FAUNA *of* AUSTRALIA

34. MORPHOLOGY AND PHYSIOLOGY OF THE EUTHERIA

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TERMINOLOGY

The language of biology is vital in imparting knowledge and exchanging ideas. The language must be precise, because confusion can (and does) arise if multiple terms are used to describe a structure or physiological process. Veterinary anatomists have attempted to overcome misconceptions in biology due to confusion in terms by developing a standard set of names for structures (*Nomina Anatomica Veterinaria* and *Nomina Histologica* 1983). Adoption of appropriate terms from that source for the Eutheria generally would be beneficial to biologists, and at the risk of offending those who fear some of their favourite terms are threatened, I shall follow the standard terms of the *Nomina*, or their English equivalents, in this chapter.

EXTERNAL BODY FORM

Eutheria in Australia range in size from the smallest bats, with body weight of 5 g or less, to the large whales, with body weights exceeding 100 tonnes.

Although bearing the basic characters that distinguish mammals generally, namely the presence of hair and mammary glands, the external form of Australian Eutheria is very variable (Fig. 34.1). This is related partly to the environment in which they live, which varies from totally aquatic to arid desert. Small rodents have a dense pelage, whereas the totally aquatic mammals (dugongs and whales) have little or no hair on the general body surface. Mammals that need to conserve body heat, notably the aquatic mammals, have fusiform bodies and small appendages, presenting to the environment a relatively small body surface area per unit weight. This advantage is augmented in many species by their very large size. Animals that inhabit hot environments, such as the camelids, have slender bodies and long limbs and, therefore, a relatively large surface area.

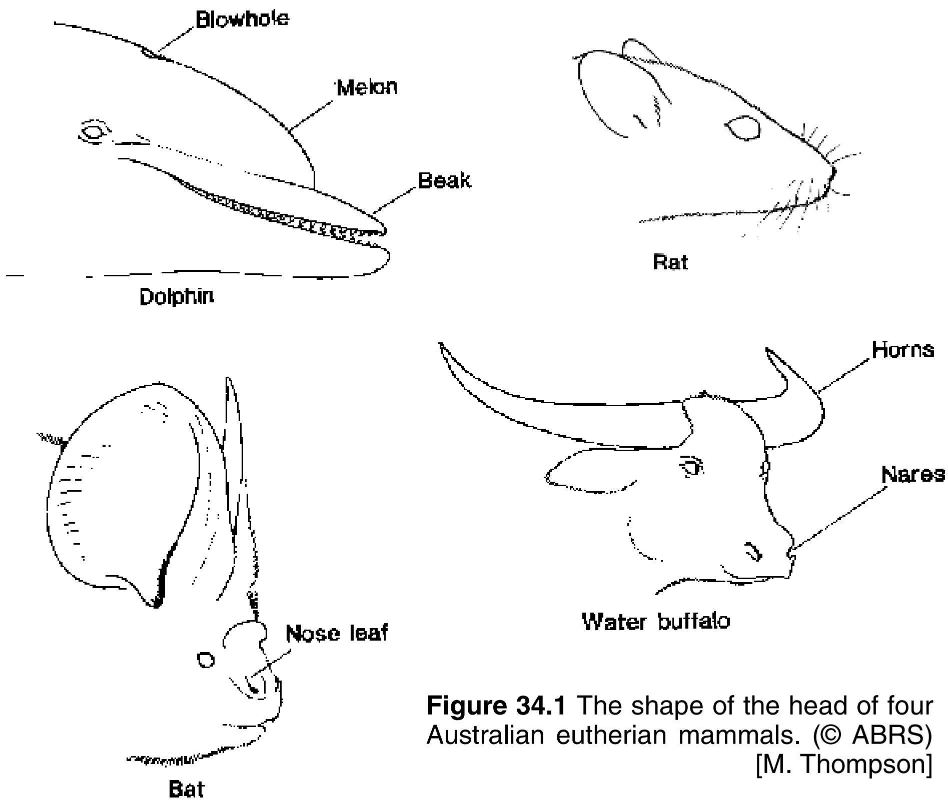


Figure 34.1 The shape of the head of four Australian eutherian mammals. (© ABRS) [M. Thompson]

The form of the limbs varies greatly. Most terrestrial species are digitigrade, but have varying degrees of reduction in the number of digits. The rodents have five digits on each foot, and the digits of the hind feet are webbed in the aquatic rats. The artiodactyls (bovids, suids, cervids and camelids) and the perissodactyls (equids) have two digits and one digit on each foot, respectively. In the flying mammals, the bats, the limbs are modified greatly to function as wings. In the aquatic mammals the limbs are adapted for swimming and, in some species, are greatly modified. The hind limbs are absent in totally aquatic mammals.

The head (Fig. 34.1) is highly variable in form, from long and narrow to short and broad. In some of the cervids and bovids it bears large antlers or horns. In many of the microchiropterids the ears and nose leaf are complex. There is a long beak and rounded melon in the dolphins.

Not all eutherian mammals have a discernible tail, but some component always remains. Even in humans, who have no tail, there are four small vertebrae that constitute the coccyx, the rudiment of a tail. The tail is long, short or absent in bats, whereas it is long and slender and acts as a thermoregulatory organ in some rodents. It bears long hairs that aid its use as a fly-whisk in the Equidae, whereas it is greatly modified to form the powerful swimming organ of the whales. In rabbits and many artiodactyls the white underside is shown as a warning of danger to others.

The shape of the body is often used as a means of communication in the social and sexual life of mammals, serving to produce appropriate responses in other individuals. Special shapes are often associated with the recognition of the sexes and in some instances this is served by body size. The most extreme example of this is seen in elephant seals, males of which are up to ten times larger than females. A direct relationship between sexual disparity in size and polygyny has been postulated. Some animals deliberately alter their shape and apparent size to express fear or aggression, for example the arching of the back and piloerection in the cat.

THE INTEGUMENT

The skin (Fig. 34.2) marks the interface between the organism and its environment. The skin of mammals has special features, not found in non-mammalian vertebrates, connected mainly with temperature control and the function of the skin as a sense organ. Investigation of the differences in the skins of various mammals shows how closely the activities of the body are related to the conditions of the environment: it varies in texture, colour, scent and temperature among other features. This conformity with the environment is maintained by control on time scales between the few seconds required for temperature regulation and the many generations for selection of a new set of genes that determine coat colour.

The Epidermis and its Appendages

The outer layer of skin, the epidermis, is a non-vascular stratified squamous epithelium. It consists of a variable number of layers of cells, the inner of which are active, continually producing cells that pass towards the surface and gradually undergo a process of cornification. The thickness of the epidermis varies according to species and the region of the body, being greatest in those areas that are subjected to wear, for example the footpads of rodents, felids and canids. The protein keratin is the distinctive component of the epidermis and its derivatives. It is virtually insoluble in water and, therefore, forms a protective outer covering for the body. The process of keratinisation is not peculiar to mammals, but it is highly developed in them and in special parts of the body it gives rise to hairs, claws (or nails), hooves or horns.

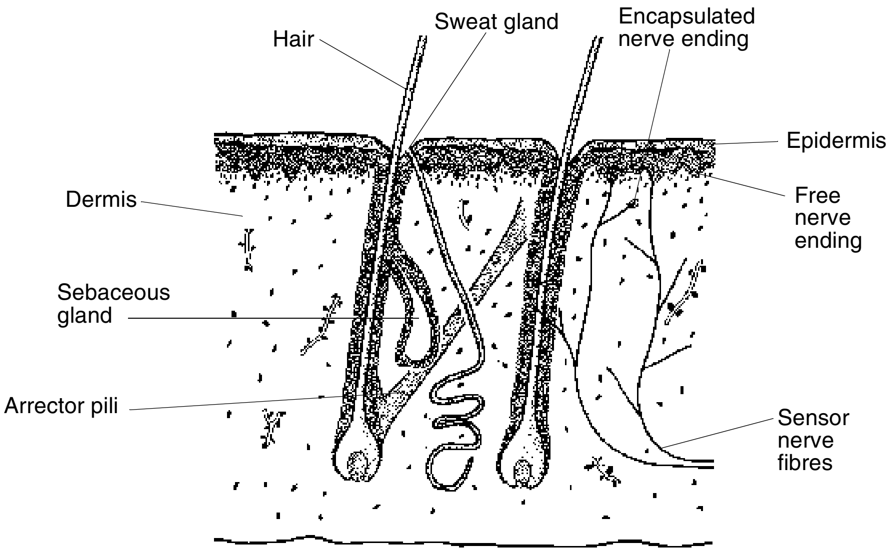


Figure 34.2 Diagram of the skin, showing some of the accessory structures - the hairs, sweat and sebaceous glands - and the smooth muscle associated with the hairs (arrector pili). Some sensory nerve fibres are shown. Not shown are the autonomic motor nerve fibres that supply the sweat glands, arrector pili and the walls of blood vessels in the skin. Magnification \X 400 (© ABRS) [S. Collin]

The hair follicles and the glands closely associated with them, the sweat glands and sebaceous glands, are derivatives of the epidermis that project inwards into the deeper layer, the dermis. Each hair consists of a rod of elongated keratinised cells, forming a thread, usually with a central medulla. The mesenchyme at the base of a developing hair forms a vascular papilla and the epidermal cells above this continue to produce keratin, thus providing the constantly growing base of the hair.

When large and dense, the hairs serve to retain heat. The associated sebaceous glands keep them and the skin surface oily and hence, waterproofed. They also are provided with nerve fibres which wrap around the base of the hair follicle. In nearly all mammals highly sensitive vibrissae, which are elongated and stiffened, have developed around the snout and make the animals sensitive to very light touch or even to small changes of air-pressure.

Each sebaceous gland consists of a few short sacs, the alveoli, opening into the hair follicle. The secretory cells become converted into the substance sebum, which keeps the hair and the adjacent skin surface greasy. Attached to each hair is a small bundle of unstriated muscle fibres, the arrector pili, in most species.

The sweat glands are tubular and highly variable in form. They are reduced in semi-aquatic, and absent in totally aquatic mammals and are confined only to certain regions of the body in some species. The secretory cells in the basal part of the gland are surrounded by myoepithelial cells that aid in expelling the secretion.

The tips of the digits of mammals are nearly always covered with hardened plates of keratin, which in their simplest form, claws, are similar to those of reptiles and birds. The coronary border (vallum) of the claw fits into the space under the ungual crest of the distal phalanx. This relationship is hidden by the skin of the claw fold. Dorsally, this fold is a modification of the hairy skin which is free from hair on one side and fused to the horn of the claw. As the horny

material is produced and grows out, it is covered by a thin stratum tectorium which adheres to the proximal part of the claw. A furrow along the palmar or plantar surface of the claw separates it from the foot pad in a similar manner.

The horns found in various mammals also are formed of keratin, produced by areas of skin overlying prolongations of the bones of the skull. The antlers of Cervidae, however, are purely bony.

Small scales occur on certain mammals, for example on the tail of rats. Cyclic epidermal cellular proliferation is a vertebrate characteristic and probably follows an autonomous rhythm regulated through neurochemical systems, in response to environmental stimuli and related to adaptive factors.

Periodic shedding of the outer epidermis, the moult, seems to be related more closely to seasonal factors in mammals and birds than in fish, amphibians and reptiles. In mammals this shedding includes the hairs. The regular moulting and hair replacement results in a seasonal variation in coat quality in most species.

The Integument and Temperature Regulation

Hair tends to trap a layer of air which insulates the body, reducing heat exchange with the environment. The air-retaining capacity is increased in some animals by a roughening of the surfaces of the hairs (examples are the wool of sheep, some goats and rabbits) causing them to stick together. The hairs are not all of the same kind. In many species long stiff hairs are found mingled with soft fur. As pointed out above, the hair of many mammals changes according to the time of year so as to provide a thicker covering in winter than in summer.

Not all mammals use an air layer for the retention of heat. The body of whales, sea cows and seals is covered with a thick layer of fat, often called the blubber, which acts as an effective insulating blanket immediately beneath the skin.

The integument has mechanisms for losing as well as retaining body heat. Some of the sweat glands produce a watery solution, which serves to cool the body through evaporation. Some mammals simulate this action behaviourally by wetting the skin periodically, for example, pigs in wallows and seals on a sunny beach. The amount of heat lost from the skin surface is also controlled by regulating the flow of blood through the capillaries and arterio-venous anastomoses. Capillary blood flow is controlled locally, whereas flow through arterio-venous anastomoses is controlled centrally in the spinal cord and the hypothalamus. The surface of the lungs also provides a means of heat loss: animals such as dogs and sheep lose excess heat by panting.

Scent Glands

Scent-producing glands are important in that they provide the mechanism for recognition of members of the species, especially in social mammals, and for bringing the sexes together. Although many mammals have good eyesight, they rely mainly upon smell for recognition. There are probably characteristic differences of scent between individuals.

Scent glands occur in the skin of various parts of the body, for example the infraorbital, interdigital and inguinal regions of certain artiodactyls, the submental and carpal regions of suids, the anal and caudal regions of canids. Some bat species have a glandular throat pouch, although its function is unknown. The characteristic smell of the rabbit is believed to be due to a pair of inguinal glands. The scents produced by these glands may be left on trees and other objects where they serve to mark the territory of an individual.

Mammary Glands

These glands are characteristic of mammals and serve to nourish their young, which are born in a relatively immature and dependent state. They are paired glands that form in the embryo along two mammary lines, extending from the axilla to the inguinal region on either side of the midline. Mammary glands may arise anywhere along these lines. The number formed and their location varies with the species. In the resting state, they consist of a branching system of ducts. During pregnancy the epithelium of these ducts divides actively to produce secretory alveoli at their ends and, after birth of the young, the alveoli produce the milk.

The functioning of the mammary glands is dependent upon the interplay of multiple and complex nervous and endocrine factors. The growth of the duct system appears to depend primarily upon oestrogen, but for complete development of the alveoli both oestrogen and progesterone are required. The hypophysis also has a direct effect upon mammary growth through its secretion of prolactin and somatotropin. To obtain full morphological development of the gland comparable to that obtained in late pregnancy, prolactin, progesterone, oestrogen, somatotropin and adrenal corticoids are all believed to be necessary.

It is thought that when the inhibiting levels of circulating progesterone and oestrogen fall abruptly at the end of pregnancy, the increased output of prolactin by the hypophysis and the secretion of adrenal cortical steroids bring about milk secretion from the fully developed mammary gland.

The continued secretion of prolactin by the hypophysis appears to be necessary for the maintenance of lactation. The secretion of normal levels of prolactin by intact animals is dependent upon a neurohormonal reflex, in which the periodic sensory stimulus of sucking acts upon the hypothalamus to promote the release of prolactin.

Removal of milk from the glands depends mainly upon the stimulus of sucking, which acts via the hypothalamus to cause release of the hormone oxytocin from the neurohypophysis. This, in turn, stimulates the myoepithelial cells of the gland to contract, ejecting the accumulated milk from the alveoli and fine ducts into the large ducts and sinuses of the gland.

The Dermis

The tissues of the dermis impart important properties to the skin as a whole. The dermis forms a tough, flexible, elastic covering over the surface of the body. Immediately deep to it the hypodermis contains a large amount of fat in some animals, for example the aquatic mammals, the pig and man. The dermis contains almost all the nerve endings of the skin and serves to support the blood vessels that extend to the epidermis. It plays a large part in the defence against bacterial invasion.

The Musculature of the Skin

The skin contains unstriated (or smooth) muscle fibres which permit a certain degree of movement. In addition to the arrector pili muscles, smooth muscle occurs in the nipples and scrotum. In most mammals there are extensive striated muscles known collectively as the cutaneous muscles. Formerly termed the panniculus carnosus, they occur in the superficial fascia beneath the skin, closely associated with the dermis. They are attached to the dermis and are anchored to the subcutaneous fascia rather than to bone, and their contraction causes movement of the skin.

General

Since the colour of the skin and its appendages serves usually for concealment rather than for recognition or stimulation as occurs in birds, the colours of the skin and hair of mammals tend to be relatively dull. The majority of mammals are colour blind. Recognition and stimulation are accomplished mostly by scent or visual cues other than colour. Many mammals have coats of different colours in different seasons. Deer become darker in winter, lighter and dappled in the summer. Some Arctic species become white in winter, but Antarctic species do not, reflecting the absence of terrestrial predators in the Antarctic region. Changes in the basic colour patterns involve alteration of the hereditary make-up by variation and natural selection.

It is clear from the foregoing that the skin is far more than a passive covering for the body. It plays a part in rapid adjustments such as temperature regulation, as well as in the slow adjustments by which a species is kept in balance with its environment. In addition to its roles in temperature regulation, protection against abrasion and infection, camouflage, the synthesis of vitamins and the secretion of sebum, sweat, milk and scents, it is an extensive sense organ that plays an important part in maintaining an animal's awareness of its surroundings and the presence of various stimuli.

THE SKELETON

The bony skeleton (Fig. 34.3) provides structural support and protection as well as levers for muscular action. It functions as a store of minerals and fat and is a site for blood cell formation. Bone is vital living tissue, supplied with blood vessels and nerves, that is metabolically active such that it may be altered in shape, size and position by mechanical or biochemical demands.

