

Swimming and crawling at microscopic scales: lessons from 1D model systems

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Drawing from **joint work** with **many** people, see list of references at the end.

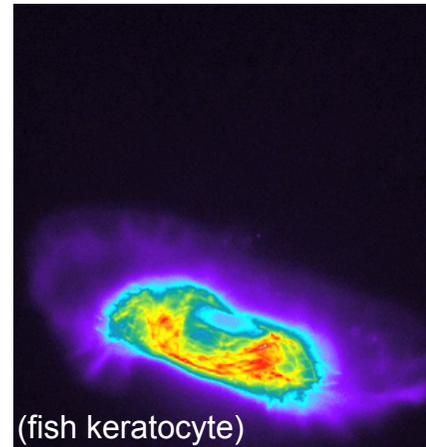
Focused Working Group on "Self-Propelled Micro-Objects", KITP Santa Barbara, 5.3.2014

Motility at the micron scale

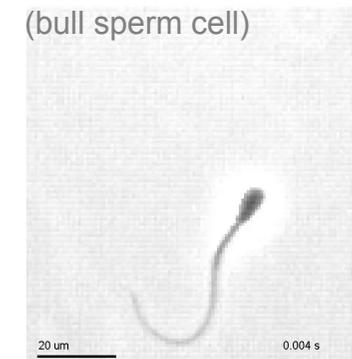
Motility is the capability of exhibiting directed, purposeful movement.

Motile cells: fascinating examples of motility at microscopic scales (1-50 μm)

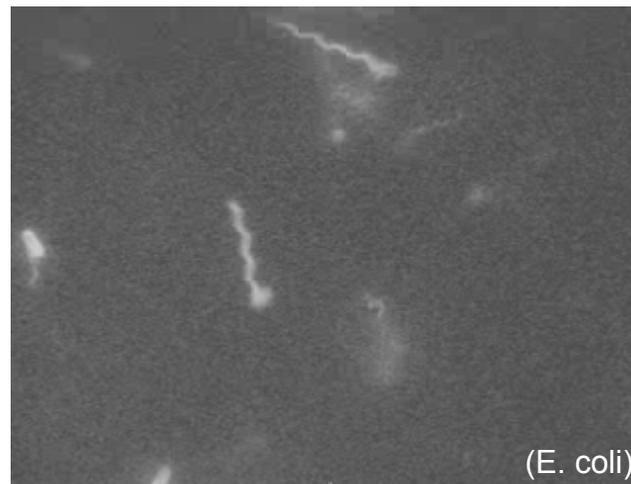
Metastatic tumor cells
(**crawling** on a solid)

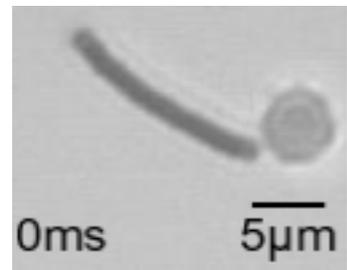
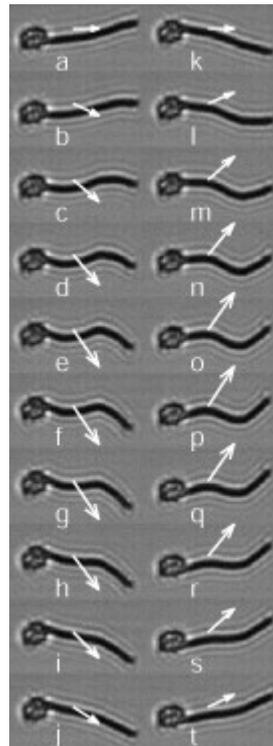


Sperm cells
(**swimming** in a fluid)



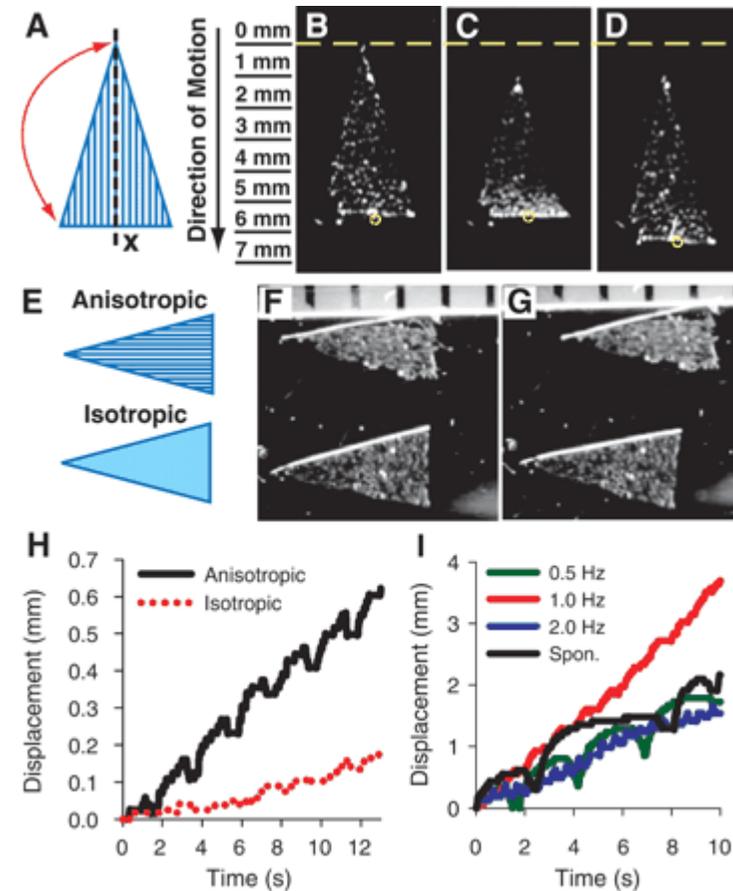
Bacteria
(**swimming** in a fluid)





