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Review

The biomechanics of solids and fluids: the physics of life

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Abstract

Biomechanics borrows and extends engineering techniques to study the mechanical properties of organisms and their environments. Like physicists and engineers, biomechanics researchers tend to specialize on either fluids or solids (but some do both). For solid materials, the stress–strain curve reveals such useful information as various moduli, ultimate strength, extensibility, and work of fracture. Few biological materials are linearly elastic so modified elastic moduli are defined. Although biological materials tend to be less stiff than engineered materials, biomaterials tend to be tougher due to their anisotropy and high extensibility. Biological beams are usually hollow cylinders; particularly in plants, beams and columns tend to have high twist-to-bend ratios. Air and water are the dominant biological fluids. Fluids generate both viscous and pressure drag (normalized as drag coefficients) and the Reynolds number (Re) gives their relative importance. The no-slip conditions leads to velocity gradients (‘boundary layers’) on surfaces and parabolic flow profiles in tubes. Rather than rigidly resisting drag in external flows, many plants and sessile animals reconfigure to reduce drag as speed increases. Living in velocity gradients can be beneficial for attachment but challenging for capturing particulate food. Lift produced by airfoils and hydrofoils is used to produce thrust by all flying animals and many swimming ones, and is usually optimal at higher Re . At low Re , most swimmers use drag-based mechanisms. A few swimmers use jetting for rapid escape despite its energetic inefficiency. At low Re , suspension feeding depends on mechanisms other than direct sieving because thick boundary layers reduce effective porosity. Most biomaterials exhibit a combination of solid and fluid properties, i.e., viscoelasticity. Even rigid biomaterials exhibit creep over many days, whereas pliant biomaterials may exhibit creep over hours or minutes. Instead of rigid materials, many organisms use tensile fibers wound around pressurized cavities (hydrostats) for rigid support; the winding angle of helical fibers greatly

affects hydrostat properties. Biomechanics researchers have gone beyond borrowing from engineers and adopted or developed a variety of new approaches—e.g., laser speckle interferometry, optical correlation, and computer-driven physical models—that are better-suited to biological situations.

Keywords: solids, fluids, Reynolds number, lift, viscoelasticity, biological materials, stress–strain curves

1. Introduction

Biologists have traditionally embraced such subdisciplines as anatomy, physiology, behavior, ecology, and genetics. Although certain aspects of physics play significant roles in these traditional areas—temperature in physiology and ecology, acoustics in behavior, for instance—physics is not really in the forefront of any of the traditional areas of biology. In contrast, physics is at the heart of biomechanics. Biomechanics uses the principles of Newtonian physics to study structures and processes of living organisms; it looks at the physical properties of organismal structures, and their physical interactions with their environments. This has traditionally included material properties of solid structures, fluid mechanics of environmental flows and of locomotion, and kinematics and dynamics of body parts. ('Biophysics' sounds as if it should include biomechanics, but by convention, biophysics focuses on intracellular and molecular-level processes, in contrast to biomechanics, which has generally focused on macroscopic structures and processes.) The goal of organismal or comparative biomechanics research is generally to understand the physical aspects of organismal functioning. This often involves analyzing physical constraints on organisms, and may include analyses of whether an organism operates at or near some physical optimum. Applied biomechanics takes the same approach but targets humans, typically focusing on improved athletic performance or on the mechanics of orthopedic repairs or prosthetics. This review will survey key concepts in the field of comparative biomechanics.

Biomechanics was first recognized as a discipline as early as the mid-20th century (Brown 1953, Bailey 1954, Weis-Fogh and Jensen 1956, Bainbridge 1958). Organismal biomechanics experienced a significant expansion in the 1960s and 1970s as biologists began to borrow many techniques from engineers. Biomechanics researchers began asking questions about, for example, the strength of organisms' supporting structures in relation to environmental loads, mechanical properties of biological materials, and the fluid mechanics of filtering, pumping, swimming, and flying. Wind and water tunnels, strain gages, and Instron-type material testing rigs all thus became familiar items in biomechanics labs. Although biomechanics researchers initially used equipment designed for engineers, they soon discovered that many such devices were not well-suited to answering biological questions; they either had to modify such equipment heavily or design and build their own. Some were simple and fundamental, such as Vogel's flow tank design (Vogel 1981, pp 297–301) whereas others were quite complex and sophisticated (see section 5). Several of these biomechanics pioneers wrote books that are still valuable references to this day (e.g., Alexander 1968, Pennycuik 1972, Wainwright *et al* 1976, Vogel 1981, Vincent 1982).

Biomechanics is somewhat complicated by the vast size range of living organisms, from a 2 μm long bacterial cell to a 30 m long blue whale—a 15-million-fold range in length and covering 20 orders of magnitude in mass. Even if we limit our focus, as in this review, to macroscopic, multicellular organisms like animals, the range from an ant to a blue whale

spans 6000-fold in length and 6×10^{10} in body mass. This great difference in linear dimensions, and the accompanying immense range in surface/volume ratios and inertia, can have dramatic physiological and physical consequences. For example, a house fly can fly full speed into a solid wall and bounce off unharmed, whereas an elephant can be fatally injured by a fall from less than its own height. A mosquito can hover but cannot soar, whereas a condor can soar but cannot hover. Although the same basic physics applies to all organisms, various scale effects—often but not entirely due to the effects of surface/volume ratios—mean that structural features that are effective for a mosquito or an ant would not work for an eagle or an elk. This is particularly true for swimming and flying, and large external flows (e.g., wind blowing on dandelions and trees or tidal currents flowing over sea anemones), where changes in scale qualitatively change the nature of the drag forces (section 3.3).

Engineers and applied physicists have traditionally treated fluid mechanics and solid mechanics as two related but largely separate areas. Biomechanics researchers have tended to follow this model, specializing in either solid or fluid biomechanics (e.g., Wainwright *et al* 1976, Vogel 1981), with some exceptions (e.g., Koehl 1977a, Koehl and Cheer 1987). In this review, the basic principles of solid and fluid mechanics will be presented separately, but later sections will cover properties of biological materials that overlap the solid-fluid boundaries.

2. Solids

Although water makes up much more of the mass of most living organisms than of engineered structures, all macroscopic organisms have at least some solid components—e.g., skin, muscle—and some such components form hard support structures—e.g., vertebrate bone, wood, insect exoskeleton. To understand the biomechanics of these structures, we first need to have a basic understanding of what makes a material a solid, and how solids deform and break; then we can look at how biological ‘solids’ are more complicated than materials used by engineers.

2.1. What is a solid?

In simple terms, solids are materials that maintain a fixed shape, in contrast to fluids (liquids and gases) that have no fixed shape and tend to conform to the shape of whatever container they occupy. In slightly more technical terms, solids are materials that resist deformation, as opposed to liquids which do not resist deformation but do resist the *rate* of being deformed. Materials scientists use the term ‘elasticity’ for the resistance of solids to deformation, and ‘viscosity’ for liquids’ resistance to rate of deformation. (Whereas the technical meaning of ‘viscosity’ is similar to its everyday meaning, the technical meaning of ‘elasticity’ is somewhat different from its everyday meaning, as we will see below.) The materials used by most engineers tend to fit into the ‘solid’ and ‘fluid’ categories neatly and unequivocally: steel is a solid, ethanol is a fluid. Most biological solid materials, however, have at least some degree of fluid-like behavior and are thus technically viscoelastic; because viscoelastic properties combine solid and fluid aspects, we need to understand both conventional solids and conventional fluids before tackling viscoelastic solids in section 4. Nevertheless, the hardest biological solids do act much like engineering solids, and the sophisticated methods that engineers have developed to analyze solid materials can be usefully applied to many stiff biological materials.

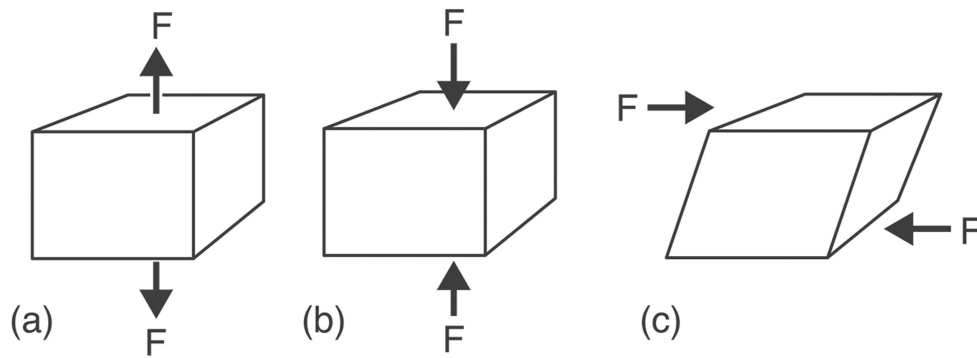


Figure 1. Three basic ways forces can be applied to deform a solid. (a) Tension; (b) compression; (c) shear. F : force; F_1 , F_2 : shearing forces (see text).

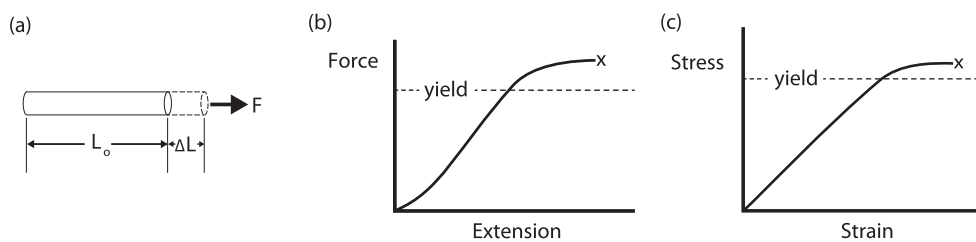


Figure 2. Terminology for a typical solid material being tested in tension. (a) A force F is applied in tension to a material sample with an initial length of L_0 , extending the sample length by ΔL . (b) A plot of the force F versus extension ΔL ; F increases until the sample breaks, or fails, at x (by convention, the curve normally just ends at the point of failure). (c) The same force–extension data, but normalized as stress and true strain. At extensions or strains above the yield strain, irreversible (plastic) deformation occurs (see text).

2.2. Deformations of solids

Solids can be deformed in different ways. A rope supporting a weight is loaded in *tension*, where the ends are being pulled apart. The concrete floor I stand on is loaded in *compression*, where the top and bottom surfaces are being pushed closer together (figure 1). *Shearing* is when forces are applied in such a way that they tend to make one part of the object slide past another part. Consider the rectangular solid in figure 1(c): force F_1 pushes on the upper left while force F_2 pushes on the lower right, so that the upper part of the object tends to slide to the right and the lower part tends to slide to the left. Some materials are flexible, and can resist tension but not compression, hence the old saying, ‘you cannot push on a rope’. Others resist compression mightily—they are ‘hard’ in the conventional sense—but do not resist tension well, such as concrete. Many biological materials are somewhere in between, with a moderate amount of tensile and compressive strength and some flexibility; Wainwright *et al* (1982) call these materials ‘pliant’, to distinguish them from materials they categorize as ‘tensile’ and ‘rigid’.

The relationship between the force applied to an object and the distortion produced is quite straightforward for many materials used by engineers, but it is much less so for most biological materials. Looking at the well-mannered behavior of ‘Hookean’ or ‘linearly elastic’

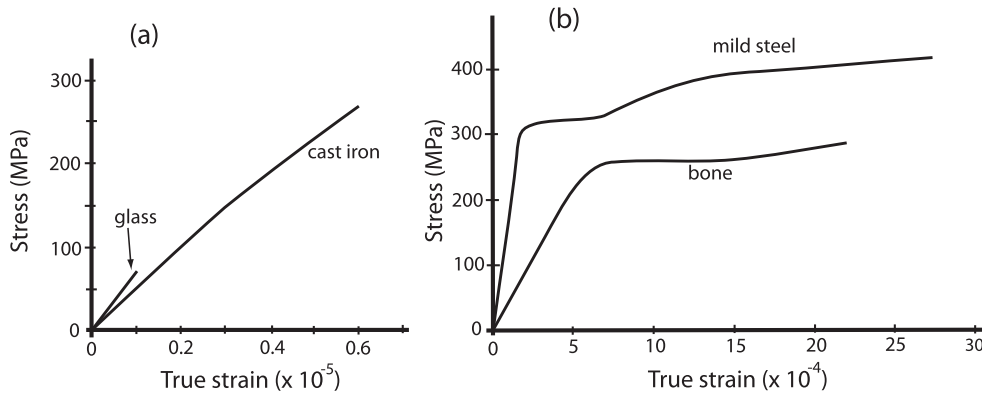


Figure 3. Sample stress–strain curves for engineering and biological materials. (a) Linearly elastic materials that show little or no plastic deformation. (b) Materials that show extensive plastic deformation.

solids like iron and glass will give us the necessary foundation to look at the more complex behavior of biological materials.

If we fix one end of an object, pull on the other end, and measure how much it elongates, we can produce a force–extension curve such as that shown in figure 2(b). If we want to know about the material (the stuff the object is made of) rather than the specific object, we need scale-independent terms for force and extension. *Stress*, σ , is the magnitude of the force applied, F , divided by the cross sectional area, S , perpendicular to the force:

$$\sigma = \frac{F}{S}. \quad (1)$$

(Note that stress has the same dimensions, force per unit area, as pressure; stress is thus measured in the same units as pressure, e.g., N m^{-2} or Pa.) *Strain*, ϵ , is the fractional elongation of the object. Engineers typically work with materials that deform very little under load and traditionally use ‘engineering strain’, ϵ_{en} , which is simply the amount of elongation, ΔL , divided by the original length, L_0 :

$$\epsilon_{\text{en}} = \frac{\Delta L}{L_0} \quad (2a)$$

(figure 2(c)). The engineering strain is a proportion, usually expressed as a percent, and while convenient and intuitively simple, it is generally reserved for extensions of up to about 10%. When materials allow extensions of greater than 10%, the true or natural strain, ϵ_{T} , gives a better representation of the incremental increases at large extensions:

$$\epsilon_{\text{T}} = \int_{L_0}^L \frac{dL}{L} = \ln \frac{L}{L_0}, \quad (2b)$$

where L is the final length of the deformed object. Both versions of strain are based on ratios and are thus dimensionless, and at strains less than 0.1, they are essentially the same.

If we plot a stress–strain curve for an engineering material like glass or cast iron, most of the curve, starting from the origin, is a straight line, hence such materials are called ‘linearly elastic’ (figures 2(c) and 3(a)). (Hooke’s law says that deflection is directly proportional to the applied force, so linearly-elastic materials are also called ‘Hookean’.) The stress–strain graph gives several useful material properties. The slope of the straight part of the stress–

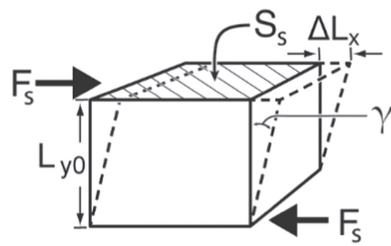


Figure 4. Terminology for shear. Equal and opposite forces (F) are applied so as to cause angular distortion γ . Strain is given by the ratio of distortion ΔL_x to unstressed thickness L_{y0} . Shear stress is normalized by the area S parallel to the forces.

strain curve is called *Young's modulus* or the *modulus of elasticity*, E . Young's modulus is given by

$$E = \sigma/\varepsilon. \quad (3)$$

Young's modulus is a measure of elasticity, which represents what we would normally call the stiffness in everyday terms (stiffness being nearly opposite from the everyday meaning of elasticity). Glass is stiffer than gelatin, so glass has a much higher Young's modulus (modulus of elasticity) than gelatin.

