Appendix to the Planta paper

Relationships between growth, morphology and wall stress in the stalk of *Acetabularia acetabulum*,

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Part Seven: Appendix

Stress and tension in the apex. Wall tension is the force per unit length exerted by the cell wall to balance the turgor pressure pushing outwards on the wall. Unless this wall tension, including both elastic and viscous components, balances turgor pressure, the wall will explode, i.e. points on the cell wall will accelerate apart. This clearly does not occur since the growth rate of parts of the cell wall slow down as they move away from the tip. Assuming the cell wall acts as a thin shell under internal pressure, then one can calculate the tension at points along the apex analytically.

By Pascal's law, the tension at a point and the pressure difference between the inside and the outside of the cell wall (P) must follow the following equation:

$$P = T_1/R_1 + T_2/R_2 \qquad \text{A1}$$

where R_1 and R_2 are the principal radii of curvature and T_1 and T_2 are the wall (or surface) tensions along the principal directions of curvature.

Furthermore, meridional tension must balance the pressure pushing the apex forwards along the midline. Note that circumferential tension acts orthogonally to the force pushing the apex forwards, so it does not enter this relationship. The internal pressure exerts a force on the apex at a particular distance from the tip equal to the pressure times the cross-sectional area of the apex at that distance from the tip (Fig. 7). Since the apex is approximately rotationally symmetric, the cross-sectional area is πr^2, where r is the radius of a cross-section at that distance from the tip. Therefore the pressure force pushing out at the apex is equal to $\pi r^2 P$. The force exerted by the cell wall on the apex will equal the component of meridional tension along the midline multiplied by the length of the circumference of the apex, i.e. at all possible meridians around the circumference (Fig. 7).

The component of meridional tension along the midline is:

$$T_m \mathrm{Cos}(\text{Ø}) \qquad \text{A2}$$

where T_m is the meridional tension and Ø is the angle between the meridian and the direction of the midline at that point. If the apex is rotationally symmetric, its circumference will equal $2\pi r$, therefore the force exerted by the cell wall will be $2\pi r T_m$. Since the pressure force is balanced by the tension,

$$2\pi r T_m \mathrm{Cos}(\text{Ø}) = \pi r^2 P \qquad \text{A3}$$

$$\text{therefore } T_m = Pr/[2\mathrm{Cos}(\text{Ø})] \text{ (Fig. 5).} \qquad \text{A4}$$

If one approximates the apex shape as a cylinder with a hemispherical top, then one can calculate the meridional tension based on the radius of the cylinder. In the cylindrical part, r is equal to R_c, the radius of the cylinder, and Ø = 0,

$$\text{therefore, } T_m = PR_c/2. \quad \text{A5}$$

In the hemispherical top, $r = R_c \operatorname{Cos}(Ø)$, Therefore $T_m = PR_c/2$ in the hemispherical top as well.

Since the apex is rotationally symmetric, one of the principal directions of curvature is along the meridian, therefore one can calculate the tensions in both principal directions of curvature by substituting T_m into Pascal's formula (above): $P = T_1/R_1 + T_m/R_m$. In the cylindrical part, the meridional curvature equals 0 and the second principal radius of curvature is the radius of the cylinder, therefore this equation reduces to $P = T_c/R_c$, where T_c is the circumferential tension,

$$\text{therefore, } T_c = PR_c. \quad \text{A6}$$

The circumferential tension is twice the meridional tension in the cylindrical part.

