Snub polyhedra and organic growth

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This paper describes a new application of polyhedral theory to the growth of the outer sheath of certain viruses. Such structures are often modular, consisting of one or two types of units arranged in a symmetric pattern. In particular, the polyoma virus has a structure apparently related to the snub dodecahedron. Here, we consider the problem of how such patterns might grow in time, starting from a given number \( N \) of randomly placed circles on the surface of a sphere. The circles are first jostled by random perturbations, then their radii are enlarged, then they are jostled again, and so on. This ‘yin–yang’ method of growth can result in some very close packings. When \( N = 12 \), the closest packing corresponds to the snub tetrahedron, and when \( N = 24 \) the closest packing corresponds to the snub cube. However, when \( N = 60 \) the closest packing does not correspond to the snub dodecahedron but to a less-symmetric arrangement. Special attention is given to the structure of the human polyoma virus, for which \( N = 72 \). It is shown that the yin–yang procedure successfully assembles the observed structure provided that the 72 circles are pre-assembled in clusters of six. Each cluster consists of five circles arranged symmetrically around a sixth at the centre, as in a flower with five petals. This has implications for the assembly of the capsomeres in a polyoma virus.

Keywords: polyhedra; snub; growth; virus; yin–yang method

1. Introduction

The protein sheath of a virus particle commonly consists of a number of nearly identical subunits, arranged in a symmetrical pattern, for reasons first suggested by Crick & Watson (1957). It was proposed by Klug & Finch (1965) that a papilloma virus (figure 1) has the symmetry of a snub icosahedron, 60 of the units being surrounded each by six neighbours, and the remaining 12 units each surrounded by five.

Snub polyhedra belong to the class of Archimedean and Platonic solids illustrated in Coxeter et al. (1954, p. 439). The two best known are the snub dodecahedron, Wythoff symbol \( | 2 3 5 \), shown in figure 2a below, and the snub cube \( | 2 3 4 \), in figure 2b; see Coxeter et al. (1954, p. 406), where this notation is explained. At each vertex of \( | 2 3 5 \) there is one pentagon, one triangle lying on a trigonal axis of symmetry of the solid, and three other triangles; also a digon, an...
edge with a twofold rotational symmetry. Similarly, on \( |2\ 3\ 4| \) at each vertex, we find one square on a fourfold axis of symmetry, one triangle on a trigonal axis, a digon and three other triangles. One may also include in this scheme the snub tetrahedron \( |2\ 3\ 3| \), which is in fact an icosahedron, having five triangular faces at each vertex. As it is well known, the 20 faces of an icosahedron fall into five sets of four triangles, each set being coplanar with a tetrahedron. If we take two such sets and mark one set red, say, and the other green (\( R \) and \( G \) in figure 2c), then it will be found that at each vertex of \( |2\ 3\ 3| \) there is one red triangle, one green triangle, a digon and three other triangles sometimes called the ‘snub triangles’.

If we wish, we may consider the regular octahedron, with four triangular faces at each vertex, as a ‘snub’, \( |2\ 2\ 2| \), derived from the degenerate regular polyhedron consisting of two coincident triangular faces joined together by three digons; or from its inverse, three coincident digons joined at two points.

Finally, the tetrahedron may be considered as a snub, \( |2\ 2\ 2| \), derived from the degenerate polyhedron consisting of two coincident digons meeting at two vertices. This ‘polyhedron’ is its own reciprocal. Some metrical properties of the snub polyhedra are cited in table 1.

Returning to the non-degenerate cases, we may note that the word snub essentially means ‘short and blunt in shape’ (Oxford English Dictionary 1993 ed.). This conveys the idea of being more spherical. Speaking quantitatively, we can say that among the Archimedean polyhedra of a given symmetry group it is the snubs that have the greatest ratio of edge length \( l \) to circumradius \( r \). Suppose that at each vertex of an Archimedean solid we draw a small circle, with centre at that vertex, on the circumscribing sphere, all the circles being of equal radii. Then, let us enlarge each circle until it touches its neighbours, as in figure 3a. We find that it is the snub polyhedra that correspond to the most complete coverage of the sphere. For, as

Figure 1. Stereo pair of micrographs of human polyoma virus particles, suggesting that they have the symmetry of a snub dodecahedron (from Klug & Finch 1965).
shown in appendix A, the maximum proportion $p$ of the sphere’s surface that can be covered by such spherical caps is given by

$$p = N \sin^2 \left( \alpha / 4 \right),$$

(1.1)

where $N$ is the number of vertices and $\alpha$ is the angle subtended by an edge at the centre of the sphere.

