Demonstration and interpretation of "scutoid" cells formed in a quasi-2D soap froth
(revised manuscript)

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ABSTRACT
Recently a novel type of epithelial cell has been discovered and dubbed the "scutoid". It is induced by curvature of the bounding surfaces. We show by simulations and experiments that such cells are to be found in a dry foam subjected to this boundary condition.

KEYWORDS
quasi-2D foams; scutoid; epithelial cells; T1 transition

1. Introduction

Recently a previously unreported form of epithelial cells has been described which appears when the epithelial tissue is curved, e.g. with local cylindrical curvature [1, 2]. The distinguishing feature of such a cell, called a *scutoid* by Gómez-Gálvez *et al.* [2], is a triangular face attached to one of the bounding surfaces of the tissue layer. Here we offer a simple illustration of this phenomenon, which is derived from the physics of foams [3], consisting of a computer simulation together with preliminary experimental observations.

In an ideal dry foam, bubbles enclose gas (which is treated as incompressible) and the energy is proportional to their total surface area. Alternatively, the soap films may be considered to be in equilibrium under a constant surface tension and the gas pressure of the neighbouring cells. Plateau's rules [4], more than a century old, place restrictions on the topology of a *dry* foam (one of negligible liquid content), which is the only case considered here.

From the earliest intrusion of physics into biology, this elementary soap froth model has attracted attention to account for the shape and development of cells [5, 6]. More sophisticated attempts to adapt it to that purpose persist today [7, 8, 9]. In the present context we show that the model largely accounts for the appearance of scutoids, in very simple and semi-quantitative terms, broadly consistent with the description in the original papers [1, 2].

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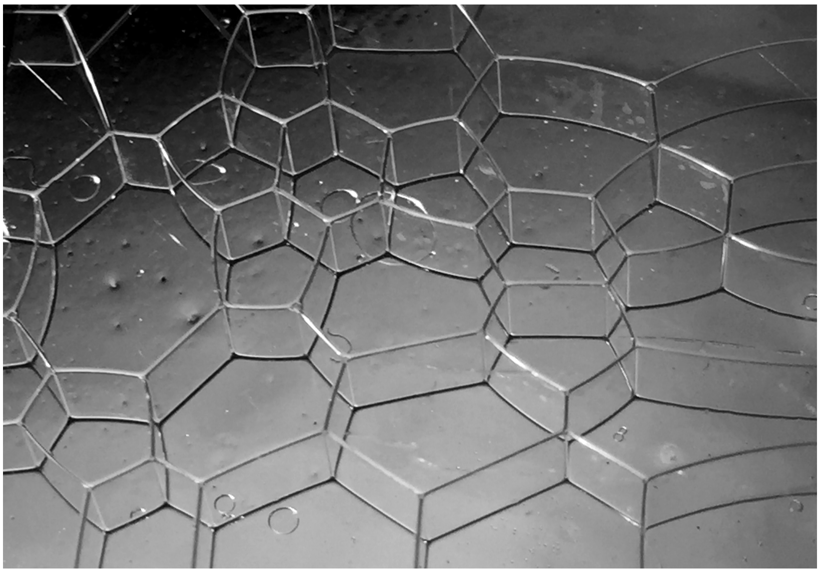

Figure 1. A quasi-2D foam showing a single layer of bubbles confined between two flat parallel glass plates (plate separation 8mm, average bubble diameter 2-3cm). Internal films meet the plates at right angles. The polygonal cells on both glass plates are identical.

2. Topology of dry foams

The relevance of foams to biology is apparent from the pioneering work of the botanist Edwin Matzke [10]. Inspired by the resemblance in shape between bubbles in foam and cells in tissues, Matzke sought to understand the forces that may be common to both. His approach was to painstakingly and exhaustively catalogue bubble shapes observed in a dry monodisperse foam, confined within a cylindrical jar. Matzke distinguished between peripheral bubbles (i.e. bubbles in contact with the walls of the cylindrical jar) and central bubbles (i.e. bubbles inside the bulk foam). Amongst the peripheral bubbles are listed two scutoids: the $(1, 3, 3, 1)$ (see Figure 9-8 of [10]) and $(1, 4, 2, 1, 1)$ polyhedra (using Matzke's notation). No triangular faces were found amongst the central (i.e. bulk) bubbles.

