In a Material World: Hyperbolic Geometry in Biological Materials

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We live in a world where matter and materials — dead or alive, synthetic or natural — play an important role. The exploration of "matter" involves a large number of scientific disciplines, from materials science and condensed matter physics to synthetic chemistry, structural biology and mathematics. Often these materials have a spatially complex structure, and geometry can be a useful tool for characterisation. An everyday example is our own skin. Human skin is a complex organ whose many layers perform a variety of different roles, from temperature regulation to the sensation of touch. Of particular interest to bathing children and discerning adults alike is the wrinkly swelling of skin after soaking in water. The swelling behaviour is a consequence of the highly symmetric geometry of keratin filaments inside the cells. The intricate structure touches on select aspects of modern geometry, from triply-periodic minimal surfaces to hyperbolic patterns. Using the filament geometry found in skin as a guide, we explore here the relationship between hyperbolic geometry, soft matter physics and biological materials, moving forward towards geometrically inspired materials.

The Geometry of Skin Swelling

The swelling of dead skin cells and subsequent wrinkling of skin is a familiar phenomenon, where exposure to water leads to the cell increasing to multiple times its original size. Experimental imaging of skin cells can nowadays resolve the internal structure, namely that the keratin filaments form a highly symmetric ordered array [23, 4]. The void space is filled mostly with water, combined with an amino acid mixture. The unique swelling property of the structure allows us to infer, via theoretical modelling, the geometry of the keratin filaments' structural arrangement. While it may appear as an unconventional perspective on a biochemical system, we argue that the ability of human skin to swell multifold when absorbing water is best understood as the geometric problem of packing helices and embedding the hyperbolic plane ($\mathbb{H}^2$) in Euclidean 3-space ($\mathbb{E}^3$).

The keratin geometry has helical filaments that align along specific axes in space that are related to each other by symmetry, as shown in Fig. 1. The so-called "cubic rod packing" is periodic in three directions (3-periodic), i.e. it is invariant under three independent translations in space, and is well known to structural chemists representing the geometry of rods of strongly bonded atoms in materials with interesting properties [25]. The rod packing can be thought of as a multidirectional braid that is 3-periodic, a more complicated version of a 1-periodic braid (Fig. 1).

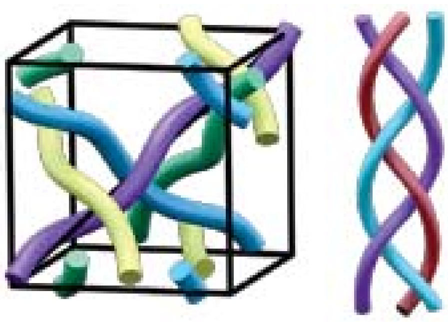

Fig. 1. The 3-periodic cubic packing of keratin fibres inside dead skin cells. It is a multidirectional version of the 1-periodic braid shown beside it.

A realistic geometric pathway from dry to swollen states of the filament packing of skin can be constructed from a combination of geometry, thermodynamics and elasticity. At all stages of the swelling process, the material maintains mechanical integrity, where the filaments are sufficiently entangled to prevent disintegration. The highly symmetric packing is shown for both dry and swollen skin cells in Fig. 2 [7].

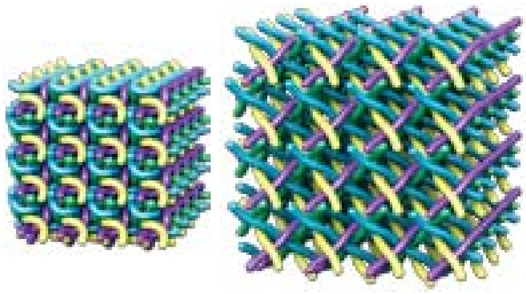

Fig. 2. The symmetric arrangement of the keratin filaments inside dead skin cells. In both the densest dry state (left) and the strongly swollen state (right), the stability of the material is guaranteed by the entangled structure [7].

The perspective of "materials geometry" for such a biomaterial is informative and of equal importance to studies of the system's biochemistry. Traditional approaches to these systems often focus on the molecular level, far smaller than the geometric assembly here, or macroscopically at the level of dermatology. The geometric approach at the "mesoscale" provides an important link between these fields, giving insight into a system with many hierarchical levels of complexity.

