Anatomy

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Introduction

The Palaeozoic-Mesozoic transition from an "icehouse" to a "greenhouse" environment resulted in greater climatic zonation with resultant isolation and diversification of organisms. In the Jurassic (mid-Mesozoic: 140-155 million years ago) the area which we know today as Bavaria (southern Germany) consisted mainly of cycads and treeferns. The climate was steamy, hot and equable; carbon dioxide levels were 2-10 times those at present, and this increased plant growth and cloud cover, resulting in a constant, humid greenhouse climate. This was the age of giant dinosaurs, flying reptiles and small mammals.

In this period a bird about 21.5 cm long (about the size of a crow) dropped into shallow water and was rapidly covered by fine, calcareous silt, thus reducing the rate of decay and becoming fossilised. The fossil lay here for 150 million years, during which it was moved hundreds of kilometres north by continental drift and raised hundreds of metres as well. Then, in 1877, the limestone matrix in which the fossil rested was split by workmen quarrying stone for the lithographic printing industry at Eichstatt. The fossil, *Archaeopteryx lithographica (Archaeopteryx*: "ancient wing"), is one of the most significant in palaeontology, for it is not a bird with which we are familiar, for it shows many characteristics which link birds with their reptilian ancestors. It was still very close to the archosaurian reptiles and was probably descended from that group. The pelvis is similar to that of ornithischisians, but the limb structure is like that of the carnivorous saurischians.

The whole skeleton is essentially like that of a reptile. It had, like modern birds, feathers, a wishbone, wings and a small breastbone. It also had, like reptiles, scales on its legs and head, a long bony tail, teeth, three-clawed forelimbs, and a small, reptile-like brain (but large within reptiles). The characteristics which *Archaeopteryx* does not share with birds of later geologic times are lack of pneumaticity, the primitive reptilian structure of the wing bones, the toothed jaws, and the long reptilian tail. This lends weight to the theory that modern birds are the descendants of dinosaurs. The Eichstatt specimen was originally thought to be a small coelurosaur, until feather impressions were noticed some 20 years after its discovery.

The jaws are not modified into a beak as in modern birds, but are bony and carried numerous undifferentiated teeth. There is no fusion of vertebrae or reduction of the tail, which consists of a long series of vertebral elements tapering to a point. The sternum had no keel for the attachment of the huge breast muscles necessary for powered flight. However, around the bones of the forelimbs and tail are the clear, unmistakable impressions of feathers which are structurally identical to those of modern birds. Feathers define birds as a class, and any organism bearing feathers is by definition a bird.

Archaeopteryx was long considered a ground-dweller that used its wings (with its associated claws), to scoop insects toward its mouth. In support of this theory was its lack of the keeled breastbone to which modern birds attach their powerful flight muscles. It is now believed that *Archaeopteryx* was not a transitional form but a fully-fledged bird, since its feathers had the same aerodynamic shape as those of living birds to achieve lift, and its hind claws were as sharply curved as those of modern perching birds (ground-dwelling birds, by contrast, have straighter claws). In addition, these feet had one fully reversed toe and claw, exactly as modern perching birds use to clutch a branch. Thus *Archaeopteryx* may not have been the equal of modern birds at powered flight but the curved claws and true feathers put the creature in the treetops and therefore made it a true bird, despite its teeth.

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The Cretaceous period (130-65 million years ago), saw the peak of development and extinction of dinosaurs and the rise of flowering plants, and also saw the rise and extinction of many toothed birds. Because fossilisation of land birds is a rare event, we only know of aquatic bird-like species such as the flightless, *Hesperornis* and the tern-like *Ichthyornis* (which might not have been toothed). During this period there must also have been terrestrial birds, since at the start of the Eocene (65 million years ago) many modern groups such as cormorants, pelicans, flamingos, ibises and rails were present. The ratites first appeared during the Eocene and must have arisen before the break-up of Gondwanaland about 100 million years ago since different ratite species have evolved in isolation in Australia, Africa and South America.

All birds other than *Archaeopteryx* may be included in the subclass *Neornithes*, characterised by a reduced tail with a fan of feathers, a well-developed sternum, usually with a good keel, and the reduction and fusion of the metacarpals.

Most Upper Cretaceous remains of birds are fragments but are sufficiently varied to indicate that by this time bird evolution was far advanced and that many of the modern bird orders were already in existence. The best known of Cretaceous birds is *Hesperornis*, which uniquely combines primitive and specialised characters. *Hesperornis* was persistently primitive in that although teeth were present in grooves in the upper and lower jaws, there were none toward the front of the jaws, so that it might be assumed that the horny beak characteristic of more advanced birds was already being formed.

Hesperornis was probably a diving bird with powerful hind legs which spread laterally at the ankles, probably giving the bird a capability for a vigorous swimming stroke. Its wings had been almost completely lost - there remaining only a slender humerus, while the sternum was unkeeled.

Skeleton

In the skeleton there are many modifications necessarily connected with flight. Air sacs are connected with the lungs and also with air-filled cavities within many of the skeletal elements, including portions of the skull, neck vertebrae, humerus, and femur.

The anterior limb consists of a long, slim, backward-slanting scapula and a single coracoid attached to the edge of the sternum. Slender clavicles usually fuse in the midline to form the wishbone. The sternum is a large plate, usually with a great keel in the middle in flying birds; and to it are attached the powerful pectoral muscles which exert the main propulsive pull on the humerus during flight.

The humerus is short in most modern flying birds, with a heavy process near the head for the attachment of the pectoral muscles. The radius and ulna are well developed and long; but the ulna, which carries the remiges at its back, is the stronger. There are four carpals, the two distal ones fused with the metacarpals. The hand is similar to that seen in dinosaurs, for only three fingers are present, the fourth and fifth having disappeared. Almost never do these fingers bear claws; they are buried and function only as supports for the remiges.

The legs are similar to those of dinosaurs in structure. The ilium is elongated and firmly bound to the synsacrum. As in dinosaurs, the acetabulum is perforated. The pubis passes down and backward, as in the ornithischian dinosaurs. The slender ischium passes down and caudally parallel to the pubis - there is usually no ventral union of the bones of the two sides, but the ischium is typically braced by an upward extension which meets the caudal end of the ilium. The pubis and ischium may join distally. The femur is short, the tibia elongated, and the fibula reduced and may only consist of a proximal end. The main joint with the foot lies in the middle of the tarsus (as in dinosaurs). The foot, too, is essentially like that of many dinosaurs. The three middle toes are generally well developed, the fifth is not present, and the first (often reduced or absent) is most commonly turned to the rear, where it aids in clutching a perch.

Skull

The distinctly appearance of the skull is due to the large orbits and large braincase. It has some reptilian features, including a single occipital condyle, moveable quadrate and pterygoid bones, and a lower jaw consisting of five bones instead of one. The sutures between most of the cranial bones have been lost, probably because of the extensive pneumatisation which occurs in embryonic life.

The facial part of the skull consists of the premaxilla and nasal bones. The premaxilla forms the major part of the upper jaw and is covered by the beak. The junction of the premaxilla and nasal bones with the frontal bone is flexible, allowing the upper jaw to open. When the bird opens its beaks, the descending lower jaw applies pressure to the quadrate bone, which rotates. Because of this rotation, the ventral part of the quadrate bone is carried rostrally. The ventral part of the quadrate bone articulates with two "rods": both articulate with the premaxilla rostrally. Thus when these rods are pushed rostrally the facial part of the skull tilts dorsally. This system is much reduced in ratite birds, and very developed in parrots, which can open the upper beak widely.

