

## Supplementary Information

### A. The case of non-equal elastic moduli.

The more general form of Eq. (2) has the form

$$\frac{d}{dt}\sigma_{ab} = \mu[\partial_a V_b + \partial_b V_a - \delta_{ab}\partial_c V_c] + \mu'(\partial_c V_c - \gamma) \quad (\text{A1})$$

where  $\mu$  is the shear rigidity modulus and  $\mu'$  is the bulk modulus, which control the magnitude of stress in response to, respectively, shear and isotropic compression.

### B. Stress relaxation and growth anisotropy.

The derivation of equation (4) relied on the assumptions of isotropic growth, and elastic behavior. While these are plausible approximations that describe some tissues, there are certainly biological tissues where these assumptions would not be appropriate. These assumptions however may be easily relaxed leading to a more general form of equation (2-4).

Anisotropic growth, such as would arise from oriented cell divisions, changes the relationship between the distribution of growth and the accumulation of stress, but equations (2,4) can be generalized to describe anisotropic growth by the introduction of a growth rate *tensor*,  $\gamma_{ab}(\vec{r}, t)$ , which replaces the isotropic growth term  $\delta_{ab}\gamma(\vec{r}, t)$  on the right-hand-side of (2). In this case the right-hand-side of (4) becomes  $\partial_b \gamma_{ab}(\vec{r}, t)$ . Animal tissues can also have stress relaxation through rearrangement or extrusion of cells and cell shape changes (Legoff and Lecuit, 2015), resulting in viscoelastic rather than elastic behavior (Doubrovinski et al., 2017). This can be incorporated into a mathematical description of changes in stress by including a stress relaxation term

$$\frac{d}{dt}\sigma_{ab} = \mu[\partial_a V_b + \partial_b V_a - \gamma_{ab}(\vec{r}, t)] - \tau_\sigma^{-1}\sigma_{ab} \quad (\text{B1})$$

where  $\tau_\sigma^{-1}$  represents the stress relaxation rate. Although stress relaxation could potentially dissipate all stress –as it would if growth stopped - the level of residual stress depends on the rate of growth compared to the rate of stress relaxation.

### C. Mathematical relation between 2D growth and surface curvature

Gauss' "Theorema Egregium" relates the Gaussian curvature  $\kappa$  of a surface embedded in 3D to the its intrinsic metric, which defines the local measure of distance  $ds$  between nearby points on the surface ( $ds^2 = e^{\phi(x,y,t)}(dx^2 + dy^2)$ , where  $x, y$  are Gauss' normal coordinates on the surface).

$$\kappa(x, y, t) = -\frac{1}{2}e^{-\phi(x,y,t)}\nabla^2\phi(x, y, t) \quad (\text{C1})$$

Because local growth expands local intrinsic area, one then finds that

$$\frac{\partial}{\partial t}\phi(x, y, t) = \gamma(x, y, t) \quad (\text{C2})$$

We observe that if  $\nabla^2\gamma = 0$  and if initially  $\gamma = 0$ , then  $\nabla^2\phi = 0$  and therefore  $\kappa = 0$  which is to say the sheet remains flat.

#### D. Conformal map of lineage flow.

The cellular flow generated by stress-less, “harmonic growth”, has some remarkable mathematical properties providing us with a particularly direct relation between growth and form. To take advantage of the mathematical beauty of the situation one defines a complex variable  $z = r_x + ir_y$  (and its complex conjugate  $\bar{z} = r_x - ir_y$ ) and a complex function

$$v(z) = V_x(\vec{r}) + iV_y(\vec{r}) \quad (\text{D1})$$

The fact that the complex number defined by the right-hand-side of (D1) turns out to be a function of a single complex variable  $z$  (and independent of  $\bar{z}$ ), i.e. an analytic function, is a non-trivial, but readily verifiable consequence of equations (6), also known as the Cauchy-Riemann conditions. The same construction applies for any instant of time,  $t$ , and  $v(z, t)dt$  defines displacement of cells, mapping positions of cells at  $t$  to their positions at  $t + dt$  so that  $z \rightarrow z + v(z, t)dt$ . More generally one can denote by  $F(z, t)$  the complexified current position of a cell originating at  $z$  (so that  $F(z, 0) = z$ ). Function  $F(z, t)$  then describes the trajectories of all cells as they progress in time and is governed by

$$\frac{d}{dt}F(z, t) = v(F(z, t), t) \quad (\text{D2})$$

which is a particular case of (1). The map  $F(z, t)$  defines the shape of the body at time  $t$ : for example if initial shape is a unit circle ( $z = e^{i\varphi}$ ), the current shape is  $F(e^{i\varphi}, t)$ . More over, function  $F(z, t)$  defines a conformal (i.e. angle preserving, see Fig. 1) map of the initial “body” into the final one, with  $|\partial_z F(z, t)|^2$  defining exactly how much growth has occurred along the lineage of a cell initially at position  $z$ . Specifically, one can show that

$$\frac{d}{dt} \ln |\partial_z F(z, t)|^2 = \gamma(x, y, t) \quad (\text{D3})$$

where  $x + iy = F(z, t)$ . (The harmonicity of the growth profile required for stress-less growth ensures that the right-hand-side of (D3) is itself a real part of an analytic function.) Stated differently, the area occupied by the descendants of a cell at  $z$  is  $|\partial_z F(z, t)|^2 A$ , where  $A$  is the area of that cell. There is of course the subtlety of reconciling the continuum approach taken here with the discreteness of cells, but it can be resolved by a more detailed analysis.

An important mathematical theorem (Carrier et al., 2005) proves that any “shape” defined by a smooth boundary (and no holes) can be conformally mapped to a unit disc (see Fig. 1), which means that one can always find a suitable function  $F(z, t)$ , that not only maps cells from initial into the final  $t = T$  positions, but also tracks

cells at intermediate times  $t < T$ . (As a math small print we warn the reader that this map is not unique, because  $z \rightarrow (cz + d)/(\bar{d}z + \bar{c})$  with arbitrary complex  $c, d$  maps a unit disc onto itself. Knowing the mapping of any three “landmark” points on the boundary, resolves the ambiguity (Alim et al., 2016; Carrier et al., 2005).) The consequence is that for any observed time history of a 2D shape, we can find a  $F(z, t)$  “lineage map” and use (D3) to define a spatio-temporal growth profile, that will generate the shape through stressless isotropic growth. This bit of beautiful mathematics provides a direct relation between growth and form, much in the spirit of D’Arcy Thompson!