CMORE, June 2010
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GOAL

To develop a basic intuition for selected small-scale biophysical processes among marine microbes → can in no way be complete

How did I get into this topic?

WANT TO LEARN MORE?

1. Ask questions and interrupt – anytime!

2. See the collection of video lectures from RS's class "Physical ecology at the microscale": **techtv.mit.edu/collections/1-961videos**

3. Recent good books

3. BOOKS

Kiørboe, A mechanistic approach to plankton ecology, Princeton University Press, 2008. *Perfect to get started, particularly for the oceans. Written by a biologist.*

Dusenbery, Living at Micro Scale: The Unexpected Physics of Being Small, Harvard University Press, 2009
Intermediate. Written by a physicist.

Berg, *Random Walks in Biology*, Princeton University Press, 1993.
Learn the fundamentals of microbial physical dynamics.

Vogel, *Life in moving fluids,* Princeton University Press, 1996.
Extremely readable, with next-to-no-math and lots of cool facts about organisms and their interaction with fluids (not just micro, mostly macro in fact)

Denny, *Air and Water,* Princeton University Press, 1995.
In the spirit of Vogel. An easy and very worthwhile read.

Kundu & Cohen, Fluid Mechanics, Elsevier, 2004
The fundamentals of fluid mechanics, well explained, at an intermediate level.

Some questions for you

1. how does the nutrient uptake by a cell scale with its radius?

2. How much does this uptake increase by, if a bacterium swims?

3. How far will a bacterium go (‘coast’) after it stops rotating its flagellum?

1. Life at low Peclet and Reynolds numbers

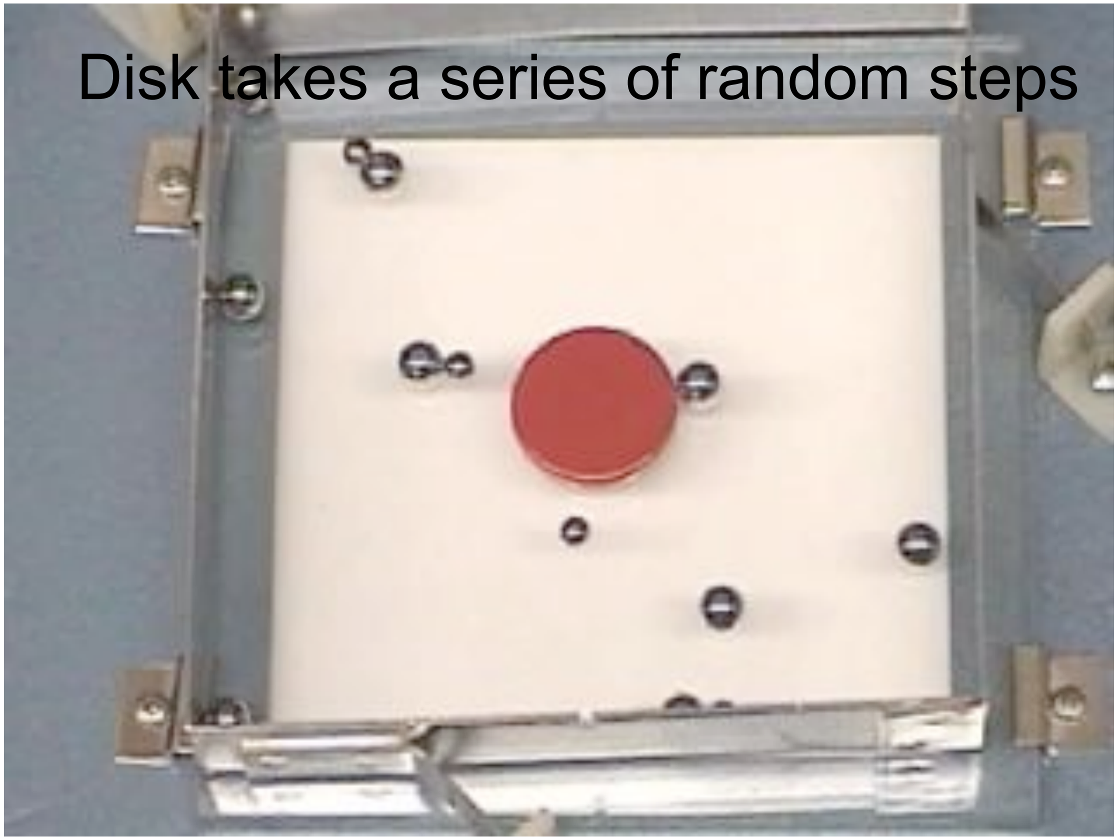
- The origin of diffusion: Brownian motion
- Diffusion-limited uptake: nutrient flux to osmotrophs
- When is it only diffusion: the Peclet number
- Swimming faster to get more food? The Sherwood number
- Low Reynolds numbers: counterintuitive fluid mechanics
  - A world with no inertia: no Brazilian free kicks
  - The perils of reversibility

Diffusion and its origins

Why start from diffusion?
A little history

The diffusion coefficient
(Einstein 1905)

$$D = \frac{kT}{6\pi\mu a}$$



Another one: http://www.phy.ntnu.edu.tw/ntnujava/viewtopic.php?t=41

Brownian motion of
0.8 um diameter
latex spheres

Glassbowl
in Aceton
Magn: 3200 x
Particle size
2 - 3 mu

Red Lead in Aceton

Slope: 6° - Magn: 800 x

Smallest visible particle: 1 um

Brownian Motion

Dept. Microbiology & Immunology
University of Leicester, UK.

