The first cells ever seen were swimming. When Anthony van Leeuwenhoek, in 1674, brought the glass bead that served him as a primitive microscope close to a drop of water taken from a pool close to his home in Delft, he was astounded to observe it full of minute particles darting here and there. Later he wrote: “... the motion of these animalcules in the water was so swift and various, upwards, downwards and round about, that 'twas wonderful to see ....” The organisms he saw were probably ciliated protozoa, each a single cell a few tenths of a millimeter in length, swimming by the agitated, but coordinated motion of thousands of hairlike cilia on their surface. The motion of such cells is so obviously directed and purposeful that van Leeuwenhoek knew it could only come from some living creature and not specks of inanimate matter.

Today, with the power and convenience of modern microscopes, we can visualize in rich detail the abundant variety of living cells, each capable of independent, directed motion through water. Sperm cells swim with a characteristic wriggling motion due to their long whiplike tails, or flagella. They often travel large distances to find an egg of the same species to fertilize, especially in aquatic species such as sea urchins. A huge menagerie of different kinds of protozoa exists including the ciliates seen by van Leeuwenhoek. Many of these swim with cilia and/or flagella, searching endlessly for food or a mate. Even minute bacteria, less than 2 μm long, are capable of moving rapidly through water with a fishlike undulating motion.

How do cells swim, and why? These questions, in various forms and at different levels of enquiry, reoccur throughout this book. In this first chapter, we start by presenting information that is visible in the light microscope, surveying the types of cells that swim and their means of propulsion. We begin by discussing some of the special problems encountered by cells traveling through water because of their minute size.

A cell suspended in water moves passively by diffusion

Because cells are so small, they encounter different physical problems when moving through water than fish or other aquatic animals. The progress of a cell through water is dominated by the viscosity of its environment; inertia, which carries a salmon or an otter forward, plays a negligible part. As for a human swimmer in a bath of honey, a cell moves
through water by using a rowing or swimming action in which viscous resistance to the backward stroke is greater than viscous resistance to the forward stroke. It follows from the principle of action and reaction that swimming cells continually push backward against the surrounding water. Usually, this is accomplished by the repetitive beating of minute surface appendages. We will see below that these appendages, called cilia and flagella, encounter greater viscous resistance when they move backward than when they move forward.

Even without cilia and flagella, however, a cell suspended in water moves passively by diffusion. Like any other particle of similar size, a cell in water is pushed first one way and then the other by the thermal motion of surrounding molecules. Since chaotic thermal motion is an ever-present factor for all objects in solution, including objects within the cytoplasm as well as cells themselves, it is useful here to summarize its physical basis.

The speed of the cell undergoing such Brownian movements is directly related to its size. The average kinetic energy of any molecular or small particle suspended in liquid is given by \( kT/2 \), where \( k \) is the Boltzmann constant and \( T \) is the absolute temperature.\(^1\) The instantaneous velocity of such a particle will change frequently as it bumps into another molecule or particle, but its average can be calculated by relating the average energy, as expressed above with temperature, and the equation for kinetic energy of any moving body: \( Mv^2/2 \), where \( M \) is the mass (kg) and \( v \) its linear velocity (m/sec) in any direction. Equating these two expressions of energy, we find:

\[
Mv^2/2 = kT/2 \quad \text{or} \quad v = (kT/M)^{1/2}
\]

Using this simple equation we can calculate that at room temperature the instantaneous speed of a protein molecule will be about 10 m/sec, whereas for a cell the size of a bacterium it will be of the order of 1 mm/sec.

Neither a molecule nor a cell will travel at this speed very far before it bumps into a water molecule and changes both its direction and speed. The continual bombardment by surrounding molecules means that a cell undergoes a random walk, wandering over an ever longer and more tortuous path. In Figure 1-1, for example, the positions of a particle about 1 \( \mu \)m in diameter suspended in water is shown every 30 seconds. The trace of this particle is marked by a succession of straight lines, but if the measurements had been made at intervals of one second instead of 30 seconds, then each straight line segment in the figure would have to be replaced by a series of 30 smaller segments in a path just as tortuous as the one shown ... and so on, at smaller and smaller dimensions. In fact, it can be calculated that in order to measure the true steps of such a particle, one would have to take measurements at less than a microsecond and over distances less than a nanometer (10\(^{-9}\) m).