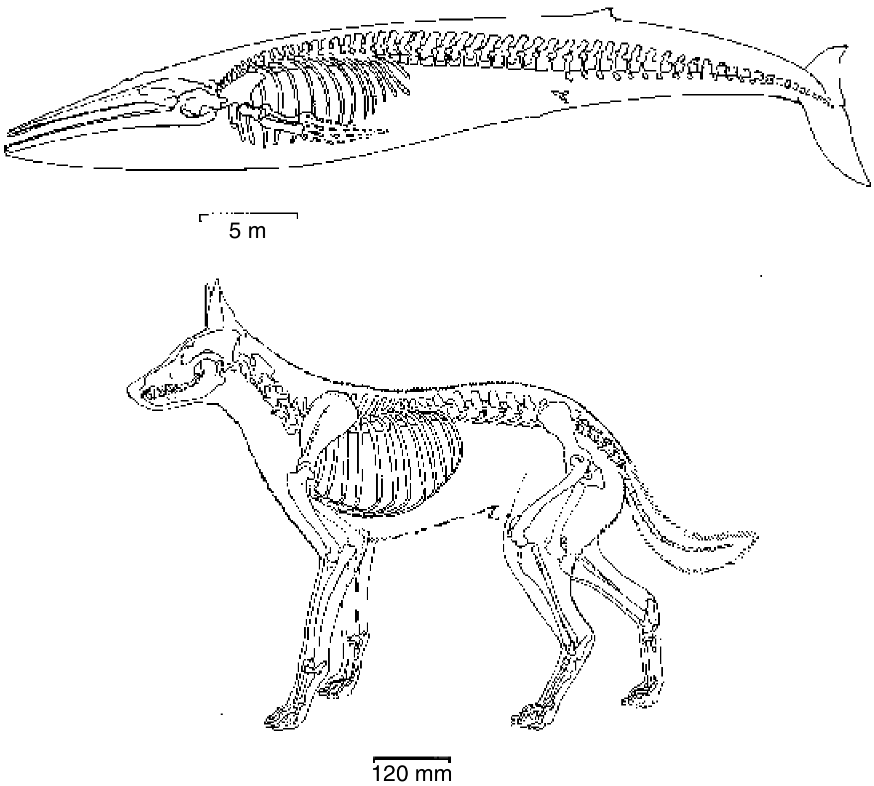


Figure 34.3 Comparison of the skeleton of a blue whale and a dog. The bones of the forelimb have been modified to form a paddle in the whale. Almost all the bones of the hind limb have disappeared. The caudal region is greatly developed to form a propulsive organ. (© ABRS) [M. Thompson]

Living bone consists essentially of connective tissue fibres impregnated with mineral substances, making it almost equally resistant to compression and tension, while giving it some elasticity. The form and structure of any bone are adapted to its function of support and of resisting mechanical stresses. The dry bones of an articulated skeleton give an impression of stability and tend to be regarded as forming a rigid inorganic framework, uninfluenced by the factors which so readily mould and modify the softer structures of the body. In fact, during growth and in adult life, each bone is continually being modified to maintain these functions as the stresses to which it is subjected change. Alteration of shape and structure is brought about by changes in the rates of deposition and absorption of bone substance. The factors controlling these processes are complex and not only involve activity by various cell types, but are also affected by more general hormonal, metabolic and nutritional changes.

Parts of the skeleton are made of cartilage, which is either a temporary formation later replaced by bone, as in the epiphyses of the long bones, or permanent and persists throughout life, as in the skeleton of the external ear and portions of the nose. Cartilage is neither as hard nor as strong as bone, but it is much more flexible.

The investigation of skeletal structures plays an important part in the study of mammalian evolution. Skeletal parts are resistant to decay in many circumstances and remain as fossils which provide the major means of following the course of phylogenesis.

To provide movement in an otherwise rigid framework and to allow for growth, the bony skeleton is divided into separate parts joined, as a rule, by tissues which are sufficiently flexible to allow movement to take place. Where the bones can move freely on each other, a joint space is present and the structure is referred to as a synovial joint. Where less movement occurs, the joint is made by fibrous connective tissue or cartilage, or both. The union may be made complete by fusion of the bones so that movement or further growth between them is prevented, as tends to occur in the joints (sutures) of the skull vault.

Movements at joints are controlled and produced mainly by muscles which are attached to the bones (and in some instances the cartilages), but the bones are held together by all the tissues which surround them. Bone and cartilage are each enclosed in a dense layer of fibrous tissue, the periosteum and perichondrium, respectively, and this sleeve runs from bone to bone, constituting the fibrous capsules of joints. Here it may be thickened to form connecting bands or ligaments which, together with the muscles and other soft tissues, maintain the continuity of the skeleton and transmit tensile stresses. Compression stresses demand something more solid and the ends of bones usually are modified in shape and enlarged to provide a good bearing surface which distributes the pressure in any normal position.

Axial Skeleton

The skull reflects the several major functions of the head. Shape is determined by genetic factors that determine such features as the size of the brain and the organs of special sense (nose, eyes and ears), the size and form of the jaws and teeth and the details of the musculature attached to the skull. The skull consists of bony capsules whose shapes correspond to the organs they contain, notably the brain, eyes, nose and mouth. The irregular shape of the skull is due partly to the multiplicity of the various capsules and passages and partly to the presence of protruberances for muscle attachments.

There is a large number of small skull bones in non-mammalian vertebrates, but a relatively small number of large bones in mammals. A large part of the skull develops in cartilage as the chondrocranium: the skull base, parts of the side walls and capsules surrounding the nasal and auditory organs. In mammals,

nearly all the chondrocranium ossifies to form cartilage bones. Early in embryonic development, membrane bones are laid down, particularly over the top of the brain, and most fuse with the cartilage bones.

The bones that make up the skull in eutherian mammals is consistent, although some variation can occur, for example, absence of the lachrymal bone in seals. The greatest degree of skull specialisation is seen in the whales, particularly the toothed whales, which shows telescoping and bilateral asymmetry with elongation of the rostrum and foreshortening and overlapping of the cranial bones. Paired frontal, parietal and occipital bones and often a small median interparietal form the vault of the skull (calvaria). The bones of the calvaria continue down over the sides and articulate with other bones. The presphenoid forms a small section of the back of the orbit, and caudal to this is the temporal wing of the sphenoid and the squamous part of the temporal. The latter is continuous ventrally with the petrous part of the temporal. The caudal end of the cranial cavity is formed by the occipital bone. The floor of the cranial cavity, extending rostrally from the foramen magnum, is formed by the basal part of the occipital and the basisphenoid with its sella turcica which houses the hypophysis. The floor is continued to its rostral extent by the presphenoid and that portion of the ethmoid that forms the cribriform plate, through which pass the fibres of the olfactory nerve.

The inside of the cranial cavity is moulded approximately to the form of the brain, whereas externally the surface is irregular where muscles are attached. Caudally, the skull is flattened to form a nuchal surface for muscle attachment. Prominences project ventrally from the skull, notably the mastoid process of the temporal for attachment of the sternomastoid muscle and the jugular process of the occipital for attachment of muscles of the tongue and hyoid. The ridges and processes on the skull are formed partly as a response to the stresses applied to the bones by muscular action.

The cranium completely encloses the brain and is pierced at its base by foramina for the passage of cranial nerves and blood vessels.

The nasal cavities are formed dorsally by the nasal bones and lateral cartilages, laterally by the maxillary and incisive (premaxillary) bones; the last two are tooth-bearing bones. Palatine processes of the incisives and maxillaries form the hard palate that makes up the rostral part of the floor of the nasal cavity. This bony palate is continued caudally by the palatine bones, then the pterygoid process of the basisphenoid. The medial wall is made up of a caudal bony part, formed by the perpendicular plate of the ethmoid above and the vomer below, and a rostral septal cartilage.

A system of spaces, the paranasal sinuses, communicates with the nasal cavity. These sinuses are present in several bones of the skull, notably the frontal, maxilla, sphenoid and ethmoid, forming a space between the outer and inner tables of compact bone, which in many bones is occupied by spongy bone (diploë). The extent and degree of complexity of the paranasal sinuses is highly variable, from the large and complex frontal sinuses in some Artiodactyla to the absence of sinuses in aquatic mammals.

The confines of the orbit are entirely bony in man, but incomplete in other mammals in which only the medial wall and part of the roof are osseous. The medial wall is formed primarily by the orbital part of the frontal bone. The orbital wing of the presphenoid forms the caudal part and contains the optic canal. The lachrymal bone, when present, contributes to a small portion of the medial wall and contains the fossa for the lachrymal sac and the caudal orifice for the nasolachrymal canal. The medial aspect of the roof of the orbit is formed by the zygomatic process of the frontal bone; the lateral aspect in some species at the rim by the frontal process of the zygomatic bone (jugal), and in other

species by the orbital ligament. Laterally the eye is protected by the zygomatic arch, made by the zygomatic bone rostrally and the zygomatic process of the temporal caudally.

The oral cavity has incomplete bony walls and is made larger or smaller by the actions on the temporomandibular joint of muscles that attach to the skull and mandible. The bony roof of the mouth is formed by the hard palate; the walls and floor are musculoskeletal. The muscles are attached to the maxilla and incisive bone above, to the mandible below. The incisive bone houses the upper incisor teeth (which are absent in ruminants).

The upper premolars and molars are lodged in the alveoli of the maxilla, all the lower teeth in the alveoli of the mandible. The size and form of the teeth vary (Fig. 34.4) from the simple, conical (homodont) dentition of the toothed whales to the heterodont and highly specialised dentition of some species, for example, the incisors of rodents and the cheek teeth of herbivores and some carnivores. The dentition is diphyodont in mammals, although in some the deciduous teeth are reabsorbed partially *in utero* and the permanent teeth formed at birth.

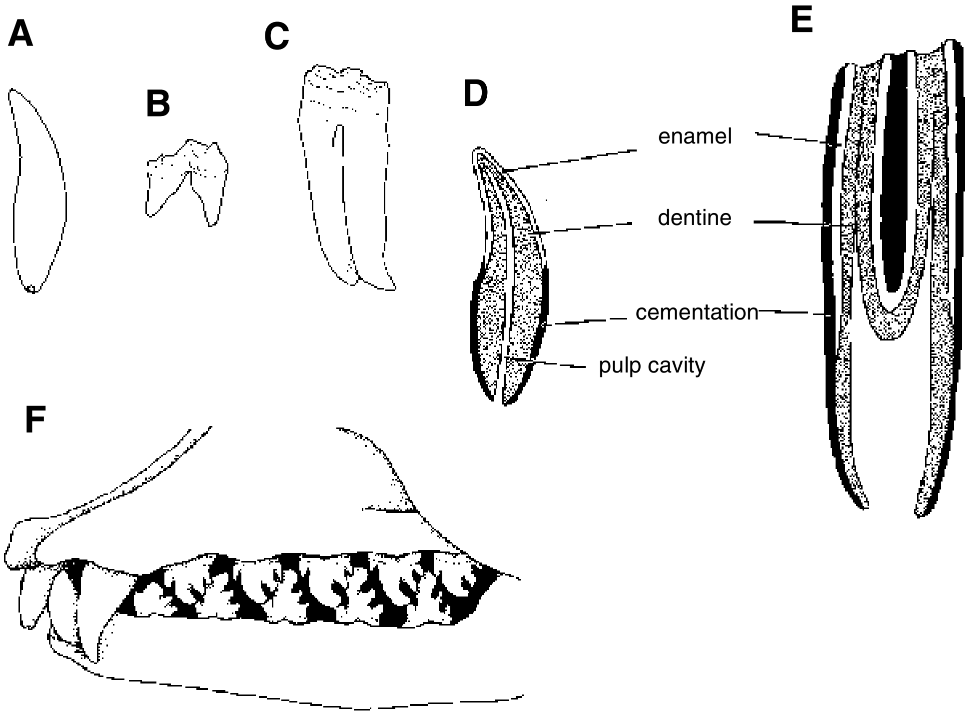


Figure 34.4 Diagrams of some mammalian teeth: **A**, canine tooth of a carnivore; **B**, sectorial (carnassial) tooth of a dog; **C**, lower cheek tooth of a horse; **D**, cross-section of A; **E**, cross-section of C; **F**, the teeth of a crabeater seal. The incisors and canines of this seal are unremarkable, but the cheek teeth are modified to function as a sieve to filter plankton. Note illustrations not to scale. (© ABRS) [B. Scott]

Each tooth develops by secretion from ameloblasts in a thickening of the ectoderm, the enamel organ, in harmony with the mesodermal dental papilla, the odontoblasts of which secrete the dentine. The tooth is thus an elevation with a mesodermal core, covered by two types of hard material (enamel and dentine) and set in the alveolus (socket). A third material, cementum, may be added to the surface of the tooth. In some herbivores it extends between the folds of the tooth so as to form part of the grinding surface.

Enamel is harder than dentine or cementum and the different rates of wear of these materials ensures the maintenance of a rough grinding surface or a sharp, cutting edge.

The tooth narrows at the base, but remains open in most species to allow blood vessels and nerves to enter the pulp cavity within the root. In teeth that grow continually, the pulp is wide open below. Usually they do not have a complete covering of enamel and are either worn away continually, as the incisors of rodents, or grow to a great size, as the tusks of pigs and dugongs.

In some species, parts of the tooth (dentine, cementum) appear laminated in sections, the layers being laid down at regular intervals. This characteristic has been used to estimate the age of individuals.

The hyoid bone of mammals (Fig. 34.10) consists typically of a body, situated in the base of the tongue, and two pairs of cornua (horns). Additional ossifications may reach up to the ear region and in some mammals (including man) the distal end of the hyoid horn may fuse with the skull as a styloid process.

The vertebral column of quadrupedal mammals forms the main compression member of a complicated girder to support their weight. The number of components comprising the girder and its flexibility differs in different mammals, but five regions can always be recognised: cervical, thoracic, lumbar, sacral and caudal (coccygeal). In the larger quadrupeds the vertebral column forms a double cantilever girder and the majority of the weight is carried on the forelimbs, the hind limbs being used for pushing. In some small mammals, such as the rabbit, the vertebral column is used in two ways: when the animal springs forward it forms a single girder, braced on the hind limbs; when standing still it is a double cantilever as in the larger quadrupeds. The vertebral elements extend dorsally from the bodies and function to protect the spinal cord.

The typical vertebra contains a body that acts as a compression strut. The bodies develop from a larger middle part, corresponding to the diaphysis of long bones, with which the smaller vertebral epiphyses fuse cranially and caudally during development. The terminal faces of the body are flat (acoelous vertebrae) and a fibrocartilaginous disc joins one vertebra with another and acts as a cushion between the bodies. These symphyses allow limited movement, particularly bending and rotation, but this is limited by the interlocking articular processes (apophyses) of the vertebrae and by the several ligaments, particularly the dorsal and ventral longitudinal and supraspinous ligaments of the vertebral column.

The base of a neural arch arises from either side of the vertebral body. Above the spinal cord the two arches fuse to form the spinous process. At the base of the arch on either side there is a transverse process. Ventral to the articular processes there are gaps, the intervertebral foramina, for the passage of the spinal nerves. The spinous processes are longest in the thoracic region. Within the thoracic region they are longest over the withers, although their length and slope vary greatly in different mammals.

In quadrupeds the more cranial thoracic spinous processes slope caudally and the lumbar spinous processes point cranially with one anticlinal vertebra almost vertical between. This represents the point between the two cantilever girders with which the vertebral column has been compared.

The number of cervical vertebrae is remarkably constant in mammals; all but a very few exceptions have seven; even an apparently neckless whale and the long-necked giraffe have seven cervicals. The number of dorsal vertebrae (thoracic and lumbar) tends to be rather constant within the limits of many mammalian families, but the ratio of thoracic to lumbar vertebrae is variable. There are three to six sacral vertebrae, some or all of which are fused together. The number of caudal vertebrae varies greatly, from three to as many as 50 vertebrae.

In ancestral tetrapods ribs were borne by every vertebra from the atlas (first cervical) to the base of the tail. Only one type of rib is present in extant tetrapods, which probably corresponds to the dorsal ribs of fishes. Only the thoracic vertebrae have discernible ribs in eutherian mammals, but embryological investigations have shown that the so-called transverse processes of the cervical vertebrae include short, fused, two-headed ribs. The transverse foramina that are characteristic of cervical vertebrae represent the gap between capitulum and tuberculum of the rib in each case. Ribs are present on all the thoracic vertebrae, the capitulum of each articulating with the body of either one or two adjacent vertebrae, and the tuberculum with the transverse process of a vertebra. Most ribs curve ventrally to reach the sternum through cartilaginous segments, but the shorter, more caudal ‘floating ribs’ do not. The lumbar vertebrae have long transverse processes but no ribs, and caudal ribs are never developed. The lumbar vertebrae have large surfaces for muscular attachment. In addition to the broad dorsal spines and transverse processes there are also mammillary processes to which are attached the tension members of the girder, the sacrospinalis muscles.

The tail of some mammals possesses a series of small elements, crescentic in end view, which are wedged ventrally in between successive vertebral bodies. These are the intercentra, to which are fused the haemal arches (chevrons), which extend down between the muscles of either side. The base of each haemal arch consists of a pair of processes that descends from the intercentrum to enclose a space in which lie the major blood vessels of the tail. The haemal arches are particularly well developed in whales, in which the two haemal processes of each arch join ventral to the vessels to give a V or Y shape as seen in end view.

The first two cervical vertebrae are modified and are given the specific names atlas and axis. The condylar articulations of the atlas with the skull are double in mammals. The dens (odontoid process) of the axis is believed to include the body of the atlas.

Appendicular Skeleton

The mammalian limbs provide support for the body and act as levers. They are struts with an axial skeleton and differ markedly from the limbs of fishes, which are flaps that project laterally from the body as fins. The hind limb of mammals is attached to the vertebral column by the sacroiliac joint. The forelimb remains relatively free. The scapula is attached to the axial skeleton only by muscles.

The forelimb (Fig. 34.5) is thus more flexible than the hind limb and has acquired functions other than support and locomotion, such as digging, collecting food and climbing. The ability to move the limb in various directions is more important than firm attachment. This ability is developed conspicuously in man.

The thoracic (pectoral) girdle in fishes, and to a lesser extent in amphibians and reptiles, is a complex structure. The body of mammals is raised off the ground and the thoracic girdle has assumed the function of transmitting the weight of the body to the limb. In so doing it has become modified and simplified such that it consists of two elements: the scapula and clavicle, or in many species the scapula alone. The entire coracoid plate has disappeared, there is no cranial coracoid and the coracoid has been reduced to a small process attached to the scapula. Even the scapula has changed radically. Instead of being a simple plate, it bears the scapular spine which separates supraspinous and infraspinous fossae. The acromion is fused to the base of the scapular spine. The glenoid cavity for articulation with the head of the humerus is a relatively shallow cup compared with the deep acetabulum of the hip joint.

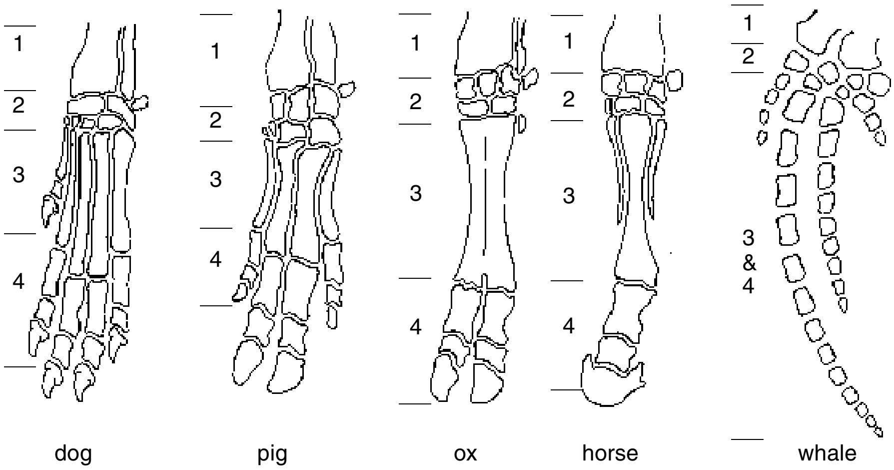


Figure 34.5 The bones of the distal end of the forelimb of several mammals. 1. distal end of radius (and ulna where present); 2. carpus; 3. metacarpus; 4. phalanges. (© ABRS) [B. Scott]

The humerus is a typical long bone, with several roughenings and protruberances where muscles are attached, for example, greater and lesser tubercles, medial and lateral epicondyles.