The geometry of this keratin structure clearly has important physical and biological functions, but it is also interesting from the perspective of applied geometry. Modern geometry can give us clues as to how such an intricate structure might form inside the living cells of the lower layers of the skin. This leads us to the relationship between biological membranes and a set of triply-periodic minimal surfaces of genus-3, and more specifically, Alan Schoen's Gyroid surface [33].

The Gyroid: A 3-periodic Minimal Surface

The Gyroid is a 3-periodic minimal surface that is space filling and divides space into two channels: It is termed "bicontinuous" for the resulting two disjoint continuous domains (Fig. 4). These two channels are exact mirror images of each other. The Gyroid was first described by Alan Schoen in the 1960s [33], and has been the subject of mathematical study since [11, 10]. The complex form of the Gyroid can be illustrated by two geometric networks, which are centred in the labyrinths. The connected network of each channel of the Gyroid, known as **srs** [24, 17], consists of identical degree-3 vertices and identical edges and is one of the most fundamental periodic networks [3]. Schoen discovered the Gyroid through exploration of the way two **srs** interthread each other in a symmetric

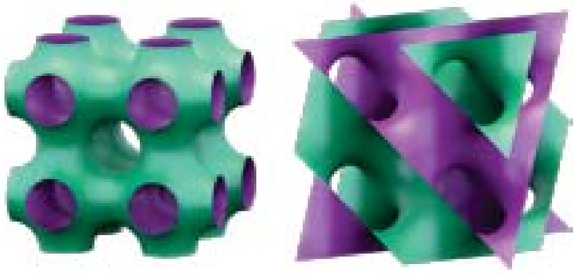

Fig. 3. The Primitive and Diamond triply-periodic minimal surfaces [37, 33].

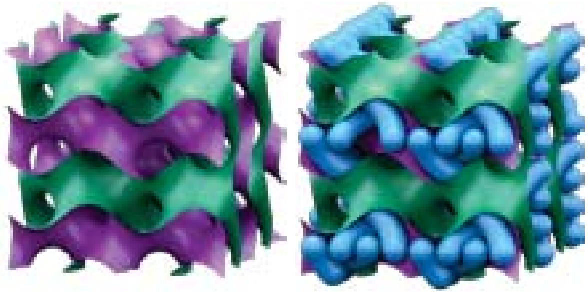

Fig. 4. (L) The Gyroid triply-periodic minimal surface divides space into two equivalent channels shown in green and purple. (R) The keratin structure of skin sitting (blue) exclusively inside one of the channels.

manner, as the minimum area surface between the two networks [32]. Schoen's Gyroid surface is closely related to two other bicontinuous surfaces, called primitive surface and diamond surface (Fig. 3), described by Herrmann Amandus Schwarz in the 19th century [37].[a]

At the same time as the mathematical description of the Gyroid by Alan Schoen, the chemist Vittorio Luzzati identified a Gyroid-like structure that had spontaneously assembled in a lipid system on the nanometre scale [21]. A rich history of the surface in soft matter science has developed since then [15]. The Gyroid is a beautiful example of how research in constructive geometry alongside the identification of complex shapes in nature have followed one another in an intertwined history.

There is a remarkable, but not surprising, connection between the Gyroid geometry and skin. The keratin filaments of the skin lie almost exclusively inside one of the channels of an appropriately sized Gyroid, leaving the second channel filled with water [4, 6]. Figure 4 shows the helical keratin filaments confined to one channel of the

[a]How close the relationship between these three surfaces is and that the Gyroid is thus actually a minimal surface was recognised by Schoen through the observation of Coxeter-Maps after discussion with Blaine Lawson, see [32].