Brownian movements are random and we cannot predict precisely where the cell will be at any time. But if many cells were to start out from the same point, then we would be able to say what their average distribution would be at different times (equivalently, we could calculate the probability that any one cell would be in a particular location after a given time).

**Diffusion is ineffective over large distances**

The distribution of diffusing particles (or cells, or molecules) in solution conforms to precisely defined spatial and temporal laws. These were first expressed mathematically in 1855 by the physiologist Adolf Fick, who adopted a set of differential equations already in use for the diffusive spread of heat in a solid. Fick's first law of diffusion says that the rate of diffusion of particles from one point to another is proportional to the difference in concentration of the particles between the two points. That is

\[
J_x = -D \frac{dN}{dx}
\]

\( J_x \) is the net flux of particles in the x-direction. The constant \( D \) is the diffusion coefficient.
Figure 1-2 One-dimensional random walk. (a) At each step the cell has an equal chance of moving to the left or the right a distance $\alpha$. If the distance of the cell from its starting point after $n$ steps is $r_n$, then

$$r_n = r_{n-1} \pm \alpha$$

squared this gives

$$r_n^2 = r_{n-1}^2 + 2\alpha r_{n-1} + \alpha^2$$

and

$$r_n^2 = r_{n-1}^2 - 2\alpha r_{n-1} + \alpha^2$$

If we average these two values of $r_n^2$ over a large population of similar cells, the terms $\pm 2\alpha r_{n-1}$ cancel (because steps to the left and right are equal in number), giving the mean square displacement

$$\langle r_n^2 \rangle = \langle r_{n-1}^2 \rangle + \alpha^2$$

Since all cells start at point zero, $\langle r_0^2 \rangle = 0; \quad \langle r_1^2 \rangle = \alpha^2; \quad \langle r_2^2 \rangle = 2\alpha^2; \quad \langle r_3^2 \rangle = 3\alpha^2$

and so on. In other words, the mean square displacement $\langle r_n^2 \rangle$ increases linearly with the number of steps, $n$, and hence with the elapsed time. That is

$$\langle r_n^2 \rangle = \text{constant} \times \text{time}$$

(b) Spreading of a population of cells undergoing a one-dimensional walk. Probability distributions at three times after commencing the random walk described in the text. The root mean square displacement (white bars) increases as the square root of time.

where $J$ is the flux of particles (the number passing through a window of unit area unit time); $N$ is the number of particles per unit volume, $x$ is the distance, so $\frac{dN}{dx}$

is the concentration gradient. The constant $D$, known as the diffusion constant, depends on the size of the particle, its shape and other factors.

Fick's law says nothing about the origins of the force driving the molecules. There is, however, an alternative description of diffusion that is more closely tied to the physical reality of the situation. This description, given by Albert Einstein in 1905, attributes diffusion to the thermal (Brownian) motions of the particles that cause them to undergo the random walk described above.

To illustrate this second approach to diffusion, consider a population of particles constrained to move along a linear track (Figure 1-2a). All of the particles start at the same initial point and then individually random steps either to the right or to the left. As time passes and more steps are taken, the particles will on average travel farther and farther from their starting point. However, the probability of a step to the right is equal to that of a step to the left, so on average the particles go nowhere! The result of many such steps by many particles is, on average, a bell-shaped distribution that becomes broader with time (Figure 1-2b).

A convenient measure of this spreading tendency is the mean square displacement of the particles $\langle r^2 \rangle$, which is always positive, a linear function of the duration of the random walk. That is

$$\langle r^2 \rangle = \text{constant} \times \text{time}$$

or, as it is usually written,

$$\langle r^2 \rangle = 2 Dt$$

where $t$ is the time elapsed and $D$ is the diffusion constant already mentioned. In one dimension $\langle r^2 \rangle = 2 Dt$ as shown; in two dimensions $\langle r^2 \rangle = 4Dt$ and in three dimensions $\langle r^2 \rangle = 6Dt$. Typical values of $D$, together with the average time taken to diffuse specific distances, are given in Table 1-1 for molecules, organelles and cells.

