Preamble.

Vogel[1] puts it succinctly: “One can argue that the boundary between the cellular and super- (or multi-) cellular worlds reflects the upper size limit of practical diffusion-based systems.”. It is important to emphasize that this is an *argument* not a statement of fact. The boundary lines are not necessarily well defined. Even so, to become multi-cellular, an organism must rely upon more than the diffusion of the ‘molecules of life’ (such as sugars to be used to generate biological energy or carbon dioxide to be fixed into metabolizable sugars). Why? Because the rate of supply is likely to be too slow, limiting the survivability of the organism. This is due in part to a higher ratio of volume to surface area, and to the need to supply cells deep within the organism’s body, far away from the surface.

Instead of diffusion, the organism must rely upon advection (mass/volume flow) to supply the ‘molecules of life’, and mass/volume flow relies upon pumps.

What are the biophysics of diffusion, advection and pumps? How do they constrain organismal size and complexity? These questions will be explored in these course notes.

To begin with, we will derive the fundamental equations describing diffusional flux, Einstein will be our guide. Then we will explore the time dependence of diffusion to show the limits of diffusion-mediated life. We will then consider the fundamental equations of mass/volume flow, and compare diffusion and advection. For the comparison of the relative contributions of diffusive and advective flow, we will use the dimensionless Peclet Number. Pumps increase the effective importance of mass/volume flow, but the pumping mechanisms used by biological organisms are so varied that we will select only a few in a case study approach to illuminate the possibilities. The case studies will look at advective stirring by the alga *Volvox*, the evaporative (vacuum) pumps of trees, and a simple valveless chamber pump in a xylem sap-sucking insects (cicadas and spittlebugs).

Two-lined Spittlebug (Prosapia bicincta) found at Shelby Park in Nashville, Tennessee. Photograph by Kaldari (http://en.wikipedia.org/wiki/User:Kaldari)

[1]Vogel, Steven (2009) Glimpses of Creatures in Their Physical Worlds. Princeton University Press. page 6.

Diffusion is the flux of molecules down a concentration gradient. The magnitude of the flux is governed by a diffusion coefficient. The molecular mechanism causing diffusion is the random walk[1] The random walk is caused by molecular collisions.

The diffusion of molecules to a cell surface provides the cell with nutrients and other needs. Waste products (and signaling molecules) secreted from the cell diffuse away into the external medium.

Within the cell, collisions between two random-walking molecules —for example, an enzyme and a substrate molecule— is the first step in an enzymatic reaction, of which there are many that are obligatory for life to occur. So diffusion is central to the life of the organisms. Life itself may be a Random Walk.

We will first introduce the diffusion equation described by Fick, then the molecular mechanisms of the random walk that underlies diffusion.

$$J = -D\frac{\partial c}{\partial x}$$

Fick's First Law of Diffusion: The flux is proportional to the concentration gradient

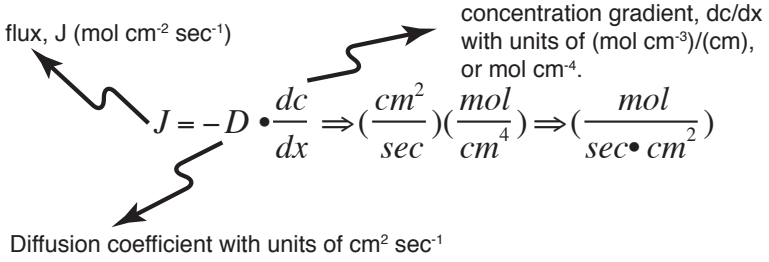
$$\frac{\partial c}{\partial t} = -\frac{\partial J}{\partial x}$$

Fick's Second Law of Diffusion: Changes in concentration over time depend upon the flux gradient

$$\frac{\partial c}{\partial t} = D\frac{\partial^2 c}{\partial x^2}$$

[1]MacDonald, DKC (1962) Noise and Fluctuations. John Wiley and Sons. (Dover Publication, 2006); and Berg, HC (1993) Random Walks in Biology. Princeton University Press.

Fick's First Law of Diffusion describes the flux of molecules. It is a phenomenological equation; that is, it was based upon experimental results when it was first formulated. It lacked a theoretical underpinning[1]. The equation is:

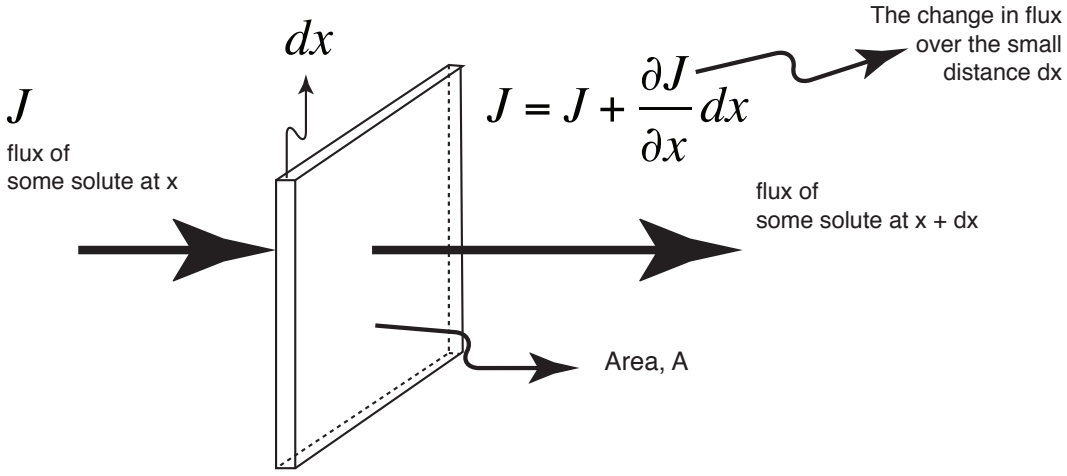


The movement of molecules depends upon the concentration gradient of molecules. This is described by Fick's First Law of Diffusion.

The diffusion equation, $J = -D(\partial c/\partial x)$, does not account for changes in concentration that will occur as molecules move from one location to another, in accordence with the flux, J. Instead, it assumes a steady state, in which the change in concentration over time is zero: $\partial c/\partial t = 0$.

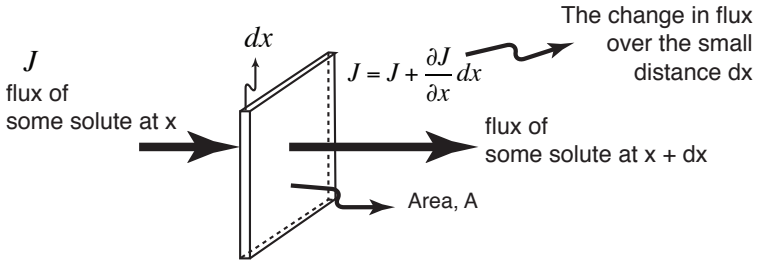
How do we account for the non-steady-state time dependence of diiffusion? The derivation of a general equation relies upon conservation of mass.

Consider the changes in flux, J, with respect to distance ($\partial J/\partial x$) through a small volume element of width x+dx and area A[2]:



The change in the amount of solute in the volume element, A•dx, is equal to the amount flowing in, J•A minus the amount flowing out, (J+(∂J/∂x)dx)•A per unit time. Note that the change in the amount of solute in the volume element A•dx can be expressed as $\partial c/\partial t$, multiplied by the volume element A•dx.

[1]MacDonald, DKC (1962) Noise and Fluctuations. John Wiley and Sons. (Dover Publication, 2006). and Berg, HC (1993) Random Walks in Biology. Princeton University Press.
[2]Noble, PS (1974) Introduction to Biophysical Plant Physiology. WH Freeman and Co. pp 9–19.



$$\frac{\partial c}{\partial t} dx \bullet A = (J \bullet A) - \left(J + \frac{\partial J}{\partial x} dx \right) \bullet A$$

The change in the amount of solute in the volume element A•dx is equal to the amount moving into the volume element minus the amount moving out of the volume element

$$\frac{\partial c}{\partial t} dx \bullet A = (J \bullet A) - (J \bullet A) - \left(\frac{\partial J}{\partial x} dx \bullet A \right)$$

$$\frac{\partial c}{\partial t} dx \bullet A = -\frac{\partial J}{\partial x} dx \bullet A$$

dividing by dx • A : $\frac{\partial c}{\partial t} = -\frac{\partial J}{\partial x}$

This is known as the Continuity Equation and is based on conservation of mass: that matter can be neither created nor destroyed.

Substituting the flux equation, J = –D(∂c/∂x) into the continuity equation, (∂c/∂t) = –(∂J/∂x):

$$\frac{\partial c}{\partial t} = -\frac{\partial}{\partial x}\left(-D \frac{\partial c}{\partial x} \right)$$

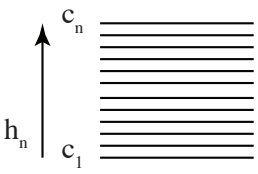
$$\frac{\partial c}{\partial t} = D \frac{\partial^2 c}{\partial x^2}$$

This is known as the Fick's Second Law of Diffusion. It describes how the concentration of the solute changes with position and with time as a result of diffusion. The solutions of this equation depend upon the geometry. Books are devoted to solutions to the diffusion equations[1].

[1]Crank, J (1975) The Mathematics of Diffusion, Second edition. Clarendon Press, Oxford.

From an historic point of view, when he developed the diffusion equation, Adolf Fick noted that the underpinning theory should be identical to that obtained for the diffusion of heat in a conducting body (developed by Fourier), and Ohm's Law describing the diffusion of electricity in a conductor[1].

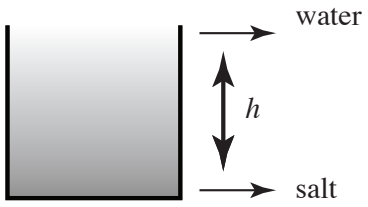
For solute diffusion through a series of concentration strata (c_1 through c_n) varying with height (h_n), Fick invoked conservation of mass:



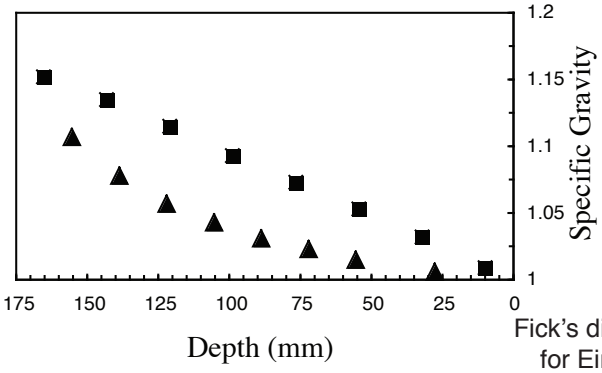
$$\frac{\partial c}{\partial t} = -k \frac{\partial^2 c}{\partial h^2}$$

That is, the change in concentration will depend upon the second derivative of concentration with respect to distance, multiplied by k, a constant dependent on the nature of the substance. Note that this is suitable for a simple system, in which the geometry and volume of each stratum are well defined.

To test this, Fick used an apparatus in which a steady state concentration gradient was created between solid salt and pure water. He then measured the specific gravity at various depths. Allowing the system to reach a steady state, where ∂c/∂t would be zero, leads to a solution of the second derivative equation: a linear gradient: c = a • h + b.



From ∂/∂h (a•h+b) = a,
and ∂/∂h (a) = 0.



In fact, this is what he found (Fick's data is graphed to the left) (square symbols). He performed a further test with a more complex geometry (a funnel), in which the steady state solution is a non-linear concentration gradient (triangle symbols).

Fick's diffusion laws were one of the starting points for Einstein's elucidation of the molecular motion underlying diffusion. The other was the behaviour of particles in solution: Brownian Motion.

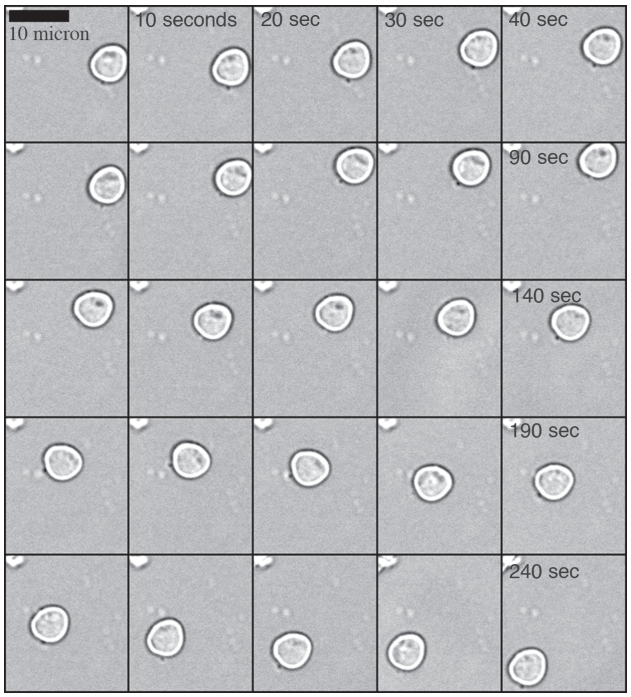
[1]The original english article (Fick, A: On liquid diffusion.) (an abstract of a longer German article) was published in 1855, and republished in the Journal of Membrane Science 100:33–38 (1995).

The theory explaining the mechanism causing diffusion is based on molecular collisions. But that explanation arrived by a circuituous route: It arose from an explanation of the enigmatic Brownian motion —the random motion of particles (dust, pollen grains etc.) that can be observed in solutions using a microscope. The example to the right is of a conidial spore of the fungus *Neurospora crassa*.

The causes of the Brownian motion were very unclear. It had been proposed that molecular bombardment of the particle could be the cause, but the momentum of a single atomic collision would be far too small to cause the motion of a large pollen grain (or conidial spore).

