theoretical aspects of the works assume a priori toroidal geometry as the stable lowest energy state with no theoretical proof \cite{21}. Moreover, compared to the theory of coil-globule transition of flexible chains \cite{7, 25, 26, 27, 28}, there is no simple microscopic theory, which contains the salient physics to demonstrate the whip-toroid transition of the semiflexible polymer. Difficulties in formulating theory results specifically from the local inextensibility constraint of the semiflexible chain \cite{8, 9}, which makes the theory non-Gaussian, and also from the non-local nature of the attractive interaction along the polymer chain, which makes the theory analytically intractable.

In this letter, we investigate the whip-toroid transition of a single semiflexible homopolymer chain with attraction, using path integral method and the nonlinear sigma model on the line segment.

In the continuum limit, the Green function (end-to-end distribution) of a stiff polymer chain with attractive interactions can be given by the path integral

\[
G(\vec{0}, \vec{R}; \vec{u}_i, \vec{u}_f; L, W) = N^{-1} \int_{\vec{r}(0)=\vec{0}, \vec{u}(0)=\vec{u}_i}^{\vec{r}(L)=\vec{R}, \vec{u}(L)=\vec{u}_f} \mathcal{D}[\vec{r}(s)] e^{-\mathcal{H}[\vec{r}, \vec{u}, W]} \tag{1}
\]

with a constraint \(|\vec{u}|^2 = 1 \). \( s \) is the proper time along the stiff polymer chain of total contour length \( L \). \( \vec{r}(s) \) denotes the pointing vector at the ‘time’ \( s \) in our three dimensional space while \( \vec{u}(s) \equiv \frac{\partial \vec{r}(s)}{\partial s} \) corresponds to the unit orientation vector at \( s \). \( \mathcal{N} \) is the normalization constant. Following Freed et al. \cite{8, 26}, the dimensionless Hamiltonian can be written by \( \mathcal{H}[\vec{r}, \vec{u}, W] = \int_0^L ds \left[ H(s) + V_{AT}(s) \right] \) where \( H(s) \) and \( V_{AT}(s) \) are the local free Hamiltonian and the attractive interaction term, respectively:

\[
H(s) = \frac{1}{2} \left| \frac{\partial}{\partial s} \vec{u}(s) \right|^2, \tag{2}
\]

\[
V_{AT}(s) = -W \int_0^s ds' \delta (\vec{r}(s) - \vec{r}(s')). \tag{3}
\]

\( l \) is the persistence length and \( W \) is a positive coupling constant of the attractive interaction between polymer segments. Thermodynamic \( \beta = 1/(k_B T) \) is implicitly included in \( l \) and \( W \). This will be revived when we consider the thermodynamic behaviours of the system. In what follows, we express \( \vec{r} \) by the unit tangent vector \( \vec{u} \) and therefore the Hamiltonian \( \mathcal{H}(\vec{u}) \) in terms of \( \vec{u} \). Hence, the Green function \( G(\vec{0}, \vec{R}; \vec{u}_i, \vec{u}_f; L, W) \) becomes a path integral over \( \vec{u} \) with a positive coupling constant \( W \), regardless of \( \vec{r} \),

\[
G = \int_{\vec{u}_i}^{\vec{u}_f} \mathcal{D}[\vec{u}(s)] \delta \left( \int_0^L ds \vec{u}(s) - \vec{R} \right) e^{-\mathcal{H}[\vec{u}, W]}, \tag{4}
\]

where we used \( \vec{r}(L) = \int_0^L ds \vec{u}(s) \) and the Jacobian is absorbed by \( \mathcal{N} \) which is neglected here. The delta function selects out the end-to-end vector. When \( W = 0 \), our free dimensionless Hamiltonian with the constraint \(|\vec{u}(s)|^2 = 1 \) can be interpreted as the low energy limit of a linear sigma model on a line segment, or quantum equivalently a nonlinear sigma model on a line segment, rather than some constrained Hamiltonian system.
We begin with $O(3)$ nonlinear sigma model on a line segment which is nothing but a quantum mechanics of a limited time $s \in [0, L]$ with a constraint. The constraint $|\vec{u}|^2 = 1$ restricts the value of $\vec{u}$ on a unit sphere $S^2$. Its polar coordinate decomposition in the free Hamiltonian $\mathcal{H}(\vec{u}) = \frac{1}{2} \int_0^L ds \, |\vec{u}(s)|^2$ gives the action:

$$S[\theta_u, \phi_u] = \frac{1}{2} \int_0^L ds \, \left[ (\partial_\theta \theta_u)^2 + \sin^2 \theta_u (\partial_\phi \phi_u)^2 \right].$$  \hfill (5)

