Chapter 7  Tendons, Bones and Joints

7.1 Introduction
In older texts, locomotion and other movements are presented as arising almost entirely from the active shortening of muscles, with skeletons and tendons acting merely as passive struts and ropes. During the last twenty years, accurate measurements of the mechanical properties and anatomical arrangement of the skeleton and tendons combined with theoretical studies have revolutionized our understanding of the exact role of muscle contraction, and the contribution of non-muscle tissues to movement, particularly cyclical, stereotyped activities such as locomotion. It is now clear that skeletal tissues make an essential contribution to the form and energy economy of movement and that the mechanical properties of muscles cannot be interpreted properly without reference to those of the tendons and skeleton to which they are attached. So this chapter describes the structure and properties of tendons, ligaments, joints and hard skeletal tissues and how their properties integrate with those of muscle (Chapters 5 and 6). Chapter 8 draws on these detailed studies of the components of the musculo-skeletal system to explain the mechanics and physiology of locomotion.

Tendon and bone are robust tissues which retain their elaborate histological structure and many of their mechanical properties for some time after they have been isolated from the animal. So, as with muscle, physicists, chemists and engineers studying isolated tissues, as well as biologists, have made major contributions to our knowledge of the properties of skeletal tissues and how they are arranged in the body.

7.2 Collagenous tissues
Collagen is found in small quantities in many kinds of invertebrates and is by far the most abundant structural protein in vertebrates, occurring at least in small quantities in almost all tissues except the brain and the blood. It is almost always in a fibrous form, but the fibres may be quite small and randomly orientated in a felt-like structure, as in skin, loose connective tissue and cartilage. Collagen occurs in a very pure form and is assembled into bundles of parallel fibres in tendons, which link muscles to the skeleton, and ligaments, which join parts of the skeleton together. Sheets of collagen fibres spread over or between the muscle fibres are called aponeuroses.* Collagenous material linking muscles to adjacent tissues such as adipose tissue and skin is called fascia. The extracellular portion of tendons consists of long parallel fibres of collagen, which, as you can see from the electron micrograph in Figure 7.1 (overleaf), are crimped along their length. If stretched beyond the point at which the crimp is straightened, these fibres resist deformation under tension, but are compliant to compression, bending and twisting.

* Singular ‘aponeurosis’. The term ‘aponeurosis’ is derived from the Greek word ‘neuron’, which means ‘sinew’. The early anatomists did not distinguish between nerves and tendons, both of which appear white and fibrous in dead mammals. So it is the terms for the skeletal tissues, not those for the nervous system, that are etymologically correct.
In its functional state, collagen is nearly always extracellular, so collagenous tissues typically consist of a high proportion of extracellular matrix, and relatively few cells. In tendons, ligaments and aponeuroses, collagen is synthesized by cells called fibroblasts and secreted into the extracellular space.

The fibroblasts mature into fibrocytes, which are small, spindle-shaped cells about 10 µm long. Fibrocytes are enmeshed between the collagen fibres throughout the tendon, sometimes in a fairly regular pattern, but they occupy only a small proportion of its volume.

Would the metabolic rate of tendons be high or low compared to muscle or liver?

The metabolic rate of the mature tissue is very low because cells are sparse and those present are not involved in contraction or secretion or any other energetically demanding biochemical process. Consequently, the blood supply to healthy tendon is very low. In fact, one of the most important features of tendons is also the most obvious: they are very pale in colour, even in living animals, because they contain little blood and no myoglobin or similar pigment.

What are the consequences of this situation for tissue repair?

Tendon healing is slow. The blood supply increases following major injury, but even so, tendons heal very slowly compared to skin, bone or muscle (Section 2.4). Tendons also do not readily ‘become fit’ with regular, strenuous exercise, i.e. their mechanical properties are little changed by repeated strain.

Although the myotendinous junction (Section 6.4.1) may be fragile compared to pure tendon or muscle, tendons make very strong attachments to bones because strands of collagen arising from the tendon penetrate into the bone, meshing with the bone collagen and weaving around and between the mineral and cellular components of the bone. If limbs are subjected to exceptionally large forces (e.g. from a fall or while skiing), a tendon or muscle may tear, or a bone may break, but the tendon–bone junctions very rarely fail.
7.2.1 Molecular structure of collagen

In mature connective tissue, collagen molecules consist of polypeptides assembled in a formation resembling a three-stranded rope. Except for short sequences at the ends of the molecules, every third amino acid residue of each polypeptide is glycine. About 36% of the rest consists of the imino acids, proline and hydroxyproline. Imino acids differ from amino acids in that the nitrogen atom is linked to two carbons, forming a ring. Their presence limits the usual rotation of one residue onto another so the resulting polypeptide is rather inflexible and does not form an α-helix as readily as other proteins. Because proline and hydroxyproline are quite rare in enzymes and in most other structural proteins, measurement of their abundance provides a sensitive assay for collagen (Section 3.2.4).

Each of the polypeptide strands is a helix with almost three residues per turn and the three such strands can coil round each other, with glycine, the smallest of the amino acids, occupying the central core of the three-stranded rope. The three strands form a right-handed superhelix with a pitch of approximately 8.7 nm. The whole molecule is about 260–300 nm in length, and 1.3 nm in diameter; a triple helix is the basic structure along all but the final 12 nm at each end of the molecule, which are rich in lysine and hydroxylysine.

In living tendons, collagen molecules are assembled into fibrils of diameter 20–500 nm which show the characteristic banding pattern, repeated every 68 nm, illustrated in Figure 7.2. The banding pattern is believed to arise from the staggered arrangement of parallel collagen molecules, as shown in Figure 7.3.

The electron micrograph stain accumulates where the head of one molecule lies beside the tail-end of another, forming a dark band; the light bands represent the spaces between the molecules in the same row. Light and dark bands therefore appear every 68 nm, although the true unit of structure involves five molecules and so repeats every 340 nm. The collagen molecules assemble themselves into this pattern, and the structure may be stabilized by covalent cross-links which form between oxidized lysine and hydroxylysine residues in the non-helical ends of adjacent collagen molecules; this structure makes the tendon strong in tension, but weak in torsion and in compression.
As in most proteins, hydrogen bonds play a central role in maintaining the tertiary and quaternary structure of collagen molecules. Bacon slices shrink and curl as they are heated, and pig skin becomes pork crackling, because the hydrogen bonds in the collagen of the skin, adipose tissue and muscle become unstable at high temperatures, causing the elaborate internal architecture of the collagen molecules to collapse; the energy so released causes irreversible shrinkage and stiffening of the tissues. Collagen from any source can be broken down into its constituent polypeptides by prolonged immersion in boiling water. The result is an amorphous, jelly-like substance, called glue* when concentrated, or soup stock when dilute; the polypeptide chains have unwound from each other, and the triple helical structure has been destroyed. Although helical collagen molecules can be disassembled and reassembled into fibrils artificially, the triple helical structure cannot be recreated once the three polypeptide strands have been completely dissociated from each other. Once assembled, collagen is among the most chemically inert proteins in the body, because most proteolytic enzymes do not attack the imino acids proline and hydroxyproline. In mammals, certain cells in the uterus and cervix, and those involved in healing and remodelling of bone (Section 2.3), secrete a specific collagenase and can thereby remodel the shape or alter the mechanical properties of the reproductive tract and skeleton. The anaerobic bacterium Clostridium histolyticum is one of the few other organisms to produce enzymes that attack collagen directly. C. histolyticum is common in soil, where it plays an essential role in completing the breakdown of dead vertebrates. However, it sometimes strays into the inadequately cleansed wounds of living vertebrates, where it destroys aponeuroses around muscles, tendons and all other collagen-containing tissues, particularly if poor blood supply or tight bandaging promote anaerobic conditions. C. histolyticum and other Clostridium species cause gangrene, a common and often fatal complication of lacerations and puncture wounds in wild animals and, until modern antibiotics became available, in humans.