The lower jaw is derived from the fusion of several small membrane bones, and also the articular bone, which is derived from the cartilages of the pharyngeal arches. The articular bone articulates with the quadrate bone, which is also derived from the pharyngeal arches. In mammals the articular and quadrate bones no longer have an articular function and have been converted into the auditory ossicles, the malleus and incus respectively.

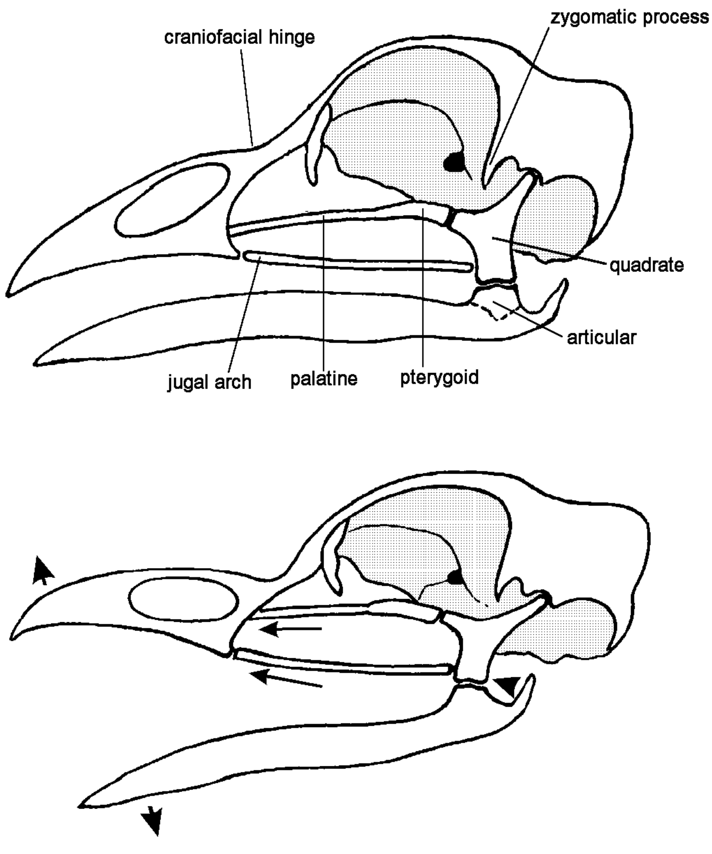

Figure 1: Diagram showing the movement of the upper jaw when the lower jaw is depressed (after King and McLelland, 1975)

Feathers

Feathers are the only distinctive feature of birds, since almost every other character can be matched in some archosaurian group. Feathers are produced by feather follicles. The scapus (feather shaft) is the longitudinal axis of the feather. It is composed of two segments: the calamus, or proximal portion - the short tubular base enclosed by the feather follicle, and the rachis, or solid part of the shaft above the skin. On each side of the rachis is a row of fine branches, individually called barbs and collectively called the vane. Barbules arise from each side (proximal and distal) of each barb. Feathers serve as protection (thermal insulation, water proofing and repellency, camouflage and threat), tactile sensation, a means of flight and (courtship).

Feathers are arranged in rows or tracts called *pterylae*. Pterylae are separated from each other by areas of bare skin called *apteria*. There are seven basic types of feathers: contour feather, semiplume, down feather, powder down feather, afterfeathers, filoplume and bristle.

1. **Contour feathers** are the predominant feathers on an adult bird's body. The contour feather consists of a pennaceous part, where the barbs are united firmly by their interlocking hooks, and the fluffy, plumaceous part. The feathers which show the outmost best adaptations to aerodynamic functions are the remiges (large wing feathers) and retrices (long tail feathers). Remiges and retrices are characterised by large size, stiffness, asymmetry, and vanes that are almost entirely pennaceous. The longest feathers on the wings are the **remiges**. The remiges (primary flight feather) arise from the back of the forearm and from the reduced fingers which form the distal part of the wing support. The secondary remiges or secondary flight feathers are attached to skin of the forearm. Covert feathers cover the remiges in several rows on the upper and under side of the wing. On the tail (which, as a bony structure, is very short) is set a spreading fan of stout feathers used as a rudder - these are the **retrices**, or flight feathers of the tail and resemble the remiges in size and structure.

3. **Semiplumes** are plumaceous feathers similar to down feathers, but differ from down feathers because their rachis is longer than their longest barb.

4. **Down feathers** are comprised by an entirely plumaceous vane, the barbs being longer than the shortest barb. They are the characteristic of the natal feathering and form the undercoat in adults of many species. **Powder down feathers** grow continuously and are never moulted. The barbs at their tips constantly break off into minute granules of keratin, forming a talc-like powder that coats the plumage. Powder downs can be found in pigeons, storks, herons, toucans, parrots and bowerbirds.

5. **Afterfeathers** have unhooked barbules arising from the distal umbilicus of plumaceous and pennaceous feathers. In most species they represent small feathers, but in the emu and cassowary the hypopennae are longer than the main feathers.

