Skeletal system

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The supporting tissues of animals which often serve to protect the body, or parts of it, and play an important role in the animal's physiology.

Skeletons can be divided into two main types based on the relative position of the skeletal tissues. When these tissues are located external to the soft parts, the animal is said to have an exoskeleton. If they occur deep within the body, they form an endoskeleton. All vertebrate animals possess an endoskeleton, but most also have components that are exoskeletal in origin. Invertebrate skeletons, however, show far more variation in position, morphology, and materials used to construct them.

Exoskeletons

Many of the invertebrate phyla contain species that have a hard exoskeleton, for example, corals (Cnidaria); limpets, snails, and *Nautilus* (Mollusca); and scorpions, crabs, insects, and millipedes (Arthropoda). However, these exoskeletons have different physical properties and morphologies. The form that each skeletal system takes presumably represents the optimal configuration for survival. *See* *See also:* ARTHROPODA; MOLLUSCA; ZOOPLANKTON.

Calcium carbonate is the commonly found inorganic material in invertebrate hard exoskeletons. The stony corals have exoskeletons made entirely of calcium carbonate, which protect the polyps from the effects of the physical environment and the attention of most predators. Calcium carbonate also provides a substrate for attachment, allowing the coral colony to grow. However, it is unusual to find calcium carbonate as the sole component of the skeleton. It normally occurs in conjunction with organic material, in the form of tanned proteins, as in the hard shell material characteristic of many mollusks. Cuticular exoskeletons are widely distributed among the invertebrates. They are formed by proteins that have been stiffened by the chemical action of phenols (the process is called tanning). Mineral salts may be incorporated within the cuticle for additional strength and stiffness.

The major advantage of a hard exoskeleton is the high degree of protection afforded to the body organs against mechanical damage and desiccation. Some disadvantages are the relatively large mass of the skeletal structure in proportion to the size of the soft tissues; the inability of some animals to remodel the skeleton and repair damage; and problems for a growing animal bounded by rigid skeletal tissues. Arthropods have solved this last problem by periodically shedding the old skeleton (molting) and replacing it with a new, larger one. Immediately after molting, the new skeleton is soft and compliant, allowing it to stretch to accommodate the increased size of the animal. During this period, the animal is more vulnerable to predation.

Endoskeletons

Internal hard skeletons are less common among the invertebrates but are a feature of some mollusks and echinoderms. There are various degrees of skeletal reduction seen in these groups, as evidenced by the urchins which have a complete rigid skeletal test formed of calcareous ossicles sutured together, and by sea cucumbers in which the skeleton is reduced to microscopic ossicles. The vertebrate endoskeleton is usually constructed of bone and cartilage; only certain fishes have skeletons that lack bone. In addition to an endoskeleton, many species possess distinct exoskeletal structures made of bone or horny materials. This dermal skeleton provides support and protection at the body surface. *See See also:* ECHINODERMATA.

Human Skeleton

Various structural components make up the human skeleton, including collagen, three different types of cartilage, and a variety of bone types.

Collagen

Collagen is the most abundant protein in the body. It is of fundamental importance in all organ systems and is found in all parts of the musculoskeletal system. Tropocollagen, a structure composed of three polypeptide chains, forms the basic building unit of collagen. The rodlike tropocollagen molecules polymerize into large collagen fibrils. Cross-links between adjacent molecules and also between fibrils give collagen its tensile strength. In tendons and ligaments, these fibrils are bundled together to form larger fibers. Tendons are formed from parallel bundles of fibers, an arrangement which allows tendons to support high uniaxial tensile loads to which they are subjected during activity. Although most ligament fibers are parallel, some have an oblique orientation. This reflects the more complex loading patterns applied to ligaments during movement, where small loads may be applied in a variety of directions. Collagen is stiff and strong only in tension. *See See also:* COLLAGEN.

Cartilage

The formation of cartilage (chondrogenesis) from mesenchyme occurs in many areas of the embryo, such as the skull, limbs, and vertebral column. Most embryonic cartilage is replaced by true bone in endochondral bone formation, but in many regions the cartilage remains throughout life. The tissue consists of cartilage cells (chondrocytes) which manufacture, secrete, and maintain the extracellular organic matrix that surrounds them. This matrix contains a dense network of collagen fibrils within a concentrated solution of protein-polysaccharide molecules called proteoglycans. The three main types of cartilage are fibrocartilage, elastic cartilage, and hyaline cartilage.

Hyaline cartilage, the most abundant form of cartilage in the body, ossifies during development to become bone. In the adult it covers the articular surfaces of bones, supports the trachea and bronchi, forms the costal cartilages linking the first ten ribs to the sternum, and reinforces the nose. This type of cartilage contains extremely fine collagen fibrils that can be seen only with the electron microscope. Hyaline articular cartilage is a special form found within synovial joints. Its material characteristics are perfectly adapted to this mechanically demanding environment.

Fibrocartilage is found predominantly in the pubic symphysis, the menisci of the knee, and the intervertebral discs. This type of cartilage is very durable and can withstand large tensile and compressive forces. It also represents a transitional material found at tendon and ligament insertions into bone and at the margins of some joint cavities. Histologically, it can be characterized by large collagen fibers running through the matrix.

Elastic cartilage is similar to hyaline cartilage but contains abundant elastin fibers which give it a yellowish appearance and make it very flexible, while still maintaining its strength. It is found in the outer ear, the auditory tube, and the larynx. *See See also:* CONNECTIVE TISSUE.

Bone

This specialized rigid connective tissue comprises cells which produce an organic extracellular matrix of collagen fibers and ground substance, and inorganic materials in the form of mineral salts. In vertebrates, the mineral portion of bone consists primarily of calcium and phosphate in the form of hydroxyapatite crystals. The organic phase gives bone its resilience and flexibility, while the inorganic phase makes the bone hard and rigid.

The functions of bone are numerous, relating to the maintenance of mineral (mainly calcium) homeostasis, formation of blood cells, and mechanical requirements.

Mineral (mainly calcium) homeostasis. Plasma calcium ion (Ca^{2+}) concentrations are maintained at about 5 mEq/L. This concentration is effectively regulated by calcitonin and parathyroid hormone and is required for normal blood clotting and nerve and muscle function. Low concentrations of calcium in the extracellular fluid that bathes the parathyroid glands elicits parathyroid hormone release. This stimulates osteoclastic breakdown of bone, releasing calcium and phosphorus into the extracellular fluid. Simultaneously, calcium absorption from the gut is increased, calcium loss via the kidneys is decreased, and urinary phosphate excretion is elevated. Calcitonin, released from the thyroid gland in response to elevated calcium concentrations, inhibits calcium removal from bone and increases urinary calcium excretion.

Formation of blood cells. During embyonic development, cellular elements of the blood (red and white blood cells and platelets) are produced by a process known as hematopoiesis. Early production occurs in the vessels of the yolk sac, but following the development of other organ systems, major blood cell production occurs in the liver, spleen, thymus, and bone marrow. At about the sixth developmental month, red bone marrow becomes the major site for the production of red and white blood cells and platelets. In adults, bone is the primary site for white cell production and the only site for red cell production, with portions of the sternum, ribs, vertebrae, skull, pelvis, scapulae, and proximal femoral and humeral heads of particular importance.

Mechanical requirements (support, protection, and leverage). Bone has a protective function, particularly with regard to the central nervous system. The skeleton is the supporting framework for the body and provides stiff levers on which muscles act to generate movement. *See See also:* CALCIUM METABOLISM; HEMATOPOIESIS; HOMEOSTASIS.

There are a number of easily recognized bone types whose microstructure can be related to the mechanical functions required of the bone. The only type of bone that does not require a preexisting surface or structure for its formation is woven bone. Woven bone is formed during early stages of development, and in adults it is encountered only in pathological conditions, including bone fracture repair. It consists of randomly oriented, small-diameter, highly mineralized collagen fibers. It is not a strong form of bone because of its unordered structure and, particularly, because much of its volume is unmineralized. Its value lies in its ability to rapidly bridge the gap between broken ends of bone to act as temporary scaffolding during the process of repair. It is later removed by bone remodeling events.