7.2.2 Mechanical properties of tendons

Tissues rich in collagen are extensible, resilient and flexible: that is, they are tough enough to be able to absorb energy without tearing or snapping, they recoil when released after a stretch, and they can transmit forces around and across joints. Tendons, which are almost pure collagen, are the most thoroughly studied of such tissues, because of their convenient size and shape and their functionally important association with muscle.

Tendons are almost always loaded in tension, so the most biologically meaningful measurements are those of tensile strength (i.e. the force required to pull the tendon apart) and tensile stiffness (i.e. the mechanical response to stretch). Stiffness can be measured by mounting a sample of tendon firmly in a movable clamp. The force required to stretch it through a measured distance is recorded. The tendons in the tail of the rat, and the Achilles tendon† of sheep or pigs (see also Section 3.2.2, Figure

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* `Collagen` means `glue-producing` and the name derives from the fact that, until the 20th century, most commercial glues were made by boiling the skins, tendons and bones of slaughtered animals.

† The Achilles tendon links the gastrocnemius muscle in the lower leg to the ankle bone. Its name refers to the mythological Greek warrior, Achilles, who was killed by an injury to this tendon at the heel.
3.7), are most frequently studied because they are readily obtainable and, being relatively long and thin, are convenient for the apparatus. However, it is important to remember that much of the collagenous material associated with muscle is in the form of strands of tendon and aponeuroses that extend deep into and through muscles (Section 6.4).

Some typical results for a limb tendon are shown in Figure 7.4; the $y$-axis is the stress ($s$), the force per unit area, measured in N m$^{-2}$ or pascals (Pa) (see Section 3.2.2), and the $x$-axis is strain ($e$), the length of extension expressed as a percentage of the unstretched length. In the ‘toe’ region of the curve, only small stresses are needed to stretch the tendon. However, once the strain exceeds about 0.6%, larger forces are needed to achieve further stretching. When these mechanical changes are correlated with changes in the ultrastructure of the collagen fibres, it is found that the ‘toe’ region of the graph corresponds to stretching out the crimp of the collagen fibres (see Figure 7.1). The linear part of the curve corresponds to stretching the bonds within and between collagen fibres; stretching in this region is completely reversible and does not permanently alter the structure of the tendon. However, if the tendon is stretched by more than about 8–10%, its internal structure starts to break down and it is permanently deformed, i.e. it does not recoil to its original length when released from stretch. At points called critical tensile stress and critical tensile strain, as well as failing to recoil, the tendon becomes weak and is easily torn apart by small additional stretch.

When comparing the mechanical properties of one tissue with those of another or with a synthetic material, it is useful to have a simple modulus that summarizes the material’s behaviour. Young’s modulus, $E$, is the slope of the linear region of stress/strain curves like the one in Figure 7.4.

$$E = \frac{s}{e}$$

Table 7.1 (overleaf) shows Young’s modulus, the critical tensile stress ($s_t$) and the critical tensile strain ($e_t$) for tendons and various other natural materials.

During fast running, the Achilles tendon of a 70 kg man is subjected to a stress of 5 kN (about 0.5 tonne force, or seven times the man’s own weight). From the data in Table 7.1, can you calculate the minimum cross-sectional area that the Achilles tendon must have in order to withstand this stress?

Stress is defined as force per unit area; the maximum stress that the tendon can withstand is 80 MPa (see Table 7.1) = $8 \times 10^7$ N m$^{-2}$, therefore the area of tendon needed = $(5,000 \text{ N})/(8 \times 10^7 \text{ N m}^{-2}) = 6.25 \times 10^{-5}$ m$^2 = 0.625$ cm$^2$.

The Achilles tendon of most men is about 0.7 cm$^2$ in area. What is the safety factor (see Section 3.2.2) under which the tendon is operating during fast running?

The safety factor is only $0.70/0.625 = 1.12$, a very low value for the normal usage of a biological material. Human athletes apparently stress their Achilles tendons almost to breaking point during fast running. Rupture of this tendon is a common sports injury.

* First formulated and measured by Thomas Young (1773–1829), a physician, biologist, physicist and Egyptologist who was born in Somerset and spent most of his working life in London.
Some properties of biological materials that are normally loaded in tension. $\sigma_c$ is the critical tensile stress and $\varepsilon_t$ is the critical tensile strain at which the material begins to suffer irreversible damage. $1 \text{ GPa} \equiv 10^9 \text{ Pa} \equiv 10^3 \text{ MPa}$.

<table>
<thead>
<tr>
<th>Material</th>
<th>Young’s modulus E/GPa</th>
<th>$\sigma_c$/MPa</th>
<th>$\varepsilon_t$/%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mammalian tendon</td>
<td>1–2</td>
<td>80</td>
<td>8</td>
</tr>
<tr>
<td>Wool fibre</td>
<td>3–4</td>
<td>60</td>
<td>2</td>
</tr>
<tr>
<td>Silk</td>
<td>4</td>
<td>800</td>
<td>&gt;20</td>
</tr>
<tr>
<td>Insect cuticle</td>
<td>20</td>
<td>500</td>
<td>3</td>
</tr>
<tr>
<td>Mammalian long bone</td>
<td>20</td>
<td>140</td>
<td>0.5</td>
</tr>
<tr>
<td>Humerus in king penguin flipper</td>
<td>22</td>
<td>290</td>
<td>n.d.</td>
</tr>
<tr>
<td>Mammalian tooth enamel</td>
<td>84</td>
<td>n.d.</td>
<td>n.d.</td>
</tr>
<tr>
<td>Molluscan shell</td>
<td>50</td>
<td>50</td>
<td>0.3</td>
</tr>
<tr>
<td>Wood</td>
<td>25–40</td>
<td>20–120</td>
<td>2</td>
</tr>
</tbody>
</table>

n.d., not determined

In adult humans, the average length of the Achilles tendon, including the aponeuroses extending into the gastrocnemius muscle, is about 30 cm.

By how much can the Achilles tendon safely be extended?

From Table 7.1, the maximum strain ($\varepsilon_t$) is 8% of 30 = 2.4 cm. If the safety factor calculated above also applies to stretching of the tendon, its normal maximum extension is $2.4/1.12 = 2.14$ cm, or about 7% of the length of the tendon at rest.

