

BONE, BONES AND SKELETONS

Part of the fascination of working with ancient bones is that they are parts of formerly living animals. Unlike potsherds or stone tools, bones have been alive, and their complexity reflects that origin. We need to understand the constituents of bone, and how they are organized, in order to understand how, and whether, bones will survive burial and excavation. Furthermore, we need to understand the basic structure of the vertebrate skeleton if we are to comprehend those excavated fragments as parts of whole animals. The purpose of this chapter is to introduce bone as a tissue, and to outline the structure of the vertebrate skeleton. There is a lot of anatomical terminology in this chapter: subsequent chapters use precise anatomical terms where necessary, and this is the place where they are introduced. Readers who are less concerned with the osteological details, or who find it all too much, may prefer to skip to the summary of this chapter before reading on, and then to return to this chapter as a source of reference as necessary.

BONE COMPOSITION

Bone is a living tissue with cells and a blood supply, just like muscle or skin. As an animal grows, so its bones grow and undergo modification and repair. Thus the form of the skeleton at the time of death is one point in a process of continuous change. By the time archaeologists deal with the bone, it is a hard, dead material, much altered since the animal's death. It is important to remember that bone in the living animal is as susceptible to damage or alteration as any other living tissue. An excellent introduction to bone, and especially to its versatility as a skeletal material, is given by Alexander (1994), and Halstead (1974) remains a useful source.

Fresh bone has three main components: a complex protein scaffolding; a mineral which stiffens this scaffold; and a 'ground substance' of other organic compounds. Although proportions vary in different tissues, about half of the weight of fresh bone is mineral, the remainder being organic matter and water.

Of the organic fraction, about 95 per cent is the structural protein *collagen* (Miller & Gay 1982; Linsenmayer 1991), which is unusual in containing high proportions of the amino acids glycine and hydroxyproline. Collagen molecules have few large side-chains and can pack together very closely, bonding at regular intervals. The macromolecules are arranged in a left-handedly spiralling triple helix, which itself spirals to the right about a central axis. The structure is a bit like a traditional hawser-laid rope, and gives collagen its characteristics of being strong under tension yet flexible.

The mineral phase is mainly *hydroxyapatite*. This may be loosely described by the formula $\text{Ca}_{10}(\text{PO}_4)_6(\text{OH})_2$, though the Ca ions may be replaced by Sr, Ra, or Pb, the PO_4 ions by CO_3 , and the OH groups by F. Other ions, mostly metals, can be attached to the surface of hydroxyapatite crystals by adsorption, which may occur in living bone, but can also occur in dead, buried bone (Lee-Thorp & van der Merwe 1981; Millard & Hedges 1995). It can therefore be difficult to tell whether the chemistry of an ancient bone reflects its chemistry during life, or the burial environment after death.

The ground substance makes up only a very small proportion of fresh bone. It serves as a packing, and probably also regulates hydration, and is composed of a mixture of mucoproteins and aminopolysaccharides.

BONE STRUCTURE

There are numerous detailed texts on bone histology and growth. A useful introduction is given by Davis (1987, 47–53), a little more detail by Alexander (1975, 74–9), and a full account in histology texts such as Bloom & Fawcett (1975). Although an old source, Frost (1973, 3–27) gives a particularly dynamic account of bone growth and remodelling.

Mineralized bone is formed by the secretion of hydroxyapatite by specialized cells (*osteoblasts*), upon and within a framework of interwoven collagen fibrils. The fibrils are roughly aligned to a common axis, determined by the stresses and strains placed upon the growing bone. In some bone, the osteoblasts are distributed throughout the tissue. This is cellular, or endochondral, bone, and is typical of most parts of mammal and bird skeletons. In acellular, or dermal, bone, osteoblasts are organized at the surface of thin laminae of bone, and not distributed throughout. Acellular bone is typical of most parts of the skeleton of the majority of fishes.

The compact bone which makes up the shafts of limb bones of birds and mammals is, at its simplest, a series of lamellae of bone deposited more or less concentrically about the longitudinal axis of the bone, and permeated by large and small channels. The cells (*osteocytes*) which are responsible for the secretion and subsequent remodelling of the bone remain enclosed in voids (*lacunae*) within the bone, which are interconnected by a branching and interdigitating network of fine channels (*canaliculi*), and the system is connected at intervals to blood vessels. This links the osteocytes to the transport system of the rest of the body, and makes bone remarkably porous, albeit on a microscopic scale. Some mammals, and a few birds and dinosaurs, show remodelling of the compact bone to produce secondary osteons. Essentially, an *osteon* is a cylindrical unit of heavily mineralized bone arranged around a longitudinally directed blood vessel. Bone which has largely been remodelled into secondary osteons is sometimes termed dense *Haversian bone* (Fig. 2.1).

A limb bone typically consists of a tube of compact bone capped at each end by strap-like pieces (*trabeculae*) arranged in a stress-bearing and shock-absorbing pattern of arches and buttresses. This is termed *cancellous* bone, or more graphically spongy bone. Other parts of the skeleton, such as ribs and shoulder blades, typically consist of thin surface layers of a form of compact bone, with cancellous bone making up most of the thickness.