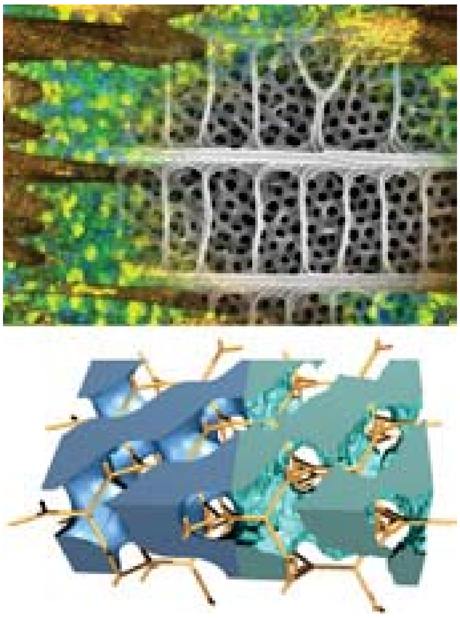

Fig. 5. Nanostructure of the wing scales of the Green Hairstreak Butterfly. The mesostructure is composed of a Gyroid-like structure with one domain filled with chitin and the other empty [29, 36].

Gyroid surface. The relationship of the skin structure to the Gyroid surface follows other precedences in the biological world. The wing scales of the Green Hairstreak Butterfly (Fig. 5) have a mesostructure composed of one channel of the Gyroid surface filled with the biopolymer chitin and the other filled with air. In the butterfly, this chiral mesostructure acts as a photonic crystal, where light of most wavelengths passes through the structure, yet light of the green wavelength is reflected because of the geometry alone (without the need for pigments), giving the wings a brilliant green colour [22, 31, 36]. Thus the soft keratin filament geometry of human skin closely resembles the hard chitin network geometry of butterfly wings.

Nature's Best Attempt at Embedding the Hyperbolic Plane in $\mathbb{E}^3$

The formation of gyroid-like interfaces in self-assembly processes is a clear demonstration of the relevance of hyperbolic geometry for the physics of soft and biological matter and materials science. It corresponds to a pragmatic interpretation of David Hilbert's famous theorem that a surface with constant negative Gaussian curvature in $\mathbb{E}^3$ does not exist [12] (see Fig. 6 for a definition of Gaussian curvature). This theorem states that the saddle-shaped counterpart of the sphere —

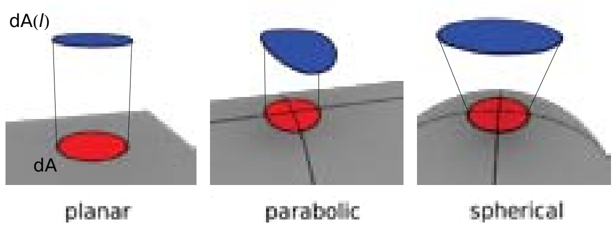

Fig. 6. Surface curvatures as area changes of parallel surfaces: Given a surface patch dA, the parallel patch is obtained by moving each point "off the surface" by a distance l. In doing so, the area changes as a polynomial $dA(l) = dA(1 \pm lH + l^2K)$ defining two coefficients, called the mean curvature H and the Gaussian curvature K.

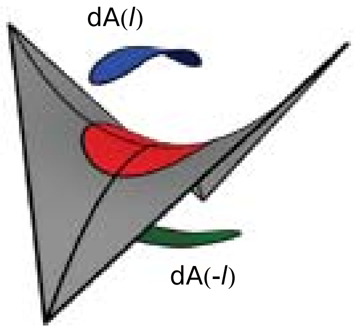

Fig. 7. A surface that shrinks equally under $\pm l$ parallel translation, is a symmetric saddle with $K \leq 0$, called *minimal surface*.

being the perfectly homogeneous convex object with uniform curvature and uniform radius — does not exist in the space $\mathbb{E}^3$ of materials science, see Fig. 7.

How will a physical system that favours saddle-shaped interfaces as well as uniform Gaussian curvature react? In the absence of a perfect solution, it adopts the best available solution, that is, the saddle-shaped surface with minimal variability of the Gaussian curvature. This phenomenon, known in physics as *frustration*, essentially provides a rationale for the ubiquity of Alan Schoen's Gyroid minimal surface geometry in soft matter self-assembly.

Lipids are amphiphilic[b] molecules composed of two parts: a "head group" that likes water (hydrophilic) and a "tail" that likes fat (hydrophobic). When mixed in sufficient concentration in water, arrangements where the tails are shielded from water emerge as the favourable configuration. Amongst these are lipid bilayers, warped sheets composed of a double layer of lipids with the tails forming the inside and the headgroups the outside surfaces (Fig. 8).

