From three-dimensional weavings to swollen corneocytes

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A novel technique to generate three-dimensional Euclidean weavings, composed of close-packed, periodic arrays of one-dimensional fibres, is described. Some of these weavings are shown to dilate by simple shape changes of the constituent fibres (such as fibre straightening). The free volume within a chiral cubic example of a dilatant weaving, the ideal conformation of the \( G_{120} \) weaving related to the \( \Sigma^+ \) rod packing, expands more than fivefold on filament straightening. This remarkable three-dimensional weaving, therefore, allows an unprecedented variation of packing density without loss of structural rigidity and is an attractive design target for materials. We propose that the \( G_{120} \) weaving (ideal \( \Sigma^+ \) weaving) is formed by keratin fibres in the outermost layer of mammalian skin, probably templated by a folded membrane.

Keywords: intermediate filaments; entangled weavings; dilatant materials

We have developed a technique to generate a variety of crystalline close-packed arrays of one-dimensional filaments, via projection of line arrays in two-dimensional hyperbolic space into conventional three-dimensional space. The procedure relies on mapping of the hyperbolic patterns onto three-periodic minimal surfaces (TPMS), generalizing a technique used to enumerate systematically crystalline nets [1]. A rich catalogue of three-dimensional weavings can be constructed using this technique, with varying degrees of entanglement between filaments. Indeed, the entanglement can be tuned by adjusting the orientation of the line arrays in the hyperbolic plane, thereby varying the pitch of filament windings around channels of the TPMS. Generic examples are woven from curved and twisted filaments, whose detailed form depends on their trajectories on the TPMS [2]. Since these weavings contain close-packed fibres that can unwind at constant fibre volume without unjamming, they offer novel geometries for dilatant structures. An intriguing natural material that can sustain significant variations in fibre-packing densities is corneocytes, which make up the bulk of the outermost layer of mammalian skin, the stratum corneum. Corneocytes contain predominantly packed keratin fibrils, whose arrangement remains uncertain. We have found a dilatant chiral weaving with cubic symmetry that admits a sevenfold increase in the free volume on straightening the fibres cooperatively. The porosity variations exhibited by this weaving match closely the observed variations in human stratum corneum water contents. Further, the geometry of keratin intermediate filaments (IFs) deduced from X-ray crystallography matches well with data for fibres within this weaving in its canonical configuration, corresponding to unhydrated corneocytes.

Since the specific curvilinear form of component filaments within a weaving can be varied without changing its entanglement, it is helpful to formulate a canonical geometry for each weaving. We have adapted algorithms developed to form canonical ‘ideal’ or ‘tight’ embeddings of knots [3,4] to arrive at these canonical embeddings. Assume all filaments have a circular cross section of equal size; the filament geometry is then determined by their diameter and the curvilinear form of the loci of centres of those circles, i.e. the filament axes. Like physical ropes, all points in neighbouring filament axes must be separated by a distance not less than the diameter. ‘Ideal’ embeddings of weavings are tight, and minimize the ratio of filament length per unit cell to diameter, similar to the canonical geometries of ideal knots [3,4]. Just as tightening a knot reduces its length for a given diameter, weavings are tightened by reducing their filament length per unit cell via adjustment of the filament’s curvilinear form. To generate the canonical ideal embedding, filaments are initially given a very small diameter, tightened and then incrementally thickened and tightened until the conformation can no longer be further optimized. We realize these embeddings numerically using our implementation of the SONO algorithm [4]. We make certain that adjacent filaments remain separated by the filament diameter at all stages of the relaxation algorithm, ensuring that the entanglement of filaments does not change by phantom moves of filaments through each other during relaxation. This process is applied repeatedly (with occasional thermal noise, akin to simulated annealing). The final ideal configurations cannot be further tightened without increasing the ratio of fibre length per unit cell to fibre

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diameter, similar to the canonical geometries of ideal knots. Since the three-dimensional weavings have three-dimensional lattices of contact points between adjacent filaments, ideal embeddings are close-packed and structurally jammed.