The upper right end of the stress–strain curve, where the sample breaks or ‘fails’ gives the *strength* of the material. Since the strength is the value of the stress at failure, strength has the same dimensions as stress, force/area (Pa in SI units, although most materials have strengths in the MPa or GPa range). The failure point also gives the breaking strain or *extensibility*, which, like the strain, is dimensionless. For rigid materials, stress, strain, Young's modulus, and strength can all be measured in both tension and compression. The exact value of E , however, may differ in tension and compression, and often the strength differs dramatically.

Whereas Young's modulus applies to both tension and compression, a different relationship is needed for shear. The shear stress, τ , is the force applied, F_s , divided by the area *parallel* to the force, S_s ($\tau = F_s/S_s$), and shear strain is the ratio of the amount of deflection parallel to the force (ΔL_x), to the object's unstressed length perpendicular to the force (L_{y0}), i.e., $\tan \gamma$ (figure 4). (At low shear strains, the deflection angle γ itself, in radians, will be essentially the same as the $\tan \gamma$, so the angle itself is usually used as shear strain for stiff materials.) The shear modulus, G , takes the same form as Young's modulus:

$$G = \tau/\gamma. \quad (4)$$

The dimensions are the same as for tension and compression: τ and G are force per unit area (so Pa in the SI system), and both $\tan \gamma$ and γ (measured in radians) are again ratios and thus dimensionless.

Elasticity in materials science means something a bit different from its everyday use. An elastic deformation is one in which the material returns to its original, undeformed shape when the load is removed. Brittle materials, like glass, show elastic deformation all the way to failure when stressed. Most materials, however, exhibit some permanent deformation when highly stressed; this permanent deformation is termed *plastic*—a meaning completely different from its everyday one. Some materials, such as modeling clay (plasticine) deform mostly or entirely plastically, whereas many rigid materials deform elastically at moderate stresses and plastically at high stresses. The point where elastic deformation stops and plastic deformation begins on a stress–strain curve is called the *yield* point (figure 2). Plastic

Table 1. Material properties of a selection of engineered and biological solids. Values of E for biological materials are tangent moduli. Strength values represent tensile strength (except values in parentheses which represent compressive strength) and should be considered as estimates for comparison only. Toughness is equivalent to strain energy storage or work of extension. (Data from Wainwright *et al* 1982, Alexander 1983, Curry 1984, Vincent 1990, Vogel 2003.)

	E (MPa)	Strength (MPa)	Extensibility	Toughness (MJ m^{-3})
Elastin	1.0	1.3	1.2	
Rubber	3.0	7	3	10
Cartilage	20	(1)	0.08	
Brick	700	5 (36)		
Tendon	1500	100	0.10	2.8
Insect cuticle	5000	100	0.02	0.03
Tree trunk	6400	200		
Cortical (dense or compact) bone	18 000	200 (170)	0.02	3.0
Tooth enamel	60 000	35 (200)	0.0005	0.02
Mild steel	200 000	400–900	0.02	1.0

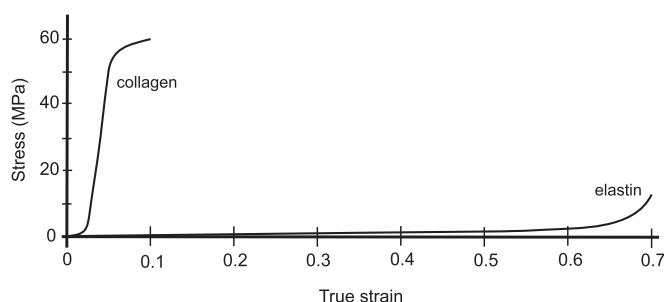


Figure 5. Stress–strain curve for two non-Hookean biological materials. (Note different scale of strain axis compared with figure 3.)

deformation can actually guard against failure: the large plastic region of the stress–strain curve of mild steel (figure 3(b)) helps it avoid breaking due to sudden shocks by absorbing energy that might otherwise go into fracturing (see section 2.3). Brittle materials like glass and concrete, with little or no plastic behavior, tend to be much weaker in tension than in compression (see table 1 and section 2.3 below).

A few biological solids behave like engineered materials. Bone, for example, has a stress–strain curve rather similar to mild steel¹ (figure 3(b)), with both large elastic and large plastic regions giving it good rigidity along with shock resistance (Burstein *et al* 1972, Curry 1984). Many biological materials exhibit very different stress–strain behavior, producing a ‘J-shaped’ stress–strain curve with an initial low slope and then a region with a dramatically steeper slope at high strains. (For a discussion of how atomic and molecular structure affects the shape of the stress–strain curve, see Alexander (1983) for rubber-like

¹ The stress strain curves shown in this review for specific materials represent typical, somewhat idealized curves based on data from multiple sources. They are intended for general comparisons, not to reflect data from any particular experiment or set of measurements.

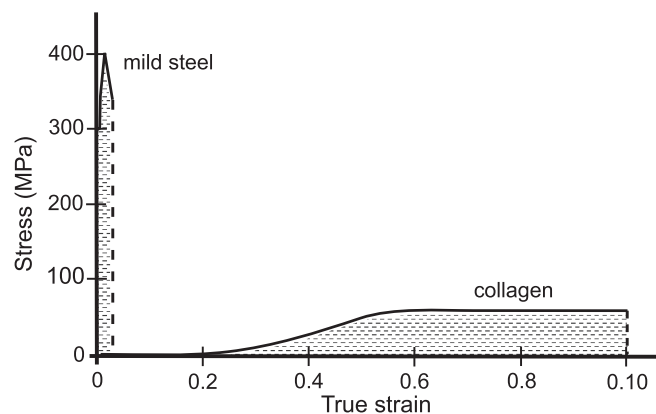


Figure 6. Strain energy (work of tension) shown as shaded area under stress–strain curves for steel and collagen.

materials and Wainwright *et al* (1982) for general solids.) Collagen, one of the most important tensile materials in the animal kingdom and the main component of our tendons, shows an initial J-shaped (concave-upward) region, and elastin from a special ligament in hoofed mammals has a completely J-shaped stress–strain curve (figure 5). Because such curves may not have much of a straight region, defining a single modulus of elasticity may be impossible. Some materials have a fairly straight region at very low strains (near zero), so the slope of this region, the ‘initial modulus’, is sometimes used. If the stresses and strains of interest are beyond this linear region, or if there is no initial linear region, researchers use the slope of a line tangent to the curve at some typical value for ϵ , thus termed the ‘tangent modulus’. Caution must be exercised when using such values for tangent moduli of biological materials reported in the literature: stiffness may be quite different at values of ϵ other than the one used in the reported measurement.

Another key property given by the stress–strain graph is the *strain energy density* (sometimes called ‘work of extension’ or ‘work of compression’ and typically referred to as simply ‘strain energy’ in biomechanics). Strain energy density is the amount of energy absorbed by the material as it is deformed, and it is given by the area under the stress–strain curve. We normalize this area by dividing it by the volume of material being deformed, and work per unit volume is dimensionally equivalent to force per unit area, so strain energy is yet another material property with the same units as stress. This key value measures how much work a material absorbs before breaking, and is sometimes referred to as ‘toughness’. Perhaps counterintuitively, some very hard, rigid materials are not very tough, whereas many floppy, easily extended materials are very tough. Figure 6 shows a comparison of idealized stress–strain curves for steel and collagen. In fact, easily extensible or *compliant* biological materials can be much tougher than many hard materials (‘compliance’ of a material is the inverse of its Young’s modulus). Such compliant biomaterials deform a lot, but in the process they absorb a lot more energy before breaking than very stiff materials. In fact, our everyday concept of brittleness is precisely the inverse of toughness. (Materials that are both compliant and brittle exist—agar or gelatin, for instance—but in pure form they seem to be absent as structural components of macroscopic organisms.)

Can we get any of that work of deformation back when the stress is removed? By definition, Hookean materials do not suffer permanent deformation when stressed within their linearly-elastic range. Thus, in principle all the strain energy should be returned when such a

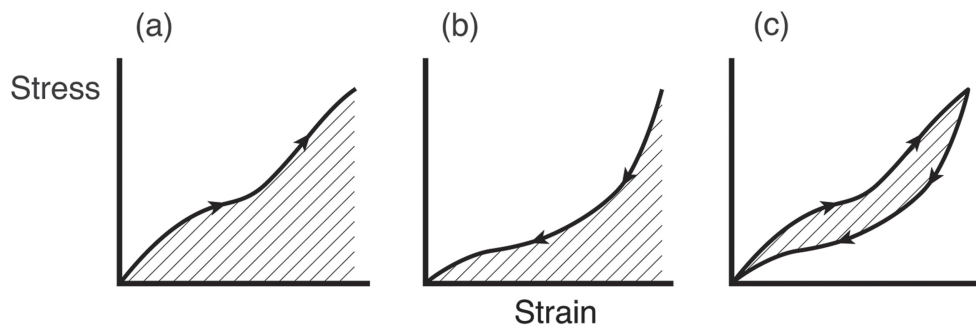


Figure 7. Loading and unloading for a hypothetical biological material. (a) Loading stress–strain curve; shaded area equals strain energy stored. (b) Unloading stress strain curve; shaded area equals strain energy returned as stress is removed. (c) Hysteresis between loading and unloading curves; shaded area shows energy lost as heat.

material is unloaded (in reality, a negligible amount may be lost as heat). The vast majority of biological materials, however, are not linearly elastic—they are non-Hookean—and they vary greatly in how much energy they return after being deformed. If we compare a material's stress–strain curve for loading with its stress–strain curve while being unloaded, we can see how well the material returns its strain energy. Recall that strain energy is given by the area under the stress–strain curve, as in figure 7(a). When the strained material is allowed to relax, the unloading stress–strain curve falls below the loading curve (figure 7(b)). The area under the unloading curve is the amount of energy returned, and we call the ratio of the area under the unloading curve to the area under the loading curve the *resilience* (usually expressed as a percentage). Resilience is thus a measure of a material's energy storage efficiency, and it tells what fraction of the energy put into stretching (or compressing) a material is returned when the material relaxes. Biological materials that are normally used to resist tension cover a huge range in resilience, from some kinds of spider silk at approximately 35%, to collagen at 93% and resilin (a rubber-like protein used as a spring in certain insect joints) at up to 96% (Jensen and Weis-Fogh 1962, Denny 1980, Wainwright *et al* 1982, Vincent 1990). When loading and unloading curves differ, the phenomenon is called *hysteresis* and it is a significant feature of most biological materials.

One final property related to stress and strain deserves brief mention. When a solid is pulled in tension it lengthens, and when it is compressed it shortens. As a solid in tension stretches in length, it also becomes narrower in width and depth (i.e., its cross-sectional area decreases), and vice versa as it shortens in compression. These changes normal to the tension are the normal strains ϵ_y —change in width—and ϵ_z —change in depth—and in isotropic materials, they are equal. The ratio of the normal strain to the parallel strain is defined as Poisson's ratio, ν :

$$\nu = -\epsilon_y/\epsilon_x = -\epsilon_z/\epsilon_x, \quad (5)$$

where ϵ_x is the strain parallel to the tension or compression, and the negative signs show that the normal strains are in the opposite sense (expanding or contracting) from the parallel strain. We might expect the normal strains to occur because the material maintains a constant volume, but that hardly ever happens, even in biomaterials containing lots of water. A constant volume would give $\nu = 0.5$ (based on true strains; Wainwright *et al* 1982, p 11), but most engineering materials as well as many biological ones have $\nu < 0.5$. For example, steel has a Poisson's ratio of about 0.3, as does cartilage and tooth enamel (Vogel 2003, p 322).

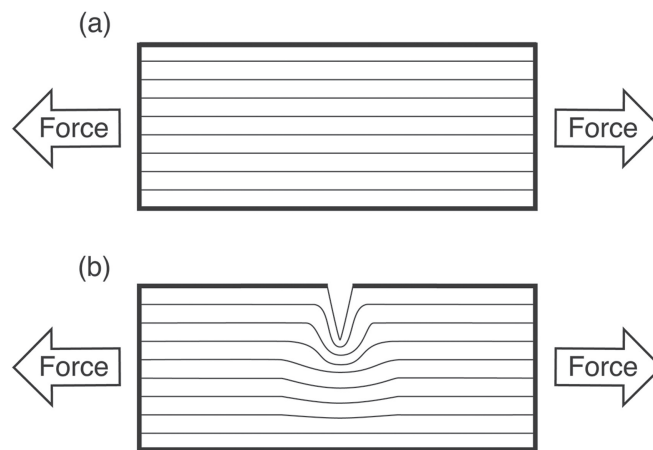


Figure 8. Force trajectories in a solid object in tension. (a) Force trajectories are parallel in a uniform material in pure tension, giving constant stress across the material. (b) Force trajectories pinch together at the end of a notch, locally increasing stress.

Poisson's ratio is notoriously difficult to measure for biological materials, and complicating matters, the anisotropic nature of most biological solids means that they have different Poisson's ratios in different directions, so any values given in the literature must be taken with a grain of salt. Mammalian bone, for example, has been reported as having values ranging from 0.13 to 0.4 (Wainwright *et al* 1982, p 12; Vogel 2003, p 322), no doubt reflecting individual variation, anisotropy, and different experimental conditions.

If engineers need to change the extensibility of a device for storing strain energy, they often do so by adjusting the shape—such as the coiled shape of a spring—while using some standard material, whereas nature might evolve materials with unusual or specialized properties so as to keep a simple shape. Insects, for instance, have evolved a rubber-like protein called resilin that often functions as a spring. Resilin is found in the wing hinges of grasshoppers (locusts) where flight muscles stretch it on the upstroke and it then retracts and returns some of its strain energy to help power the beginning of the downstroke (Weis-Fogh 1960, Andersen and Weis-Fogh 1964). Resilin is also used to help power the jump in fleas (Bennet-Clark and Lucey 1967).

Table 1 lists key material properties for a selection of biological materials with some technological ones for comparison. The values for the biological materials should be treated with caution, both due to natural variation inherent in biological processes, and due to differences in experimental methods. As one extreme example, spiders build webs from several kinds of silk, which can vary in Young's modulus by a factor of 3 and in tensile strength by a factor of almost 7.

2.3. How things break

If objects failed in tension due to breaking the chemical bonds that hold molecules together, then we should be able to calculate the strength of a material from the strength required to break those bonds. When researchers first made such calculations, they discovered that most materials broke in tension at stresses of 100–1000 times less than predicted. In fact, most solids fail in tension due to crack propagation, which only requires a tiny local failure, rather than a uniform failure all across the object's cross sectional area. And as we will see below,

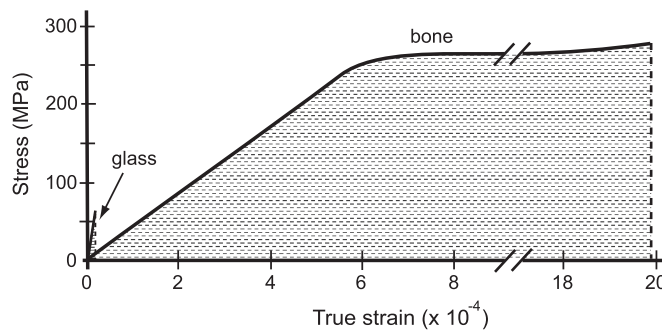


Figure 9. Work of fracture given by area under the stress–strain curve for a brittle material (glass) and a tough material (cow cortical bone). (Note scale break on strain axis.)

when beams and columns are loaded in compression and fail by buckling, they still generally fail from localized tension and crack propagation; failure in tension is thus important in other kinds of failure as well. (For a wonderfully clear and witty introduction to the science of material failure, see Gordon (1978)).