When a human or a sheep is running fast, each foot is on the ground for about 0.2 s, during which time the tendons of the lower leg are stretched. The energy thus used is stored elastically and released when the tendons recoil to their normal length. Such storage and later release of the elastic strain energy in tendons, ligaments and, to a lesser extent other connective tissues such as articular cartilage (Section 7.4.2), make an important contribution to the energy economy of fast locomotion, as explained in greater detail in Section 8.2. At the stride frequency of running, about 93% of the energy absorbed in stretching the tendons is recovered as recoil; this efficiency of energy storage is as good as that of the best quality industrial rubber. The remaining 7% of the energy used to stretch the tendon is converted into heat. The quantity of heat so generated is small compared to that produced by active contraction of muscles (Section 6.3.1) and it is normally dissipated very quickly, particularly if the tendon is situated just under the skin. Most large tendons, such as the Achilles tendon near the ankle and those in the wrist, are so close to the skin that you can see them as discrete entities in your own limbs. However, if heat dissipation is restricted by bandaging the legs, as is traditionally often done with racehorses, the temperature of the tendons and surrounding tissues can become high enough to cause inflammation during prolonged, strenuous galloping.

7.2.3 How long and how thick should a tendon be?

As explained in Section 6.4.2, the length and insertion points of a muscle–tendon system, and the relative length of the muscle determine the range of movements it can perform. The mechanical properties of the tendon are also important
because they determine how the forces generated by the muscle are transmitted to the skeleton. The main functions of tendons that are attached to muscles that are frequently used in the negative work mode (Section 6.2) are energy storage and recoil, so they should be long, thin and stretchy, like an elastic band.

- Referring back to Section 7.2.2 and to Chapter 6, what reasons could there be for not having long, thin tendons?

First, thin tendons would have a lower safety factor and hence would be vulnerable to injury from exceptionally large strains. Second, muscles that normally operate in the positive work mode need tendons that transmit precisely small changes in muscle length: precision movements, such as those of human fingers, would be very difficult to control with sensory input from muscle spindles and tendon organs (Section 6.5.1) if the mechanical properties of their tendons resembled those of elastic bands.

- What features would you expect in musculo-skeletal systems adapted for precise movement? Can you suggest which group of muscles would have these properties?

Really accurate control of length changes would require minimizing tendon length and maximizing its stiffness. Precision movements are essential (and energy storage unimportant) for the facial muscles that operate the jaws, cheeks and tongue (especially those of humans that are used for speech as well as eating). Feel your own face: it has lots of muscle and very little tendinous material. The thick, powerful muscles are attached to the skeleton by very short, stout aponeuroses. The tendons of the fingers have to be long because their muscles are in the forearm, but, in proportion to the forces that they normally transmit, they are much stiffer than those of the foot. They transmit accurately the length changes applied to them, like the stiff wires of the gears and brakes of a bicycle.

Tendons become stiffer by ossifying into bone. When eating your Christmas dinner, you may have noticed that certain tendons in the lower legs of domestic turkeys are ossified to form thin ‘needles’ of bone.

- Under what conditions would ossified tendons be inappropriate?

Where the tendons are required to transmit forces around joints or other curved planes. The other way in which tendons become stiffer is to become thicker, as is the case with the stout, stiff tendons that operate the fingers. The dimensions of tendons, like the physiological properties of muscles, are adapted to particular functions at the expense of maximum efficiency of other properties.

Both the red kangaroo (*Macropus rufus*, body mass about 40 kg) and the smaller and unrelated kangaroo rat (*Dipodomys spectabilis*, a rodent of body mass about 100 g) have similar body proportions: short forelimbs and long, powerful hindlegs. At first glance their posture and locomotory adaptations also appear to be very similar: they usually stand bipedally and, instead of trotting or galloping, they hop using only the hindlegs. The gastrocnemius muscles are large and powerful and they and the attached Achilles tendons extend and recoil at each hop (there are further details of this mechanism in Section 8.3.1). However, studies of the mechanical properties of their muscles and tendons, and the strains they undergo *in vivo*, reveal subtle but ecologically important differences.
The Achilles tendons of *Dipodomys* are relatively thick; their maximum stress during hopping is only 8 MPa and they absorb only 14% of the total mechanical work used for each stride. The gastrocnemius muscle exerts a force equivalent to only 70 kPa, about 35% of its maximum isometric stress (Section 6.2). In comparison, the tendons of *Macropus* are thinner and longer (relative to body mass) and the stress in them is about 55 MPa at maximum; about 62% of the strain energy is recovered. The gastrocnemius muscle exerts a stress of up to 180–240 kPa, close to its maximum possible isometric stress.

Under what safety factors (Sections 3.2.2 and 7.2.2) do the Achilles tendons of these species operate?

Tendon is permanently deformed by stresses of 80 MPa (Table 7.1) and breaks at stresses of 100 MPa. So the safety factor for the Achilles tendons of *Dipodomys* is 80/8 = 10 and that for *Macropus* is 80/55 = 1.5.

What do these facts imply about activities other than hopping in which the hindlegs of these species might be involved?

These observations show that in hopping, the muscles and tendons of *Macropus* experience forces close to the maximum that their tissues can sustain, but that those of *Dipodomys* are capable of withstanding much higher forces, and do not store strain energy very efficiently. The tendons and muscles of *Dipodomys*, but not those of *Macropus*, are probably used for activities such as jumping that involve much higher accelerations, and hence greater maximum stresses in both muscles and tendons. In fact, observations on *Dipodomys* in its native habitat of deserts and dry scrub in southwestern USA and northern Mexico show that it cannot hop very fast (only about 1.5 m s\(^{-1}\), compared to 3.9 m s\(^{-1}\) for *Macropus*) but when pursued by predators such as owls, rattlesnakes and foxes, it jumps to heights of at least 0.5 m (ten times its hip height).

*Macropus*, being larger and living in Australia where there are very few vertebrate predators, does not jump much, and hops mainly to travel long distances between feeding grounds rather than to escape predators. *Macropus* retains the ability to leap safely away from predators at the expense of having tendons that store less energy. The importance of energy storage in tendons and other collagenous tissues for the energetic cost of locomotion as a whole is described in Chapter 8.

Similar analysis shows that most mammalian and avian tendons are much thicker than would be necessary for adequate strength. Like muscle, the arrangement and properties of tendons are intricately adapted to their roles in the animal. Thus the long tendons that operate human fingers, which can be felt easily through the skin of the wrist and the back of the hand, are relatively thick compared to those of the ankle, although the muscles in the forearm just below the elbow that move the fingers are much smaller than the gastrocnemius muscle of the lower leg. Most limbs taper towards the ends, with the more massive muscles nearest to the trunk, and lighter tendons extending to the tips of fingers and toes. The ends of the limbs are the fastest moving parts and minimizing their mass reduces the total energetic cost of movement. Thinner tendons would be more stretchy so the muscle fibres would have to be longer to take up the slack, thus increasing the combined mass of the muscle–tendon system.
Chapter 7  Tendons, Bones and Joints

Although the human hand is capable of a wider range of movements than almost any other limb in the Animal Kingdom, the arrangement and mechanical properties of the muscles and tendons make certain combinations of actions impossible.

Grasp the index finger of one hand with the other, and bend the joint between the finger and the hand, and that between the first two segments of the finger into right angles. Now try to flex the finger tip.

The most you can achieve is a shallow, weak movement, although coiling the whole finger towards the palm as a single action is easy. Once the tendon and muscle have been stretched over two of the three bent joints, the muscle, which is located high up the forearm, is incapable of shortening with sufficient force to produce significant flexion of the last joint.