red blood cell + flexible magnetic filament

J. Bibette, H. Stone et al.: Nature (2005)



polymer film + muscle cells

G. Whitesides et al., Science (2007)

Reynolds number



$$\text{Re} = \frac{VL\rho}{\eta}$$

Velocity (typical order of magnitude) V

Diameter (typical size) L

Mass density of the fluid ρ

Viscosity of the fluid η

For water at room temperature $\rho/\eta = 10^6 \text{ (m}^2\text{s}^{-1})^{-1}$.

Orders of magnitude for swimmers:

Men, dolphins, sharks: $L=1\text{m}$, $V=1-10 \text{ ms}^{-1}$ $\text{Re}=10^6-10^7$

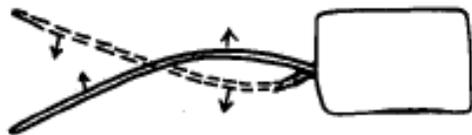
Bacteria: $L=1 \times 10^{-6}\text{m}$, $V=1-10 \times 10^{-6} \text{ ms}^{-1}$ $\text{Re}=10^{-6}-10^{-5}$



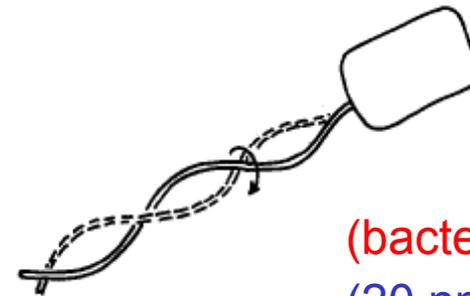
in a flow regime obeying **Stokes equations**, whatever forward motion will be produced by closing the valves, it will be exactly canceled by a backward motion upon reopening them

Micro-motility as a struggle against the scallop theorem

Nature:



(eukaryotic flagella, cilia)
(bending of 9+2 μ -tubule bundles)



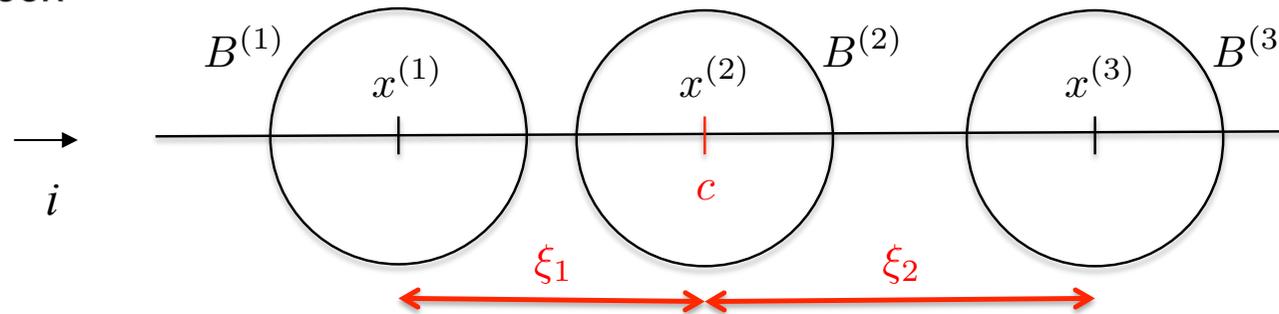
(bacterial flagella)
(20 nm rotary motor)

Design:



3-sphere swimmer (Najafi and Golestanian, 2004)

Positional change from shape change



$$\begin{aligned}\dot{x}^{(1)} &= \dot{c} - \dot{\xi}_1 \\ \dot{x}^{(2)} &= \dot{c} \\ \dot{x}^{(3)} &= \dot{c} + \dot{\xi}_2\end{aligned}$$

$$0 = F = i \cdot \int_{\partial\Omega} \sigma_{visc}(x) n(x) dA$$

$$= \varphi_1(\xi, \kappa) \dot{\xi}_1 + \varphi_2(\xi, \kappa) \dot{\xi}_2 + \varphi_3(\xi, \kappa) \dot{c}$$

<0 (nonzero)

by transl. inv.

Then \dot{c} is uniquely determined and depends linearly on $\dot{\xi}_1$ and $\dot{\xi}_2$