One of the reasons solid materials break in tension at lower stresses than chemistry might predict is that flaws or voids in a material can cause localized stress increases. If a uniform material sample is loaded in tension, the stress is uniform across the whole object and we see ‘stress trajectories’ that are parallel to the object’s surface (figure 8). If the sample is notched, however, the stress trajectories will now be pinched together as they pass the notch (figure 8). In other words, the local stress right at the tip of the notch will be much higher than elsewhere in the sample. Thus, notches, cracks, and voids produce stress concentrations (‘stress raisers’). Moreover, the sharper the tip of the notch, the higher the stress at the tip. In fact, for a crack or notch perpendicular to the tension, if the stress far from the crack is σ_0 , the stress at the tip of the crack, σ_T , is given by

$$\sigma_T = \sigma_0 \left(1 + 2\sqrt{\frac{l}{r}} \right), \quad (6)$$

where l is crack length and r is the radius of the crack tip (Gordon 1978). Given that crack tips usually have exceedingly small radii, σ_T can easily be hundreds or thousands of times higher than σ_0 . Any imperfection, flaw, or tiny void can act as the beginning of a crack.

Stress concentration matters, but the way the material absorbs energy can be even more important in tensile failure. Some materials are brittle; a small scratch or flaw causes them to crack right across and break at relatively moderate stresses, e.g., glass. Others can contain sizeable notches and cracks, and still resist breaking until much higher stresses are applied; these are tough materials, like some kinds of mammalian bone, or mild steel. The key difference is how the material absorbs energy as it deforms under load. In order for a crack to extend, new surface area must be created, which requires energy. Energy is released when the advancing crack gapes slightly and relieves some stress from the material on each side of the newly-opened part of the crack. The ratio between the work of fracture, W_f —the energy needed to create each new unit of surface area—and the strain energy released by the advancing crack, W_s , gives the critical crack length, l_c :

$$l_c = \frac{W_f}{\pi W_s}, \quad (7)$$

where W_f is energy per unit area and W_s is energy per unit volume, thus giving dimensions of length. When a crack reaches a length of l_c , any further crack extension releases more than enough strain energy to balance the work of fracture necessary to form new surface. This in turn usually leads to positive feedback and rapid, catastrophic failure. For Hookean materials, engineering handbooks give the formula:

$$l_c = \frac{2W_f}{\pi \sigma \epsilon} \quad (8)$$

(Vogel 2003). Note that $\sigma\epsilon/2$ is simply the area under the (Hookean) stress–strain curve, and for a brittle material like glass, this area is quite small. For materials that experience plastic deformation beyond their yield points, the area under the stress–strain curve is quite a bit larger (figure 9) and (8) does not apply. In simplest terms, this increase is due to the energy that goes into deforming the material plastically. Thus, tough materials—those with a high work of fracture—have various mechanisms that absorb energy and prevent crack propagation.

Even though they only apply exactly to Hookean materials, a number of practical consequences flow from a qualitative analysis using (7) and (8). The first is that any material will be much tougher in tension if it is divided up into fine strands rather than in one thick rod or cord. Assuming flaws and defects are randomly distributed, larger objects will tend to have larger flaws, so that they will experience critical crack lengths at lower stresses (Wainwright *et al* 1976, p 22). Thus, cracks that might propagate through a solid rod at a moderate stress are much less likely to propagate through a bundle of fine fibers. Certain rare, deep ocean sponges have a skeleton made of bundles of hair-fine strands and rods of silica (essentially glass) in a complex lattice; the lattice is both more flexible and much tougher than a solid layer of glass. Similarly, tendons formed from bundles of microscopic collagen fibers are much tougher than a uniform rod of collagen of the same cross section would be.

Second, a material that contains oval or rounded voids can inhibit crack elongation. When a crack reaches such a void, the void's much larger r will greatly reduce the local stress concentration and so require much greater tension to cause the crack to continue past the void. Even better is to have long voids or discontinuities parallel to the stress trajectories. Whenever a crack encounters such a discontinuity, r becomes essentially infinite and the crack is stopped dead. Wood in tension parallel to the grain is a good example.

Most of the basic theory and analysis to this point is based on isotropic materials, i.e., materials that have the same properties in every direction. Few biological materials are isotropic. The wood in the preceding paragraph is an example of an anisotropic material. In tension parallel to the grain, it is extremely tough, due to the combination of fine parallel fibers and elongate parallel voids. Across the grain, however, wood is typically a couple of orders of magnitude less tough. Anyone who has ever split firewood knows that the only practical way to split it is to apply ax or wedge so that it penetrates between the fibers, thus applying force perpendicular to the grain. A wedge applied across the grain (which basically tries to form cracks across the wood fibers rather than between them) usually just bounces off.

Composite materials take this toughening a step further. If thin fibers of a stiff, brittle material are embedded in a matrix of a more compliant (less stiff) material, any cracks that get through the stiff fibers encounter the compliant matrix, which immediately blunts the crack and reduces stress concentrations. This is the principle behind fibreglass and graphite-epoxy ('carbon-fiber') composites. In fact, almost all hard biological materials—bone, tooth enamel, mollusk shells, sclerotized insect cuticle—are composites. The ratio of stiff material to

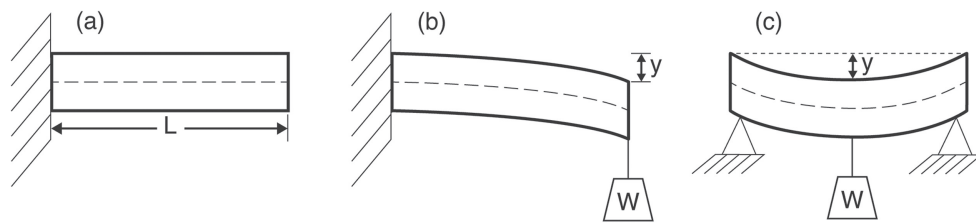


Figure 10. Beam and bending terminology. (a) Unloaded cantilever beam of length L fixed rigidly at the left end; dashed line shows neutral surface. (b) Cantilever beam loaded with weight W and deflected by distance y . (c) Simply-supported beam loaded in the center by weight W and deflected by distance y .

compliant material covers a huge range. Tooth enamel is mostly hydroxyapatite with only about 2% protein matrix, and is rather brittle for a biomaterial. Cartilage, in contrast, is a mixture of roughly equal proportions of collagen fibers and mucopolysaccharide matrix, and is considerably tougher, though more flexible, than tooth enamel.

Obviously, solid objects can break in response to compression and shear loads as well as in tension. Unlike failure in tensions, failure in compression (and to some extent, in shearing) depends as much on shape as on material properties. Moreover, in bending, structures are usually loaded so that different parts simultaneously experience compression and tension. We will now turn to structures, and consider how structures can fail in more complex ways than pure tension.

2.4. Structures

So far, we have looked at solid materials, which have particular values of Young's modulus or work of fracture independent of their shape. We now turn to structures, where the arrangement or shape of the object affects its mechanical properties. Engineering analysis uses a hierarchy, from simple to complex, of materials, structures, and structural systems, the more complex levels being composed of elements from the lower levels. The distinction between categories is usually obvious for engineered objects, but not always clear-cut for biological objects. Nevertheless, a consideration of the mechanics of simple structures can give us insight into the physical performance of, and constraints on, particular body parts of animals and plants. Engineers traditionally divide the 'structure' category into beams and columns (usually elongate) and shells (typically curved, thin-walled vessels or containers).

A beam is an elongate structure that is loaded by forces acting perpendicular to its long axis. (By convention, beams are analyzed as if they were horizontal—as opposed to columns, analyzed as if vertical—but elongate supporting structures in animals and plants often function as beams regardless of actual orientation.) Beams can be *cantilevers*, with one end firmly attached and the other end free; or they can be *simply-supported beams*, resting on a support at each end (figure 10). ('Fixed beams' with immovable, rigid attachments at both ends are essentially unknown in nature.) Because the load on a beam is perpendicular to its long axis, beams deflect by bending (figure 10). How beams resist bending depends on both the material and the shape of the beam.

When a rod of some uniform material is attached at one end and loaded at the other, the loaded end deflects downward, bending the beam. The bend will cause the top to be stretched, putting it in tension, while the bottom will be shortened, putting it in compression. Tension and compression both decrease with distance away from the top or bottom, respectively, so

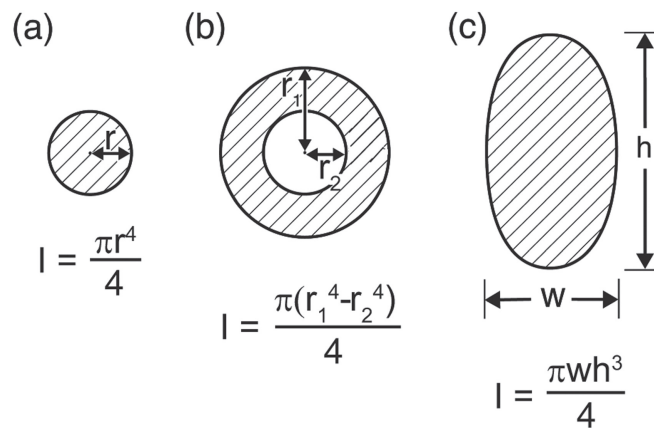


Figure 11. Examples of second moment of area for beams of simple cross section. (a) Solid circular cross section. (b) Hollow cylinder of outside radius r_1 and inside radius r_2 . (c) Solid elliptical cross section of major axis h and minor axis w .

that there is an imaginary surface somewhere in the middle of the beam that experiences neither compression nor tension. This is the *neutral surface* and it is exactly in the middle of a beam of isotropic material with a symmetrical cross section. (In some cases, the neutral surface may not be stress free, however; in a cantilever, for instance, it experiences a small amount of shear.) The farther a bit of the beam is from the neutral surface, the more it is strained, so one key concept from simple beam theory is that material farther from the neutral surface is more important for resisting deflection. How much does such a beam deflect under a given load? The deflection is governed by the *flexural stiffness*, which is the product of Young's modulus times the second moment of area, I , of the beam's cross section. The second moment of area (commonly but inaccurately called the 'moment of inertia') is a measure of the distribution of material relative to the neutral surface. See figure 11 for formulas for I for some common shapes. Since material farther from the neutral surface carries more of the load, I helps define how the load is distributed across the cross section. The flexural stiffness does not have its own symbol, but is simply referred to as EI . The deflection at the end of a cantilever of isotropic material and constant cross section is:

$$y = \frac{FL}{3EI}, \quad (9)$$

where F is the applied force (load) and L is the beam's length. In many cases we actually wish to know EI of a biological beam, such as an insect leg segment or a plant stem, so we might consider testing it as a cantilever. Firmly attaching one end of a structure of biological material can be quite challenging, however, so a three-point bending test is usually more convenient (figure 10). For a simply-supported beam (with the same material and symmetry conditions as above) in three-point bending, with the force applied in the exact center between the supports, the formula for deflection can be rearranged to give EI :

$$y = \frac{FL^3}{48EI} \text{ or } EI = \frac{FL^3}{48y}. \quad (10)$$

Beams may also be twisted, causing them to deflect in *torsion*. A beam in torsion experiences compression perpendicular to the outer surface, shear parallel to the outer surface, and tension at 45° to the long axis. (The compression is why we wring out towels to remove

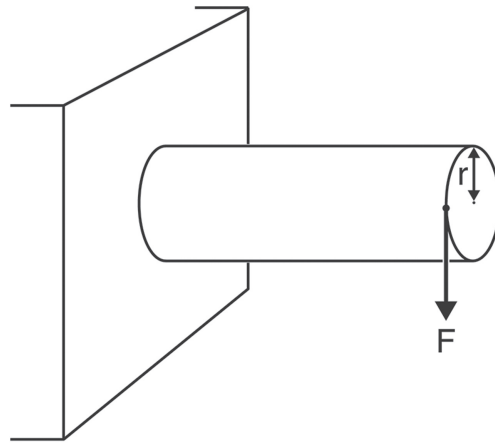


Figure 12. Terminology for cylindrical cantilever of radius r in tension. Force F is applied tangent to the surface at the end of the beam.

excess water.) The resistance to torsional deflection or *torsional stiffness* is GJ , where G is the shear modulus (from section 2.2) and J is the polar second moment of area (similar to I but with respect to a neutral axis rather than a neutral surface). For technological materials, G can often be calculated from E , but for biological materials—non-Hookean, anisotropic— G (or GJ) must be measured separately. Standard formulas exist for calculating J for simple shapes (e.g., for a solid cylinder: $J = \pi r^4/2$) but biological structures are rarely simple enough to apply such equations. Thus, in practice, researchers usually measure the composite variable GJ , similarly to measuring EI . In this case, one end of the sample must be fixed so that a moment can be applied to the other end (figure 12). (For biological materials, this may require being glued into a holder with epoxy or cyanoacrylate cement.) The torsional stiffness is then given by:

$$GJ = \frac{ML}{\theta}, \quad (11)$$

where θ is the angular deflection in radians and M is the applied moment or torque (for a force F tangent to the surface of a circular cylinder of radius r , $M = Fr$).

If a beam is loaded in pure compression, then by convention it is referred to as a column. Short, stubby columns being compressed act much like tensile structures in reverse: the structure shortens with a stress–strain relationship that may have the same or very similar E , and they fail by crushing or by cracks allowing shearing. Narrow columns, however, may fail at much lower stresses due to buckling, that is, sideways distortion. Euler buckling involves the whole column, whereas local buckling occurs in a limited region and is typically initiated by some local flaw, analogously to tension cracks. In the simplest form of Euler buckling, as the ends of the column are compressed, it bulges to one side, forming a smooth curve with the convex surface (to the outside of the bend) in tension, and the concave, inner surface in compression. Such a column usually breaks when cracks form and extend on the tension side. Local buckling is mainly a problem for thin-walled tubes and takes the form of a kink or crease that allows catastrophic collapse. The critical force, F_c , is the force that is just enough to cause breakage by buckling. For Euler buckling

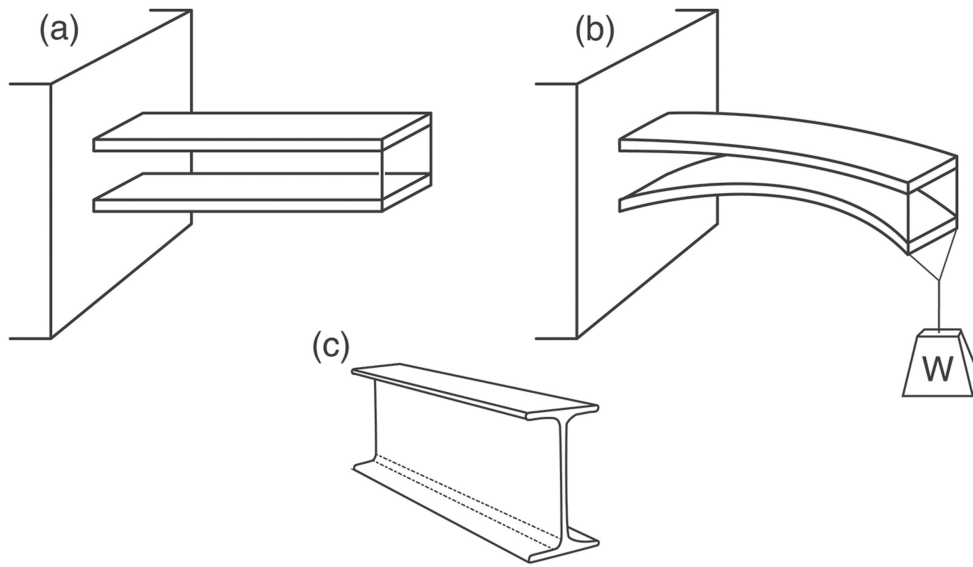


Figure 13. The extreme case of moving material away from the neutral surface to carry bending loads more efficiently. (a) Material moved entirely to top and bottom face. (b) When loaded, upper and lower plates pinch together, bringing them closer to the neutral surface and increasing stress. (c) To keep the upper and lower surfaces a constant distance away from the neutral surface, engineers add a vertical ‘web’ to parallel bars to produce the standard I-beam.

$$F_c = \frac{n\pi^2 EI}{L^2}, \quad (12)$$

where n is a coefficient that is specified by how the ends are held (for both ends ‘pinned’ or free to rotate, $n = 1$, and for both ends firmly fixed, $n = 4$). So for Euler buckling, F_c is proportional to the flexural stiffness and inversely proportional to L^2 . Thus, geometry matters a lot: increasing I increases F_c , whereas a small increase in L produces a large decrease in F_c .