The cause of the random motion was elucidated by Albert Einstein in 1905[1].

Einstein used a two-pronged approach: One was based on thermodynamic principles, that is, the ensemble properties of the system. The other approach was based on the statistical analysis of the random motion of the individual particles.

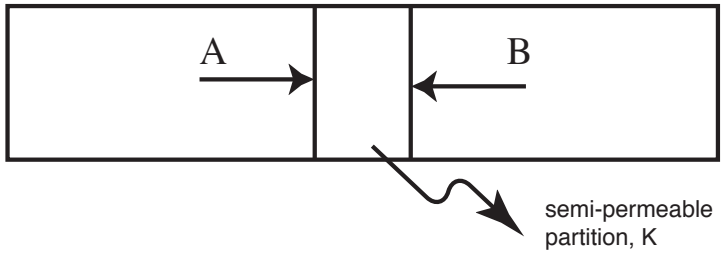


Robert Brown (1828) noted that "while examining the form of these particles immersed in water, I observed many of them vary evidently in motion. These motions were such as to satisfy me ... that they arose neither from currents in the fluid, nor from its gradual evaporation, but belonged to the particle itself"[2]. In the example shown above, the slight displacements of the conidial spore (images were taken every 10 seconds, as shown, bar = 10 micron) appear to be random, with net displacements occurring in multiple directions. Over time, it is expected that the average displacement (using an x-y coordinate system) would be zero.

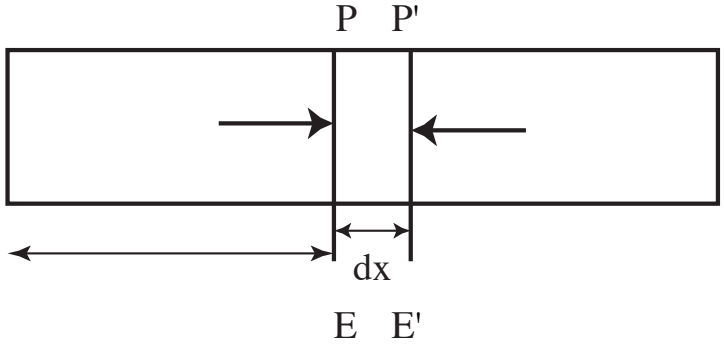
[1]Einstein, A (1905) On the movement of small particles suspended in a stationary liquid demanded by the molecular-kinetic theory of heat. Annalen der Physik, ser. 4, XVII, 549-560. (Dover Publication, 1956: Investigation on the Theory of the Brownian Motion. pp. 1–18.)
[2]MacDonald, DKC (1962) Noise and Fluctuations. John Wiley and Sons. (Dover Publication, 2006). pp.8.

Using a thermodynamic approach, Einstein proposed a way to predict the value of the diffusion coefficient of a substance dissolved in the solution based on the properties of the substance (dimensions) and the solvating medium (viscosity).

The starting point was to consider a cylinder separated into two compartments (A and B) by a membrane that is impermeable to the solution (usually water) but not the dissolved substance[1]. This is a typical starting point for considerations of diffusion and osmotic pressure, based on experiments by Pfeffer pre-dating Einstein.



Einstein invoked a diffusive process within the cylinder, but with modifications, removing the semi-permeable barrier:



Diffusion between the planes E and E' create an osmotic pressure difference: P - P'. The distance dx in the cylinder is a unit volume of the cylinder, so the osmotic pressure difference P - P' can be expressed as:

$$K = \frac{P - P'}{dx} = -\frac{P' - P}{dx} = -\frac{dP}{dx}$$

the osmotic pressure in unit volume

[1]Einstein, A (1908) The elementary theory of the Brownian motion. Zeit. fur Elektrochemie. 14:235-239. (Dover Publication, 1956: Investigation on the Theory of the Brownian Motion. pp. 68–85.)

Another expression for pressure can be obtained from the van't Hoff relation:

$$P = RTc$$

Where c is the concentration, R is the gas constant (2.437 m^3 Pa mol^{-1} $^oK^{-1}$) and T is the temperature (^{o}K). This follows from the ideal gas law (PV = nRT, or P = RT(n/V)), assuming that there is thermodynamic equilibrium between gas and liquid phases.

Incoporating the van't Hoff relation into the osmotic pressure gradient in the unit volume, the force (K = dP/dx) becomes:

$$K = -\frac{dP}{dx} = -RT\frac{dc}{dx}$$

To determine the flux of the solutes due to diffusion, it is necessary to consider the resistance to solute motion. Specifically the resistance of the solvent to the movement of the dissolved substance.

The velocity of the substance depends upon the force acting on the substance (in this case, the osmotic force K) versus the frictional resistance of the molecule to movement ($F_{frictional}$):

$$\nu = \frac{K}{F_{frictional}}$$

Assuming that the particle is a spherical shape, than the frictional resistance ($F_{frictional}$) is known:

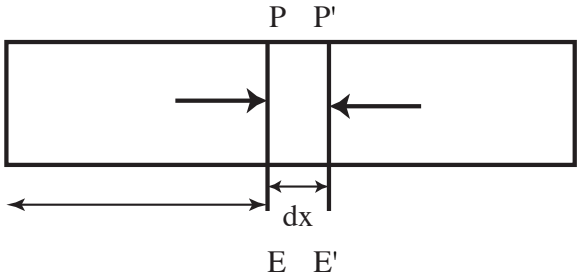
$$F_{frictional} = 6 \bullet \pi \bullet \eta \bullet r$$

Where η is the viscosity of the solution, and r is the radius of the particle. This is the Stoke's Relation, obtained from hydrodynamics. It can be experimentally validated. The derivation for Stoke's Law is presented in Appendix 1.

Einstein assumed that the dissolved particle is large compared to the molecules of the solvent, an assumption which is not necessarily true in the biological world.

[1]Einstein, A (1908) The elementary theory of the Brownian motion. Zeit. fur Elektrochemie. 14:235-239. (Dover Publication, 1956: Investigation on the Theory of the Brownian Motion. pp. 68–85.)

The number of molecules of the solute diffusing across the cross-section of the cylinder (from E to E') would be the concentration, c (in Einstein's time, called a gram-molecule) times the number of molecules in a mole: c • N. When Einstein published his paper[1], the value for the number of molecules per mole, N, was not accurately known (Einstein uses a value of $6 \bullet 10^{23}$, and notes the uncertainty is 50%).



Rather than force, K, applied to all of those molecules (c • N), we need to consider the force applied to a single molecule. So, the velocity term:

$$\nu = \frac{K}{F_{frictional}} \quad \text{becomes} \quad \nu = \frac{1}{c \bullet N} \bullet \frac{K}{F_{frictional}}$$

For one molecule.

$$\text{Since} \quad K = -\frac{dP}{dx} \quad \text{or} \quad K = -RT\frac{dc}{dx} \quad \text{then}$$

$$\nu = -\frac{1}{c \bullet N} \bullet \frac{RT}{F_{frictional}} \bullet \frac{dc}{dx} \quad \text{or}$$

$$\nu \bullet c = -\frac{1}{N} \bullet \frac{RT}{F_{frictional}} \bullet \frac{dc}{dx}$$

where $\nu \bullet c$ has units of flux, J

(cm • sec^{-1} mole • cm^{-3}, or mole • cm^{-2} • sec^{-1})

The last equation allows the thermodynamic relation derived by Einstein to be related directly to the Diffusional flux equation (Fick's Law of Diffusion) J = -D•(dc/dx). It created a predictive relation for D, the diffusion coefficient:

$$D = \frac{RT}{N} \bullet \frac{1}{F_{frictional}}$$

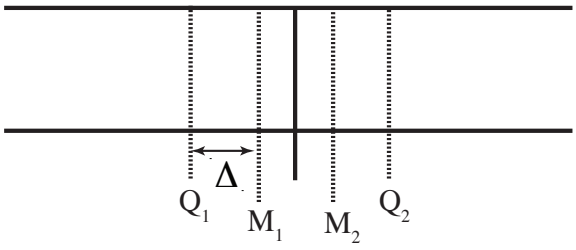
or

$$D = \frac{RT}{N} \bullet \frac{1}{6 \bullet \pi \bullet \eta \bullet r}$$

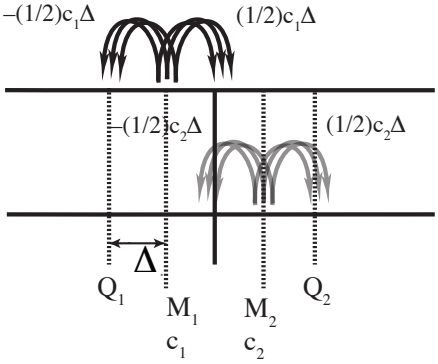
for a spherical particle. In this case, the size of the molecule can be inferred.

[1]Einstein, A (1908) The elementary theory of the Brownian motion. Zeit. fur Elektrochemie. 14:235-239. (Dover Publication, 1956: Investigation on the Theory of the Brownian Motion. pp. 68–85.)

Having established a thermodynamic description of the random motion of particles by considering a gradient of molecules and relating their properties (and the properties of the solution) to diffusional movement, Einstein now turned to a molecular approach ("The molecular theory of heat affords a second point of view, from which the process of diffusion can be considered")[1]. The initial construct is similar to the one for diffusional flux:



The solute molecule will move in the time interval t to t + τ, where τ is a time interval short enough that solute concentration is unaffected. During this short time interval, each of the molecules will move by a displacement Δ_1, Δ_2, Δ_3, etc. with some displaced in a positive (rightward) direction and some displaced in a negative (leftward) direction[2]. Assuming that the molecules do not interact, the displacements will average to Δ, even for regions with different concentrations of molecules. If the probability of rightward and leftward displacements are equal, then the net movement is:



The difference is the net movement of molecules from M_1 to M_2:

$(1/2)c_1\Delta - (1/2)c_2\Delta$

or,

$(1/2)\Delta(c_1 - c_2)$

Einstein is multiplying the concentration, c, by the unit volume, Δ (the height of the cylinder is given as unity).

Einstein notes that the difference in concentration, $(c_2 - c_1)/\Delta$, is a solution to the derivative dc/dx. That is, $(c_2 - c_1)/\Delta = dc/dx$, or $(c_1 - c_2) = -\Delta(dc/dx)$. Substituting this equation into the equation for net movement of molecules, $(1/2)\Delta(c_1 - c_2)$, the net movement of molecules (moles cm^{-2}) is $-(1/2)\Delta^2(dc/dx)$.

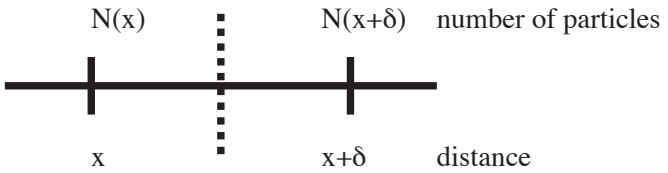
The net flux per unit time (J) (with units of moles cm^{-2} sec^{-1}) is:

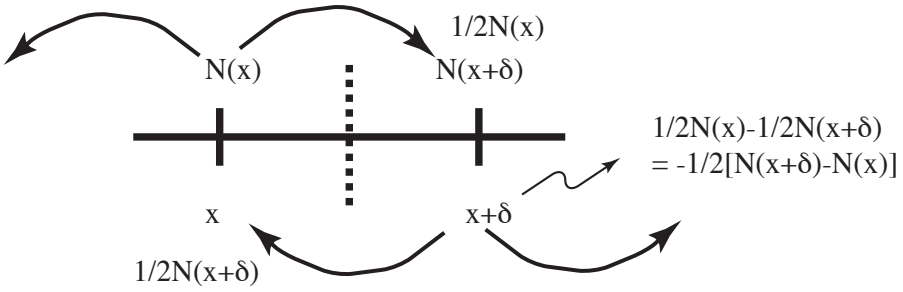
$$J = -\underbrace{\frac{1}{2} \bullet \frac{\Delta^2}{\tau}}_{\text{Diffusion coefficient}} \bullet \frac{dc}{dx}$$

[1]Einstein, A (1908) The elementary theory of the Brownian motion. Zeit. fur Elektrochemie. 14:235-239. (Dover Publication, 1956: Investigation on the Theory of the Brownian Motion. pp. 68–85.)

[2]Note that this is a simplification of Einstein's approach, but leads to the same conclusion.

Berg[1] uses an alternative approach that leads to the same outcome, Starting with a one-dimensional case: With N(x) particles at x and N(x+δ) particles at x+δ (the symbol, δ, refers to a small distance away). How many particles will move across the boundary from point x to point x+δ in a given time? If the probability for a particle to move to the left is the same as the probability to move to the right, then at time t+τ, half the particles at x will have moved to x+δ, and half the particles at x+δ will have moved to x.





The net number of particles going from x to x+δ will be -1/2[N(x+δ) - N(x)], and the flux, J (obtained by dividing by area and by time) will be:

$$J_x = -\frac{1}{2}\Big[N(x+\delta) - N(x)\Big]/A\tau,$$

multiplying by $\frac{\delta^2}{\delta^2}$

$$J_x = -\frac{1}{2}\frac{\delta^2}{\delta^2}\frac{1}{A\tau}\Big[N(x+\delta) - N(x)\Big]$$

δA has units of volume

$$J_x = -\frac{1}{2}\frac{\delta^2}{\tau}\frac{1}{\delta}\left[\frac{N(x+\delta)}{\delta A} - \frac{N(x)}{\delta A}\right]$$

N divided by volume is concentration

$$J_x = -\frac{1}{2}\frac{\delta^2}{\tau}\frac{1}{\delta}\Big[C(x+\delta) - C(x)\Big]$$

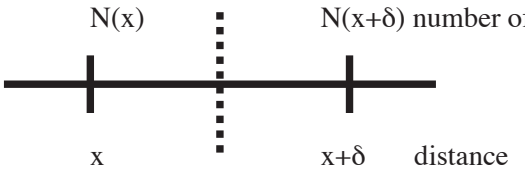
re-arranging

$$J_x = -\frac{1}{2}\frac{\delta^2}{\tau}\left[\frac{C(x+\delta) - C(x)}{\delta}\right]$$

[1]Berg, HC (1993) Random Walks in Biology. Princeton University Press. pp.17–21.