Lamellar bone is the dense hard material that constitutes most of the skeleton. In a typical bone, such as the femur, lamellar bone has two distinct types of organization. In the shaft (diaphysis) the material is deposited in layers to form compact or cortical bone. A transverse section through the diaphysis would show a tree-ring-like arrangement of bone. Bone cells (osteocytes) occupy spaces between adjacent lamellae. They interconnect with vascular spaces and one another by fine cellular extensions running in narrow channels (canaliculi). These cells maintain the integrity and normal functioning of bone. Two other main cell types important in normal bone are the bone-forming cells (osteoblasts), and the bone-destroying or bone-resorbing cells (osteoclasts).

Trabecular (spongy) bone is another form of lamellar bone found particularly in the expanded ends (epiphyses) of long bones and in the vertebrae. Although it is made of the same material as cortical bone, the mechanical characteristics of trabecular bone differ as a result of the honeycomb arrangement of bone into interlacing struts (trabeculae). This spongy bone is less dense and stiff than cortical bone, and has a large surface area which makes this tissue important for the exchange of calcium between the skeleton and the bloodstream.

Plexiform or fibrolamellar bone is a medium-density, relatively strong bone. It is found at sites of rapid growth where strength is also needed, such as in the limbs of large, fast-growing animals, which include humans during the growth phase in puberty.

Haversian systems or secondary osteons are structural units of bone that are formed secondarily within preexisting bone. This intracortical remodeling involves the formation of a tunnel through bone, achieved by the action of osteoclasts generating a resorption cavity. Following a reversal phase, in which a cement lining is deposited around the perimeter of the cavity, the tunnel is refilled with concentric rings of new bone by osteoblastic activity. A small-diameter central canal containing blood vessels is left unfilled. A completed

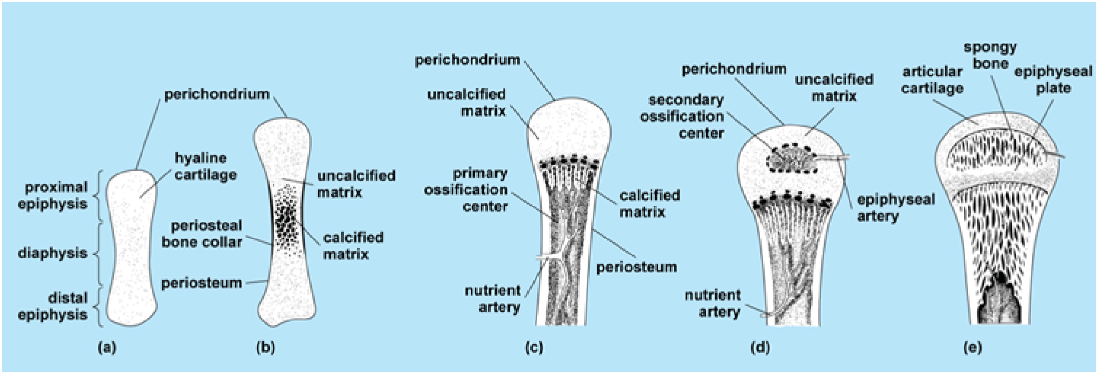

Fig. 1 **Development of endochondral ossification in a long bone. (*a*) Mesenchymal cells differentiate into chondroblasts which form the hyaline cartilage model. (*b*) The cartilage model grows, and chondrocytes in the midregion calcify the matrix. (*c*) The primary ossification center and the medullary cavity form. (*d*) Postnatal development of the secondary ossification center occurs. (*e*) Remnants of hyaline cartilage as articular cartilage and epiphyseal plate persist. (*After G. J. Tortora, Principles of Human Anatomy, 6th ed., Harper Collins, 1992*)**

secondary osteon is a branched structure. Secondary osteons form throughout life and are implicated in skeletal adaptation, repair processes, and mineral exchange between blood and bone (**Fig. 1**). *See* *See also:* BONE.

Development of the skeleton

All the components of the skeleton are derived from mesenchyme of either mesodermal or neural crest ectodermal origin. The majority of bones in the human body develop by the process of endochondral ossification; that is, the mesenchyme first forms a cartilaginous model which is subsequently replaced by true bone. The facial bones and certain bones of the cranium are formed by intramembranous ossification, in which mesenchyme is converted into skeletal elements by forming bone directly, without need of a cartilage stage. Sesamoid bones are specialized intramembranous bones that form within tendons.

Ossification

The development of bone from the embryo to the adult depends on the orderly processes of mitotic division, growth, and remodeling. These are determined largely by genetics, but are strongly influenced by hormonal action and nutrition. In endochondral ossification, the cartilaginous model is gradually calcified, resulting in cartilage cell (chondrocyte) death. Osteoblasts, together with a blood supply, invade the model and begin to secrete osteoid, which subsequently mineralizes and forms a primary ossification site. This process is repeated in the epiphyses of long bones to form secondary ossification sites. It is normal for the primary ossification site to form earlier, grow more rapidly, and cease ossification later than the secondary sites. The locations and ages at which ossification sites are active in the developing human skeleton are well documented. Hand and wrist x-radiographs are used to determine the skeletal age of individuals because of the orderly progression of ossification in these regions. Such information is important for checking whether an individual's growth rate is abnormal and whether hormone treatment is indicated. Applications also exist in the forensic field, where age at death can be accurately predicted from skeletal remains.

Two parts of developing bones remain as cartilage: epiphyseal plates and articular cartilage. Epiphyseal plates are situated between the diaphysis and the epiphysis. Longitudinal bone growth occurs by chondrocyte proliferation on the diaphyseal sides. The plates are finally obliterated by an extension of diaphyseal ossification into these regions, thus preventing further growth in the length of the bone. Articular cartilage never ossifies except in pathological situations such as osteoarthritis. *See See also:* ARTHRITIS.

Changes in the radial dimensions of long bones occur by new material being deposited beneath the periosteum, a connective tissue membrane surrounding the bone. The endosteal membrane is the equivalent structure lining the internal surfaces of tubular bones. Bone tissue can be added or removed at either site by the action of osteoblasts or osteoclasts, respectively. During growth and aging, there is a tendency for net bone deposition periosteally, with net resorption endosteally.

Bone growth and fracture repair can be increased by mechanical and electrical stimulation. Mechanical deformation of bone causes fluid flow through microscopic channels in bone, resulting in fluid shear stresses on cell membranes and/or production of strain-generated electrical potentials. Both effects have been shown to have osteogenic effects, with osteocytes responding to fluid flow changes, and osteoblast-mediated bone deposition occurring subsequent to mechanical loading in which strain-generated electrical potentials are recorded. In addition, electrical stimulation alone can promote osteogenesis under a wide range of conditions, including nonunion bone fractures and the maintenance of bone mass even in the absence of mechanical function. The mechanisms appear to involve insulinlike growth factors and/or transforming growth factor-β. Elevated levels of both accompany electrical stimulation, and insulinlike growth factors are capable of stimulating proliferation and differentiation of osteoprogenitor cells. Transforming growth factor-β is known to have important effects on bone formation, osteoblast proliferation and differentiation, and matrix synthesis. Furthermore, in vertebrates, there are transforming growth factor-β related signaling proteins (bone morphogenetic proteins and activin) that effectively regulate animal development, can induce cartilage and bone formation, and play critical roles in modulating mesenchymal differentiation.

Joints

In the human body there are fibrous, cartilaginous, and synovial joints. Functionally, these joints can be considered as immovable (synarthrosis), partly movable (amphiarthrosis), and freely movable (diarthrosis) joints, respectively.

