On the perfect hexagonal packing of tubes

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Abstract

In most cases the hexagonal packing of fibrous structures extremizes the energy of interaction between strands. If the strands are not straight, then it is still possible to form a perfect hexatic bundle. Conditions under which the perfect hexagonal packing of curved tubular structures may exist are formulated. Of particular interest are closed bundles like DNA toroids or spools. The closure or return constraints of the bundle result in an allowable group of automorphisms of the cross-sectional hexagonal lattice. The structure of this group is explored. Examples of an open helical-like and closed toroidal-like bundles are presented. A possible implication on a condensation of DNA in toroids and its packing inside a viral capsid is briefly discussed.

1 Introduction

It is known that the densest packing of infinite straight cylinders is hexagonal when all their axes are parallel [1]. It evidently corresponds to hexagonal packing of disks in a plane. The hexagonal packing of tubular objects occurs in numerous instances at nano to macro scale. Among examples there are nanotubes [19], high density columnar hexatic liquid crystalline DNA mesophases [12] and others. In most cases, this packing extremizes the interaction energy between filaments. Geometrically, it means that all pairs of neighbouring axes are located at constant distance to each other.

In some instances, the filaments are not straight. Then, the natural question arises of whether it is still possible to reach the same maximal density of packing. If yes, then the second question can be formulated as: what is the set of configurations of infinite (or closed) tubes that have the maximal density? By a tube (or a tubular neighbourhood) here we understand the set of all points in space whose distance from the smooth axial curve does not exceed the constant thickness radius. We can set the scale by fixing this radius to 1. Moreover we will assume that the global radius of curvature of the axes is less or equal to 1. Thus, the tubes cannot overlap, but they are perfectly flexible. It will be shown in the following that the densest packing class includes curvilinear axes, which should be relatively parallel. This implies that an arbitrary small twist of one axis around another immediately destroys the hexagonal packing.

In most cases, one is interested in the optimal packing in some particular domain. In this paper we do not deal with the disturbing influence of the boundaries. The packing will be considered as optimal if in any section orthogonal to the axis of a tube at some point P, the cross-sectional discs are hexagonally packed within a connected domain which includes the point P. In this sense, any single curvilinear perfect tube, which does not contact itself is optimally packed. This degenerate case just shows that the set of such locally optimal hexagonal packs is richer then the global packing.

A complicated structure arises when the tubes are in contact with themselves. An important example is a condensation of DNA in toroids [6, 8, 9] or a DNA arrangement inside of viral capsids [4, 11, 3]. In this paper, particular attention is given to closed bundles of hexagonally packed tubes. The closedness condition imposes a strict constraint on the whole structure. Indeed, take an orthogonal cross-section of the bundle. Then, we study the mapping of the 2D hexagonal lattice in the cross-section onto itself. The automorphisms that preserve both the distances and the connectivity form a discrete infinite group. Its study results in characterization of all possible closed hexagonally packed bundles: the writhing number [7] of each axis that realizes the mapping should equal $n/6$, where n is integer. One consequence of the automorphism group structure is that it is impossible to form a closed hexagonally packed bundle with a single filament: frustration is inevitable [14]. Examples of closed bundles made up with several strands are presented and the inverse spool model of the DNA packing inside a viral capsid is briefly discussed.

2 Unconstrained tube packing

We start with consideration of a perfect tube of some length with axis $\mathbf{r}_0(s)$, s being the arclength parametrization. Let the tube be in a continuous contact with the maximal allowed number of other tubes of the same thickness. This number equals 6 [18], thus it may be said that the tubes are hexagonally packed. Denote the axes of the neighbouring tubes by $\mathbf{r}_j(s)$, $j = 1, \ldots, 6$. We can choose the same parametrization for all the tubes such that for every s the points $\mathbf{r}_j(s)$, $j = 1, \ldots, 6$ are the closest to the central axis $\mathbf{r}_0(s)$ and they lie in the vertices of a regular triangular lattice. Note that s is not obliged to be an arc coordinate for $\mathbf{r}_j(s)$, $j = 1, \ldots, 6$. The vector field $\mathbf{m}_{j0}(s) \equiv \mathbf{r}_j(s) - \mathbf{r}_0(s)$ is relatively parallel [2]. It implies that there is no twist of vectors $\mathbf{m}_{j0}(s)$ about the central axis. We can add more layers of the tubes in the same manner as first six tubes. Proceeding this way will allow us to build a bundle of parallel tubes that fill up some domain in space. The hexagonal packing provides the maximal density in this domain. In particular, if all the tubes are straight, we have the packing of cylinders [1].