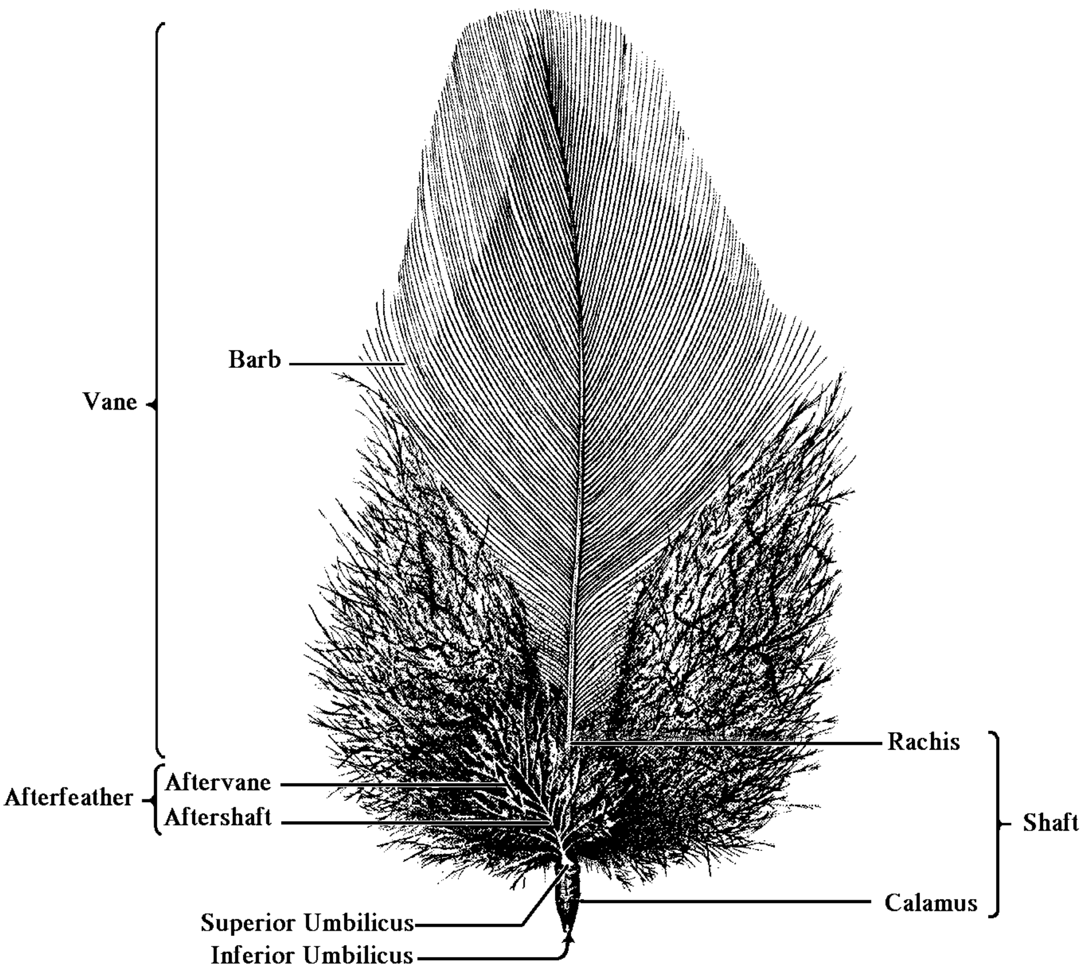

Figure 2: Main parts of a typical contour feather

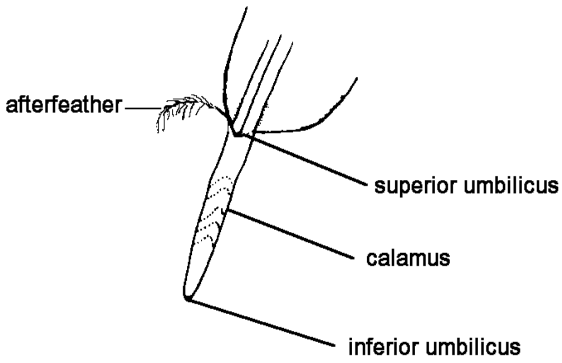

Figure 3: A body feather with an afterfeather at the superior umbilicus

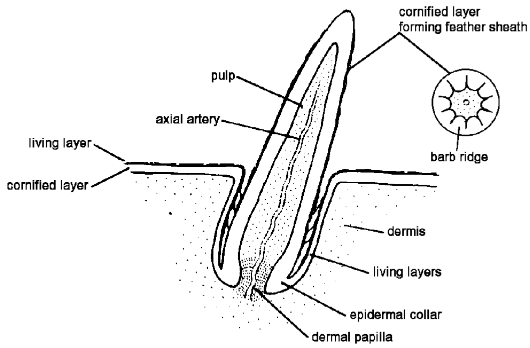

Figure 4: A developing feather, consisting of an axial core of dermis forming the pulp, enclosed by epidermis from the epidermal collar.

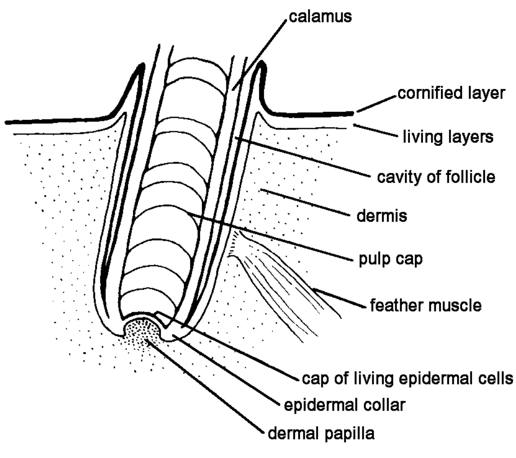

Figure 5: A mature follicle

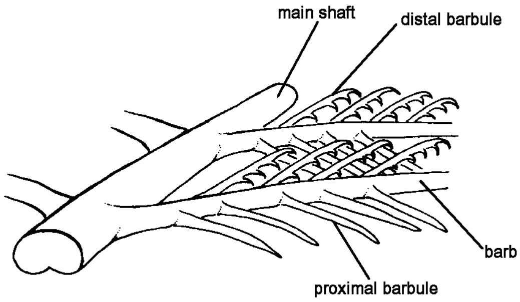

Figure 6: Showing the interlocking barbules of two barbs of a flight feather (after King & McLelland 1975)

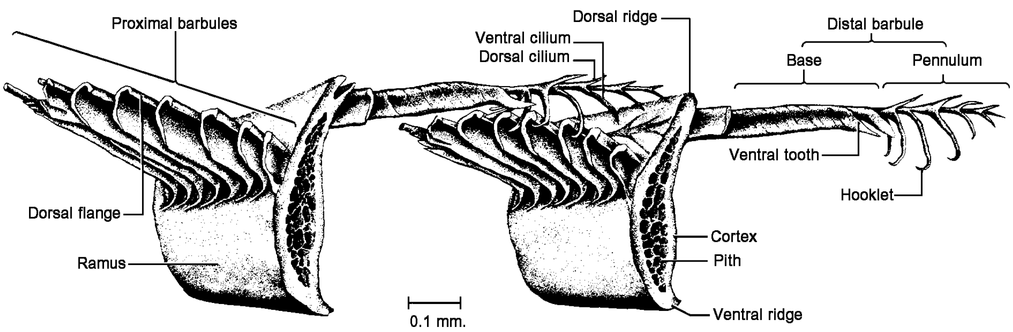

Figure 7: Segments of two pennaceous barbs from a contour feather, seen obliquely from the distal end (after Lucas and Stetnheim, 1972).

6. **Filoplumes** have a long hair-like rachis with a bunch of flexible barbs at the tip. They are the only feathers which do not have muscles attached to the follicles. They are present in all birds but the ostrich, emu and cassowary.

7. **Bristles** have a stiff rachis and barbs occur at its proximal end only. In most birds bristles are found as eyelashes around the nostrils and the mouth.

Feather Colour

Feather colours are the result of pigments and feather structure. Pigments are chemical compounds that absorb light of certain wavelengths, whereas structural conditions are physical features that modify or separate the components of white light. Colour patterns are displayed by each individual feather and the whole plumage. The most exposed feathers show the brightest colours while those beneath are white (e.g., down feathers).

The colours are caused by melanins, carotenoids and porphyrins. Melanins are the most common, and result in dull colours by themselves. Carotenoids comprise two groups according to their different chemical composition: The carotenes and xanthophylls. These pigments are derived from plants - birds cannot synthesise them. Porphyrin pigments show an intense red fluorescence under ultraviolet light and produce green colours in feathers. Structural colours result from the modification and separation of the components of white light. They may be either iridescent, changing with the angle at which they are viewed, or noniridescent, which do not change with angle of incidence.

Digestive System

Beak

1. **Genetic**

   a. Scissor beak
   b. Mandibular prognathism

2. **Trauma**

   a. Cracks, fissures + intralaminar haemorrhage
   b. Fractures
   c. Avulsion, separation
   d. Overgrowth due to insufficient wear

3. **Bacterial**

   a. Chronic rhinitis - deformation of beak.