Continuing Berg's alternative approach[1]:

$$J_x = -\frac{1}{2}\frac{\delta^2}{\tau}\frac{1}{\delta}\left[C(x+\delta) - C(x)\right]$$



If we take the term

$$\left[\frac{C(x+\delta)-C(x)}{\delta}\right]$$

to the limit $\delta \rightarrow 0$, then

$$\frac{C(x+\delta)-C(x)}{\delta} = \frac{dC}{dx}$$

therefore

$$J_x = -\frac{1}{2}\frac{\delta^2}{\tau}\frac{dC}{dx}$$

or (Einstein):

$$J = -\frac{1}{2} \bullet \frac{\Delta^2}{\tau} \bullet \frac{dC}{dx}$$

These are the same form as Fick's Law of Diffusion ($J = D \bullet dC/dx$)

where $\frac{1}{2}\frac{\Delta^2}{\tau}$ is the Diffusion coefficient, D

with units of: $\frac{cm^2}{sec}$

The molecular definition of the diffusion coefficient:

$$D = \frac{1}{2} \bullet \frac{\Delta^2}{\tau}$$

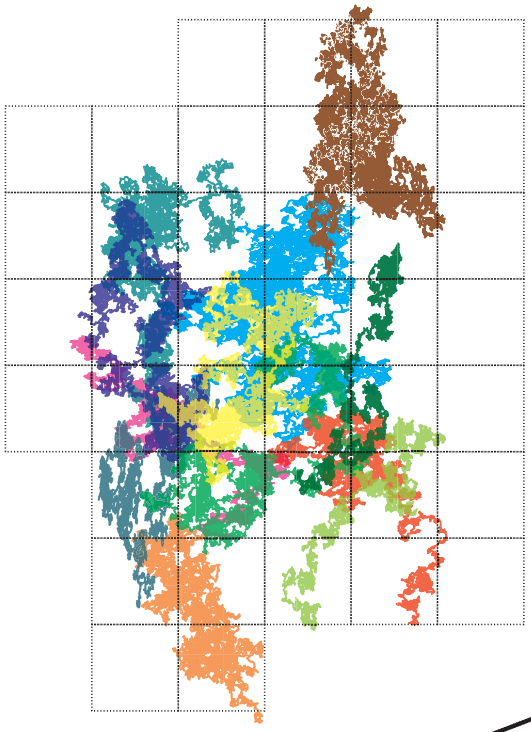
can be recast to show that the average displacement, Δ, is a function of the square root of time:

$$\Delta = \sqrt{2 \bullet D \bullet \tau}$$

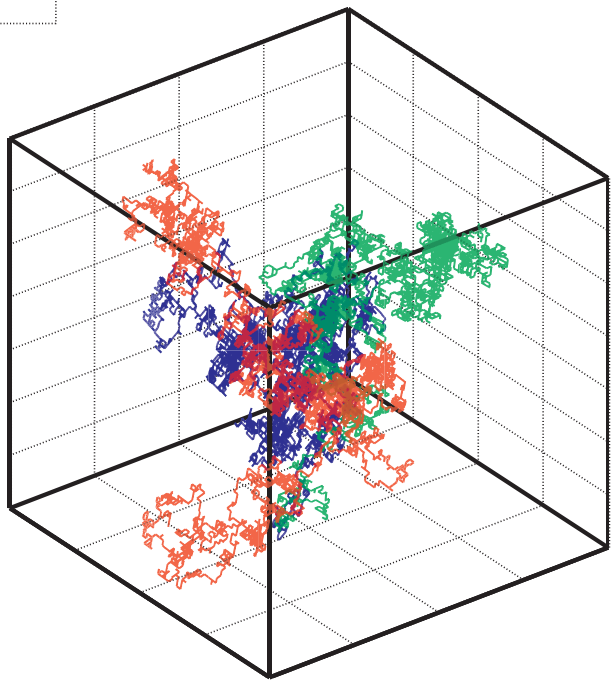
This prediction was used to verify Einstein's theory of Brownian Motion. Since then, random walks have, in one form or another, permeated biophysical research.

[1]Berg, HC (1993) Random Walks in Biology. Princeton University Press. pp.17–21.

Below are some simulations of random walks. For real particles, the distance from the origin was carefully measured by Perrin to confirm Einstein's prediction of a $t^{1/2}$ dependence. In these simulations, each particles starts at a different location on the grid. This could be a model for the random movements of enzymes and substrates, such that overlaps may represent opportunities for collision, leading to an enzymatic reaction.



And a three-dimensional random walk of three particles starting from the same location. Similar "tracks" are observed for bacteria swimming through a medium



To assess whether diffusional fluxes are relevant to biological situations, we need to know how far can a particle randomly walk in a given period of time. We cannot use the average displacement. The particles can move in either a positive or negative direction. So the average displacement will be zero. Summing over all particles:

$$< x(t) >= \frac{1}{N}\sum_{i=1}^{N}[x_i(t-1) \pm \delta] = 0$$

Instead, the root mean square is used, directly from Einstein's result ($D=(1/2)(\Delta^2/\tau)$, which yields the result for one dimension,

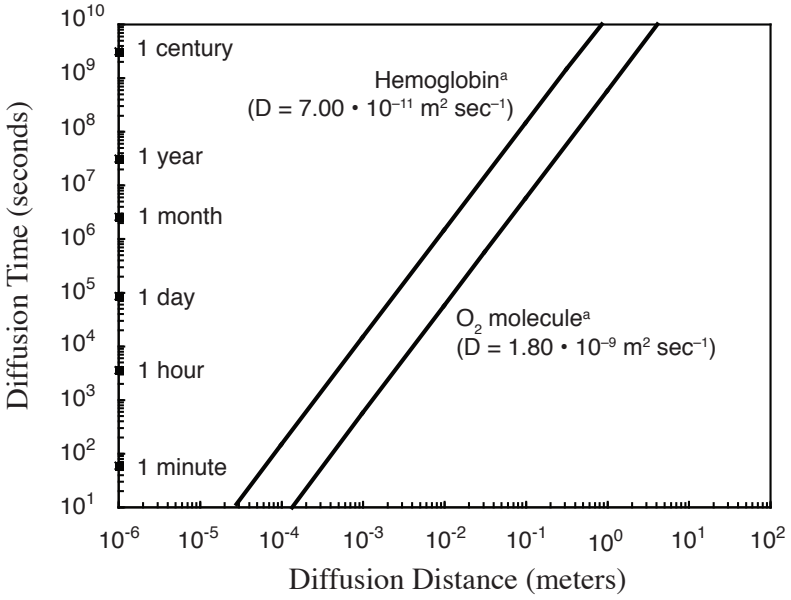
$$< x^2(t) >= 2Dt$$

or, for three dimensions (summing the x, y, and z coordinates):

$$< r^2(t) >= 6Dt$$

Thus, $r = \sqrt{6 \bullet D \bullet t}$

Time versus diffusion distance are shown for real molecules in the graph below.



Diffusion works best at small distances.

[a]Brouwer ST, L Hoof, F Kreuzer (1997) Diffusion coefficients of oxygen and hemoglobin measured by facilitated oxygen diffusion through hemoglobin solutions. Biochim Biophys Acta. 1338:127–136.

$$J = -D\frac{\partial c}{\partial x}$$

So, Fick's First Law of Diffusion has a molecular meaning that explains how flux, J (moles cm^{-2} sec^{-1}) depends upon the concentration gradient ($\partial c/\partial x$)(moles cm^{-4}) and the Diffusion coefficient D (cm^2 sec^{-1}).

But, as we have seen, diffusion is slow, especially for distances greater than about 1 mm. At the scale of multi-cellular organisms, diffusion alone is insufficient. Instead, transport must rely on mass flow:the hydrodynamic movement of nutrients, etc., as a consequence of volume flow.

The term that is used to describe mass transfer of matter (or heat) by the flow of a solution is ADVECTION.

The closely related term CONVECTION refers to the movement of fluid caused by the tendency of hot material to rise. That is, heat-induced flow.

The mathematics of advection are daunting, because in a three-dimensional space, the transport of material will rely on the velocity of the solvating medium (for example, water, the norm for biological systems) in three dimensions:

$$\nabla \mathbf{v} = u\frac{\partial}{\partial x} + v\frac{\partial}{\partial y} + w\frac{\partial}{\partial z}$$

velocity vector
—the notation grad v
is sometimes used

with velocity components, u, v, and w,
in the three dimensions, x, y, and z.

The use of partial derivatives acknowledges that the velocity factors sum across the x, y, and z coordinates, and each must be evaluated while the other two are held constant.

The meaning of the differential equation is clear: The rate of material transfer will depend upon the velocity and flow direction of the solvating medium.

Including mass flow in the flux equation, simplified to one (x) dimension:

$$J_x = -D\frac{\partial c}{\partial x} + v_x \bullet c$$

units: moles cm^{-2} sec^{-1}

$(cm^2\ sec^{-1})(moles\ cm^{-4})$

$(cm\ sec^{-1})(moles\ cm^{-3})$

The relative contributions of diffusive flux and advective flow will depend upon the concentration gradient ($\partial c/\partial x$) (and the Diffusion coefficient), and the velocity v_x (and concentration).

What will cause mass flow, such that $v > 0$?

In a biological organisms, (and the environment in general), the primary driving force for mass flow is pressure. In its simpest form, mass flow J_V is proportional to the pressure gradient:

$$J_v \propto \frac{\partial P}{\partial x} \quad \text{or} \quad J_v = L_p \frac{\partial P}{\partial x}$$

V denotes mass (or volume) flow

the pressure gradient

the hydraulic conductivity

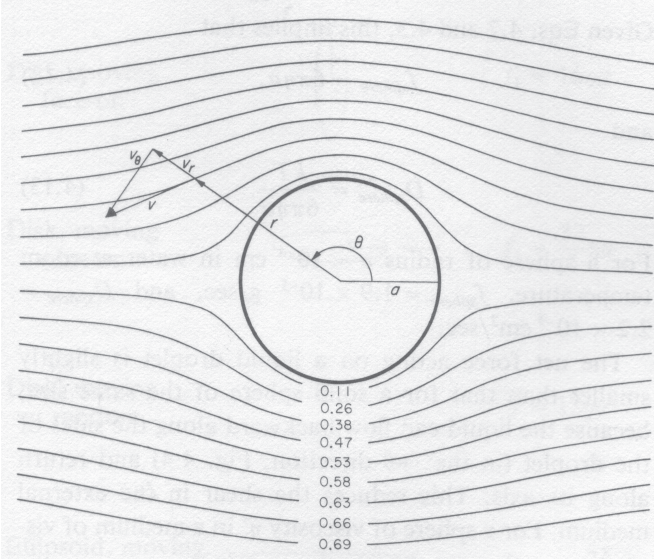
For flow through a pipe (a model for arterial/venal blood flow, or water flow through the xylem vessels of a vascular plant):

$$J_V = -\frac{r^2}{8 \bullet \eta} \bullet \frac{\partial P}{\partial x}$$

The $r^2/8$ term refers to the cylindrical area of the 'pipe'. The term 'nu', η, is the viscosity of the solution.

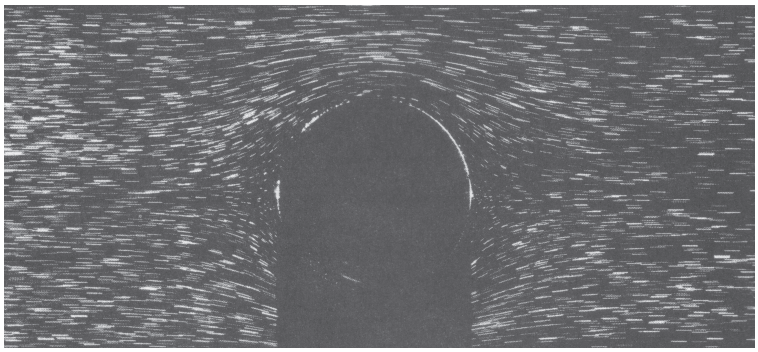
This is known as Poiseuille's Law, and, importantly, assumes that there is no turbulent mixing of the fluid as it flows: no eddies or counterflow, only laminar flow.

It is easier to visualize laminar flow than to explain it:



Although the diagram shows a sphere moving through the solution, movement of solution around the sphere would be very similar (see below). Velocity 'isovelocities' are shown. These 'isovelocities' are for the velocites at $\theta = -90°$, the velocity of displacement perpendicular to the sphere (or volume) flow
Source: Berg HC (1993) Random Walks in Biology. Princeton Univ. Press.

The image to the right documents laminar flow by photographing metal flakes as they flow around an anchored sphere. The Reynolds number is about 0.1.
Source: Nelson P (2004) Biological Physics. WH Freeman.



The 'test' for laminar flow is the Reynolds number, the dimension-less ratio of inertial forces to viscosity:

density (water = 1 gm cm^{-3})
velocity (cm sec^{-1})
tube diameter (cm)

$$R_e = \frac{\rho \bullet v \bullet l}{\eta}$$

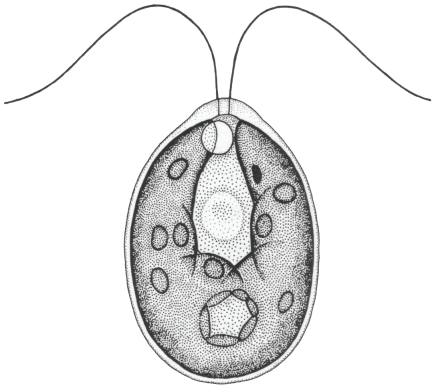
viscosity (water = 0.01 gm cm^{-1} sec^{-1})

The cut-off for turbulent flow in a tube is normally considered to be about 2000[1]. For a sphere in medium, the cut-off is about 1[2].