[b]Composed of the greek words for "both" (amphis) and "love" or "friendship" (philia).

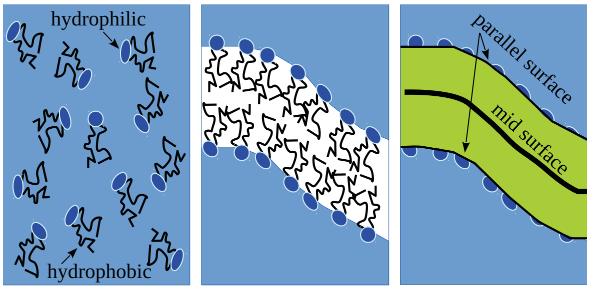

Fig. 8. The amphiphilic nature of the lipids leads to the formation of bilayers, whose mid-surface enables a differential geometric treatment.

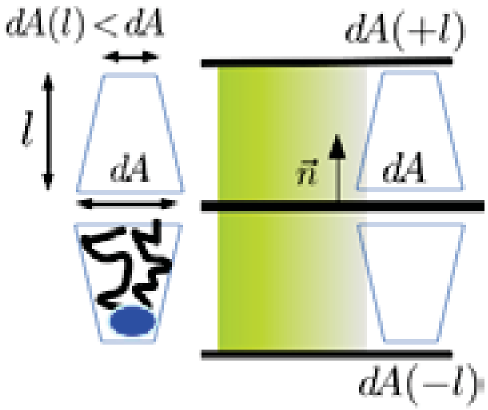

Fig. 9. Interpretation of a lipid membrane through parallel surfaces and the link between molecular form and surface curvature.

The formation of negatively curved interfaces in lipid self-assembly appears as a natural consequence of "molecular shape" [18, 15], stemming from a packing problem of soft particles of a given shape, neglecting chemical detail. The effective molecular shape is characterised by the length l, the area of the tail ends and the area of the head group. Identification of the tail area with dA and of the head group area with $dA(l)$ allows the connection between molecular shape and interface curvatures (Fig. 9). In order for the bilayer to be symmetric it needs to be a minimal surface and in order for the parallel head group surfaces to be compressed relative to the mid-plane surface, the Gaussian curvature needs to be on average negative. Put simply, negative curvature results naturally because the bilayer is a symmetric sheet whose mid-surface is bulkier than its two bounding surfaces! This, as Stephen Hyde has pointed out [13], is a property shared with a slice of toast. Selectively grilling one side will induce positive curvature. When grilling the other side, such that both outer surfaces have shrunk relative to the mid-surface, the slice of toast adopts a saddle-shape.

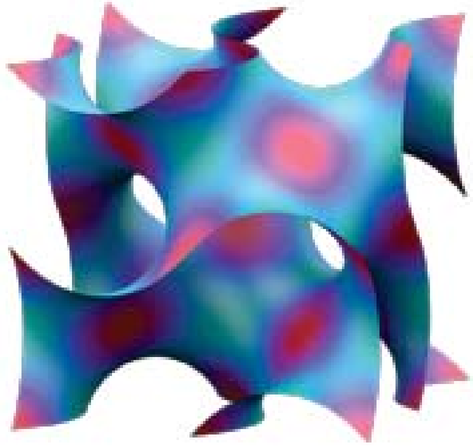

Fig. 10. Minimal surfaces cannot have constant Gaussian curvature. The Gyroid appears to be the minimal surface with the most uniform curvature and with finite average Gaussian curvature. Colour corresponds to Gaussian curvature.

The most subtle question relates to why three particular periodic minimal surfaces — Primitive, Diamond (Fig. 3) and Gyroid — appear in lipid self-assembly, but not any of the many other saddle-shaped minimal surfaces. The degree of curvature uniformity, that is, variations of the Gaussian curvature over the surface, holds the answer: Considering that molecular shape relates to interface curvature, one expects that an assembly of identical molecules favours an interface with uniform curvature. Variations of the Gaussian curvature over the structure loosely correspond to "deficiencies" of the molecular packing. Numerical analysis gives a clear indication that these three cubic minimal surfaces have the most uniform distribution of Gaussian curvature [14, 9, 35] amongst all minimal surface forms.[c,d] The Gaussian curvature variations over the Gyroid are shown in Fig. 10.

