Microbial locomotion

18.S995 - L24-26

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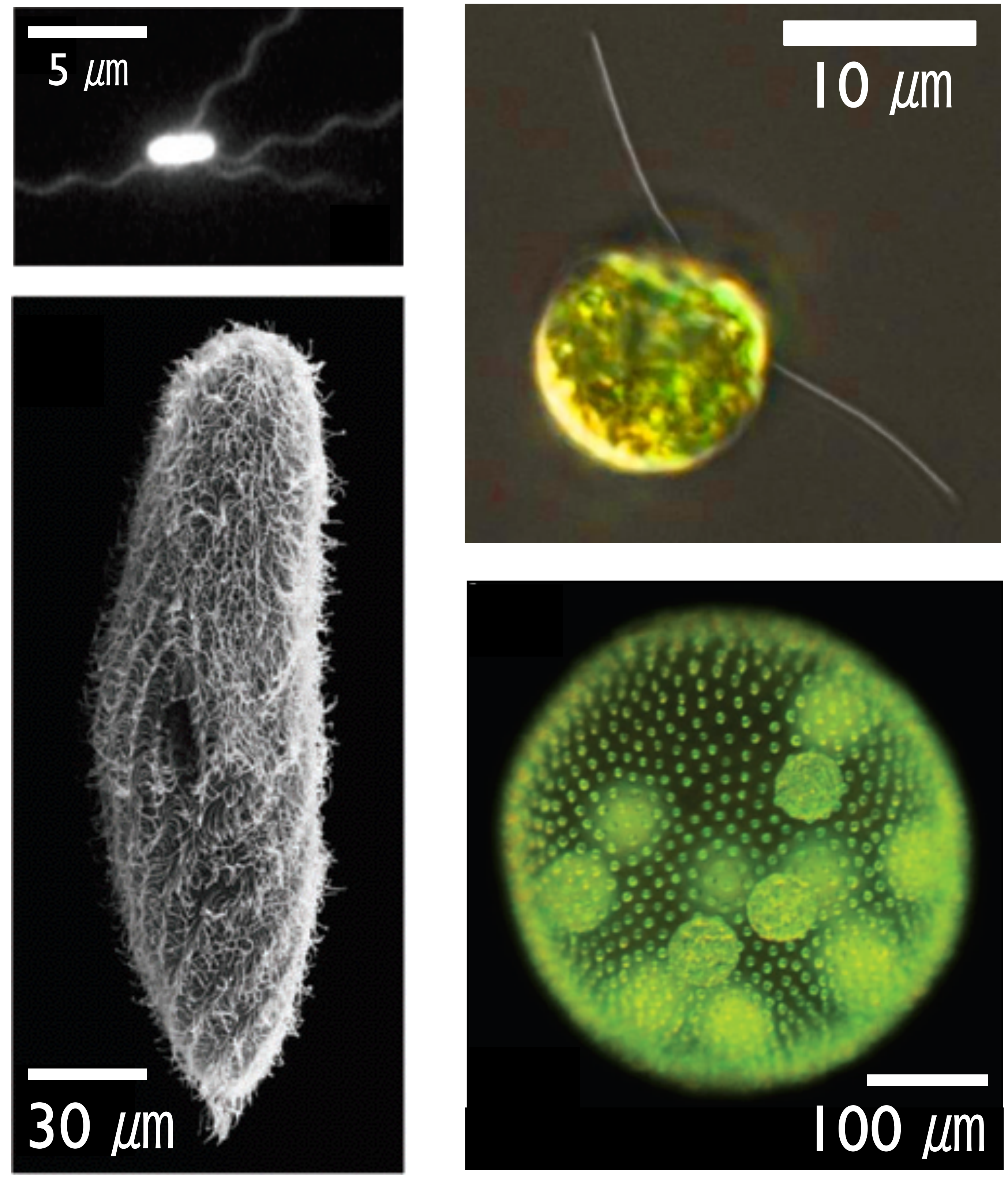
Why microbial hydrodynamics ?

- micro-machines
- hydrodynamic propulsion
- > 50% global biomass
- gut flora, biofilms, ...
- global food web
- > 50% global carbon fixation

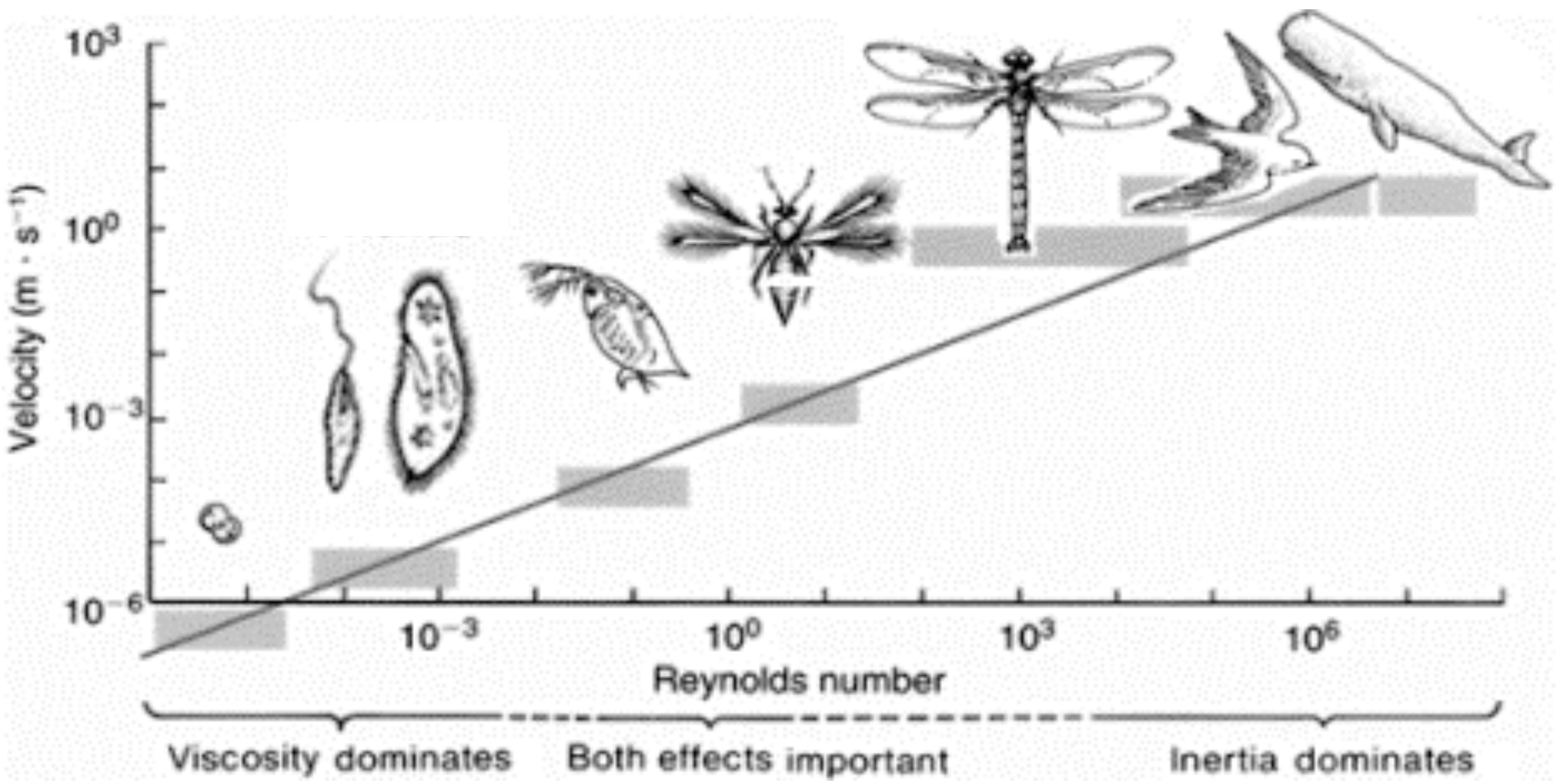
Whitman et al (1998) PNAS



Guasto et al (2012) Annu Rev Fluid Mech

Reynolds numbers

$$Re = \frac{\rho U L}{\mu} = \frac{U L}{\nu}$$



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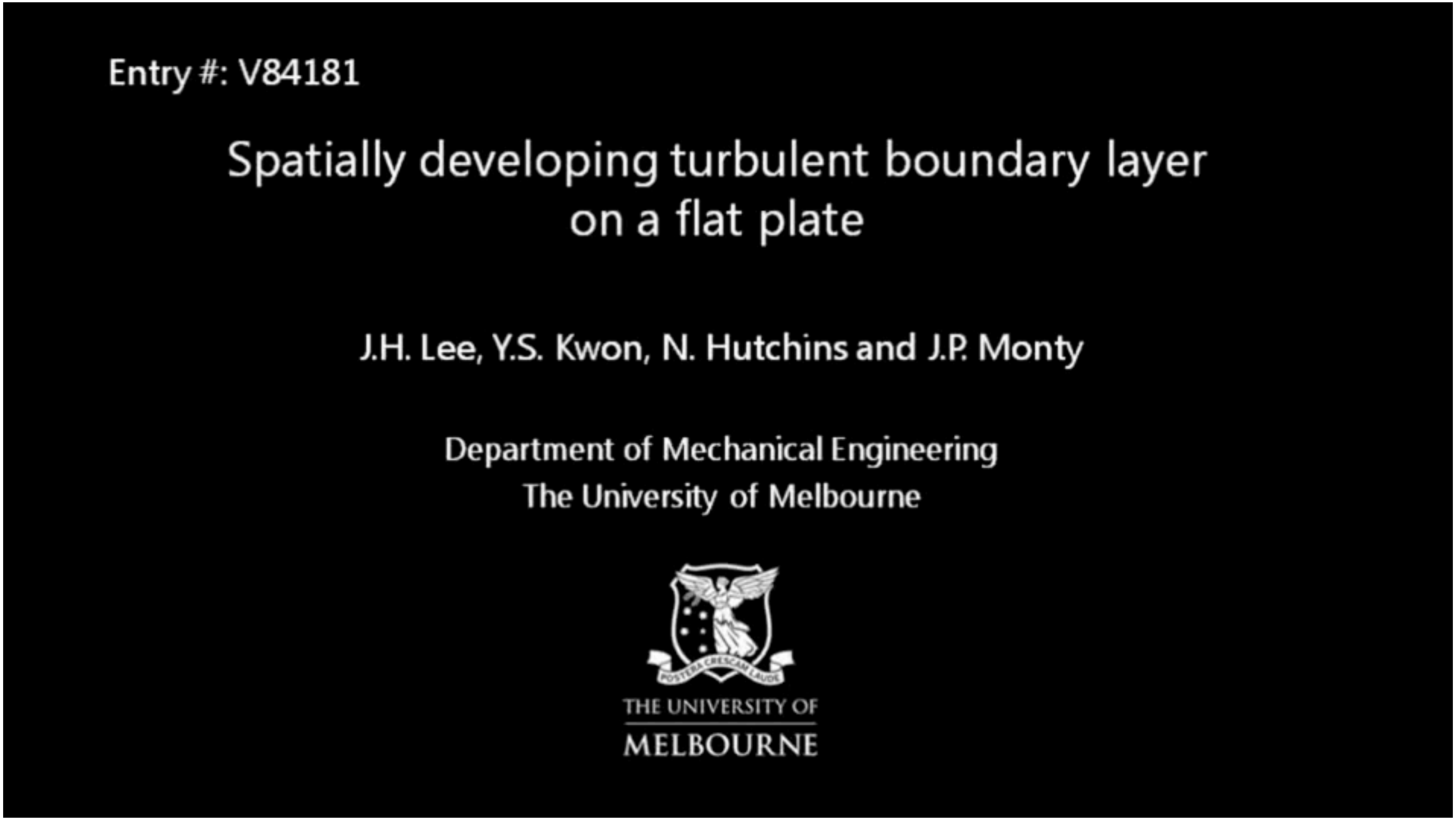
Turbulence


Entry #: V84181
Spatially developing turbulent boundary layer
on a flat plate
J.H. Lee, Y.S. Kwon, N. Hutchins and J.P. Monty
Department of Mechanical Engineering
The University of Melbourne
POSTERA CRESCAM LAUDE
THE UNIVERSITY OF
MELBOURNE

Swimming at low Reynolds number

Navier - Stokes:

$$-\nabla p + \eta \nabla^2 \vec{v} = \cancel{\rho \frac{\partial \vec{v}}{\partial t}} + \cancel{\rho (\vec{v} \cdot \nabla) \vec{v}}$$

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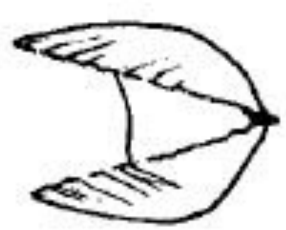
The Scallop Theorem



American Journal of Physics, Vol. 45, No. 1, January 1977

Geoffrey Ingram Taylor

James Lighthill

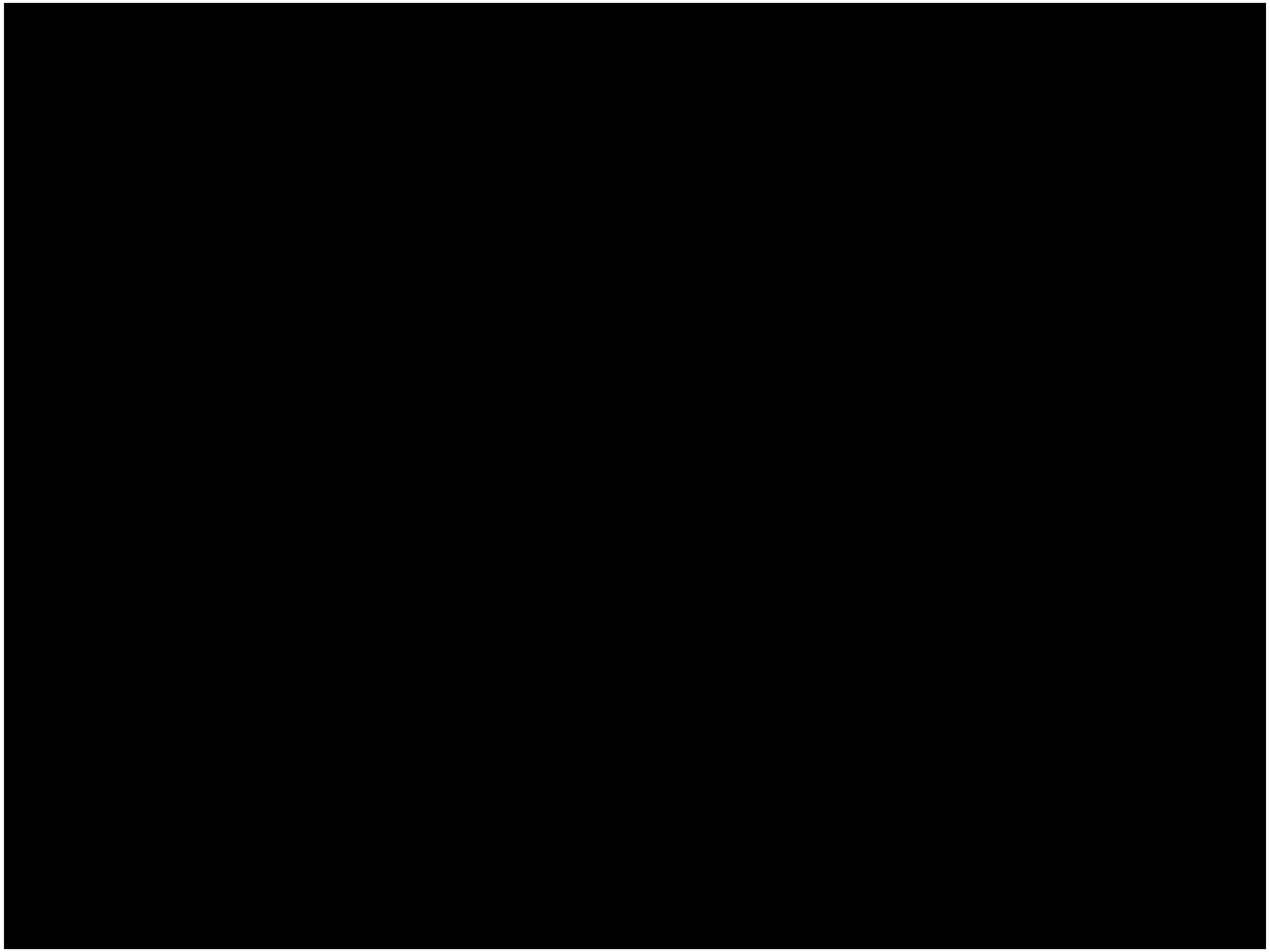
$$\begin{aligned} 0 &= \mu \nabla^2 \boldsymbol{u} - \nabla p + \boldsymbol{f}, \\ 0 &= \nabla \cdot \boldsymbol{u}. \end{aligned}$$