The bones of the antebrachium, carpus and manus vary greatly with the use to which the forelimb is put, but all mammals possess a radius and ulna which articulate with a proximal row of carpal bones, which in turn articulate with a distal row of carpals and these with the metacarpals. The ulna is reduced in many species, particularly in its distal portion. The terminology for the carpals is at times confusing and has been simplified in the *Nomina Anatomica Veterinaria* (NAV) (Table 34.1).

Table 34.1 Comparison of simplified carpal terminology found in the Nomina Anatomica Veterinaria (NAV) and that commonly found in the zoological literature.

NAV	ZOOLOGICAL TERM
Proximal row	
(Central)	Central
Radial	Scaphoid
Intermediate	Lunate
Ulnar	Triquetrum or Cuneiform
Accessory	Pisiform
Distal row	
Carpal I	Trapezium
Carpal II	Trapezoid
Carpal III	Capitate or Magnum
Carpal IV	Hamate or Unciform

Fusion of adjacent carpal bones occurs in some species. Movement at the intercarpal and carpometacarpal joints is very limited, but in most mammals there is considerable movement between the metacarpals and phalanges.

Five toes were present in the manus of ancestral mammals and are found in many forms today. The first digit (pollex) is more or less opposable to the others in arboreal forms and man, to give a grasping power. This digit is, however, of little use in terrestrial locomotion and is reduced or lost in most species. Further digital reduction or modification occurs in a great variety of mammals.

The hind limb shows less tendency to modification than the forelimb for special functions, because it is involved mainly in propulsion and support. The weight of the hind end of the body is carried by the hind limb in a quadrupedal animal when it is standing. Movement is produced by extension at the hip joint with the foot fixed, when the entire limb is used as a lever. Propulsion also is effected by lengthening of the limb by its intrinsic muscles, acting especially at the knee and tarsus in plantigrade and at the knee in digitigrade types.

The pelvic girdle articulates with one or more sacral vertebrae at the sacroiliac joint. A small amount of movement can occur at this joint, which is a synovial joint reinforced by short, very strong sacroiliac ligaments.

Compared with non-mammalian vertebrates, marked changes associated with altered limb posture and musculature have occurred in mammals. The ilium, which primitively extended mainly caudally, extends cranially to articulate with the sacrum. The pubis and ischium have moved caudally. The primitive mammalian ilium is a rather slender rod, but in heavy-bodied ungulates (for example, horse, cow) or bipeds (man) which possess powerful gluteal muscles, this bone is expanded considerably. These three bones that make up the pelvic girdle, the ilium, ischium and pubis, enclose an aperture, the obturator foramen, which in life is closed by the obturator membrane except for a small portion cranially that allows the passage of the obturator nerve and vessels. The obturator membrane gives attachment to internal and external obturator muscles inside and outside the pelvis.

The pelvic opening is broader in the female in many species, associated with viviparity and in some the symphysis which joins the girdle of either side (mainly between the pubes) is loosened under hormonal control at the time of parturition.

The acetabulum is a deep cup into which the head of the femur fits. The joint capsule is greatly thickened in some parts to form powerful ligaments which limit the movements of the joint mainly to the sagittal plane.

The lines of the trabeculae in the spongy bone of the proximal end of the femur are arranged to distribute weight downwards onto the tubular compact bone in the body. The head is attached to the body of the bone by a long neck that holds it out at a distance from the body and permits a swinging motion of the limb. There are protruberances where muscles attach (for example, major and minor trochanter, medial and lateral epicondyles) and, distally, condyles for articulation with the tibia and a trochlea for articulation with the patella.

The tibia is the main supporting element of the crus and is always developed fully. On the cranial aspect at the proximal end is the tibial tuberosity for attachment of the quadriceps tendon. The fibula bears little weight, and in consequence tends to undergo reduction. It persists in almost all mammals, but its ends may fuse with the tibia, or the shaft may be lost.

In the pes, the bones of the tarsus form a structure that is somewhat similar to the carpus. There are three bones in the proximal row, one central element and four elements in the distal row. The terminology tends to be confusing, as in the carpus (Table 34.2). As in the carpus, adjacent elements may be fused.

Table 34.2 Comparison of simplified tarsal terminology found in the Nomina Anatomica Veterinaria (NAV) and that commonly found in the zoological literature.

NAV	ZOOLOGICAL TERM
Proximal row	
Talus	Astragalus
Calcaneus	Calcaneum
Central	
Central tarsal	Navicular
Distal row	
Tarsal I	Medial or Internal Cuneiform
Tarsal II	Intermediate or Middle Cuneiform
Tarsal III	Lateral or External Cuneiform
Tarsal IV	Cuboid

The description given for the digits of the manus applies in general to the pes, but the proximal bones are termed metatarsals.

Heterotopic Skeleton

Heterotopic bones occur in certain organs, generally replacing fibrous connective tissue otherwise present there. Bone may form directly from such tissues or pass through an intermediate cartilaginous stage.

Small cartilages or bones form in several tendons of the body in mammals, at points of potential friction. Termed sesamoids, these frequently occur in the manus or pes. The patella is an unusually large sesamoid structure.

The os penis (baculum) is formed in the fibrous tissue of the corpora cavernosa in bats, rodents and carnivores, among other mammals. Its shape is the most highly varied of all bones. A homologous cartilaginous or bony os clitoridis is present in some species.

Ossa cordis develop in the fibrous skeleton of the heart of deer and bovids.

THE MUSCULATURE

Mammals possess an elaborate system for receiving information from the environment. This system is linked inextricably to correspondingly elaborate effectors, the muscles which respond to motor signals received from the nervous system. The muscles can transfer static energy (derived from food and oxygen) into kinetic energy (movement) in response to nerve stimuli. The activity of the nervous system has little mode of expression other than the contraction of muscle fibres. The musculature constitutes one third to almost one half of the mass of an individual mammal.

Muscle Function

Movement is achieved by an articulated framework, the skeletal parts, joined by ties that can be varied in length, the skeletal muscles. The muscles serve to fix as well as to move the skeletal parts. They can act as braces, holding the organs of the body in place.

Muscles operate by exerting tension. If the ends of a muscle are fixed, contraction exerts a force along its length without any actual movement occurring and is known as isometric contraction. If a muscle is allowed to shorten without increase of tension, the contraction is said to be isotonic. In practice the two types of contraction are unlikely ever to be fully separated.

The power of holding is developed most fully in the unstriated (smooth) muscle of the viscera. This muscle produces slow movements such as peristalsis. Unstriated muscle occurs in the wall of the gut, respiratory passages, urogenital ducts and blood vessels, in the skin and the iris. Myofibrils within the cells are thought to be the contractile material of unstriated muscle. They are doubly refractile under the polarizing microscope, but show no sign of the alternating isotropic and anisotropic transverse bands that are characteristic of the myofibrils of striated skeletal muscle.

Contraction of unstriated muscle may be initiated by autonomic nerve impulses, hormonal stimulation or local changes arising within the muscle itself. Stretching the muscle fibres can change the membrane potential and initiate a wave of contraction, a local stimulus that is particularly important in the physiology of the bladder, gastrointestinal tract and other hollow viscera.

Unstriated muscle in the walls of blood vessels behaves rather like striated skeletal muscle in that its activity usually is initiated by motor nerve fibres and there is little evidence of conduction between cellular units. In contrast, visceral unstriated muscle functionally resembles cardiac muscle to some extent: the cells behave like single muscular units and impulses are freely conducted from cell to cell. Two forms of contraction occur in visceral smooth muscle, namely rhythmic and tonic contraction, which appear to be independent; in addition, there is a continuous state of partial contraction known as muscle tone.

Cardiac muscle is found only in the heart wall. It shows cross striations similar to that seen in skeletal muscle, but in other respects cardiac muscle differs greatly from skeletal muscle. The heart musculature is a continuous network of dividing and recombining strands with prominent cross bands, intercalated discs, separating this network into short units. The heart beat is influenced by autonomic nerves, but the cardiac musculature is essentially autonomous.

The majority of movement in mammals is performed by the striated skeletal muscles which also play an important part in posture. Their fibres are much larger than those of unstriated muscle and contain many nuclei. The most obvious characteristic of skeletal muscle fibres (Fig. 34.6) is the transverse striations that make up the contractile units; a more delicate longitudinal striation also is detectable within the fibre, attributable to the parallel arrangement of myofibrils.

Large numbers of parallel muscle fibres are grouped into fasciculi, visible to the naked eye, which are arranged into various patterns to form several types of muscles - straplike, sheetlike, unipennate, bipennate, multipennate.

When a muscle contracts at its maximum power, it is capable of contracting to about half its stretched length. The force of contraction of a given muscle at any time depends on the number of fibres that are contracting. The contraction is initiated by a nerve impulse travelling over a nerve axon to the muscle fibres. Each axon supplies several muscle fibres, the neuromuscular unit comprising a motor unit. The number of motor units functioning at any one time determines the activity of the muscle. The precision of movement is greatest in those muscles that have many motor units, each of which includes only a few muscle fibres, for example the extrinsic muscles of the eyeball.

Pennate muscles, that is those with tendons throughout their length, are stronger than straplike or sheetlike types because they are composed of many short, oblique fibres which have an additive effect upon the insertion. The straplike

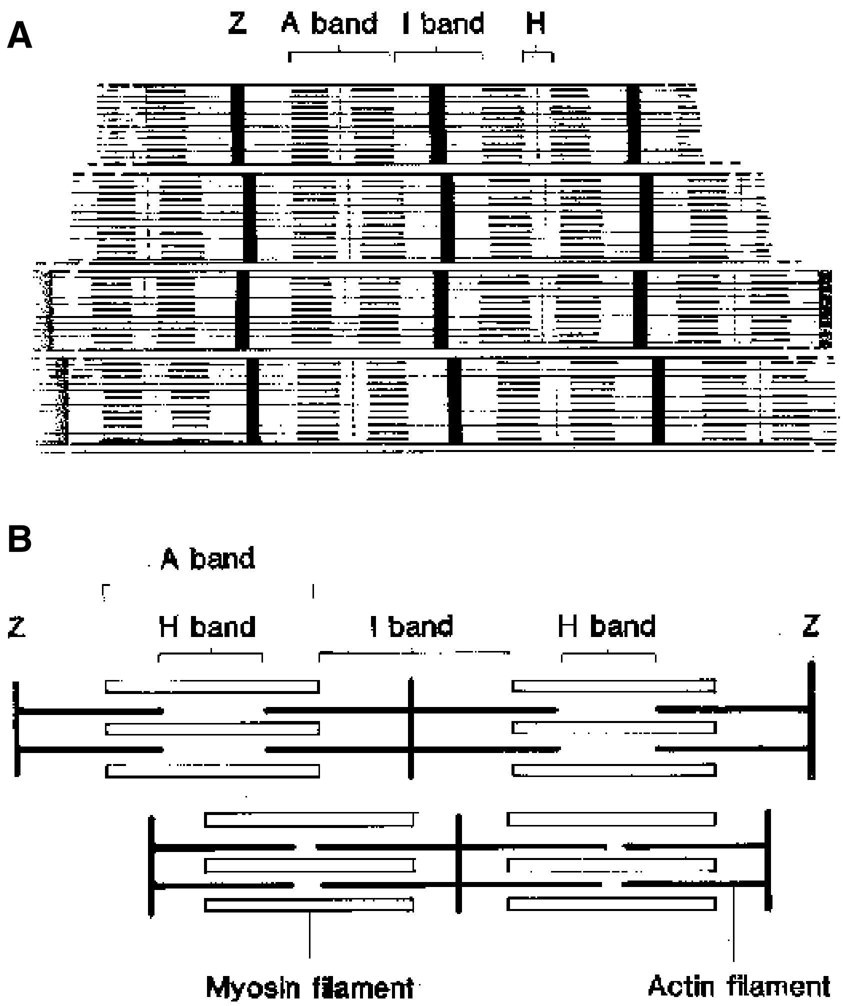


Figure 34.6 Diagrams showing the structure and mechanism of sliding filaments in striated skeletal muscle: **A**, four within a single muscle cell at high magnification; A band = anisotropic band; I band = isotropic band; **B**, the arrangement of the filaments of actin and myosin when the muscle cell is stretched (above) and contracted (below). (© ABRS) [M. Thompson]

and sheetlike types contain long fibres that are almost parallel with one another and with the long axis of the muscle. They have the ability to contract to a greater degree than pennate muscles, but with less strength.

The muscle fibres, the fasciculi and the entire muscle are each invested by connective tissue (endomysium, perimysium and epimysium, respectively) that forms a continuous stroma serving to bind together the contractile units and groups of units and to integrate their action. It also permits a degree of freedom of movement between them such that each fibre is independent of adjacent fibres to some degree and each fasciculus can move independently of neighbouring fasciculi. The connective tissue framework of muscles, therefore, is vital to normal muscle function. The epimysium of some muscles is indistinguishable from the more extensive investing fascia, a connective tissue forming fibrous membranes which separate organs and invest them. Fascia also forms extensive sheets, such as the extensive sheet of fascia that connects the skin with deeper structures. In relation to the muscles, sheets of dense fascia provide attachments, serve as elastic sheaths, form specialised retaining bands (retinacula) and fibrous sheaths for tendons and permit the gliding of one muscle

on another. The development of fascia to form an extensive, highly elastic sheet, termed the tunica flava abdominis, is seen in the abdominal wall of large herbivores such as the horse.

In the more distal parts of the limbs, especially in the lower limbs of humans, venous return is impeded by gravity and aided by muscular contraction. The muscles are prevented by the fascia from swelling and bulging excessively with blood during contraction. The fascia serves as a resistant stocking and makes muscular contraction more efficient in moving blood upward. This important function of the fascia is enhanced by its attachment to the bones in some regions to form fascial compartments that surround groups of muscles with similar function and nerve supply.

The attachment of muscles to bone or other tissue is usually by a long, cord-like tendon (sinew) or by a broad, relatively thin aponeurosis. Where they are attached to bone, the bundles of collagenous fibres fan out in the periosteum. Although some muscles appear to have an extensive, fleshy attachment to bone with no interposing tendon or aponeurosis, there is always some connective elements between the muscle fibres and the attachment of the muscle.

The Contractile Mechanism

Detailed examination of the submicroscopic organisation of muscle by electron microscopy and X-ray diffraction has led to a new concept of the mechanism of muscle. contraction

The cross-banded pattern of striated skeletal muscle (Fig. 34.6) reflects the arrangement within the myofibrils of two sets of submicroscopic filaments, thicker myosin filaments and thinner actin filaments. The explanation of their function necessitates some preliminary description. The fibrils bear cross-striations which tend to be in register within a muscle fibre, giving the entire fibre its distinctive cross-banded appearance under the light microscope. Each fibril is made up of alternating light and dark portions. The former are only slightly bi-refringent, the isotropic or I bands, the latter are strongly bi-refringent and, therefore, are termed the anisotropic or A bands. Cutting across the I band is a thin dark line, the Z line, and in the middle of the A band a thin clear line is sometimes seen, the H band.

When a muscle contracts, the thick and thin filaments maintain the same length, but slide past each other so that the ends of the actin filaments extend into the A band, narrowing and ultimately obliterating the H band. As a consequence of the deeper penetration of the A band by the actin filaments, the Z line is drawn closer to the ends of the adjacent A bands and there is an overall shortening of the myofibril. Calcium is required in the tissue fluid for muscular contraction and it is believed that neural excitation of the muscle fibre membrane is conducted inwards by tubules that are continuous with the membrane, causing the endoplasmic reticulum to release calcium ions to the myofibrils and triggering their contraction. When contraction is completed, calcium ions are recaptured by the endoplasmic reticulum and relaxation occurs.

The energy required for contraction is provided ultimately from the glycogen abundant in muscle fibres. The rapid release of energy within the muscle necessary for contraction is effected by the conversion of adenosine triphosphate (ATP) to adenosine diphosphate (ADP). The energy for rebuilding ATP is derived from the oxidation of glycogen.

Muscle Action and Homeostasis

The chemical processes within functioning muscle result in the production of energy, some of which is in the form of heat. Mammals make use of this in the control of body temperature. If cooled blood reaches the temperature-regulating

centres of the central nervous system, shivering, which consists of muscular contraction with the production of heat, may result. Non-shivering thermogenesis also may involve the muscles, when specific mechanisms for release of heat energy are involved in response to a fall in blood temperature.

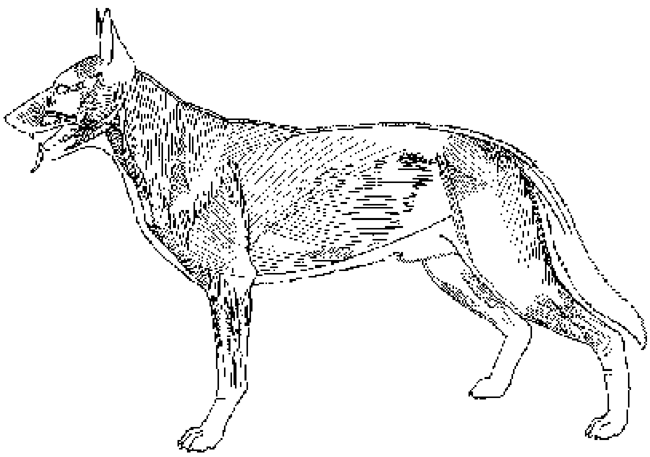
Vigorous exercise helps to maintain body temperature in cold conditions by the release of heat from working muscles.

Muscular Organisation

Several terms are used to describe muscles according to their action. An extensor muscle tends to open out a joint, a flexor closes it. An adductor draws a segment toward the median plane of the body, an abductor does the reverse. A levator raises while a depressor lowers the structure. Constrictor or sphincter muscles surround orifices and tend to close them. Dilators do the opposite.

The two major trunk muscle groups (Fig. 34.7) are the epaxial and hypaxial groups. The epaxial musculature, which in fishes is a massive column of segmented muscle lying lateral to the vertebrae, is in the main restricted to the channel along the vertebral column between the spinous processes and the transverse processes. It comprises three longitudinal divisions, with little of the original metameric arrangement. Laterally is the iliocostalis system, medial to which the longissimus system lies dorsal to the transverse processes of the vertebrae. Most medially, between the longissimus and the spinous processes, is the transversospinalis system. In the lumbar region the iliocostalis and longissimus unite into a powerful sacrospinalis. The epaxial musculature serves to extend the vertebral column, and to flex it laterally when acting on one side. Parts of it are capable of producing more subtle movements of rotation, flexion and extension between neighbouring vertebrae.