The ideal configuration for a lipid bilayer would hence be $\mathbb{H}^2$, with constant negative curvature throughout. Its nature as a three-dimensional material, however, forces the bilayer into adopting the imperfect saddle-shaped geometries

[c]When further considering extrinsic surface properties, such as domain size variations, the Gyroid emerges as more homogeneous than the Primitive and Diamond surfaces [34, 35].
[d]In order to study curvature variations, conditions on the length scale (called norms) must be imposed (see [10, 35]). The optimality of the Gyroid results for various physically motivated normalisations (same volume/surface area ratio and same average Gaussian curvature). The optimality comes only from the comparison with some classes of known minimal surfaces. A mathematically rigorous statement on minimum curvature variations would be useful.

commensurate with $\mathbb{E}^3$. In this sense, the cubic triply-periodic minimal surfaces appear to be nature's best (but not perfect) attempt at immersing $\mathbb{H}^2$ in $\mathbb{E}^3$.[e]

The critical reader may ask, what evidence does soft matter physics offer that the geometric mechanism for the formation of saddle-shaped lipid membranes actually reflects the dominant mechanisms? One indication comes from lipid systems that form two different cubic minimal surfaces: the Diamond and Gyroid. Such systems are often dominated by particular length scales (i.e. crystallographic lattice constants observed in scattering experiments): the two minimal surfaces adopt equivalent average values of the Gaussian curvature, where the average curvature value and the degeneracy with respect to the curvature variations are consistent with the above outlined conceptual link between molecular shape and interfacial curvature [39]. The size ratio is known in physical chemistry as the *Bonnet ratio* [39], and the transformation between the surfaces as the Bonnet transformation. The framework proposed in Refs. [9, 35] for the transformation mechanism now seems to be confirmed by experiment [38].

Hyperbolic Materials Geometry: New Designs for Space-filling Morphologies

We have seen that the cubic triply-periodic minimal surfaces (Gyroid, Primitive and Diamond) appear to be nature's best attempt at immersing $\mathbb{H}^2$ in $\mathbb{E}^3$. An interesting approach to increase complexity is to take $\mathbb{H}^2$ decorated by a simple pattern, such as a symmetric tiling, and build the minimal surfaces from this decorated hyperbolic plane. What we end up with is a triply-periodic minimal surface decorated by a symmetric hyperbolic pattern. This tiling pattern gives a partition of the surface, but the tile boundaries can also be considered as tracing paths in $\mathbb{E}^3$, describing a network-like structure. The projection of the patterns to periodic bicontinuous minimal surfaces naturally leads to periodic network-like structures.

The cubic structure of the mineral Sodalite (Fig. 11) in $\mathbb{E}^3$ is a good example of the projection of tilings from $\mathbb{H}^2$ to $\mathbb{E}^3$. The structure can be designed using a high symmetry tiling of $\mathbb{H}^2$ projected to the Primitive cubic minimal surface [27].

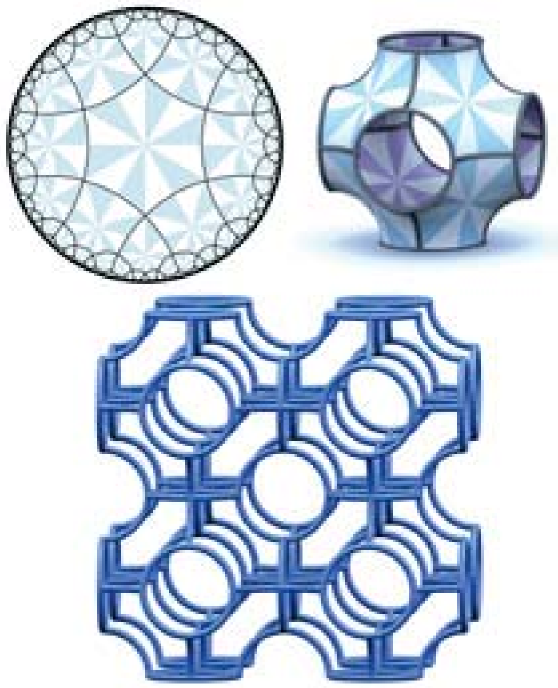

Fig. 11. The cubic structure of the mineral Sodalite can be described by a tiling of $\mathbb{H}^2$ projected to the Primitive cubic minimal surface.