This is called the nonlinear sigma model since the action is $O(3)$ symmetric but some of its transformations are realised nonlinearly. Minimizing the action (5) in terms of $\theta_u$ and $\phi_u$ yields the classical equations of motion:

$$\left[ -\partial^2 + \frac{\sin 2\theta_u}{2\theta_u} (\partial_\phi \phi_u)^2 \right] \theta_u = 0, \quad \left[ -\partial^2 + 2 (\partial_\theta \theta_u) \cot \theta_u \partial_\phi \phi_u \right] \phi_u = 0. \quad \hfill (6)$$

Our aim is now to explore classical solutions of eq. (6) and to study the whip-toroid phase transition in the presence of attractive interactions. Consider classical solutions of eq. (6) with a trial solution $\theta_u = 0$. The first equation of (6) leads to $\sin 2\theta_u (\phi_u)^2 = 0$. Thus the solution is either $\theta_u = 0$, $\pi$, or $\phi_u = 0$. The solutions $\theta_u = 0, \pi$ or $\phi_u = 0$ are equivalent to having a constant $\vec{u}$. Accordingly, classical solutions reduce to $\theta_u = \frac{\pi}{2}$ or $\vec{u} = \text{const.}$ Substitution of $\theta_u = \frac{\pi}{2}$ into the second equation of motion (6) gives $\partial^2 \phi_u = 0$. Therefore, we have two types of classical solutions:

$$\vec{u}(s) = \text{const.}$$

or

$$\theta = \frac{\pi}{2} \quad \text{and} \quad \phi_u = as + b, \quad \hfill (7)$$

where $a, b$ are constants. By symmetry argument, we state that the solutions (7) represent the general solutions 29. That is either a constant $\vec{u}(s)$ (rod solution) or a rotation at a constant speed along a great circle (toroid solution).

Now we consider the attractive interaction term 3. It is difficult to interpret it in the context of quantum theory due to its non-local nature along the polymer chain. However, we can solve it with our classical solutions (7). Let us rewrite eq. (3) by\[ \vec{r}(s) - \vec{r}(s') = \int_0^s \! dt \, \vec{u}(t) - \int_s^{s'} \! dt \, \vec{u}(t) = \int_s^{s'} \! dt \, \vec{u}(t), \] that is, $V_{\text{AT}}(s) = -W \int_0^L ds \, \delta \left( \int_s^{s^*} ds \, \vec{u}(t) \right)$. Hence the problem is now reduced to the one in the $\vec{u}$ space: finding nonzero values of $\delta \left( \int_s^{s^*} \! dt \, \vec{u}(t) \right)$ with the classical solutions (7). That is to find $\vec{u}(s')$ for a given $s$, which satisfies $\int_s^{s^*} \! dt \, \vec{u} = 0$. In the polar coordinates, this is expressed by $\int_s^{s^*} \! dt \, \sin \theta_u \cos \phi_u = 0, \int_s^{s^*} \! dt \, \sin \theta_u \sin \phi_u = 0$, and $\int_s^{s^*} \! dt \, \cos \theta_u = 0$. The first classical solution does not satisfy these equations and thus derives no attractive interactions. If we substitute the second classical solution of eq. (7) into the equations, we have $\cos \theta_u(s) = 0, \int_s^{s^*} \! dt \, \cos(at + b) = \frac{1}{2} \left( \sin(as + b) - \sin(as' + b) \right) = 0$ and $\int_s^{s^*} \! dt \, \sin(at + b) = \frac{1}{a} \left( \cos(as' + b) - \cos(as + b) \right) = 0$. Hence we have solutions: $s - s' = 2n\pi/a > 0, n \in \mathbb{Z}$.