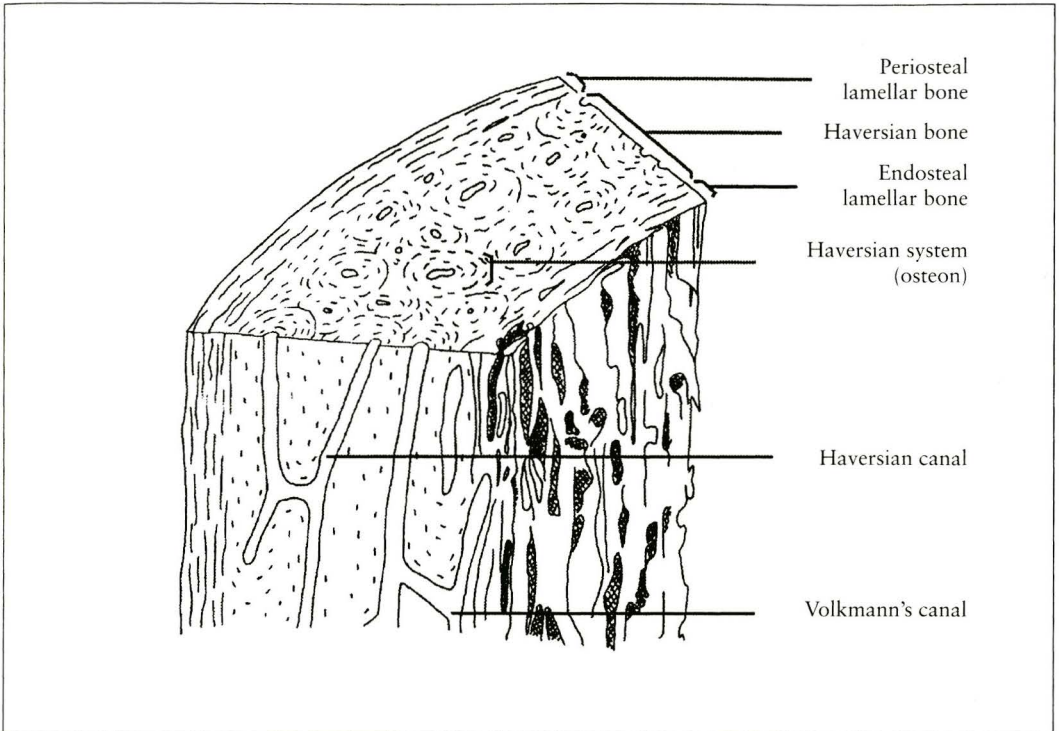


Fig. 2.1. Schematic diagram of the microstructure of mammalian compact bone, to illustrate some of the terms used in the text.

THE VERTEBRATE SKELETON

In evolutionary terms, bone developed as stiffened cartilage, to provide a flexible support through the long axis of the body, support for the gills and jaws, rigid plates to protect the brain and sensory organs, and a jointed structure against which muscles pull in order to move the body. A good review of the vertebrate skeleton from an evolutionary perspective is given by Romer (1970). The earliest vertebrates were fish-like creatures, and very far removed in appearance from modern mammals or birds. None the less, all vertebrates have much the same skeleton, developed or modified to particular functions: one body-plan encompasses mammals, birds, reptiles, and amphibians. Fish also conform to the basic vertebrate plan, but have modifications not seen in land-dwelling vertebrates. In agnathan fish (lampreys, etc.) and the cartilaginous fish (skates, rays, sharks) the skeleton is composed of cartilage, though some stress-bearing elements may be partly mineralized. This is seen, for example, in the jaws of some sharks, and in the vertebrae of some sharks and rays (Wheeler & Jones 1989, 80–1).

In order to describe the vertebrate skeleton, it is necessary to use specific terms of direction and location. These are summarized in Table 2.1. Figs 2.2 to 2.4 show the main skeletal elements of a typical mammal, bird and fish.

Table 2.1 *Terms for Location and Direction*

When trying to describe where you are around the skeleton or on a piece of bone, it is important to be consistent in the use of terms. These are some of the more commonly used terms for describing direction and location around the body.

Dorsal:	towards the back of the body.
Ventral:	towards the underside of the body.
Anterior:	towards the front; i.e the direction in which an animal normally faces.
Posterior:	towards the rear.
Medial:	towards the mid-line of the body.
Lateral:	away from the mid-line of the body.
Proximal:	towards the point of attachment of a limb.
Distal:	away from the point of attachment of a limb.
Cranial:	towards the head.
Caudal:	towards the tail.
Palmar:	the palm of the hand or sole of the foot.
Volar:	the 'back' of the hand or foot.

Thus a limb bone has proximal and distal ends, and has anterior, posterior, medial and lateral surfaces (or 'aspects'). Your knee joint consists of the distal end of the femur and the proximal end of the tibia, plus the patella, which is positioned anterior to the other bones. A vertebral centrum has a cranial surface and a caudal surface. Your navel, should you wish to contemplate it, is on your ventral surface, medial to your hips, and faces anteriorly. The meaning of a manual 'V-sign' depends on whether the palmar or volar aspect of your hand faces anteriorly.

Note also directions around the mouth:

Mesial:	towards the mid-line of the jaws; i.e. where left and right sides meet.
Distal:	away from the mid-line of the jaws.
Buccal:	towards the inner surface of the cheeks.
Lingual:	towards the tongue.
Occlusal:	the 'chewing surface' of a tooth.

(Note: the term *labial* is sometimes used synonymously with *buccal*, though sometimes only to refer to the 'towards the lips' surfaces of canine and incisor teeth. Because of this ambiguity in use, it is best avoided.)