Let us now obtain an equation that governs the position of the neighbouring tube for a given central axis. We omit the index j for clarity. Since $\|\mathbf{m}\| = const (= 2)$, we can write

$$\frac{d\mathbf{m}}{ds} = \omega \times \mathbf{m}, \tag{1}$$

and the vector ω may be represented as $\omega = \omega_1 \mathbf{m} + \omega_2 \mathbf{T} \times \mathbf{m}$ [18], where we denote by $\mathbf{T} = \frac{d\mathbf{r}}{ds}$ the tangent to the central axis.

By definition, the vector $\mathbf{m}$ connects the closest points on two curves, which implies $\mathbf{m} \cdot \mathbf{T} = 0$. Differentiating this equation and further substitute eq. (1) for $\frac{d\mathbf{m}}{ds}$, we come to $\omega_2 \mathbf{m}^2 = \mathbf{m} \cdot \frac{d\mathbf{T}}{ds}$, or, with the help of the Serret-Frenet equations, $\omega_2 \mathbf{m}^2 = \kappa \mathbf{m} \cdot \mathbf{N}$. Finally, the differential equation for the orientation vector $\mathbf{m}$ can be given the form

$$\frac{d\mathbf{m}}{ds} = -\kappa (\mathbf{m} \cdot \mathbf{N}) \mathbf{T}. \tag{2}$$

This is the main equation that describes the arrangement of tubes in the hexagonally packed bundle.

The infinite number of infinitely long cylinders can fill in the entire space. This is not possible for curvilinear tubes. Suppose the axis $\mathbf{r}(s)$ has the curvature $\kappa_0 > 0$ in some point $\mathbf{r}(s_0)$. The tangent $\mathbf{T}(s_0)$, the principal normal $\mathbf{N}(s_0)$ and the binormal $\mathbf{B}(s_0)$ form the othonormal Frenet frame in the same point. The normal plane Q spanned by $\mathbf{N}(s_0)$ and $\mathbf{B}(s_0)$ is that of the orthogonal cross-section of the bundle. Now take some vector $\mathbf{R} \in Q$. Then the curvature of a tube's axis that passes through the point $\mathbf{r}(s_0) + \mathbf{R}$ is $\kappa_1 = \kappa_0 (1 - \kappa_0 \mathbf{R} \cdot \mathbf{N}(s_0))^{-1}$. Since $\kappa_1 \leq 1$, we come to an ineqality $\mathbf{R} \cdot \mathbf{N}(s_0) \leq \kappa_0^{-1} - 1$. In other words, all the axes of the tubes in the bundle may only cross the plane Q in the region bounded by the straight line which is parallel to the binormal $\mathbf{B}(s_0)$ with the offset distance $\kappa_0^{-1} - 1$. Therefore, the thickness radius of the bundle cannot exceed κ_0^{-1} in the direction of the principal normal. As the coordinate s varies, the boundary straight line sweeps out a ruled surface which bounds a domain in space where the bundle can exist.

By way of example let us take a look at the regular helical curve: $\mathbf{r}(s) = (\cos as, \sin as, \sqrt{1-a^2}s)$, $0 \le a \le 1$. Equation (2) transforms to the system

$$\frac{d\xi}{ds} = a\eta, \quad \frac{d\eta}{ds} = a(a^2-1)\xi, \quad \frac{dm_z}{ds} = a^2\sqrt{1-a^2}\xi, \tag{3}$$

and the first two components of the vector $\mathbf{m} = (m_x, m_y, m_z)$ are expressed as $m_x = \xi \cos as - \eta \sin as$, $m_y = \xi \sin as + \eta \cos as$. The explicit solution of eq. (3) is easy to find:

$$\begin{aligned} \xi = c_1 \cos \tau s + c_2 \sin \tau s, \quad \eta &= \sqrt{1-a^2}(c_2 \cos \tau s - c_1 \sin \tau s), \\ m_z &= a(c_1 \sin \tau s - c_2 \cos \tau s), \end{aligned}$$

where $\tau = a\sqrt{1-a^2}$ is the torsion and $\mathbf{m}^2 = c_1^2 + c_2^2$. Figure 1 shows a bundle of six tubes arranged at constant distance from the central tube and from the neighbours. At every section which is orthogonal to their axes the crossing points form the hexagonal lattice.