A



B

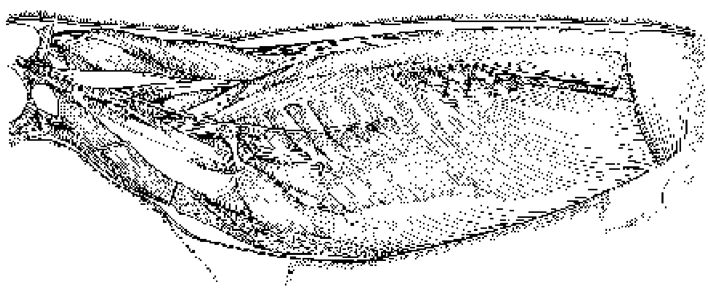


Figure 34.7 The superficial **A**, and deep **B**, musculature of the dog. (© ABRS) [M. Thompson]

The hypaxial muscles of fishes lie ventral to the horizontal septum and extend around the outer body wall to the ventral midline. They are reduced considerably in relative bulk in mammals. Some of them form muscle sheets around the belly and flanks and, aided by the rib cage, enclose and support the thoracic and abdominal cavities and their viscera. The hypaxial trunk musculature includes a series of subvertebral muscles, ventral to the transverse processes and the ribs. They function broadly to flex the vertebral column and, with the epaxial muscles, laterally flex it when they act together on the one side only. Among these muscles are the psoas muscles, quadratus lumborum and the longus colli. The hypaxial flank muscles follow the curve of the trunk from the transverse processes of the vertebrae to the ventral region and include the external and internal abdominal oblique and transverse abdominal muscles. Ventrally, the rectus abdominis runs craniocaudally from the sternum and costal cartilages to the pelvis. Thin, transverse, tendinous inscriptions often are present in the rectus, which may represent to some degree the original segmental condition of the muscle. The hypaxial muscles that attach the forelimb to the axial skeleton form slings that suspend the body between the scapulae. They mainly extend from the vertebral border of the scapula to the ribs. The muscles which form those slings are derivatives of the external oblique muscle. The major elements of the system spread out from the deep surface of the scapula in a fanwise manner to attach caudally to the ribs and cranially to the cervical vertebrae. They include the serratus ventralis, levator scapulae and the more dorsally placed rhomboideus.

The development of the diaphragm is a characteristic of mammals. It is a partition, partly muscular and partly tendinous, separating the thoracic and abdominal cavities and is of major importance in respiration.

There is a basic pattern of six extrinsic muscles of the eyeball in vertebrates, namely the four rectus muscles (dorsal, ventral, medial and lateral) and the two oblique muscles (dorsal and ventral). As in the majority of tetrapods (birds and primates are exceptions), there is a retractor bulbi which tends to pull the eyeball deeper into its socket in almost all mammals. The levator palpebrae superioris is derived from the eyeball muscles, but attaches to the upper eyelid and, in some cases, to the plica semilunaris conjunctivae (third eyelid).

In the head, the facial skin muscles are commonly referred to as the muscles of facial expression. They have a special importance in the primates because they play a large part in social organization. The jaw arch musculature of mammals comprises the muscles of mastication: the temporalis, masseter and medial and lateral pterygoids. Ventrally, a group of muscles attaches to the hyoid bone and acts as an elevator and depressor of the hyoid and, indirectly, the larynx. The main depressor of the mandible is the digastric muscle.

The limb muscles of mammals are bulky and complex. Early in the development of the limb, a mass of premuscular tissue is formed on both the dorsal and the ventral surfaces of the developing limb skeleton. These two masses are equivalent to the opposed dorsal and ventral muscle masses which raise and lower the paired fins in fishes. From the dorsal mass arise all the complex muscles on the extensor surface of the limb and related muscles of the girdle region. From the ventral mass arise the flexor muscles of the opposite limb surface. The reader should refer to an anatomy text for a description of the individual muscles of the limbs that are responsible for movement by flexion, extension, abduction, adduction, rotation, supination or pronation of the whole or components of the limb. It should be borne in mind, however, that a given muscle almost never has a single function. The action of a muscle is restrained and modified by several factors, such as the action of other muscles and whether the limb is fixed or swinging freely. The action of living muscles can be determined by electromyography.

THE BODY CAVITIES

The body cavities are large serous sacs, the pericardial, pleural and peritoneal cavities. They are derived from one continuous cavity, the coelom, whose cranial end surrounds the heart during embryonic development to form the pericardial sac. This is connected caudally to the peritoneal sac by two pericardioperitoneal canals, one on either side of the midline. The peritoneal sac becomes reduced by the developing abdominal viscera while the pericardioperitoneal canals accommodate the developing lungs and form the pleural sacs. These different parts of the coelom are soon separated off from each other. The large common cardinal veins carrying blood to the heart encircle the openings from the pericardial sac to the pleural sacs and finally occlude them altogether. Slightly later, the developing diaphragm cuts off the pleural sacs from the peritoneal cavity. In the male, a fourth subdivision of the coelom is formed by herniation of part of the peritoneal sac which surrounds the testicle in the scrotum. This becomes separated off as a closed sac, the vaginal cavity or cavity of the tunica vaginalis.

The body cavities thus become, after development of the viscera, empty potential cavities the lining membrane of which is reflected over the viscera. The viscera, thereby, become covered by a visceral layer of the serous membrane which is continuous, often through mesenteries, with the parietal lining layer which lines the body wall. This suspension of viscera into the potential space of the cavities permits free movement of the viscera. The smooth surface of the visceral layer of the serous membrane can glide freely over the opposed parietal layer, lubricated by a small amount of fluid secreted by the serous membrane. The serous membranes lining the pericardial and peritoneal cavities and the pleural sacs are referred to as serous pericardium, peritoneum and pleura, respectively.

THE DIGESTIVE SYSTEM

Animals possess a mechanism that provides a ‘drive’ to seek food. The source of the food drive, or how it relates to the needs of the organism, are not well understood, but in mammals it is strong indeed. In most species a pattern of food intake at intervals, that varies with the species, develops during early postnatal life. Probably it is triggered partly by hunger contraction (movements of the empty stomach) and partly by complex memories within the central nervous system.

It is remarkable that animals seek out and obtain the raw materials they require for their particular metabolic needs. Chemoreceptors probably play a large part in finding the right food, olfaction acting as a distance receptor and taste serving to test the food at the point of intake. Other senses may play a part as well, such as vision and, in bats and whales, sonar. Whether any given stimulus leads to acceptance or rejection of an object as food probably depends largely on past experience as recorded in the cortex.

Digestion

The features of the digestive system that are peculiar to mammals occur mainly in the mouth, where the dry exterior meets the moist interior at the mucocutaneous junction of the lips. The teeth, tongue and enzymes of the saliva begin the physical and chemical process of breaking up the food. The rest of the alimentary canal completes this process and absorbs from the products the molecules needed by the individual.

Chemical digestion is accomplished by the enzymes secreted by the alimentary canal and its associated glands and the action of symbiotic micro-organisms living within the gut. The high temperature of the body assists the fermentation process, which in herbivorous species is extensive and highly specialised in forestomach of ruminants and the large intestine of rabbits, horses and dugongs. Food is mixed and moved along the gut by rhythmic peristaltic movements regulated by neural reflexes and chemical (hormonal) signalling. Gut motility also is influenced by centres in the medulla oblongata, hypothalamus and cerebral cortex.

The Mouth

Food is taken into the mouth in various ways, in herbivores for example, by the cutting action of the incisors as in the horse and rabbit or by the prehensile action of the tongue as in cattle. Some herbivores have reduced anterior teeth, for example the ruminants, but the hard palate may be ridged such that the action of a rough tongue against it aids in breaking up the food. Production of vast quantities of saliva in certain herbivores, particularly the ruminants, also assists the initial breakdown of the food. The ducts of three major salivary glands, some or all of which are present in mammals, open into the mouth. These are the parotid, mandibular and sublingual glands. The nature of their secretions differs somewhat. The tongue bears numerous papillae of various forms (filiform, fungiform, vallate, conical, lentiform, foliate, marginal) on its surface. Taste buds occur in the epithelium of some papillae. The filiform papillae are developed to function in grooming in the cat.

The food is held in the mouth and masticated at length by herbivores and may be masticated more than once as in the ruminants. Carnivores tend to swallow the food quickly, tearing and chewing only when it is necessary to render the food portions small enough to swallow. The teeth have been considered in an earlier Section (see Section on Axial Skeleton).

The Oesophagus and Stomach

The oesophagus is a simple tube through which the food passes within a few seconds. The oesophageal musculature is partially striated and partially unstriated. Nonetheless the food is pushed along its entire length by the involuntary process of peristalsis. Food reaches the oesophagus by the voluntary act of swallowing, which involves raising the tongue and then contracting the levator muscles of the soft palate and superior pharyngeal constrictor, thus closing off the nasopharynx. The food passes through the oral and laryngeal parts of the pharynx and into the oesophagus by the stripping action of the pharyngeal constrictor muscles and the simultaneous raising of the hyoid and closing of the laryngeal aditus (Figs 34.8 & 34.9).

Portions of the stomach develop into enormous fermentation vats in the ruminants (Fig 34.8). Although the rumen, reticulum and omasum often are termed the forestomachs and are lined by stratified squamous epithelium like the oesophagus, they develop embryologically from the primitive stomach. The fourth compartment, the abomasum, is similar morphologically and functionally to the simple stomach of other mammals. Digestion of plant materials, particularly cellulose, occurs in the forestomachs, with breakdown to short chain fatty acids that form an important source of energy in herbivores. Considerable volumes of fluids are reabsorbed through the wall of the omasum.

The glandular portion of the stomach has a lining of tall columnar mucus-secreting cells, folded to form gastric pits, into the bases of which open the ducts of glands. The histological structure and the secretion products differ in different parts of the stomach. Some food, particularly liquid material, passes through the

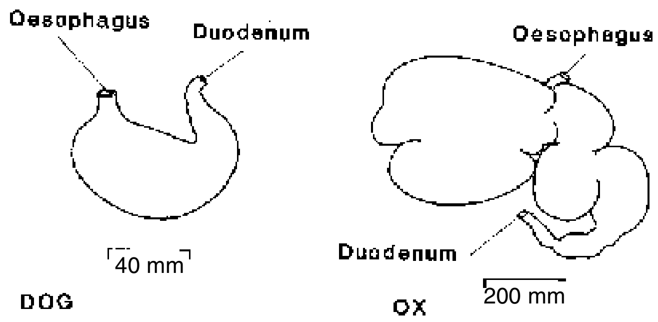


Figure 34.8 The appearance of the simple stomach of the dog compared with the complex stomach of the ox. Fermentation occurs mainly in the first compartment of the stomach of the ox. The first three compartments are referred to collectively as the forestomachs, while the fourth compartment is glandular. 1 = rumen; 2 = reticulum; 3 = omasum; 4 = abomasum. (© ABRS) [M. Thompson]

stomach within minutes, while the more solid food may remain in the stomach for up to four hours. In the glandular stomach the ingesta is acted upon by pepsin which in the acidic environment breaks down proteins into peptones and proteoses. These molecules are not absorbed until they have been further broken down in the intestine. Little food is absorbed from the stomach, but under some conditions small molecules may be. Milk clots in the stomach, aided in newborn mammals particularly by the production of the enzyme rennin.

The secretion of the gastric glands is controlled partly by reflex action, whose neural afferent pathway may be the sight or smell of food or the presence of food in the mouth or stomach itself. In addition the presence of food in the stomach causes the liberation into the blood of a hormone that stimulates secretion of gastric juice.

The Small Intestine

Food passes from the stomach into the intestine in liquid condition (chyme). This passage is controlled by the pyloric sphincter between the stomach and duodenum. The reaction of this region is only faintly acidic, and in addition to enzyme digestion in the intestines, intestinal microflora continue the process of fermentation. Although there are certain distinguishing features of the different parts of the small intestine (duodenum, jejunum and ileum), the food is mixed with the several enzymes responsible for breaking down all the chief classes of foodstuffs and absorption of the products begins along its length. Absorption is either direct into the blood stream, when metabolites pass in the hepatic portal system to the liver, or into the lacteals when the products (mainly the products of digestion of fats) pass indirectly to the bloodstream via the lymphatics. Certain hormones are passed into the blood from the small intestine, although the exact cellular source of some of them is unknown. These hormones influence the functions of the pancreas, gall bladder, intestinal glands and the vasculature.

As the chyme enters the duodenum it is mixed with pancreatic juice, bile from the liver and secretions from the glands of the duodenal wall. The chyme is rendered less acid and its composition is altered rapidly by the digestion process.

In general the small intestine tends to be relatively longer in herbivores than carnivores, presumably associated with fermentation of plant materials. But there are exceptions, as in the carnivorous Elephant Seal and Sperm Whale which have remarkably long intestines.

The Liver and Pancreas

These are large glandular structures whose prominent ducts empty their secretory products into the duodenum. The pancreas has both exocrine and endocrine components. The endocrine function is the production of insulin, important in glucose metabolism.

The secretion of the pancreatic juice, the exocrine component of pancreatic function, is controlled both by nervous and hormonal means. Food present in the duodenum stimulates the production of secretin and pancreozymin by the duodenum and these hormones in turn stimulate the release of pancreatic juice. Parasympathetic (vagal) stimulation also results in pancreatic secretion into the duodenum. Several digestive proenzymes are elaborated by the pancreatic alveoli, the chief derivatives being trypsin, amylase, lipase and the enzyme-like rennin.

The liver is a vital organ with many functions, which may be grouped under four headings: (a) those concerned with metabolism of the food and storage; (b) secretion and excretion; (c) activities concerned with composition of the blood; (d) protective and detoxicating activities. Its cells are primarily digestive in function.

The actions of the hepatic cells on the food depend on the condition of the animal at the time. For example, if amino acids are needed for building the body, they are passed directly into the general circulation to required sites. But in the adult, as a rule more amino acids are taken up from the intestine than are needed for building, and the excess is de-aminated in the liver, the nitrogen being converted to urea which is excreted by the kidney, while the remaining parts of the molecules are available for energy production. Similarly, carbohydrate either may be passed on from the liver or converted into glycogen, in which form it is stored in the liver. Vitamins, particularly A and B, are also stored in the liver, as are enzymes, hormones and fat. Fat is usually stored in a masked form; it can arise from carbohydrates and be transformed into carbohydrates.

The secretory product of the liver is the bile. We may consider the columns of hepatic cells as tubular glands, whose secretory products are released into the bile canaliculi. The latter join to form major bile channels that eventually unite

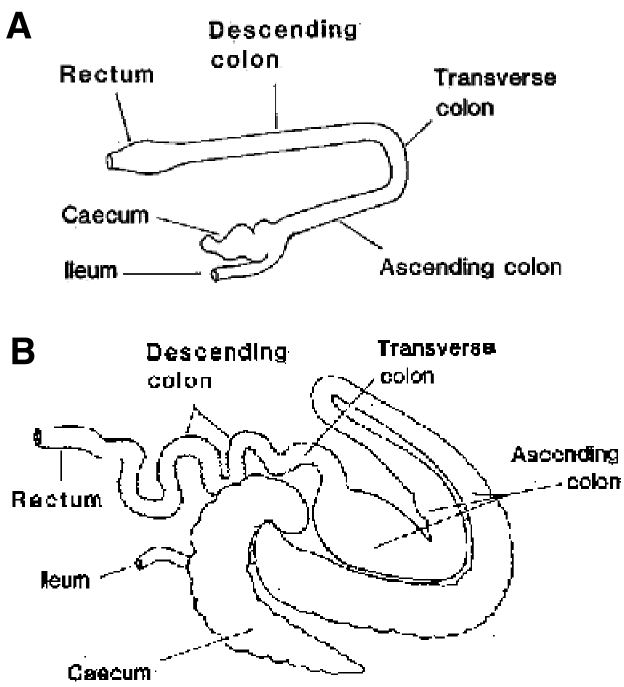


Figure 34.9 The appearance of the large intestine of a carnivore, the dog (A) and a herbivore, the horse (B). The horse has a simple stomach and the very extensive large intestine acts as a fermentation chamber. (© ABRS)
[M. Thompson]

to form the hepatic duct. In some species there is a diverticulum off the main hepatic duct, the cystic duct leading to the gallbladder, but a gallbladder is lacking in the rodents, horses, certain ruminants and Cetacea.

Bile is released from the bile duct (the duct resulting from the joining of the hepatic and cystic ducts) into the duodenum. The bile salts aid in the emulsification of fats during intestinal digestion, thereby rendering the fats vulnerable to the action of lipase, and are reabsorbed in part by the intestine and re-used. Bile pigments, the breakdown products of haemoglobin through the activity of reticulo-endothelial cells, are excreted via the bile duct into the duodenum and eliminated in the faeces. Cholesterol, lecithin and fats also are excreted via the bile.

Many substances that have a pronounced action when introduced into the body, such as alcohol and anaesthetics, are broken down in the liver.

The Large Intestine

The contents of the caecum and colon are nearly neutral and contain many micro-organisms. Their action on the colonic contents, especially on proteins, produces a variety of putrefactive products. In simple-stomached herbivores such as the horse, rabbit and dugong, there are other micro-organisms in this region that play an important part in breaking up refractory foodstuffs, particularly complex carbohydrates, such as cellulose. An important function of the large intestine is the absorption of water from the gut contents.

THE RESPIRATORY SYSTEM

The high energy requirements of a mammal, resulting from the warm-blooded condition and high level of activity, are met ultimately by the oxidation of foodstuffs by oxygen taken in from the atmosphere. The apparatus of the thoracic cavity and respiratory tree ensures that a supply of oxygen from the air is available continually.

An oxygen debt may be accumulated for a short time during powerful muscular effort, but if the tissues are without oxygen for more than a few minutes they become impaired permanently.

Gaseous exchange between the air and the blood occurs in the terminal portions of the respiratory tree, mainly the alveoli. This arrangement is made to function by the enclosure of the lungs in a chamber, the thoracic cavity, whose walls can be expanded by muscular contraction, causing air to be drawn in.

The Nasal Apparatus

The nasal passages (Fig. 34.10) function in olfaction, to moisten and warm the air before it passes to the lungs and to filter dust and other particles from the air. The nasal passages are modified greatly in the totally aquatic mammals that lack olfactory sense and have no special structures for moistening inhaled air. The air inspired immediately above the water surface in these species probably is saturated.

The olfactory function is considered later (see Section on Olfaction). The moistening and warming of the air is accomplished by the extensive, richly vascularised epithelium of the delicate nasal conchae. These are particularly large and intricate in polar mammals. The mucous membrane lining the nasal cavity and covering the conchae is a ciliated, mucus-secreting epithelium to filter out small particles.