Thus your incisors are positioned mesial to your canines. The mesial surface of LM₂ (lower molar 2) abuts the distal surface of LM₁. The distal surface of LM₃ abuts nothing, as it's the most distal part of the tooth row in a normal mammal. When you smile, you expose the buccal surfaces of your incisors (and canines in a really big grin), but few people apart from the dentist ever see the lingual surfaces. When you close your mouth, the occlusal surfaces of your upper and lower molars and premolars meet.

THE SKULL AND BACKBONE

The most primitive relatives of vertebrates, such as sea-squirts, are stiffened by a simple cartilaginous rod which runs along the length of the body (the *notochord*). In vertebrates this is replaced by a backbone comprising vertebrae which articulate with each other to give limited flexibility and support. Each vertebra comprises a roughly cylindrical structure called the *centrum*, attached to which is the *neural arch*. This arch carries

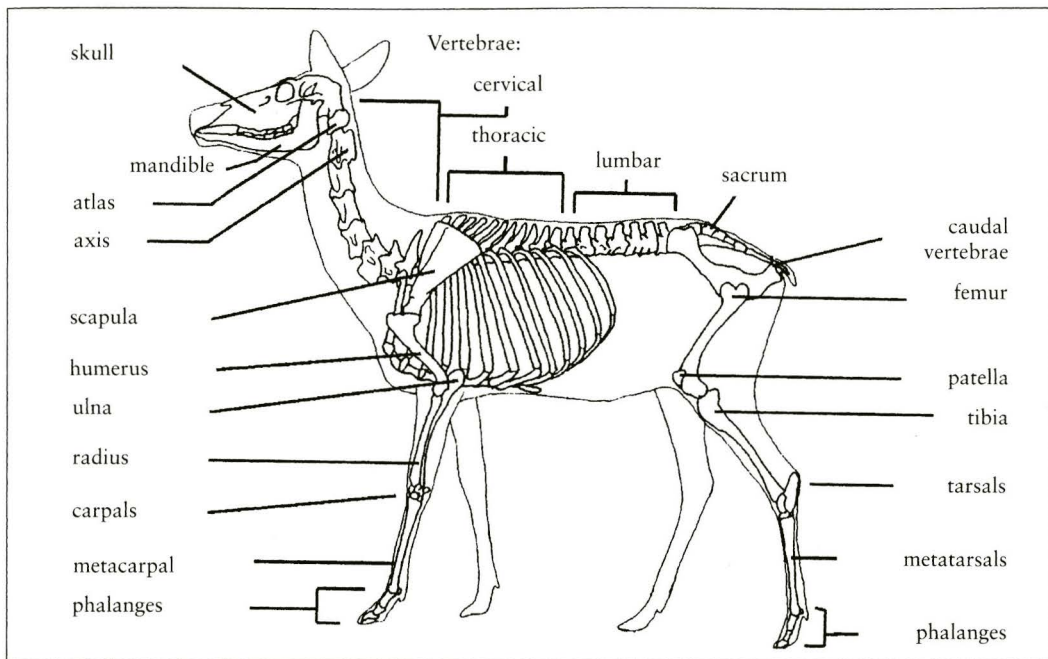


Fig. 2.2. The essentials of the mammalian skeleton, as illustrated by the skeleton of a red deer.

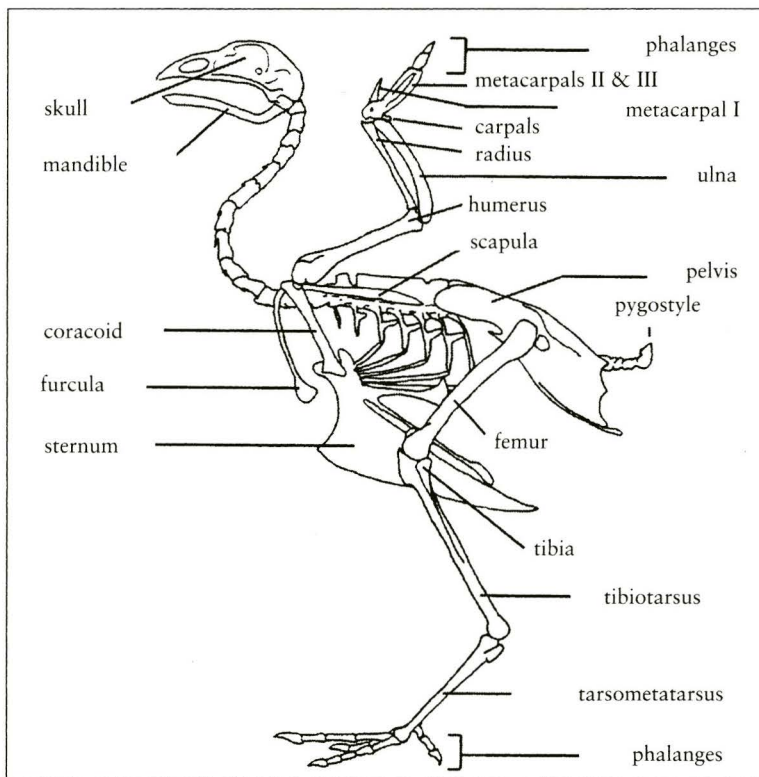


Fig. 2.3. The skeleton of a domestic fowl as a typical bird. Note in particular the massive sternum, and compare the forelimb with that of a mammal.