[1]Source: Nobel PS (1991) Physicochemical and Environmental Plant Physiology. Academic Press. pp.505–513.
[2]Source: Vogel S (1988) Life's Devices. The physical world of animals and plants. Princeton University Press. pp. 127.

So, diffusive fluxes may be slow, so slow that mass flow may be required. We need to characterize this in a biological context. Here begins our first case study: Advective flow around *Volvox* colonies (at Reynolds numbers low enough to avoid the complexities of chaotic turbulent flow)

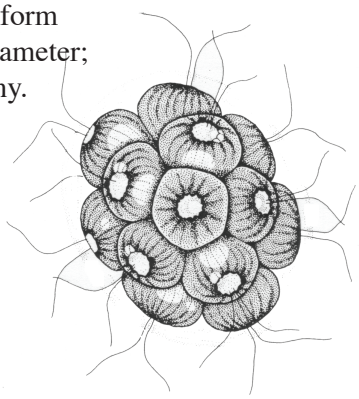
Volvocalean algae are a model system in which the relative significance of diffusive and advective transport can be explored experimentally. The Volvocalean algae exist as either small unicellular algae (for example, *Chlamydomonas reinhardtii*); small (4–64 cells) multi-cellular colonies (for example *Gonium* and *Eudorina*)(in these groups, the cells do not differentiate); and large (1,000–50,000 cells) multi-cellular colonies in which cells are either reproductive (germ cells) or vegetative (”sterile” flagellated cells).

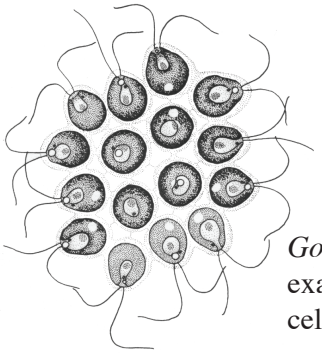


Chlamydomonas, a unicellular example of Volvocalean algae is a typical photosynthetic protist, with a cell length of 15 to 30 μm.

Multi-cellularity, implying coordinated development, represents an increase in complexity in an evolutionary context (and increased organismal size). It arose many times among the Volvocalean algal groups.

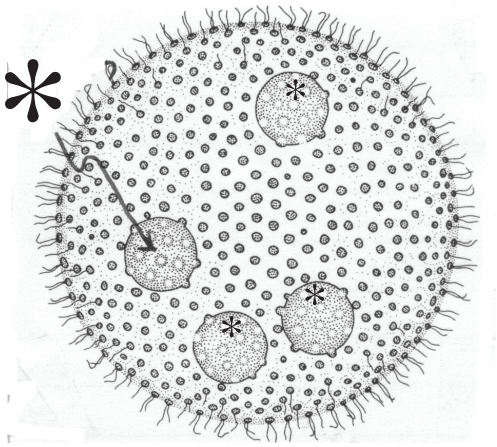
Pandorina is a simpler multi-cellular form (right). Each cell is about 20 μm in diameter; eight or sixteen cells comprise a colony.





Gonium (left) is another example (5 to 15 μm cells).

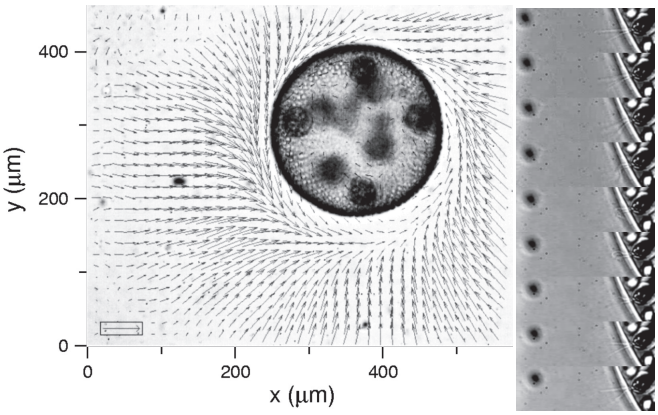
Volvox cells are relatively small (about 10 μm in diameter), but the total number of cells is many (1,000–50,000 cells), creating a large multi-cellular colony up to 1000 μm in diamater. Daughter colonies (*) develop (from the germ/gonidial cells) within the parental colony. In these large many-cell colonies, the cellular differentiation into germ (gonidial) and vegetative cells implies a 'higher' level of evolutionary complexity.



It is worthwhile to emphasize that multicellularity does not appear in a fixed phylogenetic sequence, but exists in divergent Volvocalean genera that are phylogenetically unrelated. Multicellular or not, all the species have survived a very long time.

We have to evaluate diffusive and mass fluxes in the context of nutrient requirements for continued growth of the organism. Nutrient requirements for a photosynthetic organism like *Volvox* include inorganic minerals (especially nitrogen and photphate required for proteins and nucleic acids) and carbon dioxide (to be fixed into carbohydrate by photosynthesis). All will be transported into the colony through the outer 'membrane' of the algae. We need to consider the ability of diffusion and mass flow to supply the outer perimeter of the colony.

Volvox colonies are ideal for such analyses, since they create flow patterns around the colony perimeter (shown as flow vectors in the left panel) due to the coordinated action of out-facing flagella on the peripheral cells (right panel).



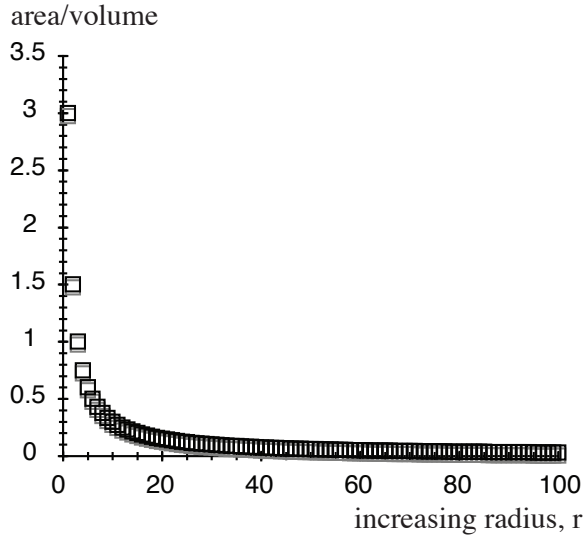
In the multi-cellular forms of the Volvocalean algae, one constraint on transport is the surface area relative to the volume of the colony.

Assuming a spherical shape: $\text{area} = 4 \bullet \pi \bullet r^2$

$$\text{volume} = \frac{4}{3} \bullet \pi \bullet r^3$$

The ratio of area/volume:

$$\frac{4 \bullet \pi \bullet r^2}{\frac{4}{3} \bullet \pi \bullet r^3} = \frac{3}{r}$$

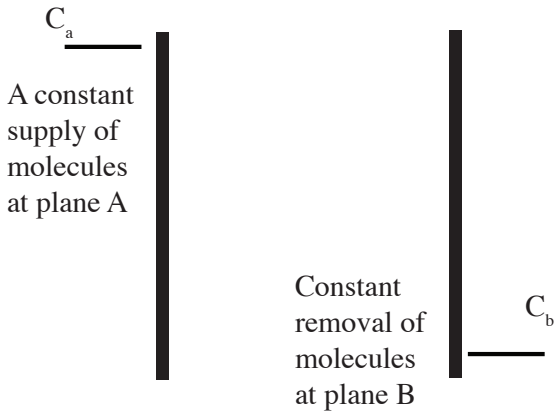


As colony size increases, the surface area available to supply the increasing volume declines precipitously.

Put another way, the metabolic requirements of the cell(s) scales with volume, r^3, but the surface available to supply metabolic requirements only scales as r^2.

We can imagine nutrient molecules 'random walking' in the external medium. Molecules that collide with the colony surface can be taken up to be used for growth of the colony. This is known as *diffusion to capture* at the colony perimeter.

Diffusion to capture can be explored using a simple model that assumes infinite absorptive capacity at the colony perimeter, so that we need consider only diffusive supply:



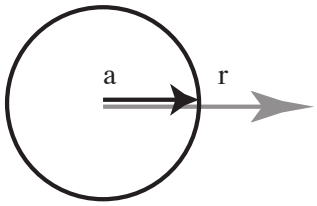
Initially, there will be many molecules at plane A, diffusing away. Then, in the long term, a steady state gradient of molecules will appear, such that $\partial C/\partial x$ is time invariant (that is, $\partial C/\partial t = 0$).

The time dependence (Fick's Second Law) is:

Under steady state conditions, $\partial C/\partial t$ is equal to 'zero', simplifying analysis.

$$\frac{\partial C}{\partial t} = D\frac{\partial^2 C}{\partial x^2}$$

Since Volvox is spherical, we are not interested in $\partial C/\partial x$, but instead $\partial C/\partial r$, where r is the radial distance from the spherical cell.



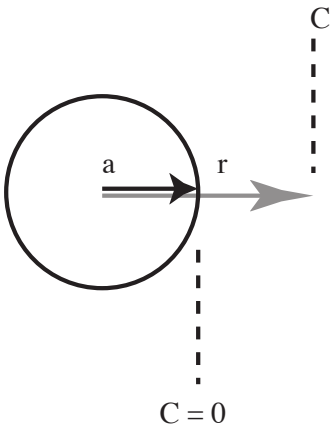
$$\text{Fick's First law : } J_r = -D\frac{\partial C}{\partial r}$$

$$\text{Fick's Second Law : } \frac{\partial C}{\partial t} = D\frac{1}{r^2}\frac{\partial}{\partial r}\left(r^2\frac{\partial C}{\partial r}\right) = 0$$

(steady state)

[1]Berg, HC (1993) Random Walks in Biology. Princeton University Press. pp. 19–27.

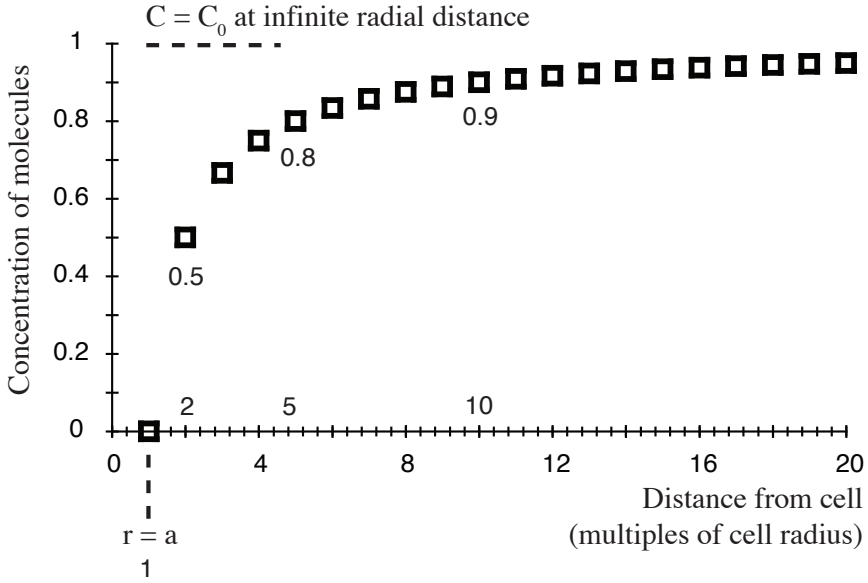
For a spherical (colony) "absorber" of radius a:



With the boundary conditions that C = 0 at the surface of the colony of radius a, and C = C_0 at an 'infinite' distance away, the spatial distribution of molecules, C(r) is:

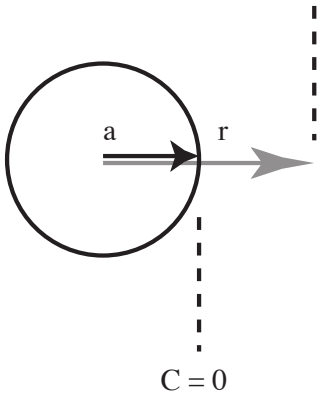
$$C(r) = C_0\left(1 - \frac{a}{r}\right)$$

Graphically:



[1]Berg, HC (1908) Random Walks in Biology. Princeton University Press. pp. 19–27.

The flux for the spherical (colony) is:



$$J_r = -D\left(\frac{\partial C}{\partial r}\right)$$

$$J(r) = -D \bullet C_0\left(\frac{a}{r^2}\right)$$

from $\frac{\partial C}{\partial r}$ of $C_0\left(1-\frac{a}{r}\right) = \frac{\partial C}{\partial r}$ of $C_0 - \frac{C_0 \bullet a}{r}$

$\frac{\partial}{\partial r}C_0 = 0$ and $\frac{\partial}{\partial r}C_0 \bullet a \bullet r^{-1} = C_0 \bullet a \bullet r^{-2}$

On an area basis, from the sphere area equal to $4 \bullet \pi \bullet a^2$, setting r = a and multiplying J(r) by the area:

J(r) = $(D \bullet Co \bullet (a/a^2) \bullet (4 \bullet \pi \bullet a^2)$. Simplifying:

$$J_r(a) = -D \bullet C_0 \bullet 4 \bullet \pi \bullet a = I_D \text{ (diffusive current)}$$

(units of mole sec^{-1})

That is diffusive supply. We now need to consider the metabolic demand of the cell which is dependent on the metabolic rate per unit area of the cell (β):

(mole cm^{-2} sec^{-1})

$$I_m = 4 \bullet \pi \bullet a^2 \bullet \beta \text{ (metabolic current)}$$

(cm^2) (units of mole sec^{-1})

Setting the diffusive and metabolic current equation equal to each other reveals the critical size of the cell, where diffusive currents cannot fulfill the colony's metabolic requirements:

$$I_D = 4 \bullet \pi \bullet a \bullet D \bullet C_0 = 4 \bullet \pi \bullet a^2 \bullet \beta = I_m$$

(cm^2 sec^{-1}) (mole cm^{-3})

$$a_{critical} = \frac{D \bullet C_0}{\beta} \quad \text{(units of cm)}$$

(mole cm^{-2} sec^{-1})

Concentration and metabolic rate both affect the critical size of the colony, as does the diffusion coefficient for the nutrient molecule.