Generic three-dimensional weavings are sufficiently entangled to preclude straightening of the individual filaments without (disallowed) phantom moves of filaments through each other. While this situation is the rule, there are exceptions: simpler weavings can be formed by arrays of infinite cylindrical filaments whose axes are straight. These examples are related to crystallographic 'rod packings', known to crystal chemistry [5]. Intuition suggests that straight fibres will minimize the fibre length per unit cell; hence, ideal embeddings should, where possible, correspond to rod packings. For the three-dimensional weaving $G_{123}^\perp(2)$, a generic version of cubic rod packing $\Gamma^\perp$ [5], this intuition is well placed: the ideal embedding contains straight rods, giving a fibre-packing fraction of 0.680. The weaving is illustrated in figure 1.

In general, however, this intuition is flawed, since it turns out that tightening most three-dimensional weavings to realize their ideal embeddings yields curvilinear filaments that are helices whose axes follow generic space curves. An example is the three-dimensional weaving, $G_{124}^\perp$, derived from a tiling in the gyroid minimal surface, whose ideal geometry contains helical filaments, as shown in figure 2. The constituent fibres form space curves that lie just to one side of the gyroid, within one of the two labyrinths. If all the filaments are straightened, the weaving is the chiral cubic rod packing known as the $\Pi^\perp$ structure [5].

The existence of curvilinear filament geometries in tight weavings has an unexpected consequence, namely the possibility of three-dimensional weavings that exhibit dilatancy, accompanied by a lowering of the fibre-packing fraction and the formation of a more open weave, while remaining tight and close-packed.

To determine whether a three-periodic weaving is dilatant, end-state configurations of the weaving under potential dilation must be prescribed. The initial configuration is the ideal configuration; this has maximum filament diameter (for normalized unit cell volumes) and a maximum number of interfilament contacts per filament length. We call the terminal configuration of the process the swollen configuration, realized as follows. The unit cell is repeatedly subjected to homothetic expansion while maintaining the filament diameter, and the filaments subsequently tightened within the swollen unit cell. (This process is equivalent to shrinking the filament diameter while maintaining the unit cell size and subsequently tightening the filaments.) The swollen configuration is reached when the unit cell cannot be further expanded without losing some of the contacts between adjacent filaments. In general, swelling is induced by gradual straightening of the curvilinear filaments.

Closer analysis of three-dimensional weavings reveals a rich taxonomy, among which we find three distinct classes. The first class exhibits zero dilatancy. In these cases, the ideal configuration and the swollen configuration of the weaving coincide. For example, the ideal state of the cubic $G_{123}^\perp(2)$ weaving reproduces the exact geometry of the $\Gamma^\perp$ rod packing, with straight rods (figure 1). Further, inflation of the unit cell while maintaining the filament diameter induces a reduction in the number of contacts between the filaments per unit cell. Hence the ideal and swollen configurations of this weaving are equivalent, and we infer that the weaving is not dilatant. Indeed, any weaving whose ideal configuration contains rectilinear filaments is not dilatant; however, weavings whose ideal forms display curvilinear filaments need not be dilatant. A second class includes all weavings that dilate to a finite extent. When fully swollen, these finitely dilatant weavings retain all interfibre contacts and remain jammed; swollen finitely dilatant weavings contain rectilinear fibres. During swelling, their fibre-packing fraction decreases continuously, yet remains positive. The third class of dilatant weavings are infinitely dilatant; their fibre-packing fraction approaches zero under swelling. (In practice, infinitely dilatant weavings have fibres of finite length. These expand until they unjam owing to loss of mutual contacts, and this end-state depends on the original fibre length.) Some fully swollen infinitely dilatant weavings contain straight fibres (which, in the limit of zero density, intersect); others are composed of curvilinear fibres.

