

Plasticity and topological defects in cellular structures: Extra matter, folds and crab moulting

N. Rivier^{a,*}, M.F. Miri^b, C. Oguey^c

^a LDFC, Université Louis Pasteur, Dept. Physique, 3 r. de l'Université, 67084 Strasbourg, France

^b IASBS, Zanjan, Iran

^c Université de Cergy-Pontoise, Cergy, France

Received 2 November 2004; accepted 31 January 2005

Available online 11 March 2005

Abstract

This paper is concerned with elasticity and plasticity of two-dimensional cellular structures. The deformation of continuous media is defined by a mapping from the actual, deformed state of the material, into a reference (natural) state, where all elastic deformations have been relaxed. In two dimensions, the two states can be represented by a complex variable each, and the map, by a meromorphic function. Topological defects correspond to the singularity of the map: disclinations, dislocations and extra-matter, which appears as a fold or as a bulge. We show that these abstract concepts find a direct, geometric illustration in foams.

The dual of a two-dimensional foam is a triangulation. The triangles are the finite elements for the two states of the material, with the vertices carrying the elementary defects. The meromorphic function can be analytically continued outside the basic triangle, and finite elements joined together in a natural fashion. The mapping enables us to define topological defects geometrically, and to compute their effect by contour integrals, and their image in the reference state. Disclinations alone can be defined intrinsically in the actual state of the material, without mapping into the reference state. For dislocation and extra matter, the mapping determines the (Burgers) contour integral, in its non-closure or its integral content, respectively.

Before moulting, the crab has prepared its new shell that lies under the old one, folded, but metrically perfect and with all its topological intricacies. It stretches just after moulting through ingestion of salt water. Successive cellular divisions create the necessary folds.

© 2005 Elsevier B.V. All rights reserved.

Keywords: Two-dimensional cellular structure; Foam; Moulting; Dislocation

1. Introduction: plasticity and extra matter

Any solid material is stretched if one pulls on it. If the material recovers its initial shape when one stops pulling, the deformation was elastic. If it does not, the deformation is plastic. Stretched spring is elastic, whereas chewing gum is plastic. Cell division, like any topological transformation, is plastic. But human skin, when pinched slightly, is elastic. It is plastic when pinched hard. Plasticity describes how solids flow, through the motion (chiefly glide) of dislocations. Dislocations were introduced in the 1930s to explain why metals could flow, and how this flow could be prevented (by alloy-

ing or by hammering, technologies known since prehistory) [1]. A foam (cellular material) behaves collectively as a (soft) solid (plug flow, dislocation glide) in spite of the fact that it is made of liquid (interfaces) and gas (bubbles) [2].

The deformation of a material is measured by comparison with a reference state that is locally not deformed. Thus, the elasticity and plasticity of a material are given by a mapping $z(w)$ from the actual, deformed state of the material (described in 2D by a complex coordinate w), into a reference state, originally called natural state [3], where all stresses have been relaxed. The reference state (described in 2D by the complex coordinate z) has no elastic strain: Only topological, plastic deformations remain and the material is free of any constraint except connectivity along paths. The source of plastic deformation is a topological defect, characterized

* Corresponding author. Tel.: +33 390240651; fax: +33 390240669.
E-mail address: nick@fresnel.u-strasbg.fr (N. Rivier).

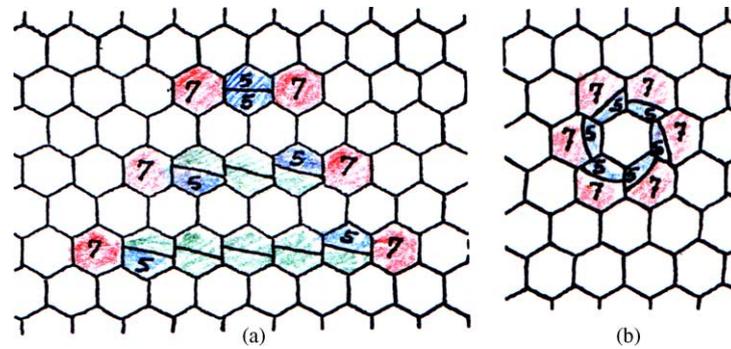


Fig. 1. Extra matter (additional layer of cells) produced by successive mitoses, i.e. by climb of one dislocation (5/7) from the other; from [5], with permission. (a) If the first division is symmetrical ($6 \rightarrow 5/5$), the tissue remains topologically flat (it has a smooth fold, a ridge (Λ -shaped) or a groove (V-shaped) between the two 7-sided cells). (b) If the first division is asymmetric ($6 \rightarrow 4/6$), a bump or a dip is produced. (There are no 3-sided cells in mammalian epidermis or in the crab's cuticle.)