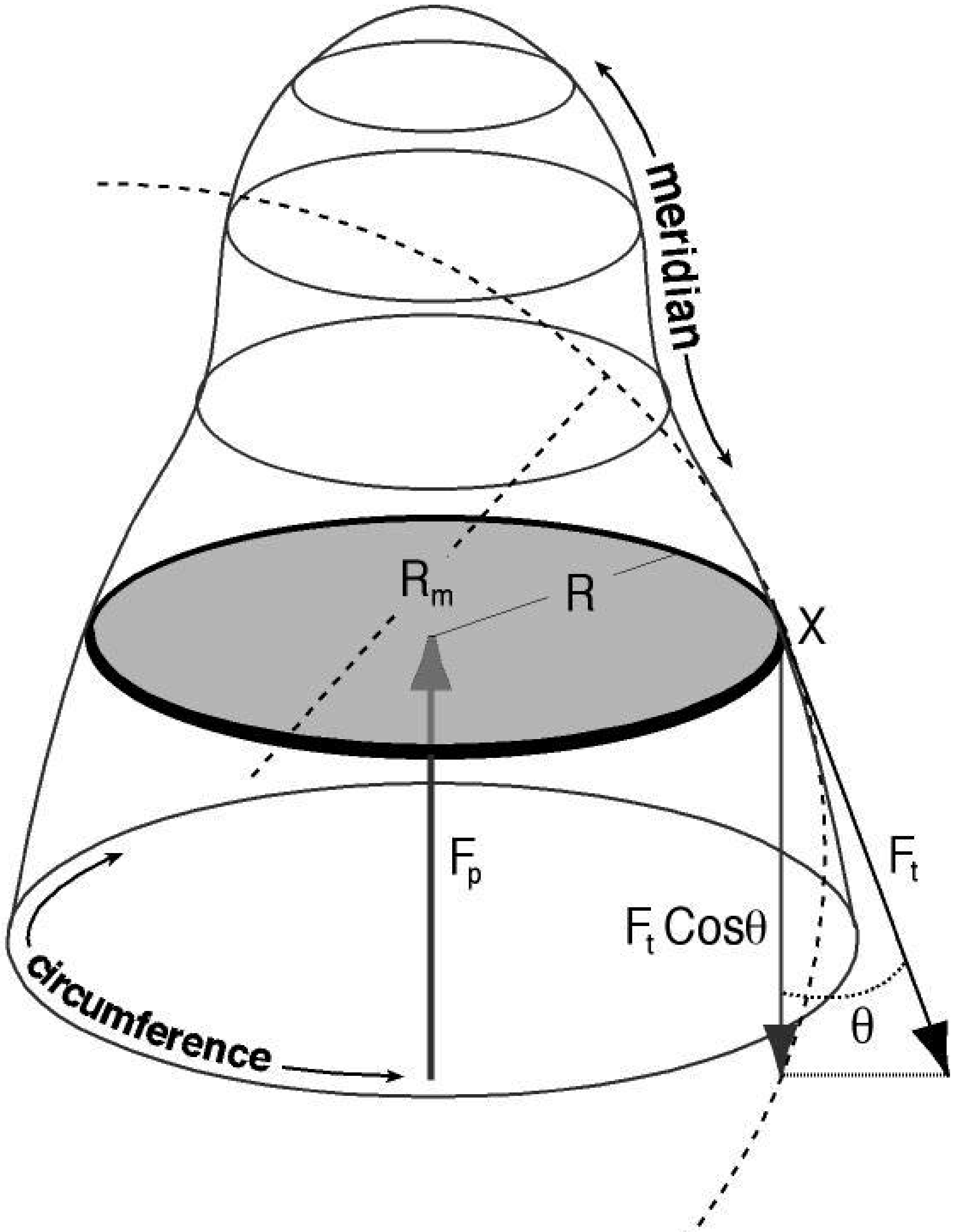
In the hemispherical top, both principal radii of curvature equal R_c, therefore $P = T_1/R_c + T_m/R_c$. Since $T_m = PR_c/2$, this reduces to $P = T_1/R_c + P/2$, therefore, $T_1 = PR_c/2$. In the hemispherical top, the stress around the circumference will be tangent to T_1,

$$\text{therefore } T_c = PR_c/2, \quad \text{A7}$$

where T_c is the circumferential tension. Thus, circumferential tension in the hemispherical top is half the circumferential tension in the cylindrical part.