Immovable joints are represented by cranial sutures and epiphyseal plates prior to their ossification. Little or no movement is available at these joints. Instead, their primary function is to allow bone growth at their margin (**Fig. 2**).

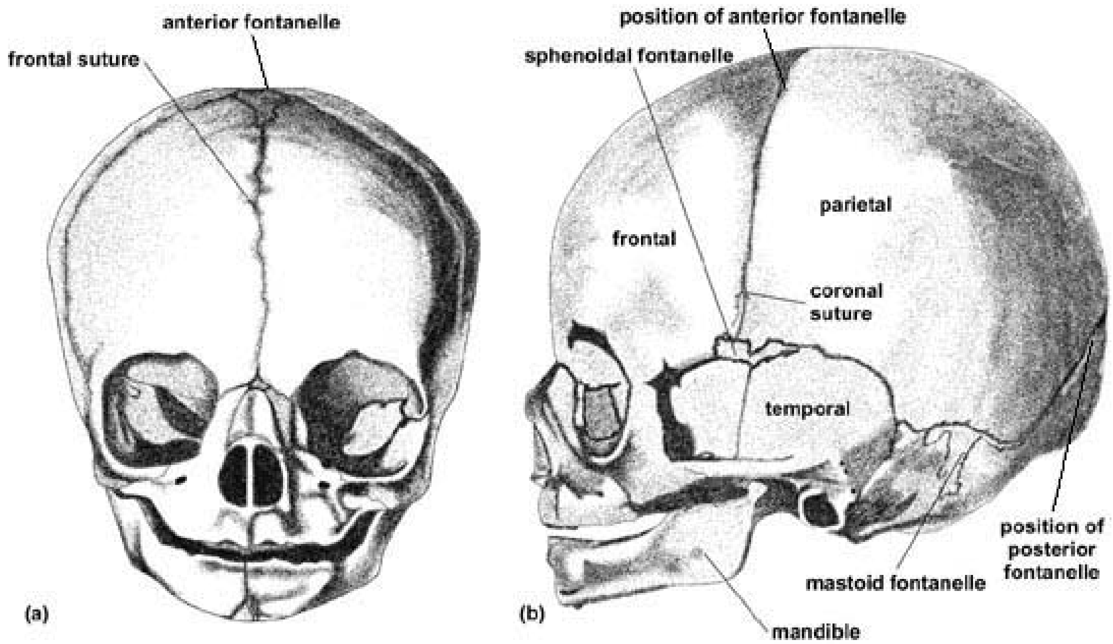

Fig. 2 **Skull in a human newborn infant. Cranial sutures and areas of temporary cartilage (fontanelles) form articulations between bones. (*a*) Frontal view. (*b*) Lateral view. (*After G. J. Romanes, Cunningham's Textbook of Anatomy, 10th ed., Oxford University Press, 1964*)**

Partly movable joints include the pubic symphysis that joins the two halves of the pelvis anteriorly and the fibrocartilaginous intervertebral discs. While the amount of movement between adjacent vertebrae is quite limited by disc stiffness, the vertebral column as a whole is quite flexible. Flexibility is achieved by combining each of the small movements permitted by individual discs.

Freely movable joints are the most complex and varied of the three types of joint, with their sizes and shapes matched to the functional requirements of the skeletal system at each location. At each joint, the surfaces of opposing bones are covered with a layer of articular cartilage that is a few millimeters thick. The joint is enclosed within a flexible joint capsule, the internal surface of which is lined by the synovial membrane that secretes the lubricating synovial fluid into the joint space. The main functions of articular cartilage are to distribute compressive loads over a wide area in order to reduce contact stresses, and to allow relative movement of opposing joint surfaces with minimum wear and friction. The combination of articular cartilage and synovial fluid gives these joints these remarkable properties. *See See also:* JOINT (ANATOMY).

Articular cartilage

Collagen fibrils, enmeshed within a proteoglycan solution, form the superficial part of articular cartilage. Beneath the relatively soft articular cartilage lies an interface (the tidemark) that indicates the start of the calcified cartilage layer. Beneath the cartilage lies a layer of subchondral bone which itself lies over the trabecular bone of the epiphysis. A gradient of increasing stiffness exists from the articular surface to the trabecular bone that helps protect the cartilage from splitting under loading conditions.

Synovial joints are subjected to an enormous range of forces. For example, the joints in the lower limb of humans have to support transient forces between two to five times body weight during running and jumping, and moderate but prolonged loading during standing. The nearly frictionless operation of joints is thought to be a function of lubricating films of synovial fluid between, and an adsorbed boundary lubricant on, the articular cartilage surfaces. The ability of cartilage to resist deformation when subjected to high stresses resides in complicated interactions between collagen fibrils, water, and proteoglycans, particularly keratin sulfate, chondroitin sulfate, and hyaluronic acid.

Damage to cartilage is thought to be a function of both the magnitude of applied forces and the speed at which forces are applied (with impact loading causing more damage). Due to its avascular nature, articular cartilage has a limited capacity for repair of such damage.

Vertebrate Skeletal Anatomy

The vertebrate skeleton consists of the axial skeleton (skull, vertebral column, and associated structures) and the appendicular skeleton (limbs or appendages). The basic plan for vertebrates is similar, although large variations occur in relation to functional demands placed on the skeleton.

Axial skeleton

The axial skeleton supports and protects the organs of the head, neck, and torso, and in humans it comprises the skull, ear ossicles, hyoid bone, vertebral column, and rib cage.

Skull. The adult human skull consists of eight bones which form the cranium, or braincase, and 13 facial bones that support the eyes, nose, and jaws. There are also three small, paired ear ossicles—the malleus, incus, and stapes—within a cavity in the temporal bone. The total of 27 bones represents a large reduction in skull elements during the course of vertebrate evolution. The three components of the skull are the neurocranium, dermatocranium, and visceral cranium. *See See also:* EAR (VERTEBRATE).

The brain and certain sense organs are protected by the neurocranium. All vertebrate neurocrania develop similarly, starting as ethmoid and basal cartilages beneath the brain, and as capsules partially enclosing the tissues that eventually form the olfactory, otic, and optic sense organs. The basal and ethmoid plates expand to meet the olfactory and otic capsules to form a floor on which the brain rests. The optic capsule becomes the fibrous sclerotic coat of the eyeball and remains free to move independently of the skull. Further development produces cartilaginous walls around the brain. Passages (foramina) through the cartilages are left open for cranial nerves and blood vessels. The largest opening is the foramen magnum, through which the spinal cord passes. Endochondral ossification from four major centers follows in all vertebrates, except the cartilaginous fishes.

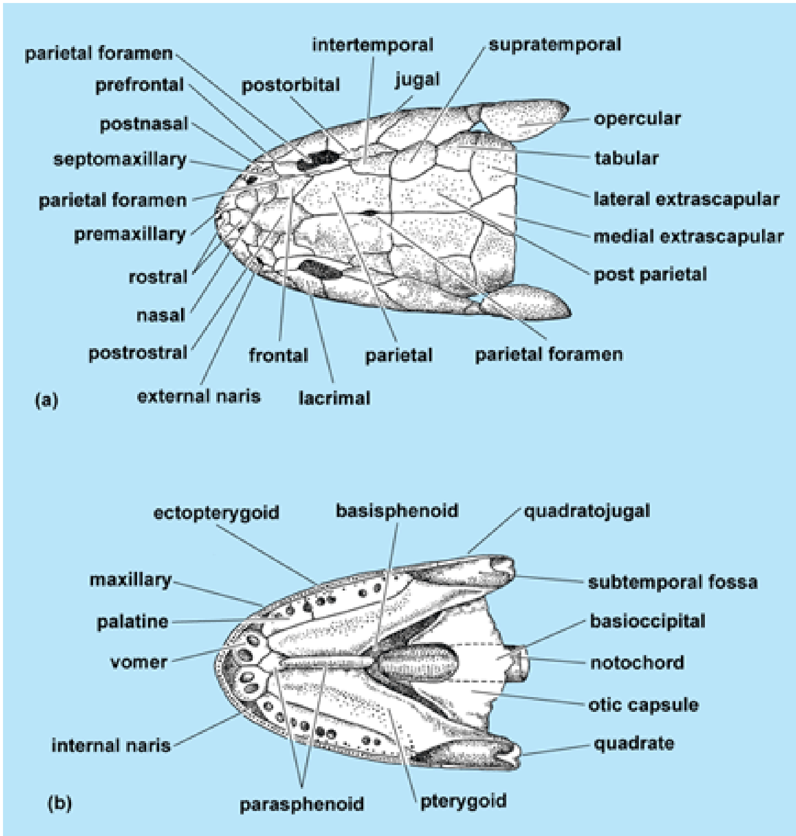

Fig. 3 **Skull of *Eusthenopteron*, a generalized fossil crossopterygian fish from Devonian time. (*a*) Dorsal aspect. (*b*) Ventral aspect. (*After A. S. Romer, The Vertebrate Body, 3d ed., Saunders, 1962*)**