Local buckling is not as amenable to theoretical analysis, so a number of partly-empirical relationships have been developed. One given by Ennos (2012) is:

$$F_c = k\pi t^2 E, \quad (13)$$

where t is wall thickness and k is a coefficient that accounts for imperfections, which ranges from 0.5 to 0.8.

Very few biological structures actually consist of a uniform, isotropic material of constant cross section, but these basic equations provide a useful starting point and are often sufficient for a useful first approximation. Moreover, they illustrate important properties and relationships qualitatively even when they cannot be used to give a precise answer. For example, both for resisting bending in beams and resisting buckling in columns, the greater the I , the better. One way to do this while conserving material is to make a strut hollow. The material close to the neutral surface or axis experiences very little stress, so if mass or weight is limiting, why not take that material from the center and move it to the periphery where it can carry some useful load? In fact, for resisting bending, torsion, and Euler buckling, a hollow cylinder can be over an order of magnitude stiffer than a solid one of the same cross sectional area (and thus, same mass). The farther the material can be placed from the neutral

axis, the stiffer the strut will be, except that if the wall gets too thin local buckling can become a danger.

Consider a beam that is only subject to bending in one plane, such as a horizontal cantilever supporting a weight at one end. The most efficient arrangement of material would be to have it concentrated at the top surface—to resist tension—and bottom surface—to resist compression—which amounts to two parallel, flat bars (figure 13). When loaded, however, the upper and lower bars would tend to pinch together, reducing their I and hence their bending stiffness. This is why engineers use I-beams: the vertical ‘web’ keeps the top and bottom surfaces spread apart to maintain a high I . Many struts must resist bending from arbitrary directions, so a hollow, circular tube is the most efficient arrangement of material. Moreover, a hollow tube also turns out to be the most efficient shape for resisting torsion, due to the conceptual similarity of J and I and the need to maximize J . Minimizing stress or maximizing stiffness of a tube in bending, torsion, and Euler buckling would all lead to struts with the largest possible diameter and the thinnest possible walls, but in fact large-diameter tubes with paper-thin walls are not practical due to local buckling. Some insight into the relative importance of Euler versus local buckling is given by comparing the slenderness ratio (length/radius) and the thickness ratio (diameter/wall thickness); high values of either ratio suggests higher risk of local buckling (Wainwright *et al* 1982). Very long, slender stems, such as onion and dandelion flowering stalks, are hollow tubes with high slenderness ratios of over 150, but they are so lightly loaded that they appear to be at nearly the same risk of Euler buckling and local buckling.

Nature makes regular use of hollow, tubular struts, such as vertebrate long bones, insect leg segments, and various plant stems, and these must be compromises: they need a large enough diameter to limit bending, twisting, and Euler buckling, along with a thick enough wall to limit local buckling. A hollow tube can, however, be reinforced in such a way as to reduce local buckling and still allow thin walls. One way is to place transverse septa or partitions (‘bulkheads’ in engineering terms) perpendicular to the long axis of the tube, such as the nodes in bamboo stems. These limit local buckling by keeping the cross section round and preventing kinks (Ennos 2012). Obviously a rigid septum would resist compression and limit distortion of the cross section, but the nodes in plants generally seem to work instead in tension, like bicycle spokes, which allows them to be much thinner and lighter. Another way to reinforce the circular shape of a hollow tube is to fill it with a light-weight substance like air-filled pith. In some plant stems, pith is stiff enough to resist compression, but in many others, it again functions mainly in tension to keep the cross section round (Ennos 2012).

Whereas engineers generally try to prevent significant structural deflections in bending or twisting, Vogel observed that many organisms seem to have evolved more toward controlled, rather than minimized, deflections (Vogel 1992, 1995). He pointed out that the relationship between their resistance to bending (EI) and their resistance to twisting (GJ) could be biologically significant. The ratio EI/GJ thus represents the ratio of bending stiffness versus torsional stiffness. Vogel suggested that what matters biologically is not so much the stiffness but the ease of deflection, so he called this ratio the twistiness-to-bendiness ratio (Vogel 2003, pp 383–6). Many, if not most, biological struts have high twistiness-to-bendiness ratios, such as maple tree trunks at 8.3 (Vogel 1995) and daffodil stems at 13.3 (Etnier and Vogel 2000), so apparently being ‘twisty’ is beneficial whereas being ‘bendy’ is not. For example, high flexural stiffness allows the daffodil stem to support its flower, but low torsional stiffness—being twisty—allows it to reorient in wind to reduce drag.

Whereas very few plants produce active movements of body parts, movement might be considered a hallmark of animals. Most animal movements are produced by muscles. Discussion of the mechanics of muscle is beyond the scope of this review, and is well-described

in many physiology textbooks (e.g., McMahon 1984, Schmidt-Nielsen 1990, Vogel 2001, Hill *et al* 2012). For an animal with a rigid skeleton, muscles alone are not sufficient to allow it to move: the skeleton must also possess joints or articulations.

Arthropod joints are based on interspersing the hard or ‘sclerotized’ parts of the exoskeleton with small regions of thinner, flexible material—places where the exoskeleton never ‘tans’ or hardens. These can be as simple as narrow lines or folds between plates that allows a body region to expand and contract. In small crustaceans, a limb may have a small region with thinner walls and a flattened cross section. This is essentially an intentional local buckle or kink, usually with slightly more flexible walls than other parts of the leg. Larger crustaceans and most insects have ‘dicondylic’ joints, consisting of a ring of soft cuticle straddled by a pair of condyles. Each condyle is a tiny knob or projection from one leg segment that fits into a pit or groove in the next leg segment. By having a pair of condyles at each joint, one on each side of the leg, they define a hinge axis, so these joints only allow bending in one plane (like our knees). Some insects have an arrangement very much like a universal joint, with two dicondylic joints very close together and at right angles, essentially allowing the compound joint to bend in two orthogonal planes. Arthropods can get by with such joints because they are very small, very smooth, and support very little weight, so they have little friction (Ennos 2012).

Most vertebrate joints have a completely different structure, with very smooth surfaces that slide over each other, lubricated with synovial fluid. Because the cartilage that forms the bearing surface of the joint is much weaker than bone (or insect cuticle), the joint needs lots of surface area: the ends of bones that carry much weight are always expanded to form a knob or cup to increase the surface area. Also unlike the continuous exoskeleton of an insect, the bearing surfaces of bones are separate and can easily move apart, so vertebrate joints usually have an elaborate arrangement of collagen straps called ligaments holding them together, often reinforced by tendons and muscles. The ligaments play a major role in limiting joint movement, because, depending on how a ligament crosses a joint, it may become taut at one extreme of the range or the other (or even both) (Alexander 1983, p 41, Alexander and Bennett 1987). While the vertebrate joint may be structurally more complex than an arthropod joint, it allows types of movement not available to arthropods. The ball-and-socket joint—such as our hip joint and shoulder joint—is the extreme exemplar of this difference. An animal can bend a ball-and-socket joint in two planes (e.g., up and down versus left and right) as well as rotate the bone about its long axis, separately or simultaneously. A ball-and-socket joint thus has more degrees of freedom than even the universal-joint-type double insect joint.

This brief survey barely scratches the surface of research and analyses in solid biomechanics. Excellent sources for further reading in this area include books by Ennos (2012) and Vogel (2009a, 2013). Despite its age, Wainwright *et al* (1982) is still one of the best starting points for theoretical analyses, practical applications, and empirical data. And finally, James Gordon’s book *Structures, or Why Things Don’t Fall Down* (Gordon 1978) is one of the most entertaining and readable introductions to a technical topic ever written.

3. Fluids

3.1. What is a fluid?

‘Fluids’ as used by physicists, engineers, and biomechanics researchers include both liquids and gasses. Obviously liquids and gasses differ in properties like compressibility and whether they have a fixed volume, but for macroscopic, subsonic flows, liquids and gasses obey the same rules and follow the same flow patterns. For all conditions of relevance to biologists,

fluid flows can be treated as incompressible, so in these circumstances the same fundamental equations and scaling relationships apply equally to liquids and gasses. (For an outstanding introduction to a biomechanics-oriented view of fluids, see Vogel 1994.)

The fundamental mechanical difference between a solid and a fluid is that a solid resists being sheared—resists changes to its shape—but a fluid, having no fixed shape, instead resists *rate* of shear. Imagine a fluid being made up of many infinitely thin layers: for a fluid to flow, some of these layers must slide past each other, and the resistance to flow is proportional to the speed these layers slide past each other. This resistance is called *viscosity*, and is effectively the form that friction takes in a fluid.

One important fluid property is the *no-slip condition*. This condition says that fluid actually in contact with a solid surface has zero velocity relative to the surface—fluid at the fluid-solid interface stops (or moves) with the solid. Thus for any fluid to flow, it must have a velocity gradient near a solid surface where the velocity decreases to zero at the surface (such gradients are the source of the concept of ‘boundary layers’). For biologically-relevant flows, another important property is that such flows are incompressible. This condition does not mean that gasses cannot change volume, but it does mean that the forces associated with such flows are not large enough to significantly compress the gas. So for biological aerodynamics, the density of air is constant, which simplifies the analysis of air flows.

Finally, incompressibility dictates the principle of continuity: for a fluid moving through a rigid conduit, the volume moving per unit time through any one cross section must be the same as the volume per time through any other cross section of the conduit. Symbolically

$$A_1 v_1 = A_2 v_2, \quad (14)$$

where A_1 is the cross section of the pipe and v_1 is the flow speed at location 1, and similarly for A_2 and v_2 at location 2. $A_x v_x$ is the *volume flow rate* at location x , so the principle of continuity says that the volume flow rate in a conduit must be constant at any location. This can be seen as a statement of the conservation of mass for a moving fluid.

A set of formidably intricate differential equations known as the Navier–Stokes equations relate fluid flow patterns to pressures, shear stresses, densities, and viscosities. In general, the Navier–Stokes equations cannot be solved analytically, although with simplifying assumptions, they can be solved for a couple specific cases of limited biomechanical relevance. (Protists and tiny planktonic animals experience flow patterns that fit one of these cases, but the focus of this review is on macroscopic organisms, for which no useful analytical solutions exist.) Nowadays, given sufficient computing power, the equations can be solved numerically, which engineers routinely do. Animal locomotion, however, is fundamentally unsteady, with continuous and complicated changes in motion and body configuration that greatly complicate the analysis. So far, only a small handful of researchers have attempted to use Navier–Stokes-based models of situations as complex as a flying animal’s flapping wings, and such analyses are usually limited to the conditions of a single, specific wing beat cycle.

3.2. Bernoulli’s equation

Bernoulli’s equation (or principle) is actually a basic equation and several variations that define the relationship between static pressure, dynamic pressure, and manometric pressure. The derivation is beyond the scope of this article (Fox *et al* 2003, see Vogel 1994); although derived from fundamental force and momentum principles, it is often viewed as an expression of conservation of energy. The basic Bernoulli equation is:

$$P + \frac{1}{2}\rho v^2 + \rho gh = \text{constant}, \quad (15)$$

where P is static pressure, ρ is fluid density, v is fluid speed, h is height above some datum, and g is the acceleration of gravity; the second term in (15), $\frac{1}{2}\rho v^2$, represents dynamic pressure and the third term, ρgh , represents manometric pressure ('hydrostatic head'). Bernoulli's equation has some quite restrictive assumptions: no viscosity, steady flow (i.e., no changes with time), and measured along a streamline; streamlines are paths through the fluid where the velocity is always tangent to the path, meaning that flowing fluid cannot cross streamlines. One variation (which applies to two points along a streamline with no significant height difference) is particularly informative:

$$\Delta P + \frac{1}{2}\rho\Delta v^2 = 0, \quad (15a)$$

where ΔP is the difference in pressure between two points on a streamline, and Δv is the difference in speed at those two points. In this form, Bernoulli's equation illustrates that pressure varies inversely with the square of speed along a streamline: doubling the speed will produce a 4-fold drop in pressure. As a practical matter, Bernoulli's equation is primarily useful for illustrating that the static pressure will change approximately in inverse proportion to the (speed)² for large-scale external flows well away from solid surfaces (to avoid shearing and thus viscous effects). Bernoulli's equation is fundamental to fluid mechanics, but situations where it can be applied accurately in biomechanics are relatively rare, partly because of viscous effects and partly because wind and water speeds experienced by organisms are rarely high enough to significantly change the pressure. For a more detailed discussion of Bernoulli's principle and its significance (and limitations) in biomechanics, see Vogel (1994, pp 52–62; 2013, pp 115–212).

3.3. Drag

Drag is any force resisting steady (non-accelerating) fluid flow or resisting the steady movement of an object through a fluid. Drag must be overcome to move air through a trachea, water through a clam's gills, a hummingbird's wing through the air, or a salmon's body through water. The cost of performing any of these movements is thus the cost of overcoming drag. Drag has several different sources, and the relative importance of the two main ones turns out to be strongly dependent on size, as discussed below.

The most obvious source of drag is viscosity; after all, we define a fluid as a material that resists rate of shear, and viscosity is a measure of this resistance. Viscosity is given by

$$\tau = \mu \frac{d \tan(\gamma)}{dt}, \quad (16)$$

where τ is the shear stress and $\tan(\gamma)$ is the shear strain (as in (4)) and μ is the *coefficient of viscosity*, also called the *dynamic viscosity*. Unless otherwise specified, 'viscosity' is usually taken to mean 'dynamic viscosity', and I will follow that convention. A useful simplification uses the same shape shown being sheared in figure 1(c). Imagine this shape represents a region of fluid. If the surface area of the top and bottom are equal, the distance between top and bottom is d , and the top moves past the fixed bottom at speed v , then the shear stress can be written:

$$\tau = \frac{\mu v}{d}. \quad (17)$$

Equation (17) and arrangements of plates or cylinders sliding past each other are the basis for common devices used to measure viscosity.

Dynamic viscosity is a material property. If the viscosity of a fluid does not change with shear rate, the fluid is called 'Newtonian'; air and water are both Newtonian fluids. Non-

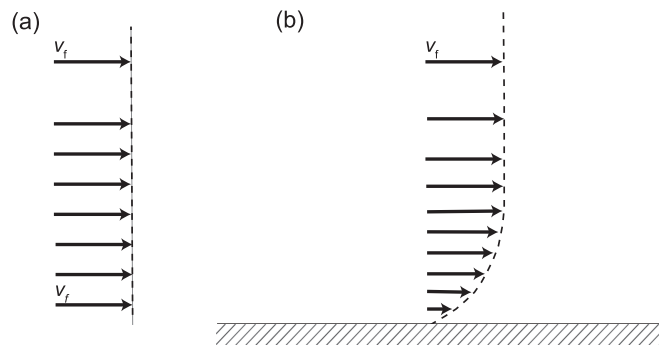


Figure 14. (a) Far from solid surfaces, velocity is constant throughout a region of fluid; this is the free-stream velocity, v_f . (b) When fluid flows over a solid surface, the no-slip condition leads to a smoothly increasing flow profile, from zero at the solid surface to asymptotically approaching the free-stream velocity far from the solid surface. Length of arrows proportional to flow speed.