3 Cycled bundles

Consider a bundle of tubes that are hexagonally packed. Take a plane Q of an orthogonal cross section of some tube with an axis point P. Let $\Psi \in Q$ be a connected domain which includes all the cross-sectional discs of tubes in the bundle touching each other. Clearly, this plane is orthogonal to all the axes of the tubes that cross Ψ. Thus, the axes' points are the vertices of a triangular lattice $i\mathbf{e}_1 + j\mathbf{e}_2$, $i, j \in \mathbb{Z}$ and $\mathbf{e}_1^2 = \mathbf{e}_2^2 = 2\mathbf{e}_1 \cdot \mathbf{e}_2 = 1$. Actually, eq. (2) defines a parallel vector field in the 3D space and if a 2D lattice is specified in a plane orthogonal to the field, then the structure of this lattice remains invariant when the plane moves along the field. This opens the way to generalizations for tubes of different thickness.

Now we are interested in such arrangements of tubes in space that, when starting at some particular vertex, the axis comes back to the same plane at the same point or another vertex. Moreover, we will assume that the tubes originating from two neighbouring vertices will remain in permanent contact and thus return to neighbouring vertices. Then, the general question to be

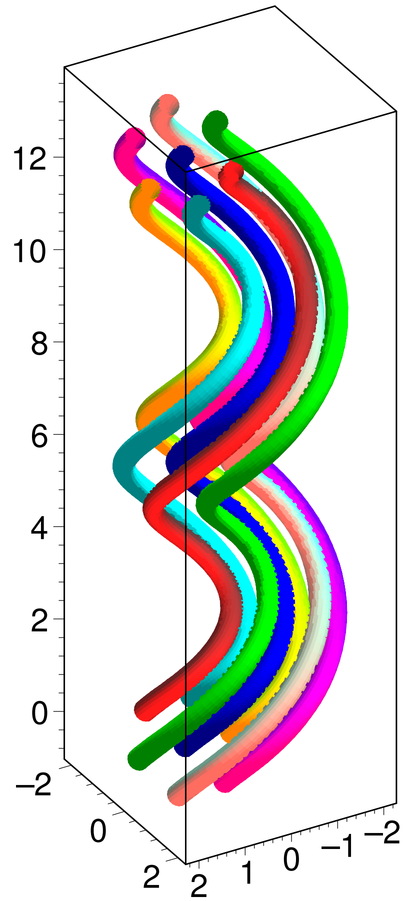

Figure 1: The perfectly packed bundle of 1+6 tubes. The axis of the central one (shown in blue) is a regular helix, six others are relatively parallel to it. The tubes are shown thinner to ease representation.

asked is: what are allowable automorphisms of the lattice induced by the three-dimensional shape of the bundle?

Let us fix the origin of the reference frame in some vertex in the plane Q. Without loss of generality, we can study the tube that starts in the origin, we call it the core. Let it come back next time at the vertex $\Delta\mathbf{r} = k\mathbf{e}_1 + l\mathbf{e}_2$, $k, l \in \mathbb{Z}$. Now take the neighbouring starting vertex $\mathbf{p}_1$; without loss of generality we can take $\mathbf{p}_1 = \mathbf{e}_1$. It is enough to consider only one neighbour, because, if we know the shape of two neighbouring tubes we can reconstruct the entire bundle uniquely, including the automorphism of the lattice. Let the neighbouring tube end up in the vertex $\mathbf{p}_2 = \Delta\mathbf{r} + \Omega^n\mathbf{p}_1$, where Ω^n is a rotation linear operator with matrix

$$\Omega^n = \begin{pmatrix} \cos\frac{\pi}{3}n & -\sin\frac{\pi}{3}n \\ \sin\frac{\pi}{3}n & \cos\frac{\pi}{3}n \end{pmatrix}, \quad n \in \mathbb{Z}_6, \tag{4}$$

and $\Omega^1\mathbf{e}_1 = \mathbf{e}_2$, $\Omega^2\mathbf{e}_1 = \Omega^1\mathbf{e}_2 = \mathbf{e}_2 - \mathbf{e}_1$, $\Omega^3\mathbf{e}_1 = -\mathbf{e}_1$, $\Omega^4\mathbf{e}_1 = -\mathbf{e}_2$, $\Omega^5\mathbf{e}_1 = \mathbf{e}_1 - \mathbf{e}_2$, $\Omega^0\mathbf{e}_1 = \mathbf{e}_1$.

