Updated: Jun 23 2021

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**FOR TWO CELLS (numerics)**

Let **index 1 denote leader cell** while **index 2 denotes trailer cell**.

An inverse approach where the morphological measurements are known, and the forces (tensions) and velocity are unknown.

| Symbol | | Meaning (non-dimensional quantities) |
|---|---|---|
| $f$ | $\frac{\Delta F}{F}$ | Maximal adhesion/protrusion |
| $t_1$ | $\frac{T_1}{F}$ | Leader membrane tension |
| $t_2$ | $\frac{T_2}{F}$ | Trailer membrane tension |
| $t_{cc}$ | $\frac{T_{cc}}{F}$ | Cell-cell adhesive forces |
| $t_0$ | $\frac{T_0}{F}$ | Characteristic tension that breaks cell-substrate adhesion |
| $\tau$ | $\frac{T}{F}$ | Ratio of membrane tension to adhesion/protrusion |
| $\xi$ | Effective viscous drag | Effective viscous drag |

** Start with a guess for tensions. Set $t_1 = 1$, and guesses for $t_2 \in [0.5,2]$ and $t_{cc} \in [0.01,0.5]$.

** Choose arbitrary values for $w$ and $h$.

Updated: Jun 23 2021

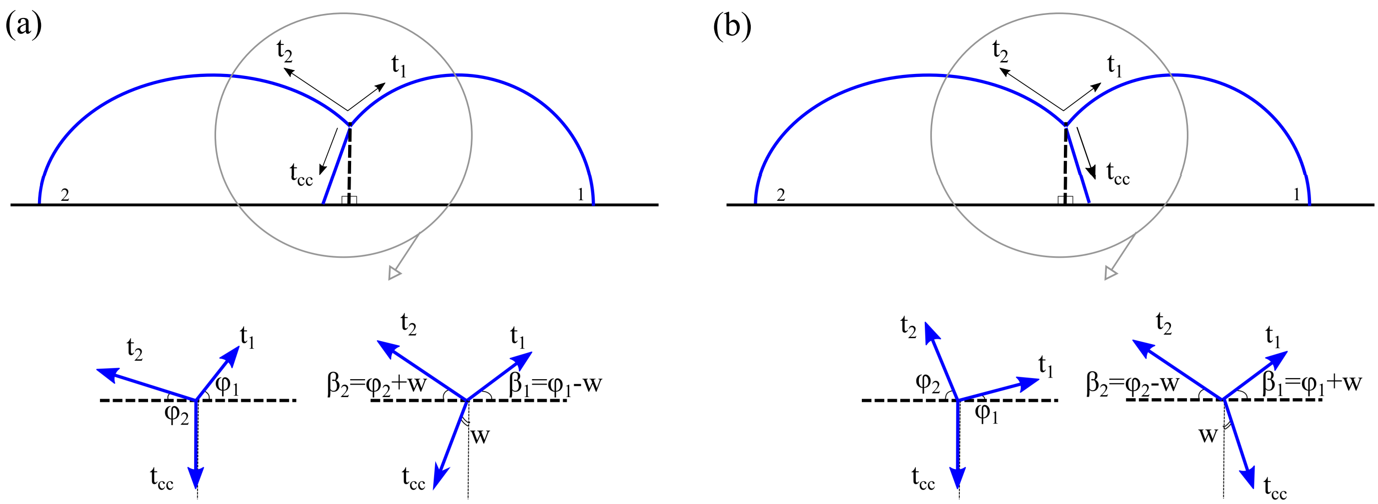



**Figure 1**. Side-view of the two cells. Two possibilities are considered including (a) negative $w$ angle and (b) positive $w$ angle.

## 1) FORCE BALANCE AT THE TOP OF CELL-CELL INTERACTION REGION given $t_1, t_2$ and $t_{cc}$ (*__plus a choice of__* $w$) to obtain $\phi_1, \phi_2$ then $\beta_1, \beta_2$

(1.a') $t_1 \cos \phi_1 - t_2 \cos \phi_2 = 0$ (x-direction)

(1.b') $t_1 \sin \phi_1 + t_2 \sin \phi_2 - t_{cc} = 0$ (y-direction)

and

(1.a) $t_1 \cos \beta_1 - t_2 \cos \beta_2 + \dfrac{w}{|w|} t_{cc} \sin|w| = 0$ (x-direction)

(1.b) $t_1 \sin \beta_1 + t_2 \sin \beta_2 - t_{cc} \cos|w| = 0$ (y-direction)