Diffusion: a random walk (molecules, viruses, bacteria, …)

Random Walks in Biology, Berg 2003

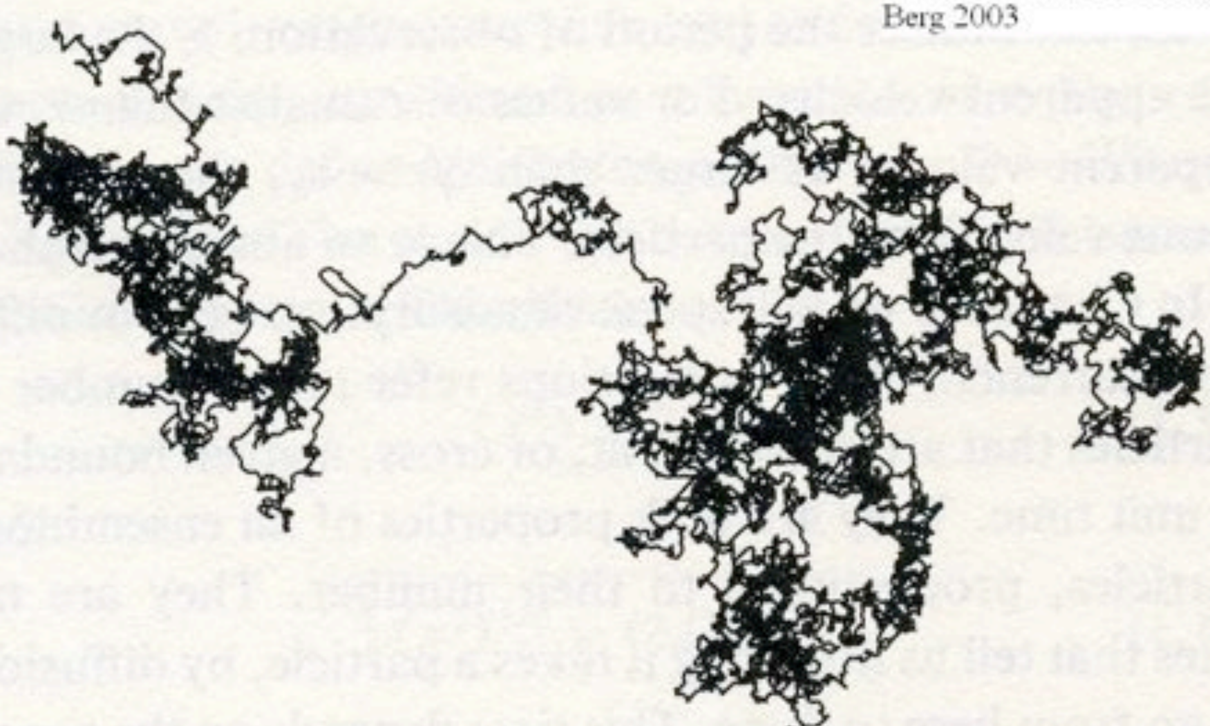
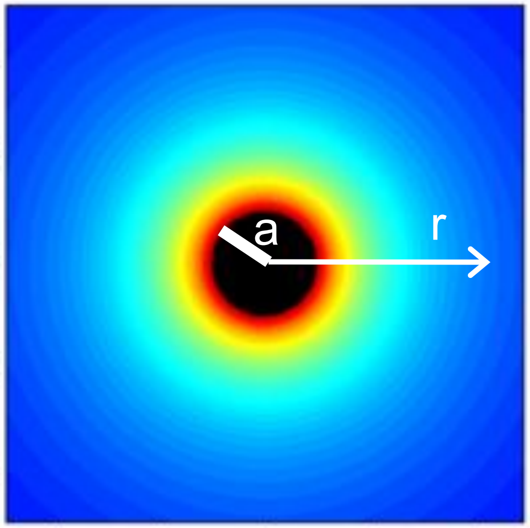


Fig. 1.4. An x, y plot of a two-dimensional random walk of n = 18,050 steps. The computer pen started at the upper left corner of the track and worked its way to the upper right edge of the track. It repeatedly traversed regions that are completely black. It moved, as the crow flies, 196 step lengths. The expected root-mean-square displacement is $(2n)^{1/2}$ = 190 step lengths.

Osmotrophs: nutrient uptake

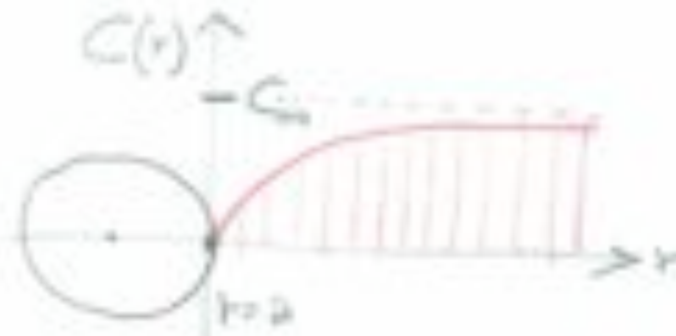
Concentration of nutrients around cell

(question: can you predict the uptake?)



$$c(r) = c_\infty \left(1 - \frac{a}{r}\right)$$

Concentration field around the cell



[Reverse (exudation) → phycosphere]

Flux J of nutrients into the cell → Fick's law: flux = - diffusivity * gradient

$$J(r) \overset{\downarrow}{=} -D\frac{dc}{dr} = -D\frac{c_\infty a}{r^2} \quad \text{(radially inward)}$$

At the cell surface $(r=a)$ → $$J(a) = -\frac{D c_\infty}{a}$$

Uptake rate

Uptake rate U

= flux × area

$= J \times 4\pi a^2$ =

$= (Dc_\infty/a) \times 4\pi a^2$

$= 4\pi D a c_\infty$

E.g. if c_∞ is in mol_C/cm^3 and a is in cm → Uptake rate U is in mol_C/s

Note: **U ~ a** (NOT a^2)

Volume-specific uptake rate

= U / Cell Volume

$= 4\pi D a c_\infty / (4\pi a^3/3)$

$= 3Dc_\infty / a^2 \sim 1/a^2$

→ small cells are strongly favored,
large cells are at a competitive disadvantage
in oligotrophic waters