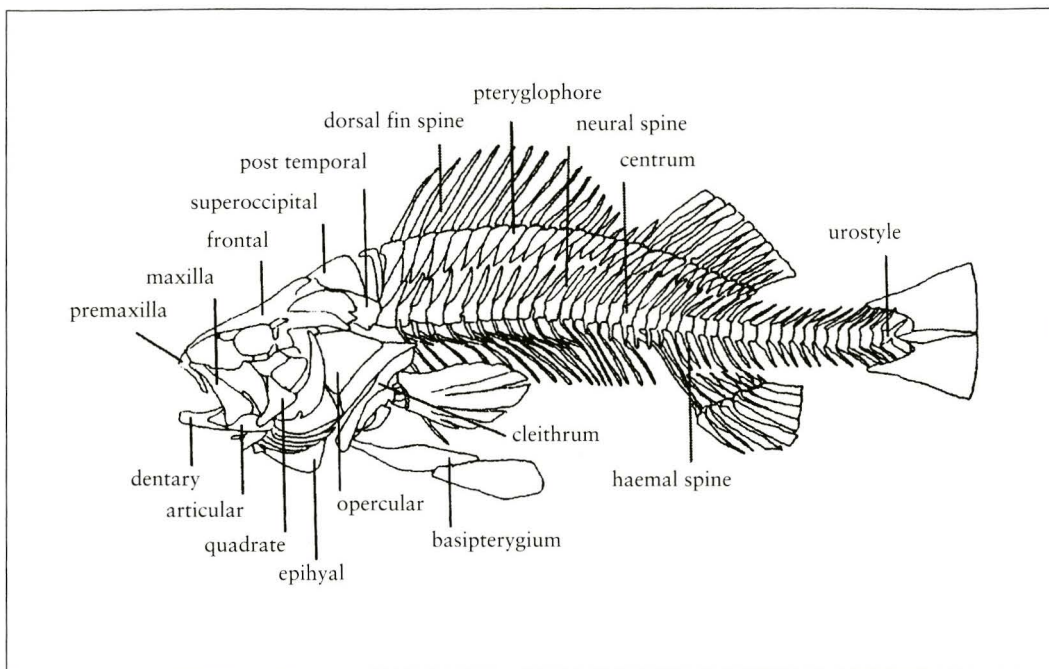


Fig. 2.4. The skeleton of a perch, shown here to illustrate only the major elements of a typical bony fish.

articulations for the adjoining vertebrae, bears the muscles which run along the backbone, and encloses the neural canal. In the neural canal in life is the spinal cord, which distributes impulses from the brain to the outlying parts of the limbs and entrails. In fish the ventral aspect of the more posterior vertebrae (Fig. 2.4) carries another arch, the *haemal arch*. In different classes of vertebrates, the vertebrae may also bear enlarged attachments for tendons and ligaments, notably the neural spine at the apex of the neural arch, and the transverse processes on either side. Because vertebrae lie along the mid-line of the body, they are bilaterally symmetrical.

The vertebral column is conventionally divided into sections. The first few vertebrae (normally seven in mammals) counting back from the skull are the *cervical vertebrae*, which constitute the skeleton of the neck. The first cervical vertebra (*atlas*) is modified to provide a point of attachment and articulation for the skull. The second cervical vertebra (*axis* or *epistropheus*) provides a 'peg' for axial rotation of the skull and atlas. The vertebrae of the chest, or *thoracic vertebrae*, have points of articulation for the ribs: mammals generally have twelve to fifteen thoracic vertebrae. Continuing down the backbone, we come to the *lumbar vertebrae* of the lower back. These have no rib articulations, but often have prominent transverse processes. The hind limb-girdle is fixed to the backbone by way of a block of fused and modified vertebrae called the *sacrum* in mammals, and *synsacrum* or *lumbro-sacrale* in birds. Beyond this lie the *caudal vertebrae* of the tail, a highly variable number of vertebrae often reduced to a simple short rod of bone.

In bony fish the vertebrae are not so obviously differentiated into groups, though there is some variation in form all along the length of the vertebral column. Some authorities (e.g. Wheeler & Jones 1989, 105–6) recognize three groups of vertebrae in fish: the *anterior abdominal vertebrae*, which lack rib attachments; the *abdominal vertebrae*, which have rib attachments; and the *caudal vertebrae*, in which the haemal canal along the ventral side of the vertebrae is closed, forming a haemal spine. In other texts, the terms *thoracic*, *precaudal* and *caudal* vertebrae are also used. Fish have more vertebrae than birds and mammals: typically fifty to sixty in members of the salmon family, for example. In reptiles and amphibians vertebrae are highly variable in number, and usually are not clearly differentiated. Frogs, for example, lack ribs and typically have only nine vertebrae, the ninth of which fulfils the function of the mammalian sacrum.

The chest of a bird or mammal is enclosed by the *ribs*, which curve away from the thoracic vertebrae to meet along the front of the chest. The ribs have an articulation at their vertebral ends which allows movement, to expand and contract the chest during breathing. At the front of the chest, or ventrally, the ribs of most mammals and birds meet the *breast-bone* or *sternum*. In mammals this is usually an elongated plate or rod, often of two or more distinct sections. In birds the sternum is a large, flat plate from the mid-line of which a ‘keel’ projects forwards to anchor the hugely developed pectoral muscles with which birds flap their wings (Fig. 2.3).