+ time-dependent BCs

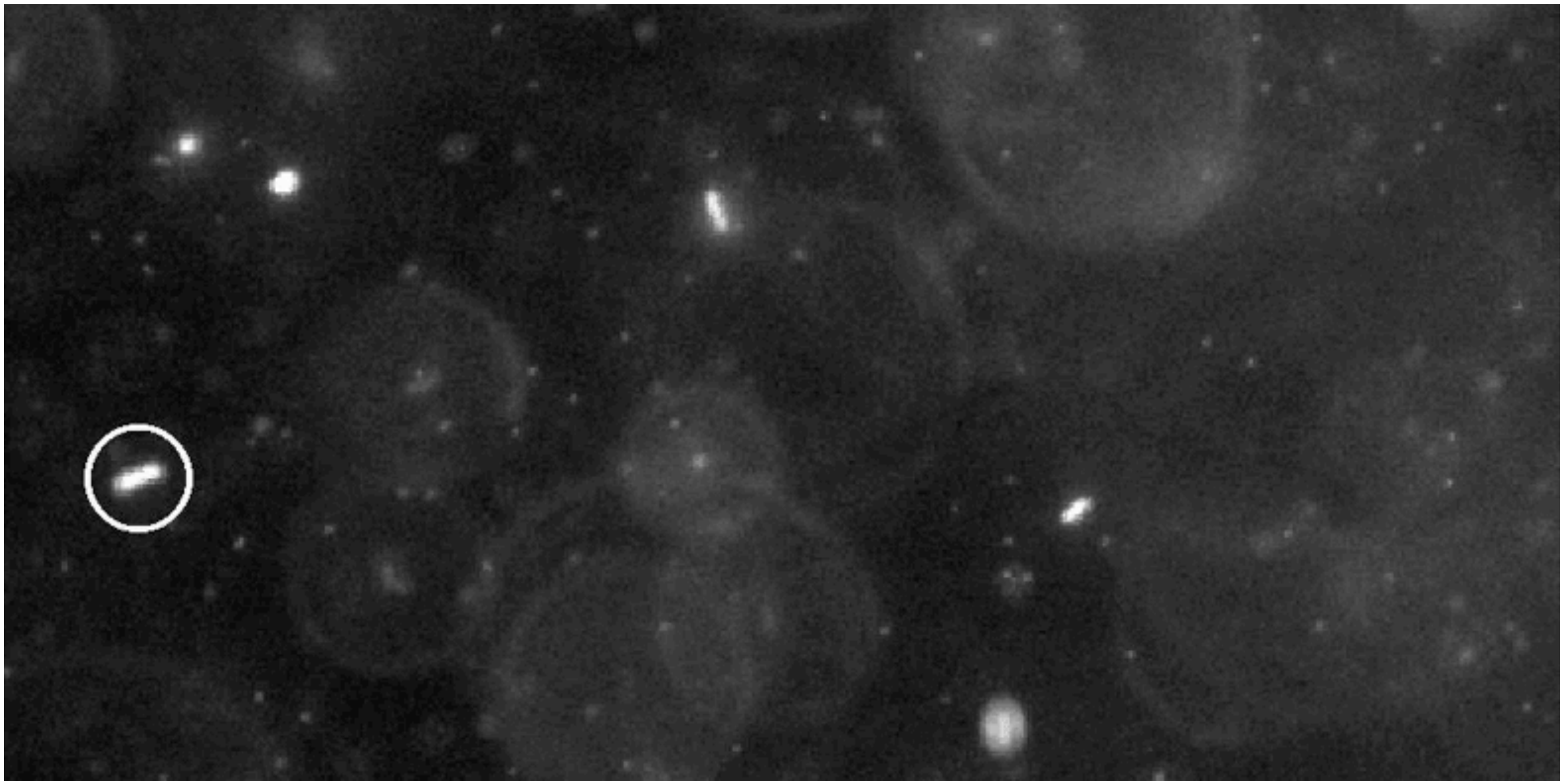
Edward Purcell

Shapere & Wilczek (1987) PRL

Zero-Re flow



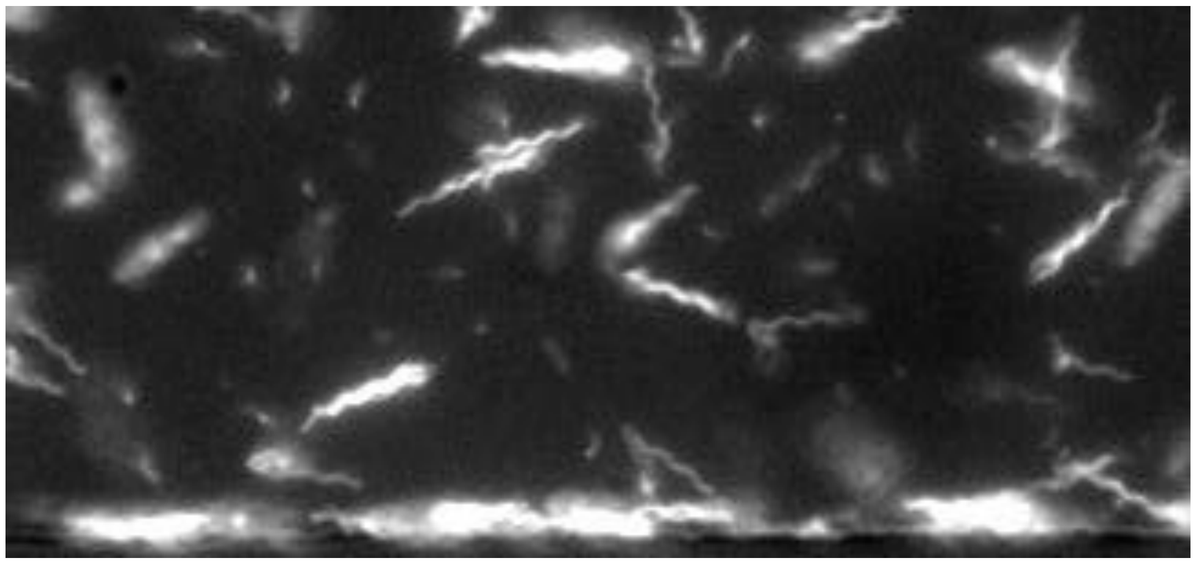
E.coli (non-tumbling HCB 437)



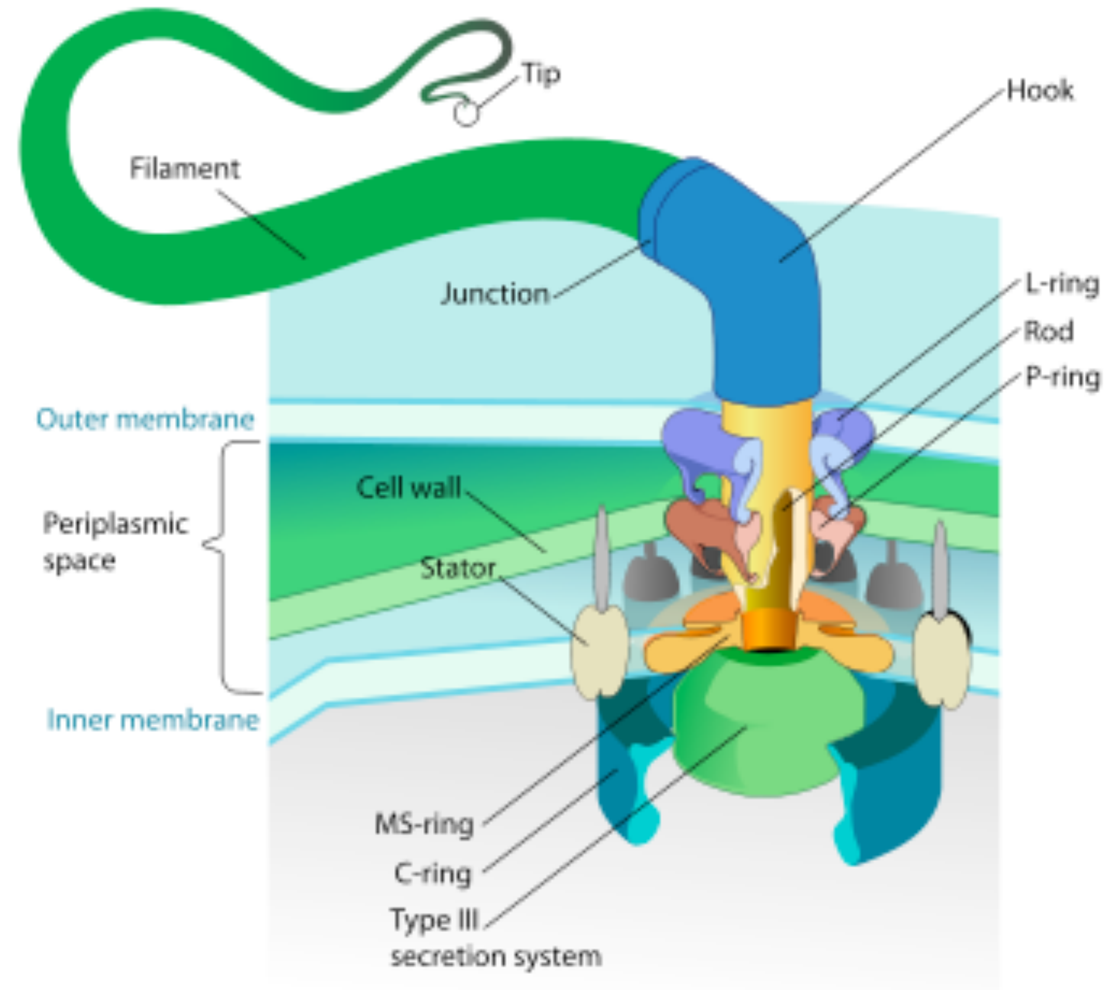
Drescher, Dunkel, Ganguly, Cisneros, Goldstein (2011) PNAS