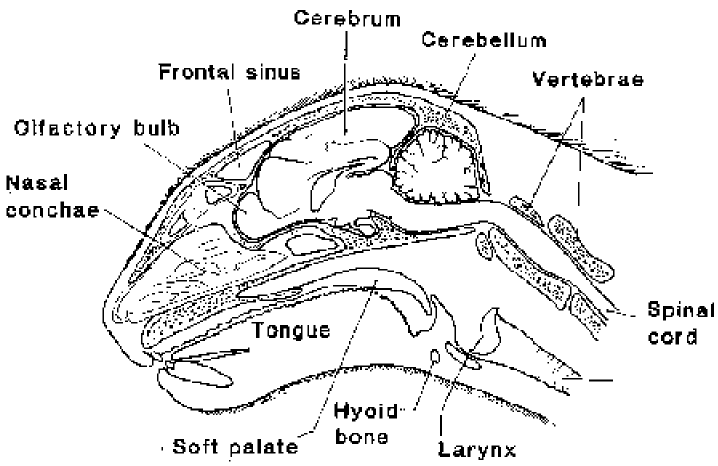


Figure 34.10 Sagittal section through the head of a cat, showing the nasal conchae in the lateral wall of the nasal cavity and related structures. Scale approximates actual size. (© ABRS) [M. Thompson]

A further system of spaces communicates with the nasal cavity, the paranasal sinuses, whose lining mucous membrane is continuous with that of the nasal cavity. The function of these sinuses is not understood fully, but they are particularly well developed in flying vertebrates, the birds and bats, but absent in aquatic mammals.

The Larynx and Phonation

The larynx functions as a vestibule to the trachea, as a valve preventing the entrance of food into the respiratory tree and in phonation. The laryngeal cavity is surrounded by a complex of cartilages. Associated muscles adjust the laryngeal cartilages and open and close the glottis. The entrance to the larynx from the pharynx, the aditus, can be closed by the action of muscles and by folding the epiglottis back over it.

Voice production is accomplished by the presence of a pair of vocal cords. These cords consist of ridges of mucous membrane containing an elastic ligament, stretched across the larynx. The two cords can be set in vibration by the passage of a current of expired air between them and their relative positions are controlled by the action of the intrinsic laryngeal muscles.

Trachea and Lungs

The trachea is continuous with the larynx, and consists of a tube whose walls are supported by incomplete rings of cartilage that prevent collapse during inspiration. At its caudal end the trachea divides into the bronchi. Division of each bronchus occurs and subsequent division leads to the bronchioles, from which a system of irregular alveolar ducts leads to the terminal alveoli. The effect of this branching system of tubes is to allow air to penetrate to every portion of the lung.

The walls of the alveolus are excessively thin. This allows a very close relationship between the air in the alveolus and the blood in the capillaries of the alveolar walls.

The walls of the alveoli and bronchioles contain many elastic fibres, which give them the power to contract during expiration. Thus, expiration is largely a passive process. The walls of the bronchioles also contain unstriated muscle which receives motor innervation from the vagus and inhibitory sympathetic innervation.

The trachea, bronchi and large bronchioles are lined by ciliated cells, which beat in such a way as to transport particulate matter towards the pharynx and protect the respiratory tree.

Respiratory Exchange

Only a partial change of air in the lungs occurs with each breath. The lungs are not emptied completely during each expiration, but much of the alveolar air is swept into the bronchioles and mixed with fresh air at the next inspiration. The gases in the alveoli come into rapid equilibrium with the blood by diffusion across the thin alveolar walls, as oxygen is taken up by the plasma and from this by haemoglobin in the red blood cells, while carbon dioxide is given up to the blood.

Under the conditions in which haemoglobin occurs in the blood, it becomes 95% saturated with oxygen at the partial pressure of oxygen in alveolar air (100 mm mercury). The haemoglobin remains saturated to as much as 80% if the oxygen tension is reduced to 50 mm Hg, but below this tension it begins to give up oxygen. This occurs normally in the capillaries. Here haemoglobin is surrounded by an environment poor in oxygen and it yields its oxygen to the plasma, then through the capillary wall to the tissues. The form of the oxygen dissociation curve depends on the composition of the blood.

The uptake of oxygen in the lungs is often termed external respiration, in contrast to the process of oxidation within the tissues, internal or tissue respiration. Tissue respiration takes place by a system of enzymatic changes, making the oxygen capable of undertaking chemical transformations that would not otherwise occur under these conditions.

Control of Respiration

The regular rhythm of respiration is produced by the action of the respiratory centre in the medulla oblongata. Afferents reach the centre via the vagus nerve from receptors in the walls of the alveoli. Cells in the region of the respiratory centre are sensitive to carbonic acid in the blood. Receptors in the aorta, carotid bodies and atria are sensitive to the pressure and oxygen content of the blood and they influence respiration. Some vagal afferents influence the respiratory centre directly.

There is, thus, an elaborate system of chemical and neural influences acting on the respiratory centre. Other receptors are present that respond to tactile and chemical influences and effect the cough reflex.

THE CIRCULATORY SYSTEM

Mammals possess a closed circulatory system. Blood never leaves the vessels that contain it and, therefore, never comes into direct contact with the cells of the body as occurs in many non-vertebrate animals. The cells of the tissues are bathed in interstitial fluid and the blood serves the tissues by diffusion of materials through the small, thin-walled capillaries. Blood is pumped by the heart, through the arteries to the capillaries, and returns to the heart through the veins.

To maintain a high and constant body temperature, mammals need to transport large quantities of fuel for combustion and oxygen with which to burn it, to the tissues. Circulation needs to be rapid and adjustable to meet the changing needs of the animal; it would be inefficient to maintain a maximum circulation of blood to all parts of the body simultaneously.

Functions

As well as transporting fuel and oxygen to the cells (via the interstitial fluid), circulation is the means by which waste products from combustion are removed from the tissues. The tissues must be supplied constantly with oxygen from the lungs and food materials from the intestine or from storage and manufacturing centres, notably the liver. Waste products must be removed continually, carbon dioxide is taken to the lungs for removal, nitrogenous wastes and excess metabolic water are excreted by the kidneys.

Another important function of the circulation is the maintenance of the steady internal environment necessary to permit efficient functioning of the cells. Uniform composition of the interstitial fluids is maintained by constant circulation of liquid throughout the body. Circulation plays a vital role in the maintenance of a steady body temperature.

The circulatory system aids in the struggle against disease and in the repair of injuries. It carries substances (the hormones) produced in one part of the body that affect others.

Blood is a connective tissue, consisting of cellular components floating freely in a liquid matrix. The fluid fraction is plasma, whose salt content is approximately the same as that of the interstitial fluid. The plasma contains, in addition, the blood proteins albumin, globulin and fibrinogen. These proteins consist of large molecules unable to pass through the capillary walls and whose presence (particularly the albumins) raises the osmotic pressure of the blood above that of the interstitial fluids, a point of importance in capillary function. Fibrinogen makes up only a small percentage of the total blood protein, but it is important when converted to fibrin in blood coagulation. One globulin type takes part in the formation of the blood clot; other specific globulins are sensitive to ‘foreign’ proteins and will, for example, cause the agglutination of red blood cells of another species. Certain globulins are active agents (antibodies) in protection against disease.

The blood cells have various functions, the most obvious is the constant transport of oxygen by the erythrocytes (red blood cells). This is achieved by the presence of haemoglobin, a protein molecule which includes in its complex structure four iron atoms, each capable of carrying an oxygen ion. Haemoglobin is also a factor in the transport of carbon dioxide from the tissues. The structure of the erythrocyte is unusual in mammals. It is round rather than oval (the camel is an exception) and the mature red blood cell lacks a nucleus, a fact that presumably increases the efficiency of oxygen carriage in the total mass of the erythrocytes.

The leukocytes, or white blood cells, are far fewer in number than the erythrocytes. Leukocytes are able to leave the blood stream to play an active role in connective tissues. Two major groups of leukocytes are distinguishable, the agranulocytes and the granulocytes. The common forms of agranulocytes are the lymphocytes, present in all classes of vertebrates, which play an important role in immunological protection of the organism. The other type of agranulocyte, the monocyte, may be merely a large lymphocyte.

The granulocytes include acidophils (eosinophils), basophils and neutrophils. They seem to be essentially inert while in the blood stream, but are capable of amoeboid movement and in this way move out of capillaries between the endothelial cells to accumulate rapidly in injured, inflamed or infected tissues.

A further cellular component of the blood is the thrombocytes (platelets), which take part in the process of blood clotting.

Haematopoiesis

Proliferation and differentiation of blood cells continues throughout life. The life of an individual blood cell is short, a few months at the most in the case of erythrocytes, days or even hours for leukocytes.

In mid-foetal life and almost up to the time of birth, the liver is concerned actively with haematopoiesis. Blood cells also are produced in the foetal spleen, which is actively haematopoietic in the later stages of foetal life. Towards the end of intrauterine life most haematopoietic activity shifts to the red marrow of bones, although the agranulocytes continue to be produced by the spleen and lymph nodes throughout life. Much of the red marrow of the bones is replaced by fatty tissue (yellow marrow) during postnatal life, but in certain regions the cancellous tissue of the bones persists as actively haematopoietic tissue throughout life, particularly the ribs, vertebrae, sternum, skull bones and pelvis. The yellow marrow may be replaced again by red marrow under exceptional circumstances, such as in certain types of anaemia. In extensive destruction of the bone marrow (for example, in myelofibrosis), the liver and spleen may revert to their former haematopoietic functions.

The thymus is a source of rapid production of lymphocytes during late foetal and early postnatal life (see Section on the Lymphoid Organs).

The Heart and Major Vessels

There is complete separation in the mammals of the systemic and pulmonary circulation. By this means, oxygenated blood can be delivered to the capillaries at a far greater pressure than can be achieved in a plan such as that of the fish. There the blood passes first through the gill capillaries before passing to the capillaries of the body, under the influence of a single pressure source in the heart. A particular advantage of the arrangement in mammals is that quick and sustained movements are possible because fuel and oxygen can be transported efficiently to the muscles.

The separation of the systemic and pulmonary circulations has occurred by septation of the heart to form four chambers and concurrent septation of the ventral aorta. The pulmonary trunk, therefore, arises from the right ventricle, and the aorta arises from the left ventricle.

The arteries become progressively smaller as they branch in their peripheral course from the aorta and pulmonary arteries. The sum of the luminal diameters of all branches also increases progressively, so that the rate of blood flow through the peripheral vessels steadily diminishes as they get farther away from the heart.

The structure of the arterial wall varies to a considerable extent in relation to the size of the vessel. In the larger arteries, elastic tissue predominates in the middle coat. The elastic tissue permits them to expand with each cardiac systole and recoil with each diastole, a pulsation which continues to drive the blood peripherally. As the vessels get smaller, the blood flow is converted gradually from an intermittent series of propulsions derived from the rhythmic contraction of the heart to a steady and continuous stream. No pulsation is evident in the capillaries under normal conditions.

The presence of unstriated muscle in the smaller arteries enables them, under the influence of the autonomic nervous system, to contract or dilate and so regulate the distribution of blood to the areas they supply.

Veins commonly run with arteries. Medium arteries often are accompanied by two veins (venae comitantes), although in some parts of the body, the brain for example, there is no close association between arteries and veins. Most veins are characterised by the presence of valves arranged at intervals along their course and so disposed as to direct the blood flow towards the heart. The flow of blood along veins is primarily dependent on a pressure gradient, the pressure decreasing from the periphery to the heart. This is the result of pressure changes related to the cardiac cycle and of the varying negative pressure in the pleural sacs produced by respiration. Muscular action further assists the venous circulation in peripheral vessels (see Section on Muscle Function).

In some regions of the body, particularly the limbs, veins course superficially in addition to the axial veins accompanying the arteries. These superficial veins have no accompanying artery, but anastomose freely with the deeper veins. They serve a thermoregulatory function by permitting heat radiation from the skin surface when they are engorged with blood. Countercurrent heat exchange can occur between the arteries and accompanying veins, serving a heat conservation function.

Supplementary to the venous system is a second series of vessels that returns fluids from the tissues to the heart, the lymphatics. They are not connected with the arteries, but arise from their own capillaries which end blindly. There is, thus, no arterial pressure behind the fluid in the lymphatics and flow in them is sluggish. The intestinal lymphatics (lacteals) are important in the uptake of fats from the intestine.

The lymphatics are most highly developed in tetrapods. The functional explanation is that because the blood circulates at a higher pressure than in fishes, the entrance of tissue fluids into the capillaries is more difficult. The lymphatics offer a relatively low pressure system of drainage into the great veins where the blood pressure is at its lowest.

Regulation of the Circulation

The rate of the heart beat varies greatly among mammals. Larger mammals have a lower rate than smaller ones. It also varies with 'emotional' and other factors, with activity and training. There are receptors in the heart, in the great blood vessels and in the lungs which influence the rate of the heart beat.

Afferent impulses which arise in the aortic body and pass in the vagus result in a lowering of blood pressure by action through a centre in the medulla oblongata. The aortic body is stimulated when the blood pressure is raised. Other receptors, the carotid body and carotid sinus, possess cells sensitive to changes of oxygen and carbon dioxide content of the blood as well as to pressure changes.

In the peripheral circulation, an elaborate system of instructions ensures that each part of the body receives an adequate supply of blood according to its functional state. When any tissue, such as muscle or intestine, becomes active there are corresponding alterations in its blood supply produced through the autonomic nervous system under the overriding control of the central nervous system.

THE URINARY SYSTEM

The major functions of the urinary system are the regulation of the internal environment and the elimination of wastes. Although some products of metabolism such as lactic acid can be used again, others, such as urea, usually

cannot and have to be excreted. This filtration occurs in the kidney in mammals. In the kidney excretory products are transferred from a vascular structure, the glomerulus, to a tube. Water and solutes filter out from the blood flowing through the glomerulus and part of the filtrate is reabsorbed during passage down the tube. Only unwanted water and solutes are excreted. The tube leads to a system of ducts that eventually passes to a storage organ, the urinary bladder and from there to the body surface.

The Kidney

The structure of the kidney (Fig 34.11) is similar in all mammals, even though there is considerable variation in its external morphology. The basic excretory unit is the nephron, consisting of a spherical renal corpuscle and a complex tubule which empties into the duct system.

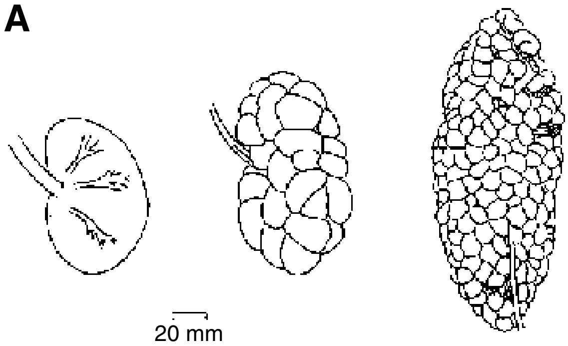
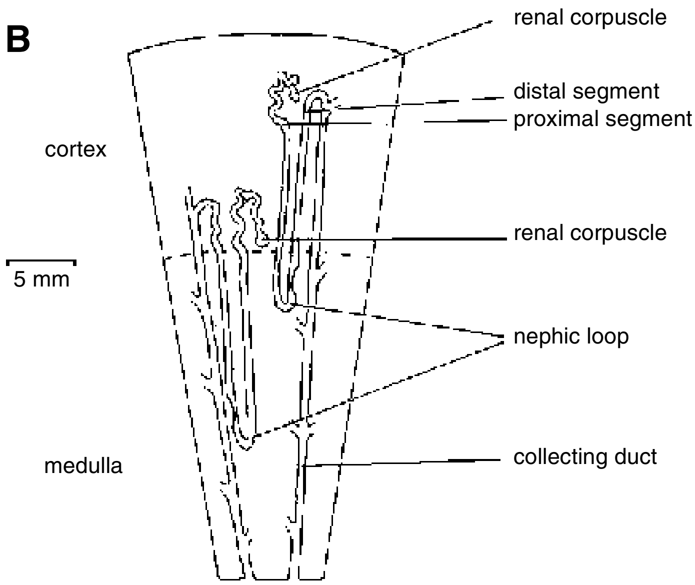
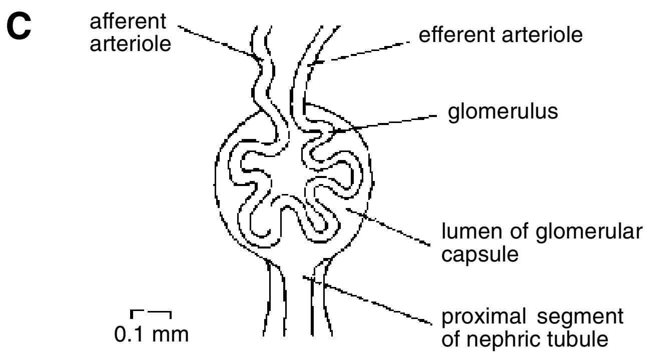


Figure 34.11 **A**, Diagrams of the kidney of a cat, ox and dolphin;
B, diagrammatic representation of two nephrons, draining into the collecting ducts;
C, diagrammatic representation of a renal corpuscle.
(© ABRS) [B. Scott]





The renal corpuscle consists of two parts, a glomerulus and a glomerular capsule. The glomerulus is a compact cluster of small blood vessels; the capsule is a proximal part of the tubule, whose shape is that of a double-layered hemisphere. The inner part is closely adherent to the vessels of the glomerulus, so that only thin membranes separate the blood stream from the lumen between the two parts of the capsule. This lumen is continuous with that of the renal tubule, a long structure with distinguishable proximal and distal segments. Along its course the tubule is bordered closely by a network of capillary vessels. Groups of cells adjacent to the glomerulus, referred to as the juxtaglomerular cells, produce the hormone renin, which raises arterial blood pressure.

Filtration and Reabsorption

The result of the activity of the renal corpuscle and the renal tubule is the production of urine. Urine is composed mainly of water, but contains to a variable degree other substances in solution. These include salt ions, particularly sodium, potassium, chloride and sulphate, and waste materials, mainly simple nitrogenous compounds generally in the form of urea.

The cells of the body require among other things an environment containing, in solution in the interstitial fluids surrounding them, appropriate amounts and proportions of specific simple salts. The maintenance of proper salt content in body fluids demands a proper balance between intake and output. The renal tubules furnish the main means of eliminating excess salts, or of removing excess amounts of liquid which tend to dilute the body fluid.

As blood flows through the glomerulus under pressure, a filtrate of it passes through the internal part of the renal capsule into the capsular lumen. Apart from blood cells and large molecules such as the blood proteins, all other materials including food materials such as glucose as well as wastes, pass readily through into the capsular lumen. The amount of fluid filtered is excessive. During passage of this filtrate along the renal tubule, the volume is reduced greatly and the composition changes as a result of reabsorption. Most of the water is reabsorbed and food materials (mainly glucose) are withdrawn in the proximal part of the tubule. Salt is reabsorbed more distally. Further active secretion of waste substances occurs through the tubule cells into the urine.