The snub dodecahedron has $N=60$ and $\alpha=26.82^\circ$, giving $p=0.81801$. In other words, 82 per cent of the surface is covered by the spherical caps. The next most complete coverage corresponds to the small rhombic dodecahedron, illustrated in figure 4. In this case, we find $\alpha=25.88^\circ$ (see appendix A) and hence $p=0.76176$; only 76 per cent of the spherical surface is covered.
The problem of determining the most dense possible packing of a given number \(N\) of equal circles on a sphere is sometimes called the Tammes problem (see Tammes 1930; Coxeter 1961) and has been the subject of many studies. In particular, when \(N=24\) it was conjectured by Van der Waerden (1952) and proved by Robinson (1961) that the solution to the Tammes problem has the symmetry of the snub cube. Thus, when \(N=60\) it might be expected that the closest arrangement of circles is as in figure 3a, but we shall show later that this conjecture is false.

In this paper, we address a somewhat different but related problem: given \(N\) equal, non-overlapping circles placed at random on the surface of a sphere, suppose they are subjected to small random displacements and are allowed at the same time to increase in size at equal rates. What kind of configuration will they ultimately tend to assume?

The latter problem, unlike the first, involves time as well as static geometry; also the additional concept of randomness. Clearly, if the process is to converge, the magnitude of the perturbation and the rate of growth must each become increasingly small.

We shall approach the problem experimentally, using a random number generator to generate perturbations within a certain range. The range must tend to zero as time increases. We can expect that if the rate of growth is too large, i.e. the room left for growth is too small compared with the perturbations, then the circles will tend to jam against each other before the maximum coverage is attained. Hence, the numerical programme must involve a certain balance between perturbation and growth.

There is a not entirely fanciful analogy between the two processes of perturbation and growth on the one hand, and the two ancient Chinese principles of yin and yang on the other. The reader will recall that, in Chinese philosophy, yin denotes the principle of yielding or accommodation, while yang denotes the more thrusting or expansive principle. Optimal success is often achieved by a judicious combination of the two.

In this paper, we shall describe some applications of this method to the problem of virus growth.

2. The yin–yang method

Let us begin by choosing \(N\) spherical caps whose centres are chosen at random points on the unit sphere, by the method outlined in appendix B. In figure 5, for example, \(N=12\). The angular radius \(\delta\) of each cap is chosen small enough that
the caps nowhere overlap. In figure 5a we chose $\delta = 0.1$. Now, without changing $\delta$, let the centre of each cap in turn be jostled, by applying to it a random perturbation. If the cap overlaps any of the others, that perturbation is cancelled, and the cap is returned to its original position. Otherwise, the cap remains in its perturbed position. After $N$ such perturbations are performed, we calculate the minimum angular distance $\theta_{\text{min}}$ between the centres of any two of the caps.

At the end of this ‘yin’ phase, let the radius $\delta$ of each cap be allowed to increase by an amount proportional to $\theta_{\text{min}}$. Thus, let $\delta$ take the new value

$$\delta^* \rightarrow \delta + F \left( \frac{1}{2} \theta_{\text{min}} - \delta \right), \quad (2.1)$$

Figure 5. A random distribution of 12 spherical caps over the surface of the unit sphere $S$; (a) $z > 0$ and (b) $z < 0$.

Figure 6. Positions of the spherical caps after 50 yin–yang cycles; (a) on the upper hemisphere ($y > 0$), (b) on the lower hemisphere ($y < 0$) and (c,d) similarly, after 5000 cycles.
where $F$ is some constant, $0 < F < 1$. It is found convenient to take $F = 0.4$. The ‘yang’ step is now complete.

The process is then repeated. After 50 such yin–yang cycles the position of the caps, on the near side of the sphere ($z > 0$), was as in figure 6a. The far side is shown in figure 6b. After 5000 cycles the near side was as in figure 6c and the far side as in figure 6d. The process is thus converging convincingly to the icosahedral arrangement, for which

$$\delta = \arcsin(\tau + 2)^{-1/2},$$

(2.2)

where $\tau$ denotes the golden ratio $(\sqrt{5} + 1)/2$, i.e.

$$\delta = 0.55357 = 31.72^\circ.$$  

(2.3)

The behaviour of $\delta$ as a function of the repetition number $m$ is shown in figure 7.

**3. The snub cube**

The snub cube, shown in figure 2b, has 24 vertices. Setting $N = 24$, we generate randomly a set of 24 small spherical caps as in figure 8. The initial radius $\delta$ is 0.03.