4. **Viral**

   a. PBFD
   b. Poxvirus

5. **Fungal/yeast**

   a. *Candida albicans* - ulcerative, necrotic lesions - tumour-like growths with *C. neoformans*
   b. *Cryptococcus neoformans* - tumour-like growths with *C. albicans*

6. **Parasitic**

   a. *Cnemidocoptes* sp in psittacine birds - deformation, malocclusion.
   c. *Trichomonas* sp - necrosis of commissures of beak

7. **Neoplasia**

   a. Fibrosarcoma

8. **Nutritional**

   a. Vitamin A, D
   b. Biotin, pantothenic acid, folic acid deficiencies - deformed upper mandible in domestic fowl

Oropharynx

The palate contains the choana, a longitudinal fissure, through which the oral and nasal centres communicate. In herons (*Ardeinae*), ducks (*Anatidae*) and ratite birds,, the choana is very short and occupies the caudal part of the palate. Birds have no soft palate. The roof of the pharynx contains the pharyngeal cleft, a median longitudinal fissure which is the common opening to both auditory tubes. The tongue shows great morphologic diversity. In some birds the floor of the mouth ventral to the tongue contains one or more sac-like diverticula, the oral sacs (*sacci orales*), which carry food or are used as display chambers during the breeding season. The oropharynx is lined by stratified squamous epithelium which in some areas is keratinised. The salivary glands are compound tubular structures distributed in the walls of the oropharynx. In birds which eat a lubricated diet, for example, fish-eaters, these glands are small or absent. Some birds have greatly enlarged mandibular glands:

a. woodpeckers - sticky mucous secretion coats the tongue and enables the bird to use it as a probing instrument to capture insects.
b. swifts - secrete a mucilaginous substance which is used as cement in the construction of nests.
c. jay - mucous secretion used in the production of boli which are stuck to conifer needles for winter food.

1. **Bacterial**

a. *Salmonella typhimurium* - yellow green diphtheritic deposits base of tongue and palate.
b. *Spirillum pulli var nova* in chickens - stomatitis
c. *Mycobacterium* sp - nodules at commissure of upper and lower beaks, oral cavity, tongue and hard palate in parrots, galliform birds and falcons.
d. *Pseudomonas aeruginosa* - abscesses.

2. **Viral**

a. Avian pox
b. Infectious laryngotracheitis
c. Pigeon herpesvirus infection
d. Duck enteritis virus - ulcers in ducks
e. Pigeon herpesvirus - diphtheritic lesions

3. **Fungal/Yeast**

a. *Candida albicans*
b. Mycotoxin from *Fusarium tricinctum* caseous raised lesions in chickens and pigeons.

4. **Parasitic**

a. *Capillaria* sp
b. *Theromyzon* sp in *Anseriformes* (nasal leeches)
c. *Oxyspirura* sp in cranes
d. Spirurid worms in native birds
e. *Contracaecum* sp in seabirds
f. *Seratospiculum amaculatum* in raptors
g. *Synhimanthus falconis* in owls

5. **Neoplasia**

a. Papilloma
b. Plasmacytoma
c. Melanoma
d. Squamous cell carcinoma
e. Papillomas in psittacine birds

6. **Nutritional**

a. Necrosis of epithelial glands (especially in pigeons)
b. Vitamin A deficiency

Oesophagus

The internal surface of the oesophagus is longitudinally folded, which allows it to be greatly distended. Some birds have an oesophageal sac, which can be inflated with air for courtship display, or used as a resonating chamber for mating calls. The Australian Bustard (*Choriotis australis*) and the Sage Grouse (*Centrocercus urophasianus*) are two birds with well-developed oesophageal sacs.

1. **Mucosal gland hypertrophy**

    a. Courtship feeding of mate and nestlings.
    b. Continuous regurgitation of food on toys, mirrors, etc.
    c. Male Emperor Penguin (*Aptenodytes forsteri*) feeds chick a fluid consisting of desquamated oesophageal epithelial cells. This is fed by male for 10 days, after which the female returns and takes over, feeding fish to chick.
    d. Male and female Greater Flamingo (*Phoenicopterus ruber*) feed a reddish fluid to chicks (produced by merocrine oesophageal glands).

2. **Viral**

    a. Avian pox
    b. Newcastle disease - oedema, haemorrhage
    c. Duck plague - swans, geese, ducks - haemorrhage, necrosis

3. **Fungal/Yeast**

    a. *Candida albicans*

4. **Parasitic**

    a. *Trichomonas gallinae*
    b. *Capillaria contorta*, *C. annulata* in wall of oesophagus and crop of quail, pheasant, chickens, turkeys and others.
    c. *Streptocarpa* sp
    d. *Gongylonema ingluvicola*, *Echinura unicinata* and *Dyspharynx nasuta* can invade up to oesophagus.

5. **Neoplasms**

    a. Squamous cell carcinoma
    b. Fibroleiomyoma

6. **Nutritional**

    a. Vitamin A deficiency
    b. Heavy metal poisoning - impaction

Crop (Ingluvies)

In some species the oesophagus has an expanded portion, the crop or *ingluvies*. The crop acts as a temporary food storage where food is moistened and partly digested. It also acts as a store of food for regurgitation, and in pigeons produces 'pigeon milk' for squabs. The simplest crop is a spindle-shaped enlargement, such as occurs in the puffin, cormorants, ducks, storks, owls and some finches. In falcons and gallinaceous birds the crop lies on the right-hand side of the oesophagus. In parrots it lies on both sides, and in the pigeon it is a large, bilobed diverticulum. In the hoatzin (*Opisthocomus hoazin*), the crop consists of cervical and thoracic parts. The cervical crop is very large and thick-walled. The thoracic part runs a tortuous course before joining the proventriculus. The kakapo (*Strigops habroptilus*) also has a very large cervical crop, but it is thin-walled. The crop is absent in ratite birds.

1. **Viral**

   a. Avian pox
   b. Newcastle disease - hyperaemia, oedema, petechiae.

2. **Bacterial**

   a. *Pasteurella multocida*
   b. *Mycobacterium* sp
   c. *Clostridium perfringens* - necrosis of mucosa

3. **Fungal/Yeast**

   a. *Candida albicans*

4. **Parasitic**

   a. *Capillaria contorta*, *C. annulata*
   b. *Gongylonema ingluvicola* - burrows in mucosa
   c. *Acuaria uncinata* - nodules in mucosa - ducks, geese, swans
   d. *Acuaria hamulosa* - attaches to mucosa of crop in chickens, turkeys, guinea fowl, pheasants - shaggy appearance
   e. *Hystrichio tricolor* - cysts in ducks.
   f. Trichomoniasis
   g. *Leucocytozoon caulleryi* - megaloschizonts in serosa in hens.

5. **Neoplasms**

   a. Papilloma
   b. Round cell carcinoma
   c. Leiomyosarcoma

6. **Nutritional**

   a. Vitamin A deficiency

7. **Miscellaneous**

   a. Patulin, a mycotoxin produced by *Aspergillus*, *Penicillium* and *Byssoschlamys* --> watery crop contents and haemorrhage throughout GIT
   b. Copper sulphate --> coagulative necrosis
   c. Phosphorus --> necrosis of crop, proventriculus and small intestine
   d. Silver nitrate - budgies chewing silver nitrate sticks - cauterised crop
   e. Arsenic - catarrhal ingluveitis
   f. Impaction - by fibrous material, litter, goitre
   g. Pendulous crop - genetic in turkeys

8. **Functional**

   a. Ingluvolith - calculus
   b. Crop stasis
   c. Crop impaction

9. **Trauma**

a. Lacerations, fistulas, strictures.

Proventriculus

The proventriculus is the glandular part of the stomach. It is best developed in piscivores, frugivores and granivorous insectivores. In such birds the proventriculus is an extendible sac-like structure. The proventriculus of the ostrich is large, dilated and thin-walled.
Most carnivores, insectivores, granivores and herbivores have a small proventriculus. The proventriculus of the orange-winged parrot (*Amazona amazonica*) and the peafowl (*Pavo cristatus*) is very small.