Reduce to:

(1.a) $$\beta_1 = \cos^{-1}\left(\frac{t_2}{t_1} \cos \beta_2 - \frac{w}{|w|} \frac{t_{cc}}{t_1} \sin|w|\right)$$

(1.b) $$t_1 \sin \left[\cos^{-1}\left(\frac{t_2}{t_1} \cos \beta_2 - \frac{w}{|w|} \frac{t_{cc}}{t_1} \sin|w|\right)\right] + t_2 \sin \beta_2 - t_{cc} \cos|w| = 0$$

Solve 1.b with fzero in Matlab for $\beta_2$. Then use equation 1.a to solve for $\beta_1$.

Updated: Jun 23 2021

**Alternative**: eqs. (1.a') and (1.b') reduce to:

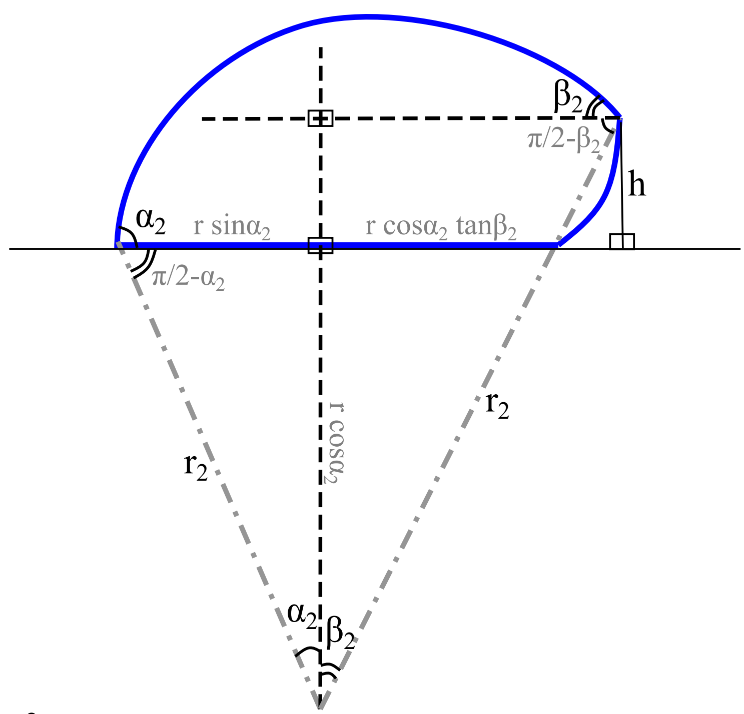
(1.a') $\phi_1 = \cos^{-1}\left(\frac{t_2}{t_1}\cos\phi_2\right)$

(1.b') $t_1 \sin\left[\cos^{-1}\left(\frac{t_2}{t_1}\cos\phi_2\right)\right] + t_2 \sin\phi_2 - t_{cc} = 0$

Solve 1.b' with zero in Matlab for $\phi_2$. Then use 1.a' to solve for $\phi_1$.
Finally, $\beta_1 = \phi_1 \pm w$ and $\beta_2 = \phi_2 \pm w$ depending on sign of $w$.

## 2) USE AREAS AND TRIGONOMETRY given $\beta_1, \beta_2, h$ to find $r_1, r_2, \alpha_1$ and $\alpha_2$

From Fig. 2 the **shaded** area of the second cell (trailer) is




$$A_2 = \frac{\pi r_2^2}{2}\frac{(\alpha_2+\beta_2)}{\pi} - \frac{1}{2}r_2^2 \sin\alpha_2\cos\alpha_2 - \frac{1}{2}r_2^2\cos^2\alpha_2\tan\beta_2 \equiv 1$$

which yields the following expressions for the radii:

(2.a) $r_1 = \left[\frac{(\alpha_1+\beta_1)}{2} - \frac{1}{2}\sin\alpha_1\cos\beta_1 - \frac{1}{2}\cos^2\alpha_1\tan\beta_1\right]^{-1/2}$

(2.b) $r_2 = \left[\frac{(\alpha_2+\beta_2)}{2} - \frac{1}{2}\sin\alpha_2\cos\beta_2 - \frac{1}{2}\cos^2\alpha_2\tan\beta_2\right]^{-1/2}$