Now let the spherical caps be alternately jostled and enlarged by the yin–yang method of §2. After 100 cycles the caps were as shown in figure 9a,b, and after 10 000 cycles they were as in figure 9c,d.

If now we join by a straight line the centres of any two adjacent spherical caps, as in figure 10, it becomes clear that the centres are arranged as the vertices of a snub cube (compare figure 3b). Moreover, from figure 11 it will be seen that as $m$ increases, $\delta$ approaches the theoretical value $\delta = 0.3861$, which is indicated by the upper horizontal line.
Figure 8. Initial positions of 24 spherical caps chosen randomly on the unit sphere; (a) $y > 0$ and (b) $y < 0$.

Figure 9. Positions of the caps after 100 cycles; (a) $y > 0$, (b) $y < 0$ and (c, d) after 10 000 cycles.

Figure 10. (a, b) The result of joining the centres of adjacent caps in figure 9, revealing the form of a snub cube.
4. The snub dodecahedron

For the snub dodecahedron (figures 2a and 3a) let us try N=60 initial caps at random, as shown in figure 12. After $m=10^5$ cycles the pattern has not converged, as can be seen from figure 13. Examination of the plot of $\delta$ against $\log m$ (figure 14) shows that $\delta=0.2358$ has actually exceeded the theoretical value for the snub dodecahedron, indicated by the upper horizontal line, $\delta=0.2341$ (table 1). In other words, the snub dodecahedron does not correspond to the most complete covering of the unit sphere by 60 spherical caps. This conclusion is in agreement with the solution of the Tammes problem for $N=60$ as found numerically by Erber & Hockney (1991), namely $2\delta=0.474241$ or $\delta=0.2371$.

A similar conclusion evidently applies to Kepler’s plane tessellation 2 3 6 (see Coxeter et al. 1954, table 8). At each vertex of this tessellation there is one digon, one triangle on an axis of symmetry, three other (snub) triangles and a regular hexagon.
If we place a circle with centre at every vertex, room is left also for an additional circle at the centre of each hexagon, thus increasing the density of the circle packing.

5. Random flowers

When considering the structure of the polyoma virus (figure 1) it is natural to apply the method to the case \( N = 72 \). The structure proposed by Klug & Finch (1965) requires that the 12 ‘holes’ of a snub dodecahedron are each filled by a circle, or ‘capsomere’ of the same size as the 60 other circles. However, it was found that a straightforward application of the yin–yang method did not lead to this result; although some pentagonal holes appeared, these were not filled by other circles at the centre. Clearly, this was because it was unlikely that the holes would be large enough to accommodate equal circles at their centre. The question then arose, what further restrictions on the circular caps are necessary to ensure that the desired arrangement of the 72 circles shall arise?

Figure 13. Positions of the 60 caps of figure 12 after \( 10^5 \) cycles; (a) \( y > 0 \) and (b) \( y < 0 \).

Figure 14. Plot of \( \delta \) against \( \log m \) for figures 12 and 13.

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Now many organic structures such as fruit blossoms, and the fruits themselves, possess a fivefold symmetry. In the biography of Donald Coxeter, Roberts (2006) recounts how Coxeter used to demonstrate the fivefold symmetry of an apple, by dissecting it in a plane at right angles to the axis of the core. Let us then assume that the 60 spherical caps have initially a strong tendency to occur in symmetric clusters of five caps. A typical cluster is shown in figure 15. We name such clusters ‘flowers’ and the five surrounding caps ‘petals’. The five centres of the petals in each flower will lie on a circle of angular radius $d_0$ equal to twice the radius $d$ of each petal, as in figure 15.

Each flower is then defined by four independent parameters: two for the position of its centre or the surface of the sphere, one for the radius $d$ and one for its orientation. A set of 12 such flowers, chosen at random, is shown in figure 16. We may alternately perturb and enlarge them, by the yin–yang method described above. One parameter $\epsilon_1$ is used for the perturbation of the centres and a second parameter $\epsilon_2$ is used for the perturbation of the orientations of the flower. After 300 cycles the pattern becomes as shown in figure 17a, and after 10 000 cycles it is as in figure 17b. Only the upper side of the sphere is shown. The centres of the flowers are marked by small circular plots. The 72 circles are now seen to be arranged in the pattern of capsomeres in figure 1. A plot of the angular radius $\delta$ of each petal is shown in figure 18 as a function of the number $m$ of cycles performed. By $m=10^4$, we find that $\delta$ has reached the value 0.2165.
Thus, whereas the direct application of yin–yang to 72 random circles on a sphere will not generally lead to the desired configuration, nevertheless when the circles are first grouped into 12 flowers, scattered at random, the desired configuration, or its mirror image, will emerge. Whether the final configuration is laevo or dextro depends on the initial configuration.