by a singularity in the mapping. In a two-dimensional foam, the reference state is a honeycomb. An $n \neq 6$ -sided cell is a plastic deformation from the 6-sided, reference cell. It carries a topological charge $q = 6 - n$. The coordinate z of the reference state is non-holonomic¹ in general: it only counts the number of steps along a path. We will see (Section 4) that the mapping is from a single-valued, meromorphic function² of a continuous variable w , into a multivalued, geometrical, equilateral triangulation.

In classical electromagnetism, a charge is identified by the integral (Gauss) of the electric field over any contour (a surface) enclosing it; a current, by the integral (Ampère) of the magnetic field over any line contour enclosing it. Similarly, a topological defect in elasticity is measured by the integral of the deformation field over a closed contour surrounding it. The closed contour in the actual state is mapped, in the reference state, into a path that is generally no longer closed. The mismatch between end points in the reference state also measures the topological defect. If it is a missing number of steps, the distance between end points is called Burgers vector; it identifies a dislocation. If the mismatch involves a rotation, the defect is a disclination.

In continuous materials, there are three types of topological defects, disclination (source of curvature—the Riemann tensor \mathbf{R}), dislocation (source of torsion—the torsion tensor \mathbf{T}), and extra matter [3] (source of non-metricity \mathbf{Q} , defined by $\mathbf{D}_k \mathbf{g}_{ij} = \mathbf{Q}_{kij} \neq 0$, where \mathbf{D} is the covariant derivative, and \mathbf{g} is the metric tensor, related in elasticity theory to the strain tensor $\mathbf{e} = (1 - \mathbf{g})/2$ [4]. All these tensors can be expressed in term of the mapping $z(w)$.

In two-dimensional foams, discrete, random cellular materials, a disclination is a non-hexagonal cell: an n -sided cell has topological charge $q_n = 6 - n$. The elementary disloca-

tion (with smallest Burgers vector) is a dipole 5/7.³ Extra matter consists of additional cell(s), for example through cell division(s). The first division creates a pair of opposite dislocations. Then, one of the dislocations climbs away from the other through successive divisions (Fig. 1). Thus, in a cellular material like a biological tissue, growth, the intrinsic production of extra matter by cellular division, is plasticity, the motion (climb) of dislocations, induced by very specific stresses (mitotic pressure and mechanical stress caused by overcrowding and rigid boundary conditions).⁴ We consider crab moulting as an illustration [5,6].

Plasticity is a global property of the foam as a cellular network. Cells are simply the seat of elementary topological transformations of specific types (T1, T2 in soap froths, cell division as symmetrical as possible in the crab's cuticle). At this level, we take for granted the existence of stable interfaces between geometrical cells through interfacial tension (surfactant in soap froths, magnetic interactions in ferrofluid foams [7], belt desmosomes for the crab [8]).

2. Cell division, extra matter, and crab moulting

It is well-known that the basal layer of the epidermis (of mammals), and epithelia (of plants), are two-dimensional foams, random cellular materials subject to local topological transformations [9–11]. The renewal of the epidermis of mammals is a problem of establishing steady state (an invariant population distribution of n -sided cells, p_n , with a number of cells N fluctuating but bounded above and below) under the local topological transformations of cell division

¹ Not integrable: it depends on the path from an origin.

² “A function is said to be meromorphic in a region if it is analytic in the region except at a finite number of poles. The expression is used in contrast to holomorphic, which is sometimes used instead of analytic” [18], p. 110.

³ M.F. Ashby [19] was the first to study the elasticity and plasticity of ordered cellular solids, notably in terms of topological dislocations.

⁴ A foam under shear undergoes a more conventional kind of plasticity: The shear stress creates first, through a T1 transformation, a pair of dislocations. Then, one of the dislocations glides away from the other through successive T1 [2,9].