Summary of Section 7.2

Collagen, which consists of a highly ordered assembly of triple-stranded, helical molecules, is the major component of the tendons and aponeuroses by which muscles are attached to the skeleton. In tendons, the collagen molecules are assembled in a parallel array, stabilized by covalent bonds. Tendons are strong in tension and can undergo reversible extension to about 8% of their original length: further extension breaks intermolecular bonds and causes damage that can only be repaired by new growth processes that may take a long time to complete. Up to 93% of the energy absorbed by stretching reappears as recoil shortening when the tendon is released. The rest is dissipated as heat. The length and thickness of tendons are intricately adapted to their roles in the animal’s normal actions. Thick, short tendons absorb less energy but are stronger and transmit muscle length changes more exactly than long, thin tendons, which store strain energy more efficiently under the moderate stresses imposed on them in locomotion.

7.3 Hard skeletal tissues

The main stiff components of musculo-skeletal systems are bone and arthropod cuticle. Bone is found only in vertebrates and is the major skeletal material of almost all adult terrestrial vertebrates and most fishes except the chondrichthyans. Its unique mechanical properties and mode of growth (Section 2.3) are believed to be among the main factors that have enabled vertebrates to become large.

7.3.1 Bone structure

The basic framework of bone (and similar tissues such as tooth and antler) is an extracellular matrix of collagen fibres of diameter up to 100 nm, and hydrated crystals of an inorganic salt, hydroxyapatite, \( \text{Ca}_10\text{(PO}_4\text{)}_6\text{Ca(OH)}_2 \), in the form of long, thin crystals about 4 nm by 40–400 nm. The hydroxyapatite crystals lie parallel to the collagen fibres, and together they form a composite material. The collagen is strong in tension, and can withstand considerable strain (Section 7.2.2); crystalline materials such as hydroxyapatite are strong under compression, but break at very low strains. Bone is strong in both tension and compression: its high mineral content makes it stiff, but the presence of collagen stops cracks from running through the brittle crystals of hydroxyapatite.
Bone differs from most invertebrate skeletal materials in that, in most but not all forms of bone, the living cells, called osteocytes (Section 2.3), which secrete the precursors of the collagen fibres and the hydroxyapatite, are incorporated into the mineralized skeleton. Like all other living cells, osteocytes require nourishment, and cellular bone is permeated with small channels containing blood vessels, and is surrounded by a soft, metabolically active periosteum. The rich blood supply means that most mammalian bones bleed profusely when bruised or broken.

Both the cellular and the extracellular components of bone are replaced during growth and, particularly in mammals, during adult life; osteoclasts (Section 2.3.1) invade the functional bone through the vascular channels and break it down, thereby making way for the formation of new bone. As the bone is dismantled, calcium and phosphate ions and amino acids are released into the bloodstream; often the new bone is formed from these same mineral and amino acid precursors, but they may also be taken up by other tissues that have a greater affinity for them. If ions of similar shape to calcium, notably barium and strontium, are present in the blood, they are sometimes incorporated in place of calcium. Such substitution distorts the crystal structure of the hydroxyapatite and may make the bone mechanically weaker.

Fluoride ions (F\(^{-}\)) can replace the OH\(^{-}\) ion in the crystal, distorting the entire structure in a way that (by a mechanism still not completely understood) increases its resistance to bacterial attack. This property has been exploited to protect teeth from decay caused by dental caries.

Why is the application of fluoride to teeth particularly beneficial for young children? Why is it of some value even for mature adults?

Ideally, fluoride ions should be incorporated into hydroxyapatite into the entire tooth as it grows, so it should be administered to children aged 4–11 as their adult set of teeth is forming (Section 1.2.3). Secondary dentine forms and a small amount of ion substitution takes place in adults, so fluoride toothpaste can still offer some protection from decay.

The main categories of bone in terrestrial vertebrates are distinguished by their arrangement of osteocytes and blood vessels and their mode of growth. By far the most abundant is lamellar bone, so called because it is composed of sheets (lamellae) of collagen and mineral elements a few micrometres in thickness between which are the osteocytes and blood vessels. Within any one lamella, all the collagen fibres are more or less parallel, and the bone is built up of many layers of lamellar, each with a different preferred orientation. Less abundant but more spectacular is Haversian bone, named after Clopton Havers, the British anatomist who first described its remarkable microscopic structure early in the 18th century. In Haversian bone, most of the lamellae form concentric cylinders (that appear as rings in sections), called osteons, around central canals containing blood vessels.

Haversian bone is always formed as a replacement for a less highly organized and probably flimsier kind of bone, often called woven bone (Section 2.3.1), that forms during periods of rapid growth or repair of fractures. It is therefore found mainly in adult mammals, in which there has been extensive bone remodelling. For reasons that are not understood, much of the bone of adult carnivores and primates (including Homo) is Haversian in form, but this type of bone is much rarer in cattle, and almost absent in rodents. Ectopic bones are normally woven bone.
At the macroscopic level, compact bone is characterized by the absence of cavities other than those containing the osteocytes and the blood vessels and is up to 90% calcified. In cancellous bone the hard tissue is reduced to thin strands called trabeculae, interspersed with soft bone marrow. In fetal, neonatal and juvenile mammals, the bone marrow is the principal site of synthesis of red and white blood cells; the newly formed blood cells are released into the small blood vessels which permeate the bone and thence travel to the rest of the body. The haemopoietic red marrow is gradually replaced by a fatty tissue called yellow marrow, and in adult terrestrial mammals, including humans, only the cavities in the ribs, vertebrae and skull contain red marrow.

Most trabeculae and some cortical regions of the skeleton are made of lamellar bone, and Haversian bone forms the cortex of many long bones, with the osteons running approximately parallel to their long axes. Figure 7.5 is a section of a dried specimen of a talus, a small weight-bearing bone in the hock (ankle joint) of the hindleg of a cow; the outer cortex consists of compact bone but the interior is filled with cancellous bone organized into trabeculae. The thickest trabeculae appear to be aligned in the direction in which the greatest forces are normally applied. In adult humans, trabecular bone accounts for only about 20% of the mass of the skeleton.
The density of some very stiff skeletal elements (e.g., the ear ossicles) that are composed of compact bone is up to 2.4 g cm\(^{-3}\), mainly because of the high density (3.2 g cm\(^{-3}\)) of the hydroxyapatite mineral. The mass of the entire skeleton is reduced by replacing compact bone with trabeculae and tissues such as haemopoietic marrow (density about 1.0 g cm\(^{-3}\)) and adipose tissue (density 0.93 g cm\(^{-3}\)), in places where the flimsier kind of bone is strong enough to withstand the forces normally applied to it.

The cavities of most long bones of flying birds (and the extinct flying reptiles, e.g., pterodactylys) contain air sacs that reduce the overall density of the skeleton. The limb bones of certain marine mammals and birds such as penguins lack proper marrow cavities. The humerus of the king penguin (\textit{Aptenodytes patagonia}) is very dense and stiff, with an exceptionally high Young’s modulus (Table 7.1), possibly as an adaptation to the forces it sustains when the animal swims fast using its wings as flippers.