6. Conclusions and discussion

We may describe as ‘maximal’ any arrangement of \( N \) equal circles, or of spherical caps, on a unit sphere, which cover the greatest possible surface area for a given \( N \). We have examined, by a yin–yang method, the arrangements corresponding to all of the snub Archimedean polyhedra, and have confirmed that the snub cube \( \{4\{3\}2 \} \) and the snub tetrahedron \( \{3\{3\}2 \} \) do indeed correspond to maximal

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**Figure 17.** The arrangement of flowers (a) after 300 cycles, \( y>0 \) and (b) after 10 000 cycles, \( y>0 \). The centres of the flowers are indicated by small circular plots.

**Figure 18.** Graph of \( \delta \) versus \( \log m \) corresponding to figures 16 and 17. When \( m<300 \) \( \epsilon_1=0.025 \), \( \epsilon_2=0.01 \); when \( m>300 \), \( \epsilon_1=0.0025 \). \( \epsilon_2=0.001 \).

Thus, whereas the direct application of yin–yang to 72 random circles on a sphere will not generally lead to the desired configuration, nevertheless when the circles are first grouped into 12 flowers, scattered at random, the desired configuration, or its mirror image, will emerge. Whether the final configuration is laevo or dextro depends on the initial configuration.
arrangements of 24 and 12 circles, respectively, as do the octahedron $|3\ 3\ 2|$ for which $N=6$, and tetrahedron $|3\ 2\ 2|$ for which $N=4$. On the other hand, neither the snub dodecahedron $|5\ 3\ 2|$ for which $N=60$, nor Kepler’s snub tessellation, for which $N=\infty$, are maximal.

In the case $N=72$, the results described in §5 suggest that the ultimate construction of the sheath of the polyoma virus from 72 capsomeres is preceded by a preparatory phase in which the capsomeres are assembled into 12 clusters; each cluster consists of a central capsomere surrounded symmetrically by five others, like the petals in a pentagonal flower. This, indeed, is the sequence of events proposed by Casper & Klug (1962) and by Klug & Finch (1965) on other grounds.

A referee has kindly pointed out the paper by Zandi et al. (2004). These authors perform Monte Carlo simulations in which $N$ interacting circles are placed at random on a spherical surface, and equilibrium (minimum energy) states are sought. The circles are of two types, $P$ (fivefold) and $H$ (sixfold), according to the number of their neighbours. The interaction between a $P$ and an $H$ differs from that between two $H$’s. By this method, certain favoured configurations are found, particularly when $N=12, 32, 42$ and $72$. This approach differs from ours in several respects: (i) only the final states are considered, whereas in the present paper our aim has been to elucidate the time development and growth of a virus sheath. (ii) In their model, the capsomeres, which are also represented by circles on the surface of a sphere, are allowed to overlap, whereas in our model overlapping is not allowed. (iii) In our model, no forces are invoked, except of course those involved when the circles come into contact.

In other respects, the models are similar. Note that Zandi et al. (2004) contains an excellent list of references, which is recommended for further reading.

In conclusion, it should be pointed out that the enlargement of a circle on the surface of a sphere is equivalent, geometrically, to a contraction of the sphere’s radius. Instead of growing physically, the capsomeres may instead be drawn inwards towards the centre of the virus by electrostatic or other forces. The choice as to whether the final configuration is laevo or dextro could also be affected by such forces.

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Appendix A. Proof of equation (1.1)

Since the edges of any Archimedean solid are of equal length $l$, say, those vertices adjacent to any given vertex $P$ must all lie on a sphere $\Sigma$ centre $P$ and radius $l$. The sphere $\Sigma$ will intersect the circumsphere $S$ of the solid in a circle, $\Gamma$, say. $\Gamma$ passes through each of the vertices adjacent to $P$ in turn. The irregular polygon formed by this sequence of vertices is called the vertex figure of the solid (Coxeter et al. 1954).

Figure 19a shows the vertex figure of a snub dodecahedron. The radii of $\Gamma$ and $S$ are denoted by $\rho$ and $r$, respectively.