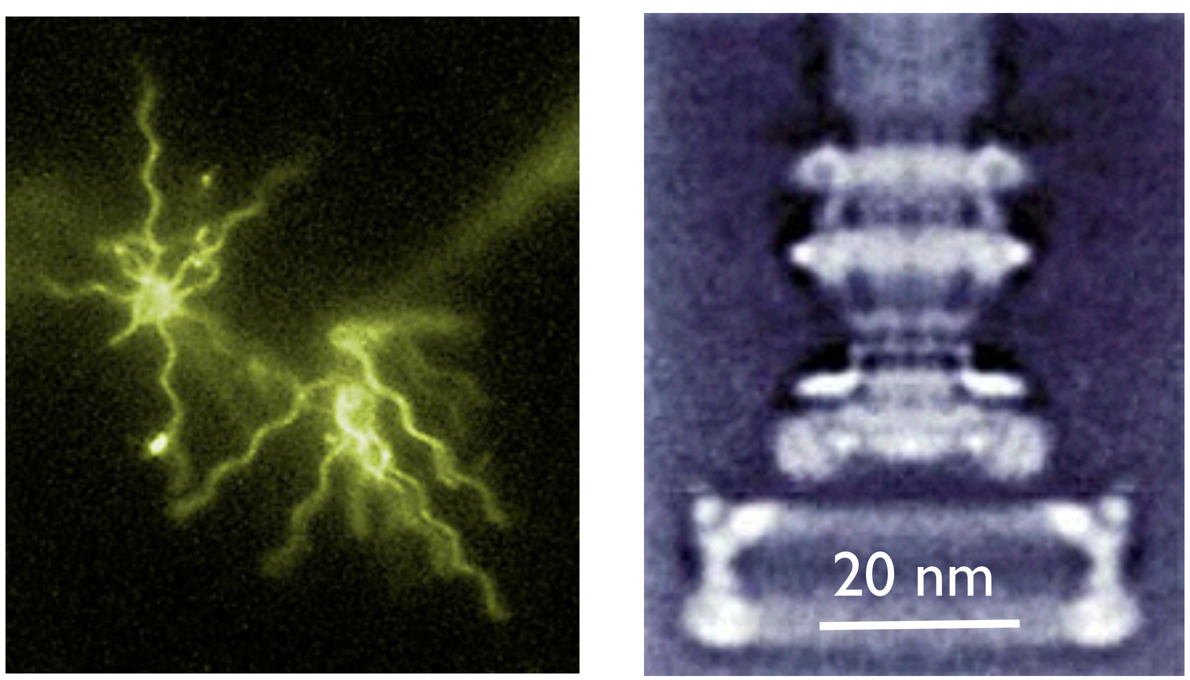
Bacterial motors

movie: V. Kantsler



~20 parts





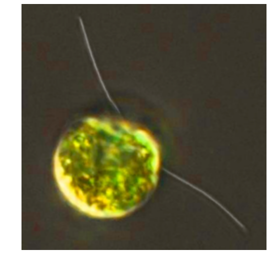
Berg (1999) Physics Today

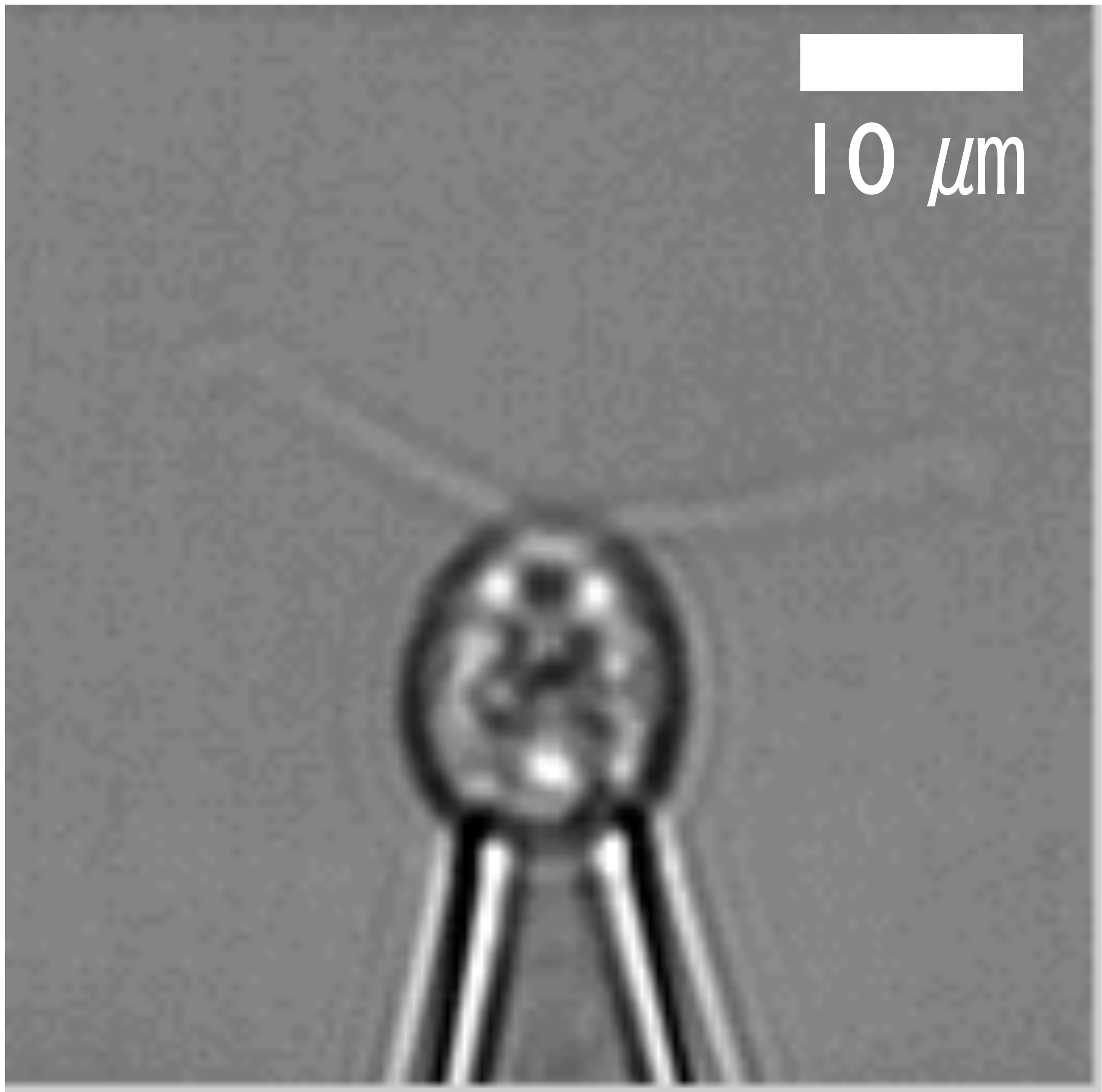
Chen et al (2011) EMBO Journal

source: wiki

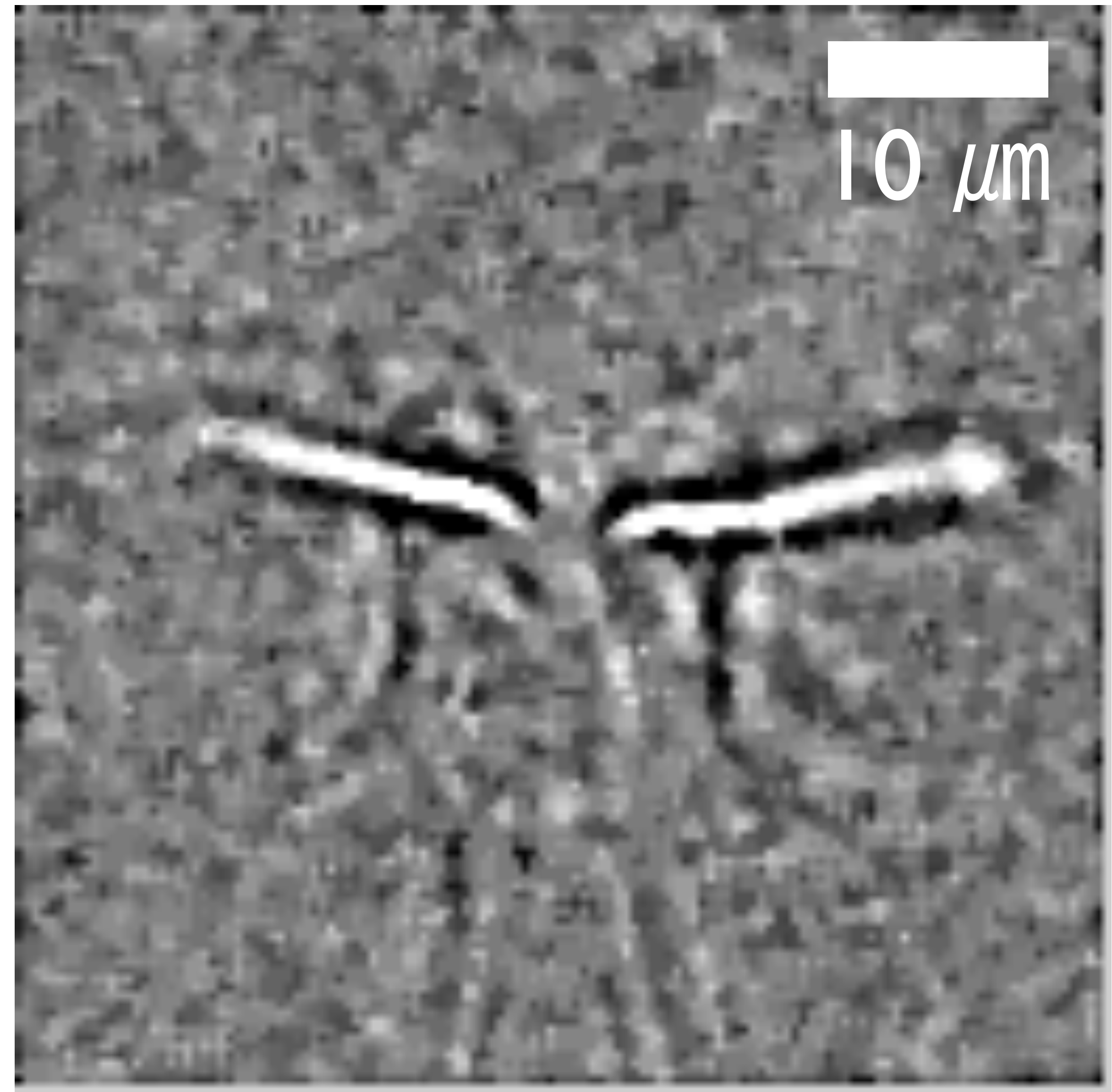
dunkel@math.mit.edu

Chlamydomonas alga





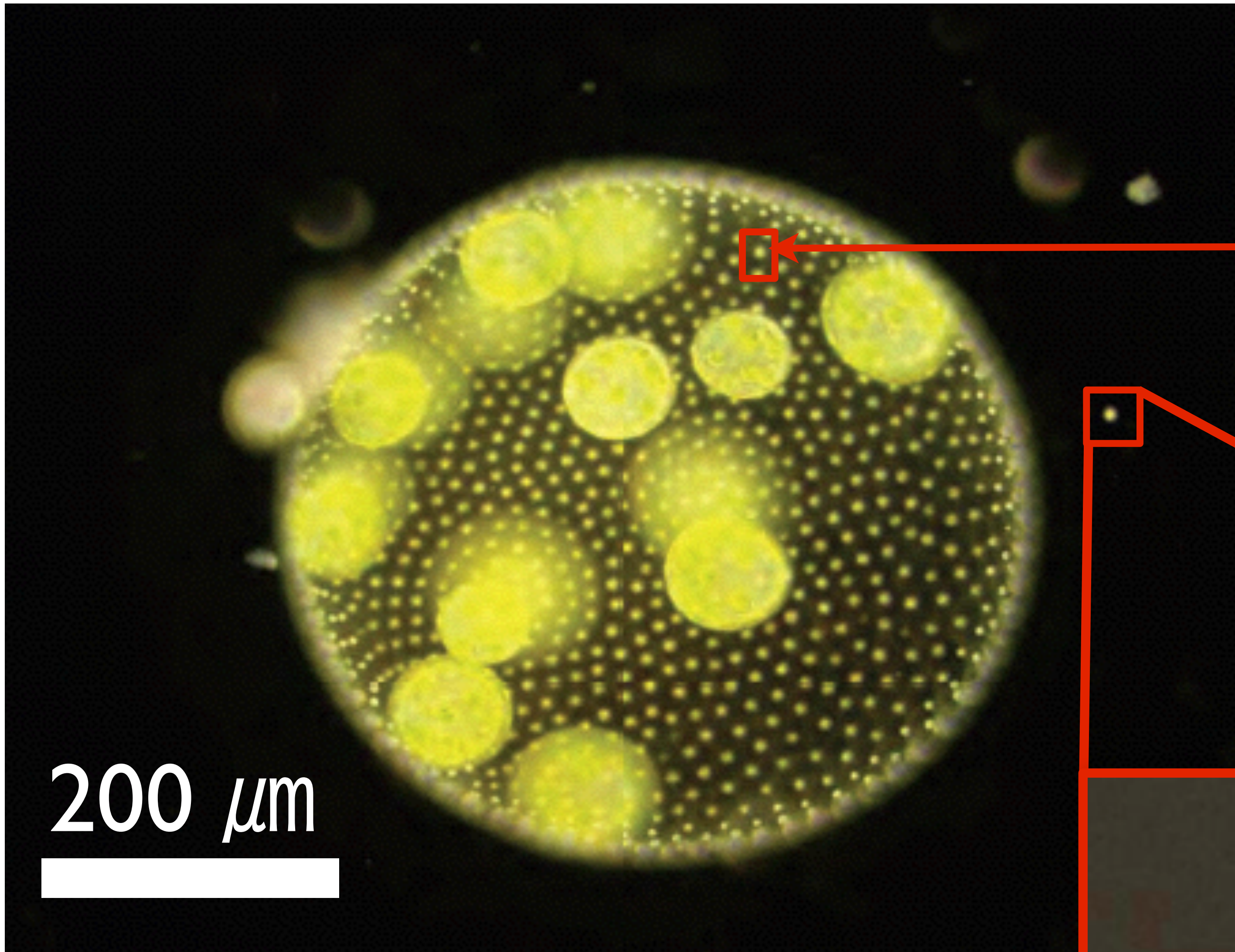
~ 50 beats / sec



speed ~100 μm/s

Goldstein et al (2011) PRL

dunkel@math.mit.edu



Volvox carteri

Chlamydomonas reinhardtii

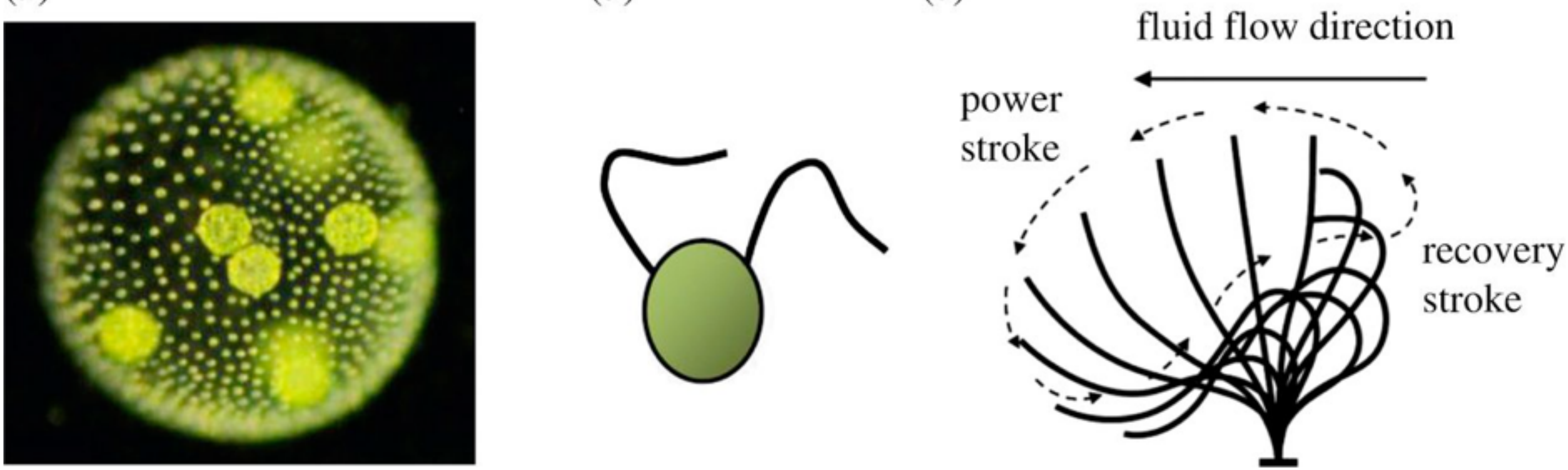
dunkel@math.mit.edu

Stroke

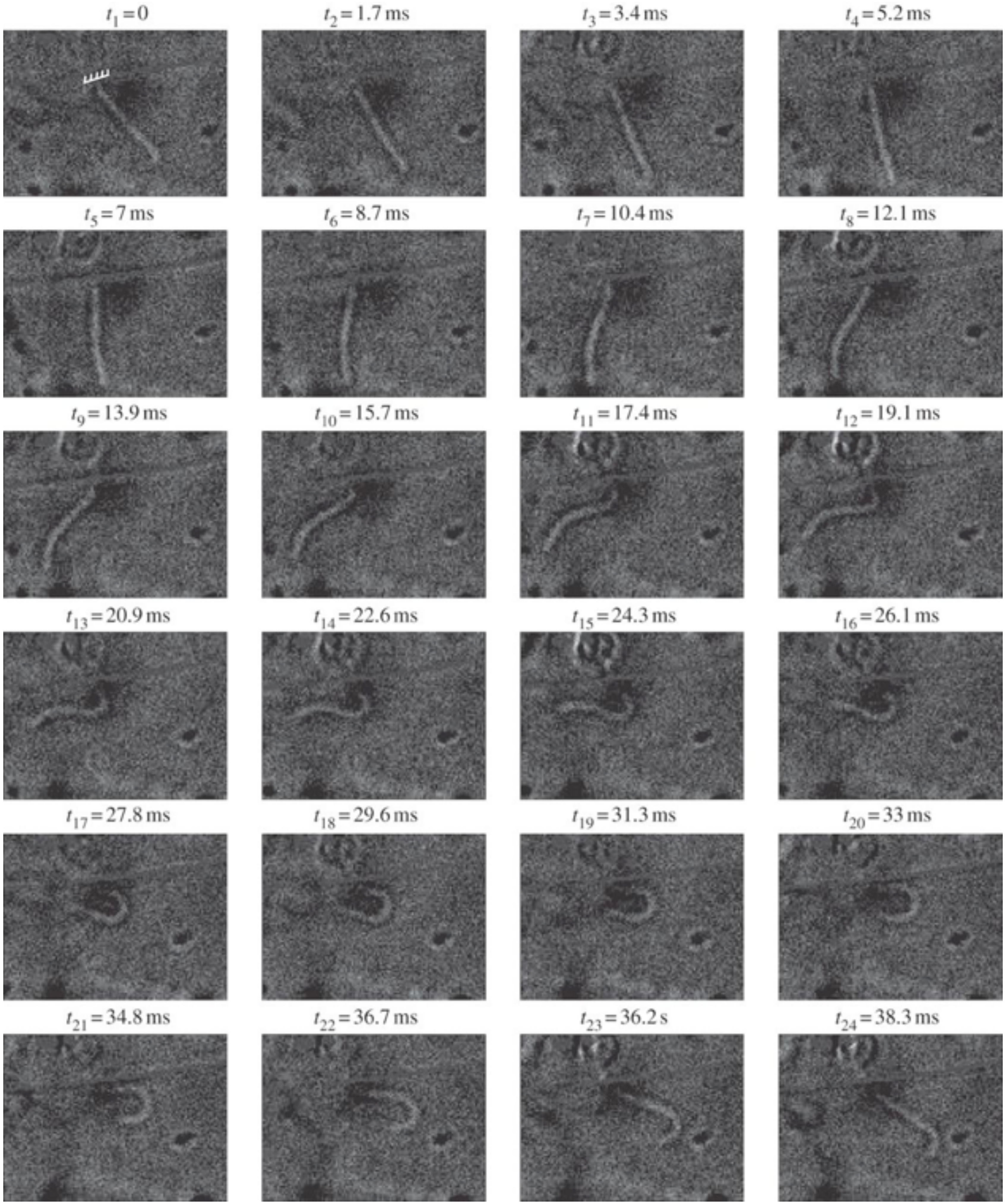
(a)

(b)

(c)