Remarkably, a decorated Gyroid surface provides a possible explanation for the biological formation of the keratin filament geometry in skin. The keratin filament packing can be constructed by a symmetric and dense packing of lines in the hyperbolic plane, subsequently embedded as a decorated Gyroid surface [5, 6]. Figure 12 shows the specific hyperbolic pattern in solid black lines on the Poincaré disk[f] representation of $\mathbb{H}^2$. We can then warp this decorated $\mathbb{H}^2$ into the Gyroid to form a decorated surface. Interpreting these lines as cylindrical tubes with finite diameter and allowing them to minimise their length while retaining the tube diameter and avoiding overlaps, they relax to the structure of the keratin in the skin (during the relaxation, the lines leave their paths on the Gyroid and move into one of the two domains). Given the findings of the previous section that gyroid-like membranes result from self-assembly in biological matter [1], the existence of gyroid membranes appear possible in living skin

[e]There is no length preserving immersion of $\mathbb{H}^2$ in $\mathbb{E}^3$ as the Gaussian curvature of the surface is not constant. In fact, a length preserving immersion of $\mathbb{H}^2$ in $\mathbb{E}^3$ is impossible according to Hilbert. However, the length distortion of the immersion is small and therefore the variations of the Gaussian curvature are small. In this respect, we consider these surfaces as a best attempt at an immersion of $\mathbb{H}^2$ in $\mathbb{E}^3$, and in this sense call the surfaces a good immersion of $\mathbb{H}^2$.

[f]The Poincaré disk is a conformal model (angles on the disk correspond to angles in $\mathbb{H}^2$) that represents $\mathbb{H}^2$ as the interior of a circle, where $\mathbb{H}^2$ approaches infinity at the boundary of the circle. A geodesic is an arc of the circle that is incident at right angles to the boundary. Parallel lines in the hyperbolic plane are signified by lines that meet at the disc boundary [2].

Fig. 12. (L) The hyperbolic pattern in solid black lines on the Poincaré Disk representation of $\mathbb{H}^2$. (C) One unit cell of the decorated Gyroid that forms from forcing the decorated $\mathbb{H}^2$ into $\mathbb{E}^3$. (R) The paths that these Gyroid lines trace in space are shown: they are the paths of the keratin filaments in the skin structure [6].

cells. The described geometric construction would then correspond in broad terms to a polymerisation of keratin in a Gyroid membrane, where the keratin used the gyroid membrane as a polymerisation scaffold.

A similar process is presumed to happen in the butterfly wing formation, where chitin uses a Gyroid membrane as a self-assembly scaffold. A Gyroid membrane exists in the living cells before the chitin structure solidifies at a subsequent step of the life cycle. This idea of "membrane templating" is a broad concept observed in numerous biological systems. What is curious in the case of the keratin filament geometry in skin is that the structure that is formed has such high symmetry in the hyperbolic plane.

Another example of a hyperbolic pattern on the Gyroid comes from the self-assembly of star-like molecules [20]. The system is a numerical simulation of a mixture of Y-shaped star polymers, essentially a polymer with three arms (A-B-C or A-B-D). In these polymeric system, we observe a phenomenon known as "micro-phase separation": the attraction of A-type polymers to other A-types and a repulsion from all other types of polymer causes the system to segregate into domains composed solely of each type of polymer. In the pattern that self-assembles in our simulation system, the C and D domains fill the two channels of the Gyroid. The A and B domains together form a film between these channels that trace the Gyroid surface. But these A and B domains must also segregate, and they do so in a symmetric hyperbolic pattern, related to that associated with the skin packing (Fig. 13). These mesostructures are among the most topologically complex morphologies identified to date. The labyrinths within the gyroid film are densely packed and contain convoluted intergrowths of multiple nets.

The keratin structure of the skin and the pattern in the Y-star polymers (as well as simpler poly-continuous materials [8]) are examples that demonstrate that self-assembly processes can result in patterns, whose structure takes on fundamentally hyperbolic form. We now turn to the question of how the mapping from $\mathbb{H}^2$ into $\mathbb{E}^3$ via the triply-periodic minimal surfaces can be useful for the enumeration of new structures, such as design motifs for artificial micro-or nano-structured materials, from artificial bone [19] to photonic materials [28].