1. **Bacterial**

   a. *Erysipelothrix rhusiopathiae* - mucosa sloughs (turkeys)
   b. Tuberculosis
   c. Megabacterial proventriculitis - "going light" syndrome

1. **Viral**

   a. Newcastle disease
   b. Virulent avian influenza
   c. Duck plague
   d. Reticuloendotheliosis

   All produce haemorrhages and oedema in *mucosa* and *lamina propria*, with necrosis and sloughing.

   e. Avian pox - canary pox causes lesions in proventriculus, air sacs and serosa. A systemic disease.
   f. Haemorrhagic enteritis turkeys - haemorrhages at junction of proventriculus and gizzard.
   g. Infectious Bursal Disease - haemorrhages
   h. Avian encephalomyelitis - lymphoid cell infiltration in *muscularis*
   i. Marek's disease
   j. Lymphoid leucosis.

3. **Fungal/Yeast**

   a. *Candida albicans*

4. **Parasitic**

   a. *Dyspharynx nasuta* - grouse, pigeons, parrots
   b. *Cyrnea colini* in quail, turkey, prairie chicken - wall of proventicular-gizzard junction - petechiae
   c. *Echinuria uncinata* forms tumour-like fibrous nodules in wall of proventriculus of waterfowl
   d. *Eustrongyloides ignotis* - nematode in proventricular glands of fish-eating birds -> peritonitis
   e. *Tetrameres americana*, *T. crami* - red worms - swollen mucosa
   f. *Tetrameres mohtedae* - thickened wall, petechiae in chickens. Females live in glands.
   g. *Spiroptera incerta* - adenomatous hyperplasia of mucosa of psittacine birds
   h. Trematodes - regarded as less pathogenic than nematodes
   i. *Ribeiroia ondatrae* - causes enlargement of proventriculus and greyish exudate in

fish-eating birds.

j. *Trichomonas gallinae* - necrotic ulceration
k. *Leucocytozoon caulleryi* - megaloschizonts in serosa and mucosa.
l. *Contracaecum* sp. pelicans and cormorants.
m. *Synhimantus falconis* in owls
n. *Gongylonema ingluvicola*

5. **Neoplasms**

a. Marek's disease
b. Leukosis
c. Adenocarcinoma
d. Fibroleimyoma
e. Carcinomas
f. Papillomas

6. **Nutritional**

a. Vitamin E/Selenium deficiency - proventricular necrosis
b. Vitamin K deficiency - haemorrhages
c. Patulin toxicosis
d. Trauma from ingestion of sharp objects
e. Impaction
f. Heavy metal poisoning
g. Myoventricular dysgenesis - finely ground feed - small ventriculus, proportionally large proventriculus

7. **Miscellaneous**

a. Intussusception of proventriculus into gizzard

Gizzard (Ventriculus)

The gizzard is the muscular part of the stomach. It is very much less developed in carnivorous and piscivorous birds which feed on soft food than in birds which feed on food which needs to be broken down before it can be digested (insectivores and granivores). The gizzard of an intensively-reared domestic fowl may be only **a** the size of a similar range-reared chicken, because it feeds exclusively on pelletised food, which readily breaks down on contact with water. The mucosal surface of the gizzard is covered by the *tunica cuticula* or *cuticula gastrica* (koilin layer or cuticle). This cuticle is a carbohydrate-protein complex and is NOT keratin. It is being continuously worn away and replaced. The cuticle may be shed completely in some birds, and in some male hornbills is shed, regurgitated and fed to the nesting female.

1. **Bacterial**

a. *Erysipelothrix rhusiopathiae* - increased thickness of wall
b. Tuberculosis
c. *Salmonella pullorum* - white foci in chickens
d. Mycoplasmosis - reticuloendothelial cell hyperplasia

2. **Viral**

a. Marek's disease
b. Avian encephalomyelitis

3. **Parasitic**

a. *Amidostomum anseris* in geese and waterfowl. Destroy koilin lining and haemorrhage may result
b. *Cheilospirura hamulosa*, *Chilospirura spinosa* - nodules in mucosa and muscularis - finches
c. *Streptocara pectinifera* - haemorrhagic ulcers in mucosa
d. *Leucocytozoon caulleryi*
e. *Epomidiostomum uncinatum*

4. **Neoplasms**

a. Carcinomas
b. Marek's disease
c. Leukosis

6. **Miscellaneous**

a. Impaction
b. Koilin dysgenesis secondary to degeneration and necrosis of koilin anlage
c. perforation - sharp objects - peritonitis

5. **Nutritional**

a. Mycotoxicosis - haemorrhages
b. Sulphonamides - haemorrhages
c. Se and Pb deficiency - haemorrhages
d. Vitamin K deficiency - haemorrhages
e. Vitamin E/Selenium deficiency - muscular dystrophy

Small Intestine

At hatching, the alimentary tract of psittacine birds is normally sterile, but in parent-reared birds a gram-positive flora, primarily anaerobes, becomes established. The aerobic bacteria most commonly present are *Lactobacillus*, *Streptococcus*, *Corynebacterium*, and *Micrococcus*. The intestinal flora of parrots, finches and waxbills is Gram-positive. If Gram-negative are present, they should be treated and eliminated if they are a potential pathogen. There is a mixed population in gallinaceous birds, waterfowl, columbiformes, raptors, omnivorous and insectivorous birds. The duodenum is generally a U-shaped loop on the right side of the gizzard. The jejunum and ileum are arranged in a variable number of U-shaped loops.

1. **Viral**

a. Haemorrhagic enteritis of turkeys
b. Coronavirus enteritis of turkeys
c. Newcastle disease
d. Avian influenza
e. Duck virus enteritis - free blood
f. Pacheco's disease
g. Pigeon herpesvirus infection

2. **Bacterial**

a. *Mycobacterium avium*
b. Ulcerative enteritis - *Clostridium colinum*
c. Necrotic enteritis - *Cl. welchii*
- *Cl. perfringens* type C
d. *Salmonella pullorum*
Salmonella typhimurium
Paratyphoid

e. Necrotic enteritis ducks - *E. coli*, trichomonads, *Hexamita* spp.
f. *Yersinia pseudotuberculosis*, catarrhal enteritis with granulomas in liver and spleen
g. *Campylobacter* sp
h. *E. coli* enteritis - parrots
i. Chlamydiosis
j. Necrotic enteritis - *Clostridium perfringens* type C
k. Ulcerative enteritis - *Clostridium colinum* - quail
l. Spirochaetosis - *Borrelia anserina* infection
m. *Erysipelothrix rhusiopathiae*
n. *Pasteurella multocida*
o. *Pasteurella anatipestifer* (new duck disease)

3. **Parasitic**

a. *Leucocytozoon caulleryi*
b. *Ascaridia galli*
Ascaridia columbae
c. *Capillaria obsignata* - extensive mucosal destruction --> fluid-filled gut.
d. *Ornithostrongylus quadriradiatus* - in anterior small intestine of pigeons --> blood sucking - petechiae and necrosis
e. *Davainea proglottina* - duodenum - petechiae, haemorrhage, mucosal thickening
f. *Raillietina cesticillus* - nodular TB-like lesions in ileum
g. *R. tetragona* - ileal distension
h. *R. echinobothrida* - degenerative villous changes in ileum
i. Trematodes -
(i) *Echinostomatidae*
(ii) *Psilostomatidae*
(iii) *Strigeidae*
(iv) *Notocotylidae*
(v) *Plagiorchiidae*
(vi) *Microphallidae*
(vii) *Brachylaemidae*
(viii) *Paramphistomidae*

e.g. **Echinostoma revolutum* in intestine, caeca and cloaca can cause haemorrhagic enteritis
**Echinoparyphium recurvatum* causes a severe enteritis
**Sphaeridiotream globulus* - ulcerative enteritis
**Plagiorchis megalorchis* - necrotic enteritis
**Cotylurus flabelliformis* causes epithelial cell necrosis in ducks and chickens

k. *Porrocaecum* sp. larvae burrow in gizzard, adults in intestine.
l. *Choanataenia* sp. in finches
m. *Strongyloides avium* and *S. tenuis* - haemorrhagic typhilitis in heavy infections.