---

\[1\] Boltzmann's constant, $k$, has a value of $1.38 \times 10^{-16}$ erg/degree. $kT$ at room temperature is around $4 \times 10^{-14}$ erg, or $4 \times 10^{-14}$ g cm$^2$/sec$^2$. A typical protein molecule (with molecular weight 30,000) has a mass of $5 \times 10^{-20}$ g. A typical bacterium has a mass of $10^{-12}$ g.
Table 1-1 Diffusion times in water

<table>
<thead>
<tr>
<th></th>
<th>Diffusion coefficient cm²/sec</th>
<th>Typical time taken to diffuse</th>
<th>1 µm</th>
<th>10 µm</th>
<th>1 mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>small molecule</td>
<td>(5 \times 10^{-6})</td>
<td></td>
<td>1 msec</td>
<td>0.1 sec</td>
<td>15 min</td>
</tr>
<tr>
<td>protein molecule</td>
<td>(5 \times 10^{-7})</td>
<td></td>
<td>10 msec</td>
<td>1 sec</td>
<td>3 hr</td>
</tr>
<tr>
<td>virus particle</td>
<td>(5 \times 10^{-8})</td>
<td></td>
<td>0.1 sec</td>
<td>10 sec</td>
<td>1 day</td>
</tr>
<tr>
<td>bacterial cell</td>
<td>(5 \times 10^{-9})</td>
<td></td>
<td>1 sec</td>
<td>100 sec</td>
<td>10 days</td>
</tr>
<tr>
<td>animal cell</td>
<td>(5 \times 10^{-10})</td>
<td></td>
<td>10 sec</td>
<td>20 min</td>
<td>100 days</td>
</tr>
</tbody>
</table>

Approximate values are given solely to indicate the magnitudes involved. The times are calculated for three-dimensional diffusion and represent the average, or root mean square displacement, of the population (see Figure 1-2). For sources see Hille (1992), Berg (1993), and Atkins (1994).

Note that according to the above equations—and also as shown in Table 1-1—the average distance traveled by diffusion is proportional to the square root of the time elapsed. Short distances are traveled rapidly; long distances much more slowly. It takes 100 times as long for a cell to wander 10 times farther.

Brownian movement and diffusion are relevant not only to the movement of individual cells suspended in water. We shall see in later chapters that they are also important in understanding the movements of molecules inside cells. On the molecular scale, the interior of a living cell is a place of ceaseless motion due to the agitated thermal motion of small and larger molecules.

The movement of cells through water is governed by viscous forces

Brownian movements are aimless and provide no net motion in a particular direction. They are consequently an inefficient way to travel toward a source of food or away from a noxious stimulus. Not surprisingly, therefore, many cells have evolved special structures that drive them purposefully through the surrounding water. As they swim, such cells encounter two kinds of resistance to forward motion. There is a viscous drag which is a frictional resistance, and there is an inertial resistance of the fluid that must be displaced, a function of the density of the fluid. The relative importance of inertial and viscous forces is expressed in a dimensionless constant, termed the Reynolds number (Re). As a rough guide, an Re greater than 100 signifies that resistance to movements is mainly inertial whereas an Re less than 0.001 means that movement is governed largely by viscous forces. We will see shortly that the Re for single cells is extremely small.

The Reynolds number was originally determined by studying the passage of water down a long pipe. At low Re the fluid flows smoothly, following the contours of the obstacle, but as Re increases small vortices develop. These are at first stationary with respect to the obstacle but at higher Re they are shed periodically. At very large Re fluid movements downstream of the obstacle become chaotic.

![laminar flow](image1)
laminar flow

![vortices form and are maintained](image2)
vortices form and are maintained

![vortices form and are periodically shed](image3)
vortices form and are periodically shed

Figure 1-3 Fluid flow at different Reynolds number (Re). At low Re the fluid flows smoothly, following the contours of the obstacle, but as Re increases small vortices develop. These are at first stationary with respect to the obstacle but at higher Re they are shed periodically. At very large Re fluid movements downstream of the obstacle become chaotic.

When used to describe a swimming organism, the Reynolds number depends on the size (average diameter) of the organism \(L\) and its velocity \(v\) as well as the density \(\rho\) and viscosity \(\eta\) of the liquid:

\[
Re = \frac{vL^2 \rho}{\eta v L \eta} = \frac{vL^2 \rho}{\eta v L \eta} = \frac{vL^2 \rho}{\eta v L \eta}
\]

This equation indicates that for a large body (large \(L\)), the Reynolds number is also likely to be large. The value of Re for a swimming mackerel, about \(10^5\), indicates that the progression of this organism through water
Figure 1-4 Jet propulsion at low Reynolds number. (a) An organism such as a scallop that works at large Reynolds number can propel itself by slowly opening and then suddenly shutting the two halves of its shell. By periodically ejecting spurts of water, the organism makes net progress. (b) A hypothetical microscopic bivalve the size of a single cell that tried to operate at low Reynolds number could not swim by such a mechanism. Viscous drag would bring the organism back to its starting point after each slow opening.

is governed principally by inertia: a mackerel propels itself mainly by accelerating water. On the other hand, a very small body, like a single cell will have a very small Reynolds number: for a protozoan 100 μm long, swimming through water at top speed, Re might be around $10^{-3}$ and for a 1 μm long bacterium around $10^{-5}$. In such cases, viscous forces dominate motion.