Bone, especially trabecular bone, acts as a reserve of essential metabolites such as calcium ions, which may be present in only small quantities in the diet (Sections 1.2.3 and 2.3). The mammalian skeleton accumulates calcium during pregnancy: herbivores such as rats and deer whose diet is low in calcium may gnaw old dried bones, antlers or even chalky soils. The calcium is released during lactation and secreted in the milk and is thereby incorporated into the skeletons of the growing young. Because of the profuse blood supply, the mineral component of the mother’s bone can be withdrawn very rapidly in response to calcium-releasing hormones. As you would expect, alteration of the mineral content of bone profoundly affects its mechanical properties; the bones (and teeth) of lactating female mammals become less dense and much more fragile towards the end of lactation because of calcium depletion.

### 7.3.2 Mechanical properties of bone

The limb bones of cattle, pigs and sheep slaughtered for meat are a convenient source of material for studies on the mechanical properties of bone. Figure 7.6 shows a typical stress–strain curve for samples of bones prepared from freshly isolated cattle femurs. In the linear region of the curve, the bone behaves elastically; it can be strained to about 0.5% of its original length without damage, and returns to normal when the extending force is removed. Young’s modulus for this region is about 20 GPa, almost 10 times greater than that of tendon. Beyond a strain of about 0.5%, the bone is permanently damaged by stretching, and it snaps suddenly when extended by about 3%.

Most components of the skeleton are much more frequently subjected to compression, torsion and bending (see Figure 3.3, Section 3.2.1), than to stretching along the axis. The bone shaft is tubular in shape, like a scaffolding pole, with the densest material around the circumference (Figure 7.5). When the limb is bent, tissue on one side is compressed, while that on the other side is loaded in tension; the bone almost always fails first on the side loaded in tension.

The chemical composition and mechanical properties of different kinds of bones are adapted to particular functions. Deer antlers (Young’s modulus 2–12 GPa) are often subjected to bending and to sudden impact forces during fights and when tangled in trees: bone that has a high collagen content is tougher and more compliant and...
hence less likely to break under such forces. High-frequency vibrations are transmitted most efficiently by very stiff materials. Earbones are adapted to this role: their Young’s modulus is up to 30 GPa and they have almost twice as much hydroxyapatite as more pliant tissues such as deer antlers. But such bones are much more brittle: the earbone of a whale (among the few that form pieces large enough for mechanical testing) is crushed by stresses of only 33 MPa, compared to 179 MPa for antler, and 247 MPa for cow femurs. Since earbones are never subjected to bending, twisting or crushing forces, the risk of breakage in situ is slight.

As explained in Section 7.3.1, there is great variation in the microscopic and gross structure of bone in different regions of the skeleton. It is difficult to relate mechanical properties to microscopic structure because there are very few histologically homogeneous samples of bone that are large enough for mechanical measurements to be made from them. Haversian bone, which always forms as a reconstruction of previously laid down bone, is weaker and has a lower Young’s modulus than lamellar bone of similar density: indeed, it is far from clear what mechanical advantages arise from the formation of Haversian bone. Although weaker than lamellar bone, it may be stronger than the material formed when the trabeculae of cancellous bone are filled in to form compact bone. Haversian bone is often found near the points of attachment of large muscles, where cancellous bone has gradually thickened during growth to form compact bone. Cancellous bone is found particularly in the middle of the joint regions of long bones and as the ‘filling’ between sheets of compact bone in broad flat structures such as the hip, shoulder and ribs. It is much weaker but more compliant than Haversian bone and behaves mechanically rather like a stiff sponge.

The bending and recoil of bones during locomotion can be measured directly by attaching small strain gauges onto the bone shafts and allowing the animal to move normally. Figure 7.7 shows some data on the compressive strain (i.e. the small changes in bone length caused by compression forces) measured from the posterior surface of the radius bone in the upper part of a horse’s foreleg. The forces that cause the bending are produced both by the muscles and by the weight of the body when the leg is on the ground. As you would expect, the compression increases sharply with increasing speed in both walking and cantering. You might be surprised, however, that there is no significant difference in the average compression and recoil recorded during walking and during cantering, in spite of the fact that the horse travels more than four times as fast when using the latter gait. The bending of the radius bone is also about 50% greater during the trot than during walking or cantering at the same speed, and does not increase with increasing speed. These observations seem at odds with the elementary laws of mechanics; the change in gait must somehow alter the distribution of forces between the skeleton, muscles and tendons. How these changes might be achieved is discussed in Chapter 8.

For reasons that are not yet fully understood, the bone remains healthy and well mineralized only if frequently subjected to compression and extension (Section 2.3.1). Such forces are easily generated by a few hours of walking or cycling, but they are lacking in a weightless environment such as living in space or submerged in water. The bones of astronauts start to lose mineral and protein after only a few days in space and become fragile and painful when stressed. The effects can be partially counteracted by regular exercise on apparatus such as rowing machines, but most astronauts become too weak to stand up on Earth after a month or more in space. Marine mammals spend a large proportion of their time swimming.
7.3.3 Ontogenetic changes in bone structure and properties

Bone plays a central role in growth and ageing: as explained in Chapter 1, growth of skeleton ‘sets the pace’ for the growth of the soft tissues, and cells of the epiphyses respond readily to growth-regulating hormones. In mammals, closing of the epiphyses is closely linked to the endocrinological changes at puberty (Section 2.3). Among terrestrial species, the skeleton of larger animals is relatively massive compared to smaller ones (Section 3.2.1, Figure 3.5). Ontogenetic changes in the mechanical properties of femurs have been investigated in only a few species, among them humans, a slow-growing relatively light species, and polar bears, a fast-growing, very massive animal. Femurs (Figure 7.8) are the parts of the skeleton most frequently used for such comparisons as they are large and of a convenient shape for making test pieces. In the sample of polar bear femurs shown in Figure 7.8, the femur of the half-grown male is about the same length as that of the almost fully grown female, but the former is more massive, with larger joints and thicker shafts.

Is growth in thickness controlled independently of growth in length?

Yes. Bone thickening is due endosteal and periosteal osteoblasts but growth in length occurs only at the epiphyses, which close around sexual maturity (Section 2.3).
Figure 7.9  Young’s modulus for samples of bone from humans (blue squares), a deer (black circles) and polar bears (open diamonds) of different ages.

Figure 7.10  Young’s modulus as a function of calcium content for samples of bone from humans (blue squares), a deer (black circles) and polar bears (open diamonds).

Figure 7.9 shows data obtained from bones taken from human cadavers and from wild polar bears whose femurs are shown in Figure 7.8, that range in size from a suckling cub to an adult male. The data for the deer (*Axis axis*) came from an unborn full-term fetus and its 2.5-year-old mother, which weighed 53 kg.

In all three species, Young’s modulus increases with age, but it does so much faster in the deer than in bears or humans.

- How can you explain the species differences in the age changes of Young’s modulus?

Like most ruminant mammals, deer fawns at birth are large relative to the size of the mother and grow rapidly to adult size. Growth stops and they become sexually mature at an early age. Bears also grow fast but they are relatively very small at birth. Their adult size is so big that even the females, which as adults are only about half the maximum size of males, do not breed until they are four or five years old. Deer fawns have to run with the herd within a day or two of birth, but polar bear cubs remain in a den for the first three months of life, so they can probably manage with bones of a much lower Young’s modulus than the deer. Humans are not particularly large as adults, but they grow very much more slowly than other mammals (Section 1.3.2).

Additional measurements from the same bones shown in Figure 7.10 help to explain these age changes. Young’s modulus increases with increasing mineralization in a more or less similar way in all three species.