4. **Protozoa**

a. *Giardia* sp
b. *Histomonas meleagridis*
c. *Hexamita* sp
d. Coccidiosis
e. *Cochlosoma* sp
f. *Chilomastix gallinarum*
g. Cryptosporidiosis

4. **Neoplasms**

a. Adenocarcinoma
b. Marek's disease
c. Leukosis
d. Fibroma
e. Fibroleiomyoma
f. Haemangioma

5. **Nutritional**

a.	Thiamine	)	
b.	Riboflavine	)	Degeneration in
c.	Pantothenic acid	)	crypts in duodenum
d.	Niacin	)	
e.	Vitamin K. deficiency - haemorrhage		

6. **Miscellaneous**

a. Mycotoxins - petechiae
b. Nitrofurazone - catarrhal enteritis
c. Copper sulphate - catarrhal gastroenteritis
d. Salt - oedema of *lamina propria*
e. Phosphorus - necrosis of intestinal mucosa
f. Amyloidosis in Pekin ducks
g. Trauma - intussusception
h. Obstruction

Caeca/Colorectum

Caeca absent or vestigial in parrots, finches, waxbills, falcons, hawks, eagles, vultures, humming birds, some pigeons, swifts, penguins and woodpeckers.

Caeca are well developed in galliform, anseriform birds and owls. In the grouse, they are so large that their combined length equals or even exceeds the length of the intestinal tract. In the ostrich the two ventral caeca open at a common orifice. Some species (grebes and herons) have a single caecum, the other being rudimentary.

Cloaca

The cloaca is a dilation of the end of the rectum. In immature birds the cloacal bursa is situated dorsally and is much larger than and compresses the cloaca on its dorsal aspect. The urogenital ducts pass over the dorsolateral surface of the cloaca and open into it dorsolaterally just caudal to its widest part. The cloaca is divided internally by two mucosal folds into three compartments: the coprodeum, urodeum and proctodeum.

Coprodeum

The coprodeum is the most cranial part of the cloaca. In the domestic fowl, there is no barrier or mucosal fold between the rectum and coprodeum - this "boundary" is indicated by the abrupt expansion in diameter which occurs where the rectum is continued by the coprodeum.

Urodeum

The urodeum is the middle compartment of the cloaca, but is only partly separated from the other two compartments by two circular mucosal folds. The more cranial of these two folds, the coprourodeal fold, is an annular ridge between the coprodeum and urodeum. If the coprodeum is full of faeces this fold becomes a thin diaphragm with a central circular aperture. The pressure of faeces can eventually cause the aperture to be everted through the vent. This diaphragm-like fold with its central aperture is also visible externally during full erection in the male bird. The more caudal fold, the uroproctodeal fold, is a semicircular dorsolateral fold between the urodeum and proctodeum which is not present ventrally. It is everywhere lower then the coprourodeal fold.

The urogenital ducts open into the urodeum. Their openings are on the dorsolateral mucosal surfaces of the urodeum, the ureters being relatively dorsal and the genital ducts lateral in position. In the male domestic fowl the *ductus deferens* opens on the end of a conical projection, the papilla of the *ductus deferens*. The red, oval vascular glomus may be found on the ventro-lateral wall of the urodeum. In the female the left oviduct opens ventro-laterally relative to the left ureter.

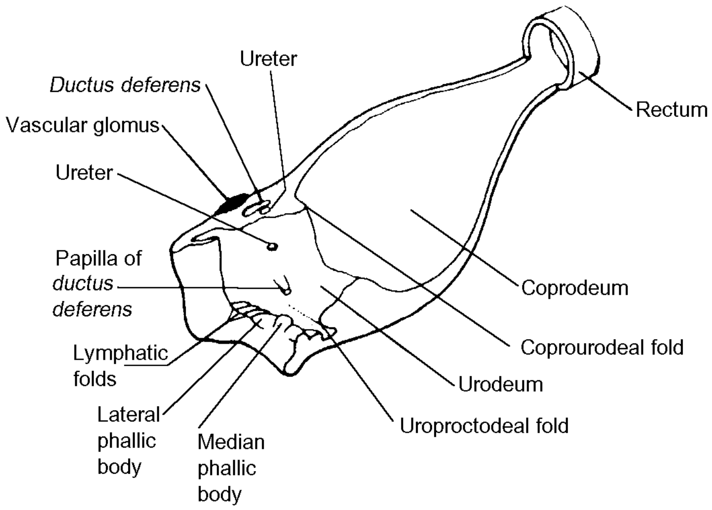

Figure 8: The cloaca of a male domestic fowl (after King and McLelland, 1975)

The proctodeum

The proctodeum is the short compartment between the uroproctodeal fold and the lips of the vent. In immature birds an opening in the dorsal midline leads into the globular cloacal bursa. In most birds this orifice is narrow but in the Ostrich it is relatively wide and this may account for reports of a true urinary bladder in this species. In the domestic fowl, in the midline immediately caudal to the opening of the cloacal bursa, the roof of the cloaca carries an oval glandular mound about 1 cm long. This is the dorsal proctodeal gland.

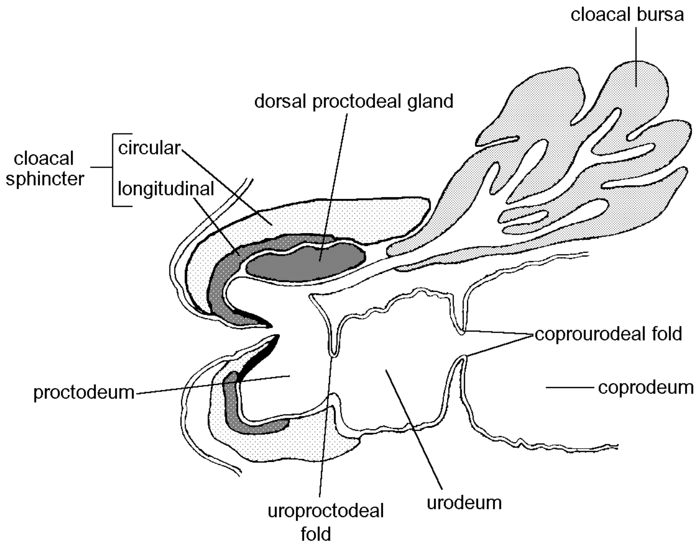

Figure 9: Median section of the cloaca of a 16-week-old hen (after King and McLelland, 1975)

1. **Bacterial**

   a. *Salmonella pullorum* - multiple necrotic foci
   b. Paratyphoid in ducks - enlargement of rectum
   c. Tuberculosis
   d. *E. rhusiopathiae* turkeys - yellow nodules in caeca
   e. *Mycoplasma* sp, *Neisseria* sp and *Candida albicans* - venereal disease of geese.