Because they move at low Reynolds number, cells find no advantage in having a streamlined shape. The smooth contours of an airplane or racing car are needed to reduce drag in an inertial flow situation by reducing turbulence. Cells do not create turbulence and need not be streamlined. Secondly, any thoughts of jet propulsion as a means of locomotion for cells can be rejected. A microorganism that tried to move like a scallop or jellyfish, by slowly filling a chamber with water and then rapidly expelling the water in a jet, would get nowhere (Figure 1-4). Jet propulsion works well in inertial situations but is extremely inefficient when the flow of liquid is entirely laminar.

In fact, most swimming cells are propelled through water by the repetitive movement of hairlike cilia or flagella, the movements of which are governed by viscosity. A typical cilium that is 0.2 μm in diameter and projects 10–20 μm from the surface of a cell will have no more tendency to continue motion when its driving force is removed than a bamboo stick in tar. Consequently a cilium can propel a cell only by altering its shape in a cyclical fashion, maximizing viscous resistance in one direction (during its ‘power stroke’) and minimizing viscous resistance in the other ‘recovery stroke.’ In other words, cilia propel cells by viscous shear. The same is true of flagella: if the flagella on the surface of a bacterium were instantaneously arrested, for example, inertia would carry the cell a distance of less than 0.01 nm—less than one-tenth the diameter of a hydrogen atom!

Swimming consumes only a small fraction of the cell’s energy

The power required to propel a cell in water is quite small. It may be calculated as the viscous drag multiplied by the velocity. For a spherical cell

$$\text{power} = (3\pi \eta L v) \times v$$

where $\eta$ is the viscosity of water ($10^{-2}$ g/(cm·sec)), $L$ the length (or diameter) of cell, and $v$ its velocity. Thus, if the cell has a radius of 1 μm and is traveling at 10 μm/sec, the power consumed is $2 \times 10^{-11}$ erg/sec ($2 \times 10^{-18}$ J/sec).

What is this power requirement in terms of ATP molecules, the principal currency of energy in the cell? Hydrolysis of one gram-molecule of ATP (about 500 g) releases about 40 kJ of useful energy; hydrolysis of a single ATP molecule releases about $10^{-19}$ J. The cell in the above calculation therefore must split about 20 molecules of ATP every second in order to maintain its speed of 10 μm/sec. If we assume a plausibly low efficiency such as 2%, then the ATP hydrolysis required for swimming might be 1000 molecules per second. Although this sounds a large number at first hearing, in fact it is very small compared to the total expenditure of
energy by the cell: the metabolic rate of a typical cell is around $10^7$ ATP molecules per second. Evidently, swimming per se is not a major energy cost—although building the apparatus that drives swimming could be expensive.

**Bacteria swim by means of flagella**

A powerful advantage is gained by any single-cell organism that can move more rapidly than its competitors toward a source of food or away from a potentially harmful environment. Bacteria, with characteristic versatility, have evolved a rich variety of mechanisms for this purpose. Species of bacteria are known that are attracted, or in some cases repelled, by sugars, amino acids, metal ions, extremes of temperature, pH, oxygen, light, hyper- or hypo-osmotic solutions, and magnetic fields. In some cases movement is achieved by indirect or passive means, as in the myriad small organisms that float to the ocean surface by developing small gas vacuoles in their cytoplasm, or that glide slowly over surfaces by the secretion of viscous slime. But the most common and effective mode of transport is provided by bacterial flagella.

The swimming of a single bacterial cell of a species such as *Escherichia coli* (the common intestinal bacterium) or *Salmonella typhimurium* is impressively rapid. Although the cell itself is only about 2 μm long, it swims at speeds of 20–30 μm per second following an undulating path, like a small fish swimming against the current. Careful analysis of the motion reveals that a swimming bacterium alternates rapidly between two swimming modes: smooth swimming, during which it progresses in a roughly constant direction for a second or so, interrupted by brief periods of tumbling during which it changes its direction in a highly erratic manner (Figure 1.5).