- Can you suggest why the bone of the adult female deer has such a high mineral content?

Bones also act as a calcium store, especially for breeding females whose diet provides barely enough calcium. This female was about to give birth and begin lactation, so her calcium stores may have been near maximal (Sections 3.4.2 and
The high mineralization and Young’s modulus may thus be seen as an adaptation to her breeding condition rather than directly related to the mechanical requirements of the bone.

### 7.3.4 Osteoporosis

Bone is replaced and repaired continually throughout life (Section 2.3). In children, the rate of deposition is faster than the rate of absorption, so the bones grow thicker, longer and stronger. In young adults, the two processes are in equilibrium so the mass of the skeleton remains approximately constant, but in older humans, the activity of osteoclasts exceeds that of osteoblasts so bones become thinner, lighter and weaker. The rate of bone loss is much lower in men, only about 0.4% per year from about the age of 50, so men’s skeletons are not greatly weakened until they are about 80 years old. But women lose bone at 0.75–1% per year from age 30, reaching a rate of 2–3% per year during the five years after menopause, so at age 70 years, the mass of women’s skeletons are only 60% that of their average mass at age 30. This depletion of bone causes a syndrome of structural and mechanical abnormalities called osteoporosis, the most obvious manifestation of which is an increased probability of fractures.

What kinds of bone would be most susceptible to reabsorption in osteoporosis?

Osteoclasts attack bone on its surface (Section 2.3.1). Trabecular bone (Section 7.3.1), although very strong, has a larger surface area than cortical bone, and so would incur faster reabsorption. By the age of 90, most women have lost about 35% of their dense bone in the cortices, and about 50% of trabecular bone.

In humans, trabeculae are most abundant in vertebrae, the pelvis and other flat bones, and in the ends of long bones such as the femur, and the radius and ulna in the forearm, so it is these bones that are most frequently weakened by osteoporosis. The vertebrae often collapse as a crush fracture, causing a reduction in standing and sitting height as well as chronic, sometimes severe, backache. Such fractures in several thoracic vertebrae lead to a permanent forward curvature of the upper spine, called a ‘dowager’s hump’ (Figure 7.11). Older readers probably remember when advanced cases of this condition were common among old ladies. These days, treatment with hormones and calcium supplements slows the progress of osteoporosis, and severe, untreated cases are becoming rare.

Fracture of the head of the femur is the most common serious injury among elderly people. It happens nearly five times as often in old women as in men of the same age, although the latter are more likely to engage in strenuous or dangerous activities. During the 1980s, the injury occurred at a rate of nearly 1% per year among women aged 75 years or older, often following only a very minor fall from standing height. Several factors in addition to osteoporosis contribute to the susceptibility of this part of the skeleton to injury. Correct coordination of the activity of the hip muscles is essential to mechanically sound walking. Anomalous forces may be imposed on the skeleton if the muscles become weak in old age (Section 4.3.2), or their neural control is impaired (Section 6.5).
Would fractures in osteoporotic bones heal as fast as similar injuries in younger people unaffected by the disease?

No. Osteoporosis is caused by a disorder of osteoclasts and osteoblasts, the very cells that are essential to bone healing (Section 2.3.1).

Most mammals lose body mass in extreme old age (Section 4.5.1), much of it due to loss of skeleton mass, but osteoporosis in middle age seems to be an exclusively human disease. Indeed, some biologists believe that its origins are inextricably related to the unique features of reproduction in human females: menstruation and menopause. Osteoporosis is less common and less severe among mothers of large families than among childless women, suggesting that depletion of bone calcium during lactation (Section 7.3.3) does not promote it. The decrease in oestrogen at menopause seems to be the root cause of most of the symptoms, and synthetic oestrogens are widely used for treatment and prevention of osteoporosis. Oestrogens promote uptake of calcium from the intestine, and stimulate the thyroid gland to secrete calcitonin, a hormone that inhibits demineralization.

Nutrition is also important. Obviously adequate calcium intake is essential to support bone formation, but a high protein diet, high alcohol consumption and smoking promote calcium excretion, which can lead to net calcium loss, even when intake is high. However, obesity per se seems to protect people against osteoporosis (although it increases the risk from many other disorders including heart disease and some forms of cancer): it is thin, elderly women, eating a sophisticated Western diet rich in protein and alcohol who are most at risk.

Can you suggest how obesity could protect older women from osteoporosis?

The greater body weight imposes more stress on the leg bones and vertebrae during standing and walking. Regular stress promotes the formation of new bone (Section 2.3.1). For the same reason, bones stressed by regular exercise are less likely to become osteoporotic than those of inactive or bedridden people. Adipose tissue also secretes small amounts of oestrogen, formed from androstenedione, even after secretion from the ovaries has stopped, thereby preventing bone loss throughout the skeleton. Well-padded bones may also be less susceptible to fracture.

Regular stress is important for the maintenance of all bones, not just those of the limbs. The classic facial appearance of a stereotyped witch is a long-term consequence of missing or defective teeth combined with osteoporosis in old age. In the absence of the stresses generated by biting and chewing, the jaws gradually shrink, with the lower jaw sometimes being reduced to a thin band of bone in edentulous (toothless) skulls. Consequently, the chin and cheeks are greatly reduced, but, because the nose is mainly cartilage, it is less affected and so appears relatively prominent. This facial structure is much rarer now, thanks to modern dentistry and the wide availability of false teeth that stress the jaws nearly as efficiently as natural teeth.
Summary of Section 7.3

Bone consists of crystals of hydroxyapatite embedded in a matrix of collagen fibres. It also contains numerous living osteocytes which are nourished by blood vessels permeating the bone. The different histological types of bones are distinguished mainly by the arrangement of the osteocytes and blood vessels. The structure and mechanical properties of bone change with age, maturation and, in female mammals, reproductive status, at very different rates in different species. Osteoporosis is a specifically human disorder that affects women more severely and at a younger age than men. Bone, particularly trabecular bone, is eroded away when the activity of osteoclasts is faster than that of the osteoblasts, leading to weakening and greatly increased risk of fracture.

7.4 Joints

Where there is little movement between skeletal elements, bones are usually linked by suture joints in which numerous short, stout bands of collagen bind the articulating surfaces together; sutures are usually found where sheets of bones at joined along their edges, as in the skull, the pelvic girdle and the tortoise’s shell. In growing animals, the edges of the bones that form the sutures are relatively straight, and there is significant movement at the joint; at many such joints, the bands of collagen gradually ossify and the sutures close as growth ends, but sometimes the capacity for movement is retained throughout life. One of the most thoroughly studied suture joints is that between the two halves of the lower jaw; in many mammals, including humans, elephants and camels, the two jawbones are almost completely fused, but in many carnivores and in kangaroos, the small movements across the suture joint between the two halves of the lower jaw are an integral part of the biting and chewing mechanism.

In many adult vertebrates, movements at suture joints, particularly those of the skull, are greatly limited by the formation of crenulations at the edges of the bones, which interlock tightly like pieces of a jigsaw puzzle. In Figure 7.12, the sutures of the antelope skull are elaborately frilled near the horns where the skullbones risk sudden and uneven impact forces, but they are almost straight around the less vulnerable nasal region. Although there is almost no movement at frilled suture joints, they are very important for limiting the propagation of minor cracks in the bone: homogeneous sheets such as a window pane or a dinner plate usually shatter into several pieces once cracks form, but in a tiled or mosaic floor, cracks in one tile do not spread across the grouting, so adjacent ones remain intact. In this respect, vertebrate skulls resemble a mosaic: instead of splitting like a broken jam jar, weakening the entire structure and causing massive bleeding, cracks remain localized and the broken surfaces well aligned, so healing quickly and often perfectly.