[1]Berg, HC (1993) Random Walks in Biology. Princeton University Press. pp. 19–27.

Now, in the Volvocalean multi-cellular colonies, the flagella extend out into the medium. With coordinated flagellar beating, the colonies are motile, moving either uni-directionally, or sometimes simply spinning in place. Are these advective flows generated by the flagellar beating important in nutrient supply?

To determine the constraints of advective supply on the colony is more complicated than the constraints of diffusive supply.

To the diffusive flux equation $$\frac{\partial \mathrm{C}}{\partial \mathrm{t}} = D\frac{\partial^2 C}{\partial r^2}$$

we need to add another term

$$\frac{\partial \mathrm{C}}{\partial \mathrm{t}} = u \bullet \frac{\partial C}{\partial r} \bullet C + D\frac{\partial^2 C}{\partial r^2}$$

flow velocity; concentration gradient; concentration

Note that this is not completely accurate, since the velocity is a vector that will vary both with distance from the colony and its polar location. Analogously, the concentration gradient may vary as a vector (that is, ∂C/∂x, ∂C/∂y, and ∂C/∂z).

There is a test for the flow rate at which u•(∂c/∂r)•C becomes more important (larger than) diffusive supply, the dimension-less Peclet Number:

where a is the cell radius, u the velocity, and D is the Diffusion coefficient.

$$P_e = \frac{2 \bullet a \bullet u}{D}$$

The leap from the combination of diffusive and advective fluxes to the Peclet Number is not very intuitive.

The terms $u \bullet \frac{\partial C}{\partial r} \bullet C$ and $D\frac{\partial^2 C}{\partial r^2}$ are simplified by considering characteristic velocities and lengths, so that

where U is the characteristic velocity (average fluid velocity), and L is the characteristic length (for example, the diameter of the cell).

$u \bullet \frac{\partial C}{\partial r} \bullet C$ becomes $\frac{U \bullet C}{L}$

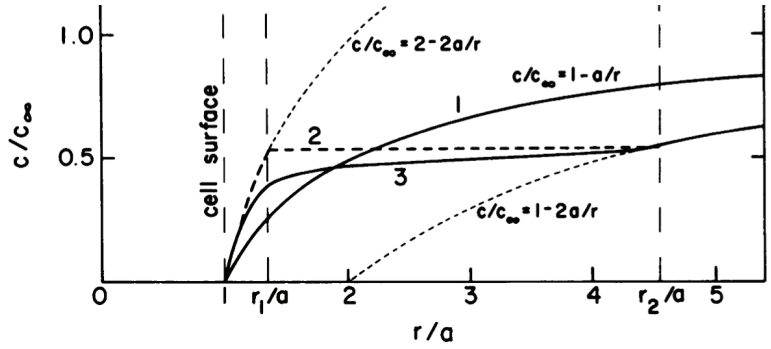
and $D\frac{\partial^2 C}{\partial r^2}$ becomes $\frac{\mathrm{D} \bullet \mathrm{C}}{\mathrm{L}^2}$

The ratio can be simplified $$\frac{\frac{UC}{L}}{\frac{DC}{L^2}} = \frac{UL}{D} = \frac{2 \bullet a \bullet u}{D}$$

For Volvox colonies, the Peclet number is about 100[1]. Advective flow dominates.

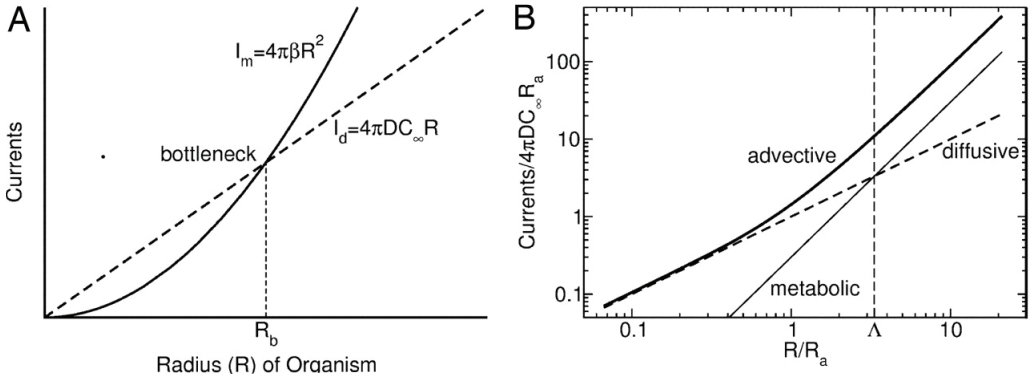
[1]Solari CA, Drescher K, Ganguly S, Kessler JO, Michod RE, Goldstein RE (2011) Flagellar phenotype plasticity in volvocalean algae correlates with Peclet number. J. R. Soc. Interface doi:10.1098/rsif.2011.0023

The relation between advective and diffusive flow may be easier to understand by considering the effect of flow rate on the concentration gradient (C(r)) near the spherical colony and the concept of a bottleneck where diffusive current becomes limiting. Three cases are shown below: (1) Diffusive supply alone. Uptake at the cell is described by $J_0 = 4 \bullet \pi \bullet a \bullet D \bullet C_0$. (2) Infinitely fast stirring between r_1 and r_2, fluid stationary elsewhere; uptake is is $2 \bullet J_0$. (3) Finite stirring speed; region inside r_1 still dominated by diffusion; uptake is $2 \bullet J_0$.



Source: Berg HC and EM Purcell (1977) Physics of chemoreception. Biophysical Journal 20:193–219.

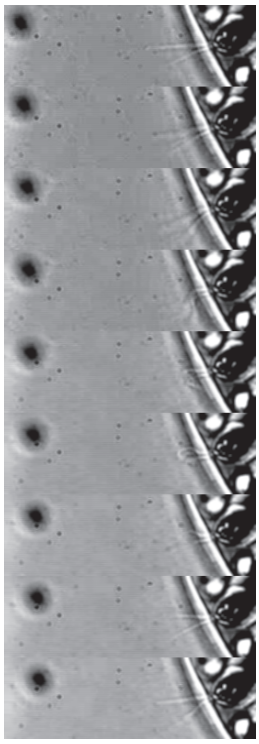
Inter-relation between diffusive supply and metabolic current, and the effect of advective flow.

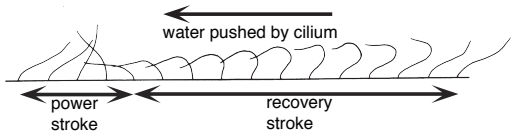


(A) There is a diffusive bottleneck (R_b) when the metabolic demand current (solid line) (quadratic in organism radius R) exceeds the diffusive current (dashed line) (linear in R). Metabolism is constrained by diffusion. (B) The log–log plot shows how the advective current (thick solid line) circumvents the diffusive bottleneck. At radii greater than the advective radius R_a , the advective current grows quadratically with R, allowing metabolic needs to be satisfied for any arbitrary size.

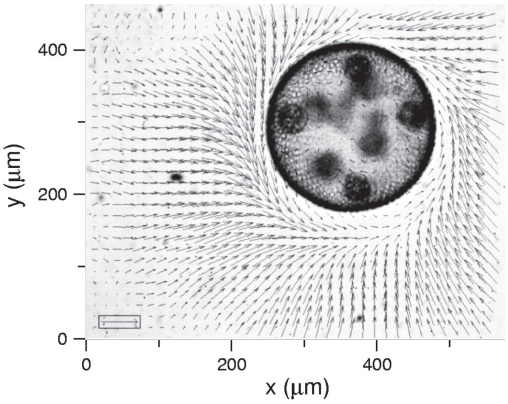
Source: Short MB, CA Solari, S Ganguly, TR Powers, JO Kessler, RE Goldstein (2006) Flows driven by flagella of multicellular organisms enhance long-range molecular transport. Proc. Natl. Acad. Sci. USA 103:8315–8319.

Experimental tests of the relative roles of diffusive and advective fluxes were provided using multi-cellular colonies of *Volvox*. In these colonies, the outer perimeter has flagellated cells which undergo coordinated beating that moves the solution near the cell. The cilia beating pattern is shown to the left. These were obtained from a high-speed video produced by the Goldstein lab ("High-speed movie (125 fps) showing flagella (brightfield)" (http://www.damtp.cam.ac.uk/user/gold/movies.html).

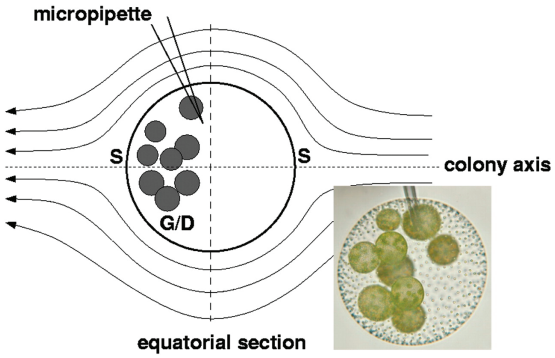




The flow rates are shown (right) as vectors in an x-y plane at a medial location of the Volvox colony.

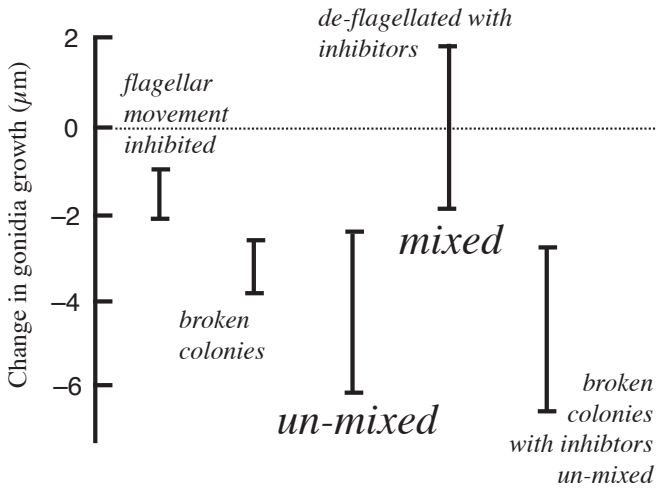


To test for a role of advective flow, the growth of Germ cells /Daughter colonies (marked 'G/D' in the figure) were assessed under various conditions of inhibited flagellar flow, or, as a control, artifically applied advective flow.



Source: Solari CA, Ganguly S, Kessler JO, Michod RE, RE Goldstein (2006) Multicellularity and the functional interdependence of motility and molecular transport. Proc. Natl. Acad. Sci. USA 103:1353-1358.

The data show how gonidia (germ cell) growth is affected by treatments that modify the activity of the flagella that create flow around the colony. The changes in growth are comparisons with normal flagellated colonies in standard medium. DIB results illustrate the restoration of normal growth with artificial bubbling.[1]



Growth of germ (gonidial) cells was unaffected in normal colonies with or without mixing. Inhibiting flagellar beating inhibited gonidial growth somewhat (–1.6±0.6 μm) (the flagellar beating-induced flow can be observed under a microscope with the appropriate optical conditions). De-flagellating the colonies and inhibiting regeneration inhibited growth a great deal (–4.3±1.8 μm), but recovery was complete if the colonies were artificially mixed (–0.0±2.0 μm) (by 'sparging' the cells, that is bubbling air through the solution). Thus, advective flow enhances nutrient supply, enhancing gonidial cell growth.

A cautionary note is in order: Many organisms (some unicellular, most multi-cellular) exceed the critical size limit derived by Short et al. (2006)[2] of about 50-200 μm where diffusive transport becomes limiting. They lack flagellar-induced flow, or any other mechanisms for creating flow around themselves. Even so, they have survived for a long time, 1,500 milllion years or so. The example that comes to mind is Chara, whose internodal cells are cylindrical, about 1000 μm in diameter and 6 cm long. Transport constraints are not a universal constraint on biological form and function.

Even so, it should be clear that flow is important in survival. Organisms have evolved many types of flow-inducing mechanisms —that is, pumps— besides cilia.

[1]Solari CA, S Ganguly, JO Kessler, RE Michod, RE Goldstein (2006) Multicellularity and the functional interdependence of motility and molecular transport. Proc. Natl. Acad. Sci. USA 103:1353–1358.
[2]Short MB, CA Solari, S Ganguly, TR Powers, JO Kessler, RE Goldstein (2006) Flows driven by flagella of multicellular organisms enhance long-range molecular transport. Proc. Natl. Acad. Sci. USA 103:8315–8319.