The *skull* consists of many different bones, the details varying from one class of vertebrates to another. Basically, the skull can be divided into the *neurocranium*, plates of bone that surround and protect the brain, and the *viscerocranium*, which carries the sensory organs and the mouth. In the higher vertebrates, the major bones of the neurocranium are the *frontal*, *parietal*, *occipital*, *temporal*, *sphenoid* and *ethmoid* bones. The viscerocranium provides a mounting for the eyes (with parts of the neurocranium), the nose and olfactory organs, and the upper and lower jaws. The major bones of the viscerocranium are the *zygomatic*, *maxilla*, *premaxilla*, *nasal* and *lachrymal* bones. The maxilla and premaxilla bear the upper set of teeth. The lower teeth are borne on the *mandible* in higher vertebrates. In fish, reptiles and amphibians the lower jaw is a more complicated structure comprising the *dentary* (which bears the teeth), *angular* and *articular* bones (Fig. 2.4). In mammals the mandible articulates with the temporal bone near the *auditory meatus*, or ear-hole. In birds, fish and other lower orders the articular bone articulates with the *quadrate*, an element of neurocranium which we mammals manage without. The elongated quadrate bone of some snakes allows them to open their mouths in a dramatically wide gape.

The bony fish have remarkably complex head bones, which take their own nomenclature (Harder 1975). The jaws consist of a tooth-bearing *dentary* bone in the lower jaw and a tooth-bearing *premaxilla* in the upper jaw. In some fish the *maxilla* is also toothed, and some carry teeth on the *palatine* and *prevomer* bones in the roof of the mouth. As if that were not enough, some fish have yet more teeth located on the upper and lower *pharyngeal bones*, located in the throat. The fish neurocranium is founded on the *basioccipital*, *basisphenoid* and *parasphenoid* bones, which form the base of the neurocranium, and the *frontal* and *supraoccipital* bones which form the ‘crown’ of the neurocranium. To either side of the posterior part of the neurocranium lie the bones of

the gill covers, and of the *branchial skeleton*, which supports the gills. Immediately posterior to the head lies the pectoral girdle, which includes a major element not present in other vertebrates: the *cleithrum*. This articulates with the *coracoid*, which in turn articulates with the *scapula* and the *radial bones*, to which the pectoral fin is attached. The closest approximation which fish have to a pelvic girdle is the *basipterygium*, which in some families is located close to the pectoral girdle, while in others it is towards the posterior end of the abdomen. A more detailed overview of the fish skeleton is given by Wheeler & Jones (1989, 87–125), and Cannon (1987) gives useful illustrations of the disarticulated bones of four representative species.

TEETH

This is too big a subject to be considered in great detail here, and a useful general source is Hillson (1986). Fig. 2.5 shows the dental layout and terminology for a typical mammal.

Mammals, fish, reptiles and some amphibians have teeth, of which mammal teeth are the most complex. Most mammals are *heterodont*; that is, their mouths contain different forms of tooth, adapted for cutting, grinding and crushing. All teeth can be divided into a *crown*, which in life is above the gum, and the *root(s)* which anchor the tooth into the mandibular bone. Where the crown runs into the roots, there may be a clearly defined *neck* or cervical zone. Most of a mammal tooth is made of *dentine*, which is a specialized form of bone. The cells that mineralize dentine retreat as the dentine forms, and so are not encapsulated within it as osteocytes are within bone. At the core of the tooth is the *pulp cavity*, containing blood vessels and nerves. The crowns of most teeth in

the majority of mammals are covered with *enamel*, which is essentially a form of hydroxyapatite.

Mammalian adult teeth can be divided into *incisors*, *canines*, *premolars* and *molars*. Mammals normally have the same distribution of teeth in the left and right halves of each jaw, but may not necessarily have the same distribution of upper as of lower teeth. For example, sheep have lower incisors, but no upper incisors. The most teeth a mammal will normally have in any one quarter of the jaws is three incisors, one canine, four premolars and three molars, distributed in that order from the front of the jaw (mesially) to the

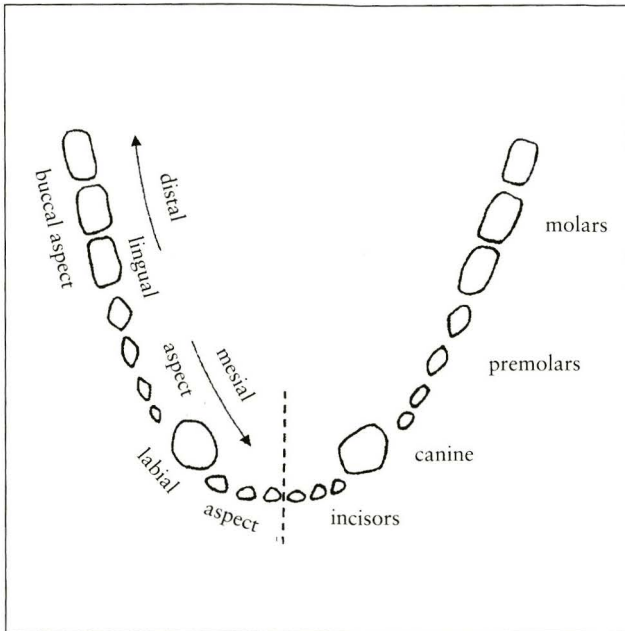


Fig. 2.5. Mammalian dentition summarized to show the application of terms to typical heterodont dentition.

back (distally). Many mammals have far fewer teeth than this: humans have two incisors, one canine, two premolars and three molars per quarter-jaw. Some mammals have two sets of teeth throughout their life: the *deciduous* ('milk') teeth and the *permanent* teeth which replace them in adult life. A species generally has fewer deciduous than adult teeth, and deciduous teeth are usually only differentiated into incisors, canines and premolars. True molars are a feature of permanent dentition, though the deciduous premolars are sometimes confusingly referred to as 'deciduous molars', especially in studies of human bones.