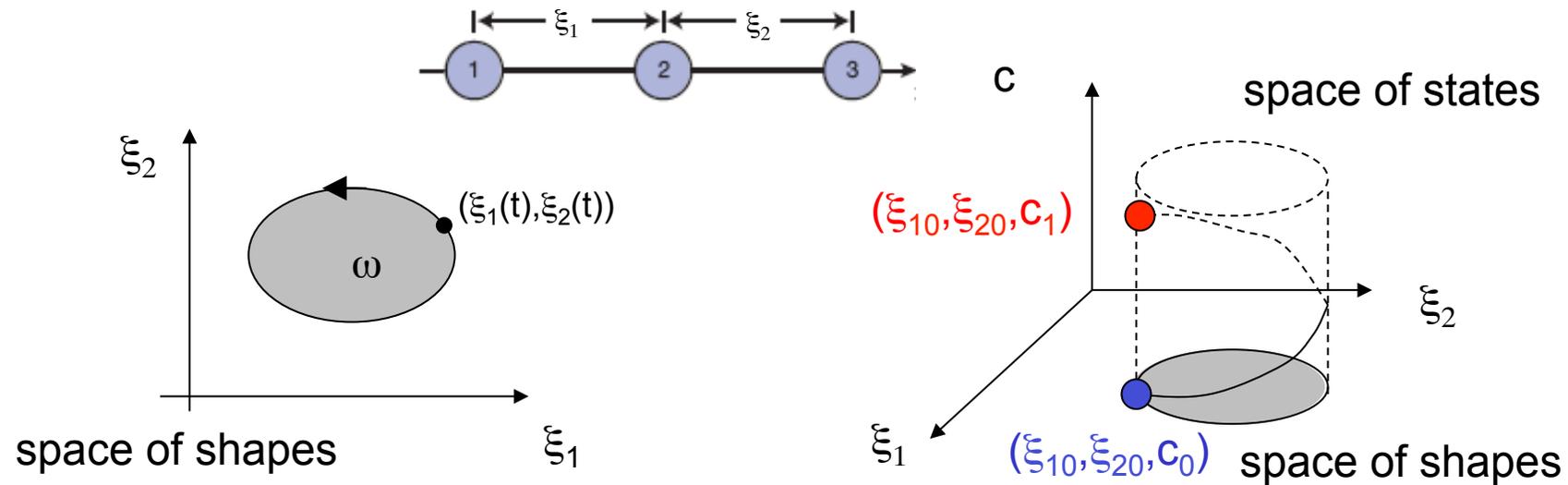
$$\frac{dc}{dt} = V_1(\xi) \frac{d\xi_1}{dt} + V_2(\xi) \frac{d\xi_2}{dt}$$

**non-linear ODE if
non-trivial depend. on ξ !**

$$V_i(\xi) = -\varphi_i(\xi) / \varphi_{n+1}(\xi)$$

Swimming with one formula

$$\Delta c = \int_0^T \dot{c} dt = \int_0^T (V_1 \frac{d\xi_1}{dt} + V_2 \frac{d\xi_2}{dt}) dt = \int_{\omega} \text{curl}_{\xi} V(\xi_1, \xi_2) d\xi_1 d\xi_2$$



$V(\xi)$ summarizes hydrodynamic interactions and swimming capabilities of a swimmer

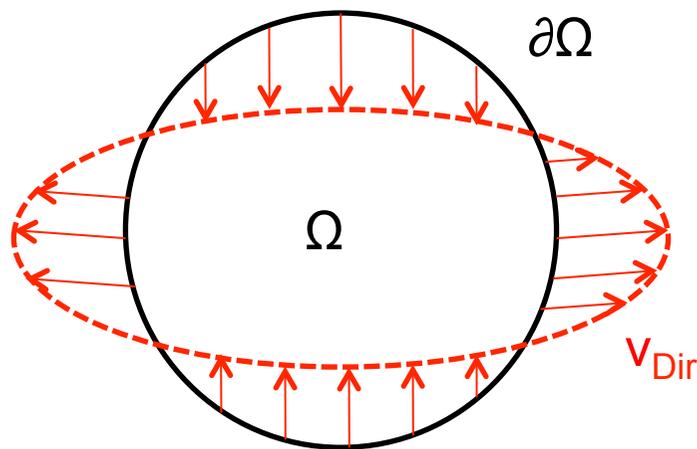
Need to solve infinitely many outer Stokes problems to compute $V(\xi)$!!!

F. Alouges, ADS, A. Lefebvre: J Nonlinear Science **18**, 277-302
Lie-bracket generating or totally non-holonomic affine control system

Motility = Action/Reaction

(theory = eq of motion of fluid + eq of motion of swimmer)

1. Find u, p in the surrounding fluid induced by swimmer's shape changes:



$$\begin{cases} -\eta \Delta u + \nabla p = 0 \\ \operatorname{div} u = 0 \end{cases} \quad \text{on } \mathbb{R}^3 \setminus \Omega$$

$$u = v_{\text{Dir}} \quad \text{on } \partial\Omega$$

$$u \rightarrow 0 \quad \text{at infinity.}$$

$$\sigma_{\text{visc}} n = DN_{\Omega} [v_{\text{Dir}}] \quad \text{stress, viscous "reactive" force p.u. area on } \partial\Omega$$

Not all of v_{Dir} is a-priori known (only shape is given, not position)

2. Find swimmer's translational and rotational velocities by solving 6 ODEs:

$$\text{Total (viscous) force} = 0$$

$$\text{Total (viscous) torque} = 0$$

From equations of motion to non-holonomic constraints

- Viscous forces, reaction to shape change by surroundings (c position, ξ shape):

$$F(c, \xi; \dot{c}, \dot{\xi})$$

- Equation of motion of the swimmer (no inertia, no other forces but viscous drag):

$$\cancel{ma} = F(c, \xi; \dot{c}, \dot{\xi}) + \cancel{F_{\text{gravity}}} + \cancel{F_{\text{other ext}}}$$

$0 =$

- c constrained to ξ :

$$0 = F(c, \xi; \dot{c}, \dot{\xi})$$

net motion from cyclic shape change = constraint must be non-holonomic

- Viscous forces linear in velocity, but shape-dependence introduces the nonlinearity:

$$0 = F = F_c(\xi) \dot{c} + \sum_i F_i(\xi) \dot{\xi}_i$$

Crawling motility

- From swimming motility....