It is likely that the bones of the dermatocranium derive from the dermal armor (bony scales) of early fishes. In modern vertebrates, these bones form via intramembranous ossification from subdermal mesenchyme.

The basic structure from which the tetrapod dermatocranium probably evolved is seen in the primitive crossopterygian fishes and early amphibians. Four kinds of bones are involved. (1) Roofing bones form above and on each side of the brain and neurocranium. These comprise paired nasal, frontal, parietal, and postparietal bones that cover the dorsal parasagittal area, while prefrontal, postfrontal, post- orbital, infraorbital, and lacrimal bones form a ring around the orbit. The posterolateral part of the skull is formed from the paired intertemporal, tabular, supratemporal, squamosal, and quadratojugal bones. (2) Dermal, tooth-bearing bones (premaxillae and maxillae) form the margins of the upper jaw. (3) Bones of the primary palate form the roof of the mouth in lower tetrapods and the oropharynx of fishes, and are the paired vomers, palatines, pterygoids, and ectopterygoids and the unpaired para-sphenoid. (4) Opercular bones extend posteriorly from the hyoid arch to cover the gill slits. These are paired bones, represented by large opercular bones and smaller subopercular, preopercular, and interopercular bones (**Fig. 3**). *See See also:* TETRAPODA.

Visceral skeleton. This skeleton of the pharyngeal arches is demonstrated in a general form by the elasmobranch fishes, where all the elements are cartilaginous and support the jaws and the gills. Each pharyngeal arch is typically composed of a number of cartilage elements, most of which support gills, but the first and second arches are modified to function in feeding. The mandibular (first) arch consists of two elements on each side of the body: the palatoquadrates dorsally, which form the upper jaw, and Meckel's cartilages, which join ventrally to form the lower jaw. The hyoid (second) arch has paired dorsal hyomandibular cartilages and lateral, gill-bearing ceratohyals. This jaw mechanism attaches to the neurocranium for support. Variations in this articulation occur between species and effectively determine jaw movement, and hence, the feeding abilities of fishes.

Evolution of neurocranium and dermatocranium. Modern amphibian skulls differ considerably from the primitive forms. Most changes involve the loss of roofing bones, particularly those from around the orbit, and massive reduction of the primary palate. These changes allows the eyes, which normally protrude from the head for good vision, to retract until they bulge into the oral cavity.

Early reptiles maintained the primitive pattern of the skull roof, with loss of only the intertemporal bone. Later reptiles exhibited large losses of bony elements, mostly from the temporal region and the back margin of the skull. Major changes in the roof of the skull are associated with the development of temporal fenestrae, resulting in four recognized design types: anaspids exhibit a primitive condition with a solid skull roof (turtles and stem reptiles); diaspids have two openings on each side of the skull (archosaurs and the ancestors of lizards and snakes); euryapsids have a single, dorsal opening on each side (ichthyosaurs and plesiosaurs); and synapsids have a single, lateral opening (pelycosaurs and therapsids). Birds derive from archosaurian reptiles and have, essentially, a diaspid skull design. The pelycosaur stock, with a synapsid skull, gave rise to the mammals.

A secondary palate appears for the first time in the reptiles as a horizontal shelf of bone dividing the oral cavity into separate nasal and oral passages. The remaining bones of the more primitive primary palate are located in the nasal passageway. Only the crocodilians, among the reptiles, have a complete secondary palate formed from medial extensions of the maxillae, premaxillae, pterygoid, and palatine bones. *See See also:* REPTILIA.

The avian skull has been modified from the diaspid reptilian type in line with increased brain size and changes in lifestyle, particularly feeding and flight behavior. Premaxillae and dentary bones form the majority of the upper and lower beak, respectively. Some birds can raise the upper portion of the beak relative to the rest of the skull by a hinge mechanism between the frontal bone and the premaxillae, maxillae, and nasal bones. This is one of the many forms of cranial kinesis, where motion (usually of the upper jaw) is possible, partially independent of other parts of the skull. Most vertebrates other than mammals are capable of cranial kinesis, which is a feeding adaptation. *See See also:* AVES.

The therapsids are mammallike reptiles that evolved large temporal fenestrae in the dermal bones of the cheek region. Other notable changes involved the loss, fusion, or reduction of roofing bones and a large variation in bone proportions and sizes. A secondary palate formed from the premaxillae, maxillae, and palatines separates

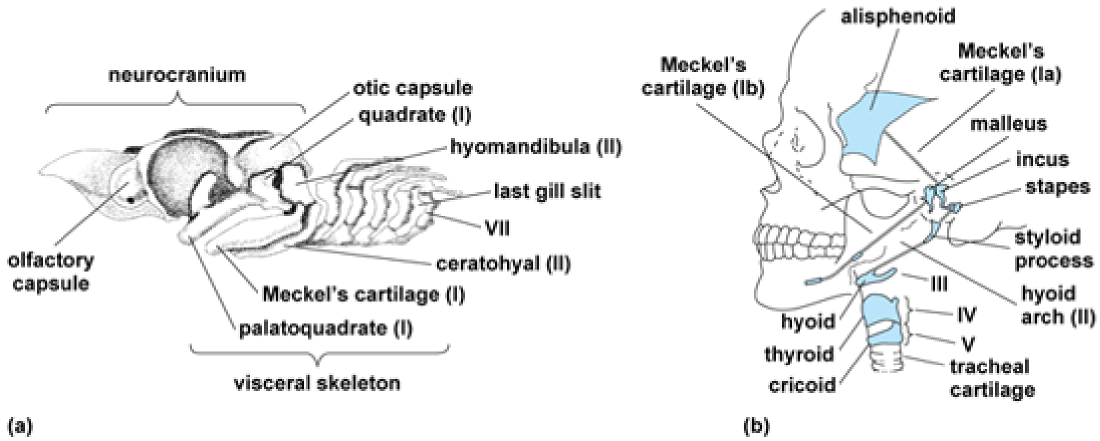

Fig. 4 **Skull and visceral skeleton. (*a*) Shark. The skeleton of the first, second, and seventh pharyngeal arches is indicated. (b) Human. Shaded regions show the components of the human skull and neck that are derived from the visceral skeleton. (*After G. C. Kent, Comparative Anatomy of the Vertebrates, 7th ed., Mosby-Year Book, 1992*)**

the nasal and oral cavities in a manner that was similar to the crocodilians. This palate continues posteriorly as a fold of skin, the soft palate. The value of a divided airway is that it gives the animal the ability to breathe while the mouth is full. *See See also:* THERAPSIDA.