The meandering path that results from this kind of swimming differs fundamentally from Brownian motion. First, the distance traveled in a given time is much greater than that traveled by a bacterium carried passively by thermal motion. This is because a swimming bacterium will travel in one direction for a second or more, whereas a bacterium undergoing thermal motion changes direction every few nanoseconds. Second, although the track of a swimming bacterial cell appears aimless, it can, unlike a cell exhibiting Brownian motion, be influenced by its local chemical or physical environment. As we shall describe in Chapter 3, a bacterium that senses it is approaching a source of nutrient is less likely to undergo a tumble, and hence is less likely to change its current direction of travel. This is enough to ensure that over the course of many runs and tumbles the bacterium moves toward the distant source.

The structures that drive a bacterium become visible if the cell is illuminated by a very intense light and viewed against a dark background. Fine threadlike flagella can then be seen streaming from the cell (Figure 1.6). The flagella are seen even more clearly if the viscosity of the medium is

---

**Figure 1-5** Bacterial swimming.

(a) Schematic diagram of *Escherichia coli* swimming. The cell body is a cylinder about 2 μm long and 0.5 μm in diameter and has 6–10 flagella on its surface, each up to 10 μm in length. Coordinated rotation of flagella drives the cell at speeds of about 30 μm/sec through water. (b) Under normal conditions, the bacterium alternates between periods of smooth swimming ("runs") and intermittent chaotic changes in direction ("tumbles").
increased by adding a substance such as methylcellulose. This slows the movements of the cell to the extent that the flagella can be seen to form visible sinusoidal waves that appear to travel backward from the cell.

The higher resolution available in a scanning electron microscope shows the propulsive unit of a bacterium to consist of a bundle of flagella, each a thread about 14 nm in diameter and 10 μm long. In *Escherichia coli*, 6–10 flagella emerge from random points on the side of the body and extend into the surrounding medium. When the cell is swimming smoothly, the flagella collect into a smoothly undulating bundle that drives the cell along (see Figure 1-6).

**Bacterial flagella are rigid helical structures that rotate**

The cilia and flagella of sperm cells and protozoa are autonomously active structures that propagate bending waves from their base to the tip. Bacterial flagella are smaller and more rigid structures that are rotated by a minute motor in the bacterial cell wall. This was first demonstrated by observing bacteria tethered to a glass slide (or to each other) by treatment with specific antisera. Cells prevented from swimming by this strategy rotate about the point of attachment, continually switching from a counterclockwise to a clockwise direction and then back again (Figure 1-7). Similar behavior was also shown by nonmotile mutant bacteria that lacked flagella, or in which the flagella were straight rather than helical. Experiments such as these demonstrated that the flagella must be turned by a structure at their base—a rotary motor embedded in the cell wall. A detailed description of this motor and its mode of action is given in Chapter 16.

At first sight, a rotating flagellum seems a poor design—a propeller of this shape would indeed be a very inefficient way to drive a submarine. But we must remember the relative importance of viscosity for microorganisms. If each segment of the flagellum is thought of as a short cylindrical rod, then it is clear that this rod will encounter less viscous resistance if it moves end-first rather than sideways through the water (Figure 1-8). Rotating the flagellum will push each rodlike segment in a circular path about the long axis of the flagellum. But each segment will encounter a resistance to motion due to viscosity that will be least if it moves end-first. The net result (summing all of the small rodlike segments together into a helical structure) is motion parallel to the long axis of the flagellum. It is rather as though the bacterium screws itself through the water by rotation of its helical flagella, much as a corkscrew can be forced through a cork simply by being rotated.

**Flagellated bacteria come in a menagerie of different forms**

*E. coli* and *Salmonella* are not the only bacteria with flagella. Many other bacteria swim by means of flagella, and show great variation in the number, length, and distribution of bacterial flagella they employ. *Proteus mirabilis* has a similar number and distribution of flagella to *E. coli* and...
swims in a similar manner when grown in liquid broth. When grown on the surface of a semiliquid agar plate, however, the cells sprout many more flagella and begin to swarm—a form of motility that appears to depend on cell–cell contact. Dual motility systems of this kind are common in bacteria that inhabit complex environments, allowing them to move efficiently in surroundings with different physical properties. Another life style is seen in stalked bacteria of the genus Caulobacter, which spend most of their life attached to a substratum. When they divide, one daughter becomes a motile cell bearing a single flagellum at one end, while the other cell retains its attachment to the substratum. The salt-loving bacterium Halobacterium halobium swims by means of flagella inserted at either pole of the cell. It spontaneously reverses its direction of swimming every 10–15 seconds, the interval being influenced by the intensity of light.\footnote{The flagella at either end of a Halobacterium cannot be identical in every respect or else the bacterium could not swim. The motors at either pole of the cell probably rotate in different directions (looking out from the cell). Alternatively, if they rotate in the same direction, then the flagella must have opposite handedness, with one a right-handed helix and the other a left-handed helix.}