2. **Viral**

   a. Duck virus enteritis - haemorrhagic mucosa
   b. Newcastle disease
   c. Virulent avian influenza

3. **Fungal/Yeast**

   a. *Mycoplasma* sp, *Neisseria* sp and *Candida albicans* - venereal disease of geese.

4. **Parasitic**

   a. Coccidia. *Eimeria* spp
   b. Enterohepatitis - *Heterakis gallinae*
      - *Histomonas meleagridis*
   c. Trematodes
      (i) *Echinostoma revolution*
      (ii) *Echinoparyphium recurvartum*
   d. *Tetratrichomonas gallinarium*
   e. *Tritrichomonas eberthi*
   f. *Leucocytozoon caulleryi*

5. **Neoplasms**

   a. Neurofibrosarcoma

b. Reticulum cell sarcoma
c. Adenosarcoma
d. Papilloma
e. Cloacoliths
f. Cloacal papilloma

6. **Nutritional**

a. Vitamin K deficiency
b. Salt poisoning - haemorrhagic inflammation intestine and cloaca

7. **Miscellaneous**

a. Prolapse of cloaca - cannibalism
b. Cloacitis - vent gleet
c. Cloacal impaction
d. Prolapse of phallus

Respiratory System

Nasal Cavity

The nasal cavity is defined by the nasal process of the incisive bone dorsally and the nasal and lacrimal bones both laterally and dorsally. Its floor is formed by the palatine processes of the palatine bones and the vomer. In many birds the nasal septum completely separates the right and left cavities, but in some (mainly waterfowl) the nasal septum is perforated cranially. Thus waterfowl are said to have *nares perviae* while others have *nares imperviae*. The nasal cavity serves as both the portal of entry to the respiratory system and the organ of smell. The nostrils are mostly located at the base of the beak, and can be placed dorsally, ventrally or laterally. They are placed at the tip of the beak in kiwis. The nostril may be hidden by feathers, or closed by cornified cell overgrowth, as in gannets, which breathe through the mouth. In the domestic fowl and turkey an operculum slightly overhangs the dorsal margin of the nostril. In doves, psittacine birds and some other birds, the external nares are set in a swollen, sensitive cere.

Nasal conchae

In the majority of birds there are three nasal conchae, which arise from the lateral nasal wall:

a. rostral (vestibular) nasal concha (*concha nasalis rostralis*);
b. middle nasal concha (*concha nasalis media*); and
c. caudal (olfactory) concha (*concha nasalis caudalis*).

The nostril acts as a nozzle which directs the incoming air into the rostral concha, which acts as a baffle plate. From here the air is directed dorsally into the olfactory region (caudal concha), along the middle concha and into the choana.

Rostral nasal concha

This is the most variable region in birds. The rostral concha is a rostrally pointed cone, C-shaped in transverse section. It is absent in quail, the emu (*Dromaius novaehollandiae*), the Indian white-backed vulture (*Gyps bengalensis*), and pelicans (*Pelecanus* sp). and very much reduced in gannets.

Middle nasal concha

This is the largest concha, decurved or scroll-like in transverse section. It is rarely missing (except in some cormorants). A nasal "valve" is found in water birds, firmly attached to the nasal roof, with its rostral edge free. This valve lies in close apposition to the roof when the bird is out of water, allowing inspired air to enter the olfactory region. When the bird places its head under water, as in feeding or diving to obtain food, the valve flips shut, deflecting water from the olfactory region, thus protecting it from insult (see Figure 10). Diving kingfishers have nasal valves, as do kiwis (*Apteryx* sp), the laughing kookaburra (*Dacelo novaeguineae*) and the woodland kingfisher (*Halcyon senegalensis*).

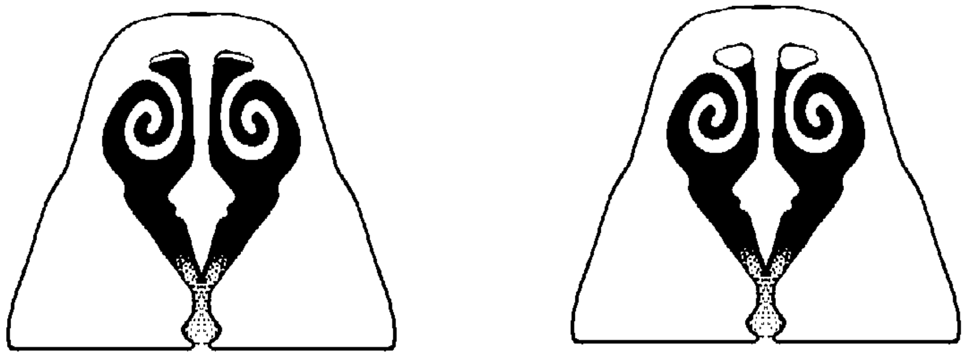

Figure 10: Nasal valves. The valves on the left are in the resting position, in close apposition to the roof of the nasal cavity. The valves on the right are almost occluding the dorsal airway - the position of the valve when the bird is diving, swimming or feeding.

Caudal nasal concha

This is usually a hollow mound projecting from the lateral nasal wall. Unlike the other conchae its cavity connects with the infraorbital sinus, and not with the nasal cavity. The epithelial lining of its outer (nasal) surface is olfactory. It is absent from some species, like the White-bellied or Glossy Swiftlet (*Collocalia esculenta*), and has been rumoured to be absent from some falcons.

The **infraorbital sinus** is a paranasal sinus which lies ventral and caudal to the eye. It extends nuchally under the bulb of the eye. This nuchal part expands as the bird ages and becomes larger than the apical part. Immediately anterior to the orbit the sinus extends up to the roof of the nasal cavity where it communicates with the interior of the caudal nasal concha. In some birds the sinus may also communicate with the nasal cavity just below the ventral border of the olfactory epithelium. The sinus is absent from the great cormorant (*Phalacrocorax carbo*) and pelicans (*Pelecanus* sp). In psittacine birds the right and left infraorbital sinuses communicate with each other and also have diverticula which pneumatise extensive areas of the skull. In Amazon parrots these diverticula extend dorso-laterally on each side of the neck as far back as the seventh cervical vertebra.

The nasal (salt) gland

In the majority of birds the salt gland consists of lateral and medial lobes, each with its own duct and ostium. It discharges into the nasal vestibule at the rear of the rostral concha. In the domestic fowl and turkey only the medial lobe is present, with its duct and ostium. In these two species the gland lies over the dorsal aspect of the eyeball and continues rostrally in the lateral wall of the nasal cavity. The gland secretes a 5% NaCl solution in marine birds, and has an osmoregulatory function in desert species (*Struthio camelus*) and some *Falconiformes*. The gland is missing from cassowaries (*Casuarius* sp), screamers (*Anhima* sp), sandgrouse (*Pterocles* sp), toucans (*Ramphastos* sp) and the hoatzin (*Opisthocomus hoazin*).

Choana (palatine cleft, choanal cleft)

Inspired air passes from the nasal cavities into oropharynx through a median slit-like opening between the left and right palatine bones and the palatine processes of the maxillae. At this point, the septum between the right and left nasal cavities is incomplete, so that they are in communication. Caudal to the choanal cleft is the infundibular cleft, which leads into the dilated tubopharyngeal space, the infundibulum tubarum, which contains the openings of the eustachian tubes.

Larynx

The laryngeal mound protrudes into the caudal part of the oropharynx. On its rostral surface is the slit-like opening into the larynx, the glottis. The glottis is formed by the arytenoid cartilages. On the caudal part of the laryngeal mound are backward-facing papillae which presumably are used to scrape food into the oesophagus.