Notable increases in the size of the brain during mammalian evolution have resulted in considerable changes to the neurocranium. The zygomatic arches are the true remnants of the original lateral walls of the skull. The temporal bone, as seen in humans, is a single unit, but is really a composite of a large number of fused skeletal elements of endochondral and membranous origin. The occipital bones are usually fused, and the single occipital condyle, present in reptiles and birds, divides to become a paired structure as in modern amphibians. Large changes occur in the organization of the otic capsule, with the inclusion of a new skull bone (the entotympanic) and dermal bone (derived from the angular bone of the reptilian jaw) in a protective role for the middle ear. *See See also:* MAMMALIA.

Evolution of visceral cranium. In all jawed vertebrates except mammals, an articulation between the posterior ends of the palatoquadrate and Meckel's cartilages (which may be ossified or ensheathed in bone) occurs between the upper and lower jaws (**Fig. 4**). The bony fishes have elaborated on the primitive condition, where the upper jaw was fused to the skull and the lower jaw or mandible could move only in the manner of a simple hinge. Teleosts are able to protrude the upper and lower jaws. This motion, coupled with expansion of the buccal cavity, enables these fishes to generate the large suction forces used to draw food into the mouth.

In the course of mammalian evolution, the dentary of the lower jaw enlarged and a ramus expanded upward in the temporal fossa. This eventually formed an articulation with the squamosal of the skull. With the freeing of the articular bone (seen as an ossified posterior end of Meckel's cartilage in teleosts) and the quadrate from their function in jaw articulation, they became ear ossicles in conjunction with the columella, that is, a skeletal rod that formed the first ear ossicle, arising in the amphibia to conduct sound waves from the eardrum to the otic capsule.

The remaining visceral skeleton has evolved from jaw and gill structures in the fishes to become an attachment site for tongue muscles and to support the vocal cords in tetrapods.

Vertebral column, ribs, and sternum. The vertebral column is an endoskeletal segmented rod of mesodermal origin. It provides protection to the spinal cord, sites for muscle attachment, flexibility, and support, particularly in land-based tetrapods where it has to support the weight of the body (**Fig. 5**).

1. Vertebrae. Hard, spool-shaped bony vertebrae alternate with tough but pliable intervertebral discs. Each typical vertebral body (centrum) has a bony neural arch extending dorsally. The spinal cord runs through these arches, and spinal nerves emerge through spaces. Bony processes and spines project from the vertebrae for the attachment of muscles and ligaments. Synovial articulations between adjacent vertebrae (zygapophyseal joints) effectively limit and define the range of vertebral motion.

Vertebral morphology differs along the length of the column. There are two recognized regions in fishes (trunk and caudal) and five in mammals (cervical, thoracic, lumbar, sacral, and caudal), reflecting regional specializations linked to function. Humans have seven cervical, twelve thoracic, five lumbar, five (fused) sacral, and four coccygeal vertebrae. Most amphibians, reptiles, and mammals have seven cervical vertebrae regardless of neck length (giraffes have only seven), whereas the number is variable in birds. Specific modification to the first two cervical vertebrae in most reptiles, birds, and mammals gives the head extra mobility. In humans, the occipital condyles articulate with the atlas, which in turn articulates with the axis, all via synovial joints. The atlas is a ringlike vertebra whose centrum is represented as a peg of bone fused to the axis. This odontoid process provides a pivot about which the atlas, and hence the head, swivels. The nodding movement is provided by rotational motion at the atlanto-occipital joint.

The presence of large ribs in the thoracic region often limits spinal flexibility. Birds utilize fusion of thoracic vertebrae to provide a rigid structure, adapted for the demands of powered flight. Additionally, fusion of the lumbar, sacral, and proximal caudal vertebrae produces a rigid back, the synsacrum.

In typical tetrapods, the sacral region is usually modified for support of the pelvic girdle, while the number of caudal vertebrae varies greatly (from 0 to 50) between and within animal groups. Birds have a specialized end cap to the caudal vertebrae (pygostyle) for the attachment of feathers. *See See also:* VERTEBRA.

2. Sternum and ribs. Jawed fishes have ribs that help maintain the rigidity and support of the coelomic cavity. These ribs typically follow the connective tissue septa that divide successive muscle groups. In the caudal region, they are often small paired ventral ribs, fused on the midline to form the haemal arches. Ancestral tetrapods had ribs on all vertebrae, and their lengths varied between the vertebral regions. Modern amphibia (frogs and toads) have few thoracic ribs, and these are much reduced and never meet ventrally. Reptiles have varied rib

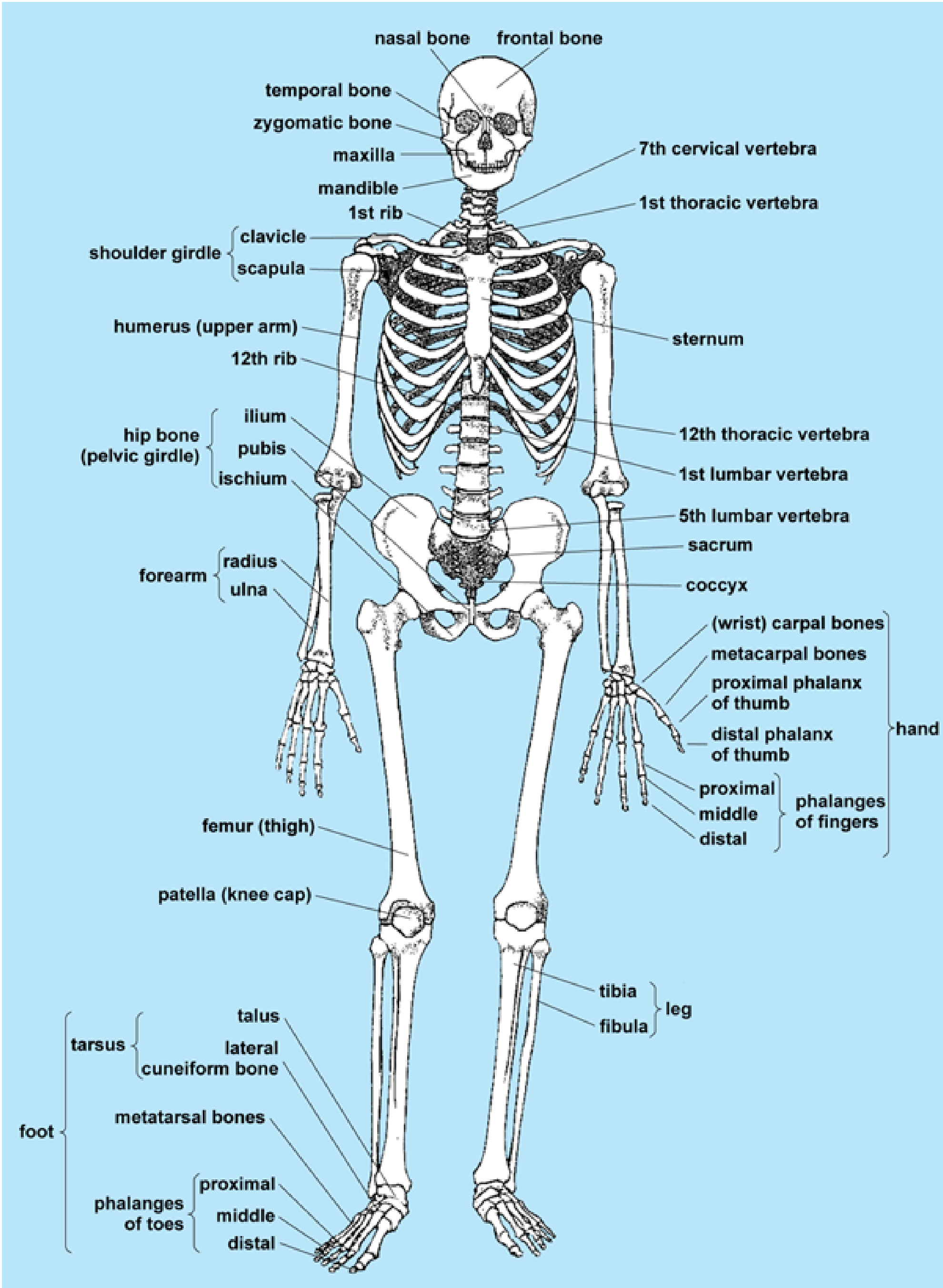

Fig. 5 **Human skeleton (anterior view). (*After G. J. Romanes, ed., Cunningham's Textbook of Anatomy, 10th ed., Oxford University Press, 1964*)**

arrangements, ranging from snakes with ribs on each vertebra (important for locomotor requirements) to turtles with only eight ribs which are fused to the inside of the carapace. Flying birds and penguins have a greatly enlarged sternum that links the ribs ventrally. This provides a large surface area for the origin of the powerful pectoralis muscles that are used to power the downstroke of the wing. In humans, there are twelve pairs of ribs which form a strong but movable cage encompassing the heart and lungs.