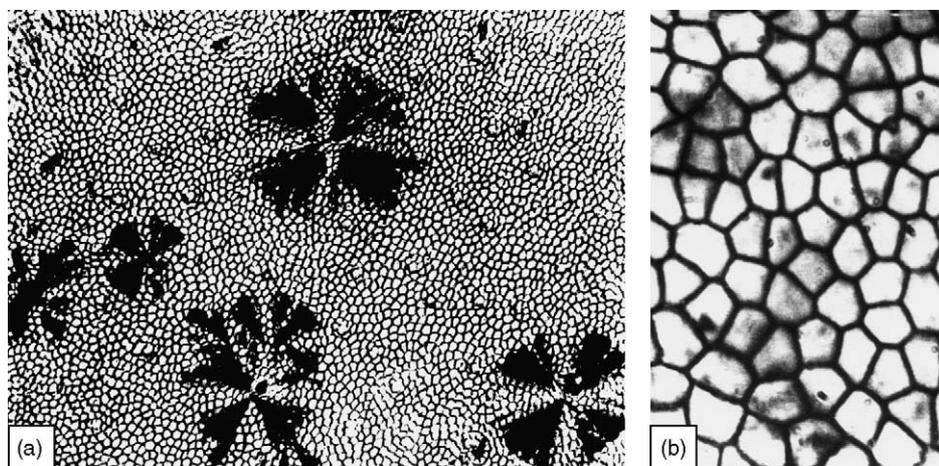


Fig. 2. The crab's new cuticle shortly after the molt resembles a 2D foam. (a) The new cuticle, observed here in polarizing microscopy between parallel polarizers. The "Maltese crosses" correspond to the radial development of calcite, in the first stages of mineralization. The boundaries of epidermal cells remain visible as traces on the cuticle. (b) This mosaic is well resolved in the cuticle, through detection of carbonic anhydrase. Micrographs due to Y. Bouligand (a) and M.-M. Giraud-Guille (b).

(mitosis) and cell detachment from the basal membrane [10], that are combinations of the elementary T1 and T2 in soap froths. The physical constraints are moderate: slight, steady mitotic pressure, for a structure that remains statistically invariant over eighty years (for humans) whereas a basal cell divides or detaches every week.

The renewal through moulting of the crab's carapace ("cuticle") operates, by contrast, under extreme physical constraints, even though its structure is, at first sight, no different from that of a two-dimensional soap froth or of an epithelium (Fig. 2).

The crab's carapace (old cuticle) is a protective shell, that is fairly hard and cannot grow. It must be shed (moulting) at intervals. The replacement cuticle is prepared under the old one on the epidermis, a single layer of cells responsible for its architecture, notably for its curvature through disclinations. Upon moulting, the new cuticle is exposed, a folded, larger and conformal copy of the old cuticle. The crab then absorbs a considerable amount of water to unfold its cuticle. It has thus prepared, without cutting or sewing, a much larger new cloth under the old one that has become too small, a remarkable achievement of mechanical engineering [5]. The crab produces the new cuticle in a short burst of mitotic activity, squeezed between the old cuticle and the epidermis, under considerable mechanical constraints. Here, the number of cells N is not constant, so that mitosis is the main topological transformation. The relevant topological defects are disclinations (to reproduce the local curvature) and extra-matter [4].

The main mechanism for growth is cell division or mitosis. One division on a hexagonal foam produces two dislocations head-on $7/5 \setminus 5/7$. Since cells with $n > 6$ are more likely to divide, as evenly as possible [10], and the dividing interface adds a side to the two neighbour cells involved, the 7 will divide next into $6 \setminus 5$, restoring into an hexagon the pentagon in

its wake, and changing the hexagon astern into an heptagon, etc. One dislocation climbs away from the other: $7/5 \setminus 5/7 \rightarrow 7/5 \setminus 6/6 \setminus 5/7 \rightarrow \dots \rightarrow 7/5 \setminus 6/6 \dots \setminus 6/6 \setminus 5/7$, leaving behind an extra layer of cells, extra matter indeed (Fig. 1). This mechanism for tissue growth by successive mitoses (dislocation climb) has been suggested originally by Lewis [12] and discussed by Pyshnov [9,13]. It does not require any cutting and regluing, unlike the formal Volterra process (Fig. 3: $a \rightarrow b$). But it always involves pairs of opposite dislocations which may be far apart, and the total Burgers vector is zero. Fig. 1 shows also that extra-matter is a podium in the stratification of Oguey et al. [14] (a), or even a full shell (b).