Maximum and optimum cell size

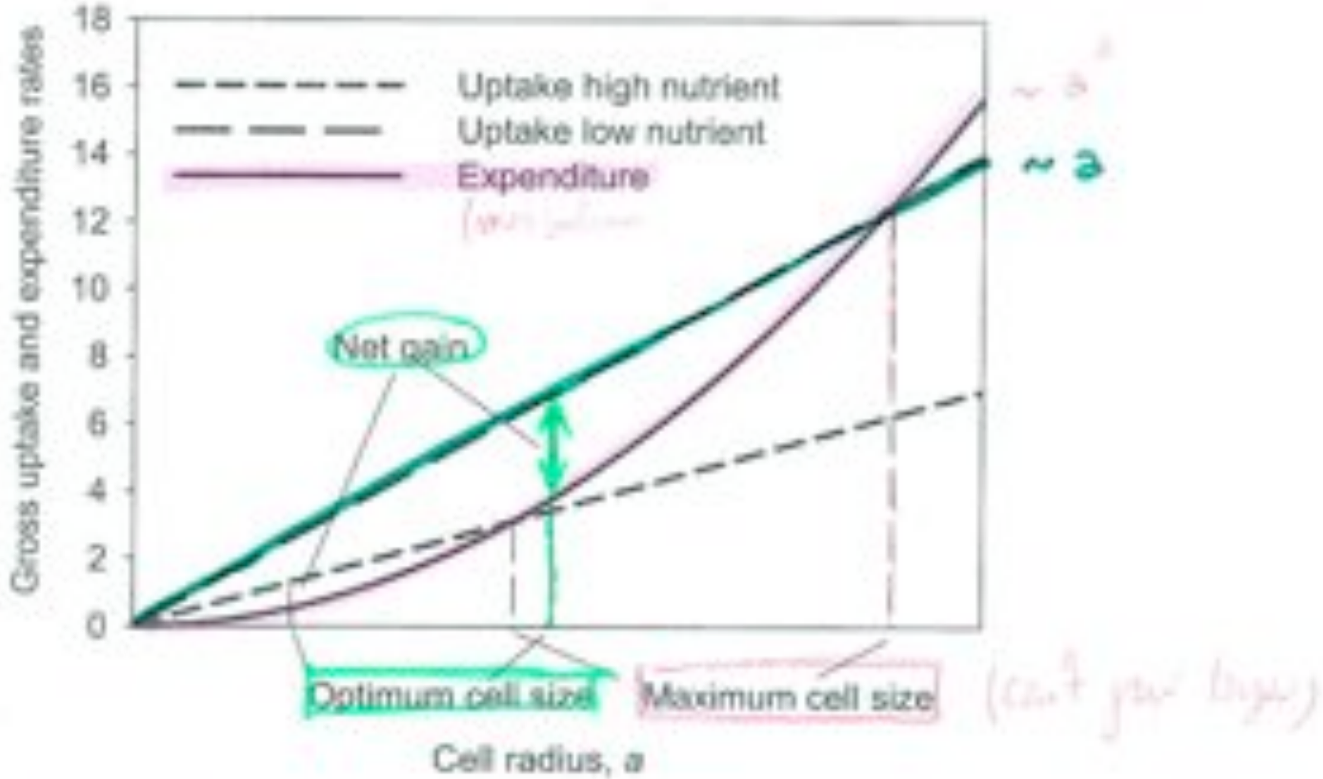
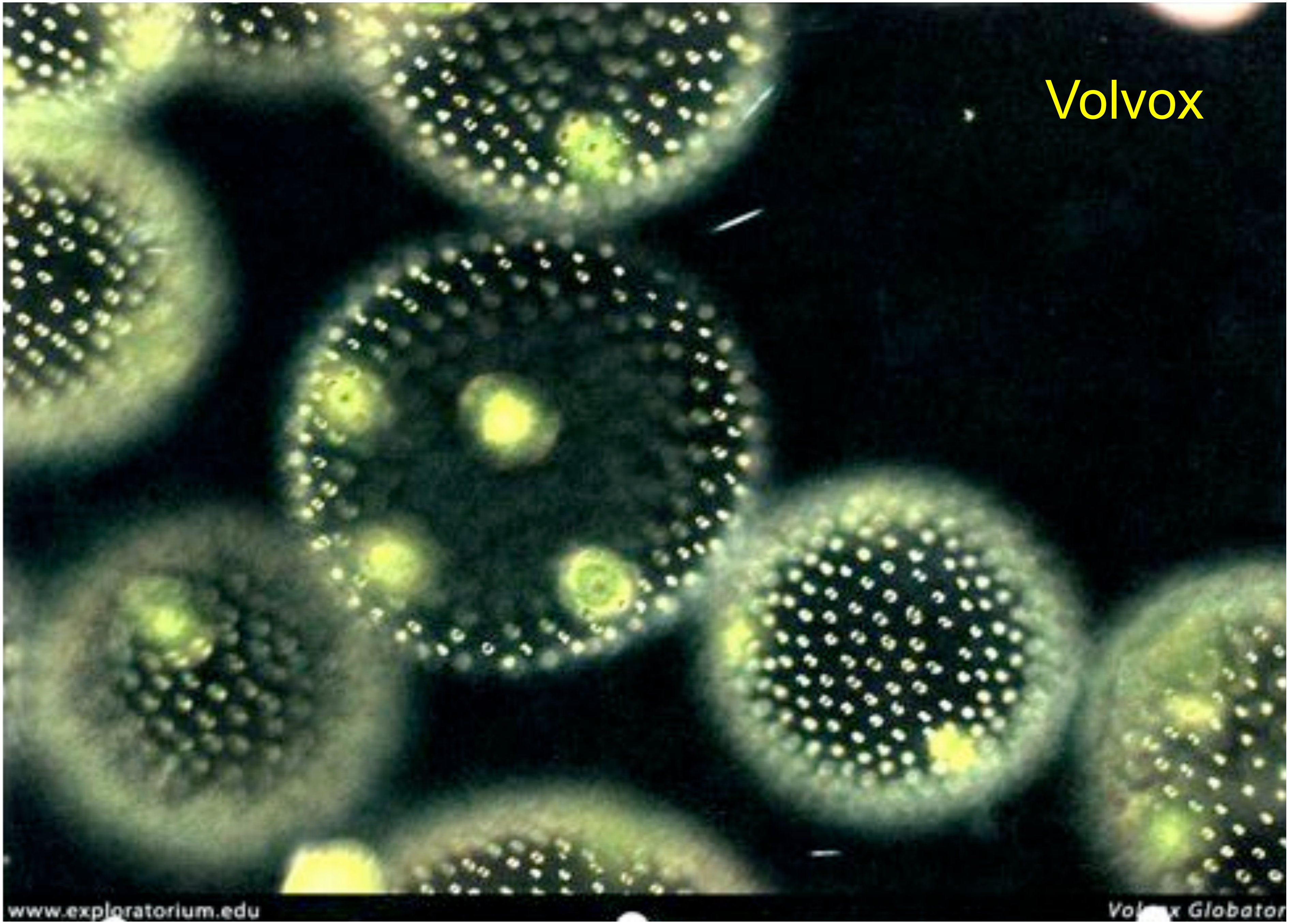


Fig. 2.6. Optimum and maximum cell size of an osmotroph. For diffusive supply, uptake rate increases linearly with cell radius, and the slope is proportional to the ambient nutrient concentration (dashed lines). Expenditure (metabolism) increases as a power function of cell size. The maximum possible cell size is the size at which uptake equals expenditure, i.e., where the uptake and expenditure lines intersect. Similarly, optimum cell size, where absolute growth (uptake minus expenditure) is the largest possible, is at the cell size where the difference between uptake and expenditure curves is the largest. Both optimum and maximum cell sizes increase with ambient nutrient concentration.