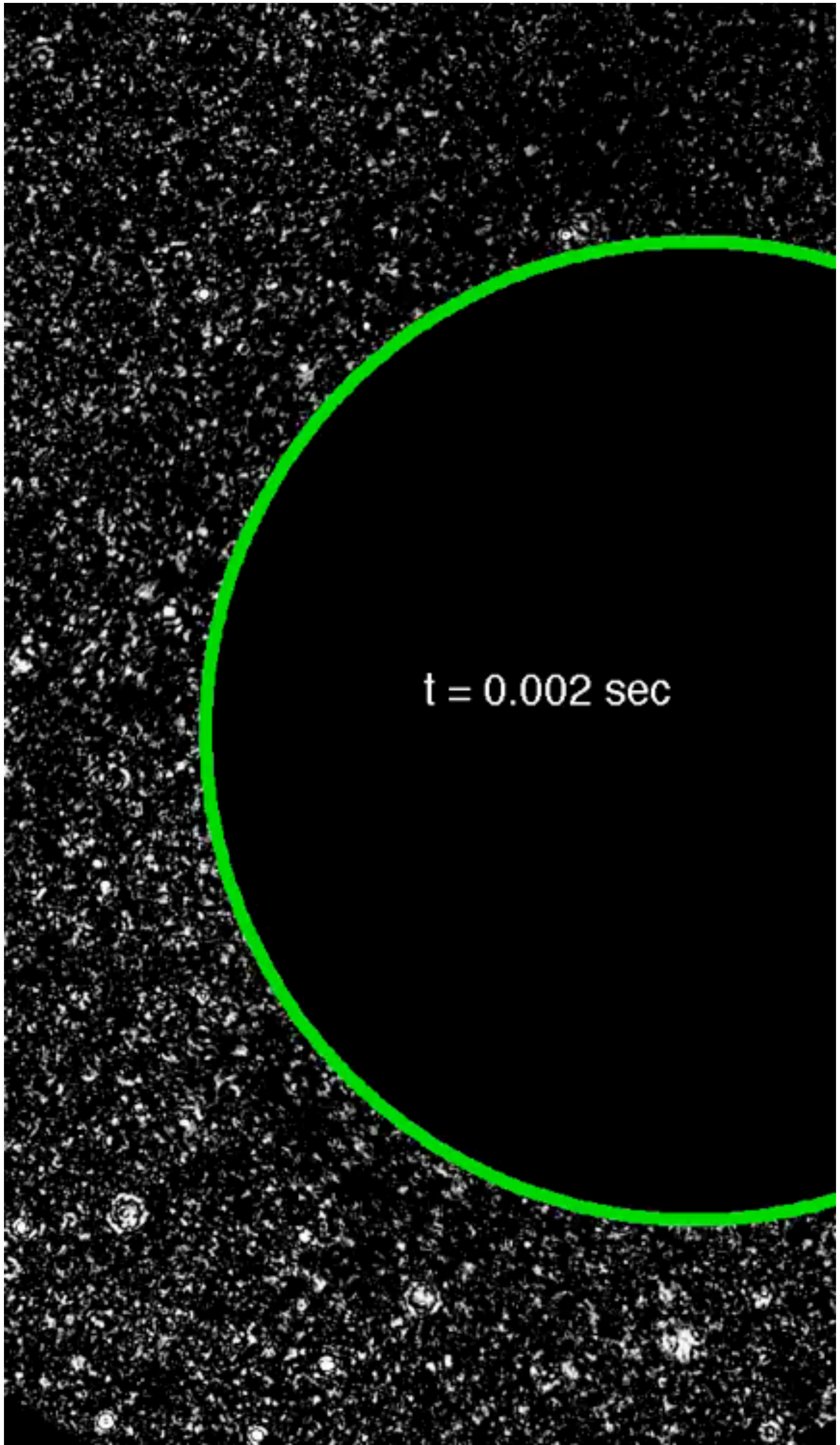
Sareh et al (2013) J Roy Soc Interface



Volvox carteri

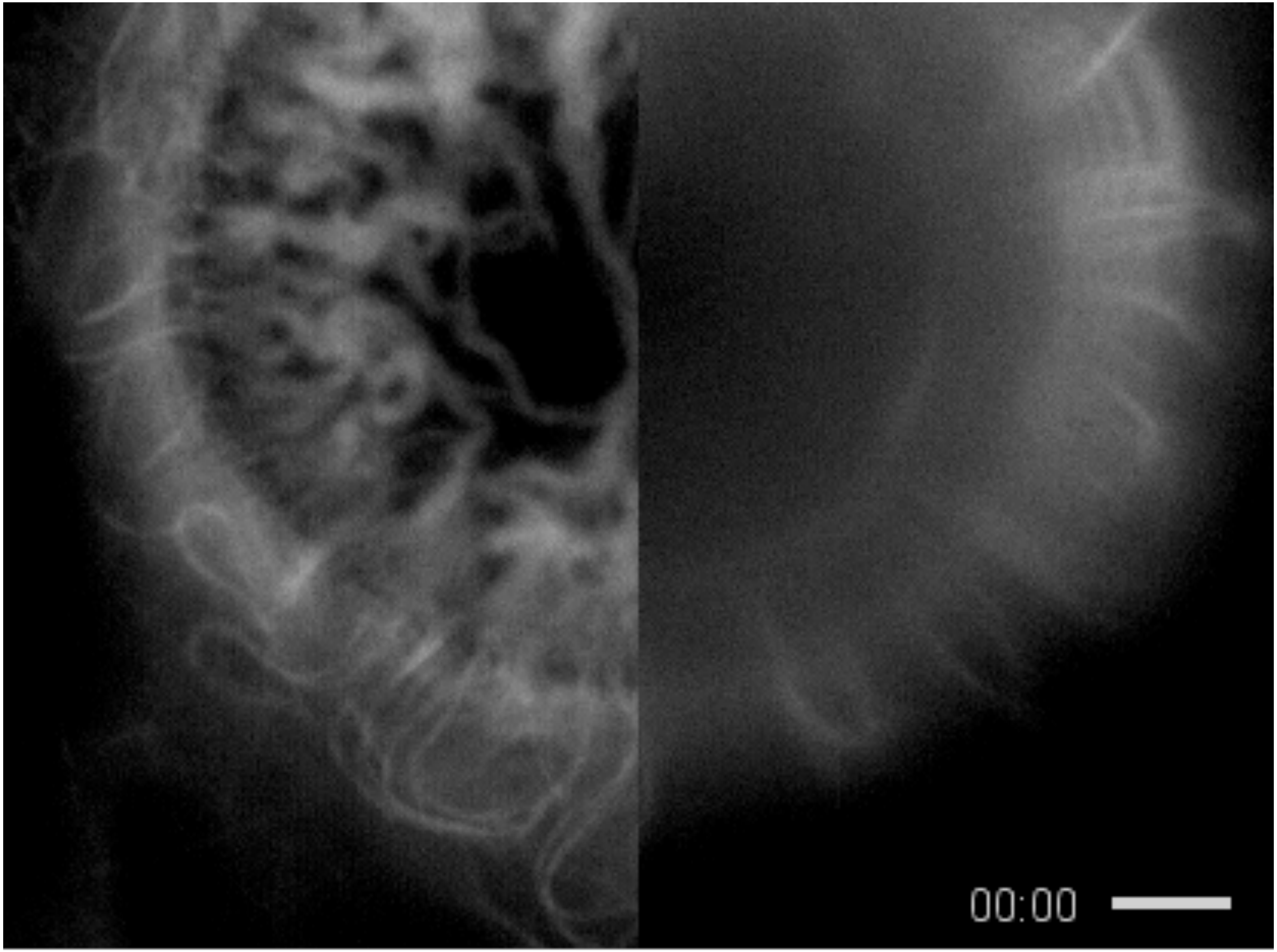
beating frequency
25Hz

Sareh et al (2013)
J Roy Soc Interface



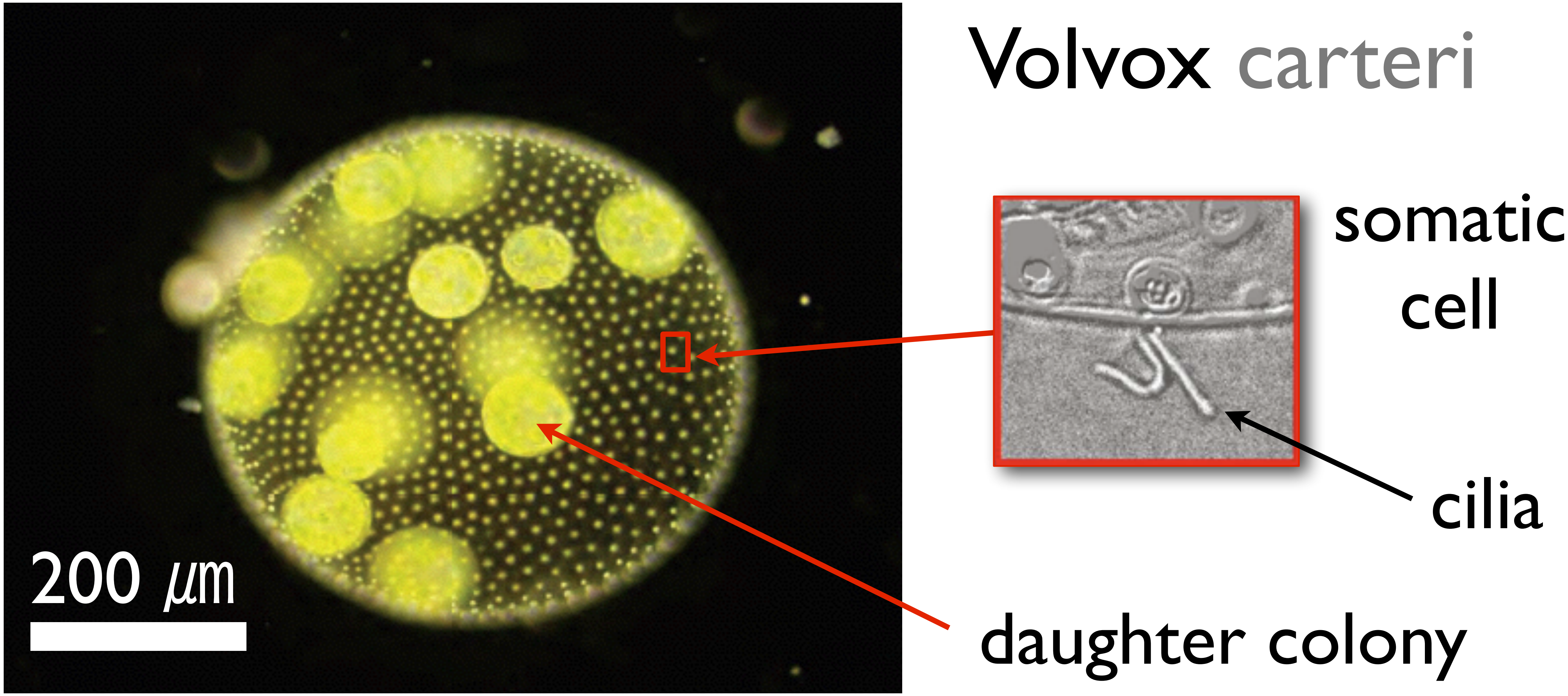
Meta-chronal waves

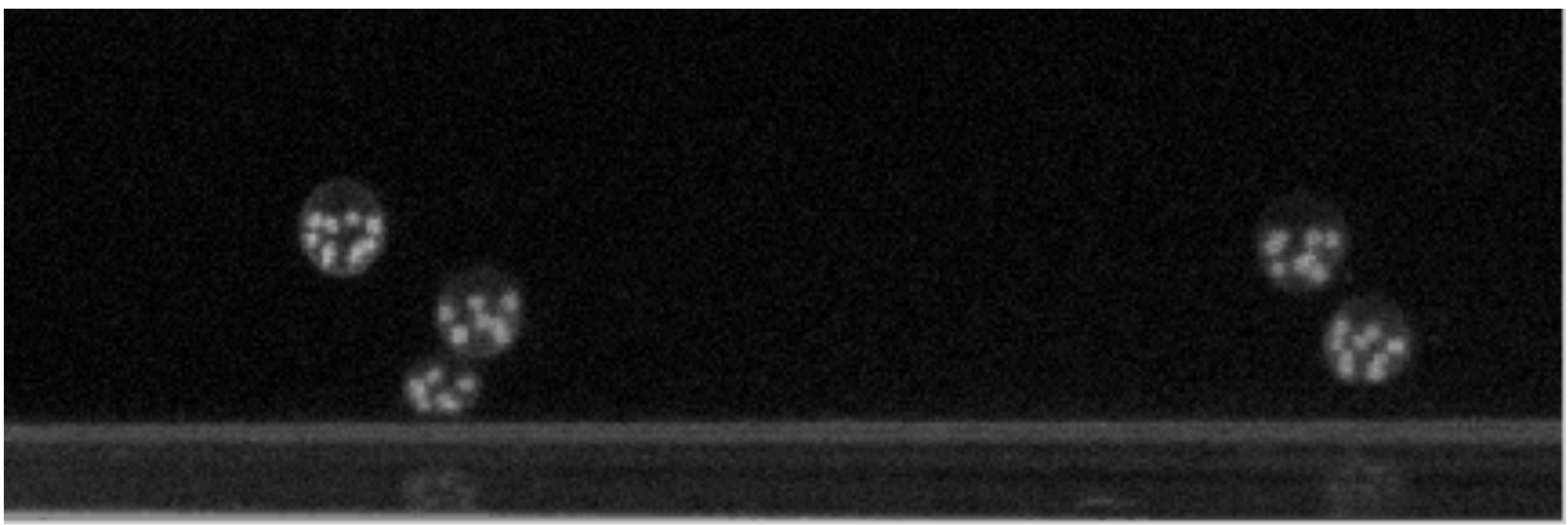
Brumley et al (2012) PRL



Dogic lab (Brandeis)

Volvox carteri





Drescher et al (2010) PRL

- How can *Volvox* perform phototaxis?

(discussed later)

Swimming at low Reynolds number

Navier - Stokes:

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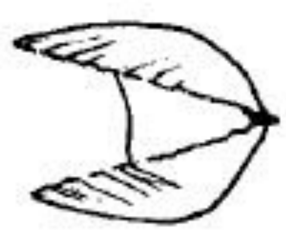

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+ time-dependent BCs

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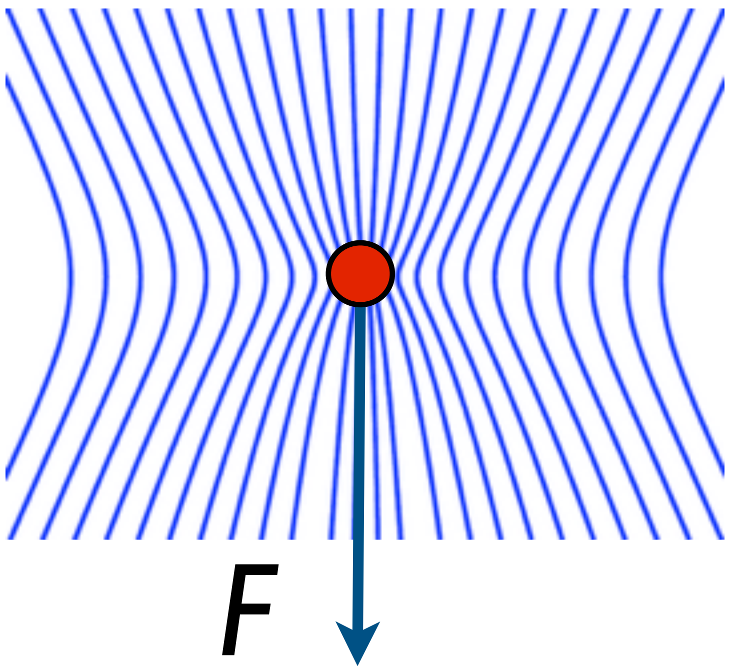
Shapere & Wilczek (1987) PRL

Superposition of singularities

stokeslet

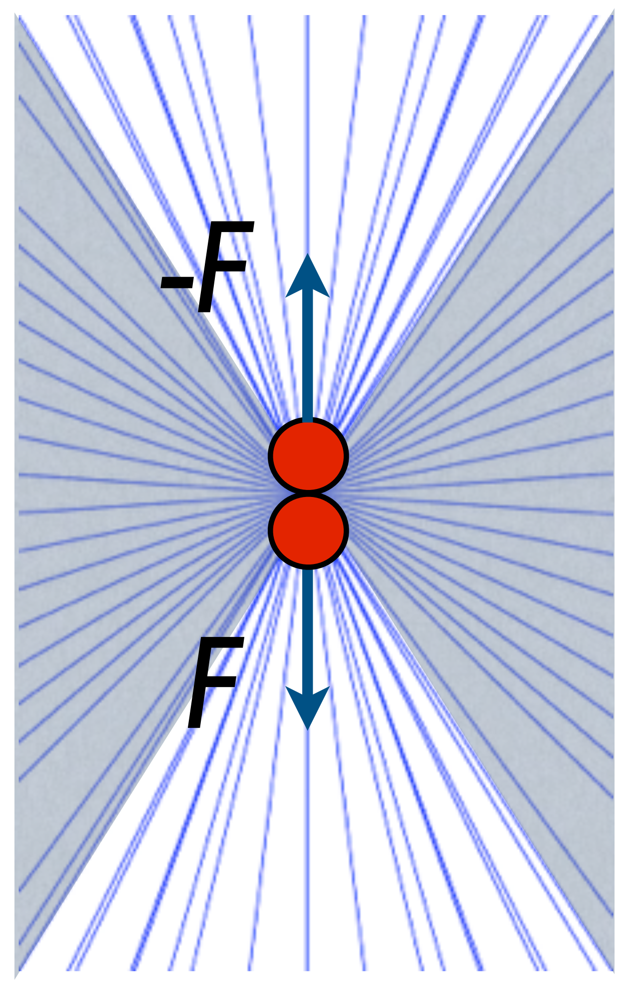


$$p(\boldsymbol{r}) = \frac{\hat{\boldsymbol{r}} \cdot \boldsymbol{F}}{4\pi r^2} + p_0$$

$$v_i(\boldsymbol{r}) = \frac{(8\pi\mu)^{-1}}{r}[\delta_{ij} + \hat{r}_i \hat{r}_j]F_j$$

flow ~ r^{-1}

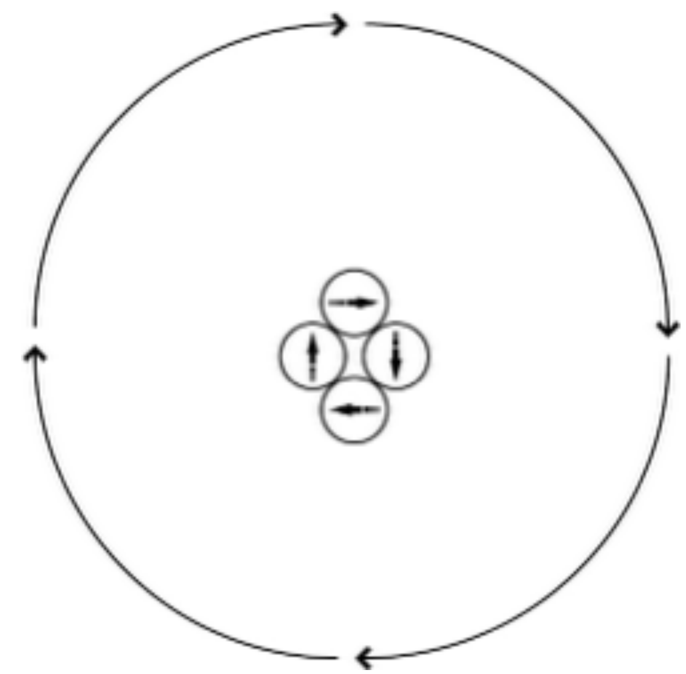
2x stokeslet =
symmetric dipole



r^{-2}

'pusher'