7.4.1 Cartilage

Cartilage (‘gristle’) is the major skeletal material of all embryonic vertebrates, and of chondrichthyan fishes throughout life. As well as being an essential stage in the growth and healing of bone (Section 2.3), cartilage is also found in parts of the skeleton of adult vertebrates, such as the tip of the nose, the outer ear and the ventral area of the rib cage, where flexibility and toughness are more important than rigidity, and at joints.
The most familiar, and in many ways the most unusual, property of cartilage is the almost complete lack of a blood supply: undamaged cartilage appears greyish-white even in living vertebrates because, unlike bone, it is not permeated by blood vessels.

What histological features would you expect in a tissue that lacks a blood supply?

The tissue would consist mostly of metabolically inert, extracellular matrix and contain very few living cells. Stained sections of cartilage show a few small oval cells about 10–30 µm in diameter called chondrocytes, embedded in an extensive and apparently homogeneous extracellular matrix. Both the density of chondrocytes and the frequency of their division depends upon their location and the age of the specimen. The density of mitotically dividing chondrocytes is 20 times higher in epiphyseal cartilage (Section 2.3) than in articular cartilage of the same species.

The matrix consists of about equal quantities of collagen and proteoglycans to which large quantities of water are bound. Proteoglycans are some of the largest of all biological macromolecules (Section 2.3), consisting of 50–150 carbohydrate molecules, mostly keratan sulphate and chondroitin sulphate, attached to a central core of protein. The M₆ of this complex is about 1–3 million, larger than all muscle proteins except perhaps titin (Section 5.2.1). Up to 100 core proteins (each surrounded by its group of carbohydrate molecules) are linked, probably mainly by hydrogen bonds, to a single unbranched molecule of hyaluronic acid. Hyaluronic acid is a polymer of the disaccharide unit (N-acetylglucosamine + glucuronic acid). Both the carbohydrate and the protein components of proteoglycans contain numerous charged sites (for example, the SO₄²⁻ components of the sulphated sugars, and the COO⁻ groups of some amino acid residues), which exert electrostatic forces on adjacent water molecules. Proteoglycan molecules are therefore able to exert forces that organize large numbers of water molecules around themselves. In a form of cartilage called hyaline cartilage, both the collagen and the proteoglycans are arranged in a three-dimensional network, and the sponge-like properties of the latter are so effective that water is, in fact, by far the largest single component of the cartilage.

Can you suggest what role the collagen might play in cartilage?

It confers strength in tension on the tissue. The major components of proteoglycans are held together mainly by hydrogen bonds, and there are large quantities of water between adjacent molecules; without a ‘framework’ of fibrous, covalently bonded collagen running through it, cartilage would be weak when twisted or stretched. The abundance of fibres and lack of crystalline minerals in cartilage make it much less brittle than bone, and considerable force is needed to break it by twisting or bending.

7.4.2 Lubricated joints

The lubricated joints of terrestrial vertebrates are remarkable in that, although there is often substantial movement between the articulating surfaces, less energy is lost as friction than in most engineering joints; furthermore, they are very hard-wearing, maintaining their superior mechanical performance for more
than 70 years in the case of many human joints. The unique properties of hyaline cartilage play an essential role in **synovial joints**, which are found where there is movement through a wide angle, including joints between the limb bones and in the hip and shoulder.

Figure 7.13 shows the general scheme of a typical synovial joint. The ends of the bones are often, but not invariably, expanded in the region of the joint so that the weight-bearing surfaces are enlarged and rounded. The articulating surfaces are lined with a layer of very smooth cartilage about 2 mm thick, and bathed in synovial fluid. This sticky, viscous fluid is secreted by the synovial membrane and is similar in composition to other intercellular fluids except that it contains hyaluronic acid (Section 7.4.1). The entire structure is enclosed within the fibrous joint capsule, which may be continuous with the periosteum surrounding the bone. The hip joint of a large marine turtle shown in Figure 7.14a was photographed in a marketplace in Costa Rica; you can see that the smooth articular cartilage and the tough flexible joint capsule are almost entirely without a blood supply in spite of their massive proportions.

Many synovial joints are subject to stretching and twisting as well as compression and bending; these forces are resisted by ligaments that run between the two bones, either around the outside of the joint or within the synovial capsule. These ligaments usually undergo only small changes in length during normal movements but are arranged so that they restrict movements that would damage the precisely matched articulating surfaces. Figure 7.14b shows the bony elements of the disarticulated hip joint of an adult macaque monkey. The rounded head of the femur fits onto the load-bearing rim of the acetabulum, which in life would be lined with articular cartilage and held in place by a short but very stout ligament. In the intact animal, several other ligaments surround the joint capsule and maintain the correct alignment of the articulating surfaces of the joint during activities such as running, sitting or rolling, that might dislocate the joint.
The synovial fluid and the two surfaces of articular cartilage together form a low-friction, compression-resistant bearing surface. When the two surfaces of the joint are compressed together, the cartilage at the bearing surfaces is deformed, and the water molecules that were ordered around the proteoglycan molecules by the charged sulphate and carboxyl groups are squeezed out of the tissue. However, this squeezing out of the water molecules brings the numerous charged sites on the proteoglycans closer together, and, since like charges repel each other, sets up forces that oppose further compression in the cartilage. At the same time, the water that is squeezed out of the articular cartilage enters the synovial fluid, making it more dilute and hence able to lubricate more efficiently.

There is also a third way in which the cartilage and the synovial fluid are together able to maintain efficient lubrication, even under prolonged compression. Figure 7.15 shows the response of two freshly excised pieces of cartilage to prolonged compression; the probe quickly dents the articular cartilage (A) to a quarter of its total thickness but the cartilage from the ribs (B) responds to similar forces more slowly and the maximum deformation is less. After the first minute, further distortion of both tissues is very slow. After the probe is removed, it takes nearly an hour for the specimens to rebound to their original shape. This slow deformation under prolonged loading is called creep; it occurs in all kinds of cartilage but, as you can see from Figure 7.15, it is much more extensive in articular cartilage than in rib cartilage.

In the intact synovial joint, the articular cartilage of the two load-bearing surfaces initially make contact over only a small area, but as they are pressed harder or for a longer time they ‘creep’, thereby increasing the area of contact between the two surfaces and so decreasing the compression per unit area of articular cartilage. From an engineering point of view, vertebrate synovial joints compare very favourably with artificial systems, both because of their very low friction during movement, and because their low-friction performance is maintained even under prolonged and heavy compression without the need for lubrication under high pressure.

It is important to emphasize that many mammalian joints are much more elaborate than those shown in Figures 7.13 and 7.14. For example, the bones of the wrist, ankle and foot are connected together by numerous synovial joints, many of which bend through only a narrow angle. Correct alignment of all the
components of these mechanically intricate structures is important: as most people know from experience, sprains or bruises of the wrist or ankle lead to much swelling, pain and loss of function. Looking closely at Figure 7.14b you can see that the acetabulum is not exactly congruent with the head of the femur; a ‘sump’ of synovial fluid forms at the back of the joint, which permits synovial fluid to reach the weight-bearing surface from the top of the joint as well as from the joint capsule. The two parts of the joint are held in place by ligaments.