Appendicular skeleton

This section of the skeletal system comprises the pectoral and pelvic limb girdles and bones of the free appendages. The girdles provide a supporting base onto which the usually mobile limbs attach.

Pectoral girdle. The pectoral girdle has both endoskeletal and dermal components. The dermal components are derived from postopercular dermal armor of primitive fishes, and are represented by the clavicles and interclavicles in modern vertebrates, except where they are secondarily lost. Endochondral bone forms the scapula. In fishes, the main component of the girdle (the cleithrum) is anchored to the skull by other bony elements. Increased mobility of the girdle is seen in amphibia as it becomes independent of the skull. Further development and skeletal reduction have resulted in a wide range of morphologies, culminating in the paired clavicles and scapulae of mammals.

Birds have fused their paired clavicles and single interclavicle to form the wishbone or furcula. This provides an increased site for the origin of the pectoral muscles, both directly and from the fascial sheet spanning the two arms. Bending of the furcula during flight is thought to assist breathing by compressing or expanding underlying air sacs. It also has a role in storing, and subsequently returning, elastic strain energy at functionally useful parts of the wing beat cycle. Clavicles have disappeared in certain groups of bounding mammals to allow greater movement of the scapula. Although humans, and most other mammals, have a coracoid process on the scapula, other tetrapods typically have a separate coracoid bracing the scapula against the sternum and forming part of the glenoid fossa.

Pelvic girdle. The pelvic girdle forms by endochondral ossification, that is, the conversion of cartilage into bone. In the fishes, it is a small structure embedded in the body wall musculature just anterior to the cloaca. Each half of the girdle provides an anchor and articulation point for the pelvic fins. In tetrapods, the girdle attaches to the vertebral column to increase its stability and assist in the support of body weight and locomotor forces. Humans, like all other tetrapods, have a bilaterally symmetrical pelvic girdle, each half of which is formed from three fused bones: the ischium, ilium, and pubis. A part of each of these elements forms the acetabulum, the socket-shaped component of the hip joint, that articulates with the femoral head. The human pelvis is bowl-shaped, helping to support the viscera in upright stance. The large ilium (a feature shared with certain heavy-bodied animals such as cattle and horses) is the site of origin of hip extensor muscles, the gluteals. They prevent the body from bending sharply at the hip and also assist powerful thigh muscle extension during the propulsive stage of running.

All urogenital and digestive products have to pass through the pelvic outlet. This accounts for the pelvic sexual dimorphism seen in most mammals, where the pelvic opening is broader in females, because of the physical demands of pregnancy and parturition. In birds (with the exception of the ostrich and the rhea), both sexes have an open pelvic girdle, a condition also found in female megachiropteran bats (flying foxes), gophers, and mole-rats.

Paired fins and tetrapod limbs. Paired fins in fishes come in different forms, but all are involved in locomotion. In the simplest form they are fairly rigid and extend from the body, functioning as stabilizers, but they are also capable of acting like a wing to produce lift as in sharks. In many fishes, the pectoral fins have narrow bases and are highly maneuverable as steering fins for low-speed locomotion. In addition, some fishes (such as the Australian lungfish) use their pectoral and pelvic fins to walk on the river bed, while others have greatly enlarged pectoral fins that take over as the main propulsive structures (for example, rays, flatfish).

The basic mammalian pectoral limb consists of the humerus, radius, ulna, carpals, five metacarpals, and fourteen phalanges (arranged as 2-3-3-3-3, starting at the thumb; reptiles tend to have a 2-3-4-5-3 arrangement); and the pelvic limb consists of the femur, tibia, fibula, tarsal, five metatarsals, and fourteen phalanges (mammals have various digital arrangements; most reptiles have a 2-3-4-5-4 arrangement). Variation in the shape and number of elements occurs primarily in the hand (manus) and foot (pes). A typical bird pelvic limb consists of a femur, tibiotarsus (formed by fusion of the tibia with the proximal row of tarsal bones), fibula, and tarsometatarsus (formed by fusion of metatarsals II–IV), metatarsal I, and four digits (each consisting of two to five phalanges).

Locomotion and skeletal adaptations

Throughout evolution, the skeletal system has adapted to the needs of many different types of organisms. Such adaptations have been made for walking and running, speed, power, digging and burrowing, locomotion without limbs, and aerial and aquatic locomotion.

Walking and running. The undulatory side-to-side flexion of the vertebral column seen in most fishes continued to play a role in early tetrapod locomotion. It still exists in the urodeles (for example, newts) and many reptiles where limbs project laterally, with the proximal element swinging in the horizontal plane. The feet provide points of firm contact with the ground in this sprawling locomotor style, with forward progression powered by lateral trunk flexion. Most terrestrial tetrapods have raised the trunk off the ground, with the limbs projecting ventrally to support the body. Changes in joint alignment resulted in the limbs and trunk flexing and extending in the sagittal plane.

Adaptations for speed. Animals use various recognizable forms of locomotion, or gaits, for traveling at different speeds. The voluntary selection of a particular gait appears to be linked to reducing locomotor forces on the limb skeleton and minimizing the energetic cost of travel.

Obvious modifications to the basic tetrapod skeleton have accompanied the acquisition of high-speed locomotion. The lengthening of limb segments allows for longer strides which, coupled with stride frequency, determine running speed. Limb elongation has been accompanied by a reduction in the number of skeletal elements in running specialists (**Fig. 6**).