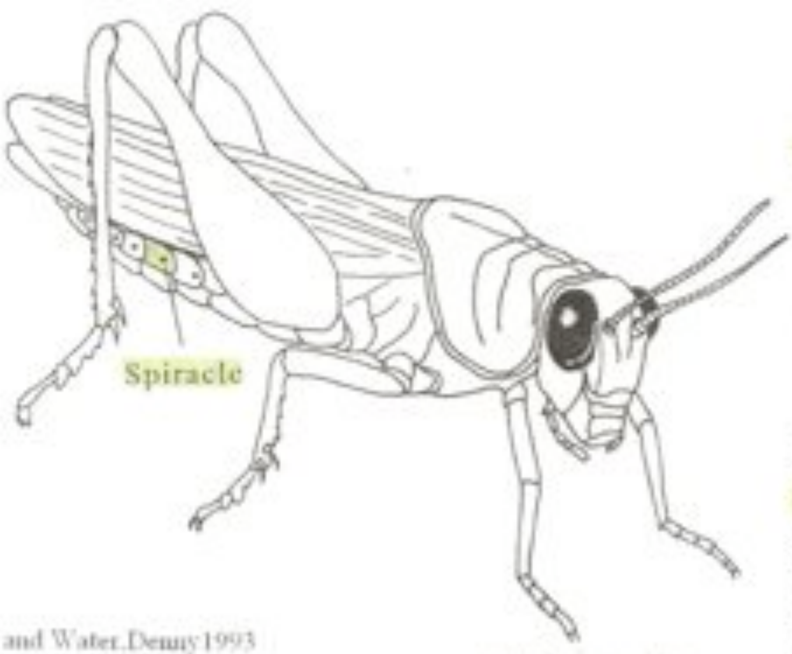
Kiorboe, 2008


Volvox
www.exploratorium.edu

Copepod nauplius

Insect tracheae

Fig. 6.12 Spiracles (located on the sides of the abdomen) are the external openings to the locust's tracheae. Internally, the tracheae go through various bifurcations.



Air and Water,Denny1993

Air and Water,Denny1993

MODEL :

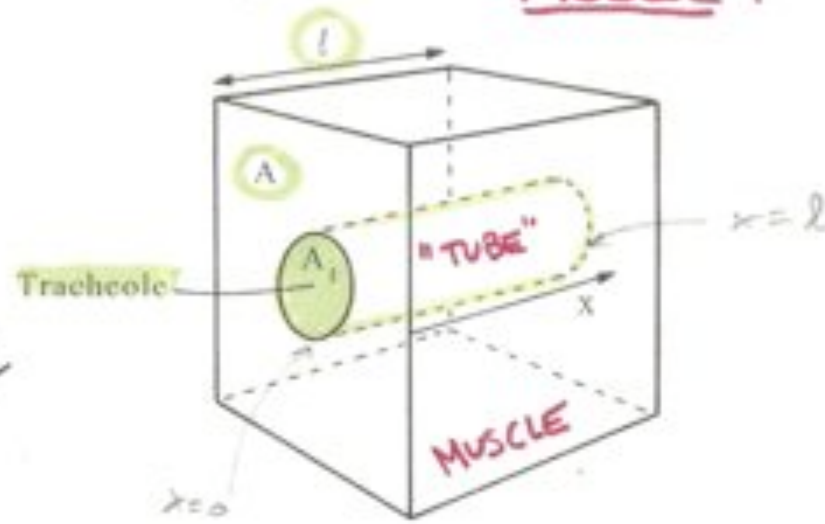


Fig. 6.13 Each tertiary tracheole supplies oxygen to a portion of muscle. The dimensions of the schematic tracheole-muscle system shown here allow us to calculate the maximal length of tracheae.

- Muscles consume O_2 → flight muscles (most demanding) $M = 6.5 \frac{mol\,O_2}{m^3 \cdot s}$
- Air is delivered to cells via blind-ended pipes
- Length of tracheole up to 1 mm; diameter up to 0.2 μm

Is diffusion sufficient to deliver enough air?

Eggs

- Why is an egg so fragile?
- How porous must an egg of given size be?
- Does this work in water?
- Mermaid's purse