- Why would a ligament within the hip joint and a sump of synovial fluid be well-developed in the monkey, but absent in the large turtle?

Joint ligaments resist twisting and extension of the joint, and the sump of synovial fluid would be particularly important as a means of maintaining lubrication during prolonged compression, as happens during standing or sitting. Maintaining good lubrication of a joint that is subjected to continuous compression is very difficult. Marine vertebrates such as *Chelonia* (Figure 7.14) are almost neutrally buoyant in the water so their joints would therefore very rarely be subjected to such continuous compressive forces. The joints are compressed by the inertial forces generated by muscular movement, but such forces usually arise from cyclical activities such as swimming so, although transiently highly, they are not as continuous as gravitational forces. Horses that are tied up for long periods, and caged parrots that are unable or unwilling to fly, keep their joints in good condition in spite of standing continuously, by shifting the weight off each leg in turn.

- From Figure 7.15, how long must the animal rest each leg for the articular cartilage to be almost completely restored to its uncompressed shape?

The body’s weight must be off the leg continuously for at least half an hour. You can observe this behaviour for yourself in any stabled horse or caged bird. Regular and strenuous compression and relaxation of the synovial joints is essential to the maintenance of low-friction, painless movement. Dancers and athletes limber up before a performance by bending the arms and legs so that the hip, shoulder and knee joints move through their full range.

Two of the three articulations between the vertebrae of the mammalian spine are synovial joints, albeit of slightly different structure from those of the limb bones. In typical quadrupedal mammals, the intervertebral discs are compressed strongly for only brief periods during fast running or when standing up on the hindlegs. But those of bipedal humans are subjected to almost continuous compression from the moment we get out of bed. Figure 7.16 shows the daily changes in standing height of a normal adult engaged in light work; the body becomes 15 mm shorter within four hours of assuming the upright posture.

This apparent shrinkage is due almost entirely to the expulsion of water from the intervertebral discs, which have been compressed by the weight of the body or by the tensing of the slow postural muscles of the back. When one reclines in an armchair or lies in bed, these postural muscles can relax, and the weight of the upper part of the body is removed from them. The cartilage slowly takes up water from the synovial fluid and expands to its original dimensions. Regular compression and expansion are essential for keeping the intervertebral discs healthy; you may be familiar with the discomfort that arises from interfering with the normal expansion of the intervertebral discs by sitting or standing up all night, or by failing to relax the postural muscles of the back satisfactorily.
Regular compression and extension of both synovial and non-synovial joints are also essential for their long-term health because the flow of fluid between the joint surfaces and the lubricating fluid is the major route for the nutrition of the articular cartilage and internal ligaments; in the absence of a blood supply, oxygen, nutrients, blood-borne hormones and drugs reach cellular components of these tissues via the synovial fluid as well as via the blood vessels in the underlying bone. Small molecules such as glucose diffuse about 40% as fast through cartilage as through water. Since nutrient transfer depends upon diffusion, the nutrition of small joints should be better than that of large ones. However, articular cartilage of small mammals such as mice, and small human joints, has up to 25 times as many chondrocytes per gram as cartilage of large joints and humans so the tissues’ supply of nutrients in relation to requirements are about the same.

The cartilage in the joints of paralysed or bedridden people, and that of astronauts, becomes thin and fragile unless the joints are subjected to regular compression and extension. Atrophy of the cartilage in joints and reabsorption of bone from the vertebrae are the main reason why a person’s standing height decreases in old age. Normal brisk walking, in which the joints of the legs, hip and spine are compressed and released at about 2 Hz, is almost ideal for the nourishment of cartilage, thereby preventing its atrophy.

Summary of Section 7.4

Cartilage is a matrix of collagen fibres and large highly charged glycoproteins called proteoglycans around which are assembled large quantities of water. It is much tougher and more flexible than bone and ‘creeps’ when deformed by prolonged application of forces. Synovial joints are lined with articular cartilage and lubricated by synovial fluid secreted from the synovial membrane of the joint capsule. Under prolonged pressure, the water bound to the proteoglycan molecules in articular cartilage is squeezed out into the synovial fluid, thereby preventing the complete elimination of the lubricating fluid from the bearing surfaces. Exchange of extracellular fluid between the cartilage and the joint capsule is also essential for the former’s nutrition.
7.5 Conclusion

‘Connective’ tissues do much more than just connect: they have many subtle and functionally important mechanical properties. Detailed biomechanical studies reveal that apparently similar structures, such as tendons, can have quite different mechanical properties, and hence must perform very different roles in movement. As in the case of muscle, some of these properties change with age and habitual usage. Like muscle, almost all skeletal tissues are living and so need a supply of nutrients. For many such tissues, regular and appropriate usage is essential to keep them mechanically sound. The next chapter is about how these passive mechanical properties of the skeleton and tendinous tissues combine with active contractions in muscle to produce locomotory movements.

Objectives for Chapter 7

When you have completed this chapter, you should be able to:

7.1 Define and use, or recognize definitions and applications of each of the bold terms.
7.2 Describe the microscopic and molecular structure of fibrous collagen.
7.3 Outline some concepts and techniques used in the study of the mechanical properties of biological materials.
7.4 Outline the implications of the gross structure of tendons for their functionally important mechanical properties.
7.5 Describe the cytological structure, mechanical properties and anatomical distribution of the principal types of mammalian bone.
7.6 Describe and provide a functional interpretation for some ontogenetic changes in the structure, composition and mechanical properties of bone.
7.7 Outline the structure and composition of the major forms of cartilage.
7.8 Outline the molecular composition and anatomical arrangement of the main tissues in vertebrate synovial joints, and explain how they function together to minimize the energy lost as friction during movement.

Questions for Chapter 7

(Answers to questions are at the end of the book.)

Question 7.1 (Objective 7.2)

In what ways do (a) the chemical composition, and (b) the anatomical distribution of collagen differ from that of most other mammalian proteins?

Question 7.2 (Objective 7.3)

Define the following terms and state their scientific units of measurement: stress, strain, Young’s modulus.

Question 7.3 (Objective 7.4)

How would the properties of a muscle and tendon system change if the tendon became (a) thicker, (b) longer, (c) ossified?
Question 7.4 (Objective 7.5)
Classify the following terms depending upon whether they refer to (a) the histological structure of bone, (b) the gross structure of the skeleton, or (c) tissues associated with bone:
- trabeculae
- compact bone
- periosteum
- Haversian bone
- osteon
- cancellous bone
- ligament
- chondrocyte
- lamellar bone
- hydroxyapatite

Question 7.5 (Objective 7.6)
Briefly describe how the structure and composition of the human skeleton changes from birth to old age. Which of these age changes are adaptive and which are non-adaptive?

Question 7.6 (Objective 7.7)
List three ways in which (a) cartilage and tendon are similar, and (b) the internal organization of cartilage and tendon differ.

Question 7.7 (Objective 7.8)
Describe the role in vertebrate joints of (a) cartilage, (b) extracellular fluids, and (c) ligaments.