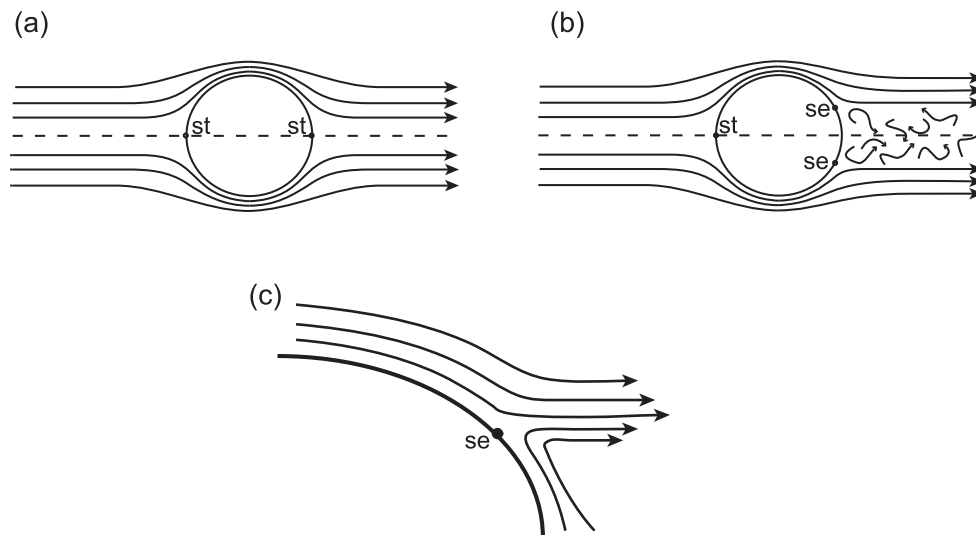


Figure 15. Fluid flowing over a cylinder. (a) In an ideal fluid (no viscosity), streamlines leaving the back are a perfect mirror image of the streamlines approaching the front; st: stagnation point. (b) In a real fluid with viscosity, streamlines do not get all the way around the back of the cylinder, leaving a low-pressure wake; se: separation point. (c) Close-up view of separation point.

Newtonian fluids can be either *shear thinning*—their viscosity decreases as shear rate increases—such as mammalian blood and modern house paint, or *shear thickening*—viscosity increases with shear rate—such as snail pedal mucus and cornstarch suspensions. A note of caution: although the dynamic viscosity of a Newtonian fluid does not change with shear rate, it is usually affected by temperature. The μ of fresh water, for example, drops by more than half as the temperature increases from 0 °C to 40 °C, whereas the μ of air actually increases slightly over the same temperature range. Viscosity can also change in response to

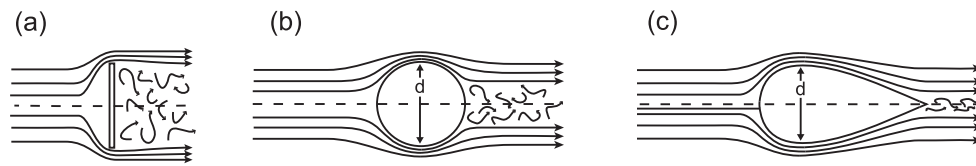


Figure 16. Wakes that produce pressure drag. (a) Flat plate perpendicular to the flow with separation points on plate edges. (b) Circular cylinder of diameter d . (c) Streamlined strut of maximum thickness d .

changing pressure, but the range of pressures experienced by living organisms are far too small to have a significant effect on air or water viscosity.

Viscosity produces drag due to the no-slip condition. Because the fluid velocity must be zero at the interface with a solid surface, fluid flowing over any solid surface will experience a velocity gradient, i.e., a region near the surface where the fluid speed increases smoothly from zero to the *free-stream velocity* v_f (velocity far from the surface; figure 14). The shearing that occurs in this velocity gradient is resisted by viscosity, and the shear stress τ divided by the surface area of the object in contact with the flow, S , gives the resisting force or *viscous drag*, D_v . Because this drag is a function of the surface area in contact with the flow, it is also called the *skin friction drag*.

Viscosity contributes indirectly to another form of drag, the *pressure drag*. Imagine a fluid flowing over a circular cylinder, perpendicular to the cylinder's long axis (figure 15). If the fluid has no viscosity, the streamlines of the fluid leaving the back will be a perfect mirror image of the fluid approaching the front. As fluid flows over the front half, the streamlines pinch together—the fluid accelerates—and as fluid flows over the back half, the streamlines spread back out—the fluid decelerates—and the fluid leaves the cylinder with the same net velocity and momentum with which it approached. A plane of symmetry divides the top and bottom flows into upper and lower mirror images; where the plane passes through the cylinder's surface, stagnation points occur, which are points where Bernoulli's equation says the flow speed is zero. (These are points in the mathematical sense and being infinitesimally small, they can be thought of as places where fluid diverges to go over the front or converges to flow away from the back.) In a real fluid with viscosity, the streamlines off the back do not perfectly mirror those on the front. Instead of traveling all the way around the back of the cylinder to the rear stagnation point, the fluid leaves the cylinder partway around at two different locations, the upper and lower separation points. Viscosity near the surface robs the fluid of some momentum by reducing its acceleration on the front, so the fluid does not have enough momentum to get all the way around the back. The flow separates from the cylinder before it gets all the way around, and the fluid directly behind the cylinder between the stagnation points forms a low pressure wake. The difference between this low pressure on the back surface of the cylinder and the higher pressure on the front produces the force we call *pressure drag*, D_p (also called *inertial drag* or *form drag*).

Pressure drag is greatest when fluid flows around sharp corners, such as the edges of flat plates perpendicular to the flow, and it can be reduced by stretching out the back face of the object and tapering it to a sharp point. Thus, a *streamlined* object has a blunt, rounded upstream surface and an extended, tapering back surface. All else being equal, pressure drag is approximately proportional to the size of the wake, and streamlining significantly reduces the size of the wake (figure 16). Consider a streamlined strut with a maximum thickness d and a cylindrical strut with a diameter of the same d (figure 16). Under some conditions, the

streamlined strut can have almost an order of magnitude less drag than the circular cylinder, even though the streamlined strut has substantially more surface area in contact with the fluid.

Viscous drag and pressure drag vary greatly in magnitude relative to each other, because viscous drag is proportional to the flow speed v , whereas pressure drag is proportional to v^2 . Researchers use a dimensionless ratio called the Reynolds number, Re , as an index of the relative importance of these two forms of drag. The Reynolds number is based on the ratio of the viscous forces to the inertial (pressure) forces, and is given by

$$Re = \frac{\rho v l}{\mu}, \quad (18)$$

where ρ is fluid density and l is some characteristic length, typically the length of an object parallel to the fluid flow. For all biologically-relevant fluid mechanical situations, knowing Re to order of magnitude, or at most, one significant figure, is sufficient precision. For $Re \ll 1$, viscosity dominates the flow and D_p can be neglected, whereas for $Re > 10^5$, pressure drag dominates and viscous drag is negligible. Most animals (and macroscopic plants) encounter flows at Reynolds numbers between these two extremes, and because living organisms tend to have complex shapes, empirical measurements may be more informative than the Re alone in determining the significance of viscous and pressure drag.

Nevertheless, the Re can be a useful way to compare organisms across size ranges. The low Re regime is the province of small, slow creatures and thick velocity gradients; at high Re , animals are big and fast and velocity gradients near surfaces are thin. The Re also helps predict turbulence. If a fluid flow follows smooth, predictable streamlines, it is called *laminar*, whereas if the flow breaks up into many tiny, chaotic swirls and eddies, it is called *turbulent*. These two states are more or less discrete and not just extremes on a continuum: a fluid flow is one or the other and normally spends very little time or space in transition. The Re was in fact developed to help predict when flows in pipes would be laminar or turbulent (Reynolds 1883). Flows tend to be laminar at low Reynolds numbers and turbulent at high Reynolds numbers, although for flows over objects, the exact transition Reynolds number is greatly influenced by factors such as surface roughness, heat transfer, and upstream fluid disturbances. Free-stream flows, wakes, and velocity gradients ('boundary layers'; see section 3.5. below) can all be laminar or turbulent, which can in turn affect drag.

3.4. Tubes, vessels, channels: interior flows

When a real fluid flows in a tube for any substantial distance, viscosity causes a velocity gradient to exist all the way across the tube's diameter. The velocity is zero at the wall, and if the tube is circular, the velocity is maximal in the center. Moreover, because the entire flow is being sheared, viscous forces are significant throughout the flow and Bernoulli's equation cannot be applied.

Osborne Reynolds developed the index that now bears his name while studying flow in pipes. He found that the Re (using radius or diameter as characteristic length) could be used to predict whether flow in a pipe would be laminar or turbulent. Although he showed that at an Re (based on diameter) of about 2000, pipe flow transitioned from laminar to turbulent, bear in mind that factors such as wall smoothness and upstream disturbances can shift the transition Re almost an order of magnitude in either direction. Nevertheless, the resistance to fluid flow in a pipe is lower for laminar flows than turbulent ones, so being able to predict whether a flow will be laminar or turbulent has practical significance.

Our focus will be on interior flow in organisms, such as circulatory and transport systems. Interior flows in animals and plants generally have Re values much lower than the

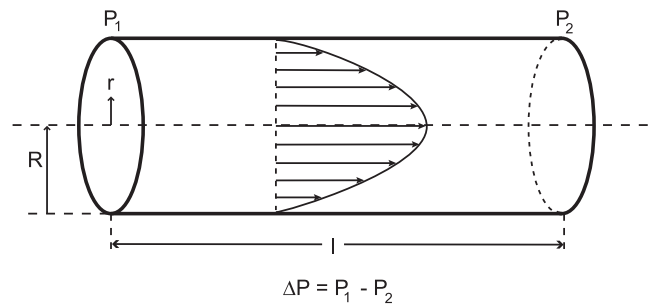


Figure 17. Fully-developed flow through a circular tube of radius R and length l . Flow velocity at any distance r from the center shown by parabolic profile (length of arrow represents speed). P_1 : upstream pressure; P_2 : downstream pressure; ΔP : pressure gradient.

transition Re of approximately 2000. Interior flows relevant to biologists will thus usually be laminar. Even very large animals with blood vessel dimensions large enough to approach the transition Re generally maintain laminar flow except during vigorous activity. Also, for reasons of material economy and wall strength, many vessels are circular, so we can apply some relatively simple equations. Because the flows are incompressible, if vessels maintain a reasonably constant volume, the continuity principle applies: the volume flow rate, Q , through any given cross section must be the same as at any other cross section. If the pipe narrows, the average flow speed must increase, and if the pipe widens, the average speed must decrease. Second, a steady-state laminar flow through a circular tube has a parabolic velocity gradient or ‘flow profile’ (figure 17). Textbooks describe ‘entrance length’ as the distance downstream from a pipe entrance for the flow profile to change from uniform ‘plug flow’ to parabolic or ‘fully-developed flow’ (Fox *et al* 2003), but entrance length is a minor factor in most circulatory systems (see Vogel 1994, pp 296–9 for detailed discussion).

Because the principle of continuity does not let viscosity slow the flow of fluid in a tube, viscosity’s effect is, instead, to reduce the pressure. Thus, the difference in pressure from the upstream to the downstream end of the flow, ΔP , is what drives the flow.

For laminar flow in a circular pipe, the flow speed v_s at any distance s from the wall is given by

$$v_s = \frac{\Delta P (R^2 - r^2)}{4\mu l} \quad (19)$$

(symbols as in figure 17). This equation gives a parabolic velocity profile as shown in figure 17. The volume flow rate, Q , is given by the Hagen–Poiseuille equation:

$$Q = \frac{\pi \Delta P R^4}{8\mu l} \quad (20)$$

which says that all else being equal, the flow rate through a tube is proportional to the tube radius to the fourth power. The maximum flow speed, $v_{\max}$, occurs at $r = 0$ (the center of the tube):

$$v_{\max} = \frac{\Delta P R^2}{4\mu l} \quad (21a)$$

and the average flow speed, $\bar{v}$, is the volume flow rate divided by the cross sectional area of the tube, which gives

$$\bar{v} = \frac{\Delta P R^2}{8\mu l}, \quad (21b)$$

so the mean speed is exactly half the maximum speed in a circular tube.

The main utility of the Hagen–Poiseuille equation in biomechanics is that it emphasizes the dramatic effect that a small change in radius can have on the volume flow rate, or in other words, a vastly greater ΔP is needed to push a given flow rate through a narrow tube than a wider one. This concept, in fact, defines the resistance to flow, R :

$$R = \frac{\Delta P}{Q} = \frac{8\mu l}{\pi R^4}. \quad (22)$$

As with many of the useful-appearing relationships we saw for solid mechanics, often these pipe-flow equations are of use to biomechanics researchers mainly as a first approximation or starting point, since the required conditions—a rigid circular pipe far from bends, forks, or constrictions—rarely apply inside animal bodies. Many vessels are circular or near circular (although our own large veins are not), but most have flexible walls and lots of bends and branches, so fully-developed flow may be rare. Moreover, hardly anything is steady—flows may be pulsatile, body fluids may be non-Newtonian (μ varying with speed), and tube dimensions may change with body movements.

Although they may not apply exactly, the Hagen–Poiseuille equations and the continuity principle suggest certain design constraints on circulatory systems. For transporting blood or other fluids over substantial distances, circular channels of the widest possible diameter will minimize resistance, as seen in the human aorta. To aid diffusion at exchange sites, slow flow and very short distances are beneficial, so a huge number of very tiny vessels (to reduce diffusion distances) with a very large, aggregate cross sectional area (to slow the flow) will improve exchange. This improvement comes at the expense of greatly increased resistance, so these tiny channels should be as short as possible. Mammalian capillaries neatly fit this entire description.

Although turbulence increases resistance to flow, it will also increase heat or material (diffusional) exchange because of the much blunter flow profile and substantial lateral transport. An example of such a situation may occur in the largest respiratory air passages of very large mammals during activity, where turbulent flow would actually assist in heat removal. For typical (smaller) animals with laminar internal flows, avoiding circular channels can improve exchange. For a given bulk flow, the average speed between parallel plates is slower than in a circular tube, which allows more time for diffusive exchange to occur. Indeed, many respiratory exchange surfaces—e.g., fish gills—are arranged as parallel surfaces (Vogel 1994, p 300).

3.5. Boundary layers

Velocity gradients—so-called *boundary layers*—can be of great biological significance. For a lucid discussion of the boundary layer concept, see (Vogel 1994, pp 156–9). In it, he warns that the term ‘boundary layer’ is inherently misleading, because boundary layers have no sharply-defined boundaries. Boundary layer thickness is, in fact, defined arbitrarily: the usual technological definition is the distance from the surface at which the flow reaches 99% of the free-stream velocity, although Vogel (1994) argued that a boundary layer thickness based on 90% of the free-stream velocity may have more biological relevance.

Boundary layer thickness increases as a fluid flows over an object. The farther downstream you measure from the front of the object, the thicker will be the velocity gradient. The slowing effect of viscosity affects fluid farther and farther from the surface as the flow moves

downstream. Numerous empirical equations exist for boundary layer thickness at arbitrary locations over flat plates and other simple shapes (Fox *et al* 2003), e.g.,

$$\delta = 5 \sqrt{\frac{x\mu}{\rho v}} \quad (23)$$

for laminar flow over a flat plate where δ is boundary layer thickness at a distance x from the front of the plate (Vogel 1994). Such equations are rarely useful for biologists because organisms are not flat plates or smooth, regular shapes, and they almost never rest on flat surfaces with sharp, straight leading edges. Nevertheless, such equations illustrate a number of useful principles. First, boundary layers grow in thickness as they flow over an object, often with a parabolic profile. Turbulent boundary layers are slightly thicker than laminar ones and so generally produce higher viscous drag. On the other hand, laminar boundary layers greatly limit material or heat transfer away from the surface, since the streamlines are all by definition more or less parallel to the surface: fluid cannot move across the streamlines. Turbulent boundary layers, in contrast, have eddies that carry fluid perpendicular to the general flow direction, so as Vogel (1994, p 158) emphasizes, any sort of exchange—gas exchange, heat exchange—will be greatly enhanced by a turbulent boundary layer near the exchange surface. Also, organisms can minimize some possibly dislodging fluid forces if they can remain partly or completely in the boundary layer. The fact that boundary layer equations cannot be applied explicitly in many biological situations is not a great hardship: many direct and indirect methods exist for measuring flow at very tiny scales (see section 5), so boundary layers can often be measured empirically.