Ureter and Bladder

The ureter and bladder have a muscular wall and a characteristic lining epithelium, the transitional epithelium. This type of epithelium presumably permits a considerable increase in area when stretched, especially in the wall of the bladder. The bladder has thick coats of unstriated muscle. Continual rhythmical peristaltic contractions force the passage of urine along the ureters into the bladder. The terminal portion passes obliquely through the bladder wall and acts as a sphincter to prevent reflux. The proximal end of the ureter is expanded to form the pelvis in some, but not all, mammals and portions of it abut against the kidney parenchyma to form the calyces. The renal collecting ducts open into them.

The muscle fibres in the bladder wall run in many directions and are able, like other unstriated muscle fibres, to adjust their length so that with distension of the organ the pressure increases only slightly.

As the bladder fills with urine, receptors in the wall are stimulated and ultimately by reflex action they produce the rhythmical contractions of the muscle which, together with relaxation of the sphincters of the urethra, lead to micturition. The muscle is controlled by autonomic nerves, parasympathetic

stimulation resulting in contraction of the bladder muscle and relaxation of the sphincter; sympathetic stimulation has the opposite effects. Striated muscle in the urogenital diaphragm serves as a sphincter under voluntary control.

Control of Excretion

The secretion of the adrenal cortex is necessary for the absorption of salts from the renal tubules. The amount of water reabsorbed is controlled largely by the influence of antidiuretic hormone (ADH) secreted by the neurohypophysis (posterior pituitary). The release of ADH is under the control of the hypothalamus, in which there are receptors sensitive to the degree of dilution of the blood. Excretory control is complex and is influenced by many other endocrine and metabolic factors.

THE REPRODUCTIVE SYSTEM

The reproductive system includes the ovary and testis that produce the gametes, the ducts by which the gametes are carried to the exterior and the copulatory organs which aid in internal fertilization of the eggs. Important to the reproductive process are the secondary sexual characters which provide signals to ensure that the sexes meet and pair, the mammary glands and special behaviour mechanisms for the care of the young. The whole reproductive system is coordinated by an elaborate system of chemical communication, centred upon the hypothalamo-hypophyseal axis.

The Male Reproductive System

The testis of mammals is peculiar in that in nearly all species it descends into the scrotal sac. In some mammals, particularly many rodents, the testes descend into the scrotum during the reproductive period, but are withdrawn into the abdominal cavity at other times by the action of the external cremaster muscle. In other mammals (testiconda) the testes are retained permanently in the body cavity. Some placental mammals appear to have been always testicond, whereas others may have returned secondarily to this condition.

The testis consists of a number of long, convoluted seminiferous tubules whose walls produce the spermatozoa. Throughout spermatogenesis the formative germ cells remain attached to the nutritive Sertoli cells. The testis is subject to seasonal change, which in seasonal breeders may involve the cessation of spermatogenesis during non-breeding, but it generally does not exhibit such marked differences between breeding and resting stages as does the ovary.

Between the seminiferous tubules of the testis there is a considerable amount of connective tissue in which are found collections of interstitial cells that produce testosterone.

Spermatogenesis is a cyclic phenomenon in most vertebrates, but the seminiferous tubules are permanent structures that produce successive crops of spermatozoa and in most species change little throughout the breeding life of the individual.

The spermatozoa of different mammals differ markedly in morphological details, but all have a head bearing the nucleus and acrosome and a flagellum (tail) consisting of a connecting piece and intermediate, principal and terminal parts.

The scrotum is derived from the scrotal sacs, paired pouches in the floor of the abdominal cavity lined with coelomic mesothelium. In eutherian mammals the sacs fuse ventro-caudal to the penis to form the scrotum.

The spermatozoa are carried away by a system of tubes derived from the mesonephric ducts. The seminiferous tubules open into the rete testis, from which the spermatozoa pass into the efferent ducts, the first part of the long, coiled epididymis. The morphologically mature sperms become functionally mature in the epididymis. The tail of the epididymis is continuous with the ductus deferens, a muscular tube that ascends through the inguinal canal and curves medially within the pelvic cavity to open into the urethra, but just before doing so its expanded end, the ampulla, is joined by the duct from the seminal vesicle. The combined duct thus formed, the ejaculatory duct, pierces the prostate before opening into the urethra. Paired bulbo-urethral glands open into the urethra below the urogenital diaphragm. The secretions of all these glands are mixed with the spermatozoa during ejaculation and among other functions serve to activate and nourish the sperms. Not all the accessory sex glands named above are present in all mammals and others, notably the rodents, have other accessory sex glands.

The penis consists of a tube containing three vascular erectile columns, the corpora cavernosa, one on each side, and the corpus spongiosum ventrally. The terminal part of the urethra is surrounded by the corpus spongiosum. Each corpus cavernosum is attached to the ischium of the same side. Erection is produced by relaxation of the walls of the arteries that lead to spaces in the erectile tissues so that they become engorged with blood.

The Female Reproductive System

The female genital tract of the mammal is built on the plan of other vertebrates, being derived from a pair of paramesonephric ducts leading from the coelom to the exterior.

The ovaries develop from the embryonic gonads. At the indifferent stage a series of primary sex cords is formed. These persist in the testis to form the convoluted seminiferous tubules, but degenerate in the developing ovary to be replaced by secondary sex cords. The germ cells contained in these secondary sex cords divide repeatedly and develop eventually by the complex process of oogenesis into definitive oocytes. Each oocyte becomes surrounded by a cluster of other cells derived from the sex cords to form a follicle, which is the major organ of oestrogen production. As maturity is approached the follicle enlarges and develops a liquid-filled space in its interior.

Follicles ripen at the surface of the ovary, continuously in some mammals, but seasonally in others, and burst, releasing the oocyte into the surrounding coelom. This is the process of ovulation. The oocyte is then taken up by the genital tract. The follicular cavity that remains becomes filled with a yellow cellular mass, the corpus luteum, which secretes progesterone. Many more oocytes are present in the ovary than are released by ovulation; a large proportion fail to reach maturity and degenerate.

The ovaries are usually paired, but one or the other fails to reach full maturity in some species.

Since the mammalian ova are small, the upper part of the female genital tract, the uterine tube, is a slender structure. The portion that receives the oocyte from the coelom is enlarged to form a funnel-shaped end, the infundibulum. This bears finger-like processes (fimbria), and a ciliated epithelium, the action of both of which aid in directing the oocyte, surrounded by cells from the follicle, into the genital tract. Fertilization usually occurs in the upper portion of the uterine tube.

The uterus is a thick-walled muscular structure within which prenatal development occurs. The uterine mucosa or endometrium, a vascular epithelium, is relatively thin during resting phases, but is thickened greatly at

times of reproductive activity. Its rhythms of growth and involution are controlled by ovarian hormones. In the most primitive mammalian situation the two uteri are separate and known as uterus duplex. This condition is present in many rodents and bats. In most eutherians, however, the more caudal parts of the two uteri are fused to a greater or lesser extent to form a bicornuate uterus and in higher primates there is complete fusion to form a uterus simplex. The caudal end of the uterus narrows to form a thick-walled canal, the cervix, which may be paired (uterus duplex) or single (bicornuate uterus and uterus simplex). The whole uterus lies in a fold of peritoneum, the broad ligament.

The terminal portions of the two paramesonephric ducts invariably are fused in eutherians to form a vagina. This opens into the urogenital sinus, which in many species appears like a continuation of the vagina. The exterior opening is protected by the labia which enclose the major derivative of the urogenital sinus, the vestibule. The urethra opens into the vestibule, as do the ducts of the major vestibular glands. Ventrally in the vestibule is the clitoris, which contains paired erectile corpora cavernosa as in the penis. Paired, erectile vestibular bulbs are present in the labia.

The Placenta and Fetal Membranes

The placenta which affords maternal nourishment of the developing embryo and fetus, is formed by a union of the uterine mucosa with the fetal membranes. The latter include the chorion, amnion and allantois, but the involvement of these in the formation of the placenta varies greatly and influences to some extent the type of placentation that occurs. The yolk sac plays a part in development of the placenta in some species as well.

As the early conceptus (blastocyst) grows it may lie free in the uterine lumen, the entire surface of its trophoblast in contact with the uterine mucosa. In other species the blastocyst remains attached only at the site of first contact, leaving a free surface projecting into the uterine lumen. In others, including man, the blastocyst is buried in the uterine mucosa and becomes surrounded by maternal tissues.

Intimate contact between part or all of the surface of the trophoblast with the uterine mucosa early in prenatal life results in the development of the placenta. On the embryonic side, blood vessels that develop in the chorion (that is, the trophoblast plus its associated extraembryonic mesoderm) connect with embryonic vessels by contact with the wall either of the yolk sac or the allantois.

Certain areas of the surface of the trophoblast develop villi, which penetrate into the uterine mucosa, thus increasing the absorptive surface of the chorion and providing intimate contact between the fetal and maternal tissues. In some species, for example perissodactyls and the Pig, there develops a diffuse placenta in which the chorionic villi are distributed nearly evenly over the surface of the chorion. In a placenta multiplex (cotyledonary placenta) as seen in ruminants, the chorionic villi are grouped in numerous patches, the cotyledons, which are separated by smooth chorion. Carnivores have a zonary placenta: the villi are restricted to a band around the middle of the chorionic sac. A discoidal placenta forms in primates, rodents and other species, where the villi are limited to a disc-shaped area on the chorion.

The closeness of contact between the fetal and uterine parts of the placenta varies in different eutherian groups. With the outgrowth of villi from the surface of the chorion, corresponding crypt-like depressions develop in the uterine placenta into which the villi become embedded. The most superficial cell layers of the uterine mucosa are destroyed by specific activity of the trophoblastic cells and the nutrients thus freed (histotroph) conveyed to the embryo. This process is particularly marked in some species and reduces the tissue remaining between the uterine and fetal capillaries of the placenta. The number of layers remaining

between the two circulations has been used in a histophysiological classification of placentas. Thus, there occur epitheliochorial, syndesmochorial, endotheliochorial, haemochorial and haemoendothelial types of placentas.

A further classification of placentas is based on the loss of uterine mucosa (decidua) at the time of parturition. With deciduate placentas (carnivores, primates and others) there is loss of uterine mucosa at birth because of a more intimate fusion of fetal and maternal tissues. In the simplest non-deciduate placentas (horses, pigs, ruminants), maternal and fetal parts are merely in apposition and little or no maternal tissue is lost.

Control of Reproduction

Coupling of males and females is ensured by an elaborate system of signals, receptors and effector mechanisms. The mutual attraction of males and females for the purpose of mating is brought about largely by olfactory signals in many mammals, but visual signals also play a large part and in some species auditory signals are involved. Some of the secondary sexual characters serve to provide signs for recognition and attraction.

Mating behaviour is influenced by the internal condition of the individual, mainly by the action of the endocrine system on the nervous system. Seasonally breeding mammals are sensitised by the hormones at certain times of the year, associated with environmental changes such as alteration of day length, so that they respond to stimulation by the secondary sexual characters of the opposite sex.

The production of the gametes, both oocytes and spermatozoa, is under intricate and finely-balanced hormonal control. Three protein hormones secreted by the adenohypophysis under hypothalamic control, the gonadotropins, regulate ovarian functions. Follicle stimulating hormone (FSH) causes ovarian follicles to grow and produce increased amounts of oestrogens. Luteinizing hormone (LH) causes ovulation and initiates the formation of the corpus luteum. Prolactin may have a luteotropic function in some species. The ovary is capable of producing oestrogens from cells surrounding the follicles and progesterone from the corpus luteum. A third hormone, relaxin, may be produced by the ovary also.

The oestrogens produce oestrus. Small amounts of progesterone may also play a role in the induction of oestrus in some species. The oestrogenic hormones control the development of all the female secondary sex characteristics and play a major role in development of the mammary gland. They also have major roles in modifying production and rates of release of hypophyseal gonadotropins.

Progesterone is the most important hormone of pregnancy. Implantation cannot occur in its absence; it acts synergistically with oestrogens to develop the uterine glands characteristic of the oestrous cycle and early pregnancy. Progesterone plays a vital role in maintaining pregnancy. The placenta produces some progesterone, in some species sufficient to maintain pregnancy in its latter stages in the absence of corpora lutea. This hormone is believed to be responsible for inhibiting ovulation during pregnancy and pseudopregnancy.

The factors responsible for the initiation of parturition are not understood fully. Parturition is controlled both by hormonal influences and the degree of distension of the uterus. A constant relationship exists among litter-bearing animals between the size of the uterus and the total size of its contents, despite variations in litter size and the size of individuals making up the litter. A remarkable series of hormonal changes occurs prior to and during parturition and, although there seems to be variation among species, in general these changes include a rise or fall (depending on the species) of plasma progesterone and oestrogen and a rise in prolactin and corticoids. Relaxin concentration

remains high until after parturition, but LH remains consistently low or is absent. The rise or fall of progesterone is accompanied by a reciprocal fall or rise in oestrogens.

Implicated in triggering these abrupt hormonal changes, at least in certain species, is an increased output of fetal adrenal corticoids in response to increased release of adrenocorticotrophic hormone (ACTH) from the foetal adenohypophysis. Prostaglandins and oxytocin seem to act directly on the uterine tunica muscularis (myometrium). Uterine contractions may be initiated by prostaglandins and continued by the action of oxytocin during parturition.

Androgen secretion by the interstitial cells of the testis is controlled by the adenohypophysis, the hormone LH is the primary one involved. In addition, FSH stimulates the production by the Sertoli cells of an androgen-binding protein that is secreted into the testicular fluid. Prolactin also appears to have a synergistic effect with LH in maintaining testosterone production. Spermatogenesis and spermiogenesis in the seminiferous tubules are controlled by the gonadotropic hormones FSH and LH, either directly or indirectly, because normal spermatogenesis can no longer occur after hypophysectomy.

In most mammals, testicular temperature remains several degrees below body temperature. The scrotum helps to regulate testicular temperature, important in the production of viable sperm, by two specialised mechanisms. The blood entering the testis in the long, coiled testicular artery is precooled by countercurrent heat exchange with the cooler venous blood returning in the pampiniform plexus. Temperature is regulated to some degree by contraction and relaxation of the striated external cremaster muscle and the unstriated muscle in the scrotal wall that constitutes the dartos. Exposure to cold results in these muscles drawing the testis closer to the body wall where the temperature is higher.

The accessory sex glands of the male are all dependent upon androgen for their normal functioning. Androgen also is responsible for the secondary sex characters in the male.

THE NERVOUS SYSTEM

There is an elaborate system of receptors from which information about the environment is transmitted to the spinal cord and brain. New information is combined with information stored there and translated into action by effector organs, especially the muscles. The nervous system, therefore, is the main agent regulating activity, its actions control almost every aspect of mammalian behaviour.

The nervous system in vertebrates arises from a well-organised dorsal tubular structure that enlarges cranially to form the brain. The remainder develops to form the spinal cord. These constitute the central nervous system. Running outward from the spinal cord and brain are numerous paired nerves along which occur clusters of nerve cells forming ganglia in specific regions. These nerves and ganglia constitute the peripheral nervous system.

The functional cellular units of the nervous system are the neurons, large cells that reside in the central nervous system and the ganglia, with long processes, the nerve fibres. The fibres include the dendrites which receive signals from the environment or from other neurons and transport them to the cell body and the axons that carry signals away from the cell body. Neurons differ greatly in shape, especially in the length of the dendrites and axons and their method of branching. The neurons are able to conduct impulses because they have the capacity to give discharges that serve as signals. This capacity depends on the fact that the surfaces of the cells are electrically-charged systems that are sensitive and readily discharge when a small change occurs near them. The

setting up of the charge by the cell depends upon chemical processes involving expenditure of energy and the discharge is probably initiated by molecular changes at the surface followed by movements of ions. These movements set up electrical currents that initiate discharge of neighbouring parts of the nerve fibre and thus make possible the transmission of signals.

The chemicals involved in the transmission process originate in the body of the neuron and flow outward to supply the various processes.

Nerve cells that are destroyed during postnatal life are not replaced, although the fibres may regenerate if the cell body remains intact.

Functionally, the most important part of a major nerve fibre is the neuronal process itself, the axis cylinder. This is wrapped almost always by a series of cells which form the neurolemma. These cells are capable of producing a myelin sheath of fatty material surrounding the fibre.

The distance between the sensory organ (receptor) and a muscle or glandular structure stimulated (effector) is never spanned by a single neuron in mammals. The action takes place through a chain of neurons, at least two and usually more. The point of transfer between one neuron and the next is the synapse. Minute amounts of chemical material are produced at the terminal branches of the axon and diffuse across to stimulate the dendrite of the second neuron. The chemical substance most generally concerned is acetylcholine, but there are many transmitter substances, some known, some unknown. This is currently an area of very active research.

The simplest nerve action is the reflex arc, the type of ‘automatic’ reaction such as the withdrawal of a paw that has touched a very hot object. A sensory stimulus is picked up from receptor cells and carried toward the central nervous system by a long dendrite that constitutes the afferent fibre. The cell body of the sensory neuron to which this fibre belongs lies in the dorsal root ganglion, at the level of the intervertebral foramen. The afferent fibre is continued as the axon of the neuron from the cell body to the central nervous system. Normally it does not synapse on a single successive neuron, but branches so that a stimulus may be produced in a whole series of neurons. Conversely, each neuron with which it connects may receive impulses from numerous afferent fibres, so that considerable interplay between receptors and effectors may take place. In this simplest reflex the neurons stimulated by incoming impulses may be efferent, usually motor neurons. Their cell bodies lie within the central nervous system and long axons run from them to the effector organs (usually muscle fibres). But even a simple reflex arc is slightly more complex than this and is a three-neuron rather than a two-neuron chain. The afferent fibres entering the central nervous system synapse with neurons contained entirely within the central nervous system. These internuncial neurons send out branched axons that synapse with numerous motor (efferent) cells. This further multiplies the number of possible responses which a sensory impulse may cause and, conversely, also increases the number of sensory impulses which might produce any given motor effect. In this case the effect on the motor neuron may be inhibitory rather than stimulatory, tending to counter stimuli this cell may have received from other sources. Even at this relatively simple level of nervous activity, there are ‘feedback’ mechanisms which increase complexity.

Spinal and Cranial Nerves

The so-called peripheral nervous system, which includes the spinal and cranial nerves, penetrates to almost every region of the body.

Typical spinal nerves are paired and present in every body segment. Each nerve arises from the spinal cord by dorsal and ventral roots which unite and leave the vertebral canal as the spinal nerve before dividing into dorsal and ventral rami.