rotlet

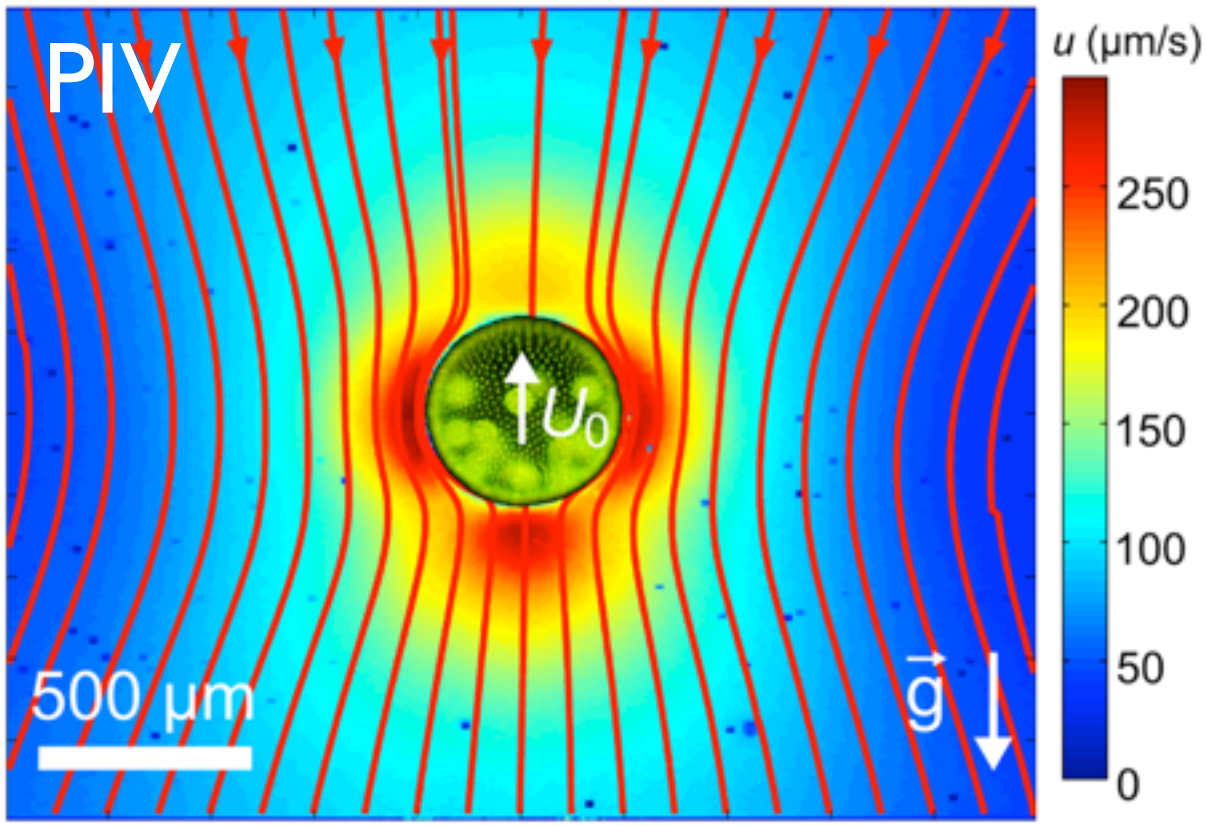


r^{-2}

Volvox

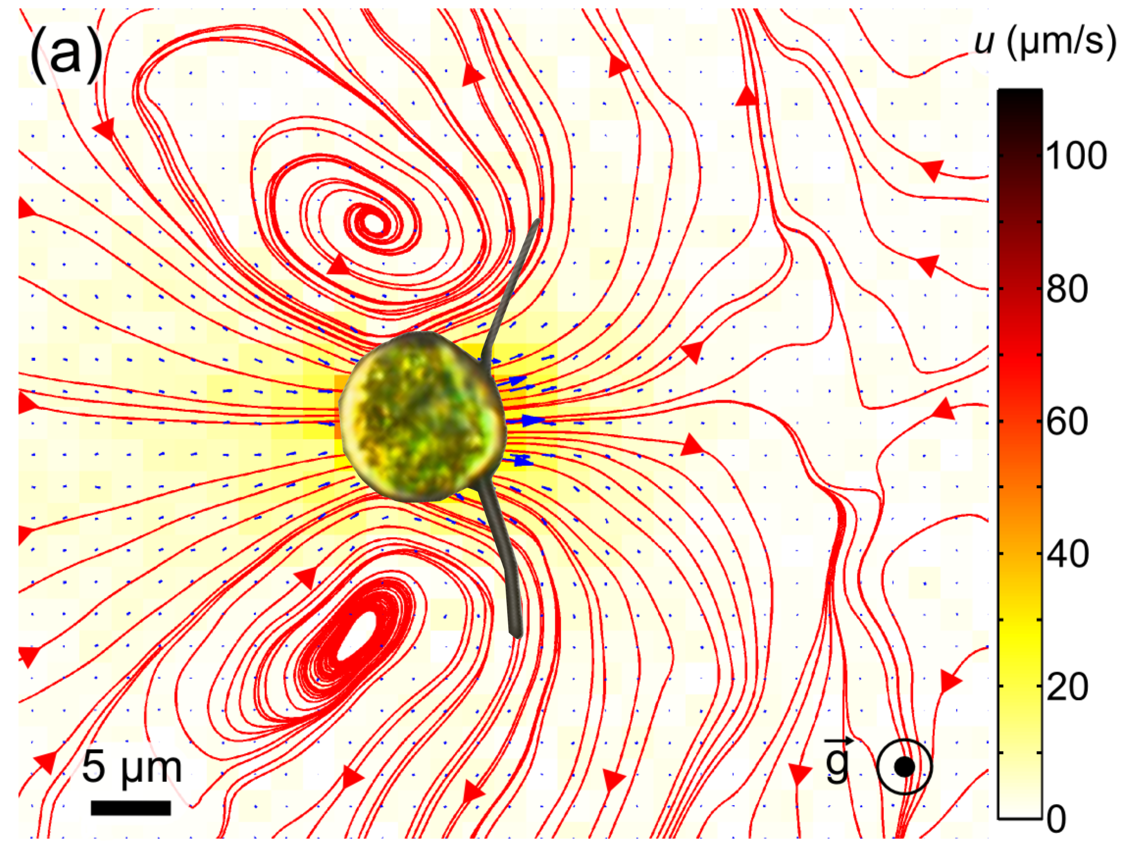
Chlamy

swimming speed ~ 100 μm/sec



$$\mathbf{v}_{fit}(\mathbf{r}) = -\ U_0\,\hat{\mathbf{y}} - \frac{A_{St}}{r}\left(\mathbf{I} + \hat{\mathbf{r}}\hat{\mathbf{r}}\right)\cdot\hat{\mathbf{y}} + \frac{A_{str}}{r^2}\left(1 - 3(y/r)^2\right)\hat{\mathbf{r}} - \frac{A_{sd}}{r^3}\left(\frac{\mathbf{I}}{3} - \hat{\mathbf{r}}\hat{\mathbf{r}}\right)\cdot\hat{\mathbf{y}} \qquad (1)$$

swimming speed ~ 50 μm/sec



$$3\text{D}: \quad \boldsymbol{v} \sim 1/r^2$$

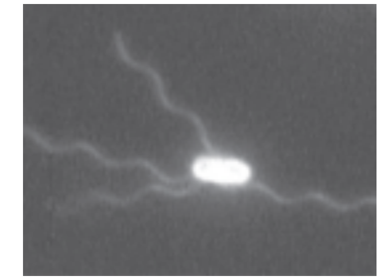
$$2\text{D}: \quad \boldsymbol{v} \sim 1/r$$

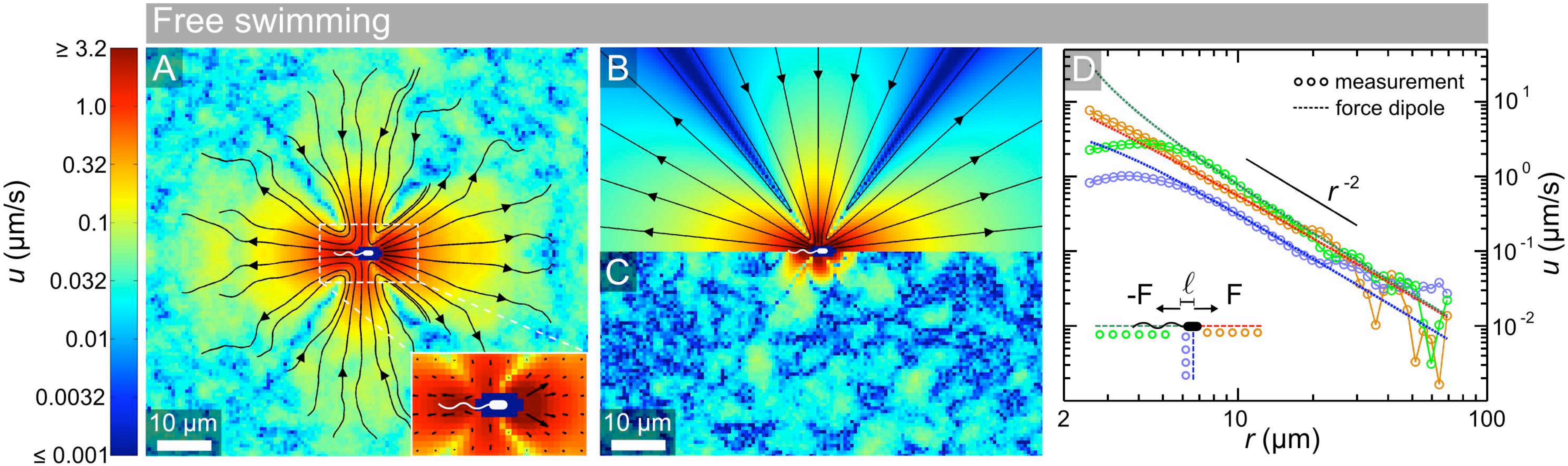
... no dipoles !

Drescher et al (2010) PRL

Guasto et al (2010) PRL

E.coli (non-tumbling HCB 437)





$$\boldsymbol{u}(\boldsymbol{r}) = \frac{A}{|\boldsymbol{r}|^2}\left[3(\hat{\boldsymbol{r}}.\hat{\boldsymbol{d}})^2 - 1\right]\hat{\boldsymbol{r}}, \quad A = \frac{\ell F}{8\pi\eta}, \quad \hat{\boldsymbol{r}} = \frac{\boldsymbol{r}}{|\boldsymbol{r}|}$$

$$V_0 = 22 \pm 5 \;\; \mu\mathrm{m/s}$$

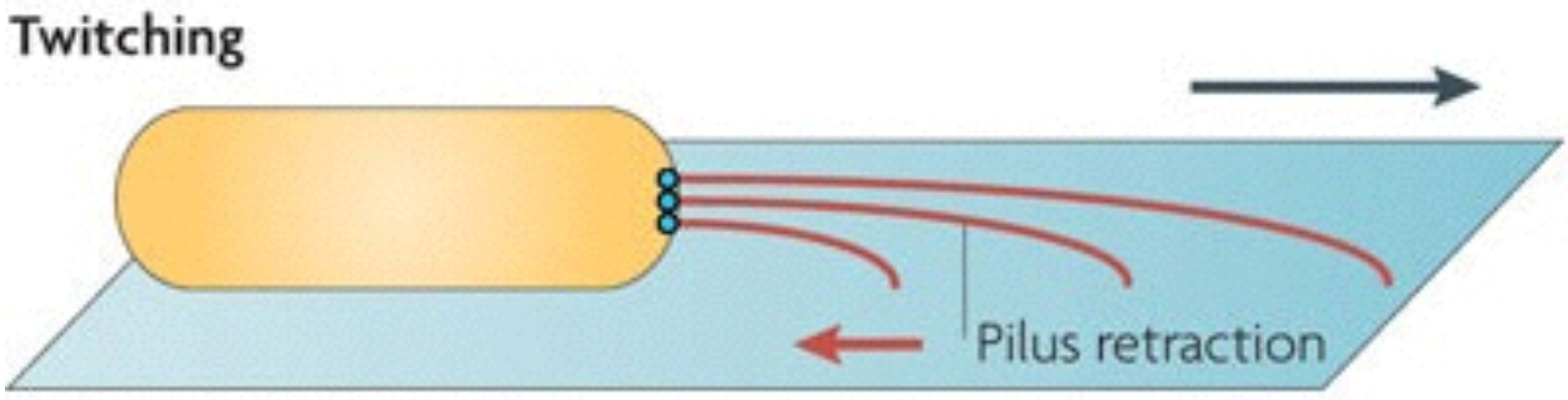
$$\ell = 1.9 \;\; \mu\mathrm{m}$$

$$F = 0.42 \;\; \mathrm{pN}$$

weak 'pusher' dipole

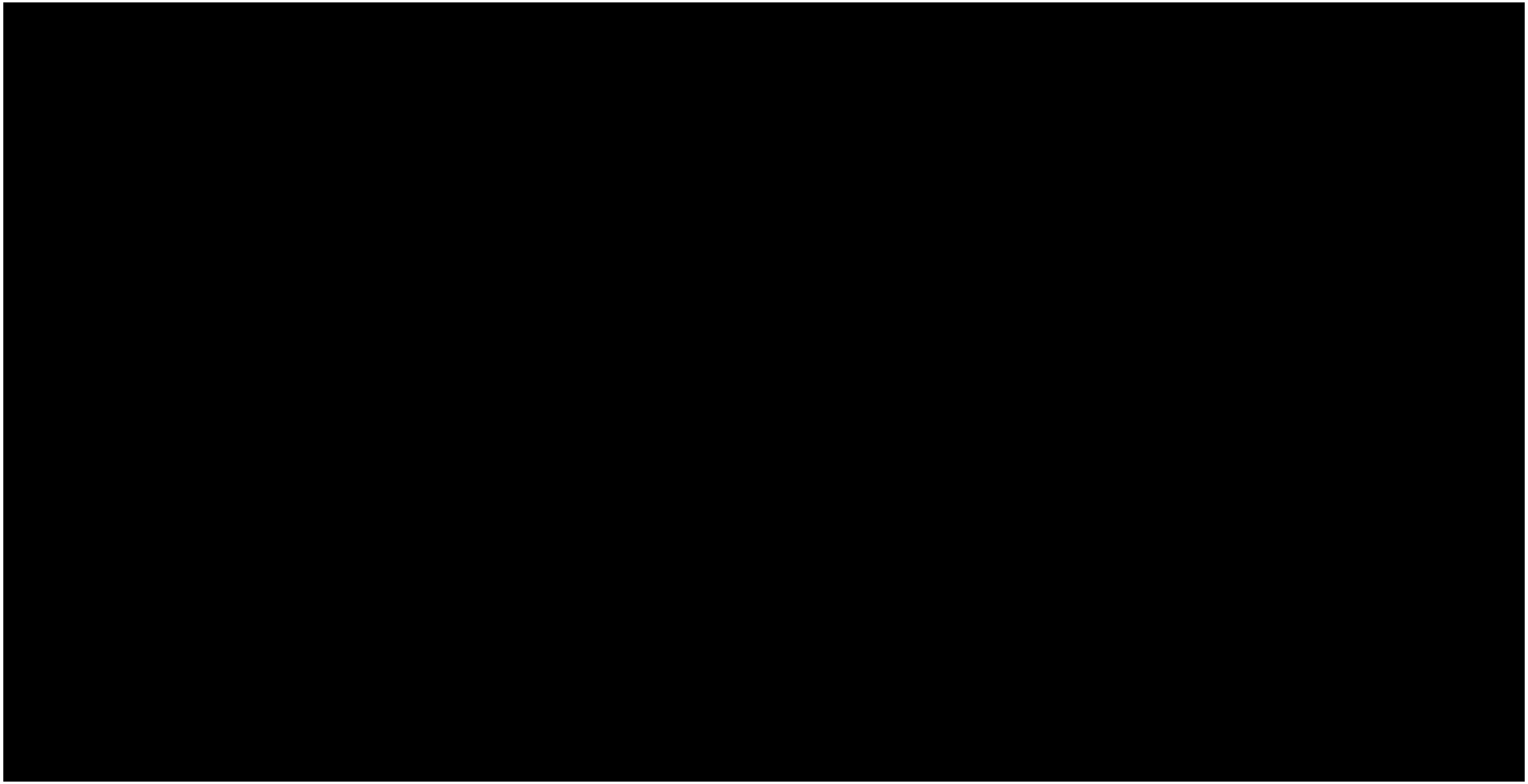
Drescher, Dunkel, Ganguly, Cisneros, Goldstein (2011) PNAS

Twitching motility



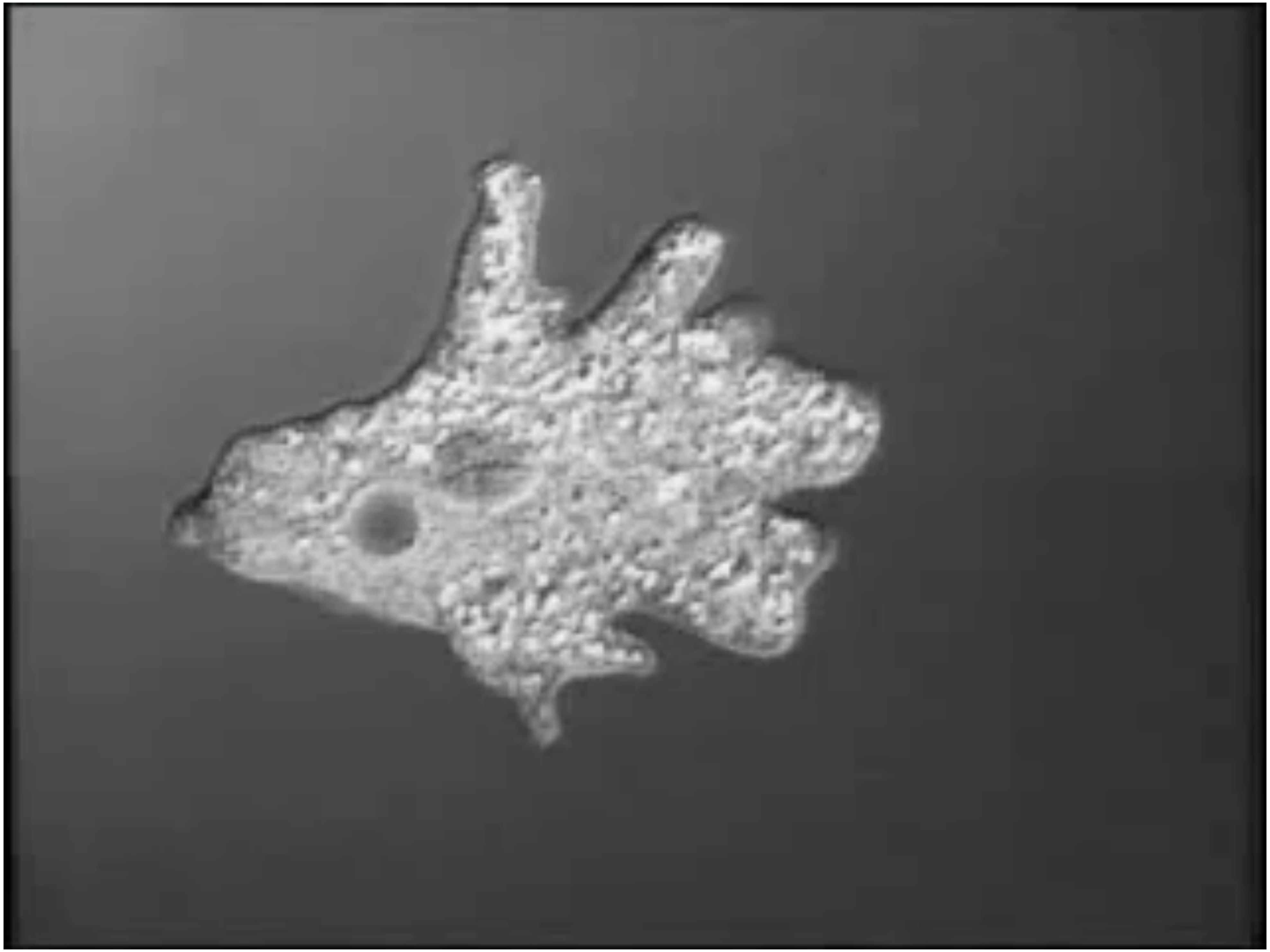
Type-IV Pili

Twitching motility



Pseudomonas

Amoeboid locomotion



5.1 Navier-Stokes equations

Consider a fluid of conserved mass density $\varrho(t, \boldsymbol{x})$, governed by continuity equation

$$\partial_t \varrho + \nabla \cdot (\varrho \boldsymbol{u}) = 0, \tag{5.1}$$

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where $\boldsymbol{u}(t, \boldsymbol{x})$ is local flow velocity. According to standard hydrodynamic theory, the dynamics of $\boldsymbol{u}$ is described by the Navier-Stokes equations (NSEs)

$$\varrho \left[\partial_t \boldsymbol{u} + (\boldsymbol{u} \cdot \nabla)\boldsymbol{u}\right] = \boldsymbol{f} - \nabla p + \nabla \cdot \hat{T}, \tag{5.2}$$

where $p(t, \boldsymbol{x})$ the pressure in the fluid, $\hat{T}(t, \boldsymbol{x})$ the deviatoric[2]) stress-energy tensor of the fluid, and $\boldsymbol{f}(t, \boldsymbol{x})$ an external force-density field. A typical example of an external force $\boldsymbol{f}$,