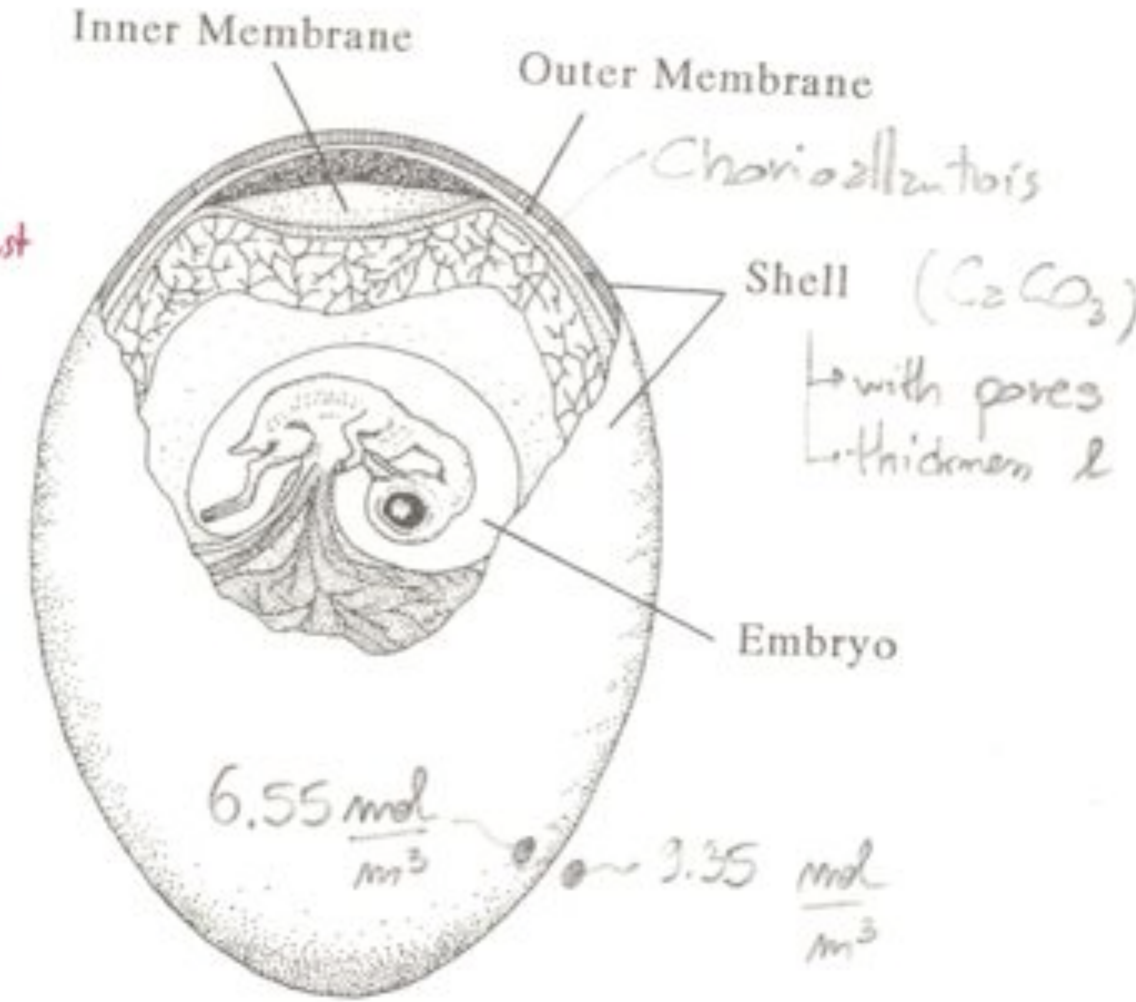
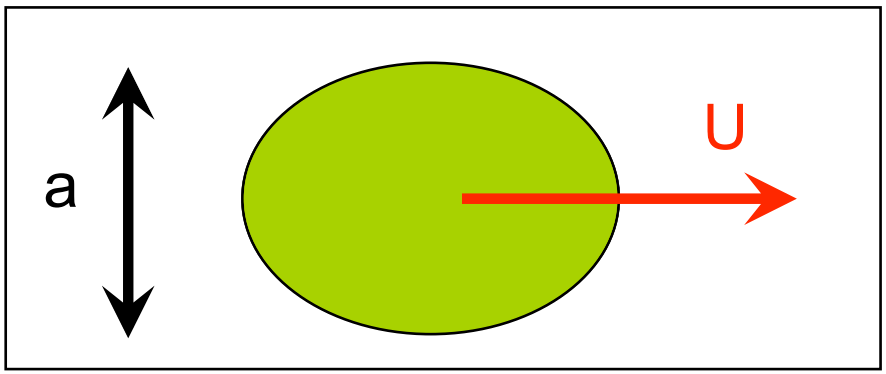


Fig. 6.15 An embryonic bird exchanges gases with its surroundings through pores in its shell.

Air and Water, Denny 1993

The Peclet number

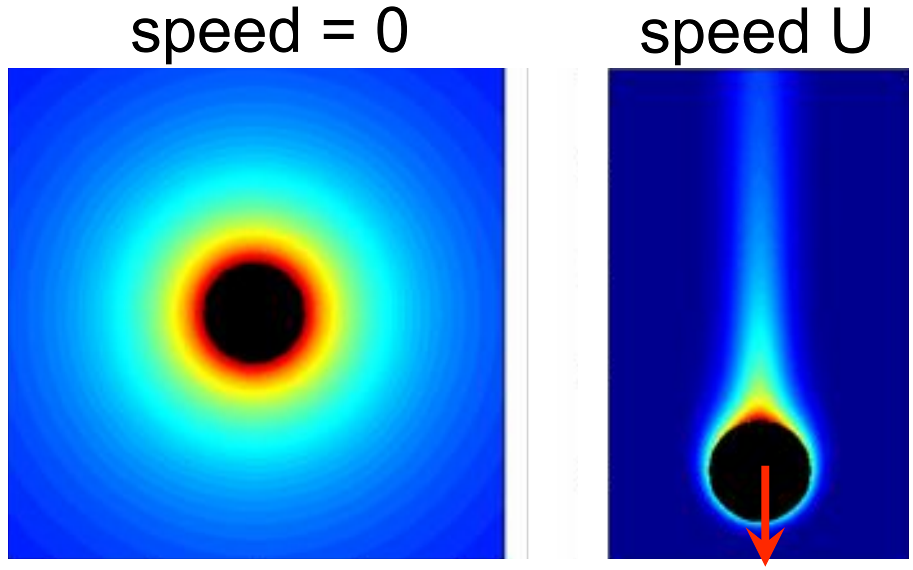
Now let the cell move, relative to the fluid
→ we will call this 'advection'
→ 'advection': many different types of flow (e.g. swimming, sinking, turbulence, …)



$$Pe = \frac{Ua}{D}$$

D : diffusivity of the solute (often ~ 10^{-9} m^2 s^{-1} in water)

Why do we like to use dimensionless numbers ?
→ Rapid classification of, and intuition about, the physical regime



The Peclet number

- $\dfrac{\text{Advection}}{\text{Diffusion}} \sim \dfrac{\text{advective flux}}{\text{diffusive flux}} \sim \dfrac{C_\infty U}{D \frac{C_\infty}{a}} \sim \dfrac{Ua}{D} = Pe =$ PECLET NUMBER

- $Pe \ll 1 \rightarrow$ diffusion dominates, advection negligible

- Swimming organisms : $U \approx 10 \cdot a$ [using meters and seconds]

  $\therefore Pe = \dfrac{10\, a^2 (m)}{10^{-9} m^2 s^{-1}} > 1$ for $a > 10\, \mu m$

The Sherwood number

$$\text{Sh} = \frac{\text{Flux by advection} + \text{Flux by diffusion}}{\text{Flux by diffusion}}$$

- How to think about the Sherwood number (catching mosquitoes)