Among the three-dimensional weavings generated from the simplest hyperbolic patterns, we have found a number of dilatant examples. For example, the $G_{124}^\perp$ weaving has an ideal configuration composed of helical filaments (figure 2). Successive unit cell expansions induce straightening of the helical filaments without loss of interfibre contacts. This expansion can be continued until a final state, in which the filaments

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Our provisional naming system for these weavings, based on the antecedent hyperbolic pattern and TPMS projection, runs as follows. The initial letter denotes the conventional name of the TPMS used to form the pattern (G:gyroid), H:henne, D:duo-). The subscript denotes the three-dimensional hyperbolic group number, tabulated for cubic surfaces in Robins et al. [6] and for the H-surface in Robins et al. [7] and the number in parentheses is a running index for each hyperbolic pattern within that group. Owing to the pair of patterns that can be formed on the gyroid [8], these weavings are appended by $+$ or $-$ to denote the (hyperbolic) handedness of the pattern.

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Figure 1. The ideal configuration of the $G_{123}^\perp(2)$ weaving, which contains straight filaments and is equivalent to the $\Gamma^\perp$ rod packing. (a) Multiple unit cells, where the filament diameter has been decreased. (b) A single unit cell. The filaments of this configuration are straight. (Online version in colour.)
are completely straight and the unit cell is finite, forming the $\Pi^+$ rod packing. This packing is the swollen configuration. The helical filaments of the ideal $G_{124}$ weaving have length 6.466 within one unit cell (set to size $1 \times 1 \times 1$), and a radius of 0.181; hence, the packing fraction is 0.665 for the ideal configuration. On dilation, the packing fraction decreases from 0.665 to 0.295 in the swollen configuration: the packing fraction is more than halved on cooperative straightening. This example is isotropic; however, anisotropic weavings may also display dilatant behaviour.

Infinitely dilatant weavings include cases whose filaments can only be partially straightened; beyond this stage further swelling cannot occur without forbidden phantom crossings (changing the weaving type). For example, a complex three-dimensional weaving $G_{118}^+(2)$ results from a hyperbolic decoration of the gyroid. The unit cell size can be expanded without limit, without the loss of any interfilament contacts, as illustrated in figure 3.

A particularly large and finite dilatant behaviour is associated with the $G_{129}$ weaving, which is related to...
Table 1. Structural measurements for various three-dimensional weavings, all normalized for (conventional) unit cells of unit volume and fibres of radius \( R \). All weavings are cubic, except \( H_{131}(1) \), which is trigonal and has a unit cell with lattice parameters \( 1, 1, 1, \pi/2, \pi/2, \pi/3 \) and volume 0.866. \( L \) is the total fibre length per unit cell; \( \gamma \in 0, \gamma_{\text{max}} \) defines the start and end-points during dilation, \( f(\gamma) \) denotes the fibre volume fraction. The dilatancy induced by fibre rectification is quantified by the fractional change in free and total volumes: \( \Delta_{\text{free}}(=V_{\text{free}}(\gamma_{\text{max}})/V_{\text{free}}(0)) \) and \( \Delta_{\text{tot}}(=V_{\text{tot}}(\gamma_{\text{max}})/V_{\text{tot}}(0)) \), where \( V_{\text{free}} \) and \( V_{\text{tot}} \) denote the volume not occupied by fibres within a unit cell and the total unit cell volume, respectively.