Let us first consider the case when the core comes back to the origin, i.e. $k = l = 0$. Then the mapping of the lattice onto itself is just a rotation through the angle $\frac{\pi}{3}n$ around the origin. If $n = 0$, then the map is identical, all the tubes come back to their starting places. Thus the whole bundle contains a set of closed tubes and every tube crosses the domain Ψ only once. Such a bundle is often used as a simplified model in studies of DNA condensation into nanostructures, in particular, toroids [20, 9] or spools [16, 15]. For $n = 1, 5$, every tube makes closure after 6 intersections with Ψ (fig. 2(a)), for $n = 2, 4$ after three crossings (fig. 2(b)) and for $n = 3$ after two (fig. 2(c)).

Take the axes of the core and of a neighbouring tube and consider a closed thin ribbon which is formed by an arbitrary short vector $\epsilon\Delta\mathbf{r}(s)$, $s \in [0, L]$, pointing from the core axis to the closest point onto the neighbouring axis. Generally, the ribbon is not closed, the closed is only its one edge, the core axis. The ribbon is untwisted, because of the parallelism of the axes. Then, the fractional part of the writhe of the closed core axis equals $-\frac{1}{2\pi}\cdot\frac{\pi}{3}n = -\frac{n}{6}$ (see Appendix A in Ref. [17]). Moreover, it is easy to see that the writhe of a piece of every axis between two intersections with Ψ is the same. Note, that for $n \neq 0$, these pieces are not closed though they have parallel tangents at their ends.

Now we come to the more general case when $|k| + |l| \neq 0$. Our aim is to find a point $\mathbf{c} = \mu\mathbf{e}_1 + \nu\mathbf{e}_2$ such that the rotation of the plane Q through the angle $\frac{\pi}{3}n$ maps the origin into the point $\Delta\mathbf{r}$ and $\mathbf{p}_1$ into $\mathbf{p}_2$. We shall

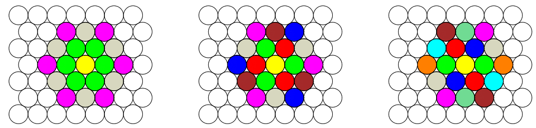

Figure 2: a) Rotation of the lattice around the central disk through $\pm\frac{1}{3}\pi \mod 2\pi$ ($n = 1, 5$). b) Rotation of the lattice around the central disk through $\pm\frac{2}{3}\pi \mod 2\pi$ ($n = 2, 4$). c) Rotation of the lattice around the central disk through $\pm\pi \mod 2\pi$ ($n = 3$).

call this point $\mathbf{c}$ the centre of rotation and it should satisfy the equation

$$\Omega^n \mathbf{c} = \mathbf{c} - \Delta\mathbf{r}, \tag{5}$$

which transforms into a system of two equations for the coordinates μ, ν. Equation (5) implies that $\Omega^n(\mathbf{c} - \mathbf{p}_1) = \mathbf{c} - \mathbf{p}_2$ which shows that the point $\mathbf{p}_1$ goes to $\mathbf{p}_2$ after rotation. This means that the transformation of the plane Q is consistent with an automorphism of the lattice.

Consider now all the possible cases of various $n \in \mathbb{Z}_6$ and find the coordinates of the point $\mathbf{c}$ explicitly. Note that the point $\mathbf{c}$ is not obliged to belong to the domain Ψ.

$\underline{n = 0.}$ The centre of rotation does not exist; the transformation is a translation along $\Delta\mathbf{r}$ (fig. 3(a)).

$\underline{n = 1.}$ The centre of rotation is located in a vertex of the triangular lattice: $\mathbf{c} = -l\mathbf{e}_1 + (k + l)\mathbf{e}_2$. The self-mapping of the lattice is rotation around the point $\mathbf{c}$ through $\frac{\pi}{3} \mod 2\pi$ (fig. 2(a)).

$\underline{n = 2.}$ The centre of rotation has the coordinates: $\mu = \frac{k-l}{3}$, $\nu = \frac{k+2l}{3}$. It can be represented as $\mathbf{c} = \frac{\sigma}{3}(\mathbf{e}_1 + \mathbf{e}_2) + s\mathbf{e}_1 + t\mathbf{e}_2$ with $\sigma = 0, \pm 1$ and $s, t \in \mathbb{Z}$, from where we see that the centre of rotation is located in a vertex of a reciprocal lattice. If $l - k = 3h$, $h \in \mathbb{Z}$ ($\sigma = 0$), then the centre of rotation coincides with the centre of a cross-sectional disk of a tube which closes after one cycle (fig. 2(b)). Otherwise, the point $\mathbf{c}$ is located in the centre of one of the equilateral triangles of the initial lattice. There exists no core tube, instead, all the lattice is decomposed into triples of disks and every triple corresponds to a single tube which closes after three intersections with Ψ (fig. 3(b)).