The scallop theorem

-to motility by crawling



The snail theorem ?

Is nonlinear rheology of mucus
necessary for locomotion ?

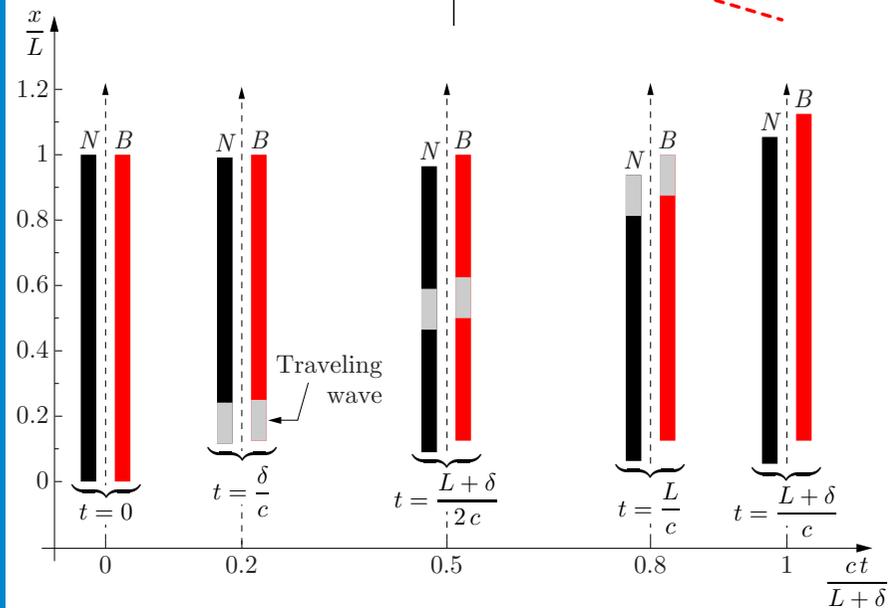
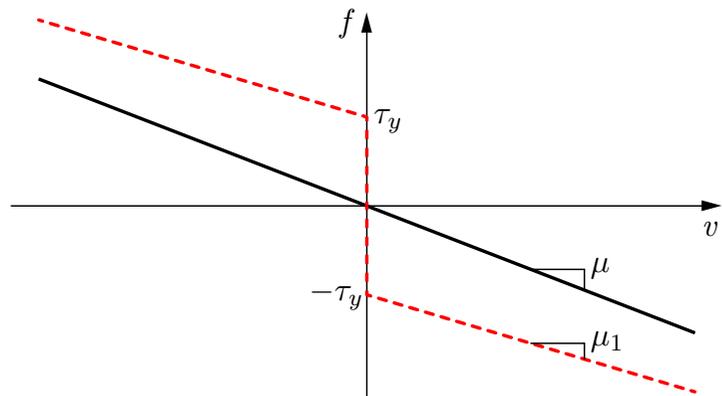
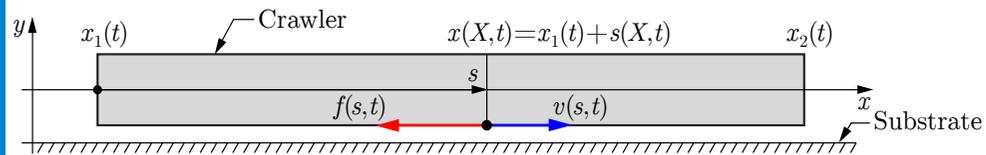
"1D" biological crawlers



