The word *skeleton* invariably conjures up an image of the articulated bones hanging in the corner of the high school biology classroom, or perhaps in the corner of the general practitioner’s office. However, jointed bones are only one form of skeletal system. Nearly all multicellular animals, even invertebrates, require a skeleton for movement. The only exceptions to this rule are those small, aquatic metazoans that may move exclusively by cilia. A functional definition of the word *skeleton* is

A solid or fluid system permitting muscles to be stretched back to their original length following a contraction. Such a system may or may not have protective and supportive functions as well.

A skeletal system is essential simply because muscles are capable of only 2 of the 3 activities required for repeated movements: Muscles can shorten or relax, but they cannot actively extend themselves. To bend your arm at the elbow, one set of muscles, the biceps, must contract. This contraction of the biceps not only causes your arm to bend at the elbow, but also serves to stretch another muscle in your arm, the triceps (Fig. 5.1). The triceps can now contract, making it possible for you to reextend your arm. Reextension of your arm, in turn, serves to stretch the biceps. The bones in your arm have functioned in these movements as the vehicle through which the triceps and biceps take turns stretching each other back to precontraction length; that is, the muscles *antagonize* (act against) each other, making controlled, repeatable movement possible. In vertebrates, the mutual antagonism of muscles is mediated through a solid skeleton. A rigid skeletal system is essential in a terrestrial environment, in part because the skeleton must also serve to support the body in a nonsupportive medium (see Chapter 1). Aquatic organisms are supported by the medium in which they live, so a rigid skeletal system is not required.
2. that this cavity be surrounded by a flexible outer body membrane, so that the outer body wall can be deformed;
3. that the volume of fluid in the cavity remain constant; and
4. that the animal be capable of forming temporary attachments to the substrate, if progressive locomotion is to occur on or within a substrate.

Let us assume that these 4 attributes are met in the hypothetical organism shown in Figure 5.2. This cylindrical being is equipped with longitudinal muscles only. If this animal attaches at point X (as shown in Fig. 5.2a) and then contracts its musculature, the increase in internal hydrostatic pressure will deform the outer body wall, resulting in a shorter, fatter animal (Fig. 5.2b). This animal can regain its initial shape only if it is surrounded by a stiff, elastic covering that will spring back to its original shape upon relaxation of the longitudinal musculature. Such a stiff covering could be difficult to deform in the first place and is not commonly encountered among unjointed invertebrates.

Instead, we add a second set of muscles (circular muscles) to our hypothetical animal. Forward locomotion then results from the series of contractions illustrated in Figure 5.3. In (a), the circular muscles are contracted, and the longitudinal muscles are stretched. The longitudinal muscles now contract while the circular muscles relax, producing the shorter, wider animal of Figure 5.3b (and generating powerful radial forces in the process). In (b), the animal releases its anterior attachment to the substrate and forms a new temporary

**Figure 5.1**
Antagonistic interaction between the biceps and triceps in the human arm. Contraction of the biceps (a) results not only in movement of the arm (b), but also in stretching of the opposing muscle, the triceps. Contraction of the triceps then returns the arm to its initial position (c) and stretches the biceps. In vertebrates, muscle pairs antagonize each other through a rigid skeleton, which is internal and jointed.

In fact, fluid can serve as the vehicle through which sets of muscles interact. Such hydrostatic skeletons are common among invertebrates. The basic hydrostatic skeleton requires:

1. the presence of a cavity housing an incompressible fluid that transmits pressure changes uniformly in all directions;

**Figure 5.2**
(a,b) Shape changes possible in a worm-like organism equipped with only longitudinal muscles. Because the fluid volume is constant, a change in the width of the hypothetical animal must be compensated for by a change in length, brought about by the increase in internal hydrostatic pressure during muscle contraction. Similarly, a shortening of the worm is accompanied by an increase in width, as seen in (b).
From this discussion, it is obvious that one addition must be made to the previous list of requirements for a functional hydrostatic skeleton:

5. the presence of a deformable but elastic covering or the presence of at least 2 sets of muscles that can act against each other.

Clearly, the skeletal system in our hypothetical organism is a fluid. Temporary increases in internal pressure are caused by the contraction of one set of muscles, and this temporary pressure increase elongates another set of muscles. I emphasize that the internal pressure increase is temporary; elongation of the opposing set of muscles relieves the pressure. The essentially incompressible fluid thus makes possible the mutual antagonism of the 2 sets of muscles, resulting in repeatable locomotory movements. Hydrostatic skeletons play a role in the movements made by representatives of nearly every animal phylum. Researchers at a number of institutions are currently trying to develop flexible, shape-changing robots based on these principles.

---

**Topics for Further Discussion and Investigation**

1. Which features of a hydrostatic skeleton do sponges (Chapter 4) possess? Which features do sponges lack?

2. Fluid-rich deformable cells can act as hydrostatic skeletal systems. Examples are the deformable muscle cells of squid tentacles ("muscular hydrostats," Chapter 12) and the parenchyma of turbellarian flatworms (Chapter 8). What sequence of muscle contractions and relaxations is likely to be involved in (a) elongating a squid tentacle, (b) mediating flatworm locomotion via pedal waves, and (c) flatworm locomotion via "looping"?