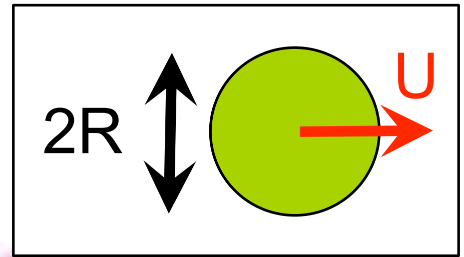
- No simple, a priori expression for Sh (like there is for Pe)

- Instead, Sh actually measures (rather than estimates) the relative importance of advection and diffusion

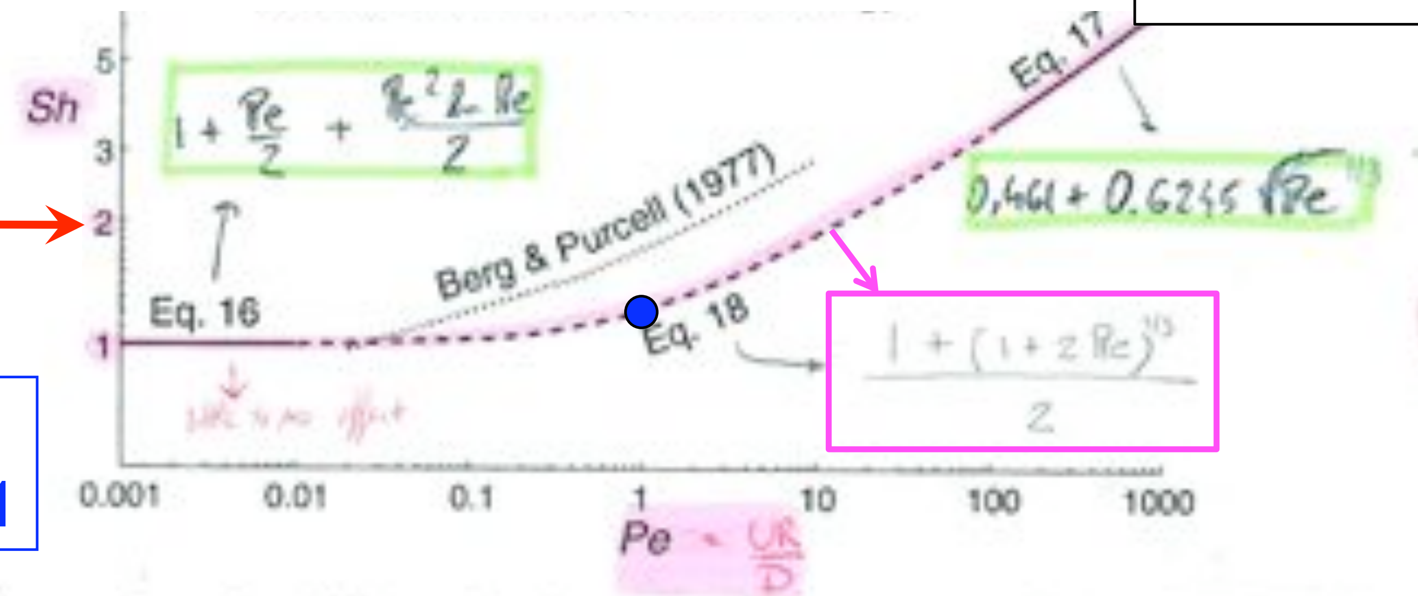
- Diffusion only → Sh = 1 (Pe = 0)

- Sh can be computed as a FUNCTION of the Peclet number, where the choice of the function depends on which flow ones is considering (e.g. sinking or turbulence)

Uptake gain due to swimming
(or sinking)



Advection doubles the uptake



Sh = 1.2
at Pe = 1

Figure 2 Sherwood number (*Sh*) as a function of Péclet number (*Pe*) for cells moving at a constant velocity in stagnant water or cells fixed in a uniform flow ($Re \ll 1$). Equation 16 was derived by Acrivos & Taylor (1962) for $Pe \ll 1$ and Equation 17 was derived for $Pe \gg 1$ by Acrivos & Goddard (1965). Clift et al. (1978) suggested Equation 18 as a fit to their numerical results; we use it for the region of intermediate *Pe* for which analytic solutions are not available. Berg & Purcell (1977) obtained their relation numerically, but provided no explicit equation. For reasons detailed in the text and in Appendix II, we believe Berg & Purcell's (1977) relation (their Fig. 4) to be inaccurate.

Karp-Boss et al., Oceanography and Marine Biology: an Annual Review 1996

How this works: compute Pe → get Sh from the graph (for THIS flow)

Uptake gain due to swimming

Examples of Sherwood numbers

0.5 μm bacterium	$U = 20$ μm/s	$Pe = 10^{-2}$	$Sh = 1.00$
5 μm flagellate	$U = 200$ μm/s	$Pe = 1$	$Sh = 1.22$
500 μm algal colony	$U = 800$ μm/s	$Pe = 400$	$Sh = 5$

So, why would bacteria want to swim??

Enhancement of nutrient uptake by sinking

Phytoplankton				
Radius, µm	*Sinking velocity,*[1] *cm s*$^{-1}$	*Re* (= *au/ν*)	*Pe* (= *au/D*)	*Sh*[2]
0.5	2.3×10^{-5}	1.1×10^{-7}	1.1×10^{-4}	1.00
5	3.4×10^{-4}	1.7×10^{-5}	1.7×10^{-2}	1.01
50	5.0×10^{-3}	2.5×10^{-3}	2.5×10^{0}	1.41
500	7.5×10^{-2}	3.8×10^{-1}	3.8×10^{2}	5.06
Marine snow aggregates				
Radius, mm	*Sinking velocity,*[3] *cm s*$^{-1}$	*Re* (= *au/ν*)	*Pe* (= *au/D*)	*Sh*[4]
0.1	0.039	0.039	39	2.6
1	0.071	0.71	710	6.4
10	0.13	13	1300	18.8

[1] u (cm s^{-1}) = $2.48a$ (cm)$^{1.17}$. Calculated from Stokes' law taking the declining cell density with cell size into account (Jackson 1989).

[2] *Sh* calculated using eq. 3.5 assuming $D = 10^{-5}$ cm^{2}s^{-1}

[3] u (cm s^{-1}) = $0.13a$ (cm)$^{0.26}$ (Alldredge and Gotschalk 1988).