Without any loss of generality, we assume $a > 0$ and $n \in \mathbb{Z}_+$. Introducing $N(s) \equiv \left[ as/2\pi \right]$ by Gauss’ symbol 31, we obtain $\int_s^{s^*} \! dt \, \vec{u}(t) = \int_s^{s^*} \! dt \, \vec{u}(t) = \cdots = \int_s^{s^*} \! dt \, \vec{u}(t) = 0$. Therefore, the attractive potential is given by $V_{\text{AT}}(s) = -W \cdot N(s)$. Note that $N(L)$ represents the winding number of the classical solution (7) along a great circle of $S^2$. Finally, an integration over $s$ yields the dimensionless Hamiltonian with our classical solutions:

$$\mathcal{H} \left[ \vec{u}, W \right] = \int_0^L ds \, H(s) + \int_0^L ds \, V_{\text{AT}}(s)$$

$$= \frac{Ll}{2} a^2 - W \left[ \frac{2\pi}{a} \sum_{k=1}^{N(L) - 1} k + \frac{2\pi}{a} \left( \frac{aL}{2\pi} - N(L) \right) N(L) \right]$$

$$= \frac{L l}{2} a^2 - WL \cdot N(L) \left\{ 1 - \frac{\pi}{aL} (N(L) + 1) \right\}. \quad \hfill (8)$$

The first term denotes the bending energy, and the second and the third terms are thought of as ‘topological’ terms from the winding number.

The non-zero winding number of the classical solution in the $\vec{u}$ space means that the polymer chain winds in the $r$ space as well. That is, when $a > \frac{2\pi}{L}$, configurations around the second classical solution (7) start forming a toroidal shape since

$$\vec{r}(s) = \begin{pmatrix} \frac{1}{\pi} \left( \sin(as + b) - \sin(b) \right) \\ -\frac{1}{\pi} \left( \cos(as + b) - \cos(b) \right) \end{pmatrix}, \quad \hfill (9)$$

and stabilise itself by attracting neighbouring segments. We call such classical solutions the “toroid states.” Whenever $a$ increases and passes through the point $\frac{2\pi}{L}$ for $n \in \mathbb{Z}_+$, another toroid state appears with the increased winding number $n$. Note that the radius of the toroid state is given by $\frac{1}{a}$. When the chain of contour length $L$ winds $N(L)$ times we have the $N(L)$ circles of each length $\frac{2\pi}{a}$ and the rest $\left( L - \frac{2\pi}{a} N(L) \right)$. The second and third terms in the second line of eq. (8) result from the former and the latter respectively. When $0 < a < \frac{2\pi}{L}$, the chain cannot wind like the toroid states. Both ends of the chain are not connected to each other, thus can move freely as well as any other parts of the chain fluctuate. As long as the total energy of the chain does not exceed the bending energy of $\frac{2\pi}{L}$ at $a = \frac{2\pi}{L}$, they can whip with zero winding number. We call such low-energy states the “whip states.” Although the definition includes fluctuations around the classical solutions, unless otherwise stated, we primarily refer to the classical solutions of such states, which are rather bowstrings than whips.

We now explore the exact energy levels of the whip and toroid states, and discuss the phase transitions between these states. The dimensionless Hamiltonian of the second classical solution (7) is a function of $l, L, W$ and $a$:

$$\mathcal{H}_{\text{cl}} \left( a, l, L, W \right)$$

$$= \frac{L l}{2} a^2 + \frac{\pi W}{a} \left( \frac{N(L)}{2} + 1 \right) - WL \cdot N(L). \quad \hfill (10)$$
This matches with the first classical solution when \( N(L) = 0 \) for \( a = 0 \) is defined. Accordingly, the above expression is valid for all classical solutions.

Consider first a case with \( L, W, \) and \( l \) fixed. By definition, \( H(a) \equiv H_0(a, l, L, W) \) is continuous in the entire region of \( a \geq 0 \) and is a smooth function in each segment: \( a \in \left[ \frac{2\pi N}{L}, \frac{2\pi(N+1)}{L} \right] \) for \( N \in \mathbb{Z}_{\geq 0} \). However, it is not smooth at each joint of the segments: \( \frac{2\pi}{N+1} \in \mathbb{Z} \). We plot, in Fig. 1, the energy level as a function of \( a \) for different values of \( c \), showing qualitative agreement with Conwell et al. [3]. Given \( N(L) = N \) is fixed, the Hamiltonian (11) takes a minimum at \( a = a_c(N) \equiv \left( \frac{N}{L} \right)^{1/3} \). Accordingly, each segment falls into one of three cases:

(i) When \( a_c(N) \leq \frac{2\pi N}{L} \), \( H(a) \) is a monotonic function in the segment and takes its minimum at \( a = \frac{2\pi N}{L} \).