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Figure 19 shows a cross section of the vertex figure 19a in a plane through L, N and the circumcentre O of S. The angle POL subtended by the arc PL at O is equal to twice the angle θ subtended at the circumference. Hence,

\[ \frac{\rho}{l} = \cos \theta, \quad \frac{l}{2r} = \sin \theta. \]  
(A1)

To find the area σ of the spherical with cap centre P and arc radius θ note that, by Archimedes’ theorem, this area equals the curved surface area of a cylinder of radius r and height \( r - r \cos \theta \). Since the circumference of the cylinder equals \( 2 \pi r \), we have

\[ \sigma = 2 \pi r^2 (1 - \cos \theta). \]  
(A2)

The surface area of S being \( 4 \pi r^2 \), we see that the proportion \( p \) of the surface area covered by \( N \) such spherical caps is given by

\[ p = \frac{1}{2} N (1 - \cos \theta) = N \sin^2 \left( \frac{1}{2} \theta \right). \]  
(A3)

Writing \( 2 \theta = \alpha \) in this formula we obtain equation (1.1).

In the special case of the snub dodecahedron, note that in figure 19a the angles subtended at the centre M of I by adjacent pentagonal or triangular edges are \( 2 \arcsin(\tau l/2\rho) \) or \( 2 \arcsin(l/2\rho) \), respectively. Hence, writing \( l/2\rho = y \) we have

\[ \arcsin(\tau y) + 4 \arcsin y = \pi, \]  
(A4)

an equation that is easily solved numerically to give \( y = 0.514016 \); hence, \( \rho/l = 1/2y = 0.972733 \) (cf. Coxeter et al. 1954, table 4). Therefore, \( \theta = \arccos(\rho/l) = 13.4106^\circ, \alpha = 2\theta = 26.821^\circ \), as stated.

On the other hand, for the small rhombic dodecahedron, where at each vertex there is one pentagon, two squares and a triangle, we have instead of equation (A4) the relation,

\[ \arcsin \tau y + 2 \arcsin \sqrt{2} y + \arcsin y = \pi, \]  
(A5)

where \( y = l/2\rho \) as before. The relevant root of equation (A5) is \( y = 0.513027 \). By similar steps, this leads to the values of \( \alpha \) and \( p \) quoted in §1.

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Appendix B. Generation of random points on the unit sphere

Since the degree of randomness of the sequence does not appear to be critical to the outcome of the present problem, we used the simple random number generator,

\[
\begin{align*}
Q &= 10^6 \sqrt{2} \ e^D, \\
R &= Q - [Q], \\
D &= R.
\end{align*}
\] (B 1)

The initial value of \( D \) is chosen as some five-digit number lying between 0 and 1. Then \( R \) is a randomized number lying with uniform probability density, within the range \((0, 1)\). The factor \( \sqrt{2} \) in \( Q \) is inserted to avoid the repetitive pair \( D = 0, \ Q = 0 \).

To obtain points \( P \) distributed with uniform probability density over the surface of the unit sphere \( r = (x^2 + y^2 + z^2)^{1/2} = 1 \), note that, by a theorem of Archimedes, every small element of area on the spherical annulus between \( z \) and \( z + dz \) is equal in area to the corresponding element on the circular cylinder \( x^2 + y^2 = 1 \) having as its axis of symmetry the \( z \)-axis (figure 20). Call this cylinder \( \Sigma \), lying between \( z = \pm 1 \). If we distribute over the curved surface of \( \Sigma \) a number of points \( Q_i \) with equal probability density on \( \Sigma \), then the corresponding points \( P_i \) on \( S \) will be distributed with equal density over the surface of \( S \). Hence, if \( R \) and \( R^* \) are two random numbers distributed uniformly over \((0, 1)\), then the point \( P \) on \( S \) having \( z \)-coordinate \((-1 + 2R)\) and azimuthal angle \( 2\pi R^* \) is distributed uniformly over the unit sphere \( S \).

To generate a random perturbation of \( P \) on the surface of the unit sphere we need to construct a point \( P' \) lying, with uniform probability density, within a spherical cap having centre \( P \) and angular radius \( \epsilon \), say. Let \( Q' \) denote the projection of \( P' \) onto a circular cylinder of unit radius and axis parallel to \( OP \). Then, by Archimedes’ theorem, \( Q' \) will be distributed uniformly over a curved strip of the cylindrical surface of circumference \( 2\pi \) and width \((1 - \cos \epsilon)\). Such a point \( Q' \) is easily constructed by the random number generator, and the \( P' \) can then be found as the intersection of the sphere with the line \( Q'P' \) perpendicular to \( OP \) in the plane \( OPQ' \).

![Figure 20. Diagram to illustrate Archimedes’ theorem.](http://rspa.royalsocietypublishing.org/)

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