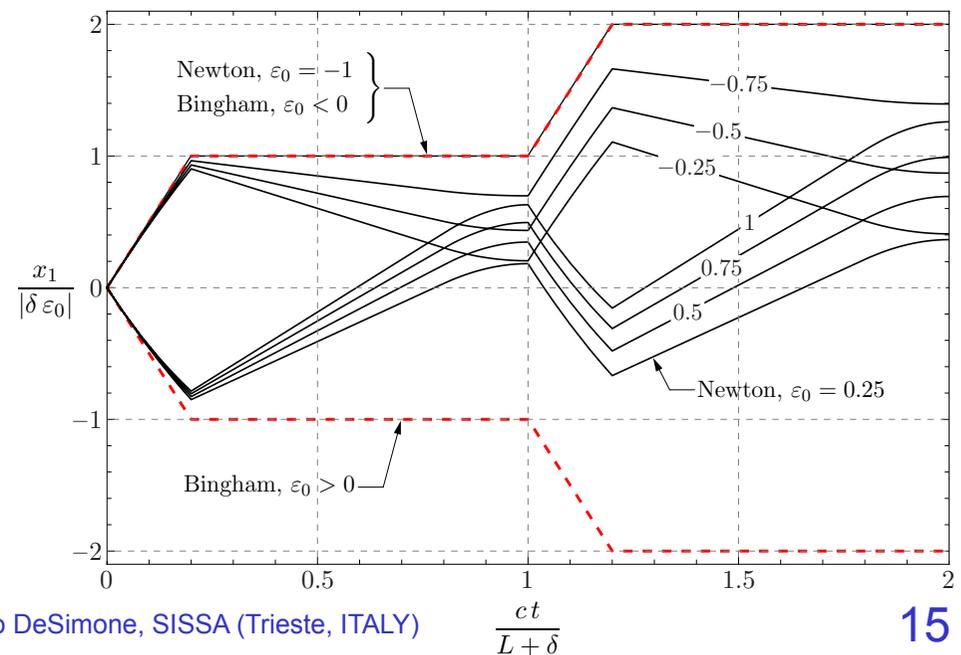
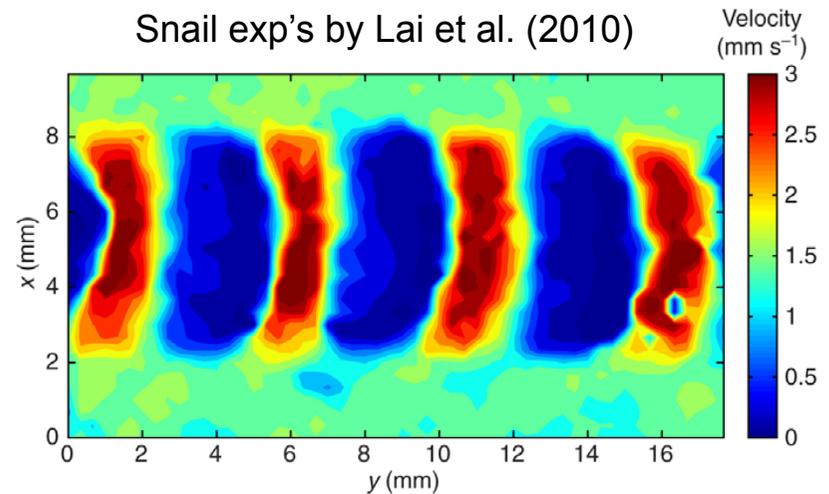
Locomotion by propagation of traveling "contraction" waves

Crawlers on fluid layers: contraction waves

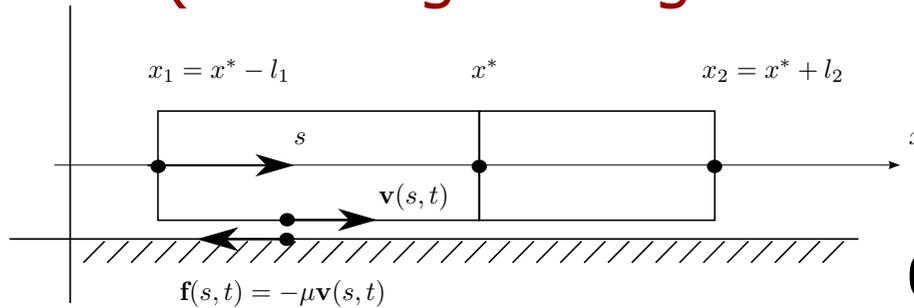
ADS, F. Guarnieri, G. Noselli, A. Tatone: Int J Nonlinear Mechanics **56**, 142-147 (2013)



Snail exp's by Lai et al. (2010)



Discrete argument (crawling analog of the three-sphere-swimmer)



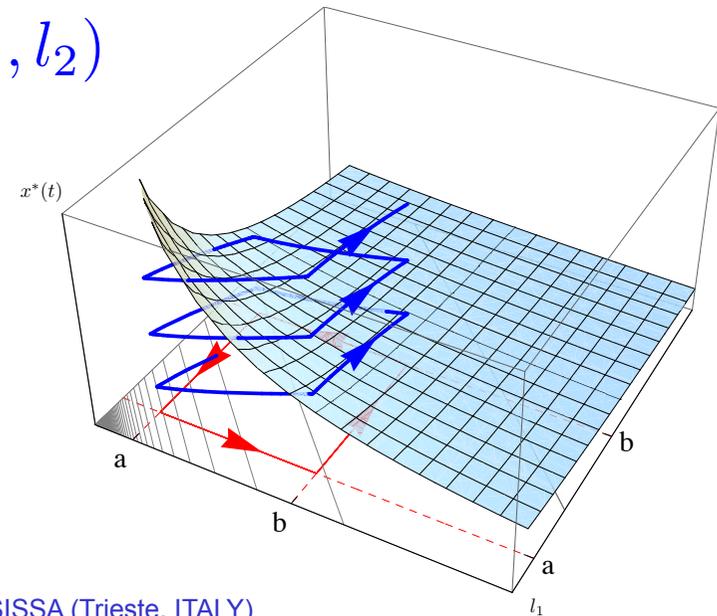
$$0 = F = \int_0^{l_1+l_2} f(s) ds$$

$$0 = -\mu \left((l_1 + l_2) \dot{x}^* - \frac{l_1}{2} \dot{l}_1 + \frac{l_2}{2} \dot{l}_1 \right)$$