3. Quasi-2D foam sandwich

Cyril Stanley Smith [11] first introduced the experimental quasi-2D foam that is formed between two glass plates. The plates are close enough together that all bubbles touch both boundaries, so that there are no internal bubbles and the internal soap films meet the glass plates at right angles (see Figure 1). The quasi-2D foam between flat parallel plates is often taken as the experimental counterpart of the ideal 2D foam, which consists of polygonal 2D cells with (in general curved) edges meeting three at a time at 120^o. Such a finite foam sandwich presents *two* such patterns on its two boundaries, and indeed on any plane taken parallel to them. However, if the plate separation is increased, this structure is overtaken by an instability, described and analysed by Cox *et al.* [12], in which individual cells cease to span the gap between two plates. This instability is not directly relevant to scutoid formation but places limitations on both experiment and theory.

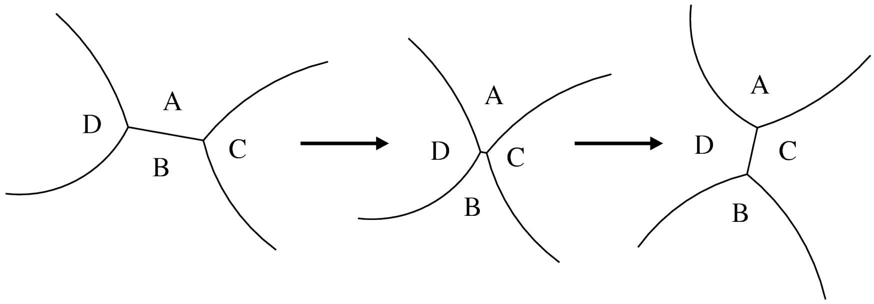

Figure 2. A schematic of a T1 transition in an ideal 2D foam or on the surface bounding a 3D/quasi-2D foam [15]. The edge shared between bubbles A and B gradually shrinks and vanishes, the resulting fourfold vertex is in violation of Plateau's laws and the system transitions to a new arrangement. As a result, bubbles A and B are no longer neighbours, while C and D (which were previously unconnected) now share a boundary.

The novel element that is brought into consideration by the work of Rupprecht *et al.* [1] and Gómez-Gálvez *et al.* [2] is the introduction of *curved* boundaries which may be represented by two concentric cylinders or a portion thereof. While there has been some work on the effects of curvature of one or both plates [13, 14], it has not addressed the case considered by Gómez-Gálvez *et al.*, which consists of two concentric boundaries.

When the separation between the two cylinders is infinitesimal there will be identical patterns on the two surfaces. However, if the separation is increased, the 2D patterns on the inner and outer surfaces become strained to accommodate the change in circumference. Eventually, this should lead to the vanishing of a 2D cell edge, and hence to a topological change, as in Figure 2 and also in Figure 1(c) of [2]. This is the so-called T1 process [15]. It necessarily entails the creation of a *scutoid* feature within the bulk of the foam (as illustrated in sections 4 and 5) which is responsible for the "apico-to-basal neighbour exchange" [1] that is observed. However, its appearance may be only transitory, as it may provoke a similar effect at the other surface, in a double-$T1$ process that restores the original columnar structure. The geometry required by Plateau's rules makes it obvious that this must be the case if the gap between the cylinders is very small. Increasing the gap is expected to allow stable scutoids to persist, provided we do not encounter the other type of instability mentioned above.

These arguments leave room for doubt as to whether such scutoid features can really be found in the foam sandwich. Both simulations and experiments, described in the following section, have yielded positive results.

4. Simulations

As in the simulations of [2], we start from a Voronoi partition of the gap between two concentric cylinders, to give a collection of hexagonal prismatic cells. This structure is imported into the Surface Evolver software [16], which permits the minimization of surface energy (here equivalent to surface area, as in the ideal foam model) subject to fixed cell volumes. We employ a periodic boundary condition in the direction of the axis of the cylinders to reduce the effect of the finite size of the simulation. Cell volumes are assigned fixed values within a restricted range so that the initial structure is polydisperse but still hexagonal. In the example shown in Fig 3a, the cylinder has