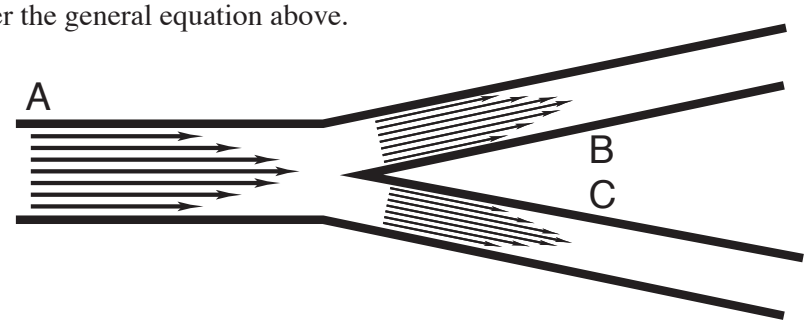
To begin with, we need to introduce a physical description of the nature of pumps. Their function is to move volume. The substance being moved can be any liquid or gas. It can be moved around and about the surroundings, or through pipes. The 'driving force' for volume flow is pressure differences to cause volume displacement. This may not be so intuitively obvious in the case of one example of biological pumping —coordinated waving of cilia causing flow along the surface of the organisms— but is readily described in another example of biological pumping —flow through a pipe (such as arteries and veins of a mammal or xylem of a plant). The general equation for flow through a tube is:

$$Q = \frac{\Delta p}{l}\frac{\pi a^4}{8\eta}$$

We have seen this equation before. It is the Poiseuille equation.

where Q is the volume flow (units of volume per time), $\Delta p/l$ is the pressure gradient, a is the radius of the tube (taken to the fourth power), and η is the viscosity of the fluid. The power (P) is equal to volume flow times pressure: $Q \bullet \Delta p$. Higher volume flows at lower pressure have similar power as smaller volume flows at higher pressure. The units are (m^3 s^{-1}) (Pa), or (m^3 s^{-1}) (N m^{-2}), or N m s^{-1} (joules s^{-1}). This is similar to the better known definition of electrical power: P = I•V (the units are the same: joules s^{-1}, or Watts). Biological pumps exhibit a wide range of volume flows and pressure differences, hence a wide range of powers.

We do need to be mindful of the conservation of mass. In a complex piping network, volume flows have to conform to the requirement that mass (or volume) will be neither destroyed nor appear unexpectedly! A pipe (A) that splits into two branches (B and C) must abide by this conformity: the volume flow through B & C ($Q_{B\&C}$) must be equal to the volume flow through A (Q_A). How this occurs will depend upon the radii of A, B and C per the general equation above.

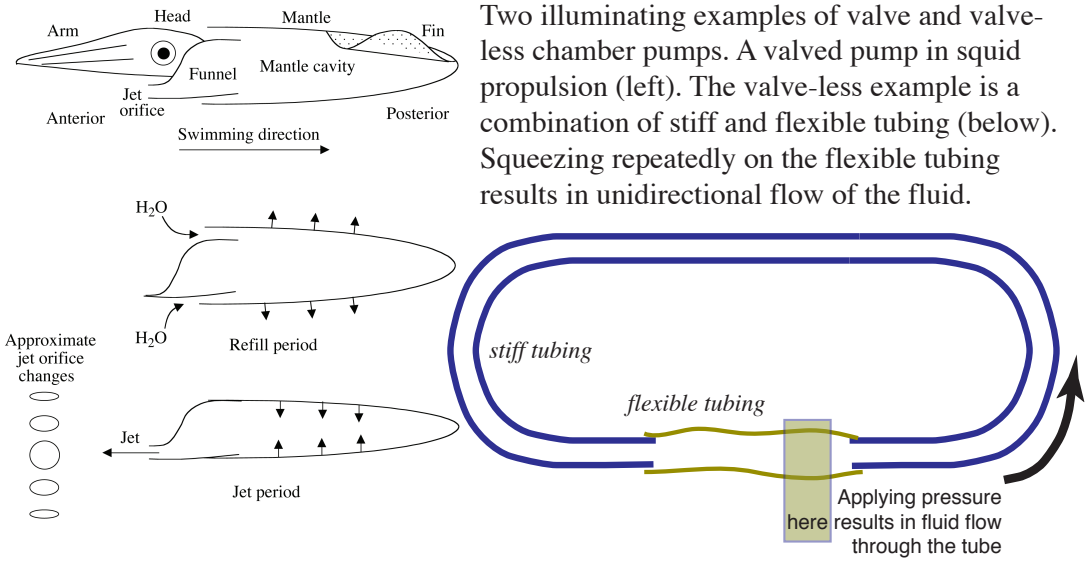


Source: Vogel, Steven (2009) Glimpses of Creatures in their Physical Worlds. Princeton University Press. pp. 184–208.

How does an organism pump fluid? In many different ways. Vogel (2009) notes that most biological pumps are displacement pumps, which use a diverse array of mechanisms to displace fluids resulting in net flow.

Valve and chamber pumps. These are the classic pumping mechanisms of hearts. The volume of a chamber is changed. Net flow is caused by valves that either allow fluid into the chamber (during volume expansion) or out of the chamber (during volume contraction). Some (like our hearts) are multi-chamber / multi-valve, some are simpler designs.

Valve-less chamber pumps. These make sense, if you think about a reciprocating flow, back and forth. It also includes single jet pumps (for example venom injection into an unsuspecting prey….) and pulsing jet pumps of small jellyfish. The jellyfish swim by expanding their bells (slowly) to collect water, then contracting them. The movement of the jellyfish is caused by the relatively rapid expulsion if water during contraction. In larger jellyfish, their muscle strength is insufficient to cause the bell to contract, so they use a rowing motion instead, something that does not quite fit the definition of a pump. Finally, many bloodsucking insects of animals (and the equivalent phloem and xylem sucking insects of plants) rely on valve-less chamber pumps.



Two illuminating examples of valve and valve-less chamber pumps. A valved pump in squid propulsion (left). The valve-less example is a combination of stiff and flexible tubing (below). Squeezing repeatedly on the flexible tubing results in unidirectional flow of the fluid.

Source: Vogel, Steven (2009) Glimpses of Creatures in their Physical Worlds. Princeton University Press. pp. 184–208. Thanks to Andrew Donini for suggesting squid propulsion. The squid diagram is from: Anderson,EJ and Demont ME (2000) The mechanics of locomotion in the squid *Loligo pealei*: Locomotory function and unsteady hydrodynamics of the jet and intramantle pressure. Journal of Experimental Biology 203:2851–2863

Valve-less moving chamber pumps. These are commonly called peristaltic pumps. Examples are our intestines and esophagus, which both rely on muscular contraction that propagates along the tube. For engineers, peristaltic pumps offer the advantage that the fluid is retained within the tube, never coming in contact with the moving contractile component.

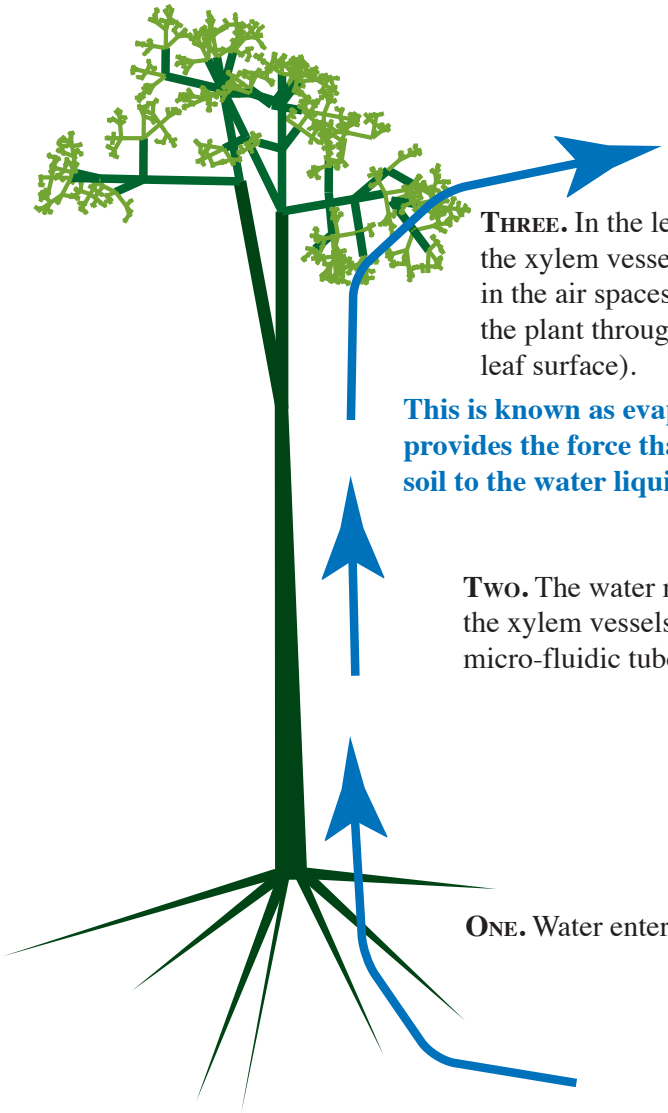
Osmotic pumps. These rely on differences in water potential that are created by accumulating osmotically active solutes. They are more prevalent than one might imagine. Nutrient flow through plant phloem relies upon differences in osmolarity at the sink (high osmolarity) versus the source (low osmolarity). An even more dramatic example is the osmotic pump responsible for generating extremely high pressures (in the range of 2000 kiloPascal) in fungi. The pressure builds within the walled cells. It is the driving force that causes the explosive expulsion of spores due to a releasing mechanism.

Evaporative pumps. Water flow through plant xylem relies upon an evaporative pulling force that 'pulls' the water to the top of the plant (as high as 100 meters in the case of Sequioia). Again the magnitude of the pressure difference is extreme (2000 kiloPascal), but the volume flow is through very small tubes, hence the power ($Q \bullet \Delta p$) is relatively low.

Ciliated pumps. All of the pumps considered so far are displacement pumps, in which fluid is somehow displaced to cause net flow. Ciliated pumps are an example of a fluid dynamic pump (rotary fans are an example of a fluid dynamic pump you would be familiar with at home). Ciliated pumps are common. They occur in our airways to 'pump' mucous out to clear the air passages. They are also found in organisms like the colonial *Volvox* (already described) which uses coordinated cilia movements to create flow around the colony, as we learned earlier in the course notes when we considered diffusive versus advective flow.

Source: Vogel, Steven (2009) Glimpses of Creatures in their Physical Worlds. Princeton University Press. pp. 184–208.

Evaporative pumps. The evaporative pump of plants is covered in the lectures on the HEIGHT OF A TREE. Here, the energetic nature of the pump will be summarized. First, the process is described below.



THREE. In the leaves, the water moves out of the the xylem vessels, is tranformed to water vapor in the air spaces within the leaves, then departs the plant through stomates (small pores in the leaf surface).

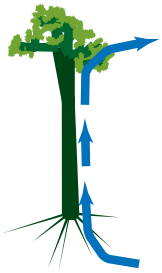
This is known as evapotranspiration, where evaporation provides the force that pulls the strand of water from the soil to the water liquid/vapour interface in the leaf.

TWO. The water moves up the plant through the xylem vessels (50 to 200 μm diameter micro-fluidic tubes).

ONE. Water enters the plant roots from the soil matrix

Source: Nobel, PS (1991) Physicochemical and Environmental Plant Physiology. Academic Press. pp. 473–536.

The energetics are described by the water potential, Ψ. The derivation is usually covered in courses devoted to physical chemistry. Basically, the water potential arises from the chemical potential of species *j* ($\partial G/\partial n_j$).



$$\mu_j = \left(\frac{\partial G}{\partial n_j}\right)_{T,P,E,h,n_i}$$

$$\mu_j^{liquid} = \mu_j^* + RT\ln a_j + \overline{V}_j P + z_j FE + m_j gh$$

Nobel calls this equation "one of the most elegant relations in all of biology" because it is so information-rich, and embodies all the energetic considerations of biological systems. Within the 'grand' equation, three terms are relevant to water transport.

$$RT\ln a_j + \overline{V}_j P + m_j gh$$

gravitational potential

$$a_j = \gamma_j c_j$$

The activity of water (a_j) is the product of the activity coefficient and the concentration of water

$$\overline{V}_j = \left(\frac{\partial V}{\partial n_j}\right)_{n_i,T,P,E,h}$$

The partial molal volume of species j is the incremental increase in volume with the addition of species j. For water, it is 18.0 X 10^{-6} m^3 mol^{-1}.

$$RT\ln a_j = \overline{V}_j \Pi$$

osmotic pressure

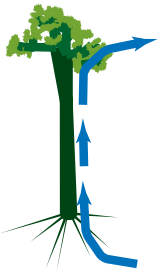
$$\Pi_s = RT\sum_j c_j$$

Van't Hoff relation

The terms inter-relate various properties of water: changes in its activity with the addition of solutes, and the relation to pressure.

Source: Nobel, PS (1991) Physicochemical and Environmental Plant Physiology. Academic Press. pp. 473–536.

The chemical potential for water vapour in the atmosphere is:



$$\mu_w^{vapour} = \frac{RT}{V_w} \ln \frac{P_{wv}}{P_{wv}^*} + \rho_{wv} g h$$

$$\Psi_{wv} = \frac{RT}{V_w} \ln \frac{\%RH}{100}$$

Ignoring the gravitational potential.
RH is the relative humidity

$$\Psi_{wv} = 135 \bullet \ln \frac{\%RH}{100}$$

(in megaPascal)

Two major things have to be considered:

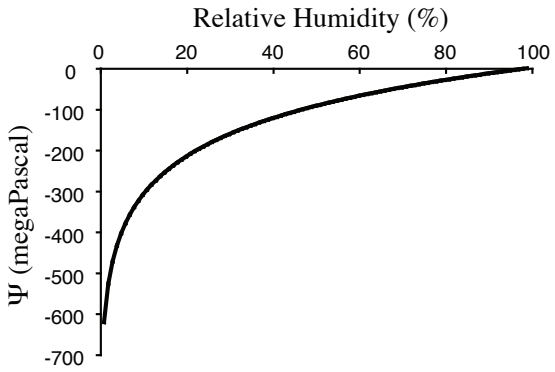
ONE. The height of the water column:

$$\rho_{wv} g h = 1000 \text{ kg m}^{-3}\ 9.81 \text{ m s}^{-2}\ 100 \text{ m} = 0.981 \text{ MPa}$$

(for 100 meter height)

TWO. The 'pulling force provided by evaporation.