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where $p(t, \boldsymbol{x})$ the pressure in the fluid, $\hat{T}(t, \boldsymbol{x})$ the deviatoric[2]) stress-energy tensor of the fluid, and $\boldsymbol{f}(t, \boldsymbol{x})$ an external force-density field. A typical example of an external force $\boldsymbol{f}$, that is also relevant in the biological context, is the gravitational force

$$\boldsymbol{f} = \varrho \boldsymbol{g}, \tag{5.3}$$

where $\boldsymbol{g}(t, \boldsymbol{x})$ is the gravitational acceleration field.

Considering a Cartesian coordinate frame, Eqs. (5.1) and (5.2) can also be rewritten in the component form

$$\partial_t \varrho + \nabla_i(\varrho u_i) = 0, \tag{5.4a}$$

$$\varrho\,(\partial_t u_i + u_j \partial_j u_i) = F_i - \partial_i p + \partial_j \hat{T}_{ji}. \tag{5.4b}$$

To close the system of equations (5.4), one still needs to

(i) fix the equation of state

$$p = p[\varrho, \ldots],$$

(ii) choose an ansatz the symmetric stress-energy tensor

$$\hat{T} = (\hat{T}_{ij}[\varrho, \boldsymbol{u}, \ldots]),$$

(iii) specify an appropriate set of initial and boundary conditions.

---

[2] 'deviatoric':= without hydrostatic stress (pressure); a 'full' stress-energy tensor $\hat{\sigma}$ may be defined by

$$\hat{\sigma}_{ij} := -p\,\delta_{ij} + \hat{T}_{ij}.$$

Simplifications In the case of a *homogeneous* fluid with [3]

$$\partial_t \varrho = 0 \qquad \text{and} \qquad \nabla \varrho = 0, \tag{5.5}$$

the associated flow is *incompressible* (isochoric)

$$\nabla \cdot \boldsymbol{u} = 0. \tag{5.6}$$

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A *Newtonian* fluid is a fluid that can, by definition, be described by

$$\hat{T}_{ij} := \lambda \, (\nabla \cdot \boldsymbol{u}) \, \delta_{ij} + \mu \, (\partial_i u_j + \partial_j u_i). \tag{5.7}$$

where λ the first coefficient of viscosity (related to *bulk* viscosity), and μ is the second coefficient of viscosity (shear viscosity). Thus, for an incompressible Newtonian fluid, the Navier-Stokes system (5.4) simplifies to

$$\begin{aligned} 0 &= \nabla \cdot \boldsymbol{u}, && (5.8\text{a}) \\ \varrho \, [\partial_t \boldsymbol{u} + (\boldsymbol{u} \cdot \nabla) \boldsymbol{u}] &= -\nabla p + \mu \nabla^2 \boldsymbol{u} + \boldsymbol{f}. && (5.8\text{b}) \end{aligned}$$

Dynamic viscosity The SI physical unit of *dynamic* viscosity μ is the Pascal$\times$second

$$[\mu] = 1\,\mathrm{Pa} \cdot \mathrm{s} = 1\,\mathrm{kg}/(\mathrm{m} \cdot \mathrm{s}) \tag{5.9}$$

If a fluid with a viscosity $\mu = 1\,\mathrm{Pa} \cdot \mathrm{s}$ is placed between two plates, and one plate is pushed sideways with a shear stress of one pascal, it moves a distance equal to the thickness of the layer between the plates in one second. The dynamic viscosity of water ($T = 20\,°\mathrm{C}$) is $\mu = 1.0020 \times 10^{-3}\,\mathrm{Pa} \cdot \mathrm{s}$.

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Kinematic viscosity Below we will be interested in comparing viscous and inertial forces. Their ratio is characterized by the *kinematic* viscosity ν, defined as

$$\nu = \frac{\mu}{\varrho}\,, \qquad [\nu] = \mathrm{m}^2/\mathrm{s} \tag{5.10}$$

The kinematic viscosity of water with mass density $\varrho = 1\,\mathrm{g/cm}^3$ is $\nu = 10^{-6}\,\mathrm{m}^2/\mathrm{s} = 1\,\mathrm{mm}^2/s = 1\,\mathrm{cSt}$.

5.2 Stokes equations

5.2.1 Motivation

Consider an object of characteristic length L, moving at absolute velocity $U = |\boldsymbol{U}|$ through (relative to) an incompressible, homogeneous Newtonian fluid of constant viscosity μ and constant density ϱ. The object can be imagined as a moving boundary (condition), which induces a flow field $\boldsymbol{u}(t, \boldsymbol{x})$ in the fluid. The ratio of the inertial (dynamic) pressure ϱU^2 and viscous shearing stress $\mu U/L$ can be characterized by the Reynolds number[4]

$$\mathcal{R} = \frac{|\varrho(\partial_t \boldsymbol{u} + (\boldsymbol{u} \cdot \boldsymbol{\nabla})\boldsymbol{u})|}{|\mu \nabla^2 \boldsymbol{u}|} \simeq \frac{\varrho U^2/L}{\mu U/L^2} = \frac{UL\varrho}{\mu} = \frac{UL}{\nu}. \tag{5.11}$$

For example, when considering swimming in water ($\nu = 10^{-6}\,\mathrm{m}^2/\mathrm{s}$), one finds for fish or humans:

$$L \simeq 1\,\mathrm{m},\ U \simeq 1\ \mathrm{m/s} \qquad \Rightarrow \qquad \mathcal{R} \simeq 10^6,$$

whereas for bacteria:

$$L \simeq 1\,\mu\mathrm{m},\ U \simeq 10\ \mu\mathrm{m/s} \qquad \Rightarrow \qquad \mathcal{R} \simeq 10^{-5}.$$

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whereas for bacteria:

$$L \simeq 1\,\mu\mathrm{m},\; U \simeq 10\,\mu\mathrm{m/s} \qquad \Rightarrow \qquad \mathcal{R} \simeq 10^{-5}.$$

If the Reynolds number is very small, $\mathcal{R} \ll 1$, the nonlinear NSEs (5.8) can be approximated by the linear *Stokes equations*[5]

$$0 = \nabla \cdot \boldsymbol{u}, \tag{5.12a}$$

$$0 = \mu \nabla^2 \boldsymbol{u} - \nabla p + \boldsymbol{f}. \tag{5.12b}$$

$$\begin{cases} \boldsymbol{u}(t, \boldsymbol{x}) = 0, \\ p(t, \boldsymbol{x}) = p_\infty, \end{cases} \qquad \text{as} \qquad |\boldsymbol{x}| \to \infty. \tag{5.13}$$

5.2.2 Special solutions

Oseen solution Consider the Stokes equations (5.12) for a point-force

$$\boldsymbol{f}(\boldsymbol{x}) = \boldsymbol{F}\,\delta(\boldsymbol{x}). \tag{5.14}$$

In this case, the solution with standard boundary conditions (5.13) reads[6]

$$u_i(\boldsymbol{x}) = G_{ij}(\boldsymbol{x})\,F_j\,, \qquad p(\boldsymbol{x}) = \frac{F_j x_j}{4\pi|\boldsymbol{x}|^3} + p_\infty, \tag{5.15a}$$

where the Greens function G_{ij} is given by the Oseen tensor

$$G_{ij}(\boldsymbol{x}) = \frac{1}{8\pi\mu\,|\boldsymbol{x}|}\left(\delta_{ij} + \frac{x_i x_j}{|\boldsymbol{x}|^2}\right), \tag{5.15b}$$

which has the inverse

$$G^{-1}_{jk}(\boldsymbol{x}) = 8\pi\mu|\boldsymbol{x}|\left(\delta_{jk} - \frac{x_j x_k}{2|\boldsymbol{x}|^2}\right), \tag{5.16}$$

as can be seen from

$$\begin{aligned} G_{ij}G^{-1}_{jk} &= \left(\delta_{ij} + \frac{x_i x_j}{|\boldsymbol{x}|^2}\right)\left(\delta_{jk} - \frac{x_j x_k}{2|\boldsymbol{x}|^2}\right) \\ &= \delta_{ik} - \frac{x_i x_k}{2|\boldsymbol{x}|^2} + \frac{x_i x_k}{|\boldsymbol{x}|^2} - \frac{x_i x_j}{|\boldsymbol{x}|^2}\frac{x_j x_k}{2|\boldsymbol{x}|^2} \\ &= \delta_{ik} - \frac{x_i x_k}{2|\boldsymbol{x}|^2} + \frac{x_i x_k}{2|\boldsymbol{x}|^2} \\ &= \delta_{ik}. \end{aligned} \tag{5.17}$$

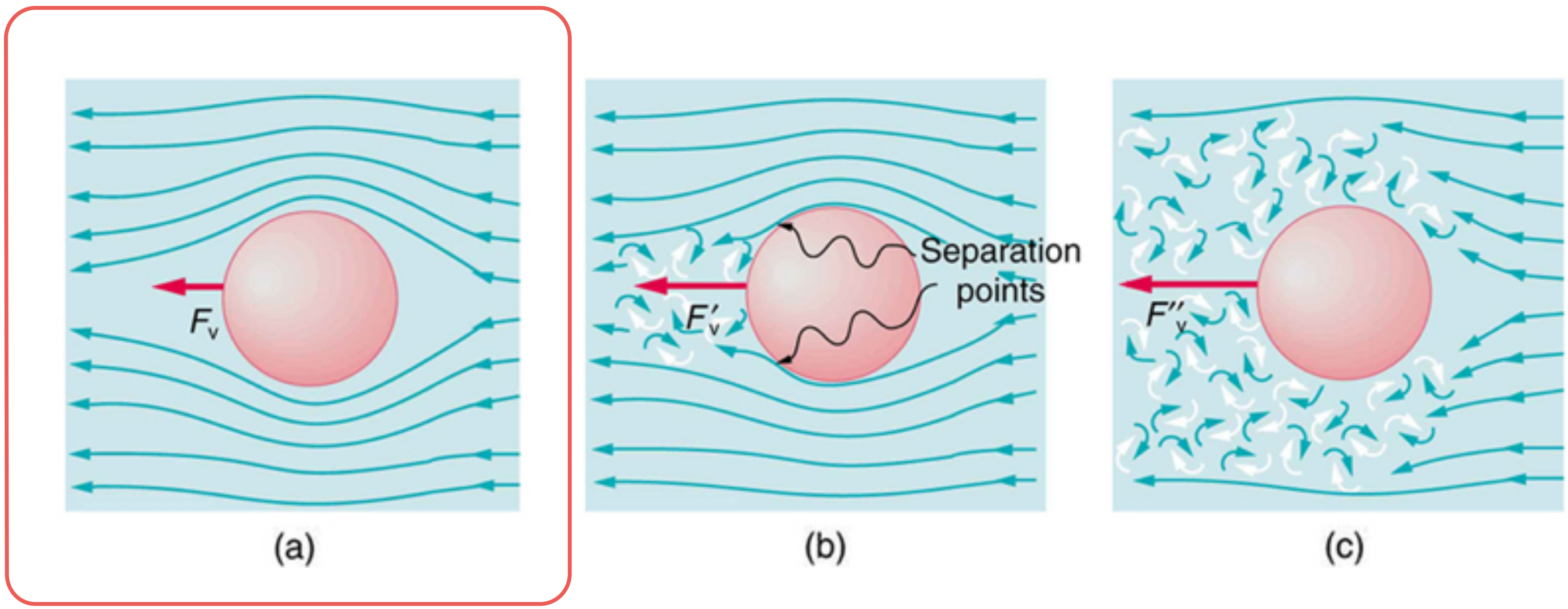
Stokes solution (1851) Consider a sphere of radius a, which at time t is located at the origin, $\boldsymbol{X}(t) = \mathbf{0}$, and moves at velocity $\boldsymbol{U}(t)$. The corresponding solution of the Stokes equation with standard boundary conditions (5.13) reads[7]

$$u_i(t,\boldsymbol{x}) = U_j \left[\frac{3}{4}\frac{a}{|\boldsymbol{x}|}\left(\delta_{ji} + \frac{x_j x_i}{|\boldsymbol{x}|^2}\right) + \frac{1}{4}\frac{a^3}{|\boldsymbol{x}|^3}\left(\delta_{ji} - 3\frac{x_j x_i}{|\boldsymbol{x}|^2}\right)\right], \tag{5.18a}$$

$$p(t,\boldsymbol{x}) = \frac{3}{2}\mu a \frac{U_j x_j}{|\boldsymbol{x}|^3} + p_\infty. \tag{5.18b}$$

If the particle is located at $\boldsymbol{X}(t)$, one has to replace x_i by $x_i - X_i(t)$ on the rhs. of Eqs. (5.18). Parameterizing the surface of the sphere by

$$\boldsymbol{a} = a\sin\theta\,\cos\phi\,\boldsymbol{e}_x + a\sin\theta\,\sin\phi\,\boldsymbol{e}_y + a\cos\theta\,\boldsymbol{e}_z = a_i\boldsymbol{e}_i$$



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Stokes solution (1851) Consider a sphere of radius a, which at time t is located at the origin, $\boldsymbol{X}(t) = \mathbf{0}$, and moves at velocity $\boldsymbol{U}(t)$. The corresponding solution of the Stokes equation with standard boundary conditions (5.13) reads[7]

$$u_i(t,\boldsymbol{x}) = U_j \left[\frac{3}{4}\frac{a}{|\boldsymbol{x}|}\left(\delta_{ji} + \frac{x_j x_i}{|\boldsymbol{x}|^2}\right) + \frac{1}{4}\frac{a^3}{|\boldsymbol{x}|^3}\left(\delta_{ji} - 3\frac{x_j x_i}{|\boldsymbol{x}|^2}\right)\right], \tag{5.18a}$$

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where $\theta \in [0,\pi], \phi \in [0, 2\pi)$, one finds that on this boundary

$$\boldsymbol{u}(t,\boldsymbol{a}(\theta,\phi)) = \boldsymbol{U}, \tag{5.19a}$$

$$p(t,\boldsymbol{a}(\theta,\phi)) = \frac{3}{2}\frac{\mu}{a^2} U_j\, a_j(\theta,\phi) + p_\infty, \tag{5.19b}$$

corresponding to a no-slip boundary condition on the sphere's surface. The $\mathcal{O}(a/|\boldsymbol{x}|)$-contribution in (5.18a) coincides with the Oseen result (5.15), if we identify

$$\boldsymbol{F} = 6\pi\, \mu a\, \boldsymbol{U}. \tag{5.20}$$

The prefactor $\gamma = 6\pi\, \mu a$ is the well-known Stokes drag coefficient for a sphere.

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The $\mathcal{O}[(a/|\boldsymbol{x}|)^3]$-part in (5.18a) corresponds to the finite-size correction, and defining the Stokes tensor by

$$S_{ij} = G_{ij} + \frac{1}{24\pi\mu} \frac{a^2}{|\boldsymbol{x}|^3} \left(\delta_{ji} - 3 \frac{x_j x_i}{|\boldsymbol{x}|^2} \right), \tag{5.21}$$

we may rewrite (5.18a) as[8]

$$u_i(t, \boldsymbol{x}) = S_{ij} F_j. \tag{5.22}$$

5.3 Golestanian's swimmer model

This part is copied (with very minor adaptations) from the article of Golestanian and Ajdari [GA07], for their excellent discussion is difficult, if not impossible, to improve.