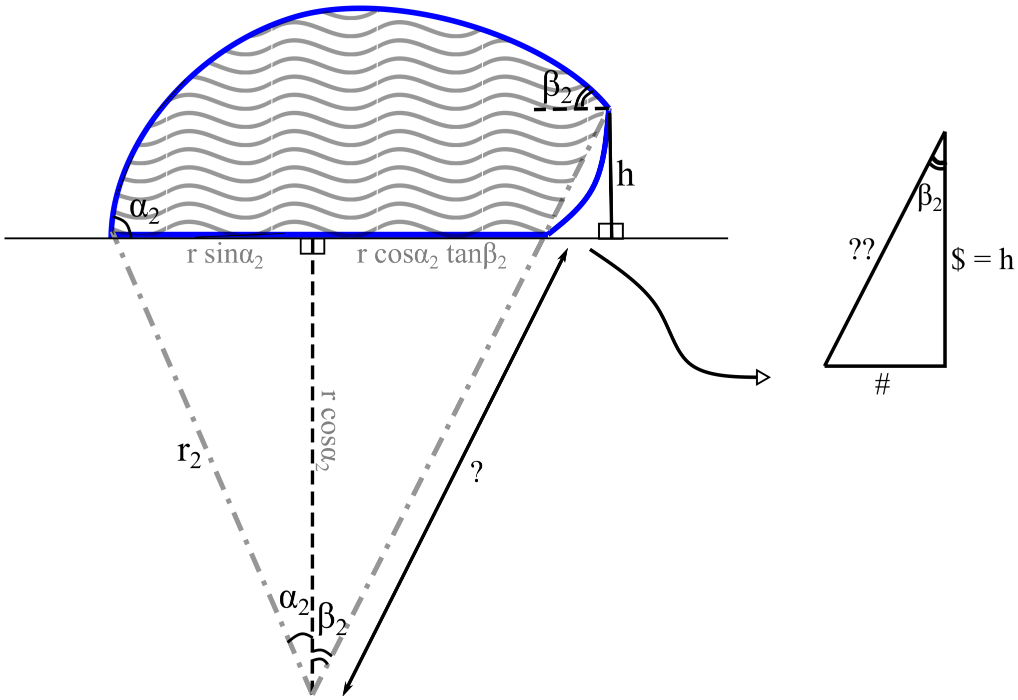



**Figure 3.** Zoom in of trailer cell to illustrate area computation for (2.a) and (2.b)

☑ *We can improve our area calculation slightly; including the small triangle on the right-side (not the arc section) in the area calculation produces*

$$A_2 = \frac{\pi r_2^2}{2}\frac{(\alpha_2+\beta_2)}{\pi} - \frac{1}{2}r_2^2 \sin\alpha_2 \cos\alpha_2 - \frac{1}{2}r_2^2 \cos^2\alpha_2 \tan\beta_2 + \frac{1}{2}r_2^2\left(\cos\beta_2 - \cos\alpha_2 \tan\beta_2\right)\left(\sin\beta_2 - \cos\alpha_2 \tan^2\beta_2\right) \equiv 1$$

The resulting radii are

(2.a)

$$r_1 = \left[\frac{(\alpha_1+\beta_1)}{2} - \frac{1}{2}\sin\alpha_1\cos\beta_1 - \frac{1}{2}\cos^2\alpha_1\tan\beta_1 + \frac{1}{2}\left(\cos\beta_1 - \cos\alpha_1\tan\beta_1\right)\left(\sin\beta_1 - \cos\alpha_1\tan^2\beta_1\right)\right]^{-1/2}$$

(2.b)

$$r_2 = \left[\frac{(\alpha_2+\beta_2)}{2} - \frac{1}{2}\sin\alpha_2\cos\beta_2 - \frac{1}{2}\cos^2\alpha_2\tan\beta_2 + \frac{1}{2}\left(\cos\beta_2 - \cos\alpha_2\tan\beta_2\right)\left(\sin\beta_2 - \cos\alpha_2\tan^2\beta_2\right)\right]^{-1/2}$$