The pulling force of evaporation is much greater than the pressure caused by the height of the water column (which the evaporative pull must overcome to draw water out of the top of the tree).



Source: Nobel, PS (1991) Physicochemical and Environmental Plant Physiology. Academic Press. pp. 473–536.

Valve-less chamber pumps. Xylem-sucking insects are an example of an organism that uses a valve-less chamber biological pump. Some of these insects can cause significant damage to the plant. This is especially important for crops. Other insects that feed on blood also use this type of pump, so there is a direct relevance to society and human health.

Xylem-feeding insects are found in the Hemiptera (or Homoptera, depending on the taxonomic authority), and include cercopids, cicadas, and cicadellas, amongst other insect groups. Of these, the cicada is best known. The males have a special sound-producing system causing a humming noise that we commonly hear during the summer months. The 17 year Cicada (Magicicada) is famous for another reason: The nymphs live underground (where they feed by sucking nutrients from xylem cells in plant roots[1]) and only emerge every 17 years in unbelievable numbers as adults. When they emerge the noise can be astonishing. After emergence from the ground, the larvae molt into adults (shedding of their outer integument), littering the ground with the empty exoskeletons. In some regions of North America, the cicada populations from a particular brood are much higher than in ordinary years, so the event of the cicada emergence is very memorable.

During 2004, "Brood X" cicadas emerged in the Virginia/Maryland region. The following quote is from a news article in the Baltimore Sun:

"Cicada song is illegally loud. Brood X's drone measured at more than 90 decibels.

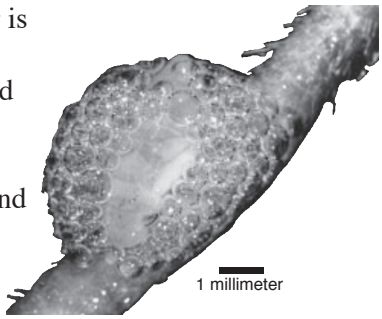
…. Yes, ears are ringing all over Baltimore as male 17-year cicadas from Brood X break their silence -- and, incidentally, a few public noise regulations -- in an earsplitting effort to land a mate.

These high-decibel pleas pack enough sonic punch to overpower lawn mowers, truck traffic and the crackle of walkie-talkies. They're forcing some softball players to holler for pop flies and homeowners to miss phonecalls ..."

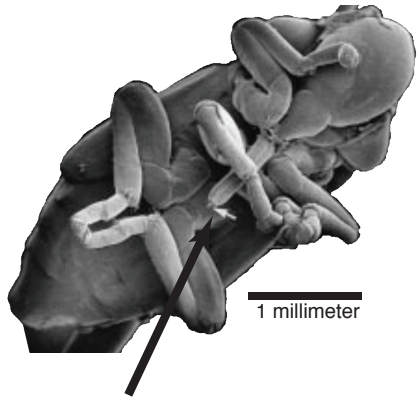
Evidence that cicadas (and other insects) are xylem feeders is based on electron microscopy demonstrating that their stylets penetrate into xylem vessels.

[1]White J, and Strehl CE (1978) Xylem feeding by periodical cicada nymphs on tree roots. Ecological Entomology 3:323–327.

Another example of a xylem feeder that might be familiar is spittlebugs. The nymphs of *Philaenus spumarius* (Cercopidae) feed on xylem aboveground. The xylem fluid contains very little nutrients, so the nymphs must ingest quantities well above their own body weight and secrete most of the water, forming the characteristic 'spittle' around their bodies[1].

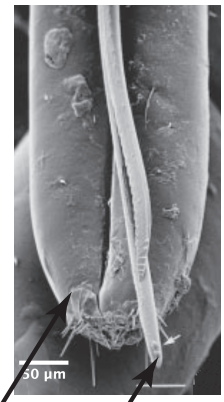


As already noted, to pull water through the narrow xylem tubes to the top of a plant requires negative pressure, created by evaporation of water at the leaves. The suction pressures can be quite dramatic at the top of a tall tree (–3 MPa or so), but are considerably less at lower heights. Even so, the xylem-feeding insects (which are usually found 1 meter above the ground) must be able to pump at a significant negative pressure to feed on xylem sap.



stylet surrounded by the mandibles

To impale the plant and penetrate to a xylem vessel, the spittlebug uses a stylet with a complex anatomy. The stylet is normally encased by mandibles.

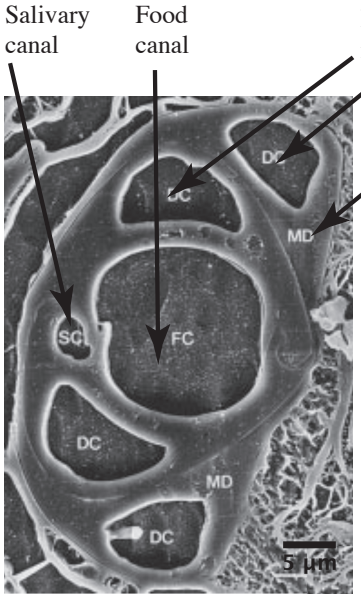


mandible

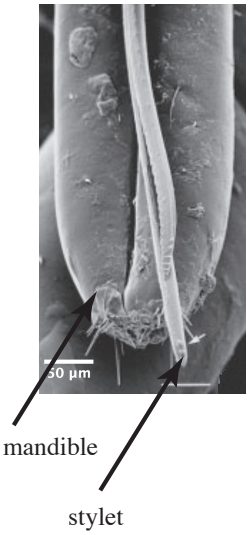
stylet

The anatomy of the mandible and stylet are probably similar for any insects that impale host tissue to feed (for example mosquitoes and the blood-sucking *Rhodnius*). The mandible can be coated with a very tough cuticle to enhance its toughness.

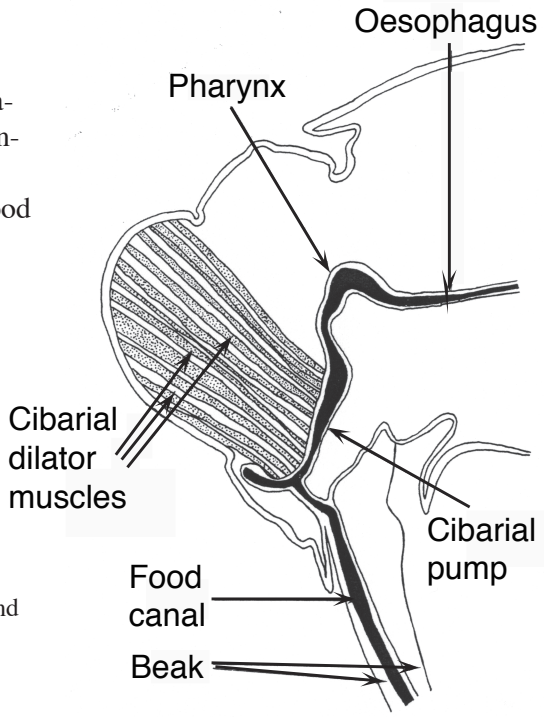
[1]Crews LJ, McCully ME, Canny MJ, Huang CX and Ling LEC (1998) Xylem feeding by spittlebug nymphs: Some observations by optical and cryo-scanning electron microscopy American Journal of Botany 85:449–460.



In cross-section, two pores exist in the stylet. One is the food canal, through which the xylem sap is extracted from the xylem vessel. The other is a salivary canal. The salivary canal secrets saliva which contains a variety of substances depending on species. Presumably this includes lubricants to assist penetration of the tissue, and cement to produce a tight seal[1].



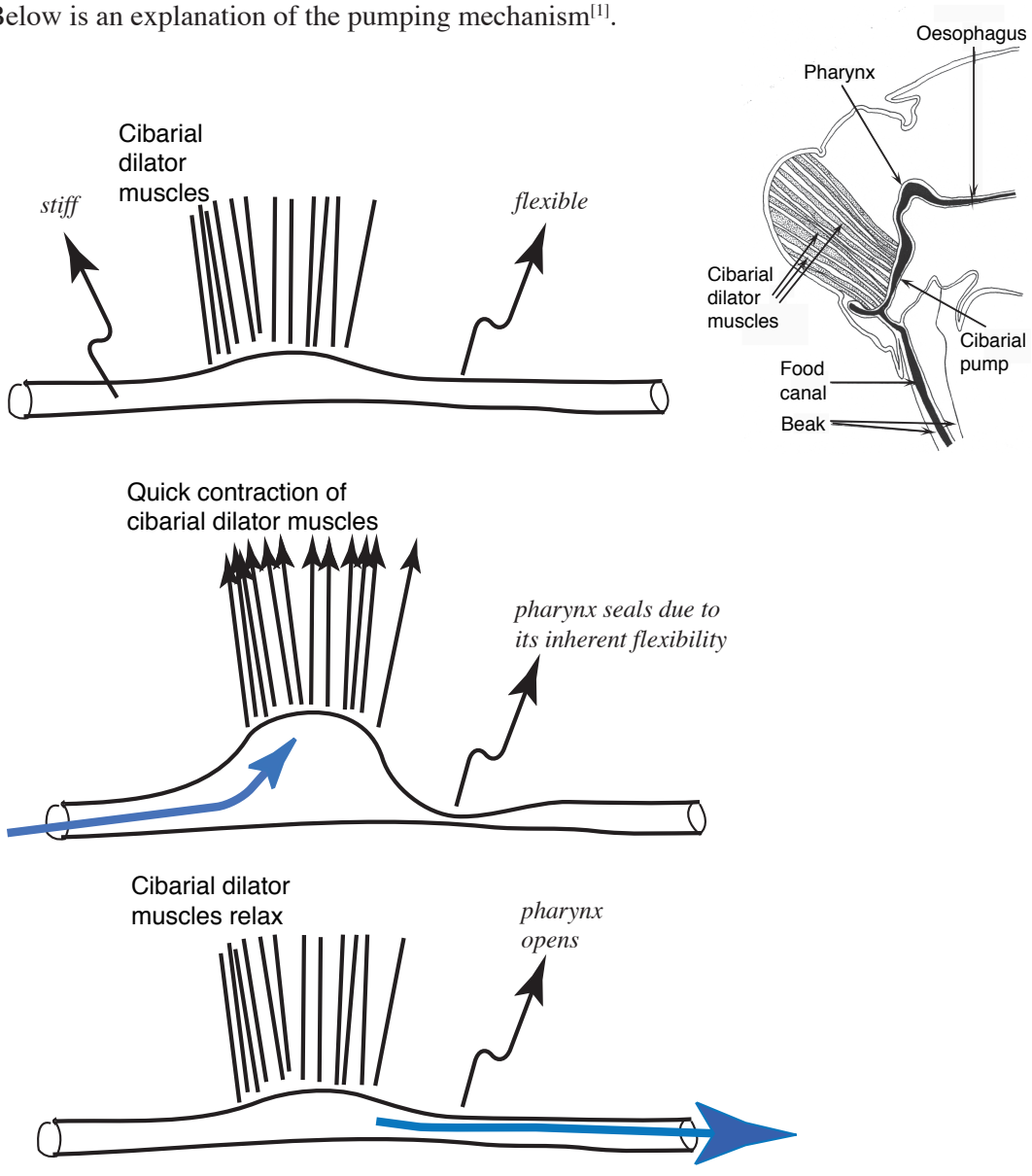
For the pump itself, the example is from cicadas. The pumping action is caused by the contraction of the cibarial muscle, enlarging the cibarial pump chamber to draw sap up the food canal, through the pharynx and into the esophagus[2].



[1]Crews LJ, McCully ME, Canny MJ, Huang CX and Ling LEC (1998) Xylem feeding by spittlebug nymphs: Some observations by optical and cryo-scanning electron microscopy American Journal of Botany 85:449–460.

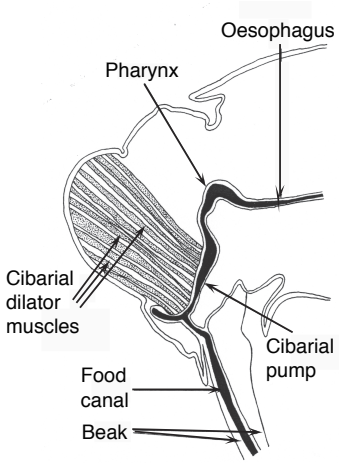
[2]Raven JA (1983) Phytophages of xylem and phloem: a comparison of animal and plant sap-feeders. In MacFadden A and Ford ED (eds) Advances in Ecological Research. Academic Press. pp.136–233.

Below is an explanation of the pumping mechanism[1].



[2]Raven JA (1983) Phytophages of xylem and phloem: a comparison of animal and plant sap-feeders. In MacFadden A and Ford ED (eds) Advances in Ecological Research. Academic Press. pp.136–233.

The energetic details of the pumping mechanism are shown below for *Rhodnius* (a blood sucking insect) and spittlebugs (*Philaenus*)[1].



	Rhodnius	*Philaenus*
Muscle tension (maximum)	600 kPa	600 kPa
Pump stroke frequency	3 Hz	1.7 Hz
Muscle contraction rate (muscle lengths per second)	1 s^{-1}	0.5 s^{-1}
Ratio of muscle/piston	2.5	10.0
Maximum muscle tension	–300 kPa	–2400 kPa

The muscle tension (600 kPa) provides a guide to the ability of the cibarial pump to suck sap from the xylem. The impluse force provided by the slower contraction of the muscle

$$F = ma = m(dv/dt)$$
$$\text{Impulse} = F(\Delta t) = m(\Delta v)$$

and the relative proportion of muscle to the 'piston' (the chamber whose volume increases upon cibarial muscle contraction) 'improve' the suction potential. To a level of –2.4 MPa in the case of *Philaenus*.