3.6. Drag of organisms in flows

For most organisms, drag is something to be minimized if it cannot be avoided. For sessile organisms like trees or barnacles, the drag produced by air or wind currents could potentially dislodge them from their substrates. For mobile organisms like sparrows or trout, drag can be a significant component of their cost of moving about. In contrast, some organisms actually use drag productively, for dispersal, as in dandelion or cottonwood seeds, or spiderlings ‘ballooning’ on long silk threads.

Drag is a force that varies with many factors, including speed, size, shape, and viscosity. The drag coefficient, C_D , a useful dimensionless index of drag, is given by

$$C_D = \frac{D}{\frac{1}{2}\rho v^2 S}, \quad (24)$$

where D is drag and S is some reference area (discussed below). Note that rearranging the equation to put D on one side of the equal sign, as it is usually written, does not define drag. It is simply a statement that the drag coefficient relates the magnitude of the drag to the dynamic pressure. The drag coefficient is the drag per unit area divided by the dynamic pressure, and it is not by any means a constant. The drag coefficient is a function of the Reynolds number, and even for simple shapes—spheres, cylinders—the function is quite complex (e.g., see figures 5.3 and 5.3 in Vogel 1994). At Reynolds numbers below about 10, the relationship between C_D and Re is hyperbolic (although D is directly proportional to v), but at higher Reynolds numbers, the changes in C_D can be quite irregular. For example, at an Re of somewhere between 10^5 and 10^6 , the C_D on a sphere drops abruptly with increasing Re as the sphere’s boundary layer transitions from laminar to turbulent; then the C_D increases again.

The reference area mentioned above is somewhat arbitrary. For blunt, unstreamlined objects, the projected area perpendicular to the flow, or *frontal area*, is used. This area would be appropriate for sessile organisms with radial or irregular symmetry. For streamlined objects, the total surface area, or *wetted area*, is preferred. By convention, wetted area is usually considered appropriate for swimming and flying animals, although it can be extremely difficult to measure on organisms with complex shapes such as arthropods (volume to the $2/3$ power has been suggested as a practical alternative to wetted area, but has yet to come into common use; Vogel 1981, p 71). See Vogel (1994, pp 90–1) for detailed discussion of appropriate reference areas.

For swimming or flying animals, minimizing body drag can be of major benefit. Power is force times velocity, and for a swimmer or flyer, the power that goes into locomotion is the drag times the speed of locomotion. For an animal operating at relatively high Re values—above approximately 10^3 —the most effective approach is streamlining. The drag reduction due to streamlining can be startling; the C_D of a streamlined strut can be more than an order of magnitude less than a cylinder with the same frontal area. A streamlined body with a length to maximum diameter ratio of 8 has a C_{Dw} (wetted area drag coefficient) of about 5% of a cylinder in the $10^4 < Re < 10^5$ range.

Measuring the drag on a swimming animal can be quite difficult. One particularly useful way to measure the drag on the body of a live, swimming animal is to measure its deceleration between bouts of active swimming. If we know the animal's mass and its deceleration, the drag is the decelerating force, so we can calculate this 'gliding' drag from Newton's second law. Assuming the animal's propulsors—sea lion flippers, boxfish fins, diving beetle legs—are reasonably well tucked away, this gliding drag is a decent estimate of the drag on the non-thrust-producing part of the body. Body drag can also be measured by towing carcasses or models, measuring sinking speed of weighted carcasses, or placing carcasses or models in flow tanks or wind tunnels. Although subject to additional sources of error (e.g., interference drag, see Tucker 1990b), these methods can provide useful comparisons for animals with largely inflexible bodies.

In comparing the drag coefficients of a variety of animals of very different shapes, Vogel (1994) used the drag coefficient of a sphere as a blunt or non-streamlined reference value, and that of a flat plate parallel to the flow as the perfectly-streamlined reference value, for any given Re . Researchers have used a variety of methods for measuring animal drag, including gliding (usually termed 'whole body drag'), towing or flow tank measurements on carcasses or models without propelling appendages (termed 'parasite drag' for drag on the non-thrust-producing parts of the body), or calculations based on other measures of thrust. Some highly streamlined animals had drag approaching the flat plate drag, such as mackerel, $C_{Dw} = 0.0043$ at $Re = 10^5$ (Webb 1975); emperor penguins, $C_{Dw} = 0.0027$ at $Re = 1.5 \times 10^6$ (Clark and Bemis 1979); and California sea lions, $C_{Dw} = 0.0041$ at $Re = 2 \times 10^6$ (Feldkamp 1987). At the other extreme, frog tadpoles seem to be completely unstreamlined, with C_{Dw} values of 0.1–0.2 at Re between 1000 and 2000 (Dudley *et al* 1991), which is essentially the same as a sphere and four times higher than a flat plate at that Re range. Tadpoles tend to live in temporary or very shallow bodies of water, where predatory fish are not normally found, and they eat algae, so have no need to chase food; they apparently face little selection pressure to swim fast or economically.

Birds ought to be under significant selection pressure to reduce drag, and most birds certainly look streamlined. Early measurements of body drag on frozen carcasses (with wings removed) sometimes gave drag coefficients closer to spheres than flat plates, e.g., pigeons (Pennycuik 1968) and vultures (Pennycuik 1971). Later drag coefficient measurements on ducks and geese came out much lower when care was taken to smooth feathers (Pennycuik

et al 1988, Tucker and Heine 1990, Tucker 1990a), but still substantially higher than flat plate drag. Indirect methods, and measurements on models, suggest that problems achieving a life-like arrangement of feathers may cause overestimates of drag coefficients on feathered car-casses (Tucker 2000).

Flying insects operate at much lower Reynolds numbers than birds, and fruit flies (*Drosophila* species) may be near the minimum size for effective flight in air. Vogel measured parasite drag on fruit fly bodies and found $C_{Dw} = 0.17$ at $Re = 300$, about half way between a sphere and a flat plate at that Re (Vogel 1966, 1994). In contrast, a classic study of locust flight found C_{Dw} values of about the same as a sphere at $Re = 8000$ (Weis-Fogh 1956), and indeed, locusts (grasshoppers) show little evidence of streamlining. Apparently factors other than drag reduction played a greater role in the evolution of locust external anatomy. The results of a study I performed on two species of isopods (small aquatic crustaceans) serve as a cautionary tale about the importance of specifying which reference area is used for C_D calculations, as well as the relative nature of the C_D concept itself. One species was shorter, rounder, wider, and slower-swimming, whereas the other species was more elongated, less rounded, and faster-swimming. When I measured the average drag on each species and calculated drag coefficients, I found that the short, stout isopod species had a lower C_{Df} (based on frontal area) than the long, narrow one, but a higher C_{Dw} (based on wetted area) (Alexander 1990) at Re between 3000 and 9000.

At Re values below 1.0, drag becomes proportional to speed (instead of speed squared as at higher Re values). This direct proportionality leads to some simple but useful relationships, such as Stoke's law for drag on a sphere:

$$D = 6\pi r\eta v, \quad (25)$$

where r is the sphere's radius. Similar equations exist for disks and cylinders (Cox 1970, Vogel 1994). Few multicellular animals operate in this regime of thick velocity gradients and dominant viscosity, where surface area matters more than streamlining (although the appendages of some very small swimmers might fall into this range). Sinking speed, however, is one possible phenomenon that might involve low Re values in macroscopic organisms. For planktonic animals, pollen grains, fungal spores, and wind-dispersed seeds, falling or sinking speed may be biologically important. *Terminal velocity* is the falling speed at which drag, D , exactly balances the force due to gravity. For a sphere, D is given by Stoke's law, and the gravitational force is the weight minus any buoyancy due to displaced fluid. For a sphere at $Re = 1.0$, the terminal velocity, v_T , is:

$$v_T = \frac{2r^2g(\rho - \rho_0)}{9\mu}, \quad (26)$$

where g is the gravitational acceleration, ρ is the object's density, and ρ_0 is the fluid's density. If a lower terminal velocity is beneficial, increasing the surface area often evolves: the mass of fine fibers that form the 'parachute' of a dandelion seed has exceedingly high surface area, greatly reducing its v_T .

Sessile or attached organisms face the possibility of being dislodged by winds or currents, so in many cases they would benefit from streamlining. Unfortunately, if they face flows from a variety of directions, a streamlined shape is no help: if the flow is any direction other than along the streamlining's long axis, the organism will actually experience higher drag than that of a simple cylinder. Many sessile organisms are thus either cylindrical or symmetrical about a vertical axis, such as sea anemones, sessile ('acorn') barnacles, or typical trees. Acorn barnacles and limpets maintain a low profile, which can keep some or all of their

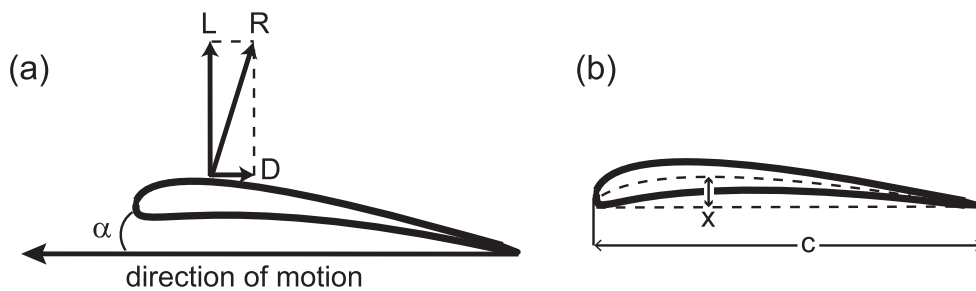


Figure 18. Airfoil (wing cross section) forces and terminology. (a) Forces on an airfoil moving at some angle of attack, α , relative to its direction of motion. D : drag; L : lift; R : resultant force. (b) A cambered airfoil of chord c with maximum height x of the mean camber line.

shells within the velocity gradient and so reduce the flow speed they experience. (Indeed, such animals may face more probability of being dislodged by lift than drag; Denny 1987.)

Some organisms seek resources best captured well away from the substrate, such as current-borne food particles captured by tall sea anemones or light captured by leaves of trees. Since these organisms cannot hide in the boundary layer, they often use shape changes to reduce drag in high current or winds. The tall sea anemone *Metridium senile* can reduce its drag by bending the tentacle-laden crown downstream, then as flow speed increases, progressively clumping the tentacles, allowing them to flex downstream and finally retracting them altogether, dropping the C_{Df} from 0.9 to 0.2 (Koehl 1977b). Or consider trees. A large, temperate hardwood tree might have a basically cylindrical trunk and a globular crown of leaves. Competition for sunlight has led most trees to evolve a long trunk without leaves or branches, and a profusion of small branches and twigs bearing most of the leaves many meters above the ground. This is a very inconvenient configuration for avoiding drag, because it puts the leaves—the main source of drag—at the end of a long moment arm, the trunk. Drag from a strong wind acting on the crown can potentially uproot the tree or break the trunk. Trees with broad leaves, however, have greatly reduced drag at higher wind speeds because they allow the leaves to deflect and reconfigure. Vogel showed how large leaves tend to roll into cones, and compound leaves collapse into cylinders, greatly lowering their drag coefficients (Vogel 1989, 2009b). He also pointed out that such leaves do not flap like flags; flapping flags have much higher drag than rigid plates of the same size, and by reconfiguring, real leaves actually showed less drag than rigid plates of the same shape.

Smaller plants also benefit from reconfiguration. Daffodils have flowers oriented horizontally and held to one side of the stem, to attract particular types of pollinators. As mentioned in section 2.4, daffodil stems have quite high twist-to-bend ratios (EI/GJ) (Etnier and Vogel 2000), so the stem twists easily. When the flower swings downwind in a breeze, the reconfigured plant's drag can be up to 30% lower than with the flower facing into the wind.

3.7. Lift

Wings are remarkable devices. For the cost of overcoming a unit of drag force, the wing generates many units of lift force. Not only do all flying animals use wings to generate lift, but the propelling appendages of most macroscopic swimmers—sea lion and sea turtle

flippers, whale and tuna tails, blue crab hind legs—function as underwater wings and generate lift.

By convention, lift is defined as a force perpendicular to the direction of the wing's movement through the fluid. Drag is defined as parallel to the motion, so lift and drag are perpendicular (figure 18). Lift and drag can be added vectorially to give the resultant force, R . Biological wings are generally cambered (convex upward), and the degree of camber is given by x/c (usually expressed as a percentage) as in figure 18. Wings are relatively large structures that operate in fast flows so they are often streamlined; the sharp trailing edge not only helps reduce drag, but aids lift production as well, as described below.

The amount of lift produced by a wing can be changed by changing the angle of attack, α (figure 18). The angle of attack is the angle between the wing's chord line and the direction of movement. Within limits, the greater the angle of attack, the greater the lift. At the risk of somewhat oversimplifying, we can think of the wing's trailing edge directing air downward as it streams off the back edge of the wing (called 'downwash'), and the downward momentum imparted to the air leads to an equal and opposite upward reaction on the wing, i.e., lift. Thus, increasing α tilts the trailing edge down and increases lift, and giving the wing camber also tilts the trailing edge downward and increases lift. Too much camber increases drag and may compromise structural strength; 10%–15% is a lot of camber.

As the angle of attack of a wing increases, the air flowing over the top must accelerate, and the higher the α , the more it accelerates. According to Bernoulli's equation, this faster air creates a low pressure zone on top of the wing, and the difference between this low pressure, integrated over the wing's upper surface, and the high pressure on the wing's lower surface, represents lift. (This and the downwash are different manifestations of the same process.) The limit to increasing the angle of attack is *stall*, which is when the flow over the top of the wing peels away from the upper surface and instead streams more or less straight back from the raised leading edge. When stall occurs on a wing, the wing's lift is greatly reduced and its drag increases. A stalled wing essentially stops flying. Stall occurs at a particular angle, the critical angle of attack, α_c , for a given wing at a given Re . At normal operating Re values, a bird's wing might stall at 20° , a large grasshopper's at 30° , and a fruit fly at 50° . The Re also affects how rapidly stalling occurs. Stalls tend to be abrupt at the Re of large birds, but quite gradual at the Re of small insects. The turbulence caused by stalling can easily be seen on high-speed videos of large birds landing; they usually stall their wings intentionally just before touchdown, causing many of the small contour feathers on the top of the wing to rise up and flutter.

The airflow over a wing, faster above and slower below, is described mathematically as a *bound vortex* (a vortex is a whirling flow like a tornado or a whirlpool). The details of such a description are beyond the scope of this review (see Alexander 2002), but the bound vortex, which can seem like a mathematical abstraction, leads to the very tangible *tip vortex* or *trailing vortex*, a swirling air pattern that trails off the tip of every wing that is producing lift. Tip vortices have been shown to have potential benefits for formation flight, such as the characteristic 'vees' of geese (Cutts and Speakman 1994, Weimerskirch *et al* 2001).

Just as the C_D is a useful way to describe drag, the lift coefficient, C_L is a scale-independent way to describe lift, and the defining equation takes the same form:

$$C_L = \frac{L}{\frac{1}{2}\rho v^2 S}, \quad (27)$$

where L is the lift force. The reference area S is always planform area (the projected area of the wing looking down on it from above) for C_L , and so for consistency, planform area should always be used as the reference area for drag coefficients of wings (and hydrofoils). Again,

note that rearranging the equation to put L on one side of the equal sign, as it is usually written, does not define lift. It is simply a statement that the lift coefficient relates the magnitude of the lift to the dynamic pressure. And as with the C_D , the C_L is not constant, but is a function of both Re and α .