A large class of tessellations, packings of branched tree-like objects and packings of lines can be designed in $\mathbb{H}^2$. All of these are candidates for projection to the 3-periodic minimal surfaces. Thanks to extensive methods to enumerate such patterns in the hyperbolic plane [26, 5, 6], a comprehensive and systematic catalogue of symmetric structures in $\mathbb{E}^3$ results via projection to the minimal surfaces, which serve as structural motifs for new or previously unidentified structures. Of particular importance is the fact that

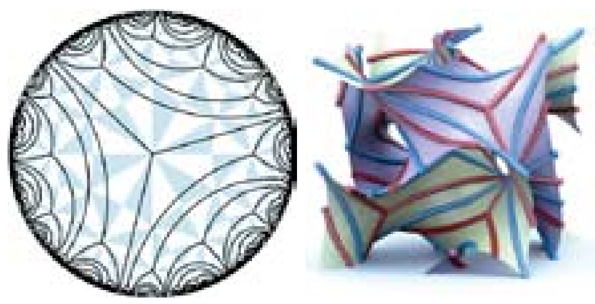

Fig. 13. The symmetric pattern in $\mathbb{H}^2$ and on the Gyroid, which describes the domains formed in a numerical simulation of polymer self-assembly [20]. The red and blue networks represent the A and B domains, respectively, as they segregate on the Gyroid.

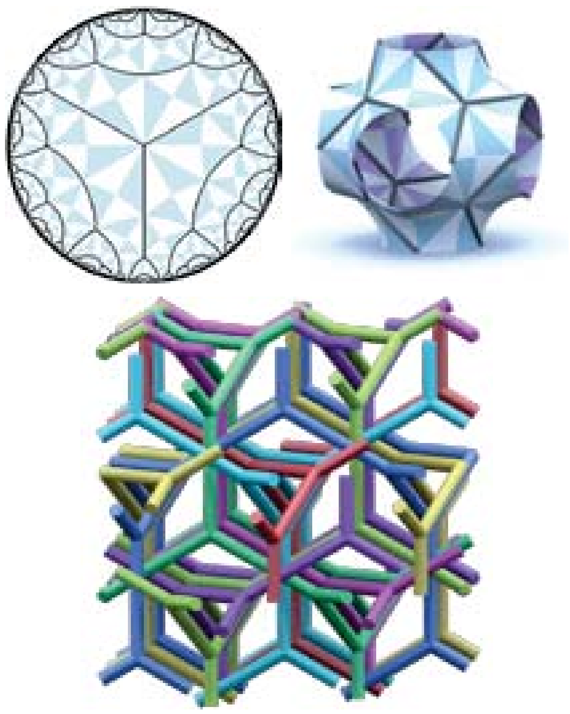

Fig. 14. An example of a hyperbolic pattern on the Primitive cubic minimal surfaces, from a hyperbolic packing of tree-like objects, which describes the interthreading of eight srs networks in space [16, 5]. The particular structure is potentially useful as a photonic material [28].

infinite patterns in $\mathbb{H}^2$ lead to periodic network-like percolating structures in $\mathbb{E}^3$, as opposed to finite structures resulting from projection onto a sphere. Such periodic structures are of particular importance for materials science and biology.

Structures that begin as hyperbolic tilings by finite disk-like tiles, where the tile boundaries form a single connected network in $\mathbb{H}^2$, end up as single connected networks when they become minimal surface decorations (Fig. 11). A database containing the simplest examples is known as the EPINET project [26][g].

Tiling $\mathbb{H}^2$ by infinite ribbon tiles gives tile boundaries that are infinite tree-like structures leading to more complicated structures in $\mathbb{E}^3$. The tree objects become networks in $\mathbb{E}^3$, and depending on how edges meet up, the number of networks interthreading each other varies (in some cases up to 64 networks sitting within each other). One such structure with 4 intergrown srs networks is shown in Fig. 14. A complete characterisation of the way that these structures interthread is still yet to be determined. In some cases, this entanglement can be visually arresting, such as in the woven structure containing four

[g]This database can be found online at epinet.anu.edu.au.