3. Plasticity in cellular networks

The actual state is a two-dimensional foam, a random, space-filling cellular network, a regular graph with vertex degree (coordination) 3. The natural, reference state is a perfect hexagonal tiling, but on a Riemann surface with branch points (Fig. 3c, e, g and i). Alternatively, one can use the dual representation, a triangulation, with vertices of random degree at the centre of the cells of the foam. In the reference state, the triangles are all equilateral and of the same size. The image of a closed contour in the actual state is, in the reference state, a band of edge-sharing equilateral triangles and the mismatch between end points is an integer in translation and in rotation by $2\pi/6$. The reference state is a triangular lattice on a Riemann surface with branch points at its vertices with $q \neq 0$.

The foam, a discrete cellular material with cells of various sizes, has a topological and combinatorial representation in the reference state, which is a tiling of identical, equilateral triangles, glued edge-on-edge. The mapping $z(w)$ maps

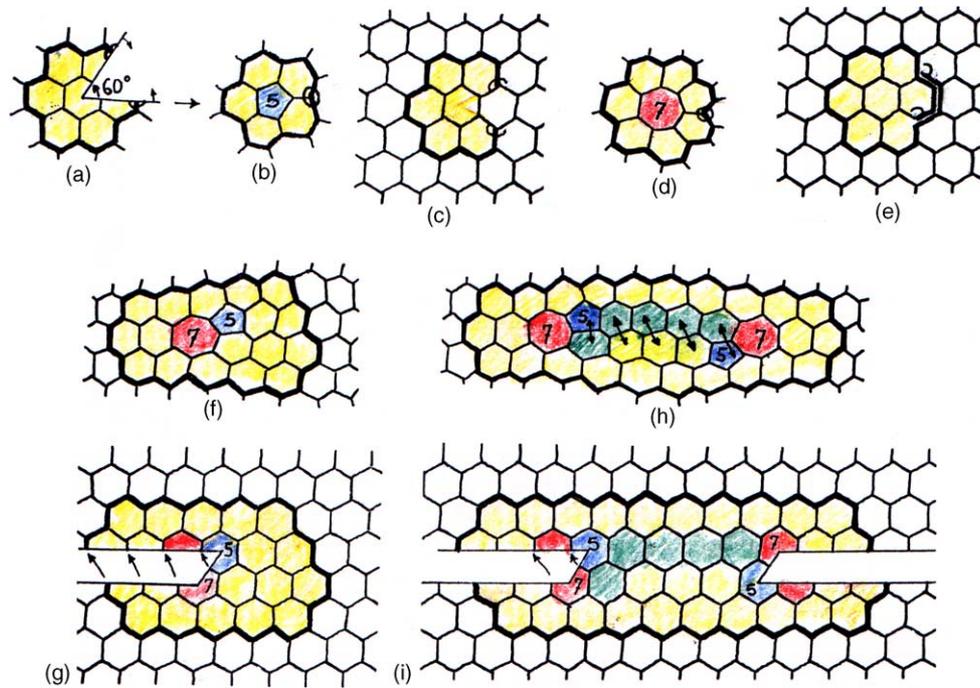


Fig. 3. Topological defects and Burgers contour (thick line) in a cellular network; from [5]. Mapping real state (b, d, f and h) \rightarrow reference state (a, c, e, g and i), in the foam representation: b \rightarrow c: disclination (5); d \rightarrow e: disclination (7); f \rightarrow g: dislocation (5/7); h \rightarrow i: extra matter, through successive cell divisions (mitotic axis shown by the double arrow), i.e. through dislocation climb (Lewis' process). The Burgers vector (single arrow) is perpendicular to the moment of the dislocation(s) (strictly, the moment of the dipole of the topological charges $+1/-1$ constituting the dislocation 5/7) enclosed. (a \rightarrow b is the formal Volterra process).

a single-valued meromorphic function into a multi-valued, geometrical tiling of equilateral triangles.

4. Burgers theorem in two-dimensional foams

A 2D foam is a discrete, random cellular structure, with minimal incidence (three edges and cells incident on each vertex, two cells on each edge). In the actual state, the structure is a tessellation: It is space-filling and single-valued, but the elements, the cells, have various sizes and shapes. In the reference state, the structure is still a foam, but it is metrically regular, and multi-valued.