From trigonometry we also know that

(2.c) $h = r_1\left(\cos\beta_1 - \cos\alpha_1\right)$

(2.d) $h = r_2\left(\cos\beta_2 - \cos\alpha_2\right)$

**3) FROM LAPLACE'S LAW the intracellular pressure is:**

$$p_1 = \frac{t_1}{r_1} \text{ and } p_2 = \frac{t_2}{r_2}$$

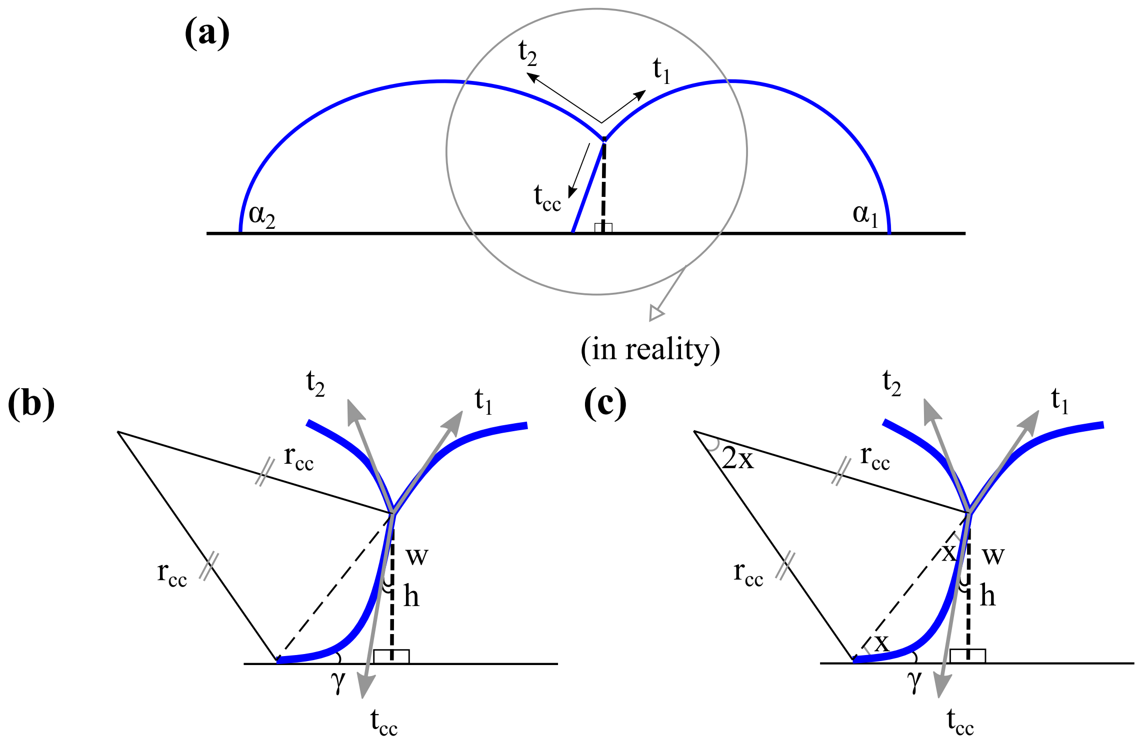



**Figure 3.** Zoom in of the cell-cell interface and the resulting angles in the wedge

**4) FROM LAPLACE'S LAW find the radius of curvature for the cell-cell junction**

$$p_2 - p_1 = \frac{t_{cc}}{r_{cc}} \rightarrow r_{cc} = \frac{t_{cc}}{t_2/r_2 - t_1/r_1}$$

**5) USE TRIGONOMETRY AT CELL-CELL INTERFACE given $h, w, r_{cc}$, to find the angle $\gamma$ at the ventral end of the cell-cell boundary**

$$(1)\ \cos(|x| + |w|) = \frac{h}{s}$$

$$(2)\ \sin(|x| + \gamma) = \frac{h}{s}$$

(3) $s^2 = 2r_{cc}^2\,(1 - \cos(2|w|))$ (where $s$ is the third side in the isosceles triangle with sides $r_{cc}$)

Combining (1) and (3), to obtain:

$$\frac{h^2}{\cos^2(|x| + |w|)} = 2r_{cc}^2\,\left(1 - \cos(2|x|)\right) \text{ fzero for } x \in [0, \pi/4].$$

Then: $\gamma = \frac{\pi}{2} - |w| - 2|x|$.

**6) LASTLY, USE THE FORCE BALANCE AT THE VENTRAL POINTS:**

Force balance at the front endpoint of the leader cell:

(6.a) $(1 + f)\left(1 - \frac{t_1}{t_0 + \tau}\right) - \zeta_1 v = t_1 \cos \alpha_1$

Force balance at the rear endpoint of the trailer cell:

(6.b) $(1 - f)\left(1 - \frac{t_2}{t_0 - \tau}\right) + \zeta_2 v = t_2 \cos \alpha_2$

Force balance at the cell-cell interaction zone:

(6.c) $t_{cc} \cos(\gamma) = \zeta_{cc} v$

Obtain velocity. (Each equation represents a plane in 3D space)