<table>
<thead>
<tr>
<th>pattern (rod pack)</th>
<th>straight fibres?</th>
<th>class</th>
<th>symmetry</th>
<th>( \gamma )</th>
<th>( R(\gamma) )</th>
<th>( L(\gamma) )</th>
<th>( f(\gamma) )</th>
<th>( \Delta_{\text{free}} )</th>
<th>( \Delta_{\text{tot}} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( G_{123}(2) )</td>
<td>( \vee )</td>
<td>non-dilatant</td>
<td>cubic</td>
<td>0</td>
<td>0.177</td>
<td>6.933</td>
<td>0.682</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>( H_{31}(1) )</td>
<td>X</td>
<td>dilatant (I)</td>
<td>trigonal</td>
<td>0</td>
<td>0.181</td>
<td>4.444</td>
<td>0.525</td>
<td>4.330</td>
<td>2.581</td>
</tr>
<tr>
<td>( G_{124} )</td>
<td>( \vee )</td>
<td>dilatant (I)</td>
<td>cubic</td>
<td>0</td>
<td>0.181</td>
<td>6.466</td>
<td>0.662</td>
<td>4.688</td>
<td>2.247</td>
</tr>
<tr>
<td>( \Sigma^+ )</td>
<td>( \vee )</td>
<td>dilatant (I)</td>
<td>cubic</td>
<td>0</td>
<td>0.125</td>
<td>6</td>
<td>0.295</td>
<td>7.899</td>
<td>5.429</td>
</tr>
<tr>
<td>( G_{118}(1) )</td>
<td>X</td>
<td>dilatant (II)</td>
<td>cubic</td>
<td>0</td>
<td>0.073</td>
<td>18.082</td>
<td>0.303</td>
<td>18.965</td>
<td>14.785</td>
</tr>
<tr>
<td>( D_{118}(1) )</td>
<td>X</td>
<td>dilatant (II)</td>
<td>cubic</td>
<td>0</td>
<td>1</td>
<td>16.965</td>
<td>0</td>
<td>16.965</td>
<td>14.785</td>
</tr>
<tr>
<td>( G_{118}(2) )</td>
<td>X</td>
<td>dilatant (III)</td>
<td>cubic</td>
<td>0</td>
<td>0.075</td>
<td>10.714</td>
<td>0.199</td>
<td>10.714</td>
<td>8.522</td>
</tr>
<tr>
<td>( G_{118}(2) )</td>
<td>X</td>
<td>dilatant (III)</td>
<td>cubic</td>
<td>0</td>
<td>0.066</td>
<td>29.074</td>
<td>0.389</td>
<td>29.074</td>
<td>22.934</td>
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</tbody>
</table>

The \( \Sigma^+ \) rod packing, a chiral, cubic arrangement [5], and is generated via a tiling on the gyroid. The ideal conformation of the \( G_{129} \) weaving contains helicoidal filaments that lie almost completely within one labyrinth of the gyroid. The swollen configuration of the weaving contains straight rods and is the \( \Sigma^+ \) rod packing (figure 4). The packing fraction of the weaving decreases from 0.387 in the ideal case to 0.075 in the swollen configuration: a more than fivefold decrease in the packing fraction. The free volume within the \( G_{129} \) weaving changes by a factor of 7.6 on swelling. This weaving, therefore, offers a fascinating target structure for rigid three-dimensional weavings capable of extreme variations in filament-packing densities.

Geometric data for the swelling process of a variety of three-dimensional weavings are listed in table 1. These dilation data are plotted in figure 5, which allows comparison of the rate of dilation, along with the range of porosities sustained by various weavings. We allow only jammed configurations of the weavings during the dilation transformation, as the number of interfibre contacts per unit cell is conserved. Note, however, that if the fibre length per unit cell is reduced during dilation, the density of interfibre contacts per unit cell for outermost fragments of the weaving is reduced, owing to this contraction. This variation leads to softening of the weaving rigidity, owing to unsupported fibres in the corona. This effect is difficult to quantify. A simple gauge is the number of contacts per unit length of the fibre, measured throughout the dilation process.

These data reveal the very distinct character of various weavings. Infinitely dilatant weavings exhibit extraordinary dilation properties; however, this is achieved at the expense of a significant reduction in the density of interfibre contacts. These cases are, therefore, expected to significantly soften on dilation, and finite volumes of these weavings are likely to unjam on swelling. It is also worth noting that these examples occupy a significantly larger total volume (for the same total fibre content; figure 5).
affords the most compact weaving, with the highest density of interfibre contacts.