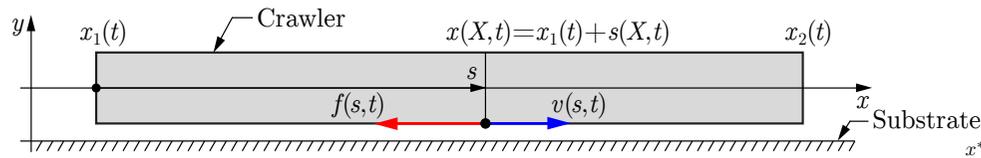
$$\dot{x}^* = \underbrace{\frac{l_1}{2(l_1 + l_2)}}_{V_1(l_1, l_2)} \dot{l}_1 - \underbrace{\frac{l_2}{2(l_1 + l_2)}}_{V_2(l_1, l_2)} \dot{l}_2$$

$$\Delta x^* = \int_{[a,b]^2} \text{curl } \mathbf{V}(l_1, l_2) dl_1 dl_2$$

$$\text{curl } \mathbf{V}(l_1, l_2) = \frac{1}{2} \frac{1}{l_1 + l_2}$$

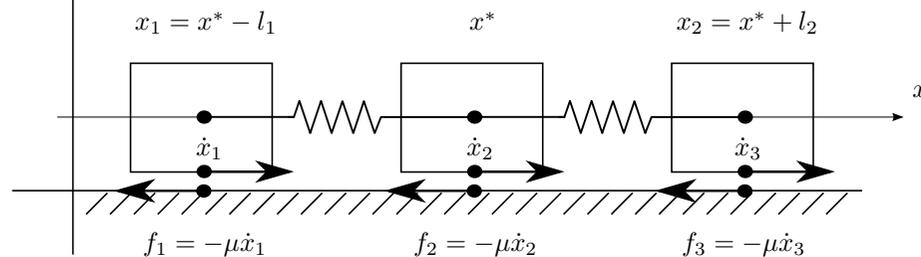
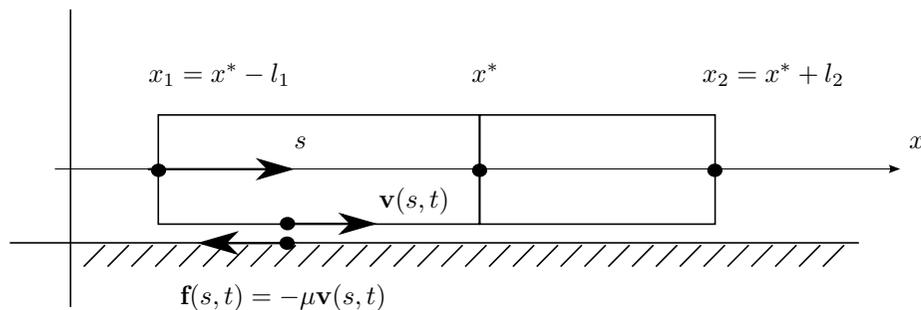
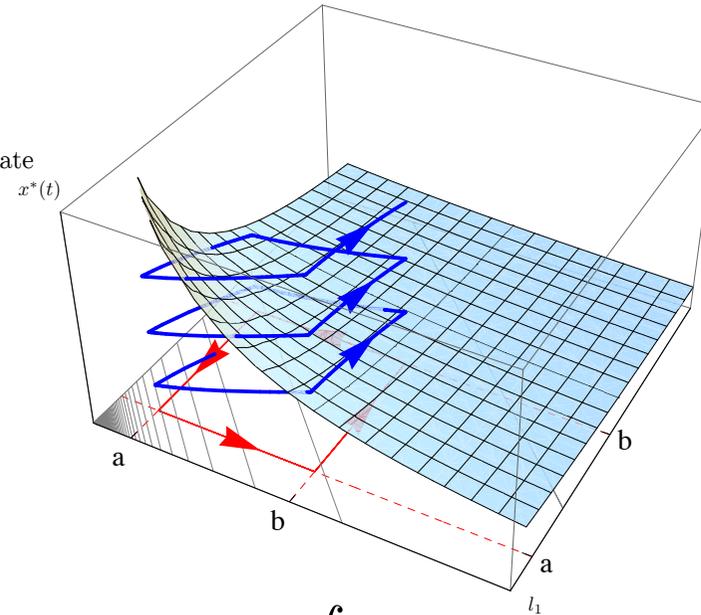