We set the foam (actual state) on a torus (periodic boundary conditions). The structure of the foam is described by an elliptic function, a doubly periodic, single-valued meromorphic function $\Phi(w)$. The singularities are disclinations located at the centre of non-hexagonal cells. They are zeroes or poles of order $q_n = 6 - n$, at $w = w_I$, the coordinate of the centre of the n -sided cell, or of the vertex in the dual triangulation.⁵ The elliptic function has a Laurent expansion around w_I :

$$\Phi(w) = c_q(w - w_I)^q + c_{q+1}(w - w_I)^{q+1} + \dots \quad (1)$$

⁵ Cells are labelled by capital latin letters (I, J, \dots), edges by greek letters (α, β, \dots) and vertices by l.c. latin letters (i, j, \dots). Edges on the contour O have index $\alpha\partial$; vertices are labelled $i\partial+$ ($i\partial-$) if the third incident edge comes from outside (resp. inside) O .

and its logarithmic derivative has a simple pole of residue q at w_I ([15], p. 684–687):

$$(\ln \Phi)' = \left[\frac{q}{(w - w_I)} \right] \left[1 + \left(\frac{c_{q+1}}{qc_q} \right) (w - w_I) + \dots \right]. \quad (2)$$

It is more convenient to work in the dual representation of the foam, a *triangulation*, with vertices at w_I . For the foam as a material, the triangles are the finite elements. The elliptic function $\Phi(w)$, analytic in one of the triangles, can be analytically continued across the edges of the triangle by Schwarz's reflection principle ([16], pp. 354–359), and defined thus on the entire torus. The reference state is a Riemann surface with branch points (at disclinations), made of equilateral triangles, or, in the foam representation, of perfect hexagons. The mapping of elasticity theory is realised simply by stacking equilateral triangles and following the analytic continuation in the actual state.

Consider a closed contour O in the actual (deformed) state, made of e edges $\alpha\partial$, v^+ vertices ($i\partial+$) with the third incident edge coming from outside and v^- vertices ($i\partial-$) with the third incident edge from inside O . We will recover the old [17] result that the total topological charge Q_O enclosed in O is the integral over O (the flux of edges across O [17]):

$$Q_O = \sum q_I = \left(\frac{1}{2i\pi} \right) \int_O [\ln \Phi(w)]' dw = 6 - (v^+ - v^-), \quad (3)$$

and show that the total first moment of the topological charge is a contour integral

$$\sum q_I w_I = \left(\frac{1}{2i\pi}\right) \int_O w [\ln \Phi(w)]' dw = \sum_C \mathbf{z}^* = -\mathbf{b}^*. \tag{4}$$

(If a single dislocation (5/7) is enclosed in O , $\sum q_I w_I = w_5 - w_7$.) Here, C is the (open) image in the reference state of the closed contour O (it is a continuous path of edges in a hexagonal lattice, see Fig. 3). \mathbf{z}^* is a vector attached to each vertex on C , of constant length and directed along the third incident edge, i.e. positive if the vertex is $i\partial+$, and negative if it is $i\partial-$. $\mathbf{b}_i^* = \varepsilon_{ij} b^j$ is the dual vector to the Burgers vector \mathbf{b} , defined as the non-closure of the contour C in the reference state.⁶

In the foam representation, C is a path of edges of a perfect honeycomb lattice (Fig. 3). In the triangulation, it is a band of equilateral triangles attached edge-on-edge. If the closed contour O encloses no net disclination, i.e. if $Q_O = 0$, one has “distant parallelism”; \mathbf{b}^* and the Burgers vector are then topological invariants, independent of the starting point on O . We have chosen the two contours of Fig. 4 accordingly.

The expressions on the left of Eqs. (3) and (4) are homogeneous polynomials, of degree 0 and 1, respectively, in the coordinates of the singularities of $\Phi(w)$, that is of the centres of the non-hexagonal cells in the foam representation, or of the non-6-valent vertices of the dual triangulation. Inside the closed contour O , the independent variables are the coordinates w_I , the vertices in the triangulation (faces of the foam). The coordinates of the other elements of the triangulation are defined by incidence relations (non-oriented):

$$\begin{aligned} \text{vertices : } w_i &= \left(\frac{1}{3}\right) (w_I + w_J + w_K), \\ \text{edges : } w_\alpha &= \left(\frac{1}{2}\right) (w_I + w_J), \end{aligned} \tag{5}$$

i.e. the centre of mass of the incident elements.

On the closed contour O , the coordinates are the vertices $w_{i\partial}$, which split in two classes $i\partial+$ and $i\partial-$, depending on the direction of the third incident edge (not on the contour). The edges on the contour have coordinates $w_{\alpha\partial} = (w_{i\partial}^{+/-} + w_{j\partial}^{+/-})/2$, when the vertices $i\partial$ and $j\partial$ are neighbours bounding edge $\alpha\partial$. Thus,

$$\sum_{\alpha\partial} w_{\alpha\partial} = \sum_{i\partial} (w_{i\partial}^+ + w_{i\partial}^-). \tag{6}$$

There are $f + v^+ + v^-$ independent variables, w_I and $w_{i\partial}$. All the incidence relations remain valid in the reference state, and if the foam is translated by an arbitrary constant.