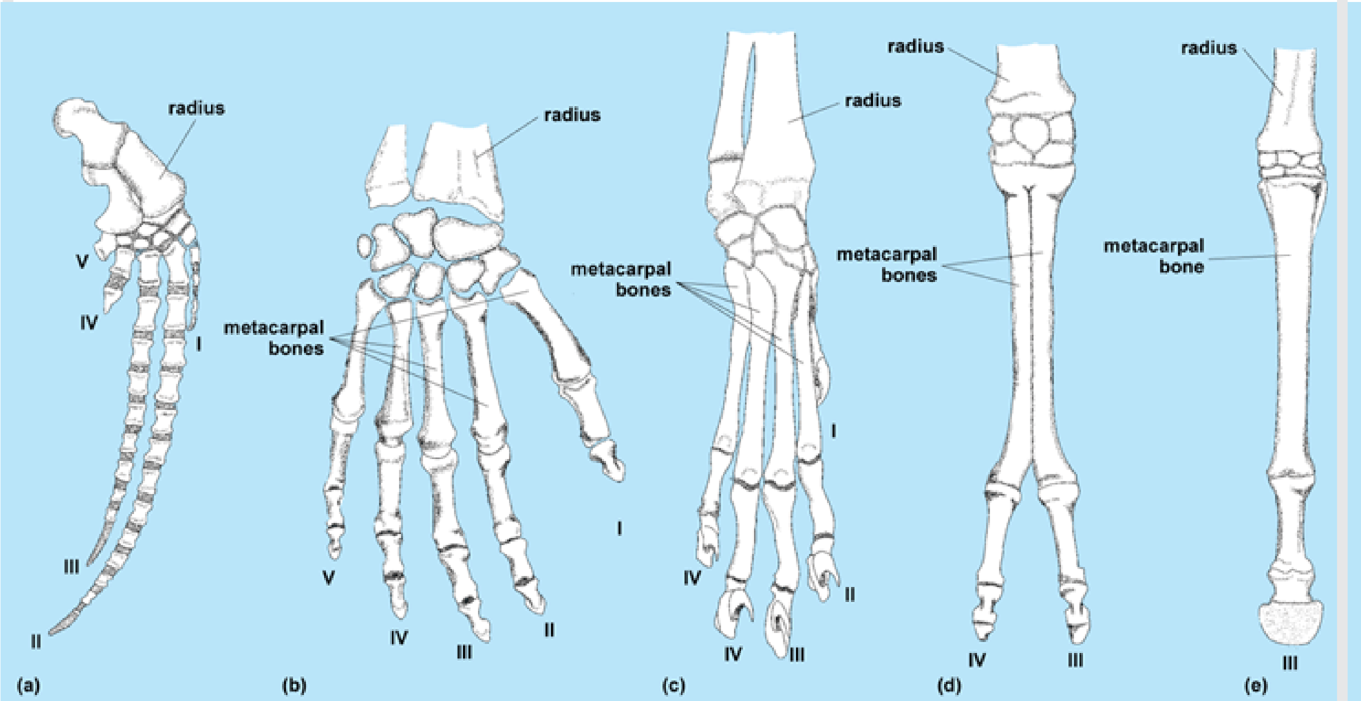

Fig. 6 **Changes in the tetrapod distal limbs in relation to different locomotor requirements. (*a*) Whale (*after A. S. Romer and T. S. Parsons, The Vertebrate Body, 6th ed., CBS College Publishing, 1986*). (*b*) Human; (*c*) cat; (*d*) camel; (*e*) horse (*after G. C. Kent, Comparative Anatomy of the Vertebrates, 7th ed., Mosby-Year Book, 1992*)**

The normal pentadactyl (five-digit) limb is seen in plantigrade animals, such as primates and insectivores, where the ankles, wrists, and all bones distal to these joints contact the ground. Humans have a bipedal plantigrade posture. A plantigrade posture typically provides stability (large foot-ground contact area) and good manual or pedal dexterity (useful for climbing, and holding and manipulating objects), but does not provide particularly good running performance (**Fig. 7**).

Many of the Carnivora, Rodentia, and Lagomorpha have either lost or reduced the first digit. They are digitigrade; that is, they walk and run on four toes, with the metacarpals and tarsals raised off the ground. The functional increase in limb length contributes to their fleetness of foot, useful for catching prey or avoiding capture; and the reduction, particularly of the metacarpals, metatarsals, and digits, can be viewed as an adaptation for speed. *See See also:* CARNIVORA; LAGOMORPHA; RODENTIA.

Hoofed (unguligrade) animals have further reduced their digits. Even-toed ungulates (sheep, cattle, and camel) and odd-toed ungulates (horse and rhinoceros) walk on the tips of the remaining digits. Claws or nails are often expanded to form protective structures such as the horse's hoof. The remaining metatarsals and metacarpals are often very elongate. Digital reduction is extreme in horses, where a single digit (digit III, equivalent to the human middle finger or toe) remains. All limb reduction results in loss of dexterity, and the horse, as an extreme example, cannot use its limbs for any function other than locomotion. However, digital reduction is extremely

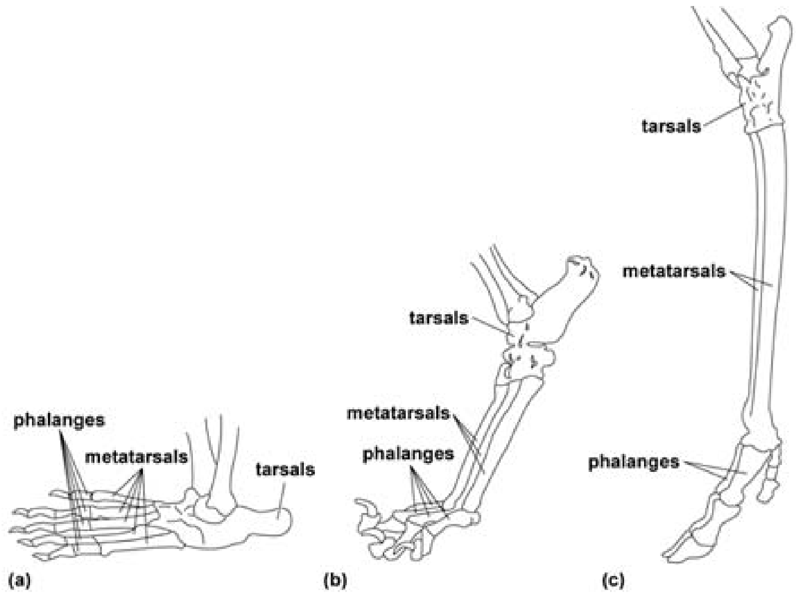

Fig. 7 **Limb postures. (*a*) Plantigrade. (*b*) Digitigrade. (*c*) Unguligrade. (*After G. C. Kent, Comparative Anatomy of the Vertebrates, 7th ed., Mosby-Year Book, 1992*)**

important for economical locomotion: multiple bones weigh more than a single element of equal strength, and thus limb mass can be reduced by reducing the number of bones without compromising limb strength.

There is a similar trend in birds. The ostrich is the only bird that has two toes (didactyl); rheas, cassowaries, emus, and others have three (tridactyl), whereas most species have four. However, variation in toe number, size, and orientation reflects more than just locomotor behavior because there are three-toed species (kingfishers, parrots) that are not runners.

Other skeletal adaptations for speed include the loss of clavicle in cats, allowing greater scapular movement which results in greater reach (greater stride length when running) and helps reduce impact forces to the axial skeleton when running; and increased flexibility of the vertebral column in the sagittal plane—another way to increase stride length.

Speed versus power. The speed of movement of limb bones is of fundamental importance for running animals. This depends on the sizes and properties of muscles and where they attach relative to the joints. A muscle that is attached close to a joint has a small moment arm (the perpendicular distance from the line of action of the force to the joint center) and will be able to move the distal end of the bone rapidly when the muscle contracts. The larger its moment arm about the joint, the slower the movement. However, the opposite is true for exertion of force at the distal end of the bone. Thus, skeletal morphologies differ, depending on whether predominantly powerful or rapid movements are required.

Digging and burrowing. Most changes in hole-dwelling animals are related to muscular insertions for increased power in their movements. However, skeletal adaptations occur in the teeth, pectoral and pelvic limbs, and vertebral column. Major modifications include limbs becoming shorter and more robust. The medial humeral epicondyle enlarges to accommodate an increased muscle bulk of carpal and digital flexor muscles and forearm pronators. Claws are either sharp to break hard soil or flattened to help shift soft soil, and often have large extensor tubercles on the dorsal surfaces. These act as passive bony stops to prevent overextension of the joints. Many joints are restricted to planar motion (flexion-extension) to increase their stability and make them less likely to dislocate.

Limbless locomotion. Frogs, birds, and terrestrial mammals have never produced limbless forms. Snakes (Ophidia) are the most diverse limbless group, but there are lizards (Sauria) and amphibia (Apoda) that show a reduction or loss of one or both limb pairs and girdles. The main adaptation accompanying limb loss is elongation of the body. More than 500 vertebrae have been documented in a snake. The overlapping bony scales used for protection and to gain purchase for movement are formed secondarily in the skin.