Oversimplifying the model



$$\dot{x}_1(t) = \frac{1}{l(t)} \int_0^L \dot{s}(X,t) s'(X,t) dX$$

$$s' \sim (1 + \epsilon) \quad \dot{s}s' \sim \dot{s}$$



$$\Delta x^* = \int_{[a,b]^2} \text{curl } \mathbf{V}(l_1, l_2) dl_1 dl_2$$

$$\text{curl } \mathbf{V}(l_1, l_2) = \frac{1}{2} \frac{1}{l_1 + l_2}$$

$$\dot{x}^* = \frac{1}{3} \dot{l}_1 - \frac{1}{3} \dot{l}_2$$

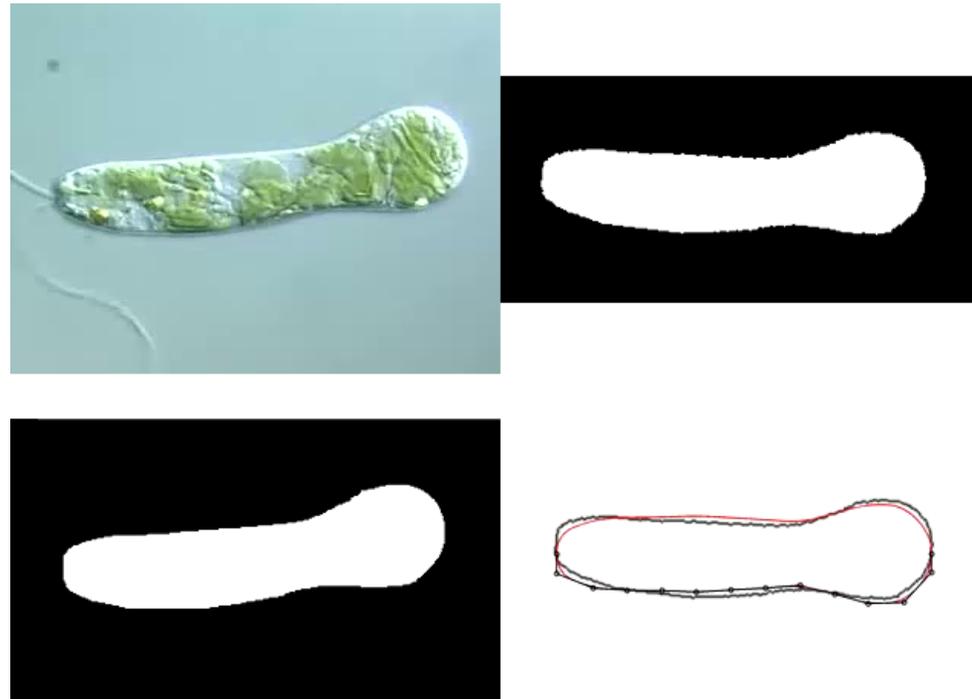
$$\text{curl } \mathbf{V}(l_1, l_2) = 0$$

From general concepts to biological detail: *metaboly* of euglenids

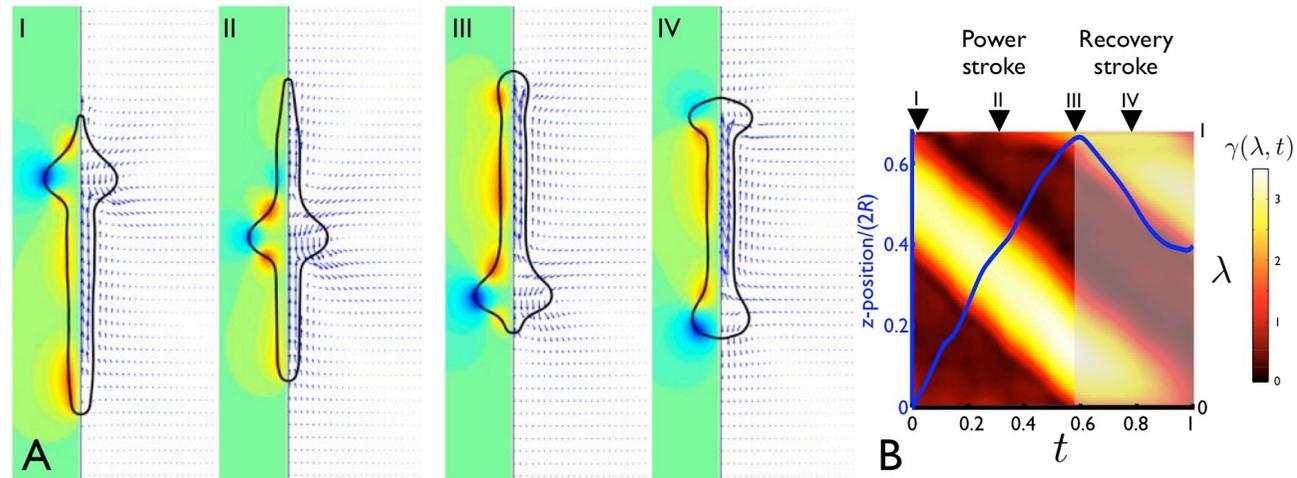
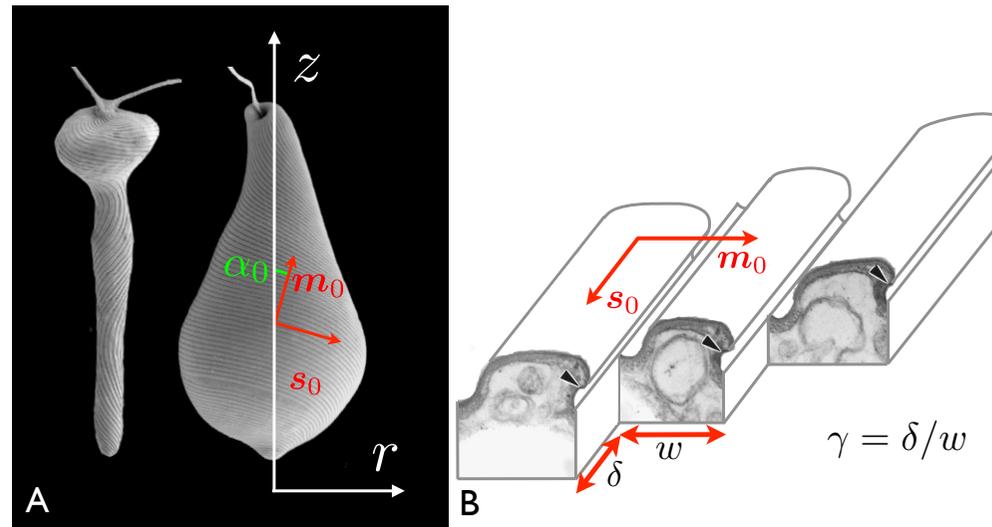


Euglenoid movement
(metaboly)