One of the most curious forms of movements is that of spirochetes, which are powered by one or more internal flagella. Spirochetes such as Treponema pallidum, the causative agent of syphilis, have a remarkable ability to swim in gel-like media. Their long helical bodies bore through high-viscosity media in a serpentine manner without slippage, as though traveling through a helical tube. These movements are generated by flagella, attached at either end, that rotate within the confines of an outer membrane sheath (Chapter 16).

**Bacterial flagella and eucaryotic flagella differ in structure and mode of action**

Many eucaryotic cells also swim by means of flagella: this is true of many species of protozoa and algae as well as most types of animal sperm. However, eucaryotic flagella are at least ten times larger than bacterial flagella in both diameter and length, and their structure and mode of action are far more complex. The differences are so great that it seems that they must have arrived at their common whiplike form by convergent evolution: different solutions to the same problem of moving a cell through water at low Reynolds number.
The flagellum of a mammalian sperm, for example, is typically 70 μm long and may be 0.8 μm wide near the cell body, tapering to 0.2 μm at its distal end (Figure 1-9). Unlike a bacterial flagellum, which is an inert structure rotated at the cell body, a eucaryotic flagellum actively propagates bending waves. If a sperm flagellum is severed from the cell body by a focused UV beam or by sonication, it remains able to swim for long periods. Another indication of internal complexity is that the waveform of a eucaryotic flagellum is not always rigidly helical but varies between cell types. The flagellum of mammalian sperm, for example, executes an almost perfectly planar sinusoidal wave.

Although larger than bacterial flagella, eucaryotic flagella still move at low Reynolds number and are therefore dominated by viscous drag. The underlying basis of their forward movement is the greater viscous drag encountered by a thin rod or filament that moves sideways through a fluid rather than moving end-on (see Figure 1-8). From the standpoint of fluid mechanics, the principal difference between the two kinds of flagella is that each small segment of the eucaryotic flagellum is driven by bending motions generated along its length by the mechnochemical interactions of adjoining segments. The segments of a bacterial flagellum move because of a rotation imposed from outside, by the motor in the cell body.

**Eucaryotic flagella generate a wide variety of waveforms**

The simplest type of waveform seen in eucaryotic flagella is a planar sinusoidal wave that travels steadily toward the rear of the swimming cell. This pattern of beating is seen in many animal sperm that are streamlined for efficient swimming. They typically have a small head region, containing highly condensed chromatin together with enzymes that enable fertilization to occur. The small head has minimal effects on the hydrodynamic performance of the cell, so that sperm flagella show some of the simplest and most regular waveforms.

By contrast, a sinusoidal waveform is only rarely encountered in protozoa, the other major group of eucaryotic cells that swim by means of flagella. The cell body of a protozoan presents much greater resistance to passage though water than the head of a sperm and often plays an important part in the hydrodynamics of swimming.

Take *Euglena gracilis* for example. This is a photosynthetic protozoan (or alga) that swims by means of a single long flagellum. The flagellum is attached to the front end of the long tapered cell; when beating it wraps around the cell to point rearward (Figure 1-10). Helical waves moving from the base of the flagellum to its tip drive the cell forward, and also

![Figure 1-9 Sperm flagellum and bacterial flagellum compared.](image)

**Figure 1-9** Sperm flagellum and bacterial flagellum compared.

![Figure 1-10 Euglena swimming. The single long flagellum generates waves that cause the cell body to spin, moving forward like a single-blade propeller.](image)

**Figure 1-10** *Euglena* swimming. The single long flagellum generates waves that cause the cell body to spin, moving forward like a single-blade propeller.
Figure 1-11 Chrysomonad swimming. This marine organism has a 'tinsellated' flagellum covered in side hairs. The flagellum propagates planar waves from its base to tip, as usual, but the side hairs change its hydrodynamic properties so that it pulls the cell rather than pushes. The cell consequently swims with its hairy flagellum foremost.

exert a torque on the cell. The organism consequently follows a gyrating path through the water in which the anterior of the cell sweeps through a larger radius than the posterior. Spinning with a frequency of about one cycle per second, the cell body acts like a counterbalance against the driving force of the flagellum. A contrasting form of flagellar-driven swimming is seen in the unicellular green alga Chlamydomonas reinhardtii, which swims forward using its pair of flagella rather as a human swimmer uses arms in a breast stroke, although in an avoidance response the flagella have an undulating waveform. We will return to Chlamydomonas swimming in Chapter 14 to discuss the many mutants of this organism known to be affected in their swimming ability.