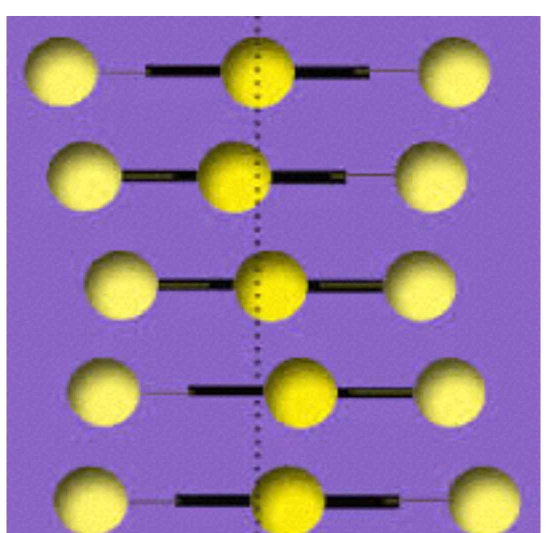
5.3.1 Three-sphere swimmer: simplified analysis

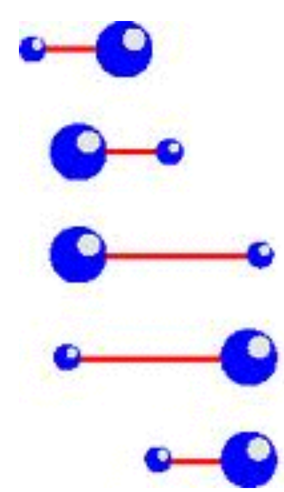
As a minimal model of a low Reynolds number swimmer, consider three spheres of radii a_i $(i = 1, 2, 3)$ that are separated by two arms of lengths L_1 and L_2. Each sphere exerts a force F_i on, and experiences a force $-F_i$ from, the fluid that we assume to be along the swimmer axis. In the limit $a_i/L_j \ll 1$, we can use the Oseen tensor (5.15) to relate the forces and the velocities as

$$v_1 = \frac{F_1}{6\pi\mu a_1} + \frac{F_2}{4\pi\mu L_1} + \frac{F_3}{4\pi\mu(L_1 + L_2)}, \tag{5.23a}$$

$$v_2 = \frac{F_1}{4\pi\mu L_1} + \frac{F_2}{6\pi\mu a_2} + \frac{F_3}{4\pi\mu L_2}, \tag{5.23b}$$

$$v_3 = \frac{F_1}{4\pi\mu(L_1 + L_2)} + \frac{F_2}{4\pi\mu L_2} + \frac{F_3}{6\pi\mu a_3}. \tag{5.23c}$$





other 'minimal' swimmer

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$$v_2 = \frac{F_1}{4\pi\mu L_1} + \frac{F_2}{6\pi\mu a_2} + \frac{F_3}{4\pi\mu L_2}, \tag{5.23b}$$

$$v_3 = \frac{F_1}{4\pi\mu(L_1 + L_2)} + \frac{F_2}{4\pi\mu L_2} + \frac{F_3}{6\pi\mu a_3}. \tag{5.23c}$$

Swim-speed

$$V_0 = \frac{1}{3}(v_1 + v_2 + v_3). \tag{5.24}$$

Force-free constraint

$$F_1 + F_2 + F_3 = 0. \tag{5.25}$$

Eliminating F_2 using Eq. (5.25), we can calculate the swimming velocity from Eqs. (5.23a), (5.23b), (5.23c), and (5.24) as

$$\begin{aligned} V_0 &= \frac{1}{3}\left[\left(\frac{1}{a_1}-\frac{1}{a_2}\right)+\frac{3}{2}\left(\frac{1}{L_1+L_2}-\frac{1}{L_2}\right)\right]\left(\frac{F_1}{6\pi\mu}\right)+ \\ & \frac{1}{3}\left[\left(\frac{1}{a_3}-\frac{1}{a_2}\right)+\frac{3}{2}\left(\frac{1}{L_1+L_2}-\frac{1}{L_1}\right)\right]\left(\frac{F_3}{6\pi\mu}\right), \end{aligned} \tag{5.26}$$

where the subscript 0 denotes the force-free condition. To close the system of equations, we should either prescribe the forces (stresses) acting across each linker, or alternatively the opening and closing motion of each arm as a function of time. We choose to prescribe the motion of the arms connecting the three spheres, and assume that the velocities

$$\dot{L}_1 = v_2 - v_1, \tag{5.27a}$$

$$\dot{L}_2 = v_3 - v_2, \tag{5.27b}$$

are known functions. We then use Eqs. (5.23a), (5.23b), (5.23c), and (5.25) to solve for F_1 and F_3 as a function of $\dot{L}_1$ and $\dot{L}_2$. Putting the resulting expressions for F_1 and F_3 back in Eq. (5.26), and keeping only terms in the leading order in a_i/L_j consistent with our original scheme, we find the average swimming velocity to the leading order.

$$
\begin{aligned}
V_0 \;=\;& \frac{(a_1-a_2)(a_2+a_3)}{3a_2(a_1+a_2+a_3)}\left[1+\frac{3}{2}\left(\frac{a_1a_2}{a_2-a_1}\right)\left(\frac{1}{L_1+L_2}-\frac{1}{L_2}\right)-3\left(\frac{a_2a_3}{a_2+a_3}\right)\frac{1}{L_2}\right.\\
&\left.+\frac{3}{a_1+a_2+a_3}\left(\frac{a_2a_3}{L_2}+\frac{a_1a_2}{L_1}+\frac{a_3a_1}{L_1+L_2}\right)\right]\dot{L}_1\\
+\;& \frac{a_3(a_1-a_2)}{3a_2(a_1+a_2+a_3)}\left[1+\frac{3}{2}\left(\frac{a_1a_2}{a_2-a_1}\right)\left(\frac{1}{L_1+L_2}-\frac{1}{L_2}\right)-\frac{3}{2}\left(\frac{a_2}{L_1}+\frac{a_2}{L_2}-\frac{a_2}{L_1+L_2}\right)\right.\\
&\left.+\frac{3}{a_1+a_2+a_3}\left(\frac{a_2a_3}{L_2}+\frac{a_1a_2}{L_1}+\frac{a_3a_1}{L_1+L_2}\right)\right]\dot{L}_2\\
+\;& \frac{a_1(a_2-a_3)}{3a_2(a_1+a_2+a_3)}\left[1+\frac{3}{2}\left(\frac{a_2a_3}{a_2-a_3}\right)\left(\frac{1}{L_1+L_2}-\frac{1}{L_1}\right)-\frac{3}{2}\left(\frac{a_2}{L_1}+\frac{a_2}{L_2}-\frac{a_2}{L_1+L_2}\right)\right.\\
&\left.+\frac{3}{a_1+a_2+a_3}\left(\frac{a_2a_3}{L_2}+\frac{a_1a_2}{L_1}+\frac{a_3a_1}{L_1+L_2}\right)\right]\dot{L}_1\\
+\;& \frac{(a_2-a_3)(a_1+a_2)}{3a_2(a_1+a_2+a_3)}\left[1+\frac{3}{2}\left(\frac{a_2a_3}{a_2-a_3}\right)\left(\frac{1}{L_1+L_2}-\frac{1}{L_1}\right)-3\left(\frac{a_1a_2}{a_1+a_2}\right)\frac{1}{L_1}\right.\\
&\left.+\frac{3}{a_1+a_2+a_3}\left(\frac{a_2a_3}{L_2}+\frac{a_1a_2}{L_1}+\frac{a_3a_1}{L_1+L_2}\right)\right]\dot{L}_2.
\end{aligned}
\tag{B.1}
$$

5.3.2 Swimming velocity

The above calculations yield a lengthy expression summarized in Eq. (B.1) of the Appendix. This result (B.1) is suitable for numerical studies of swimming cycles with arbitrarily large deformations. For the simple case where all the spheres have the same radii, namely $a = a_1 = a_2 = a_3$, Eq. (5.26) simplifies to

$$V_0 = \frac{a}{6}\left[\left(\frac{\dot{L}_2 - \dot{L}_1}{L_1 + L_2}\right) + 2\left(\frac{\dot{L}_1}{L_2} - \frac{\dot{L}_2}{L_1}\right)\right], \tag{5.28}$$

plus terms that average to zero over a full swimming cycle. Equation (5.28) is also valid for arbitrarily large deformations.

We can also consider relatively small deformations and perform an expansion of the swimming velocity to the leading order. Using

$$L_1 = \ell_1 + u_1(t), \tag{5.29}$$

$$L_2 = \ell_2 + u_2(t), \tag{5.30}$$

in Eq. (B.1), and expanding to the leading order in u_i/ℓ_j, we find the average swimming velocity as

$$\overline{V_0} = \frac{K}{2}\,\overline{(u_1\dot{u}_2 - \dot{u}_1 u_2)}, \tag{5.31}$$

where

$$K = \frac{3\,a_1 a_2 a_3}{(a_1 + a_2 + a_3)^2}\left[\frac{1}{\ell_1^2} + \frac{1}{\ell_2^2} - \frac{1}{(\ell_1 + \ell_2)^2}\right]. \tag{5.32}$$

5.3.3 Harmonic deformations

As a simple explicit example, consider harmonic deformations of the two arms, with identical frequencies ω and a mismatch in phases,

$$u_1(t) = d_1 \cos(\omega t + \varphi_1), \tag{5.33}$$
$$u_2(t) = d_2 \cos(\omega t + \varphi_2). \tag{5.34}$$

The average swimming velocity from Eq. (5.31) reads

$$\overline{V_0} = \frac{K}{2}\, d_1 d_2 \omega \sin(\varphi_1 - \varphi_2). \tag{5.35}$$

This result shows that the maximum velocity is obtained when the phase difference is $\pi/2$, which supports the picture of maximizing the area covered by the trajectory of the swimming cycle in the parameter space of the deformations. A phase difference of 0 or π, for example, will create closed trajectories with zero area, or just lines.

5.3.4 Force-velocity relation and stall force

The effect of an external force or load on the efficiency of the swimmer can be easily studied within the linear theory of Stokes hydrodynamics. When the swimmer is under the effect of an applied external force F, Eq. (5.25) should be changed as

$$F_1 + F_2 + F_3 = F. \tag{5.36}$$

Following through the calculations of Sec. 5.3.1 above, we find that the following changes take place in Eqs. (5.23a), (5.23b), (5.23c), and (5.24):

$$v_1 \mapsto v_1 - \frac{F}{4\pi\mu L_1}, \tag{5.37}$$

$$v_2 \mapsto v_2 - \frac{F}{6\pi\mu a_2}, \tag{5.38}$$

$$v_3 \mapsto v_3 - \frac{F}{4\pi\mu L_2}, \tag{5.39}$$

$$V \mapsto V - \frac{1}{3}\left(\frac{1}{6\pi\mu a_2} + \frac{1}{4\pi\mu L_1} + \frac{1}{4\pi\mu L_2}\right) F. \tag{5.40}$$

These lead to the changes

$$\dot{L}_1 \mapsto \dot{L}_1 - \left(\frac{1}{6\pi\mu a_2} - \frac{1}{4\pi\mu L_1}\right) F, \tag{5.41}$$

$$\dot{L}_2 \mapsto \dot{L}_2 - \left(\frac{1}{4\pi\mu L_2} - \frac{1}{6\pi\mu a_2}\right) F, \tag{5.42}$$

in Eq. (B.1), which together with correction coming from Eq. (5.40) leads to the average swimming velocity

$$\overline{V}(F) = \overline{V_0} + \frac{F}{18\pi\mu a_R}, \tag{5.43}$$

$$\overline{V}(F) = \overline{V_0} + \frac{F}{18\pi\mu a_R}, \qquad \overline{V_0} = \frac{K}{2}\, d_1 d_2 \omega \sin(\varphi_1 - \varphi_2)$$

for $a_1 = a_2 = a_3 = a$,

$$\frac{1}{a_R} = \frac{1}{a} + \overline{\frac{1}{L_1}} + \overline{\frac{1}{L_2}} + \overline{\frac{1}{L_1 + L_2}} - \frac{a}{2}\overline{\left(\frac{1}{L_1} - \frac{1}{L_2}\right)^2} - \frac{a}{2}\overline{\frac{1}{(L_1 + L_2)^2}}. \tag{5.44}$$

The force-velocity relation given in Eq. (5.43), which could have been expected based on linearity of hydrodynamics, yields a *stall force*

$$F_s = -18\pi\mu a_R \overline{V_0}. \tag{5.45}$$

Using the zeroth order expression for the hydrodynamic radius, one can see that this is equal to the Stokes force exerted on the three spheres moving with a velocity $\overline{V_0}$.

5.3.5 Power consumption and efficiency

Because we know the instantaneous values for the velocities and the forces, we can easily calculate the power consumption in the motion of the spheres through the viscous fluid. The rate of power consumption at any time is given as

$$\mathcal{P} = F_1 v_1 + F_2 v_2 + F_3 v_3 = F_1(-\dot{L}_1) + F_3(\dot{L}_2), \tag{5.46}$$

where the second expression is the result of enforcing the force-free constrain of Eq. (5.25).

Using the expressions for F_1 and F_3 as a function of $\dot{L}_1$ and $\dot{L}_2$, one finds for $a_1 = a_2 = a_3 = a$

$$\begin{aligned} \mathcal{P} \;=\; & 4\pi\mu a \left[1 + \frac{a}{L_1} - \frac{1}{2}\frac{a}{L_2} + \frac{a}{L_1 + L_2}\right] \dot{L}_1^2 + \\ & 4\pi\mu a \left[1 - \frac{1}{2}\frac{a}{L_1} + \frac{a}{L_2} + \frac{a}{L_1 + L_2}\right] \dot{L}_2^2 + \\ & 4\pi\mu a \left[1 - \frac{1}{2}\frac{a}{L_1} - \frac{1}{2}\frac{a}{L_2} + \frac{5}{2}\frac{a}{L_1 + L_2}\right] \dot{L}_1 \dot{L}_2. \end{aligned} \tag{5.47}$$

$$\begin{aligned}\mathcal{P} &= 4\pi\mu a\left[1+\frac{a}{L_1}-\frac{1}{2}\frac{a}{L_2}+\frac{a}{L_1+L_2}\right]\dot{L}_1^2+\\ &\quad 4\pi\mu a\left[1-\frac{1}{2}\frac{a}{L_1}+\frac{a}{L_2}+\frac{a}{L_1+L_2}\right]\dot{L}_2^2+\\ &\quad 4\pi\mu a\left[1-\frac{1}{2}\frac{a}{L_1}-\frac{1}{2}\frac{a}{L_2}+\frac{5}{2}\frac{a}{L_1+L_2}\right]\dot{L}_1\dot{L}_2.\end{aligned}$$

We can now define a Lighthill hydrodynamic efficiency as

$$\mu_{\mathrm{L}} \equiv \frac{18\pi\mu a_R \overline{V_0}^2}{\overline{\mathcal{P}}}, \tag{5.48}$$

for which we find to the leading order

$$\mu_{\mathrm{L}} = \frac{9}{8}\frac{a_R}{a}\,\frac{K^2\,\overline{(u_1\dot{u}_2-\dot{u}_1u_2)}^2}{C_1\,\overline{\dot{u}_1^2}+C_2\,\overline{\dot{u}_2^2}+C_3\,\overline{\dot{u}_1\dot{u}_2}}, \tag{5.49a}$$

where

$$C_1 = 1+\frac{a}{\ell_1}-\frac{1}{2}\frac{a}{\ell_2}+\frac{a}{\ell_1+\ell_2}, \tag{5.49b}$$

$$C_2 = 1-\frac{1}{2}\frac{a}{\ell_1}+\frac{a}{\ell_2}+\frac{a}{\ell_1+\ell_2}, \tag{5.49c}$$

$$C_3 = 1-\frac{1}{2}\frac{a}{\ell_1}-\frac{1}{2}\frac{a}{\ell_2}+\frac{5}{2}\frac{a}{\ell_1+\ell_2}. \tag{5.49d}$$

5.4 Dimensionality

We saw above that, in 3D, the fundamental solution to the Stokes equations for a point force at the origin is given by the Oseen solution

$$u_i(\boldsymbol{x}) = G_{ij}(\boldsymbol{x})\ F_j\ , \qquad p(\boldsymbol{x}) = \frac{F_j x_j}{4\pi|\boldsymbol{x}|^3} + p_\infty, \tag{5.50a}$$

where

$$G_{ij}(\boldsymbol{x}) = \frac{1}{8\pi\mu\,|\boldsymbol{x}|}\left(\delta_{ij} + \frac{x_i x_j}{|\boldsymbol{x}|^2}\right), \tag{5.50b}$$

It is interesting to compare this result with corresponding 2D solution

$$u_i(\boldsymbol{x}) = J_{ij}(\boldsymbol{x}) F_j\ , \qquad p = \frac{F_j x_j}{2\pi|\boldsymbol{x}|^2} + \partial_\infty\ , \qquad \boldsymbol{x} = (x, y) \tag{5.51a}$$

where

$$J_{ij}(\boldsymbol{x}) = \frac{1}{4\pi\mu}\left[-\delta_{ij}\ln\left(\frac{|\boldsymbol{x}|}{a}\right) + \frac{x_i x_j}{|\boldsymbol{x}|^2}\right] \tag{5.51b}$$

with a being an arbitrary constant fixed by some intermediate flow normalization condition. Note that (5.51) decays much more slowly than (5.50), implying that hydrodynamic interactions in 2D freestanding films are much stronger than in 3D bulk solutions.