$\underline{n = 3.}$ The lattice map is a rotation through $\pi \mod 2\pi$ around $\mathbf{c} = \frac{1}{2}(k\mathbf{e}_1 + l\mathbf{e}_2)$. If k and l are both even, then the map is as in fig. 2(c). Otherwise, there is no self-joining core, all the tubes have two crossings with Ψ (fig. 3(c)).

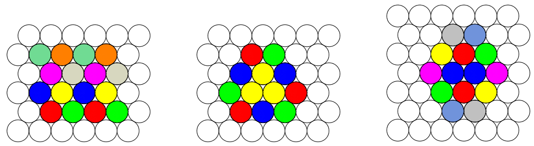

Figure 3: a) Translation of the lattice along $\mathbf{e}_1$ ($n = 0$). b) Rotation of the lattice around $\frac{1}{3}(\mathbf{e}_1 + \mathbf{e}_2)$ through $\pm\frac{2}{3}\pi \mod 2\pi$ ($n = 2, 4$). c) Rotation of the lattice around $\frac{1}{2}\mathbf{e}_1$ through $\pm\pi \mod 2\pi$ ($n = 3$).

<u>$n = 4$.</u> This case resembles that for $n = 2$. The lattice is rotated through $\frac{4}{3}\pi \mod 2\pi$ around $\mathbf{c} = \frac{1}{3}((2k + l)\mathbf{e}_1 + (l - k)\mathbf{e}_2) = \frac{\sigma}{3}(\mathbf{e}_1 + \mathbf{e}_2) + s\mathbf{e}_1 + t\mathbf{e}_2$ with $\sigma = 0, \pm 1$, $s, t \in \mathbb{Z}$. If $l - k = 3h$, $h \in \mathbb{Z}$ ($\sigma = 0$), then the point $\mathbf{c}$ lies in the centre of the disk of the one-cycle core (fig. 2(b)). Otherwise, there exist only cycles of period three (fig. 3(b)).

<u>$n = 5$.</u> The last case is similar to that for $n = 1$. The lattice is mapped onto itself by rotation through $\frac{5}{3}\pi \mod 2\pi$ around the centre $\mathbf{c} = (k+l)\mathbf{e}_1 - k\mathbf{e}_2$.

Summing up, we can say that the automorphism group of the lattice is finitely generated by the following set of transformations: 1) an identity map, 2) translations along the lattice vectors $\mathbf{e}_1$ and $\mathbf{e}_2$, 3) a rotation through $\frac{1}{3}\pi$ around the origin, 4) a rotation through $\frac{2}{3}\pi$ around $\frac{1}{3}(\mathbf{e}_1 + \mathbf{e}_2)$, 5) a rotation through π around $\frac{1}{2}\mathbf{e}_1$.

The above group includes all the transformations of the lattice which may be realized with a bundle of continuously hexagonally packed tubes. We see that the maximal number of returns of one tube is six. This implies that a thick (multi-layered) bundle may be formed only by a set of separate closed tubes. Note that in the case of translations, one may speak only about self-attached bundles, not closed in a strict sense.

The spatial configuration of the bundle determines the continuous mapping of the domain Ψ of the cross-sectional plane which moves in space as the parameter s varies. Therefore, the centres of rotation form a closed curve $\mathbf{c}(s)$. As in the above-considered particular case, the fractional part of the writhe of a piece of axis between consecutive crossings equals $-\frac{n}{6}$. To prove this in case $n \neq 0$, one has to consider a ribbon formed by a vector $\epsilon\Delta\mathbf{r}(s)$ directed from the curve $\mathbf{c}(s)$ to the closest point onto the neighbouring axis.

If $n = 0$, then we can consider a ribbon formed by the vector $\epsilon\Delta\mathbf{r}(s)$ moving along an open or closed axis of some tube on the interval between two consecutive intersections with Ψ. The ribbon is untwisted and both its edges may be not closed, but the orientation of its ends is the same. If open, such a ribbon may be made closed by adding another untwisted ribbon, hence its writhe (i.e. the writhe of the tube's axis) should be integer (details on how to deal with the writhe of open curves can be found in Ref. [17]).