A swimmer with a twist

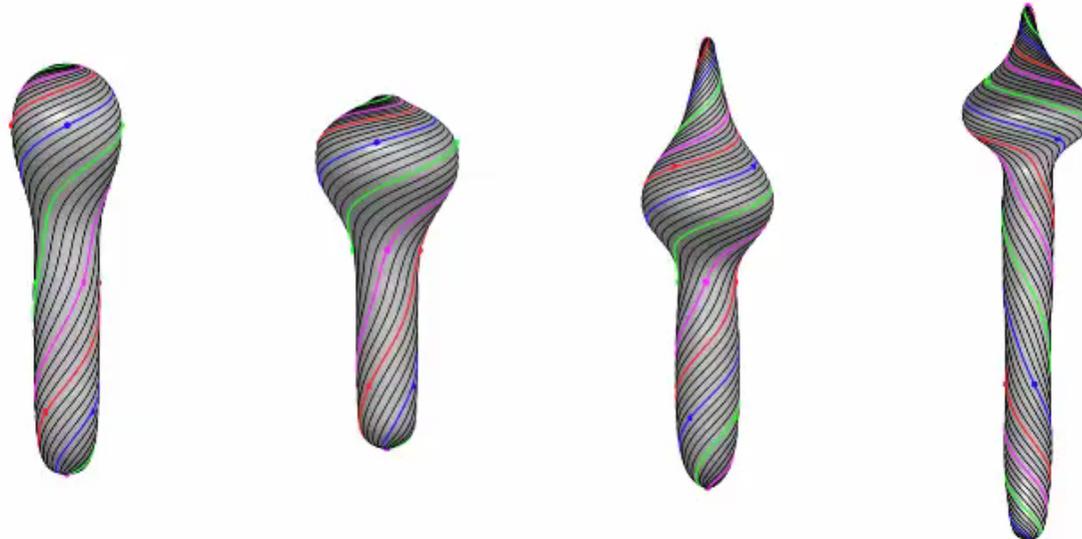


Reverse engineering the euglenoid movement

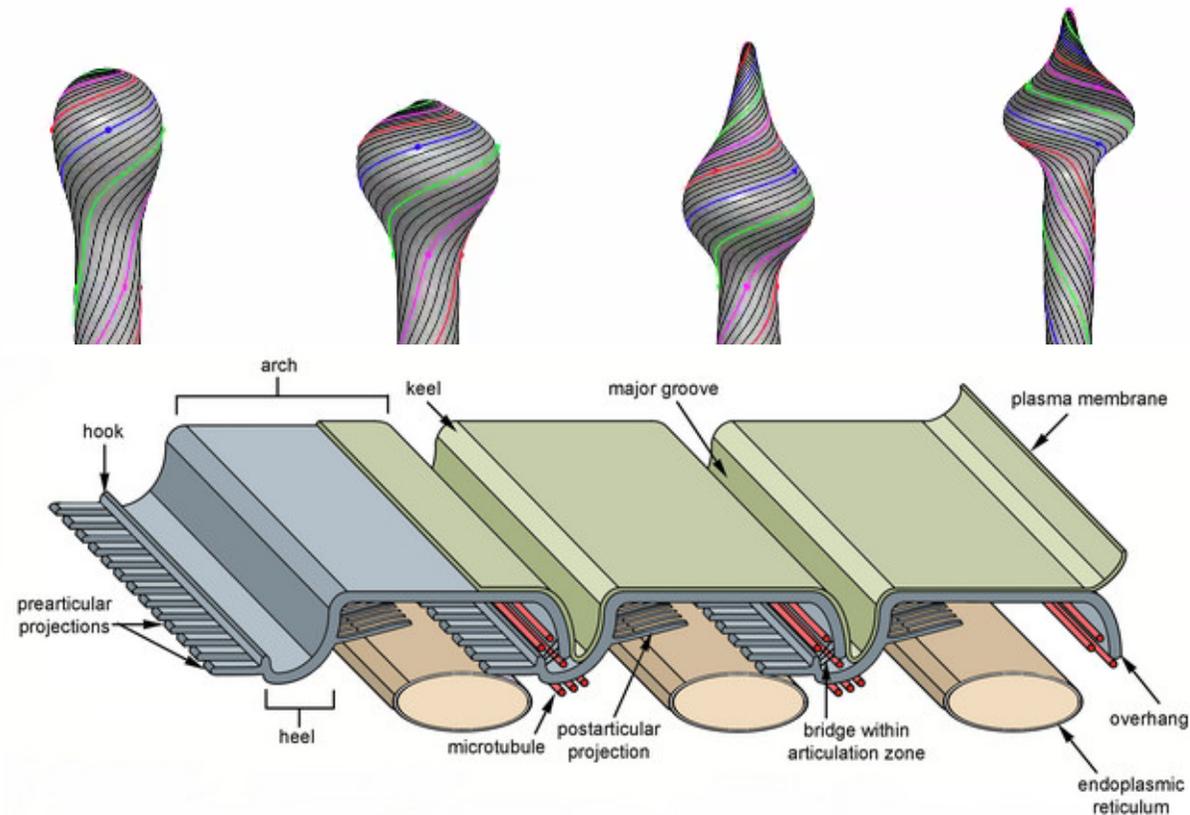


M. Arroyo, D. Milan, L. Heltai, ADS, PNAS **109**, 1784-1789 (2012)

Proposed mechanism: traveling shear wave



Proposed mechanism: traveling shear wave



Thanks

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