Denoting by f_n, e, v the total numbers of n -sided faces, edges and vertices within O (including those on the contour), and by $e_\partial, v_\partial^+, v_\partial^-$, the numbers of edges and vertices of each

class on the contour O , we have the incidence/boundary, and Euler relations:

$$\begin{aligned} 2e &= 3v - v_\partial^+; & \sum_n n f_n &= 2e - e_\partial; \\ e_\partial &= v_\partial^+ + v_\partial^-; & 6[f - e + v] &= 6 \end{aligned} \tag{7}$$

since an edge is bounded by two vertices, and three edges are incident on a vertex (two if it is a $\partial+$ vertex on the contour O); an n -sided face is bounded by n edges, and an edge separates two faces (only one if the edge is on O).

One evaluates the sum over the edges and vertices coordinates,

$$2 \sum w_\alpha = \sum_n n \sum_{I(n)} w_{I(n)} + \sum_{i\partial} (w_{i\partial}^+ + w_{i\partial}^-) \tag{8}$$

and

$$3 \sum w_i = \sum_n n \sum_{I(n)} w_{I(n)} + \sum_{i\partial} (w_{i\partial}^+ + w_{i\partial}^-) + \sum_{i\partial} w_{i\partial}^+. \tag{9}$$

in terms of the independent variables w_I and $w_{i\partial}$, by using relations (5) and (6). Here $I(n)$ labels the n -sided cells. The sums \sum on the left-hand side involve all edges or vertices, inside and on the contour O . The Eulerian combination of (8) and (9) with $\sum w_I$ yields,

$$\begin{aligned} 6 \left[\sum w_I - \sum w_\alpha + \sum w_i \right] \\ = \sum q_I w_I + \sum_{i\partial} (w_{i\partial}^+ - w_{i\partial}^-), \end{aligned} \tag{10}$$

with $\sum q_I w_I = \sum_n (6 - n) \sum_{I(n)} w_{I(n)}$. The bracket on the left depends only on the bulk variables, since the boundary contribution $-\sum_{\alpha\partial} w_{\alpha\partial} + \sum_{i\partial} w_{i\partial}$ vanishes through (6). On the boundary, there are normal, oriented edges, linking vertex $(i - 1)\partial-$ to vertex $i\partial+$, separated by isolated vertices, $j\partial^{++}$ (if j and $j - 1$ are both outwards $\partial+$) and $j\partial^{--}$ (if j and $j + 1$ are both inwards $\partial-$). Accordingly, $\sum_{i\partial} (w_{i\partial}^+ - w_{i\partial}^-) = \sum (w_{i\partial}^+ - w_{i-1\partial}^-) + \sum w_{j\partial}^{++} - \sum w_{j\partial}^{--}$.

Let us translate the foam. All the coordinates in (10) are replaced by $w + a$, where a is the position of an arbitrary origin. Thus,

$$\begin{aligned} 6 \left[\sum w_I - \sum w_\alpha + \sum w_i \right] + 6a \\ = \sum q_I w_I + Q_O a + \sum (w_{i\partial}^+ - w_{i-1\partial}^-) \\ + \sum w_{j\partial}^{++} - \sum w_{j\partial}^{--} + (v_\partial^+ - v_\partial^-) a. \end{aligned} \tag{11}$$

Arbitrariness of a yields the Gauss integral for foams (3): $Q_O = \sum q_I = 6 - (v_\partial^+ - v_\partial^-)$, relating the total topological charge enclosed by the contour to the flux of the edges through the contour [17]. Moreover, if the contour encloses no net disclination, $Q_O = 0$ (distant parallelism [3,4]), one can choose as the origin a the “centre of mass” defined by $6 \left[\sum w_I - \sum w_\alpha + \sum w_i \right] - (\sum w_{i\partial}^{++} - \sum w_{i\partial}^{--}) = 0$, so that,

$$\sum q_I w_I = - \sum (w_{i\partial}^+ - w_{i-1\partial}^-). \tag{12}$$

⁶ The Burgers vector \mathbf{b} is a lattice vector of the hexagonal lattice, which is the reference state of a two-dimensional foam, by definition.