Not all mammals show clear differentiation of their teeth. In shrews, for example, there are obvious incisor teeth, but the remainder are a row of sharply pointed teeth which defy classification. Similarly, in seals the distinction between premolars and molars can not be clearly made in adults: instead, they are generally referred to as *postcanine teeth*.

HIPS AND SHOULDERS, KNEES AND TOES

Vertebrates' limbs are attached to the backbone by way of the *pectoral* and *pelvic* girdles, which also provide a joint within which the leg, wing or fin can move. The limb girdles in fish are close to the skull, and have been outlined above (Fig. 2.4). In other vertebrates the pectoral girdle consists of three bones: the *scapula*, *coracoid* and *clavicle*. In simple amphibians the three bones extend roughly in a 'Y' shape, with the articulation for the front leg at the centre of the 'Y'. The scapula extends along the back, roughly parallel to the backbone; the coracoid extends down the sides of the body and slightly backwards; and the clavicle extends across the front of the upper part of the 'chest'. The articulation for the front leg is a socket made up of part of the scapula and part of the coracoid. In birds the scapula is a slender, cutlass-shaped bone which lies to one side of the backbone, while the coracoid is a big triangular structure which links the pectoral girdle to the *sternum* (breast-bone) and provides a rigid strut to brace the chest against the pull of the pectoral muscles which flap the wings. The two slender clavicles are fused to produce a structure called the *furcula* (wish-bone). In mammals the scapula is the major bone of the pectoral girdle, and is a flat, triangular or D-shaped structure, with an articulation for the front leg. The coracoid is reduced to a small lump beside this articulation, and the shoulder blade in many mammals, ourselves included, should properly be described as the *scapulo-coracoid* bone. Only the most primitive mammals, such as the duck-billed platypus *Ornithorhynchus*, retain a substantial, separate coracoid. The clavicles are struts which connect the pectoral girdle to the sternum, such as the human collar bone. In some mammals, such as sheep and pigs, the clavicle has faded away altogether.

The pelvic girdle is also based on three bones, but is more firmly attached to the backbone by way of the *sacrum*. Each half of the pelvic girdle is referred to as the *os innominatum*. (This means 'un-named bone', which seems a contradiction in terms.) The major orders of vertebrates have diverse modifications of the pelvis, and this is only the most basic of summaries. In amphibians the *os innominatum* comprises a long, slightly curved, rod (*ilium*), which is expanded at one end where it fuses with the 'straight' side of a D-shaped plate (*ischium*). An articulation for the back leg (*acetabulum*) is located where

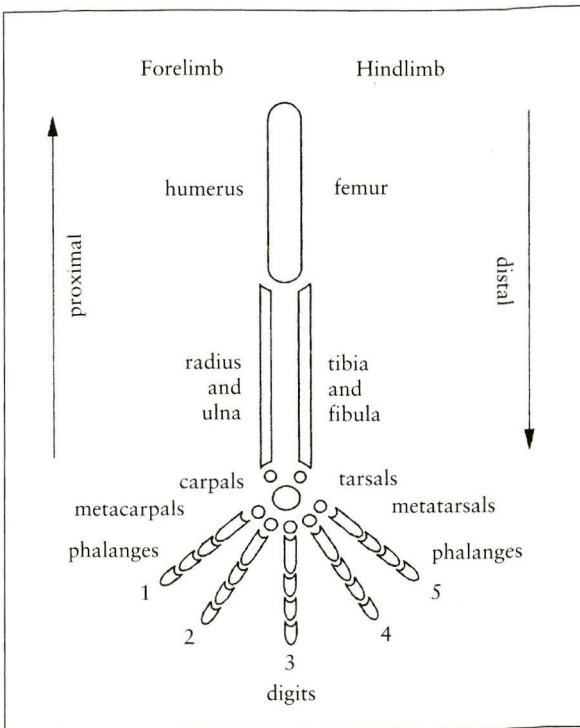


Fig. 2.6. The basic pentadactyl limb, and terms for the fore and hind limb. Note that the number of digits, and the number of phalanges, varies considerably from the pattern shown here. Horses have only one digit on each foot, while we primates have only two phalanges in our first digits.

the ilium and ischium fuse, roughly half of it on each bone. In birds the pelvis is somewhat different. The ilium is a flattened plate of bone which extends along either side of the lower part of the bird's back and is fused to the backbone. The ischium extends posteriorly, and is also broad and flattened. A third bone, the *pubis*, extends from roughly where the ilium and ischium meet, and is a blade-like bone that passes downwards and backwards across the sides of the abdomen. The acetabulum is a neat hemispherical cup located where all three bones meet. (*Acetabulum* is a Latin term meaning 'vinegar cup'.) In mammals the os innominatum is relatively simple. The ilium is generally quite flattened and has a large area of fusion with the sacrum, and the flattened ischium passes posteriorly to a substantial tuberosity (which you're sitting on). The pubis extends across the front of the abdomen to fuse with the

opposite pubis, and posteriorly to fuse with the ischium. The acetabulum consists of parts of the ilium, ischium and pubis, which fuse at a Y-shaped junction or suture.