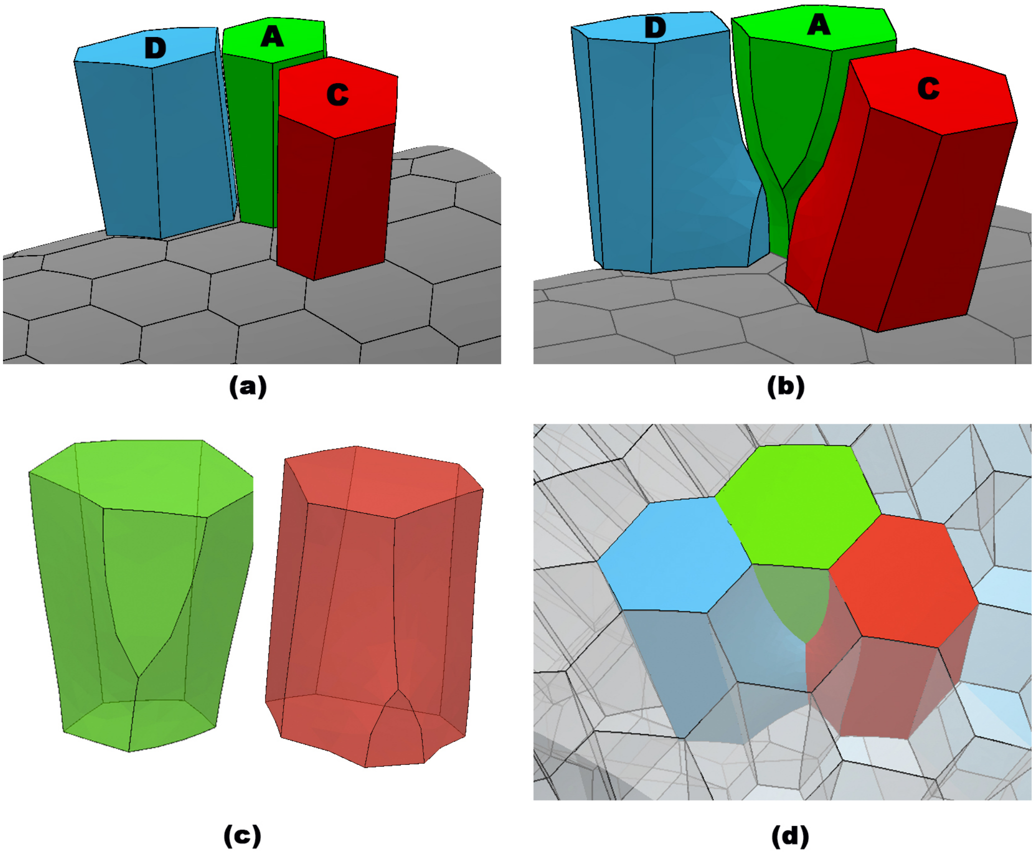

Figure 3. Cells in a Surface Evolver simulation of a polydisperse foam confined between two concentric cylinders. (a) In the initial state the 2D pattern on both boundaries is purely hexagonal (only the pattern on the substrate is shown). Red and blue bubbles are not in contact while the green bubble is in contact with a fourth neighbouring bubble (not shown for clarity). (b) The foam after a T1 transition on the substrate, resulting in four stable scutoid cells. The pattern on the substrate contains two five-sided and two seven-sided regions, while the pattern on the superstrate remains purely hexagonal. The cells are shown slightly separated for clarity. (c) The two types of scutoids cells (pentagonal and heptagonal) are shown separately. (d) A combined view showing the scutoids and the surrounding foam cells.

axis length 5.2 units, the cylinder radii are 2.8 and 4.3 units and there are 144 cells. To allow the cell walls between the cylinders to develop realistic curvature, we tessellate each face with about 40 triangles (average triangle area 0.01 units^2) and perform a standard Surface Evolver minimization of the surface area.

In this preliminary exploration, topological changes were triggered using the Surface Evolver software. A number of stable scutoids were identified of which one example is shown in Figure 3. The cell arrangement featuring the scutoids, Figure 3(b), is equilibrated, but its energy is about 0.3% higher than that of the original configuration of Figure 3(a), since it was provoked, rather than occurring spontaneously as is the case when the length of a cell edge shrinks to zero. In the continuation of this work we will examine this further by mapping out the parameter space in which such stable scutoids are to be found.

In our simulations we model cell edges as having infinitesimal thickness; however, our results are also of relevance to experimental findings, presented below, for foams with values of liquid volume fraction less than one percent. In this case the Decoration Theorem applies [17, 18], that is, the foams can be considered as essentially dry foams.