The flagella of most mammalian sperm have smooth surfaces, but this is not true of all protozoa. The flagella of some species of Euglena, for example, are decorated with a unilateral array of minute filamentous projections that project from points along their entire length and with a tuft of hairs that project at their tips. Other protozoa carry flagella adorned with lateral spines, scales, or bristles. Many of these lateral projections have an important influence on the swimming performance of the cell—even to the extent of reversing the normal direction of swimming! For example, most motile species of Chrysophytes—a group of protozoa also termed golden algae—possess a flagellum attached to their front end that propagates a planar wave from base to tip. We would expect such a motion to drive the cell rearward, but the opposite is the case because the flagellum of this organism is covered with stiff hairs that project from its side (Figure 1-11). As this 'tinsel' flagellum bends, the hairs on either side undergo a cycle of movements like side paddles that carry the cell in the forward direction.3

Parasitic species of protozoa frequently have unusual arrangements of flagella, possibly because their environment poses special problems of locomotion. The Trichomonas, for example, which are parasitic in man and other animals, typically have several flagella, one of which folds back down the cell body and may be associated with an undulating membrane (Figure 1-12). The single flagellum of Trypanosoma brucei, the parasitic protozoan that causes African sleeping sickness, is similarly attached to the margin of a delicately undulating membrane. This apparatus is capable of swift reversals, equipping the parasite for movements in the swiftly flowing bloodstream of a mammalian host. In a different stage of its life cycle the trypanosome is confined to the mouthparts of the tsetse fly and the flagellum changes from being a motile organelle to one that provides anchorage to the lining of the insect proboscis. Elsewhere among the protozoa, flagella are found that act as rudders for steerage or act as sensory whiskers, or feelers.

Many protozoa move by the coordinated beating of cilia on their surface

Cilia are a form of hairlike motile appendage found on a wide variety of eucaryotic cells. They closely resemble eucaryotic flagella in internal structure and mode of action, as discussed in Chapter 14, but they are typically shorter than flagella and are present in larger numbers arrayed

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3 Many Chrysophytes possess two flagella, one tinsellated (hairy) and the other smooth; the hairy flagellum advances in front of the cell and is the principal source of motility. A similar flagellar arrangement occurs in the sperm of fucus, a sea weed, where the tinsellated flagellum makes initial contact with the egg.
over the cell surface. Their waveform is also more complex consisting of a planar power stroke and a three-dimensional recovery stroke, the shape of which appears to be adapted to the cell's particular hydrodynamic environment (Figure 1-13). A major phylum of protozoa, the Ciliophora or ciliates, is characterized by cilia covering large portions of surface.

Ciliates of the genus Paramecium are free-living, freshwater protozoa, typically slipper-shaped and 100–200 μm in length. Their surface is covered by thousands of cilia, each about 10 μm long, that beat at a frequency of about 20 cycles per second. They work like small oars to drive water over the cell surface, enabling the cell to swim. Cilia on the surface of paramecia, and indeed most cells, work in near synchrony, showing a slight time lag between the beating of successive rows of cilia, which produces a large-scale ripple pattern on the surface of the cell, the metachronal wave. As the cell swims forward, metachronal waves sweep from the posterior left up to the anterior right of the cell (Figure 1-14). The cell consequently rotates as it swims, describing a smoothly rotating path, moving through water with a net rate of up to several millimeters a second.