The spinal nerve and its rami carry both afferent and efferent fibres, but the two roots show a sharp division of function. The ventral roots convey mainly efferent impulses and, therefore, are mainly motor, while the dorsal roots carry afferent fibres and thus are sensory. The cell bodies of the latter neurons generally lie in the dorsal root ganglion.

Although the cranial nerves lack the regular arrangement of the spinal nerves, they subserve similar functions and convey afferent impulses from the head and neck (and from the trunk in the case of the vagus), as well as efferent impulses to the muscles of the head, neck and in one case (the trapezius) the back. Unlike the spinal nerves, however, the cranial nerves do not all carry all components. The first, second and eighth cranial nerves are special sensory nerves consisting only of afferent fibres conveying to the central nervous system information only about smell, sight and hearing and balance, respectively.

The processes of peripheral nerves grow out from the central nervous system or the ganglion and reach their end organs: sensory structures, muscle fibres or gland cells. Although there is a degree of specific association in that efferent fibres do not attach to sensory structures nor afferent fibres to muscle cells, there are no specific affinities. That is, a particular nerve will not always attach to a given end organ.

Both afferent and efferent fibres can be divided functionally into two types, somatic and visceral. Somatic afferents carry impulses from the skin (exteroceptive) and sense organs of muscles and tendons (proprioceptive) to the central nervous system, whereas visceral afferents carry sensations from sensory endings in the internal organs (enteroceptive). Somatic efferents are the motor fibres to the striated muscles, while visceral efferents carry stimuli primarily to the unstriated muscles and glands in various regions. These four components are present in most spinal nerves, but this is not true of some cranial nerves. The special somatic afferents have been mentioned above.

The Autonomic Nervous System

Whereas the somatic part of the nervous system controls those organs of the body in contact with the outside world, the autonomic nervous system controls the internal workings of the body. Nonetheless, these outer (somatic) and inner (visceral) components of the nervous system work together in a coordinated way. When, for example, the muscles of the trunk and limbs are activated by the somatic nervous system, the autonomic system influences the heart and blood vessels to adjust the flow of blood to the muscles. In this way, it ensures that sufficient oxygen and fuel are carried in the blood to the muscles to permit their increased activity.

Sensory endings are present in the internal organs and blood vessels. Visceral afferent fibres pass from these to the central nervous system through autonomic nerves of either the sympathetic or the parasympathetic system.

The autonomic impulses which pass to the unstriated muscles and glands of the body are carried from the central nervous system along a two-neuron chain of efferent fibres, the visceral efferents. The first neuron, termed the preganglionic neuron, has its cell body in the central nervous system and its axon is typically myelinated. At some point along its course it enters a ganglion of the autonomic nervous system, where it synapses on a postganglionic neuron whose axon completes the passage to the end organ.

The autonomic nervous system comprises the sympathetic and parasympathetic systems, which to a large extent are distinguished anatomically, physiologically and pharmacologically. Preganglionic outflow of the sympathetic system is confined to the thoracic and lumbar parts of the spinal cord. Sympathetic stimulation tends to increase the activity of the animal, speed up the rate of heart

beating and increase the circulation, slow down digestive processes and, in general, make it fit for 'fright, flight or fight'. The tips of the nerve fibres release noradrenalin and adrenalin.

Preganglionic outflow of the parasympathetic system is from the brain and via certain cranial nerves (particularly the vagus) and the sacral part of the spinal cord. The action of the parasympathetic system tends to slow down the activity of an animal in general but promotes digestion and a relative rest phase. The fibres release acetylcholine at their ends.

The Spinal Cord

The spinal cord contains, as it did in the embryo, a central canal containing fluid, but in contrast to the embryonic structure it is relatively small in the adult, owing to the growth of nervous tissue surrounding it. The spinal cord is shorter than the vertebral column in mammals, so that in the caudal part of the vertebral canal there is merely a series of nerves passing caudally from cord segments to the corresponding intervertebral foramina.

Two distinct layers can be distinguished (even with the naked eye) in the cord, a central area of grey matter surrounding the central canal and white matter surrounding the grey matter.

The grey matter consists mainly of cell bodies of neurons, arranged into an H-shape. The dorsal and ventral projections of the 'H' are termed the dorsal and ventral horns, respectively. Cell bodies of the efferent (motor) neurons of the spinal nerves are present in the ventral horns. Their axons typically pass out in the ventral roots of successive spinal nerves. Most of the motor supply is to somatic muscles, but in the thoracic and lumbar parts of the cord preganglionic sympathetic efferents are situated dorsolateral to the somatic motor neurons in a lateral horn.

The dorsal horn is associated with the dorsal, sensory roots of the spinal nerves. Here is the seat of the cell bodies of association neurons through which afferent impulses brought in from sense organs may be relayed and distributed.

The white matter is composed of myelinated fibres, including ascending and descending fibres of sensory nerve cells, fibres which carry sensory stimuli cranially to the brain and fibres returning from brain centres to act on motor neurons. Topographically, the white matter is subdivided into dorsal, lateral and ventral funiculi, in which are found relatively discrete fibre tracts which carry information up and down the spinal cord.

The Brain

There is a considerable degree of concentration of command over bodily functions in the brain of mammals. Intermediate neurons connecting the spinal cord with the brain tend to gather in functional centres (nuclei) in many parts of the brain and fibres with like connections tend to assemble into definite bundles (tracts). The nuclei range in size from microscopic clusters of cells to the entire cerebral cortex. In the nuclei afferent impulses may be correlated and integrated for appropriate responses or motor mechanisms coordinated. At higher levels there may develop association centres whose activities are responsible for such phenomena as memory, learning and consciousness.

A primitive system persists in mammals in the form of the reticular formation. Rather than discrete nuclei and tracts, this is a band of interlacing cells and fibres associated with the motor columns of the brain stem and cranial spinal cord. It is important in motor coordination and in carrying stimuli down from

higher brain centres to the motor centres of the medulla oblongata and the spinal cord. It also acts as an agent which tends to promote activation of the higher centres of the cerebral cortex.

The brain is largely bilaterally symmetrical and, therefore, cross connections are necessary. These occur in commissures, fibre tracts which connect corresponding regions of the two sides, and decussations of tracts.

In general, the complexity of the brain increases from caudal to rostral regions. The medulla oblongata and, to a lesser extent, the pons are structurally somewhat similar to the spinal cord, with a series of nuclei of grey matter reminiscent of the grey horns of the cord, but their gross appearance is different. Dorsally, the central canal is greatly expanded to form the fourth ventricle, the roof of which is thin and membranous. Rostrally, it is covered by the cerebellum. The series of nuclei of the somatic motor column breaks down in the pons and midbrain into several small nuclei related to movements of the eyes.

The series of motor and sensory nuclei of the medulla oblongata provide all the elements required for reflex circuits in the brain for the head region, with the exception of most of the special senses. In mammals, acoustic nuclei persist as distinct centres for the vestibular and cochlear parts of the ear in the brain stem at about the level of junction of the pons and medulla oblongata, in the region of the acoustico-lateralis area of more primitive vertebrates.

The cerebellum, a large structure in mammals (particularly man), functions in the coordination and regulation of motor activities and the maintenance of posture. It acts in a passive, essentially reflex fashion in the maintenance of equilibrium and body orientation. In addition, it plays a major positive role in locomotion. Associated with these functions are the large, paired, convoluted cerebellar hemispheres which make up much of the bulk of the organ in mammals.

The midbrain and diencephalon (Fig. 34.12) show specialised functional features in mammals as in other vertebrates. Sensory and motor nuclei of more posterior origin extend some distance into the midbrain, but such structures are absent in the rostral midbrain and diencephalon. In general, the rostral brain stem centres have no direct connections outside the central nervous system other than via the optic nerve. The region of the midbrain and diencephalon, particularly the latter, is a principal relay station between lower brain areas and the cerebrum. Most auditory and other somatic sensations that reach the midbrain are relayed by way of the thalamus to the cerebrum.

The tectum (roof) of the midbrain serves in a limited way as a centre for visual and auditory reflexes.

The tegmentum, the region of the midbrain between the tectum and the crus cerebri on each side, is essentially a rostral continuation of the motor areas of the pons and medulla oblongata. As such, it functions as a region in which varied stimuli from the diencephalon, tectum and cerebellum are coordinated and transmitted to the motor nuclei of the pons, medulla and spinal cord.

The main importance of the hypothalamus is as a major integrative centre for visceral functions. It has fibre connections with the autonomic centres of the brain stem and cord. Stimuli from olfactory and taste organs as well as sensations from various visceral structures pass to hypothalamic nuclei. The hypothalamus controls the activity of the hypophysis to a considerable degree and some hypothalamic nuclei secrete hormones which pass to the hypophysis. Functions such as thermoregulation, heart beat, respiratory rate, blood pressure, sleep and gut activities are controlled or influenced by the hypothalamus.

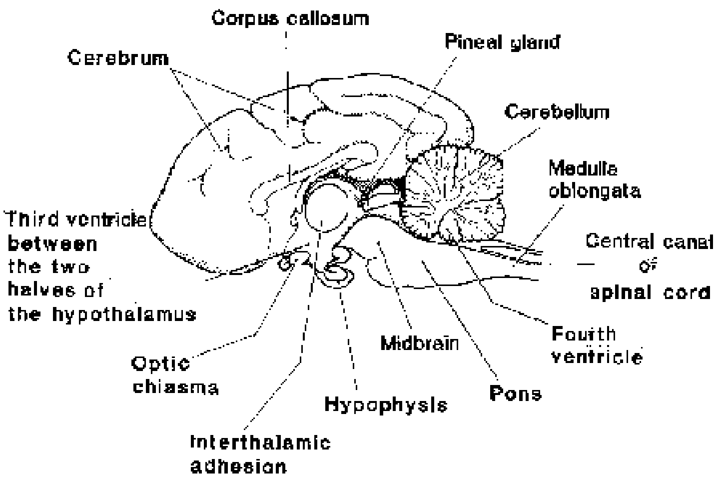


Figure 34.12 Medial view of a hemisected dog's brain. The thalamus and hypothalamus together make up most of the diencephalon. Scale approximates actual size.(© ABRS) [M. Thompson]

All sensory material (except olfaction) is relayed to the cerebral cortex via the dorsal thalamus. Other areas of the thalamus are associated with coordination of muscle function.

Much of the cerebrum of mammals is represented by the neopallium, a greatly expanded cortical area for correlation, association and learning. This area assumes the greater part of the higher functions that in lower forms are concentrated in the tectum or corpus striatum, gains a complete array of somatic sensory information through projection fibres from the thalamus and develops direct motor paths to the motor columns of the brain stem and spinal cord. A massive commissure, the corpus callosum, connects the left and right neopallial structures, permitting both hemispheres to share memory and learning. The surface of the neopallium of eutherian mammals is thrown into folds (gyri), between which are grooves (sulci).

Supporting Elements of the Nervous System

Most of this Section on the nervous system has dealt with the neural elements of the nervous system, although the sheaths of nerve fibres have been mentioned. Other types of cells and other structures are developed as part of the nervous system to support the functioning units, the neurons.

In the central nervous system, cells known collectively as neuroglia serve to protect and support the neural elements. In the ganglia, satellite cells perform a similar function.

The brain and spinal cord, enclosed within the brain case and the vertebral canal, are wrapped by the meninges. These are the outer dura mater that lines the bony cavities, the arachnoid mater and the inner pia mater, the latter two separated by a fluid-filled subarachnoid space.

The mammalian nervous system develops as a hollow tube and this tubular arrangement persists in the adult. Within the brain are the ventricles (two lateral, third and fourth) and in the spinal cord a central canal. A clear liquid, the cerebrospinal fluid, is formed in the ventricles. It passes into the central canal and also through the foramina in the roof of the fourth ventricle into the subarachnoid space, where it is reabsorbed into the venous system. The cerebrospinal fluid is produced by special vascular structures, the choroid plexuses, that project into the ventricles. The membranes of the choroid

plexuses and cerebral vessels serve as a barrier against introduction of foreign materials into the central nervous tissues. The cerebrospinal fluid further serves as a water-bed suspending brain and cord and protecting them from injury.

THE SPECIAL SENSES

Sense organs, which occur in various parts of the body, function to measure either the intensity or the extent of change of conditions. The eye measures intensity of light and its wave-length and also the distribution of patterns of change of light intensity, enabling the body to react to shapes. The skin measures mechanical movement and the ear is also a mechanoreceptor, able to detect the minute air movements we call sounds. The nose and tongue measure chemical concentrations, the skin measures temperature, and the vestibular apparatus measures changes in the position and orientation of the head. Although these various sense organs measure these changes of conditions, they do not have the capacity to interpret them. Reception of such information is of no value to the animal unless there is some channel of communication between the receptor and the organs (muscles or glands) which should make the appropriate response. Such communication may be made by hormonal action, but in general it is made by the nervous system.

The Eye and Vision

Eyes operate by translating a change in the incident radiation into nerve impulses in the fibres of the optic tract. These are then analysed by the brain to produce appropriate reactions.

There are marked differences between the eyes and their neural connections of different mammals according to the type of information required. Nocturnal animals, for example, require a high sensitivity which would be a distinct disadvantage in very strong light. With few exceptions, however, the basic plan of the eyeball is similar among species. The eyeball is roughly spherical. It is situated in the orbit and connected with the brain by a structure referred to as the optic nerve, which is really a tract. Internally, there is a set of chambers filled with watery or gelatinous fluids and toward the front of the eyeball lies the lens. The walls of the eyeball are formed of three layers: the inner retina, the choroid and the outer sclera. The retina includes the sensory part of the eye system where visual stimuli are received and transferred to the brain via the optic nerve. The scleroid coat is modified rostrally to form the transparent cornea. The outer layer of the retina is fused with the choroid and in most parts is pigmented heavily. The pigment is black over much of the extent of the eyeball, but in many species portions of it are coloured and act as a reflecting surface, the tapetum. Opposite the margins of the lens, the conjoined layers of retina and choroid expand to form the ciliary body from which the lens is suspended. Rostral to this, these layers curve inward parallel to the lens to form the iris, which is incomplete centrally. The resulting central opening is the pupil.

The cornea and lens focus the light upon the retina, which receives the image and transmits it to the brain. The iris acts as a diaphragm, under sympathetic and parasympathetic control, regulating the size of the pupil and, therefore, the amount of light entering the eye.

Accessory structures aid the efficient functioning of the eye. Ocular muscles move the eyeball, lids serve to moisten and clean the corneal surface by closing at intervals and washing the secretion of the lachrymal glands across it. Land mammals have a duct leading from the medial corner of the eye to the nasal cavity. This drains the lachrymal fluid from the eye surface and has an accessory function in moistening the nasal mucosa.

The Ear, Hearing and Space Orientation

The apparatus of the inner ear shows a remarkably constant organization among the vertebrates. It contains receptors that respond to slight mechanical deformation and give information about the direction and frequency of incident sound waves, the position of the head in relation to gravity and the angular acceleration of movement of the head in various directions.

The receptor systems of the ear are: the spiral organ within the cochlea for measuring intensity and frequency of sound waves; the cristae within the semicircular canals for response to rotational movements of the head in space; and the maculae of the utricle and saccule providing tonic gravitational receptors.

Sound reaches the receptors in the cochlea through the external and middle ears, which are developed solely for this purpose. Sound reception plays a particularly important role in the lives of aquatic forms and considerable modification of the external and middle ears of these are observed.

The auricle (pinna) is variable in shape and size among mammals and can be moved to maximise sound reception and aid in detecting the direction from which sound is coming. The remainder of the external ear consists of a tube held open by the presence of cartilage and bone in its walls. The tympanic membrane is stretched across the interior end of the tube and marks the outer wall of the middle ear. Vibrations of the tympanic membrane, set up by sound waves, are transmitted to the inner ear by the three auditory ossicles: the malleus, incus and stapes. The footplate of the stapes fits into a small opening leading to the inner ear. There are synovial joints between the ossicles. The system ensures that every inward movement of the centre of the tympanic membrane produces a movement of about one-third the extent in the foot plate of the stapes. The pressure at the stapes is several-fold greater than at the tympanic membrane. The inner ear is protected, to some extent, against loud sounds by the presence of two tiny muscles attached to the ossicles which may act to decrease the amplitude of the vibrating systems.

Special use is made of the auditory system by certain bats and whales in the system known as echolocation or sonar. Sounds are produced as a series of pulses and the echoes of these pulses provide auditory clues by which the animal navigates among objects and detects prey.

The parts of the inner ear associated with three dimensional space orientation are universal in vertebrates. The three semicircular canals, set mutually at right angles to one another, are tubes forming almost complete circles. They arise from a larger central sac, part of whose wall is evaginated to form the utricle. Each tube has an ampulla at one end, in which lies the very sensitive receptor. The utricle communicates with the saccule by a narrow duct and both contain sensory receptors, the maculae.

Taste

Most of the simpler senses and some of the complex ones such as vision and sound perception, are responses to physical stimuli, but taste and smell are responses to chemical stimulation.

The taste buds consist of barrel-like collections of elongated cells sunk within the epithelium. Taste buds are confined to the mouth and pharynx and, in mammals, are concentrated on the tongue, particularly certain papillae.

Much of what is casually thought of as taste is actually a smelling of mouth contents and, in addition, the feel of food in the mouth.

Although all taste buds are similar in structure, their receptive capabilities differ. These differences lie in the responses of the taste buds to specific sorts of molecules or ions in solution in the mouth. Sensations of sour, salty, bitter and sweet can be distinguished in man; other mammals have similar discriminatory powers.

Olfaction

Although the nose has become associated with breathing in mammals, its primary function is in olfaction. The whales, dolphins, dugongs and manatees are specialised to the extent that there is no olfactory mechanism at all. But, among the mammals and vertebrates in general, smell is in many ways the most important of all senses.

Within the nasal cavity, particularly in its dorso-caudal region, is the olfactory epithelium, which contains olfactory cells interposed with supporting elements and mucous cells. The olfactory cells differ from other receptor organs in mammals in that they not only receive sensations, but transmit them along their extensions to the olfactory bulb of the brain.

The olfactory cells are sensitive to minute amounts of chemical materials, derived from distant objects, which go into solution in the liquid covering the olfactory epithelium in the nasal cavity. The precise nature of olfaction is not well understood. Smell discrimination may be due to the presence of submicroscopic pockets of different shapes at the tips of the sensory cells and stimulation of a cell may be caused by the presence of a molecule whose shape enables it to fit into one or another type of pocket.

Apparently closely associated with olfactory sense is the vomeronasal organ (Jacobson's organ), which is an apparently functional organ in many groups of mammals, but is absent in humans, many bats and various aquatic forms. It is paired, lying in the rostral base of the nasal septum as a tubular pocket of olfactory epithelium, partially enclosed by a scroll of cartilage. Each vomeronasal organ opens rostrally into an incisive duct (or into the nasal cavity in many rodents). It is supplied by several nerves which pass through the cribriform plate of the ethmoid bone with the olfactory nerves and along the medial surface of the olfactory bulb to the accessory olfactory bulb.