[4] *Sh* calculated using eq. 3.6, assuming ν/D equal to 1000.

Kiorboe, 2008

Encounter of viruses

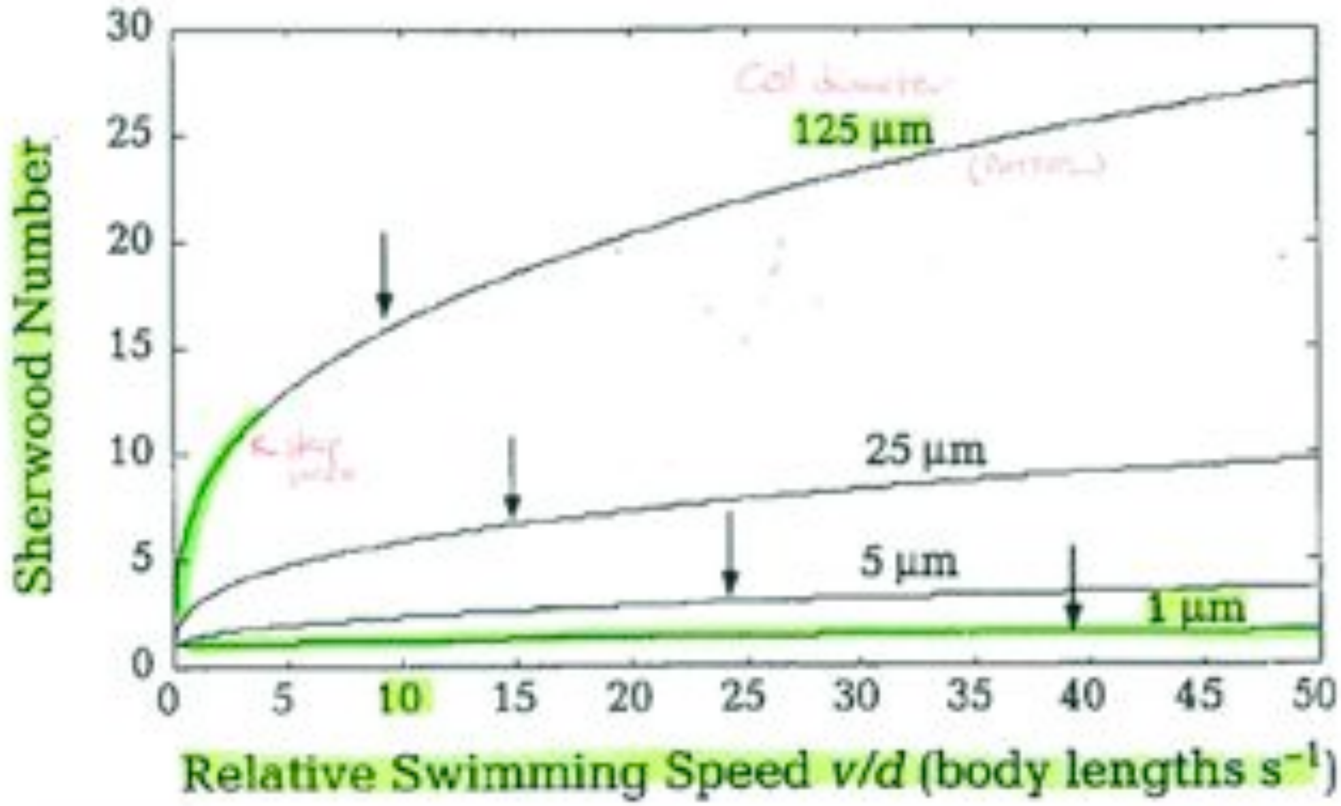
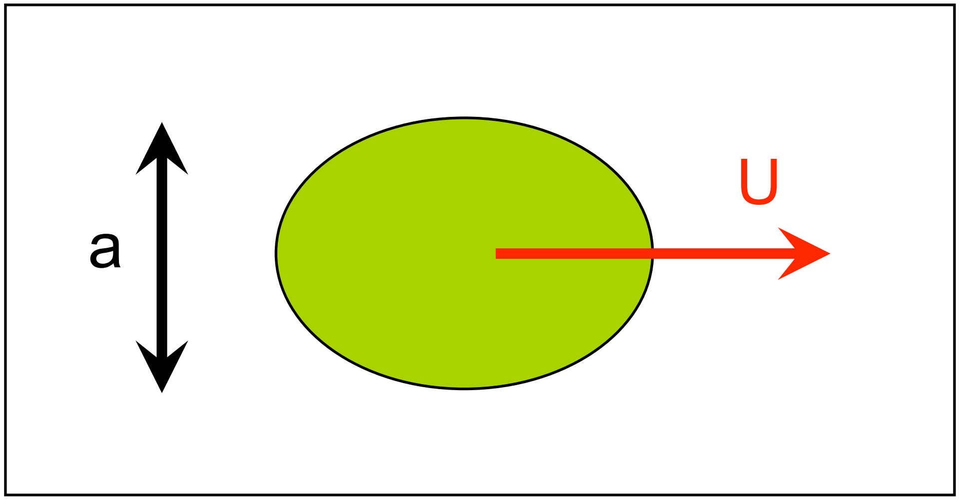


Fig. 2. Effect of speed relative to host's body length on contact rate with viruses for different particle sizes. Numbers shown are for particle diameter, arrows indicate swimming speed calculated by Eq. 11. Not only are larger hosts more sensitive to movement, they are very sensitive to small movements.