To verify that (5.51) is indeed a solution of the 2D Stokes equations, we first note that generally

$$\begin{aligned}
\partial_j|\boldsymbol{x}| &= \partial_j(x_i x_i)^{1/2} = x_j(x_i x_i)^{-1/2} = \frac{x_j}{|\boldsymbol{x}|} && \text{(5.52a)}\\
\partial_j|\boldsymbol{x}|^{-n} &= \partial_j(x_i x_i)^{-n/2} = -n x_j(x_i x_i)^{-(n+2)/2} = -n\frac{x_j}{|\boldsymbol{x}|^{n+2}}. && \text{(5.52b)}
\end{aligned}$$

From this, we find

$$\partial_i p = \frac{F_i}{2\pi|\boldsymbol{x}|^2} - 2\frac{F_j x_j x_i}{2\pi|\boldsymbol{x}|^4} = \frac{F_j}{2\pi|\boldsymbol{x}|^2}\left(\delta_{ij} - 2\frac{x_j x_i}{|\boldsymbol{x}|^2}\right) \tag{5.53}$$

and

$$\begin{aligned}
\partial_k J_{ij} &= \frac{1}{4\pi\mu}\partial_k\left[-\delta_{ij}\ln\left(\frac{|\boldsymbol{x}|}{a}\right) + \frac{x_i x_j}{|\boldsymbol{x}|^2}\right] \\
&= \frac{1}{4\pi\mu}\left[-\delta_{ij}\frac{1}{|\boldsymbol{x}|}\partial_k|\boldsymbol{x}| + \partial_k\left(\frac{x_i x_j}{|\boldsymbol{x}|^2}\right)\right] \\
&= \frac{1}{4\pi\mu}\left[-\delta_{ij}\frac{x_k}{|\boldsymbol{x}|^2} + \left(\delta_{ik}\frac{x_j}{|\boldsymbol{x}|^2} + \delta_{jk}\frac{x_i}{|\boldsymbol{x}|^2} - 2\frac{x_i x_j x_k}{|\boldsymbol{x}|^4}\right)\right].
\end{aligned} \tag{5.54}$$

To check the incompressibility condition, note that

$$\begin{aligned}
\partial_i J_{ij} &= \frac{1}{4\pi\mu}\left[-\delta_{ij}\frac{x_i}{|\boldsymbol{x}|^2} + \left(\delta_{ii}\frac{x_j}{|\boldsymbol{x}|^2} + \delta_{ji}\frac{x_i}{|\boldsymbol{x}|^2} - \frac{x_i x_j x_i}{2|\boldsymbol{x}|^4}\right)\right] \\
&= \frac{1}{4\pi\mu}\left(-\frac{x_j}{|\boldsymbol{x}|^2} + 2\frac{x_j}{|\boldsymbol{x}|^2} + \frac{x_j}{|\boldsymbol{x}|^2} - 2\frac{x_j}{|\boldsymbol{x}|^2}\right) \\
&= 0,
\end{aligned} \tag{5.55}$$

which confirms that the solution (5.51) satisfies the incompressibility condition $\nabla \cdot \boldsymbol{u} = 0$.

Moreover, we find for the Laplacian

$$\begin{aligned}
\partial_k \partial_k J_{ij} &= \frac{\partial_k}{4\pi\mu}\left[-\delta_{ij}\frac{x_k}{|\boldsymbol{x}|^2}+\delta_{ik}\frac{x_j}{|\boldsymbol{x}|^2}+\delta_{jk}\frac{x_i}{|\boldsymbol{x}|^2}-2\frac{x_i x_j x_k}{|\boldsymbol{x}|^4}\right] \\
&= \frac{1}{4\pi\mu}\left[-\delta_{ij}\partial_k\left(\frac{x_k}{|\boldsymbol{x}|^2}\right)+\delta_{ik}\partial_k\left(\frac{x_j}{|\boldsymbol{x}|^2}\right)+\delta_{jk}\partial_k\left(\frac{x_i}{|\boldsymbol{x}|^2}\right)-2\partial_k\left(\frac{x_i x_j x_k}{|\boldsymbol{x}|^4}\right)\right] \\
&= \frac{1}{4\pi\mu}\Bigg[-\delta_{ij}\left(\frac{\delta_{kk}}{|\boldsymbol{x}|^2}-2\frac{x_k x_k}{|\boldsymbol{x}|^4}\right)+\delta_{ik}\left(\frac{\delta_{jk}}{|\boldsymbol{x}|^2}-2\frac{x_j x_k}{|\boldsymbol{x}|^4}\right)+\delta_{jk}\left(\frac{\delta_{ik}}{|\boldsymbol{x}|^2}-2\frac{x_i x_k}{|\boldsymbol{x}|^4}\right)- \\
&\qquad 2\left(\frac{\delta_{ik}x_j x_k}{|\boldsymbol{x}|^4}+\frac{x_i\delta_{jk}x_k}{|\boldsymbol{x}|^4}+\frac{x_i x_j\delta_{kk}}{|\boldsymbol{x}|^4}-4\frac{x_i x_j x_k x_k}{|\boldsymbol{x}|^6}\right)\Bigg] \\
&= \frac{1}{4\pi\mu}\Bigg[-\delta_{ij}\left(\frac{2}{|\boldsymbol{x}|^2}-2\frac{1}{|\boldsymbol{x}|^2}\right)+\left(\frac{\delta_{ij}}{|\boldsymbol{x}|^2}-2\frac{x_j x_i}{|\boldsymbol{x}|^4}\right)+\left(\frac{\delta_{ij}}{|\boldsymbol{x}|^2}-2\frac{x_i x_j}{|\boldsymbol{x}|^4}\right)- \\
&\qquad 2\left(\frac{x_j x_i}{|\boldsymbol{x}|^4}+\frac{x_i x_j}{|\boldsymbol{x}|^4}+2\frac{x_i x_j}{|\boldsymbol{x}|^4}-4\frac{x_i x_j}{|\boldsymbol{x}|^4}\right)\Bigg] \\
&= \frac{1}{2\pi\mu}\left(\frac{\delta_{ij}}{|\boldsymbol{x}|^2}-2\frac{x_j x_i}{|\boldsymbol{x}|^4}\right)
\end{aligned} \tag{5.56}$$

Hence, by comparing with (5.53), we see that indeed

$$-\partial_i p+\mu\partial_k\partial_k u_i=-\partial_i p+\mu\partial_k\partial_k J_{ij}F_j=0. \tag{5.57}$$

The difference between 3D and 2D hydrodynamics has been confirmed experimentally for *Chlamydomonas* algae [GJG10, DGM+10].

5.5 Force dipole and dimensionality

To construct a force dipole, consider two opposite point-forces $\boldsymbol{F}^+ = -\boldsymbol{F}^- = F\boldsymbol{e}_x$ located at positions $\boldsymbol{x}^+ = \pm\ell\boldsymbol{e}_x$. Due to linearity of the Stokes equations the total flow at some point $\boldsymbol{x}$ is given by

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where $\Gamma_{ij} = J_{ij}$ in 2D and $\Gamma_{ij} = G_{ij}$ in 3D. If $|\boldsymbol{x}| \gg \ell$, we can Taylor expand Γ_{ij} near $\ell = 0$, and find to leading order

$$\begin{aligned} u_i(\boldsymbol{x}) &\simeq \left\{\left[\Gamma_{ij}(\boldsymbol{x}) - \Gamma_{ij}(\boldsymbol{x})\right] - \left[x_k^+\partial_k\Gamma_{ij}(\boldsymbol{x}) - x_k^-\partial_k\Gamma_{ij}(\boldsymbol{x})\right]\right\}F_j^+ \\ &= -2x_k^+\left[\partial_k\Gamma_{ij}(\boldsymbol{x})\right]F_j^+ \end{aligned} \tag{5.59}$$

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2D case Using our above result for $\partial_k J_{ij}$, and writing $\boldsymbol{x}^+ = \ell\boldsymbol{n}$ and $\boldsymbol{F}^+ = F\boldsymbol{n}$ with $|\boldsymbol{n}| = 1$, we find in 2D

$$\begin{aligned} u_i(\boldsymbol{x}) &= -\frac{x_k^+}{2\pi\mu}\left[-\delta_{ij}\frac{x_k}{|\boldsymbol{x}|^2} + \left(\delta_{ik}\frac{x_j}{|\boldsymbol{x}|^2} + \delta_{jk}\frac{x_i}{|\boldsymbol{x}|^2} - 2\frac{x_ix_jx_k}{|\boldsymbol{x}|^4}\right)\right]F_j^+ \\ &= -\frac{F\ell}{2\pi\mu}\left(-n_i\frac{x_kn_k}{|\boldsymbol{x}|^2} + n_i\frac{x_jn_j}{|\boldsymbol{x}|^2} + n_kn_k\frac{x_i}{|\boldsymbol{x}|^2} - 2\frac{n_kx_ix_jx_kn_j}{|\boldsymbol{x}|^4}\right) \end{aligned}$$

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and, hence,

$$\boldsymbol{u}(x) = \frac{F\ell}{2\pi\mu|\boldsymbol{x}|}\left[2(\boldsymbol{n}\cdot\hat{\boldsymbol{x}})^2 - 1\right]\hat{\boldsymbol{x}} \tag{5.60}$$

where $\hat{\boldsymbol{x}} = \boldsymbol{x}/|\boldsymbol{x}|$.

3D case To compute the dipole flow field in 3D, we need to compute the partial derivatives of the Oseen tensor

$$G_{ij}(\boldsymbol{x}) = \frac{1}{8\pi\mu|\boldsymbol{x}|}\left(1 + \hat{x}_i\hat{x}_j\right) , \qquad \hat{x}_k = \frac{x_k}{|\boldsymbol{x}|}. \tag{5.61}$$

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Defining the orthogonal projector (Π_{ik}) for $\hat{x}_k$ by

$$\Pi_{ik} := \delta_{ik} - \hat{x}_i\hat{x}_k, \tag{5.62}$$

we have

$$\partial_k|\boldsymbol{x}| = \frac{x_k}{|\boldsymbol{x}|} = \hat{x}_k, \tag{5.63a}$$

$$\partial_k\hat{x}_i = \frac{\delta_{ik}}{|\boldsymbol{x}|} - \frac{x_k x_i}{|\boldsymbol{x}|^3} = \frac{\Pi_{ik}}{|\boldsymbol{x}|}, \tag{5.63b}$$

$$\partial_n\Pi_{ik} = -\frac{1}{|\boldsymbol{x}|}\left(\hat{x}_i\Pi_{nk} + \hat{x}_k\Pi_{ni}\right), \tag{5.63c}$$

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and from this we find

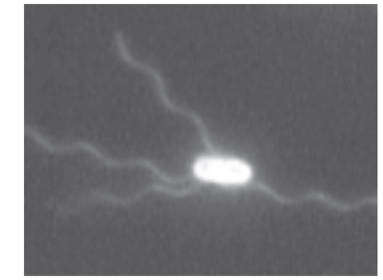
$$\begin{aligned} \partial_k G_{ij} &= -\frac{\hat{x}_k}{|\boldsymbol{x}|}G_{ij} + \frac{\kappa}{|\boldsymbol{x}|^2}\left(\Pi_{ik}\hat{x}_j + \Pi_{jk}\hat{x}_i\right) \\ &= \frac{\kappa}{|\boldsymbol{x}|^2}\big(-\hat{x}_k\delta_{ij} + \hat{x}_j\delta_{ik} + \hat{x}_i\delta_{jk} - 3\hat{x}_k\hat{x}_i\hat{x}_j\big). \end{aligned} \tag{5.64}$$

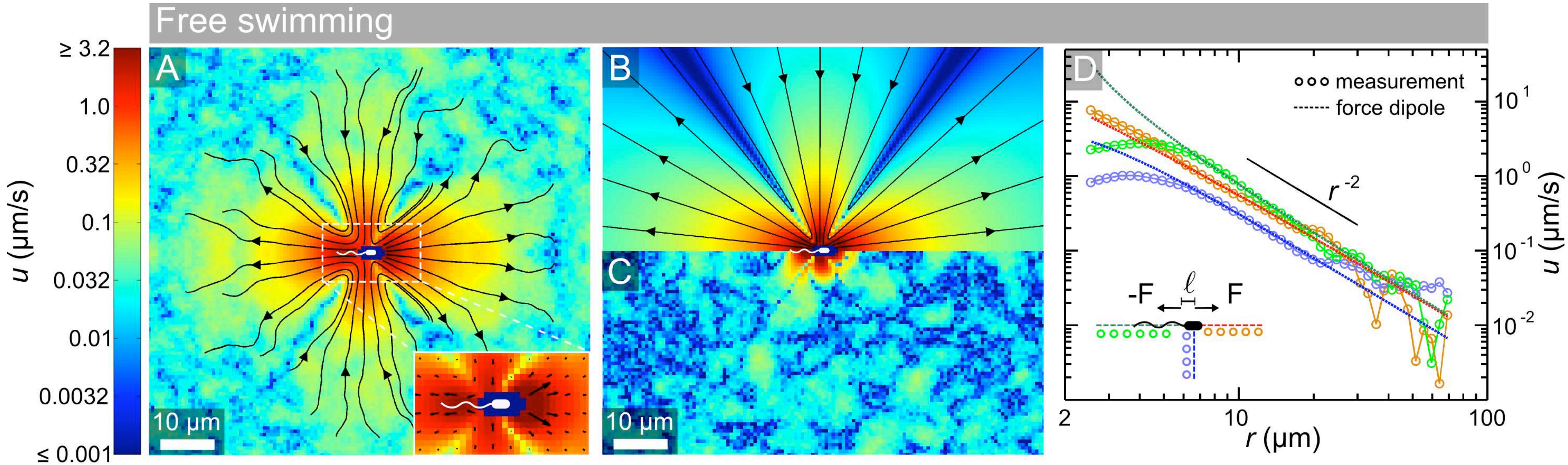
Inserting this expression into (5.59), we obtain the far-field dipole flow in 3D

$$\boldsymbol{u}(\boldsymbol{x}) = \frac{F\ell}{4\pi\mu|\boldsymbol{x}|^2}\left[3(\boldsymbol{n}\cdot\hat{\boldsymbol{x}})^2 - 1\right]\hat{\boldsymbol{x}}. \tag{5.65}$$

As shown in Ref. [DDC+11], Eq. (5.65) agrees well with the mean flow-field of a bacterium.

E.coli (non-tumbling HCB 437)





$$\boxed{\boldsymbol{u}(\boldsymbol{r}) = \frac{A}{|\boldsymbol{r}|^2}\left[3(\hat{\boldsymbol{r}}.\hat{\boldsymbol{d}})^2 - 1\right]\hat{\boldsymbol{r}}, \quad A = \frac{\ell F}{8\pi\eta}, \quad \hat{\boldsymbol{r}} = \frac{\boldsymbol{r}}{|\boldsymbol{r}|}}$$

$$V_0 = 22 \pm 5 \ \ \mu\mathrm{m/s}$$

$$\ell = 1.9 \ \ \mu\mathrm{m}$$

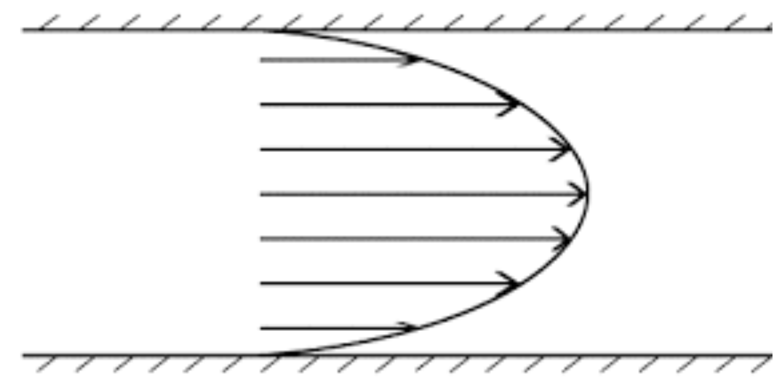
$$F = 0.42 \ \ \mathrm{pN}$$

weak 'pusher' dipole

Drescher, Dunkel, Ganguly, Cisneros, Goldstein (2011) PNAS

Hele-Shaw approximation

$$
\begin{aligned}
0 &= \nabla \cdot \boldsymbol{u}, \\
0 &= \mu \nabla^2 \boldsymbol{u} - \nabla p + \boldsymbol{f}.
\end{aligned}
$$



$$\boldsymbol{u}(x, y, z) = \frac{6z(H-z)}{H^2}\left[U_x(x, y)\boldsymbol{e}_x + U_x(x, y)\boldsymbol{e}_y\right] \equiv \frac{6z(H-z)}{H^2}\boldsymbol{U}(x, y)$$

$$\boldsymbol{u}(x, y, h/2) = \frac{3}{2}\boldsymbol{U}(x, y)$$

$$0 = \nabla \cdot \boldsymbol{U}\ , \qquad 0 = -\nabla P + \mu \nabla^2 \boldsymbol{U} - \kappa \boldsymbol{U}$$

where $\kappa = 12\mu/H^2$ and ∇ is now the 2D gradient operator.

Hele-Shaw approximation