The specific function of the vomeronasal organ is as yet unknown, although there is evidence that it plays a role in sexual behaviour and kin recognition. The behavioural 'lip curl' or 'Flehmen' reaction observed in many mammals may provide mechanical assistance in clearing the passageways to the vomeronasal organ and in aspirating odorants so they may reach the receptor sites of the organ.

Receptors in the Skin and Viscera

The sensation of pain is believed to be produced by direct stimulation of the end fibres of sensory nerves. Such nerve endings, in the skin at least, appear to be also sensitive to touch.

Many sensations are received by terminal corpuscles, specialised sensory endings of variable size (mostly microscopic) and structure. They may be present in almost any part of the body, particularly the skin, muscles and tendons and the viscera. Some five types of sensations may be distinguished in mammals: warmth, cold, pain, touch and pressure. Although it is difficult to determine accurately the function of the different types of corpuscles, there is good evidence now for the relationship of fine structure and function in some of them, notably the mechanoreceptors.

Complex nerve endings surrounding the bases of hairs, in particular the vibrissae, are important in touch reception. Proprioceptive sensations include those obtained from sensory structures located in the striated skeletal muscles and tendons as neuromuscular and neurotendinous spindles. They convey to the central nervous system, via associated afferent nerve fibres, information about the state of contraction of the muscles and the position in space of the various parts of the body.

The receptors in the internal organs provide an essential feedback system that initiates and stops many actions, particularly in the young animal, before a system for regulating rhythmic activity is fully established in the brain.

Receptors able to respond to distension probably are present in the bladder, uterus, stomach and other internal organs. Enteroceptors are present in the vascular system, important ones being in the arch of the aorta and the carotid sinus (sensitive to increased blood pressure) and the carotid body (sensitive to reduction of oxygen tension).

THE ENDOCRINE ORGANS

The endocrine organs, although they occur in many parts of the body, comprise an integrative system in which information and directives are transmitted in the blood stream by chemical messengers, the hormones, produced by the endocrine glands. The method of transmission by the endocrine system is slower than that by the nervous system. Hormonal effects often are distributed broadly over the body to a variety of tissues and organs, in contrast to the ‘pinpointing’ possible in the nervous system.

Integrative organization of the body, thus, is effected by two systems, the nervous system and the endocrine system. The two are intimately interrelated, both morphologically and functionally. The nervous system may be powerfully affected, directly or indirectly, by hormones. Conversely, the hypophysis is influenced strongly by, and some of its hormones actually are produced by nuclei in, the hypothalamus. There is a complicated series of endocrine interrelationships, which are extremely important in the integration of various physiological activities. Some of these are indicated in Fig. 34.13, which emphasises the central role played by the adenohypophysis in the endocrine system. It, in turn, is influenced greatly by the hypothalamus, which produces a variety of releasing factors that stimulates the adenohypophysis to dispense various of its hormones in a specific manner. The central nervous system in certain ways influences the discharge of releasing factors, which then reach the target cells in the adenohypophysis via the blood stream, in vessels that constitute the hypothalamo-hypophyseal portal system. The releasing factors are produced in secretory cells of the hypothalamus and released in the median eminence at the base of the diencephalon. They are then picked up by the primary plexus of the portal system and, passing to the sinusoids in the pars distalis of the adenohypophysis, stimulate hormone production there.

In some systems, the secretion of a particular adenohypophyseal hormone stimulates increased hormone production by another endocrine gland. The increased level of that hormone then acts back on the hypothalamo-hypophyseal axis, resulting in a reduction in release of the adenohypophyseal hormone. An example of this type of interrelationship is shown in Fig. 34.14.

Hormones produced by the gastrointestinal tract and those secreted by the testes and ovary have been discussed previously in this chapter. Among its other functions, the placenta synthesises hormones important in pregnancy which continue or supplement activities of the hypophysis and ovaries.

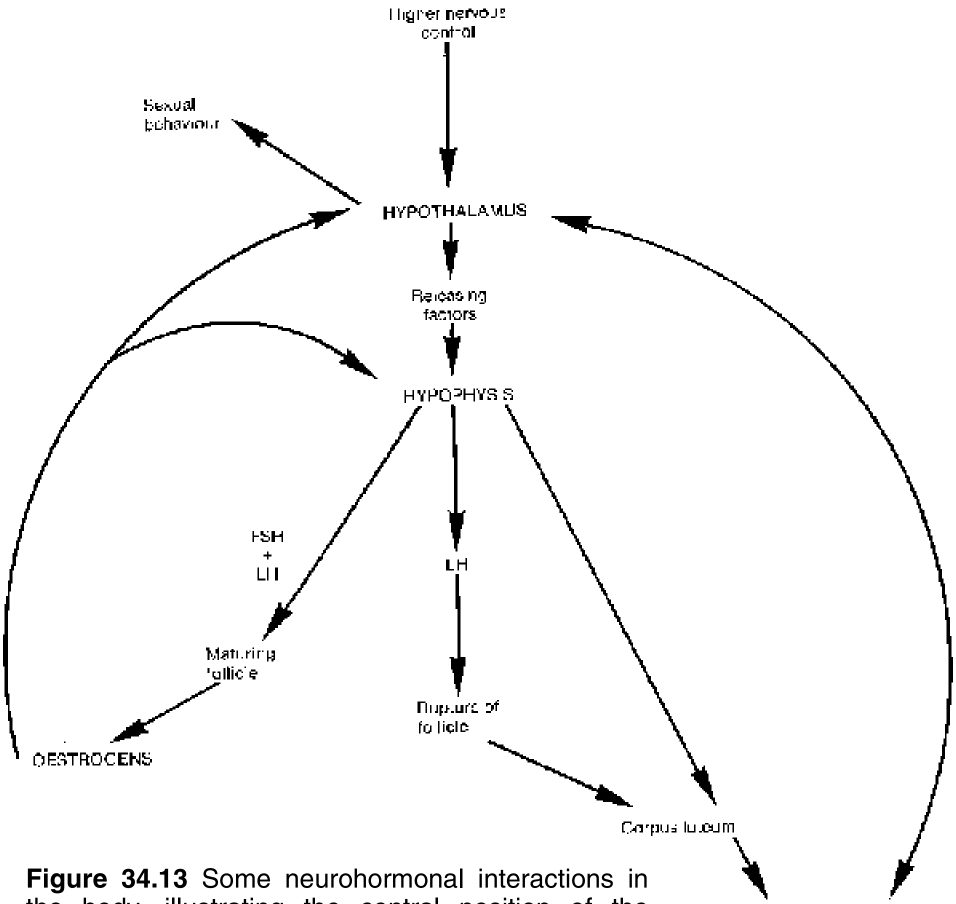


Figure 34.13 Some neurohormonal interactions in the body, illustrating the central position of the hypothalamo-hypophyseal axis in the control of endocrine function. This schema is a simplification of a highly complex system of interactions. Not shown is that many hormones act back on the brain and hypophysis (see Fig. 34.14).

The Hypophysis Cerebri

The hypophysis cerebri is a dual structure, the two portions having different embryological origins and functions. It lies in the hypophyseal fossa in the floor of the cranial cavity, immediately ventral to the hypothalamus.

The adenohypophysis lies rostral to the neurohypophysis and the bulk of it is made up of branching cords of cells separated by sinusoids, the pars distalis. Six types of cells are identifiable in the adenohypophysis, each responsible for the release of one or more hormones.

The neurohypophysis is directly continuous with the hypothalamus. The secretions found in it are not produced there, but are neurosecretions produced by cells in the hypothalamus (particularly in the supraoptic and paraventricular nuclei) and released at the tips of their axons in the neurohypophysis.

Seven known hormones are secreted from the adenohypophysis, the first six from the pars distalis. Follicle-stimulating hormone (FSH) stimulates the growth of ovarian follicles, promotes oestrogen secretion and ovulation and promotes spermatogenesis. Luteinizing hormone (LH) influences maturation of the gonads and production of sex hormones, acts in formation of corpora lutea and secretion of progesterone in the ovary and stimulates the interstitial cells of the testis, thus promoting the production of androgens and the maturation of sperm. Prolactin stimulates milk secretion and prolongs the functional life of the corpus

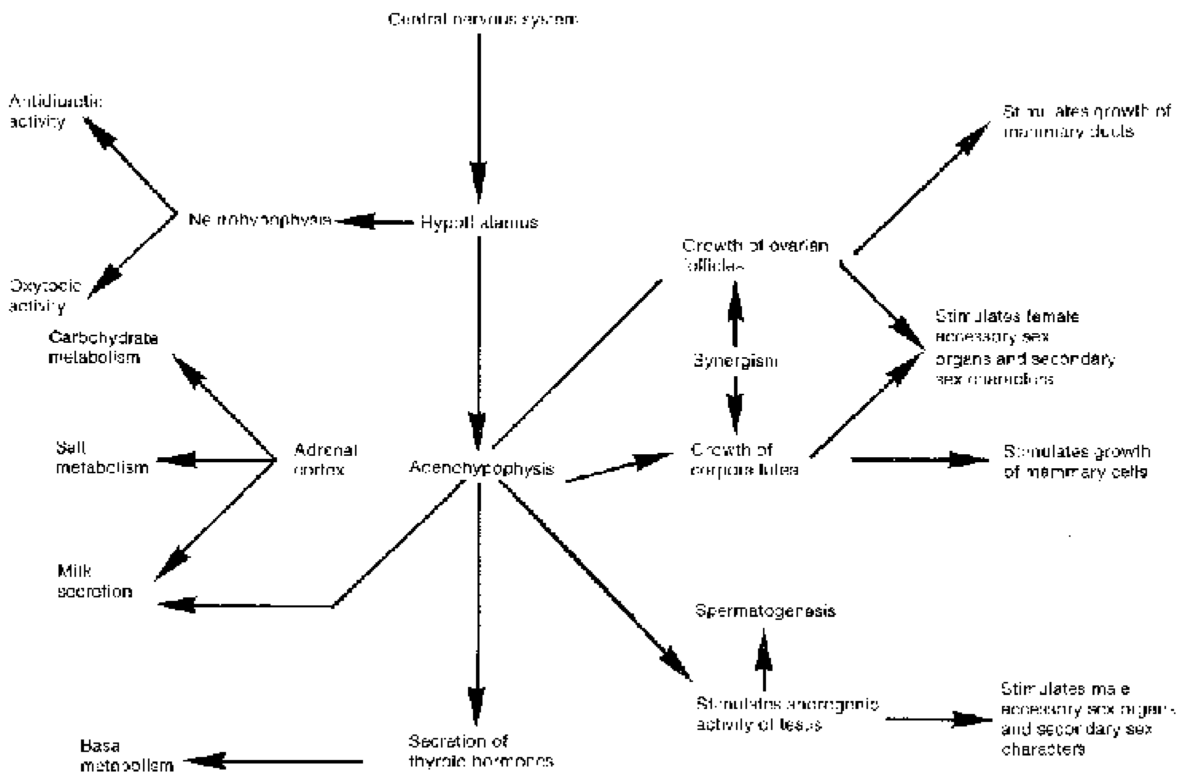


Figure 34.14 Interrelationships of the hypothalamus, hypophysis and ovary. The organs within the ovary (follicles and corpus luteum) are stimulated by hypophyseal hormones and the products of those ovarian organs, oestrogen and progesterone, act in turn on the brain and hypophysis to influence the release of hypophyseal hormones.

luteum. Adrenocorticotrophic hormone (ACTH) is vital for the normal activity of the adrenal cortex in secretion of hormones and exerts some metabolic influence in other ways. Thyroid stimulating hormone (TSH) is essential for the stimulation of the thyroid to form and release thyroid hormones. Growth hormone (GH) has a very broad influence on growth and metabolism in general, with marked influence on growth of skeleton and muscle, metabolism of fats and carbohydrates and protein synthesis. It further acts to enhance the effect of other hormones on the activity of the thyroid, adrenal cortex and reproductive organs. Intermedin, secreted by the pars intermedia, has no known function in mammals.

The secretions released from the neurohypophysis have two major functions, oxytocic and antidiuretic. The oxytocic effects are mainly contraction of the uterine muscle, mammary gland development and milk ejection after the birth of young. Antidiuretic effects are associated principally with increasing blood pressure through contraction of arterioles and controlling water output or intake through effect on the kidney.

The Adrenals

Adjacent to the kidneys at their cranial poles are the paired adrenals (suprarenals), consisting, in mammals, of distinct outer cortical and inner medullary layers. Both are endocrine glands, but of different sorts. The medullary tissue is a modified part of the nervous system, innervated by preganglionic autonomic nerve fibres, which on stimulation release into the blood stream two chemicals adrenalin and noradrenalin. The cells of the adrenal cortex secrete a series of steroid hormones which has widespread influence over bodily functions. In general, this influence involves aiding the body to meet long-continued environmental stresses. This is in

contrast to the function of the adrenal medulla, which functions in coping with more immediate, short-term stresses. Three main types of cortical steroids may be distinguished. The first includes cortisone, corticosterone and cortisol, which are potent in affecting carbohydrate and protein metabolism. The second type, for example, deoxycorticosterone, has major effects on salt and water metabolism. The third type is aldosterone, the most effective steroid in sodium and potassium metabolism. With the exception of aldosterone, the secretion of these hormones is influenced by ACTH.

The Thyroid Gland

This gland is found in the neck of mammals, lying against the trachea. Of pharyngeal origin, it migrates caudally to different levels in different species, so that it may lie near the larynx or close to the cranial thoracic aperture. The gland is composed of numerous follicles bound together by connective tissue, each follicle consisting of a cuboidal epithelium of secretory cells surrounding a central cavity that contains a colloid substance. In the colloid are found stores of thyroglobulin from which, through hydrolysis, are formed the hormones thyroxine and triiodothyronine - the former more abundant, but the latter more active.

Hormone secretion from the thyroid is controlled to a great extent by the hypophysis through the production of TSH, but a variety of environmental stimuli may be influential as well.

Pale, parafollicular cells occur subjacent to the epithelial cells and are responsible for production of the hormone calcitonin. Its secretion is induced when the concentration of calcium in the blood becomes high. Its effect is to depress the level of blood calcium by suppressing reabsorption of bone.

The Parathyroid Glands

There are usually two pairs of parathyroids in mammals, either partly embedded in the thyroid gland or beneath or just outside its capsule. They are very small and consist of closely packed cells interspersed with numerous sinusoids.

The secretion of the parathyroid glands, through the release of parathormone, causes the withdrawal of calcium from bones into the blood. An increasing calcium level in the plasma depresses parathyroid activity.

The function of the parathyroid glands and the parafollicular cells of the thyroid gland is to control the amount of calcium circulating in the blood. In performing this function they cooperate with the vitamin D introduced with the food or synthesised in the skin by the action of sunlight.

The amount of calcium in the interstitial fluids affects the surface properties of every cell, so it is obvious that the stabilisation of this ion is vitally important.

The Pancreatic Islands

Among the abundant lobules of the pancreas forming the exocrine part of the gland are isolated islands of cells, the pancreatic islands, which together constitute an endocrine gland. They produce a specific protein, insulin. Insulin has an important regulatory action on metabolism, particularly of carbohydrates, by increasing their utilisation by the tissues, moderating glucose formation in the liver, facilitating the entry of glucose into certain types of cells and maintaining the blood sugar level. Insulin secretion seems to be controlled mainly by the level of sugar in the blood passing through the pancreatic islands. The polypeptide glucagon also is produced in the pancreatic islands, but is formed in a different cell type from that secreting insulin. Glucagon offsets the influence of insulin. It affects sugar metabolism by breaking down glycogen stored in the liver so that the level of blood glucose is increased.

The Pineal Gland

The pineal gland (epiphysis cerebri) is in the dorsal part of the diencephalon. It is extremely variable in size and shape in mammals, but absent in certain species, such as the dugong.

The pineal secretes the hormone melatonin, although it is not the only site of production of this indole. Light impinging on the retina is believed to cause a change in the sympathetic output of the cranial cervical ganglion, which results in decreased production and release of melatonin. A daily rhythmic activity in melatonin synthesis dependent on environmental lighting is observed in mammals. Melatonin has been shown to be inhibitory to the gonads. Considerable emphasis has been placed on the role of the pineal gland in mediating the influence of the photoperiod on the neuroendocrine-reproductive axis. For a time this was assumed to be the primary role of the gland, but its role now appears to be more general. As currently perceived, the function of the pineal gland in mammals is to serve as an intermediary between the external environment, especially the photoperiod, and the organism as a whole.

THE LYMPHOID ORGANS

Certain regions or organs of the body contain accumulations of lymphoid tissue. These may be in simple organization in close relation to epithelial membranes, for example diffuse lymphoid tissue, solitary nodules, aggregate nodules, tonsils, or as more organised structures that comprise separate organs, for example lymph node, spleen, thymus.

Lymphoid tissue consists of two primary elements: the reticular tissue and cells which are chiefly lymphocytes. The major functions of lymphoid tissue are the production of new lymphocytes and the phagocytic activities in the tissue of free and fixed macrophages. The latter activity is directed against bacteria, spent blood cells and foreign materials associated with the filtration by the lymphoid tissue of tissue fluid, lymph or blood.

Diffuse lymphoid tissue occurs mainly in the tissue beneath the mucous membrane of the alimentary and respiratory tracts. Aggregate nodules, often called Peyer's patches, are found in the intestinal lining. Three tonsillar groups form a lymphoid ring about the entrance of the throat. The lymph nodes occur in various parts of the body and are the only organs that act as filterers of lymph. As such, they tend to form groups, either many small or few large nodes (depending on the species), at foci of lymph drainage such as the proximal ends of the limbs, around the junction of the head and neck and in the mesenteries. Some species, notably the ruminants, possess haemal nodes, in addition to the lymph nodes, along the ventral side of the vertebrae.

The spleen is the largest of all lymphoid organs and is specialised for filtering blood. Its size is variable within and among mammals. It lies on the left side in close relationship with the stomach and omentum. It is an elastic, controllable reservoir that is important in adjusting the volume of circulating blood to changing needs. In particular, it stores red blood cells in its sinuses and red pulp. The spleen is an important haematopoietic organ, generating both lymphocytes and monocytes. In early foetal life it is, like other organs such as the liver, an important source of all types of blood cells.

The thymus is a lymphoid organ found in the cranial thoracic region and in the young of some species extends the full length of the neck. Essential for the normal development and maintenance of immunological competence, it becomes relatively and often absolutely, smaller as postnatal growth proceeds. In addition, various protein substances have been isolated from the thymus and proposed as thymic hormones.

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