The equation for the lift coefficient illustrates that, all else being equal, lift will be proportional to v^2 and to S . A small change in speed thus can have a much larger effect on the magnitude of lift. Speed and angle of attack interact, so flyers in high-speed cruise mode will fly fast and at low α (hence low C_D), whereas when preparing to land, they will fly slowly at high α , which may take more effort (due to higher drag) but is slower and more precise. The amount of lift on a wing is also proportional to wing area, meaning that if an animal can change the shape of its wing to change the area, the animal can use shape change to change the lift as well. Birds, especially, are well-known to flex and extend their wings to adjust lift production (Brown 1953, Tucker and Parrott 1970).

Wings experience an additional form of drag known as *induced drag* (with the coefficient C_{Di}). A wing moving at the angle of attack that gives zero lift (this is in fact a negative α for a cambered wing) experiences friction and pressure drag but no induced drag. As soon as the angle of attack increases and the wing starts to produce lift, it also starts experiencing induced drag, and the greater the lift, the greater the induced drag. The induced drag is the 'cost' of producing lift: the power that goes into overcoming the induced drag is literally a measure of the energetic cost of generating lift.

If we want to know how effective or efficient a wing is, we need to know more than just how much lift it generates. A wing's lift-to-drag ratio, L/D , is what really describes a wing's effectiveness. (The L/D is sometimes called a wing's 'efficiency', but given that L/D can greatly exceed 1.0, it does not really fit the usual concept of efficiency.) The higher the L/D , the more effective the wing. Consider two wings, wing A with $L/D = 15$ and wing B with $L/D = 5$. If I push on wing A with a force of 100 N to overcome drag, the wing generates 1500 N of lift. If I push on wing B with 100 N, wing B only generates 500 N of lift. Although the ratio is not, itself, efficiency in the usual sense, the L/D is related to traditional efficiency because the D in the denominator of the ratio is related to the cost of producing lift; a wing with high L/D will thus be more energetically efficient than a wing with low L/D . Wings with high lift-to-drag ratios are thus advantageous for long distance or long duration flight.

Wings tend to become less effective as the Re decreases. Airplanes and large birds operate at $Re > 10^5$ and usually have lift-to-drag ratios in the range of 10–15. Small birds like sparrows typically have ratios of 5–9, as do the largest flying insect like large dragonflies. Values of L/D for small insects like fruit flies can be as low as 2 (Alexander 2002). This Reynolds-number effect is because thicker boundary layers interfere with the formation of the flow patterns (specifically, the bound vortex) that generate lift. Small, slow wings are inherently less effective than large, fast wings.

Wings that maximize L/D are typically those that minimize drag. Because the induced drag is related to the tip vortex, reducing the tip vortex strength will reduce the induced drag. This can be done by making the wing long and narrow. The distance from wingtip to wingtip is a wing's span, and by increasing a wing's span/chord while keeping S constant, the wing effectively has less tip for a given area. The span/chord is called the wing's aspect ratio, AR , and all else being equal, a wing with a high AR has a higher L/D . (Technically, the aspect ratio is only span/chord for rectangular wings; for other shapes, $AR = [\text{span}]^2/S$). Obviously, real wings face structural constraints and conflicting functional trade-offs. Bumblebees and red-tailed hawks have aspect ratios of approximately 6 or 7, fairly typical for generalist flying animals (as well as small airplanes). Specialist soaring birds—especially seabirds like pelicans and albatrosses that do not have to worry about flying through forests—

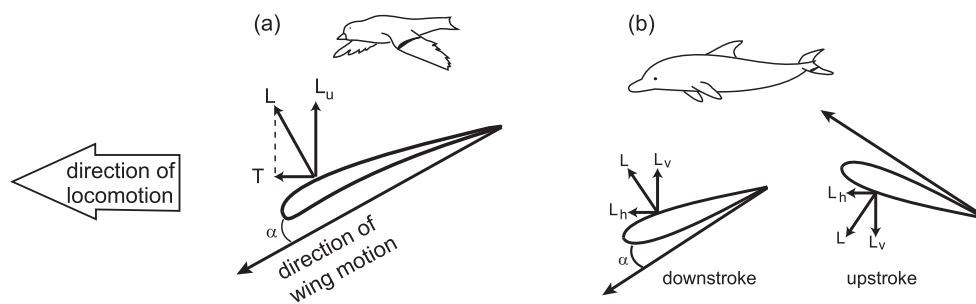


Figure 19. Forces on a flapping airfoil. (a) A bird's wing moves down and forward on the downstroke, and this tilts the lift vector forward to produce thrust as a horizontal component. (b) Upstroke and downstroke of a flapping hydrofoil (porpoise's tail), where the horizontal component of the lift, L_h , represents thrust, and the vertical components of lift, L_v , on the upstroke and downstroke cancel. L : lift; L_u : upward component of lift; T : thrust; α : angle of attack.

have aspect ratios of 11–15 (Tennekes 1996). (Conventional airplanes mostly have aspect ratios in the same range as generalist flying animals, although specialized sailplanes can have aspect ratios more than twice those of soaring seabirds; Alexander 2002.)

3.8. Flying and swimming

Contrary to popular belief, flying animals flap their wings to produce *thrust*, not lift. If a flying crow stops flapping its wings, leaving them outstretched, it will glide, and a gliding wing produces lift quite nicely.

Gliding is essentially gravity-powered flight. A glider uses gravity to accelerate downward until the resultant force, R , exactly equals its weight, at which point it no longer accelerates and is in a steady glide. Gliding thus must always be downward relative to the air. It is analogous to coasting downhill on a bicycle; as long as it is on a downward slope, the bicycle moves, just as a glider will keep flying as long as it descends. Moreover, the L/D dictates a glider's glide angle (the angle at which it descends below the horizontal). A bit of geometry shows that L/D must be the same as the *glide ratio*, which is the number of meters the glider moves forward for every meter it descends (Alexander 2002, pp 38–9). A high L/D means a high glide ratio and low glide angle, which is of great benefit to a glider.

Some animals can only glide. Flying squirrels, flying lizards, flying frogs: these animals have no way to produce the thrust needed to overcome drag and fly level, so they are limited to downward glides. They always land lower than they started. Some specialized birds engage in soaring, where they use air that is rising faster than the bird descends, so they are able to remain aloft by passive gliding. These birds all have high lift-to-drag ratios, either due to high aspect ratios or due to modified wingtips that give some of the effects of high aspect ratios (slots between tip feathers, 'separated primaries'; Alexander 2002).

If an animal flies level continuously or climbs, it needs to have some source of thrust, a forward force to overcome drag. Flying animals flap their wings to produce thrust, and the most important part of the flapping stroke is the downstroke. During the downstroke, a flapping wing moves down and forward, at some positive angle of attack. As a result of the downward movement, the lift vector tilts forward (figure 19(a)). The upward component of lift supports the flyer's weight. The lift also has a horizontal component directed forward, and this horizontal component is the thrust. Thrust production is the function of flapping, and if

thrust equals total drag, then the flyer will be able to maintain level flight, thus overcoming the downward requirement of gliding. Increasing the thrust allows climbing, and decreasing the thrust allows descent.

Upstrokes can vary greatly, depending on the type of animal. They can be a largely passive recovery stroke, with angle of attack and area adjusted to minimize forces, as in most medium and large birds. In contrast, some small flyers like houseflies can generate a significant amount of thrust during the upstroke (Alexander 2002, pp 80–5). Nevertheless, the thrust and the vertical component of the lift are largest during the downstroke even for animals with such an active upstroke. In any case, the forces must be large enough so that, averaged over the whole stroke, the thrust balances the drag and the vertical component of lift balances weight.

A great many medium-sized and large animals swim with lift-producing appendages—penguins, sea turtles, tunas, and whales, for example. These swimmers are very near the same density as the water they inhabit, so little or none of their locomotory effort needs to go into supporting their weight. Consider the tail of a cetacean such as a porpoise. It flaps up and down like a bird wing, but since the porpoise needs no net upward force to support its weight, the downstroke occurs at a positive angle of attack and generates lift upward and forward, with a horizontal component providing thrust. The upstroke uses a negative angle of attack, so the ‘negative’ lift vector points down and forward, forming an upside down mirror image of the downstroke (figure 19(b)). The vertical components (L_v) of the upstroke and downstroke cancel, and the horizontal components (L_h) provide an near-continuous forward thrust. The stroke can be tweaked a bit to give a bit of net downward force for positively buoyant animals—those slightly less denser than water, like penguins at shallow depths—or a bit of net upward force for negatively buoyant animals—like whales and seals at great depths—but the vertical forces involved are tiny compared to the horizontal forces of swimming.

Take this porpoise tail-beat pattern and turn it on its side, so the motion is side-to-side instead of up-and-down, and it becomes the tail-beat pattern of many large, fast-swimming fish such as tunas and swordfish. These animals swim with a stiff body that narrows down to a slender extension that connects to a tall, narrow, crescent-shaped tail. Such fish swing the tail vigorously from side to side while keeping most of the body rigid. Biologists call this pattern thunniform swimming (named after the genus *Thunnus*, a genus of tunas). The other extreme is the pattern used by eels (called anguilliform swimming, after *Anguilla*, the genus of the common eel) where the animal passes waves of bending down the whole body from snout to tail. The body typically has more than one full *S*-curve at any one instant, and the amplitude of the waves increase as they move toward the tail. In between is what is probably the most typical fish swimming mode, the carangiform mode (named after *Caranx*, the genus of the jacks), as used by trout, carp, perch, and other generalized fish. In carangiform swimming, the front of the body is stiffer than in the eel but not as rigid as a tuna, and the bending wave starts at the head but has very low amplitude until it is about half way down the body when its amplitude increases dramatically; also, the body always has less than one full *S*-curve at any given time. The exact physical explanation of how these waves of bending generate thrust is considerably more complex (and less well-understood) than generating lift on an airfoil or hydrofoil. One way to think of the process is to imagine the waves of bending producing a flow pattern at the outside of each curve that has properties analogous to the bound vortex of a wing, and when the curve reaches the tail, it sheds a vortex into the water as the tail reverses direction at the lateral extreme of the stroke. Vortices shed on the left side turn in the opposite direction from vortices shed on the right side, and the momentum imparted to the water when the vortices are shed reflects the equal and opposite reaction of moving the fish forward.

Although quite a few swimmers use lift-based mechanisms, at least two other categories deserve mention. One is *jetting*, used by squid and other cephalopod molluscs, jellyfish, and some dragonfly naiads (larvae). Biological jetting involves filling an expandable chamber with water, and then forcibly contracting the walls of the chamber to eject water, often through a narrow orifice. A simpler demonstration of Newton's third law of equal and opposite reactions is hard to find: a squid expels a given volume of water at a given speed from an orifice under the head to jet backward. The momentum of the expelled water in one direction must equal the momentum of the squid's body in the opposite direction. Simple it may be, but efficient, it is definitely not. The Foude propulsive efficiency, η_F , is:

$$\eta_F = \frac{2v_1}{v_2 + v_1}, \quad (28)$$

where v_1 is the fluid speed before it is accelerated and v_2 is its speed after it has accelerated (v_1 is usually the body speed of a swimming animal) (see Vogel 2003, p 142 for derivation). If the goal is to add as much momentum as possible to the water, (28) suggests that a swimmer should accelerate a lot of water a small amount rather than accelerating a little water to a very high speed. A hydrofoil like a tuna tail imparts a small speed increase to a large volume of water and is thus relatively efficient; a jetting squid imparts a large increase in speed to a small volume of water by ejecting it through a small orifice, and is thus inefficient. For a sudden burst of speed to evade a predator, the inefficiency of jetting may be tolerable, but as a form of long-distance locomotion, it is hopelessly expensive. In fact, squid use their fins (and lift-based thrust) for slow, long-distance cruising.

Many swimmers use drag-based mechanisms rather than lift-based ones. The concept for drag-based swimming is simple: orient a paddle-like appendage broad side to the flow during the power stroke, and then 'feather' it—turning the broad side parallel to the flow—on the recovery stroke. If the power stroke is backward, the drag will be high as the paddle moves backward, producing thrust as an equal and opposite reaction forward. By feathering the paddle to move it forward on the recovery stroke, the drag will be much lower. The backward force from the recovery stroke will be much lower than the forward force of the power stroke, yielding a net forward force. A duck swims this way by fanning out the toes of its webbed feet on the backward power stroke, and collapsing them together in a tight bundle for the forward recovery stroke.

Drag-based paddling is simple and easy for many partly terrestrial animals like ducks and freshwater turtles but it has a major drawback: the animal's top swimming speed is exactly the maximum speed at which the swimmer can move its paddle backward. Lift-based locomotion does not have any such strict speed limit. Vogel generated a nice thought experiment to show that similar appendages can be used for either drag-based or lift-based swimming with only minor adjustments to the motion. His key result was that drag-based methods can generate very high thrust at low speeds, which may be an advantage for quick acceleration from rest. The lift-based appendages, however, operated over a much greater speed range with a top speed five times higher than the drag-based appendages, and at those speeds tend to be more efficient (Vogel 1994, pp 284–5), at least at higher Reynolds numbers. At lower Reynolds numbers—less than approximately 1000—wings lose efficiency. Boundary layers get thick, impeding bound vortex formation, so C_L decreases. At the same time, viscous drag increases, further decreasing L/D . For small swimmers, such as small crustaceans and aquatic insects, the performance advantage of lift-based swimming may become negligible. Shrimp swimmerets and diving beetle legs, for example, have a fan of bristles that passively spread out for the power stroke and collapse down for the recovery stroke, clearly using the drag-based

mechanism. This is a common arrangement for the swimming appendages of many small, swimming crustaceans.

3.9. Suspension feeding

Many aquatic animals feed on fine organic particulates (including planktonic organisms) suspended in the water. Some such animals are sessile and depend to a greater or lesser degree on ambient water currents to bring food to them. Others are mobile and collect particles as they swim. Both were traditionally called ‘filter feeders’, but thanks to a now-classic paper by Rubenstein and Koehl (1977), a few decades ago biologists realized that few such animals actually ‘filter’ in the sense of sieving or collecting particles too large to pass through a mesh. Suspension feeders typically collect particles much smaller than the gap between elements of the filtering array. These particle capture structures, such as the feeding tentacles of coral polyps, cirri of barnacles, sieve-like gills of clams, or bristle-covered feeding appendages of tiny crustaceans like *Daphnia* (water fleas), all operate at low Reynolds numbers, usually less than 1.0. At these Re values, the velocity gradients (boundary layers) can be so thick that surprisingly little water flows between the mesh elements, even though they appear visually to be very porous. At these Reynolds numbers, a mesh that has a frontal area only covering 50% of the area perpendicular to the flow may only transmit 10% of the flow; the other 90% goes around rather than through. Appendages that look to us like filters may in fact act more like spoons or paddles, scooping up individual particles (Koehl and Strickler 1981).

If these collectors do not work as sieves, how do they catch particles? Rubenstein and Koehl described several possibilities (reviewed and expanded upon by Shimeta and Jumars 1991). For example, if a particle is denser than water, its inertia might carry it straight into a mesh element as the streamline curves away, or the particle might sink out of its streamline onto the top of a mesh element as it passes over. Many of the ‘particles’ are mobile plankton and if they move randomly or haphazardly as they are carried along by the flow, their own movements may bring them into contact with a mesh element. What causes the particle to stick (or not) and how it is handled after contact with the mesh is subject to huge variation, see work by Koehl, Loudon, and their colleagues for general discussion of the scale-dependent aspects of particle collection (e.g., Cheer and Koehl 1987, Koehl and Cheer 1987, Loudon *et al* 1994).