Given the remarkable combination of structural rigidity and variable porosity afforded by these weavings, it is worth looking for them in materials. One material that necessarily combines rigidity with variable porosity is mammalian skin. Among its many functions is its homeostatic property on exposure to humidity or water; prolonged immersion in the bath will cause our skin to wrinkle owing to swelling, yet this organ retains its structural integrity. The outermost stratum corneum of mammalian skin is composed of corneocytes, whose interior is dominated by the presence of arrays of helical keratin macrofibres [9]. On exposure to water, corneocytes can swell to many times their initial volume without significant degradation of the structural integrity of the stratum corneum [10], owing to the uptake of bulk water, which occupies the fibre interstices [11]. On hydration, the corneocytes swell with little change in their total fibre content or keratin dimensions, though their helical pitch is likely to vary. In situ measurements of the hydration levels of corneocytes in human stratum corneum give average values varying between about 0.5 [12] and 3 w/w [13]. The stratum corneum is predominantly composed of keratin fibres, water and remnant lipids and various water-soluble substances (or ‘natural moisturizing factors’ (NMFs)), including inorganics, amino acids, proteins and urea [14]. It is an essential barrier layer of skin that results by granular compaction of dead skin cells to form corneocytes, containing significant fractions of keratin fibres. During the cornification process, keratin production increases and subsequent self-assembly of the polypeptide helices results in protofilaments. Subsequent accretion forms IFs, probably mediated by specific ionic interaction between the protofilaments, which are clearly visible in electron microscopy images as distinct, long and twisted fibres [15,16].

Owing to the water-binding facility of NMFs, and variation in the NMF contents and hydration within the stratum corneum, estimation of the fraction of keratin fibres within the stratum corneum is difficult to gauge precisely. Assuming densities of 1 g cm$^{-3}$ for water and NMF and 1.25 g cm$^{-3}$ for keratin, and a dry mass of about 80 per cent w/w (i.e. NMFs constitute the other 20%) [17], the hydration limits reported in Caspers et al. [12] and Bouwstra et al. [13] correspond to keratin volume fractions between 15 and 35 per cent.

The keratin fibres in the stratum corneum, therefore, form an array whose porosity is capable of varying between 65 and 85 per cent without loss of structural rigidity. Comparison of these data with those deduced for dilatant weavings is shown in figure 5. Evidently, the fibre swelling cannot change types during the hydration process, so a single weaving must span the complete range of porosities. Both the $G_{129}$ and $G_{118}^+$ weavings offer suitable arrangements of keratin fibres with dilatancy squarely within the estimated porosity range. The structure of the soft keratin IFs that make up the fibrils as a function of hydration remains uncertain. However, dry fibrils of hard keratins are known to be helical, with pitch 470 Å and diameter 74.5 Å [18], giving a ratio of pitch to diameter of 6.3. Further, the
structure of dry soft keratin IFs, constituting the stratum corneum, is likely to be similar [18].

The $G_{[100]}^{[1]}(2)$ weaving contains fibres whose geometries are complex modulated helices, without a simple helical axis, contrary to the structure of IFs. By contrast, the $G_{129}$ weaving is made of helical filaments (with slightly triangulated cross section, rather than the circular sections of ideal helices). Further, in their tightest configuration, corresponding to the dry state, the ratio of their pitch to fibre diameter is 6.8, close to that proposed by Fraser et al. [18]. (Scaling the (tightest) $G_{129}$ weaving to give the measured pitch of 470 Å implies a lattice parameter of about 550 Å for the weaving.) The remarkable dilatancy of the $G_{129}$ weaving, which spans the measured porosity variations between dry and hydrated corneocytes, coupled with the agreement in helical dimensions in keratin IFs and the filament shape in the ideal chiral cubic weaving, suggests that keratin fibrils indeed weave within corneocytes according to the $G_{129}$ pattern. Indeed, the $G_{129}$ weaving affords a low-density, rigid three-dimensional weaving, whose economy makes it an ideal geometry for a biomaterial.

A qualitative picture of the hydration process according to this model runs as follows. Exposure to water induces the keratin fibres to unwind by sliding over each other, without compromising their structural rigidity imposed by their interfibre contacts. The number of point contacts per unit cell remains fixed, but they move along the fibres, thereby generating additional free volume accessible to the water. Cooperative unwinding occurs by a gradual increase in the pitch of the IFs without any change in their diameter, resulting in isotropic expansion of the corneocytes. We predict that swelling of corneocytes beyond the free volume accessible to the straightened rod packing will lead to dramatic weakening, since further swelling of the pattern can only occur by loosening contacts between fibres, thereby diminishing the structural integrity of the corneocytes. Indeed, there is a limit to water uptake in skin, beyond which the stratum corneum loses its protective barrier [19].