(ii) When \( \frac{2\pi N}{L} < a_c(N) < \frac{2\pi(N+1)}{L} \), \( H(a) \) behaves quadratic in \( a \) and takes its minimum at \( a = a_c(N) \).

(iii) When \( \frac{2\pi(N+1)}{L} < a_c(N) \), \( H(a) \) is monotonic in the segment and takes its minimum at \( a = \frac{2\pi(N+1)}{L} \).

The first and third cases are physically less relevant since they mean no (meta-) stable point in the segment. So, we focus on the second case. Introducing a new parameter \( c \equiv \left( \frac{2\pi}{N+1} \right)^{1/3} \), the condition for \( N \) or \( a \) to be in the second case turns out to be:

\[
N_L(c) < N < N_U(c) \quad \text{for } c \geq 4, \\
1 \leq N < N_U(c) \quad \text{for } 0 \leq c < 4,
\]

where \( N = [aL/2\pi], N_L(c) \equiv \frac{L}{2\pi} \left( 1 - \frac{c}{2} + \sqrt{1 - \frac{c}{4}} \right) \), and \( N_U(c) \equiv \frac{L}{2\pi} \left( 1 + \sqrt{1 + \frac{c}{4}} \right) \).

When \( N_U(c) \leq 1 \) (i.e. \( c \leq \frac{1}{2} \)), the above second condition vanishes and thus the whip states only survive at low energy. Therefore, at the critical value of \( c = \frac{1}{2} \), the whip phase to whip-toroid co-existence phase transition may occur. On the other hand, when \( c > \frac{1}{2} \), there always exists at least one (meta-) stable state for some non-zero value of \( a \) with positive winding number \( N(L) \).

The number of minima are roughly given by the width of the region for \( N \), i.e., \( N_U(c) - N_L(c) \). For example, when \( c \geq 4 \), \( N_U(c) - N_L(c) > 3 \), and therefore there are at least three minima with positive winding numbers greater than 1. When \( 0 < c < 4 \), the condition of having three minima is \( c > \frac{1}{6} \). To summarise, when \( c > \frac{1}{9} \) there exist at least three minima with different winding numbers. This occurrence of the multiple local minima is because the energy is given by the balance between the bending energy and the attractive potential energy. The former is a monotonically increasing function of \( a \) while the latter is monotonically decreasing but not smooth function of \( a \). This non-smoothness is a source of multiple stable states. Note that our precise analysis shows that the number of minima could be reduced in some cases, for example, one can confirm it shortly by plotting the Hamiltonian (12) with some finite size effect on.

One can plot the critical value of \( c \) where the minimum of the \( N \)-th segment emerges and vanishes. The lower bound of the \( N \)-th segment is \( c_L(N) = \frac{N^2}{N+1} \), while the upper bound is \( c_U(N) = \frac{(N+1)^2}{N} \). So, when \( c_L(N) < c < c_U(N) \), the \( N \)-th segment has a minimal and (meta-) stable point. For example, when \( \frac{1}{2} < c < 4 \), the first segment \( a \in \left[ \frac{2\pi}{N+1}, \frac{2\pi}{L} \right] \) (i.e. \( N = 1 \)) has a minimal point at \( a = a_c(1) \).

So far we have dealt with the classical solutions, which are derived from the first derivative of the action. Thus, they may correspond to the global/local minima of the action in the configuration space. However, the solutions are not necessarily stable unless we take into account the attraction, since the second derivative of the action is zero or even negative in many cases. When we take the attraction into account, we observe the followings. When \( c \geq 4 \), the toroid states become stable under the quantum fluctuations, since deviations from such toroid states will cost a large penalty in energy. When \( c \) is small, a number of the whip states become equally or more probable to any toroid state.