Some suspension feeders are entirely passive and depend on ambient currents to bring particles into their capture devices, such as the web-like traps of caddisfly larvae or the tentacles of tubeworms or sea anemones. Others actively pump water through internal collection devices, such as bivalve clams, sponges, and tunicates. Yet others, like barnacles, hold out their collecting appendages passively when currents are fast, and actively sweep them through the water when currents slow down. Active sweeping has the advantage of increasing the speed, which in turn increases the Reynolds number, allowing a greater fraction of the water to go through rather than around the collectors.

Sessile suspension feeders must deal with living to some extent in a velocity gradient. In a river, where the current direction is constant, an animal might choose to live near the upstream edge of a rock or ledge where the boundary layer would be thin, but such a location might also be dangerously susceptible to scouring by sand and gravel in high water or floods. Most sessile suspension feeders must deal with boundary layers as best they can, either being tall enough to get above it or using some active pumping or sweeping to augment ambient currents.

Several kinds of fish are suspension feeders, and they all generally use the same method. Most fish have gill rakers: tiny, finger-like structures that project into the water current

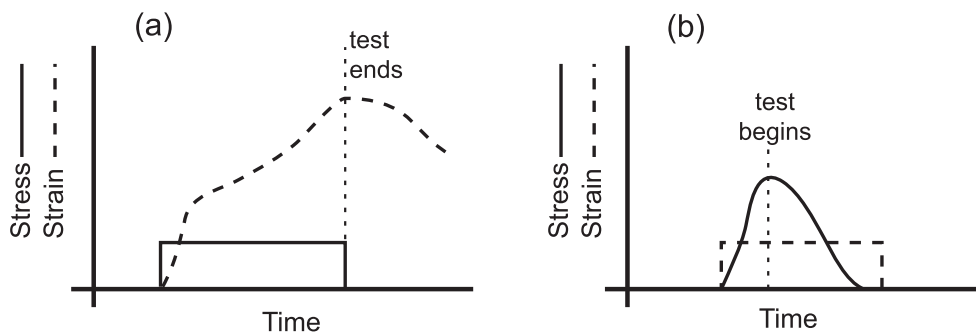


Figure 20. Tests of viscoelastic material. (a) In a creep test, a fixed stress is applied and strain continues to change over periods that can range from seconds to months. Measurement begins when stress is applied and ends when stress is removed. (b) In a stress-relaxation test, a fixed strain (deformation) is applied while monitoring stress over time. Measurement usually starts when stress begins to decrease and ends when stress reaches zero.

between the oral cavity and the gill cavity, upstream of the gills. In non-suspension-feeding fish, the gill rakers prevent debris from getting into the gills. Such fish also usually have a pumping arrangement to move water over their gills. In suspension-feeding fish, the gill rakers are finer and more numerous, and the fish simply swims through a cloud of plankton with its mouth open, forcing water through the rakers, through the gills, and out the opercular opening. For these fish, swimming provides the water currents for both swimming and gill ventilation (biologists call this ‘ram ventilation’ and in addition to suspension feeders, it is used by many fast-swimming fish like tuna and sharks).

4. Biology blurs the boundaries

4.1. Viscoelasticity

Most biological materials do not fit perfectly into the solid or fluid categories as engineers and physicists have usually defined them. Many biological structures that we would ordinarily consider solid actually have a time-dependent response to loading that gives them a partly fluid character. A proper Hookean material behaves the same way whether it is loaded for a second or a week: remove the load and it returns to its original shape. A viscoelastic solid, however, displays a property called *creep*: apply a load briefly and the material will spring back just as if it were Hookean. Apply the same load for a prolonged period, however, and the material will continue to deform gradually. When the load is removed, the material may have acquired a permanent deformation, and if so, the longer it is loaded, the greater the permanent deformation. Wooden bookshelves sometimes exhibit this trait. If the shelf is too long between supports, or if the load is too large, the shelf will gradually sag, and will retain the sag after the load is removed. Another way of viewing the same phenomenon is shown by using a constant strain. If a constant strain (deformation) is applied to a viscoelastic material and then we measure the stress, the stress in the material will start out high but then will gradually decrease. These two ways of demonstrating viscoelasticity are the basis for two of the standard tests for viscoelastic properties.

In a creep test, a constant stress is applied continuously. Some materials may creep significantly in a few seconds, whereas other may require experimental durations of many

days to show significant creep (figure 20(a)). In a stress-relaxation test, a fixed strain is applied, and the stress is measured as it diminishes over time (figure 20(b)). A viscoelastic material has no fixed Young's modulus, although the initial 'instantaneous' stress and strain are sometimes used to calculate an 'unrelaxed elastic modulus', E_u ; often the reciprocal, the 'unrelaxed compliance', $D_u = \epsilon/\sigma$, is used instead (Wainwright *et al* 1982, pp 26–8). Researchers can use the results of a creep test to plot E versus time. A further step is to measure 'retardation time', which is the time for the elasticity to fall from E_u to E_u/e (where e is the base of natural logarithms). Retardation time can be used as a single value to characterize a viscoelastic solid. More or less the same thing can be done with a stress-relaxation test, plotting σ over time and measuring the 'relaxation time', t_r , which is the time for the stress to fall from its initial value of σ_0 to σ_0/e . The relaxation time is also given by

$$t_r = \frac{\mu}{E_u} \quad (29)$$

so t_r is a direct measure of the viscous behavior of the viscoelastic solid. Due to the complex nature of viscoelastic mechanisms, retardation time and relaxation time are not typically the same.

Another way to examine viscoelastic behavior is to use dynamic testing. This consists of applying continuous sinusoidal cycles of loading and unloading, and measuring stress and strain. Such tests are analogous to the tests we saw in section 2.2 for measuring resilience, only in this case, the stress–strain graph illustrates that the stress lags the strain. The amount of lag is given by the phase angle² δ , which is given by solving for δ in the equation:

$$\sigma = \sigma_{\max} \sin(\omega t + \delta), \quad (30)$$

where $\sigma_{\max}$ is the maximum stress, ω is the angular velocity of the cycle, and t is the time when σ is measured. The phase angle can be used to calculate the storage modulus E' (energy stored elastically per cycle) and the loss modulus E'' (energy dissipated per cycle) (Wainwright *et al* 1982, p 32). Energy is dissipated by viscous properties, so materials with high δ , and hence high E'' , have a prominent viscous component to their viscoelastic behavior. Biological materials tend to have much higher phase angles than engineering materials.

Some biological materials—e.g., bone—behave more like Hookean solids and show only a little creep (and have low δ). Others are rather floppy and show substantial creep over shorter time intervals (and these have higher δ). For example, mesoglea is the soft nonliving structural material that makes up most of the body wall of sea anemones and jellyfish. It is a polysaccharide gel reinforced with collagen fibers. Sea anemones have a cylindrical body wall with a crown of tentacles at the top (see section 3.6) and they are capable of contracting the body down to a small mound of less than $\frac{1}{4}$ of its fully-expanded height. Several studies have shown that at loads that give instantaneous strains of 0.2, 10 h later the strain increases to >10 (Alexander 1962, Koehl 1977a), with a retardation time of on the order of 1 h (Vincent 1990). This correlates well with a sea anemone's biology: stiff under quick, brief loading to resist wave action, yet compliant over long periods to allow slow—minutes to hours—body contraction and expansion (Ennos 2012).

Mucus is a dilute gel of about 2% (or less) mucopolysaccharides or glycoproteins in water, forming a material with both fluid and solid properties. A huge variety of animals use mucus for a wide range of different purposes, from collecting food particles to protecting delicate surfaces. Snails and slugs use it for locomotion, and their form of locomotion would be impossible without the strange behavior of their mucus. In an elegant series of experiments, Denny showed that at strains less than about 5—very high for most solids but low for

² Not to be confused with boundary layer thickness, which uses the same symbol.

mucus—the mucus acts like a floppy solid of very low stiffness. At higher strains, the mucus softens, and flows like a viscous liquid (Denny and Gosline 1980, Denny 1984). A snail glides by using its mucus like a ratchet, pushing on it when it acts like a solid and sliding over it when it acts like a fluid, using tiny waves of contraction that travel along the bottom of its lower surface or ‘foot’ (for details, see Ennos 2012, pp 48–50; Vogel 2003, pp 362–3).

4.2. ‘Soft’ skeletons

Humans have a rigid internal skeleton of bone, so we are used to thinking of columns—like our legs—or cantilevers—like our arms—supported by hard, internal structures. Not all animals follow this pattern. Many support their bodies using pliant or flexible materials. The mesoglea of a sea anemone in the previous section is a simple example. Another common example is the hydrostatic skeleton, capable of much greater force transmission, and faster and more complex movements than those supported by mesoglea.

Hydrostatic skeletons made of pressurized cylinders can be rigid, yet with walls that only experience tension they can be made with ‘cheap’ tensile materials. Most animal hydrostats are water-filled spaces surrounded by tension-resisting fibers. One simple way to arrange such fibers is to have hoop-shaped fibers running around the circumference to resist expansion in diameter, and longitudinal fibers running lengthwise to resist lengthening; this is the ‘orthogonal’ reinforcing arrangement. This arrangement is actually very rare in nature, so far only found in mammalian penises. A much more common arrangement is for the fibers to be helically wrapped around the cylinder like corkscrews, with some fibers in left-handed helices and others in right-handed helices. Almost all biological hydrostats use such crossed, helically-wound reinforcing fibers, and the fibers usually have at least some freedom to slide past each other. Geometry plays a somewhat surprising role with such cylinders: orthogonally-reinforced hydrostats cannot change length or diameter once pressurized, and are easy to twist but hard to bend, and are prone to kinking. Helically-wound hydrostats, in contrast, resist twisting (because of the angled fiber orientation), resist kinking, are easy to bend, and under some circumstances can change length and diameter. Geometry dictates that the volume of the cylinder will be maximized when the angle of the reinforcing fibers is 54.7° relative to the cylinder’s long axis. This is strictly a geometric constraint that has nothing to do with material properties, assuming the fibers are basically inextensible at biological pressures. Because maximum volume occurs at a fiber angle of approximately 55° , if the fiber angle is high—lots of turns in a given length—then increasing the pressure will tend to lengthen and narrow the cylinder to make the fiber angle closer to 55° . If the fiber angle is low—few turns in a given length—the opposite is true: increasing pressure will tend to make the cylinder shorter and wider so the fiber angle gets closer to 55° . Oddly enough, biological hydrostats mostly use fiber angles well away from 55° . Nematodes (roundworms) for example, have a helical fiber-reinforced outer body covering or cuticle with a fiber angle of approximately 75° . Their only muscles are longitudinal, which would tend to shorten the body if they all contracted together. Because of the high fiber angle, the body would need to increase in volume in order to shorten, but with body contents mostly of water, its volume cannot change. So when the muscles contract, they produce very little shortening but a large increase (up to 30 kPa) in internal pressure. The high pressure stiffens the body and opposes bending. Thus, when muscles on one side contract, the body will form a smooth curve with the fiber-reinforced cuticle acting as an antagonist to the longitudinal muscles. In life, nematodes squirm through their environments using waves of bending, without getting shorter and using only longitudinal muscles. See Vogel (2013, pp 408–21) for many examples of biological hydrostats.

Hydrostats do not have to be hollow. Kier and Smith (1985) pointed out that many fleshy appendages—e.g., mammal and lizard tongues, squid tentacles—are nearly solid muscle, yet function as hydrostats. Because muscle tissue is mostly water, it is for all practical purposes incompressible. These ‘muscular hydrostats’ have various combinations of longitudinal, transverse, and helically-arranged muscle ‘fibers’ (cells), which can produce shortening, lengthening, bending, and twisting. Some have specialized arrangements to give them amazingly fast movements (e.g., squid tentacles, chameleon tongues), great strength (elephant trunks) or great dexterity (octopus arms, giraffe tongues). For more details of the operation of muscular hydrostats, see Kier (1992).

Viscoelastic solids and hydrostatic skeletons are just two of the better-studied topics among many areas of biomechanics that differ greatly from conventional engineering technologies. A brief sample of other such topics include non-Newtonian fluids, unsteady aerodynamic effects in animal flight, added-mass effects in animal swimming, gecko feet and other reversibly adhesive structures, boundary layer effects on cutaneous gas exchange, compliant and shape-adjustable wings, mechanics of tree roots as anchors, drag reduction by skin microstructure or mucus, mechanics of intermittent jet propulsion in squid and jellyfish, rapid movements in plants such as Venus fly traps, energy storage in elastic tissues to aid locomotion, or mechanics of plant physical defenses against herbivores. The interested reader should consult books by Alexander (2003), Ennos (2012), and Vogel (1994, 1998, 2009a, 2013) for an introduction to such topics.

5. New directions

Many biomechanics studies in the mid to late 20th century used methods and equipment borrowed straight from engineers. As research questions and theoretical analyses became more sophisticated, researchers realized that the wet, floppy, irregular bits of animals and plants that they studied were not well-matched to traditional engineering equipment. Biomechanics researchers began to develop their own techniques. Some proved to be elegant in their simplicity, such as the weight hanging from a spiral pulley that Vogel and Papanicolaou (1983) used to apply a constant stress as the cross sectional area changes in creep tests on viscoelastic material. Similarly, Farran *et al* (2008) modified a standard universal testing machine with parts from a simple pair of toenail clippers to measure fracture properties of keratinous structures. Only slightly more complex, the portable toughness tester of Darvell *et al* (1996) is designed specifically to test floppy or compliant materials in the type of field setting commonly faced by biologists. Sonomicrometry, using tiny piezo crystals to measure very small displacements acoustically, lets researchers measure soft tissue displacements in living animals (Biewener *et al* 1998). Other techniques require more expensive equipment and computerized data analysis. At the very low end of the strain spectrum, laser speckle interferometry allows researchers to measure strains of stiff materials such as teeth non-invasively and at smaller strains than permitted by traditional strain gauges (Zaslansky *et al* 2006). In contrast, large strains of compliant structures like skin can be measured by computer-aided optical correlation (Da Fonseca *et al* 2005). In the fluid realm, another laser-based technique, digital particle image velocimetry uses laser sheets to illuminate neutral-density particles in air or water that are assumed to follow the flow patterns. The particle density is too high to follow particles individually, so sophisticated autocorrelation or signal processing algorithms are used to extract flow patterns from successive, high-resolution digital video images. This allows reconstruction of very fine details of the flow pattern, all without any physical probes or flow disturbances (Crandell and Tobalske 2015). High speed

photography (nowadays normally video) has long been a mainstay of many areas of biomechanics (Alexander 1986), and prices of high-speed video systems have decreased as ease of use and versatility has increased in recent years. For instance, based on kinematics measured from such videos, researchers studying insect flight have developed a series of scaled, dynamically-similar physical models of flapping insect wings. These range from the ‘robomoth’ of Ellington’s lab that aided in the discovery of the leading-edge vortex (Ellington *et al* 1996) to the most recent computer-controlled models of crane fly wings (Ishihara *et al* 2009) and hawkmoth wings (Cheng *et al* 2011). As a result of the ever-increasing computational power of computers, modeling of animal flight continues to become more detailed and realistic, to the point that such models accurately predict forces and moments on the wings and bodies of hovering insects (Liu and Sun 2008).

Although comparative biomechanics may never achieve the number of researchers or amount of resources devoted to, for example, molecular genetics or aerospace engineering, it has become securely recognized as a valuable area of biological research. Although a small field, its productivity has grown over the past few decades, and with the recent promotion of the concept of biomimicry, it has even begun to produce useful practical insights, such as removable adhesives based on gecko feet and miniature aerial vehicles based on flying insects³.

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³ A book-length treatment of the topic of this review is in preparation by the author.

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