The vertebrate leg can be considered in very simple, general terms. All vertebrates are *pentadactylous*; that is, they have a maximum of five fingers or toes per limb (Fig. 2.6). Not all vertebrates have retained all five toes on the fore and hind feet. As natural selection has driven adaptation and bodily diversity, some animals have achieved greater 'fitness' by losing toes, leaving horses with only one toe per limb, sheep with two, rhinoceros with three, pigs with four, and ourselves and aardvarks with five. Loss of toes has generally been an adaptation to faster, more energy-efficient running, at the expense of the ability to grip and to climb.

The leg can be divided into three zones. By reference to human limbs, these are the *stylopodium*, the first segment from shoulder to elbow or hip to knee; the *zygopodium*, the second part from elbow to wrist or knee to ankle; and the *autopodium*, encompassing the wrist, hands and fingers or ankle, feet and toes. The stylopodium has one bone, with a ball-shaped articulation at the upper (proximal) end and a more complex articulation at the lower (distal) end. In the front leg, this bone is the *humerus*. In mammals the humerus is a tube of roughly circular to oval cross-section, the

proximal articulation typically being a flattened hemisphere, and the distal articulation an elongated pulley-shaped articulation (*trochlea*), which forms part of a complex hinge-joint (the elbow). In birds the humerus is similar, but the proximal end is expanded and somewhat flattened. The stylopodium element in the back leg is the *femur*. This resembles the humerus in having a roughly circular cross-section, with a prominent ball-shaped proximal articulation. The distal articulation consists of two strongly convex knobs (*condyles*), with a saddle-shaped surface on the front of the distal end to carry the knee-cap (*patella*). The femur in birds is much as in mammals and it fulfils the same function.

The zygapodium consists of two parallel bones that may be wholly or partially fused along their length. In the front leg, these are the *radius* and *ulna*. The radius has a simple concave proximal articulation, to articulate with the trochlea of the humerus, and a series of concave facets at the distal end to articulate with the bones of the wrist. The proximal part of the ulna is extended by the *olecranon process*: the knob of bone at the tip of your elbow is your olecranon process. This forms a lever with the humerus so as to allow the elbow joint to be straightened. In amphibians the radius and ulna are fused along their length into a composite bone. In birds they are separate, and the ulna is generally much the more robust of the two. In mammals the radius is usually the more robust element, and in some mammals (such as horses, cows, deer and camels) the shaft of the ulna has been reduced to a sliver of bone fused to the posterior surface of the radius, though the proximal end remains as a substantial bone.

In the back leg, the two zygapodium bones are the *tibia* and *fibula*. The proximal end of the tibia bears two, often conjoined, slightly concave articulations for the condyles of the femur, and the distal articulation is also concave. In amphibians the tibia and fibula are fused along their length. In birds the fibula is much reduced, to a roughly triangular proximal end, one corner of which is drawn out into a tapering, slender shaft. The tibia in birds is a robust bone of roughly oval cross-section, the proximal part being elaborated by a prominent crest of bone on the front (anterior) surface. In birds the proximal group of tarsals are fused with the distal part of the tibia, so the bone is more correctly called the *tibiotarsus*, and the distal articulation is distinctly convex. In mammals the fibula is often reduced, sometimes to nothing more than the distal articulation, and is never as robust as the tibia. The tibia typically has a roughly rectangular cross-section in the more distal part of the shaft, and a distinctive triangular form towards the proximal end.

Finally the autopodium. First come the bones of the wrist and ankle, the *carpals* and *tarsals* respectively, which do several jobs (Fig. 2.7). They provide the necessary flexibility for the front and back feet, act as shock absorbers and provide a means of attaching up to five digits to a zygapodium of only two bones. The nomenclature of carpals is complicated, and in species in which the number of toes is reduced, or in which the fore foot is particularly specialized, some carpals may be absent or fused with one another. The tarsals are similarly variable. The tibia articulates with the *astragalus*, attached to which is the *calcaneum*. The calcaneum has a process which extends towards the back of the heel to provide an attachment for the Achilles' Tendon. The astragalus and calcaneum (*talus* in some texts) articulate with a row of smaller tarsals,