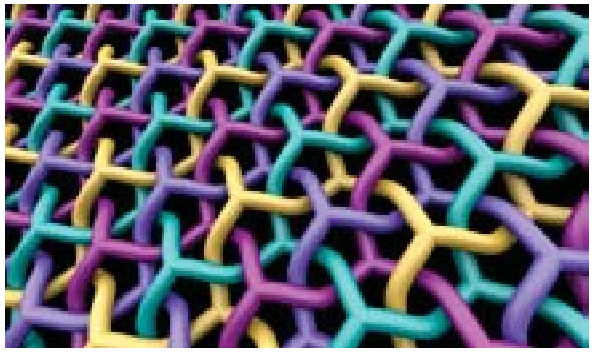

Fig. 15. A symmetric woven structure containing four interthreaded 2-periodic "honeycomb" networks.

simple 2-periodic "honeycomb" networks shown in Fig. 15.

Multiple interthreaded networks are useful in the materials sciences. A set of materials called metal-organic frameworks, where metals (vertices) are bonded together by long chain-like molecules (edges), form network-like frameworks. The length of the edges allows multiple networks to thread through each other, often resulting in very stable yet porous materials with high functionality, making them ideal for hydrogen, methane and carbon dioxide storage, among other applications [40]. Another application comes in the form of photonic materials, in which structures of multiple interwoven srs networks show remarkable properties with respect to circularly-polarised light [29, 28, 30].

When hyperbolic line packings are considered on minimal surface scaffolds, a zoo of filament weavings results, including the skin's keratin structure. Many weavings within this catalogue have similar mechanical properties to the skin structure, making them ideal candidates for new filamentous material designs. In general, the characterisation of such structures is poorly understood: A more robust characterisation is required to understand the scope of this process and identify more interesting examples in materials and nature. This is where mathematics is of great importance, creating an extension of the traditional studies of braids, knots and tangles to encompass these more complicated entangled structures.

The scope of such an enumerative process, including interthreaded networks and filament weavings, is broad and exciting. The small number of examples in soft matter and biomaterials is set to explode as more of these structures are examined. A critical part of this is the thorough characterisation of such structures, in which mathematics has a critical role to play. Through rigorous understanding of these structures comes further inspiration for the materials sciences. The reverse can also be true, where further understanding of biomaterials helps to motivate interesting geometric problems.

On the Role of Hyperbolic Geometry for Modern Materials

One way to describe the filament structure of human skin is, as we have seen, by reference to hyperbolic geometry. By virtue of the cubic triply-periodic minimal Gyroid surface, a symmetric line packing in $\mathbb{H}^2$ is transformed via a reasonably truthful embedding into the space $\mathbb{E}^2$ where all real-world materials — biological or synthetic — live. What can this description elucidate that is hidden in a simple crystallographic description of the structure? It gives us a way to think about structure in materials from a viewpoint and using a language that is close to the formation principles of the material. It also gives us a way to enumerate spatial structures and search for new material designs, in the class of topologically complex structures for which we have otherwise no agreed common scientific language.

Clearly, materials science and soft matter physics is not just geometry, and any such claim would defy the view taken in this article. However, where there is geometry (and Johannes Kepler famously declared this to be the case for all matter "*Ibi materia, ibi geometria*") a considerate and informed study of geometry can provide general insight into the formation and function of real-world materials, beyond details of a specific system. The choice of the "right" geometry is crucial, with mathematical tools and concepts well adjusted to the systems' underlying principles. When the materials of interest are network-like structures that extend spatially throughout space, then hyperbolic geometry dealing with saddle-shaped interfaces is the right choice.

This approach of *Materials Geometry* is as much of a call to natural scientists to open their minds to hyperbolic geometry as it is a call to mathematicians to draw inspiration for their field of study from the real-world problems of the natural sciences. While not disputing the need for rigorous mathematical endeavour into hyperbolic geometry, it is wise to remember that the common language for mathematics and natural sciences in this regard lies in the power of images and concepts, as well as in the sullied world of "Experimental Mathematics" where concepts of hyperbolic geometry, minimal surfaces and the like become virtual realities, accessible to both mathematicians and natural scientists.

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