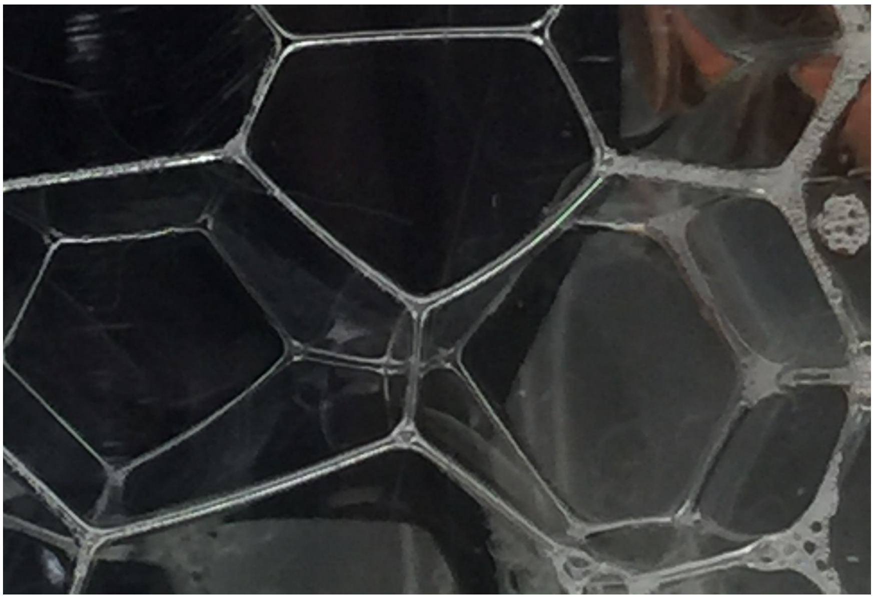

Figure 4. Photograph of scutoids in a quasi-2d foam sandwich. The bubble on the left features a hexagon in contact with the outer cylinder and a pentagon in contact with the inner cylinder while the bubble on the right shows a heptagon on the outer and a hexagon on the inner cylinder. Also visible is the small triangular face separating these two bubbles. (diameter of inner cylinder 21mm, internal diameter of hollow outer cylinder 39mm, spacing about 7mm, approximate equivalent sphere diameter of the bubbles 8 mm.)

Further simulations (and experiments) are required to study the stability of scutoids in foams of greater wetness.

5. Experiments with soap bubbles

We performed preliminary experiments with soap bubbles between curved surfaces, using a glass cylinder of diameter 21mm as a substrate and a hollow half cylinder (made from perspex) with inner diameter 39mm as a superstrate. The bubbles (approximate equivalent sphere diameter 8 mm) were produced using a simple aquarium pump with flow control and commercial dish-washing solution.

Both cylinders were placed horizontally into the vessel containing the solution; the outer half-cylinder was rested on an 8.5 mm support, resulting in a (minimum) gap between the two cylinders of approximately 7mm. This gap was initially about half filled with liquid. We then used a syringe needle attached to the pump to blow air into this gap, leading to the formation of a quasi-2D foam sandwich. By reducing the water level we created bubbles which were in contact with both cylinder surfaces, some of them forming scutoids, see Figure 4. The present process involves a measure of trial and error: repeated raising and lowering the water level allows for repeated bubble rearrangements which increases the chance of finding scutoids.

6. Conclusion

Both simulation and experiment have confirmed that stable scutoid configurations are to be found in a dry foam sandwich between cylindrically curved faces. It remains for future work, which we will undertake, to identify the conditions for this in terms of geometrical parameters.

In our simulations of an ordered foam, the scutoids (1,3,3,1,0) and (1,4,2,1,1), which were amongst the cell types listed by Matzke [10], appear in (two) pairs. In disordered foams, other scutoids should be found. If we define a scutoid to be a shape that has an N-sided face on one surface, an $N-1$-sided face on the opposite surface, and a triangular face attached to the surface with the N-sided face, then in addition there must be $(N-3)$ four-sided faces and two five-sided faces. The two scutoids above correspond to $N=6$ and 7. For $N=4$ and 5 this results in the additional scutoids (2,2,2,0,0) and (1,3,3,0,0), neither of which were amongst the cell types compiled by Matzke but which should be sought in disordered quasi-2D foams. For larger N scutoids all take the form $(1, N-3, 2, \ldots, 1, 1)$, and no other topologies are possible.

The foam model is well established in the description of biological cells and the processes by which they change their arrangements, but is at best a rough first approximation. In the present case we have noted that epithelial cells may be relatively elongated. If greater realism is called for, further energy terms may be added, stiffening the cell walls.

7. Acknowledgements

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