Here ends our exploration of diffusion, advection and the evolution of multi-cellular organisms. In no way can the presentation be considered complete! Even so, a picture, albeit hazy, emerges of an understanding of the limitations of diffusion, the need for advective nutrient supply, and the evolution (over 1000 million years) of more and more complex pumping systems that support, are probably obligatory, for the evolution of more complex organismal forms: in both size and shape.

[1]Malone M, Watson R, Pritchard J (1999) The spittlebug *Philaenus spumaris* feeds from mature xylem at the full hydraulic tension of the transpiration stream. New Phytologist 143:261–271.

Stoke's law plays a crucial role in understanding the forces that affect flow, especially at low Reynolds number. The derivation of Stoke's law and its relation to drag —frictional resistance to flow— will be explored in the following[1]. Stokes measured the rate of fall of spheres of various densities in media of various viscosity and found that the rate of fall followed the following relation:

$$\tfrac{2}{9}(\gamma_s - \gamma_f) = \eta v a^{-2}$$

where $(\gamma_s - \gamma_f)$ is the difference in specific weight of the sphere and the displaced fluid, η is the viscosity of the fluid, v is the velocity and a the radius of the sphere. Note that specific weight is equal to the density times the acceleration of gravity.

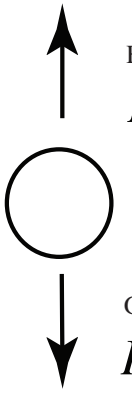
The net gravitational force (F) acting on the sphere as it falls is:

$$F = \tfrac{4}{3}\pi a^3(\gamma_s - \gamma_f)$$

The $(\gamma_s - \gamma_f)$ terms can be eliminated, resulting in the usual description of frictional force for a sphere, known as Stoke's Law:

$(\gamma_s - \gamma_f) = \frac{\eta v a^{-2}}{\frac{2}{9}}$ and $(\gamma_s - \gamma_f) = \frac{F}{\frac{4}{3}\pi a^3}$

$\frac{\eta v a^{-2}}{\frac{2}{9}} = \frac{F}{\frac{4}{3}\pi a^3}$, re-arranging $\frac{\eta v a^{-2}\frac{4}{3}\pi a^3}{\frac{2}{9}} = F$, simplifying $F = 6\pi\eta a v$



Frictional force

$$F_f = 6\pi\eta a v$$

Where the frictional and gravitational forces are balenced, the velocity reaches a steady state.

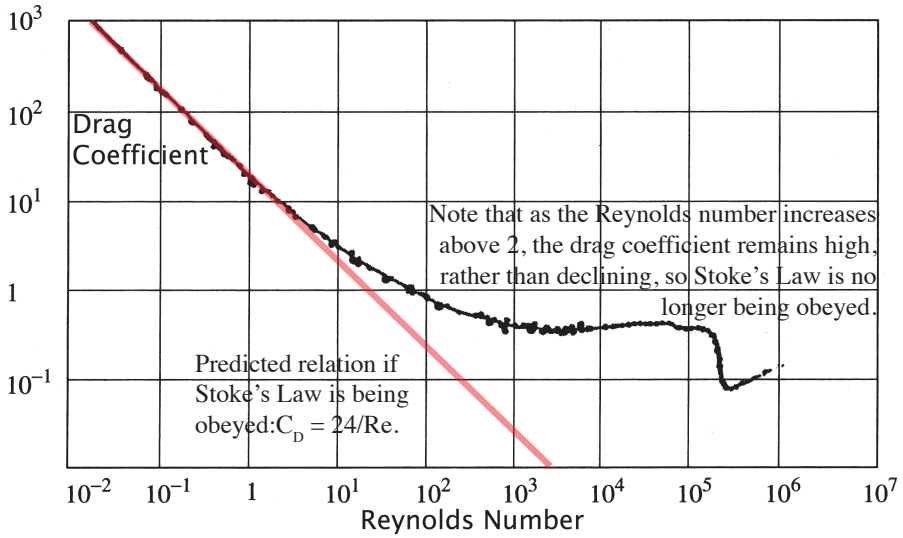
Gravitational pull

$$F_g = \tfrac{4}{3}\pi a^3 \Delta\rho g$$

[1]Dusenbery, David B. (2009) Living at Micro Scale. The unexpected physics of being small. Harvard University Press. pp. 49– 56.

$$F_f = 6\pi\eta a v$$

Stoke's law states that frictional force increases as velocity increases[1]. There is a direct relation between Stoke's Law and the Reynolds number because Re = ($\varrho v l$)/η, where ϱ is the density, v is the velocity, l is the characteristic length and η is the viscosity. Velocity is usually described as a function of the drag coefficient (C_D). The graph below shows the relation between the drag coefficient and the Reynolds number[2]. At low Reynolds number —where Stoke's Law applies— the relation is linear, and predicted by Stoke's Law to be $C_D = 24/Re$. At high Reynolds number ($Re>10^3$), the relation between the drag coefficient and the frictional force is more complex: $C_D = F_f / (0.5\varrho v^2 A)$, where ϱ is the density, v^2 is the velocity squared and A is the frontal area of the object.



We can carry the presentation one step further, focusing on high Reynolds number, and consider the terminal velocity of an object free-falling in air:

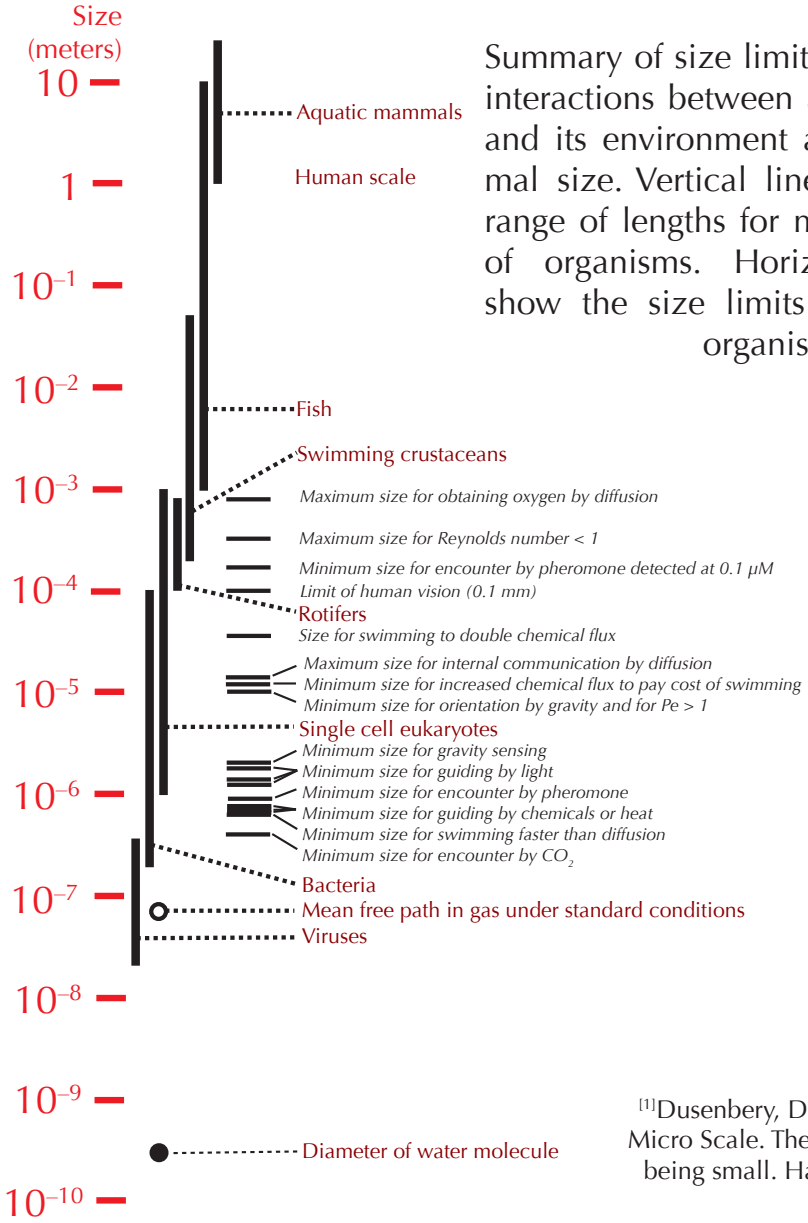
$$V_{\text{terminal}} = \sqrt{\frac{2mg}{\rho A C_D}}$$

Terminal velocity is where the drag force (F_f) is equal to the 'downward' force of gravity (mg). You should be able to assess the terminal velocity at low Reynolds number by the same analytical approach.

[1]Dusenbery, David B. (2009) Living at Micro Scale. The unexpected physics of being small. Harvard University Press. pp. 49– 56.

[2]Barenblatt, G. I. (2003) Scaling. Cambridge University Press. page 41.

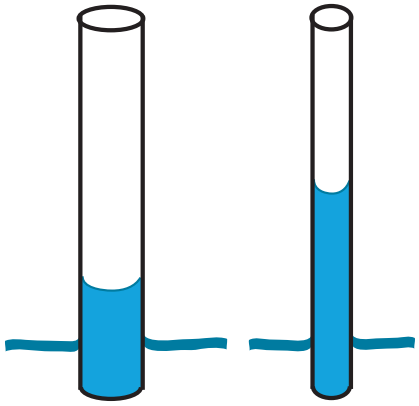
When we deal with organisms, we do have to consider scaling properties in some detail. What works for small organisms won't work for large organisms, and *vice versa*. Dusenbery[1] catalogs a variety of micro-physical limits, not just for transport but for the ability to sense gradients (like pheromones or light). His conclusory diagram is shown below —detailed explanations are provided in his book.



Summary of size limits for various interactions between an organism and its environment and organismal size. Vertical lines show the range of lengths for major groups of organisms. Horizontal lines show the size limits for various organism functions.

[1]Dusenbery, David B. (2009) Living at Micro Scale. The unexpected physics of being small. Harvard University Press. Page 330.

One of the pumping mechanisms we have not explored is capillary transport. Capillarity is easy to invoke, but for a biological organism it is difficult to implement in a practical way. Capillarity is a pulling source created because of the surface tension of water that defies gravity.



The height to which a water column can rise in a capillary depends upon the radius of the tube: the narrower it is, the higher the water will rise.

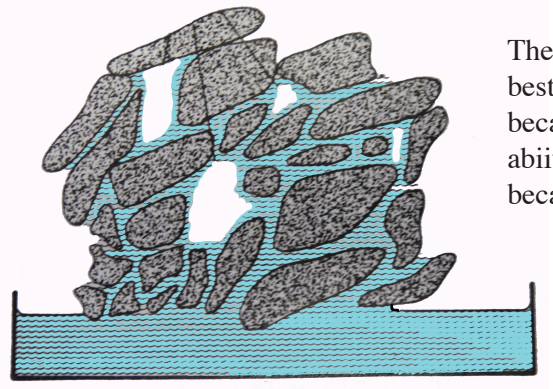
$$h = \frac{2T}{rdg}$$

where h is the height, T is the surface tension, r is the radius of the tube, d is the density and g is the gravity.

But two problems arise.

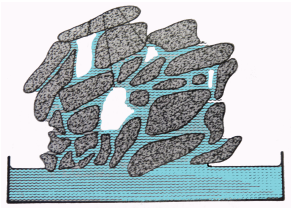
The first is a simple question: How can capillarity be harnessed for transport?

The second has to do with the speed of transport. Consider a well-studied example of capillary movement of water through soil.

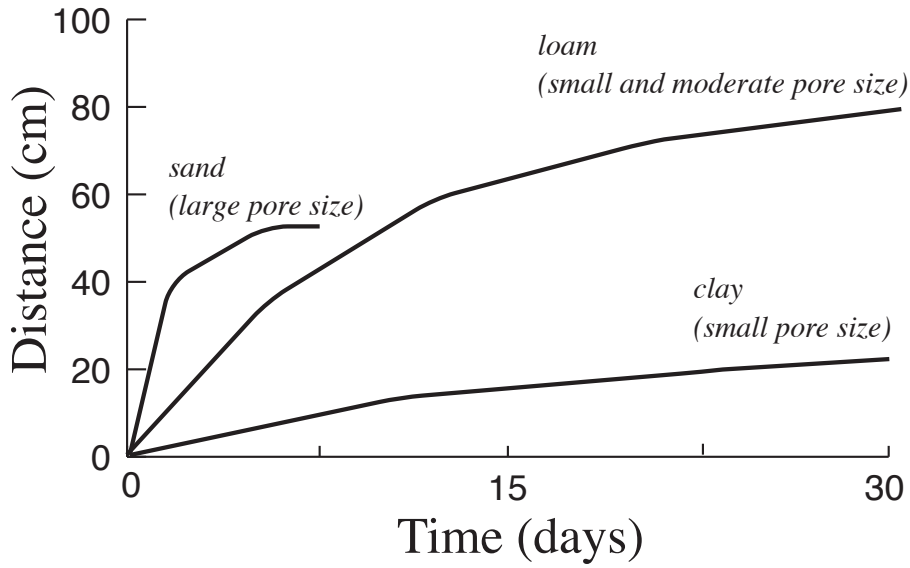


The water traverses a complex matrix, best described as extremely irregular because of the tortuose nature and variabiity in size of the soil pores and because of entrapped air[1].

[1]Brady, Nyle C. (1974) The Nature and Properties of Soill. MacMillan Publishing. Pages 178–181.



Data are available for the height of water and the time it takes to achieve that height for soils of large pore size and small pore size[1].



Clearly, average pore size has an impact, but the even greater issue is the exceedingly long time it takes for soil water to be transported by capillary action[1] (at best, moving only 1 meter in 30 days). Calculating flow velocities would be an appropriate question for an assignment, in the context of water transport in trees or even blood vessels.

[1]Brady, Nyle C. (1974) The Nature and Properties of Soill. MacMillan Publishing. Pages 178–181.