Evidently this Platonic idealization of the actual process neglects a number of factors present in the stratum corneum. First, the layer is itself very anisotropic, since it is anchored to the next layer (stratum lucidum) on its inner side while its outer face is exposed to the atmosphere; additional structural anisotropy is caused by the pancake-shaped corneocytes. The overall expansion of the layer is therefore unlikely to be isotropic. Second, the interfibre contacts are probably extended over many atoms; nevertheless, it is probable that in the presence of water keratin fibres slide over each other readily. Finally, since the length per unit cell of fibres changes with swelling, if the total fibre length is conserved—as we expect it is—the total number of interfibre contacts diminishes on swelling. The combination of this effect with the changing fibre helicity is expected to induce measurable variation in the rigidity of corneocytes with hydration, though they remain sterically jammed owing to close packing of the fibres.

It is noteworthy that the $G_{129}$ weaving is generated by a simple arrangement of geodesics in the gyroid TPMS, a particularly important structure found in a variety of soft condensed materials, including membrane organelles in vivo [20,21]. Recall also that the ideal configuration lies within a good approximation of a single labyrinth of the gyroid (figure 4). (Indeed, the ideal weaving is sufficiently porous to allow a second ideal weaving of the opposite hand $G_{129}$ to be threaded within the $G_{129}$ pattern.) The relation of this weaving with the gyroid is likely to be more than coincidental. In pioneering structural studies of the stratum corneum, Norlén and Al-Amoudi [11] noted the possible presence of lipid bilayers folded onto the gyroid surface within individual corneocytes and suggested that this geometry effectively templates an ordered arrangement of keratin fibres, corresponding to another weaving whose entanglements are those of the cubic $\Gamma$ rod packing [5]. In contrast to the $G_{129}$ weaving, this pattern is achiral and relatively dense. The $\Gamma$ embedding is not dilatant; hence, the only route to increase the available free volume per unit cell is to lose interfibre contacts, which results in a loss of structural stability. It is noteworthy that, despite their discussion of the $\Gamma$ packing, Norlén and Al-Amoudi [11] suggested a chiral arrangement, consistent with the super-dilatant $G_{129}$ pattern.

Our model suggests that the corneocytes are formed in vivo via templating and collapse to one side of a lipid membrane folded into the gyroid, as proposed by Norlén and Al-Amoudi [11]. The expected lattice parameter for the gyroid, ca 550 Å, is consistent with dimensions of cubic membranes found to date [21]. Since their initial proposal, chemical studies have revealed an identical mechanism for the formation of chiral inorganic networks in synthetic mesoporous materials [22,23]. Most recently, the presence of a chiral, cubic photonic crystal composed of chitin has been established in the wing-scales of certain species of butterflies, leading to structural colour [24,25]. Indeed, the chitin network is very similar to the geometry of the keratin fibres, though chitin forms a consolidated network (and resists swelling), in contrast to the individual keratin fibres in the stratum corneum. Prima facie, the structural likeness may suggest evolutionary convergence. However, it is most probable that the morphological correspondence between mammalian skin and butterfly wings is driven by the ubiquity of the gyroid pattern in folded membranes in vivo, since both materials are probably templated by a lipid membrane.

Can the extraordinary material properties of mammalian skin be mimicked in vitro? Our understanding of the genesis of skin via lipid membrane templating suggests a route to formulate synthetic three-dimensional filament weavings at the macromolecular scale, via templating within bicontinuous molecular mesophases. In addition, the suite of examples of three-dimensional weavings discussed in this paper suggests that this route is a realistic one to generate weavings of various types, from dilatant examples to their conventional counterparts. Evidently, three-dimensional weavings of one-dimensional filaments offer a wealth of distinct material responses as a function of filament geometry.

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