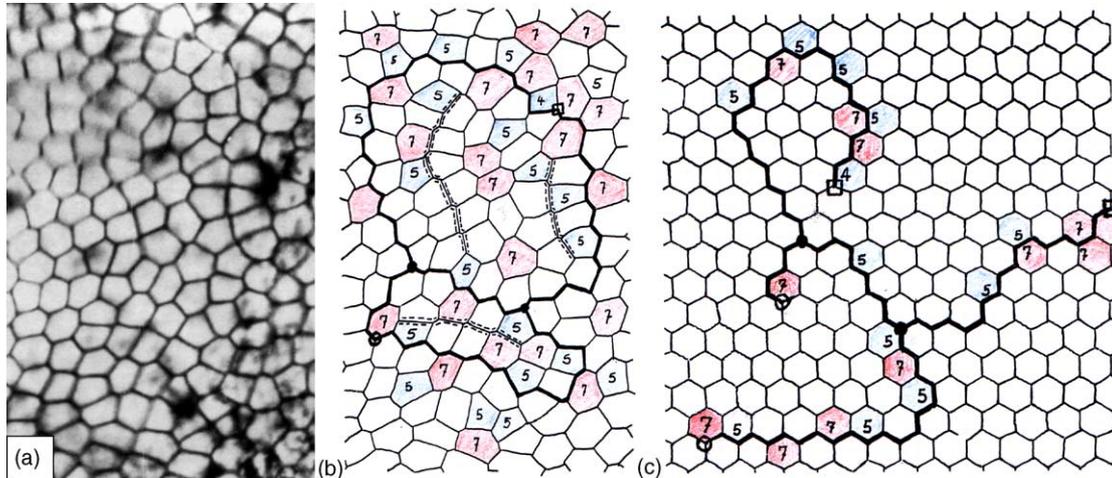


Fig. 4. Burgers contour and mapping from the real to the reference state on the crab's cuticle. (a) A fragment of the new cuticle, shortly after moulting. (b) The corresponding cellular graph, real state of the topological foam. The non-hexagonal cells are labelled. The alignments of recent interfaces are marked; they could correspond to folds (see Figs. 2a and 3h). Two contours (thick line) enclose one or two folds; the black dots mark the limits of the common segment. The arbitrary start and finish points of the two contours are indicated by a square and a circle. (c) The images of the two contours in the reference state, with the same reference points. The contours are no longer closed. For each contour, the Burgers vector joins the image of the start and finish points. It is independent of the choice of the starting point. Picture by M.-M. Giraud-Guille, from [5], with permission.

This is the contour integral (4). In the reference state, the right-hand side is perpendicular to the Burgers vector \mathbf{b} , the missing segment between end points in the band of equilateral triangles. The results (3) and (4) are geometrically evident in Fig. 3, through the principle of superposition (linearity of Eqs. (3) and (4)). Incidentally, additivity of two contours follows from the fact that an oriented edge ($w_{i\partial}^+ - w_{(i-1)\partial}^-$) of the common segment has the opposite sign in each contour.

In this paper, we have discussed the importance of topological defects in two-dimensional foams and shown how to calculate them by contour integration. Topological defects are associated with non-hexagonal cells, carrying a topological charge $q = 6 - n$. Disclinations (cells with $q \neq 0$) and dislocations (dipoles 5/7) are well-known [9]. On the other hand, extra-matter is a new concept in cellular networks. Its source is cell division (the generalized elementary topological transformation $(T2)^{-1}$). Repeated divisions make a dislocation climb, leaving behind an additional layer of cells. This plastic deformation is essential in the renewal of biological tissues.

Acknowledgements

Yves Bouligand (EPHE, Angers) has made many important contributions to this paper, besides those acknowledged specifically [5,6,8]. He has suggested to us the problem of the crab's moult, and Section 2 is his story, as written by one of us (N. Rivier). He has also prepared the figures. We are grateful to him and to M.-M. Giraud-Guille for allowing us to present them here. Last but not least, N. Rivier acknowledges many stimulating discussions with him, and his always pertinent criticisms. The referee's enlightened scepticism has also been very helpful in making this paper more intelligible in different scientific circles.