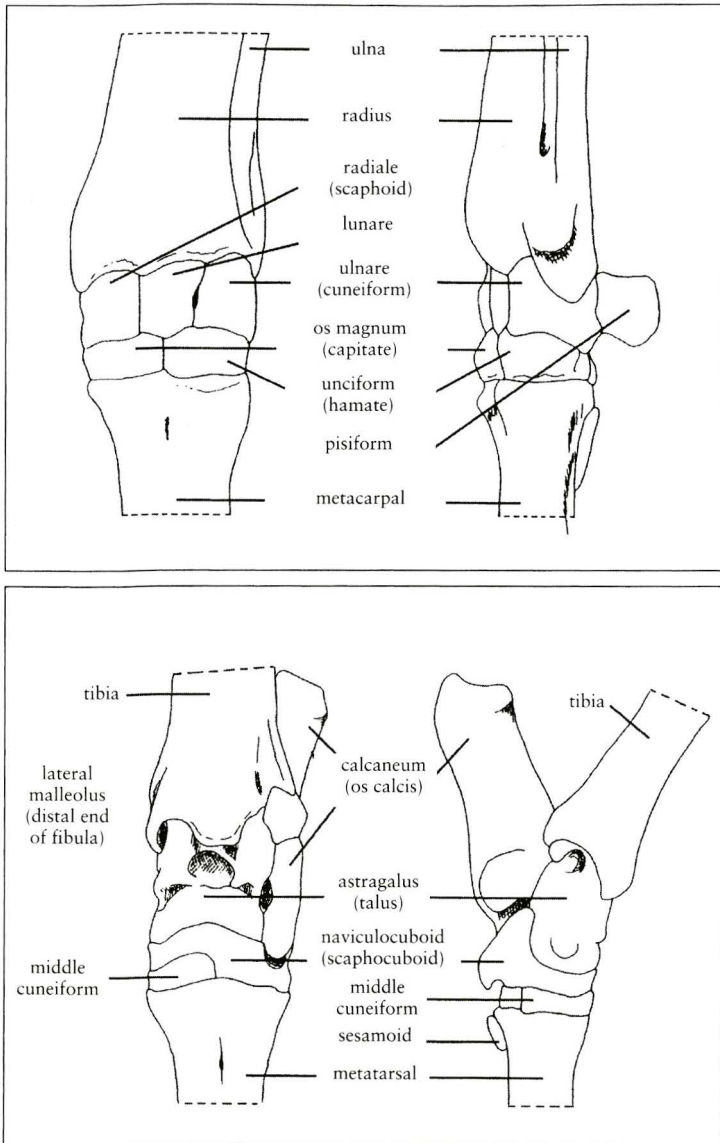


Fig. 2.7. Carpals (above) and tarsals (below) of a typical bovid, illustrated and named.

the largest of which is usually the descriptively named *cuboid*. In hoofed mammals such as cattle and sheep, this is fused to another, smaller tarsal to form a substantial bone called the *naviculo-cuboid*.

Articulating with the carpals and tarsals are the *metapodials*, which form the palm of the hand and arch of the foot. These are simple tubular bones, with a flat or concave proximal articulation and a convex distal articulation, and are termed *metacarpals* in the front limb, and *metatarsals* in the hind limb. In birds the metacarpals are reduced to a fused pair of bones which bear an uncanny resemblance to a safety-pin, and which

form the lower portion of the wing. The three metatarsals in birds are fused together along their length, with the distal group of tarsals fused to their proximal ends. The whole unit is termed the *tarsometatarsus*, of which the fused tarsal bones comprise the *hypotarsus*. Mammals with a reduced number of toes obviously have fewer metapodials. Horses have only one toe: it is the third digit, so they retain only the third metapodial. In the two toes of cattle, sheep, and other cloven-hooved animals the third and fourth metapodials are fused together along their length to produce what appears to be one bone, with an obviously doubled articulation at the distal end for the separate third and fourth toes.

The last outpost of the vertebrate leg are the *phalanges*, the bones of the fingers and toes. The first digit (the thumb or great toe in humans) has only two phalanges, while digits two to five have three each. Phalanges are rather stubby, tubular bones, with a concave proximal articulation and a convex distal articulation, except for the last (terminal) phalanges, which may show all sorts of modifications, depending on the form of the foot of the animal. In carnivorous mammals and in most birds the terminal phalanges are sharply curved, to provide a gripping claw. In the hooved mammals the shape of the terminal phalanges reflects the shape of the hoof. It is crescent-shaped in cloven-hooved species such as cattle and deer, but flattened and nearly circular in outline in horses.

The scales of fish are an additional category of vertebrate remains which may be found in archaeological deposits. In anatomically primitive fishes such as sturgeon or the garpike (*Lepidosteus*) of North America, *ganoid scales* are formed. These are typically diamond-shaped, and have a coating of a material not unlike dental enamel, termed *ganoine*. Most bony fishes have a covering of scales, and the scales of some species may be sufficiently robust to survive in favourable burial conditions. Identification of scales is often possible to family level, and sometimes to species. Most scales grow during life by the addition of increments (*circuli*), the thickness of which reflects the rate of growth of the fish. The approximate age and seasonality of growth of fishes can thus be read from the scales, and this information can survive on archaeological specimens. Scales are reviewed in greater detail by Wheeler & Jones (1989, 116–20).

Most fish also develop *otoliths*, mineralized structures carried in the neurocranium as a means of sensing and controlling bodily orientation. Otoliths consist largely of calcium carbonate, and so may differ in their survival during burial from bones in the same deposit. The form of the otoliths varies between species, often enabling identification to be made to genus or species level. Otoliths, like scales, grow incrementally, and their analysis allows investigation of the age and seasonal growth patterns of fishes (see Chapter 12).

SUMMARY

It may not seem so to a reader new to the subject, but that is a brief and fairly straightforward review of the vertebrate skeleton and its major elements. If you skipped the detail or just looked at the pictures, the important point to grasp is that birds and mammals, and to a degree reptiles and amphibians, have much the same bones, variously adapted to fit them to their way of life. It is this homology, derived from the single

evolutionary origin of the internal bony skeleton, that makes possible the identification of fragmented, disarticulated archaeological material. A femur is a femur, whether it comes from an eagle or a deer. It is relatively easy to see and understand this homology when confronted with articulated modern skeletons. However, archaeological material has usually been broken and dispersed by humans and scavengers, then buried in more or less destructive geochemical conditions, then handled by archaeologists during excavation and study. The physical attributes which typify a particular skeletal element will have been broken up and modified, and physical traces of butchering and gnawing will have been added. The next chapter reviews the process of post-mortem modification. For now, I would stress the importance of familiarity with the vertebrate skeleton in all its diverse forms as an essential start to being able to identify and describe the gnarled old fragments which excavation produces. One may never personally encounter archaeological specimens of ostrich or wallaby, but familiarity with their skeletons is a useful contribution to an understanding of the vertebrate skeleton as a whole.