Sh calculated from Eq. 5

Murray & Jackson, MEPS 1992

The Reynolds number



$$Re = \frac{Ua}{\nu}$$

ν : **kinematic** viscosity of the fluid (10^{-6} m^2 s^{-1} for water)

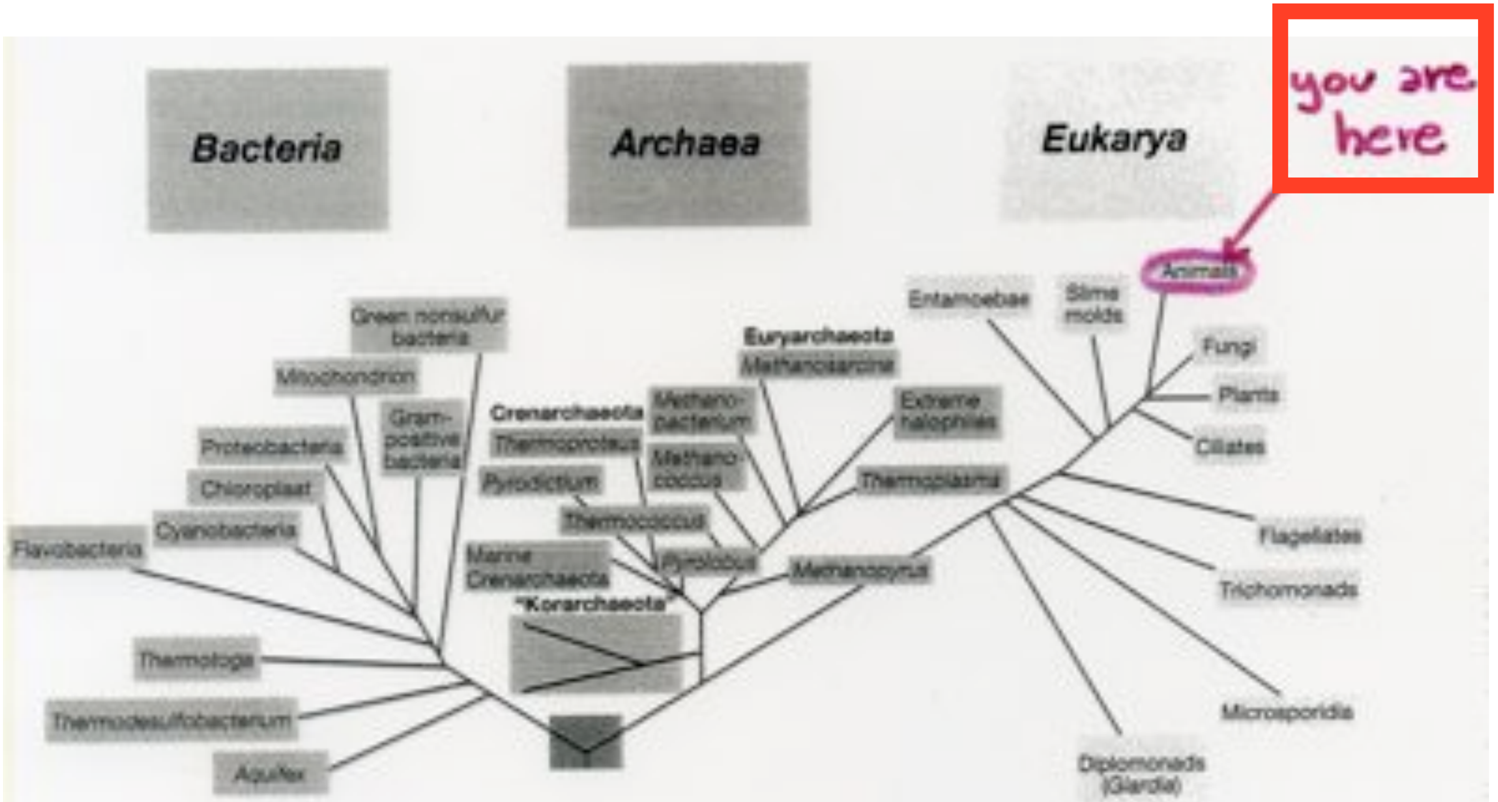
$$Re = \frac{\text{inertial forces}}{\text{viscous forces}} \quad \text{(dimensionless)}$$

Glaciers, pumping oil and swimming spermatozoa

When is the Reynolds number small?

$$Re = \frac{Ua}{\nu}$$

Note: all these processes are governed by the same fluid dynamics!!



all the others are 'small'

UNIVERSAL PHYLOGENETIC TREE. This tree is derived from comparative sequencing of 16S or 18S RNA. Note the three major domains of living organisms: the *Bacteria*, the *Archaea*, and the *Eukarya*. The evolutionary distance between two groups of organisms is proportional to the cumulative distance between the end of the branch and the node that joins the two groups. See Sections 11.4–11.8 for further information on ribosomal RNA-based phylogenies. *Data for the tree obtained from the Ribosomal Database project* **http://rdp.cme.msu.edu**

The Reynolds number

TABLE 11.2 The Body Lengths, Speeds, Relative Speeds, and Reynolds Numbers for Some Swimming Microorganisms

Organism	Body Length (µm)	Speed (mm/s)	Lengths/Time s^{-1}	Reynolds Number
Bacterium, *Escherichia coli*	3.0	0.03	10	0.00009
Sperm, *Lytechinus* (sea urchin)	5.1	0.16	31	0.0008
Flagellate, *Chlamydomonas*	13.	0.06	4.6	0.0008
Flagellate, *Euglena*	50.	0.08	1.6	0.004
Ciliate, *Tetrahymena*	70.	0.48	6.9	0.03
Ciliate, *Paramecium*	210	1.0	4.8	0.21
Ciliated flatworm, *Convoluta*	2,000	0.60	0.3	1.2

Sources: Data from Holwill 1975, 1977; Brennen and Winet 1977; Sleigh and Blake 1977; Berg 1993.

US WALKING $2 \cdot 10^6$ $2 \cdot 10^3$ (1) $4 \cdot 10^5$

Counterintuitive fluid mechanics

(1) No inertia, no coasting, no Brazilian free kicks

Example of soccer ball

How long does it take for a bacterium to come to rest after it stops propelling its flagellum? (e.g. soccer ball)

$\xrightarrow{\int} \ln U = -\frac{t}{\tau} + k_1$

$\therefore \; U(t) = U_0 e^{-t/\tau}$

↳ timescale to come to rest $= \tau = \frac{2}{9}\frac{R^2}{\nu} = \frac{2}{9}\cdot\frac{(10^{-6}\,m)^2}{10^{-6}\,m^2 s^{-1}}$ $< 1\,\mu s$

Stopping distance $\ell \sim U_0 \tau \sim 10\,\mu m/s \cdot 1\,\mu s = 10^{-10}\,m = 1$ Å

At low Re, motion exists only while force (propulsion) acts

(Aristotle's prediction!)

No inertia (no coasting) → particles/organisms faithfully follow streamlines (no Brazilian free kicks among microbes)

Counterintuitive fluid mechanics

(2) Reversibility at low Re

http://web.mit.edu/fluids/www/Shapiro/ncfmf.html

The scallop theorem!