For large \( c \), the ground state — the dominant toroid state of the winding number \( N_c \) can be estimated by the inequality relation of \( c \): \( c_L(N) < c < c_U(N) \). It reads \( N_c \approx c \). Using this, we can estimate that the radius of our ideal toroid behaves \( r_c = \frac{aL}{2\pi c} = \frac{a\pi}{c} \). Our ideal toroids have zero thickness, but the finite size effect of their cross sections can be approximated by the hexagonally arranged DNA chains with a van der Waals type interaction, i.e., with the effective nearest neighbour interactions. In the
case of \( N(L) \geq 4 \), it leads to the modified Hamiltonian:

\[
\mathcal{H}(a) = \frac{L}{2} a^2 - \frac{2\pi W}{a} \mathcal{D}(N(L)) - \frac{2\pi W}{a} \left( \frac{aL}{2\pi} - N(L) \right) \text{Gap}(N(L)),
\]

where \( \mathcal{D}(N) \equiv 3N - 2\sqrt{3}N - 1/4 \) and \( \text{Gap}(N) \equiv \mathcal{D}(N + 1) - \mathcal{D}(N) \). Following the same procedure for \( c_0^{(N)} < c < c_U^{(N)} \), one can find \( N_c \approx (2\sqrt{3}c)^{\frac{2}{5}} \) for large \( c \). By \( r_c \equiv \frac{L}{2\pi N_c} \), we now estimate the mean radius of the toroid (i.e. the average of inner and outer radii) in a physical system in more detail. A coupling constant can be given by \( W = \frac{k\epsilon}{l_m(k_BT)} \) where \( k \) is the number of the electric dipoles in a monomer segment, which create van der Waals interactions of the magnitude \( \epsilon \). \( l_m \) denotes the length of the monomer along the chain contour, taken to be \( l_m \approx 5 \text{bp} = 1.66 \text{nm} \) in the end. Substituting \( N_c \) and the above, we obtain

\[
r_c \approx (6\pi)^{-\frac{1}{5}} L^{\frac{2}{5}} \left( \frac{l}{W} \right)^{\frac{2}{5}} = (6\pi)^{-\frac{1}{5}} L^{\frac{2}{5}} (l_m l)^{\frac{2}{5}} \left( \frac{k\epsilon}{k_BT} \right)^{-\frac{2}{5}}.
\]

This \( L^{\frac{2}{5}} \) dependence agrees with the proposed exponent in the asymptotic limit \cite{18, 22, 23, 24}.

We estimate the mean toroidal radius of T4 DNA in low ionic conditions reported in ref.\cite{4}. Using \( L = 57 \mu \text{m} \), \( l \approx 50 \sim 60 \text{nm} \), and \( l_m \), the mean radius of the toroid is \( r_c = 29.09 B^{-\frac{2}{5}} \sim 31.29 B^{-\frac{2}{5}} \text{[nm]} \), where \( B \equiv \frac{k_BT}{k\epsilon} \). This result is in good agreement with the experiment \( r_c \approx 28.5 \text{nm} \) for \( B \sim 1.15 \). The same argument for Sperm DNA packaged by protamines \( (L = 20.4 \mu \text{m}) \) gives the analytic value \( r_c = 23.69 B^{-\frac{2}{5}} \sim 25.48 B^{-\frac{2}{5}} \text{[nm]} \), which is comparable to an experimental result \( r_c \approx 26.25 \text{nm} \). Note that the latter has a larger diameter of the segment and is expected to have the weaker interaction with smaller \( B \).

The exponents \( \nu \) predicted in the literature for \( r_c \sim L^{\nu} \) are \( \nu = \frac{1}{2} \) in most cases \cite{18, 22, 23, 24}. However, they are inconsistent with the experimentally well known observation that the radius is independent of the chain length \cite{22, 23, 24}. This might suggest that the real interaction is not van der Waals like, or at least is not a single van der Waals type interaction. It should be noted here that combinations of our ideal toroid and its finite size effect can give a range of \( \nu = -1 \sim \frac{1}{2} \) in some region. Another important and interesting remark is that, in fact, when we apply Coulomb like interactions to our approximation, we observe some asymptotic behaviour that the radius remains constant as \( L \) changes. The precise analysis is to be studied and given in the near future.

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