Stress is tension, T, divided by wall thickness, h. Without the value of h, T tells one nothing about the stress.

Fig. 7. The relationship between shape and meridional tension. A diagram of the forces on a thin-walled shell under pressure. Given $F_p = F_t \text{Cos}\theta$; $F_p = P\pi R^2$ and $F_t = T_m 2\pi R$, then $F_t = P2\pi R/\text{Cos}\theta$ and $T_m = PR/2\text{Cos}\theta$ where T_m = meridional tension, P = internal pressure, F_t = force at X due to the meridional tension, F_p = axial component of the force on the apex due to the internal pressure, and R = radius of the stalk. (See Original figure 5 below).



Growth rate versus curvature. We proposed that the relative growth rate in width is inversely proportional to the width such that: $(dW/dt)/W = (A/W) - (A/W_f)$, where W is the width at some time, t, A and W_f are constants such that the final width is W_f, and $(dW/dt)/W$ is the elemental growth rate in width. This differential equation reduces to

$dW/dt = A(1 - W/W_f)$, where dW/dt is the absolute growth rate in width. This differential equation is solved by the formula

$$W = W_f(1-e^{mt}) + W_0e^{mt} \qquad \text{A8}$$

where W_f is the final width, W_0 is the initial width, m is a constant. So long as $m < 0$ and $W_f > 0$, W will approach W_f asymptotically. The width after a given time interval is therefore a linear function of the width at the beginning of that time interval.

To solve for the constants A and W_f, one can take the derivative of W with respect to t:

$$dW/dt = -W_f m e^{mt} + W_0 m e^{mt} \qquad \text{A9}$$

Which can be rearranged to: $$dW/dt = m[W_f(1 - e^{mt}) + W_0e^{mt}] - W_f m \qquad \text{A10}$$

The first part on the right is equal to mW therefore this reduces to:

$$dW/dt = mW - W_f m \qquad \text{A11}$$

Therefore, $A = -W_f m$.

Note also that since the width after a time interval is a linear function of the width at the beginning of that time interval, the relative growth, $(W - W_0)/W_0$, is inversely proportional to the initial width as well, only the constant A will be somewhat different. Starting with the equation for W at some time T:

$$W = W_f(1-e^{mt}) + W_0e^{mt} \qquad \text{A12}$$

This can be expanded to: $(W - W_0)/W_0 = [W_f(1-e^{mt})]/W_0 + (e^{mt} -1)$. A13

For a given time interval, $[W_f(1-e^{mt})]$ and $(e^{mt} - 1)$ are constants. This means that the relative growth over that time interval is a linear function of the initial circumferential curvature, $1/W_0$ if the relative growth rate is a linear function of the circumferential curvature.

Meridional growth and anisotropy. If $(1/L)(dL/dt) = A_m/W - A_m/W_f$, where L is a meridional length, A_m is the proportionality between relative growth rate along the meridian and circumferential curvature, and W and W_f are as defined above, then the ratio of the relative growth rate in width to that in length (the anisotropy) is equal to A/A_m.

Since $W = W_f(1-e^{mt}) + W_0e^{mt}$, the right side of the equation for relative meridional growth rate is equal to:

$$(A_m/W_f)(W_f-W_0)e^{mt}/(W_f+(W_0-W_f)e^{mt}). \qquad \text{A14}$$

Integrating both sides gives the following relation:

$$\mathrm{Ln}(L_t/L_0) = (-A_m/(mW_f))\mathrm{Ln}(W_t/W_0), \quad \text{or} \quad \mathrm{Ln}(L_t/L_0) = (A_m/A)\mathrm{Ln}(W_t/W_0). \qquad \text{A15}$$

Where L_t and W_t are the length and width at some time, t, and L_0 and W_0 are the initial length and width. This implies that the anisotropy of growth is equal to:

$$(A/A_m) = \mathrm{Ln}(W_t/W_0)/\mathrm{Ln}(L_t/L_0) \qquad \text{A16}$$