Aerial locomotion. Birds and bats (and possibly the extinct pterosaurs) are the only examples of vertebrates capable of continuous muscle-powered flight. Many others use the more passive gliding or parachuting. Flying fishes (for example, Exocoetidae, Hemirhamphidae) have enlarged pectoral fins enabling them to glide out of water to escape predators. A number of reptiles (for example, *Draco* spp.) glide with the aid of flight surfaces formed by elongated ribs.

Birds have a highly modified forelimb complex (**Fig. 8**). The humerus, ulna, and radius have surface features linked to flight, but the real adaptation of these (and other bird and pterosaur bones) is their air-filled or pneumatic character. This reduces their mass and, therefore, the muscular work involved in moving the wings up and down. In addition, the major wing bones of bats, birds, and pterosaurs have relatively large diameters and are relatively thin-walled. These traits maximize torsional strength for any given mass of bone material, which is important for flying animals in which twisting forces on the wing skeleton are commonly encountered. Support of the primary flight feathers is provided by the bones of the carpus, carpometacarpus (a fusion of carpals and metacarpals unique to birds), and manus, which in adult birds has only three digits (recently identified as digits II-III-IV). Wing length is effectively determined by the lengths of the arm, forearm, and hand skeleton, but wing shape (breadth and sharpness of wingtips) is determined by feather morphology. Secondary adaptations to flight are seen in the pelvic girdle, with its extensive connection to the synsacrum presumed to be linked to absorbing the shock of landing.

Bats have adopted a different skeletal strategy. They use highly elongated bones (humerus, radius, metacarpals, and phalanges) to help support the whole wing, not only the leading edge as seen in birds. These bones are not pneumatic, but contain marrow. Weight savings do occur in distal elements due to a reduction in mineralization. Large pectoral muscles attach to ribs, and there is no massive, keeled sternum as in birds. Pelvic girdle reduction, thinner and straighter limb bones (they no longer have to resist large bending forces), rotation of the limb so the

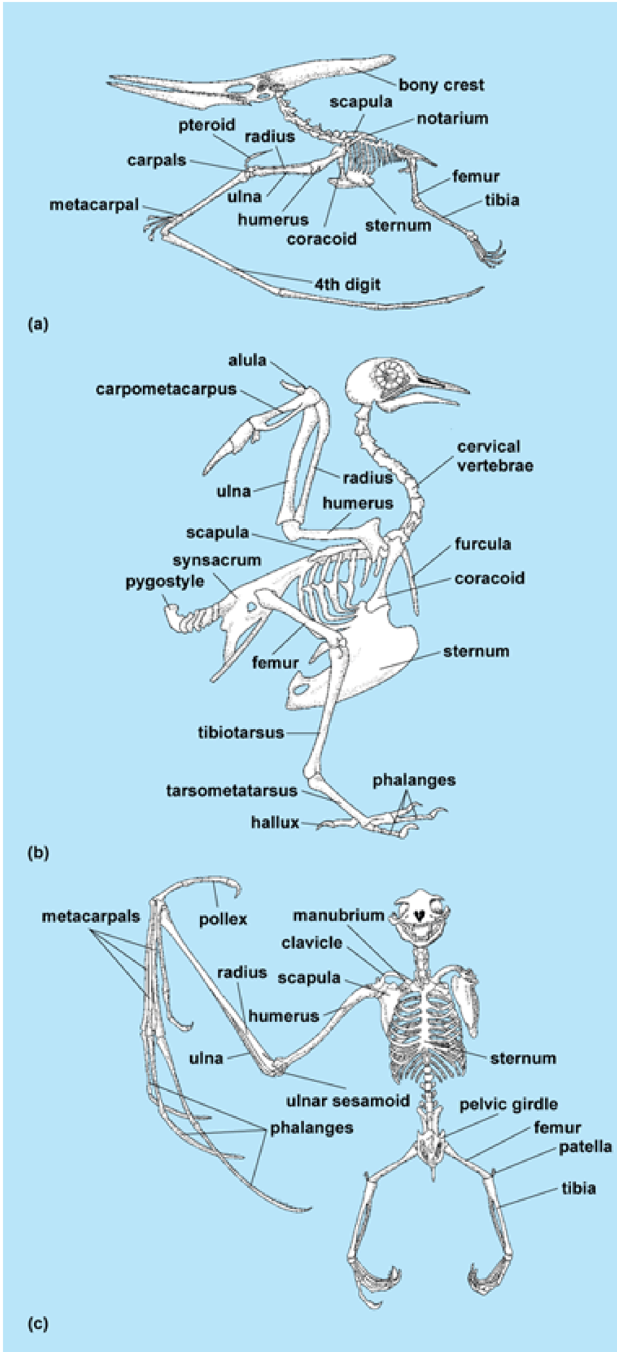

Fig. 8 Skeletons of flying vertebrates. (*a*) Extinct pterosaur (*Pteranodon*). (*b*) Typical bird skeleton. (*c*) Skeleton of a fruit bat or flying fox. (*After L. B. Halstead, Vertebrate Hard Tissues, Wykeham Publications, London, 1974*)

patella faces posteriorly, partial loss of the fibula, and possession of large claws are all skeletal adaptations for a hanging lifestyle. *See See also:* FLIGHT.

Aquatic locomotion. In contrast to terrestrial locomotion, the limbs of aquatic organisms are hydrofoils or paddles. The skeletal elements are usually the same as typical tetrapods, with altered dimensions. Some specialist swimmers (such as porpoises and whales) have increased the number of phalanges in the hand. The manus is fairly stiff, the bones being bound together with connective tissue. Reduction or loss of the pelvic girdle and limbs has occurred in cetaceans and sirenians, and thrust is supplied by dorsal-ventral flexion of the vertebral column. Seals and walruses retain the pelvic structures, swimming by lateral flexion of the vertebral column.

Skeletal strength

Bones have to be stiff in order to act as levers for effective muscle action, and strong to resist failure. Although the form of the skeleton is genetically determined, the basic plan can be modified within limits by hormone action and the mechanical environment.

The limb skeleton of terrestrial tetrapods is subjected to large dynamic forces during rigorous exercise. For example, the feet of human runners generate loads of two to three times body weight. Even larger forces are applied to the skeleton by muscle action (for example, to the heel bone via the Achilles tendon). Direct measurement of bone deformation under such conditions shows that the limb bones in most animals undergo similar levels of strain (that is, change in specimen length per original length) and are typically three to five times as strong as they need to be to resist failure.

Long bones

Lamellar or cortical bone has the same mechanical properties whether taken from a mouse or an elephant. The strength of whole bones is therefore a function of the amount of bone present and its geometric arrangement. Long bones in tetrapod limbs are typically tubular, even though the marrow contained within the hollow center appears to have little functional use. Why the bones are not solid can be explained by referring to principles of biomechanics. As most bones have a degree of longitudinal curvature, they tend to bend in a predictable direction when loaded, for example, during running. One surface of the bone will tend to be under compression (squashed), and the opposite surface will be under tension (pulled). As there is a gradient across the bone running from compression to tension, there is a position between the surfaces where the forces cancel out (the neutral axis). Bone material along and close to this axis does not contribute much strength to the bone in bending. Such redundant material can be removed (forming the marrow cavity) without compromising bone strength.

Size and the skeleton

The bones of humans and elephants are proportionately more robust than those of mice. This occurs because a doubling in linear dimensions results in a fourfold increase in area and an eightfold increase in mass. If animals simply increased in size, it would result in the bones undergoing larger stresses in bigger animals. To keep bone stresses at the same level as in small animals requires that the bones be made thicker.

Another obvious feature is that small animals adopt crouching (noncursorial) postures, while larger ones are typically cursorial, standing with straighter limbs. A more upright limb posture results in a better alignment of the forces generated during locomotion with the long axes of the bones. This reduces both the forces that muscles need to generate to keep limbs extended, and the bending moments imposed on the bones. Cursorial postures lower stresses on the limb bones but reduce agility. *See* *See also:* BIOPHYSICS.

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