Consider a helical tube in which the successive coils touch each other continuously. Fix a point on the axis of the tube and take an orthogonal cross-section of the tube at this point. It is easy to show that the plane of this section crosses all other coils non-orthogonally. But the hexagonal packing is only possible with parallel tangents to the axes at the cross-section [18]. Therefore, the packing in a cylindrical spool when the helical tubes form layers [13] is nowhere hexagonal. In other words, the adjacent coils cannot be made relatively parallel (cf. fig. 1). Additionally, the spool formation scenario from outer to inner layers [13] poses more problems: 1) it is not clear how DNA may switch to a next layer without either self-intersection or sharp bends, depending on its relative direction in the adjacent layers; 2) since the radius of the helix decreases with the number of coils being the same in all the layers, the DNA tube is forced to be compressed in the inner layers, which should lead to frustration.

An example of a perfectly packed closed bundle is shown in fig. 4. The axis of the central tube lies on the surface of a torus. It closes after one turn around the torus' hole. The writhing number of the central axis was made equal to $-\frac{1}{6}$. The second tube winds six times around the torus' hole, forming the hexagonally packed structure. Another example is presented in fig. 5, it corresponds to the lattice transformation of fig. 3(b). The mapping of fig. 3(c) takes place in the bundle shown in fig. 6. Three closed tubes are drawn. The axis of each tube may be considered as an edge of a Möbius strip. The contact line of the central tube lies on the surface of a torus and its writhing number is $-\frac{1}{2}$.

Under certain conditions, the DNA toroids may deform taking on a warped shape [5]. Generally, this deformation affects the interstrand distances and the interaction energy between strands. This effect may influence the twist-bend instability of the DNA condensates [10]. However, fig. 5 shows a perfectly packed structure with an overall shape that closely resembles the warped toroids in [5].

Figure 4: The perfectly packed bundle made up of two closed tubes. The core (dark) makes one turn and the second tube winds six times. The colour variation codes the arclength. The tubes are shown thinner to ease representation.

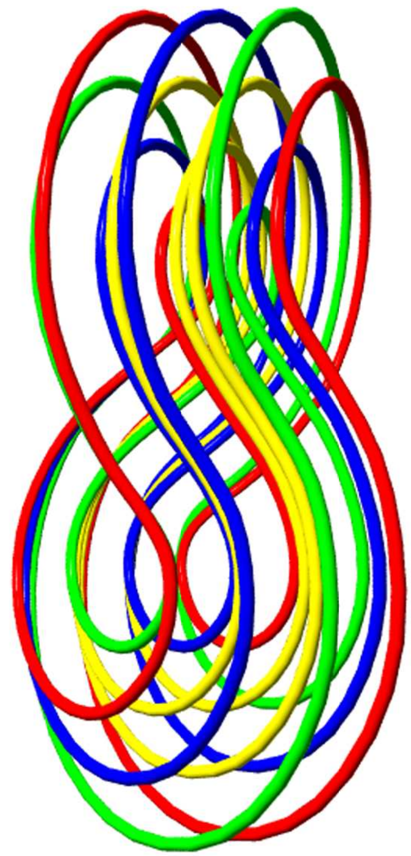

Figure 5: The perfectly packed bundle made up of four closed tubes. The tubes are shown thinner to ease representation.

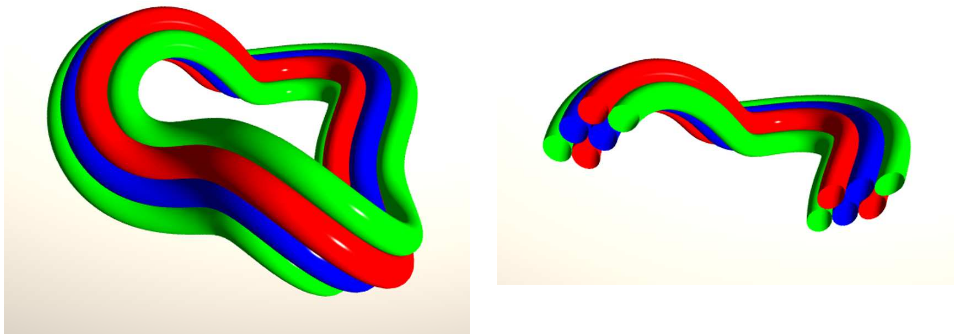

Figure 6: The perfectly packed bundle that corresponds to the case of fig. 3(c).

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