References

- [1] N.F. Mott, *La Structure atomique et la Résistance des Métaux*, Dunod, 1958.
- [2] E. Collé, N. Rivier, *Rhéologie de mousses ordonnées*. *Rheologie et Interfaces*. 39ème colloque annuel du GFR, Mulhouse, oct. 2004, pp. 22–26; D. Reinelt, P. Boltenhagen, N. Rivier, Deformed foam structure and transitions in a tube, *Eur. Phys. J. E* 4 (2001) 299–304.
- [3] E. Kröner, *Erg. Angew. Math.* 5 (1958) 1.
- [4] M.F. Miri, N. Rivier, Continuum elasticity with topological defects, including dislocations and extra-matter, *J. Phys. A: Math. Gen.* 35 (2002) 1727–1739.
- [5] Y. Bouligand, *Problèmes de morphogenèse cuticulaire chez les Crustacés*. *Aspects récents de la Biologie des Crustacés*, Xème Réunion des Carcinologistes de Langue Française. IFREMER, Actes de Colloques 8 (1988) 13–31 (S); Y. Bouligand, *La mémoire de l'épiderme chez les crabes et les autres*, Communication 2502, SFP, 5èmes Journées de la Matière Condensée, Poitiers, 2000, p. 806.; Y. Bouligand, M.-M. Giraud-Guille, N. Rivier, *La mémoire de l'épiderme chez les crabes*, unpublished.
- [6] M.-M. Giraud, Carbonic anhydrase activity in the integument of the crab *Carcinus maenas* during the intermolt cycle, *Comp. Biochem. Physiol. A* 69 (1981) 381–387; M.-M. Giraud-Guille, Calcification initiation sites in the crab cuticle, the interprismatic septae, an ultrastructural cytochemical study, *Cell Tissue Res.* 236 (1984) 413–420; Y. Bouligand, *Les solides mésoporeux d'intérêt biologique*, *L'Actualité Chimique*, 4–15 (juillet 2003); A.-N. Vitzou, *Recherches sur la structure et la formation des téguments chez les Crustacés Décapodes*, *Arch. Zool. Exp. Gén.* 10 (1882) 451–576.
- [7] F. Elias, *Organisation de motifs bidimensionnels de ferrofluide: la structure cellulaire*, PhD thesis, Université Paris VII, 1998; F. Elias, I. Drikis, A. Cebers, C. Flament, J.-C. Bacri, Undulation instability in two-dimensional foams of magnetic fluids, *Eur. Phys. J. B* 3 (1998) 203–209.
- [8] Y. Bouligand, private communication; B. Alberts, D. Bray, J. Lewis, M. Raff, K. Roberts, J.D. Watson,

- The Molecular Biology of the Cell, third ed., Garland Publ., New York, London, 1994 (chapter 19).
- [9] D. Weaire, N. Rivier, Soap, cells and statistics—random patterns in two dimensions, *Contemp. Phys.* 25 (1984) 59–99.
- [10] B. Dubertret, N. Rivier, The renewal of the epidermis: a topological mechanism, *Biophys. J.* 73 (1997) 38–44.
- [11] N. Rivier, A. Lissowski, On the correlation between shapes and sizes of cells in epithelial mosaics, *J. Phys. A* 15 (1982) 143–148.
- [12] F.T. Lewis, The geometry of growth and cell division in epithelial mosaics, *Am. J. Bot.* 30 (1943) 74–81.
- [13] M.B. Pyshnov, Topological solution for cell proliferation in intestinal crypt—elastic growth without cell loss, *J. Theor. Biol.* 87 (1980) 189–200.
- [14] C. Oguey, N. Rivier, T. Aste, Stratifications of cellular patterns: hysteresis and convergence, *Eur. Phys. J. B* 33 (2003) 447–455;
- C. Oguey, N. Rivier, Roughness and scaling in cellular patterns: analysis of a simple model, *J. Phys. A: Math. Gen.* 34 (2001) 6225–6238;
- T. Aste, D. Boosé, N. Rivier, From one cell to the entire froth, *Phys. Rev. E* 53 (1995) 6181.
- [15] M.A. Lavrentiev, B.V. Shabat, *Methods of the Theory of Functions of a Complex Variable*, Mir, Moscow, 1972.
- [16] B.A. Fuchs, B.V. Shabat, *Functions of a Complex Variable and Some of Their Applications*, vol. I, Pergamon Press, Oxford, 1964.
- [17] N. Rivier, T. Aste, Curvature and frustration in cellular systems, *Phil. Trans. R. Soc. Lond. A* 354 (1996) 2055–2069.
- [18] E.C. Titchmarsh, *The Theory of Functions*, Oxford University Press, 1932.
- [19] J.E. Morral, M.F. Ashby, *Acta Metall.* 26 (1974) 567.