**Fields of cilia move adjacent layers of water**

The coordinated beating of cilia, as we have just seen, carries currents of water over the surface of a cell. Many ciliates take advantage of this action not to swim but to feed. Thus, sessile species of protozoa, such as *Stentor* or *Vorticella*, which spend most of their life anchored to surfaces, use fields of cilia to sweep currents of water into the mouth region of the cell. Particles of food carried in the flow are thereby captured and devoured. Multicellular organisms also take advantage of the ability of cilia to create a continual directed flow of fluid and the apical (outward-facing) surfaces of many epithelial cells are covered by cilia (Figure 1-15). Ciliated cells are

![Figure 1-13 The beating of a cilium. Each cilium performs a repetitive cycle of movements consisting of a power stroke followed by a recovery stroke. In the fast power stroke (solid lines), the cilium is fully extended and fluid driven over the surface of the cell. In the slow recovery stroke (broken lines) the cilium curls back into position with minimal disturbance to the surrounding fluid. Each cycle typically requires 0.1–0.2 seconds and generates a force that is perpendicular to the axis of the cilium.](image)

**Figure 1-12** A trichomonad. One of a large family of parasitic flagellates, in this case taken from a termite gut. The cell has several flagella, one of which curves around the cell body and is attached to it by an undulating membrane. (Courtesy of A.V. Grimstone.)
Figure 1-14 Ciliary beating on the surface of a swimming Paramecium. (a) The surface of Paramecium is covered by some 5000 cilia, the repetitive beating of which propels the cell through the water. (b) Because of near synchrony in the beating of adjacent cilia, they form waves on the surface. Note that the direction of these metachronal waves is not necessarily the same as that of the individual ciliary beat. (a, courtesy of Sidney Tamm.)

present in enormous numbers on the inner surfaces of the bronchioles of the human lung, and the unceasing coordinated beating of their cilia carries layers of mucus and particles of dust that have been inhaled up to the throat to be swallowed and eliminated. Cilia on the walls of the proximal convoluted tubule of the kidney aid the collection of fluid waste; cilia on ependymal cells lining the ventricles of the brain cause circulatory movements in the cerebrospinal fluid; the mammalian egg is borne by the beating of hundreds of thousands of cilia on the inner wall of the Fallopian tube as the egg migrates from the ovary to the womb.

Modified cilia and flagella are used for purposes other than swimming

Evolution is opportunistic, and once a successful structure has appeared it is often employed in unexpected ways. Thus cilia and eucaryotic flagella form the basis of modified structures that perform functions other than swimming. We have just noted that many ciliated protozoa use fields of cilia to sweep food particles into their mouths for feeding. This typically

Figure 1-15 Ciliated cell in an epithelium. Scanning electron micrograph of the esophageal epithelium of a fetal mouse shows an isolated ciliated cell. The apical surface of the cell carries both long motile cilia and shorter, static microvilli. Later in development ciliated cells will proliferate to produce extensive fields of beating cilia. (Courtesy of Raymond Calvert.)
employs highly specific arrangements of cilia and, moreover, often includes cilia fused together to form larger (and presumably more efficient) platelike structures termed membranelles. Other free-living protozoa use cilia fused together in structures called ciliary to perform a form of locomotion similar to walking, as described in Chapter 2.

Parasitic and symbiotic protozoa also employ cilia or flagella to move and maintain their position in a suitable niche within the host organism. Many of these, such as the flagellated cell Trichonympha, show an amazing degree of specialization (Figure 1-16). Trichonympha inhabits the intestine of wood-eating termites, where it ingests the minute bits of wood in the termite’s intestine, transforming them to soluble carbohydrates, a proportion of which can be used by the insect host.

Modified cilia are found also in higher animals, often associated with sensory processes. Olfactory cells, responsible for the sense of smell, are specialized nerve cells that carry (in humans) six or eight extremely long (up to 200 μm) immobile cilia. These project out from the surface of the olfactory epithelium, and their membranes carry receptors for the detection of odors. The photoreceptor rod cells of vertebrate retina are another highly specialized form of cilium. Between the highly specialized outer segments of the photodetectors, which carry the photoreceptor apparatus, and the inner segment that contains many mitochondria, there is a slender neck region that has an internal structure very similar to that of a cilium. Evidently, during the development of an embryo, specific epithelial cells bearing a single cilium on their surface become progressively modified in form and function to produce the light-detecting cells in the adult eye. Here the genetic program that specifies the structure of a cilium has been taken over and adapted to a different purpose.

**Figure 1-16** The flagellated protozoan Trichonympha. This bell-shaped organism ingests particles of wood by means of pseudopodia that protrude from its lower part (not shown). The upper surface of the organism is covered with hairlike flagella that enable the organism to move and position itself in the termite gut, which is its home. (Micrograph courtesy of A.V. Grimstone.)
Further Reading