Trachea

The trachea in most birds is a straight tube extending from the larynx to the syrinx in the anterior part of the thorax. The trachea consists of overlapping complete cartilaginous rings. Each ring consists of broad and narrow parts, the broad part of one cartilage overlapping externally the narrow parts of the two adjacent rings. The rings progressively decrease in diameter caudally, the lumen also decreasing in diameter. In all passerines and the domestic fowl, the trachea starts in the midline, passes to the right side of the neck, and then back to the midline to enter the thoracic inlet. Within the thorax it is closely related to the clavicular air sac. In hummingbirds (*Trochilidae* sp) the trachea divides into the two primary bronchi in the mid-cervical region. In some species, the trachea is oddly elongated into convolutions or coils or bulbous expansions which lie between the skin and pectoral muscles. Tracheal coils are usually confined to the male, but when present in both sexes, are better developed in males. They develop after hatching and are fully developed at adulthood.

Tracheal loops

Gadow and Selenka (1891) divided bird tracheas into five looping arrangements:

a. a loop in the caudal part of the neck - the male Capercaille (*Tetrao urogallus*);

b. a loop which extends caudally between the pectoral muscles and skin, sometimes to the level of the cloaca. This occurs in the male Magpie Goose (*Anseranas semipalmata*); the female Painted Snipe (*Rostratula benghalensis*) - the male has a straight trachea; both males and females of Guans (*Penelope* sp); and Birds of Paradise.

c. a loop which fits into a hollow in the enlarged sternal extremity of the furcula - both sexes of Guinea Fowl (*Guttera* sp).

d. a long loop which extends caudally past the furcula and lies in a cavity of the sternum. This occurs in both sexes of several swan species, including the Whistling Swan (*Cygnus columbianus*) and the Whooper Swan (*Cygnus cygnus*). In the Black Swan (*Cygnus atratus*) the trachea forms only a short bend at the thoracic inlet.

5. the trachea extends caudally past the furcula and forms several intrathoracic loops which lie in a cavity in the sternum. This occurs in many male and female cranes (*Grus* sp and *Anthrapoides* sp), the male Yellow-billed Stork (*Ibis ibis*), and the White Spoonbill (*Platalea leucorodia*).

Tracheal sacs

A tracheal sac is present in the Emu (*Dromais novaehollandiae*) and the Ruddy Duck (*Oxyura jamaicensis*). In the emu the sac is present in both sexes and is fully developed only in adult birds. It arises from the ventral surface of the trachea ¾ of way down the neck, the ventral parts of the tracheal rings at this point being incomplete. The caudal end of the sac almost reaches the sternum. The tracheal sac of the Ruddy Duck occurs only in male ducks and opens in a depression of the dorsal wall of the trachea immediately caudal to the larynx.

Tracheal bulbous expansions

The trachea of many male ducks is enlarged to form a rigid bulbous expansion. There may be one or two expansions, and they are usually found in the middle of the neck or its caudal two-thirds. In the *Freckled Duck* (*Stictonetta naevosa*) the second expansion lies in the cranial third of the trachea.

"Double" tracheas

A median septum which divides the trachea into right and left channels has been described in some penguins (*Spheniscidae*) and petrels (*Procellariidae*). This septum extends cranially from the bronchial bifurcation and is thus similar to the transient tracheal septum seen in bird embryos. The length of the septum varies widely.

Syrinx

The syrinx occurs at the junction of the end of the trachea and the beginnings of the left and right primary bronchi. The syrinx is composed of variably ossified cartilages (the tympanic cartilage, the pessalus and the caudal syringeal cartilages) and soft structures (a pair of medial tympaniform membranes, a pair of lateral tympaniform membranes and labia) and syringeal muscles.

In male *Anatinae* there is a symmetrical dilation of the left side of the tympanum, the syringeal bulla (*bulla tympanica* or *bulla syringealis*). In the Common Shelduck (*Tadorna tadorna*) there is a bulla on both sides, but the right is larger. Whistling Ducks (*Dendrocygna* sp) have a bilaterally symmetrical bulla.

Lung

Avian lungs are dorsal in position and can be either quadrilateral or triangular in shape. In no species of bird is the lung lobed. The dorso-medial aspects of the lungs are deeply embedded in the vertebral ribs.

The trachea divides at the syrinx into the extrapulmonary parts of the right and left primary bronchi. The intrapulmonary parts of the bronchi continue through the lung to open into the abdominal air sacs. The secondary bronchi include all bronchi arising from the primary bronchus. Secondary bronchi terminate at the ostiums of various air sacs.

Air sacs

The air passages of the lung communicate with transparent, thin-walled chambers, the air sacs.

a. **Cervical air sac**. This sac lies between the lungs and dorsal to the oesophagus and gives rise to a pair of tubular diverticula on each side of the vertebral column, one inside the neural canal and one outside. The latter penetrates and pneumatises the cervical and thoracic vertebrae and vertebral ribs. The cervical sac is absent from loons and grebes. It fuses with the clavicular sac in turkeys and the House Sparrow. Subcutaneous diverticula are present in some species (Great Indian Hornbill, *Buceros bicornis*; the Northern Screamer (*Chauna chavaria*) and the *Accipitridae*.

b. **Clavicular air sac** - originates from four primordial sacs, a medial pair and a lateral pair, which fuse along the midline to form a single unpaired sac. It occupies the cranioventral part of the thorax. It pneumatises the sternum, sternal ribs, pectoral girdle and humerus.

c. **Cranial and caudal thoracic air sacs**. Paired sacs with no diverticula.

d. The abdominal air sac is paired in all birds. When artificially inflated this sac has a large capacity, but in reality it is merely a potential space. The abdominal sac pneumatises the synsacrum, pelvis and head and body of the femur.

In the embryo there are six pairs of primordial air sacs: cervical, lateral clavicular, medial clavicular, cranial thoracic, caudal thoracic and abdominal. Thus there is a potential of 12 sacs. However, the actual number is always less than 12, because of the fusion of the four primordial clavicular sacs into a single sac, making the more usual total of 9. In storks the caudal thoracic sac is divided into two, making 11 sacs. In the domestic fowl there are 8 sacs, dur to the fusion of the cervical sacs.

Pneumatisation of bones is poor in non-flying birds, and many small flying birds (swifts - *Apodidae*; swallows - *Hirundinidae*). In powerful fliers such as swans (*Cygnus* sp), albatrosses (*Diomedea* sp) and eagles (*Aquila* sp) pneumatisation is very extensive.

Urinary System

The paired kidneys are retroperitoneal and lie generally symmetrically in contact with the pelvis and synsacrum, and extend from the lungs cranially to the end of the synsacrum caually. They are buried into bony depressions in the synsacrum, called synsacrum fossae, and are divided into cranial, middle and caudal divisions. The external iliac artery and vein separate the cranial and middle divisions, while the ischiadic artery and vein separate the middle and caudal divisions. In most non-passerine birds these divisions are distinct, but in passerine birds they are largely fused (close inspection will reveal the divisions, however). In addition, the relative sizes and shapes of the divisions vary greatly. In some birds (herons, puffins and penguins) the caudal divisions are fused in the midline. In hornbills there is no middle division, only separate cranial and caudal divisions.

Blood supply

The blood supply to the kidney is via the arterial and portal systems.

Arterial blood supply

Three pairs of arteries supply the kidneys, cranial, middle and caudal. The left and right cranial renal arteries arise directly from the aorta, and supply the cranial lobes, while the left and right middle and caudal renal arteries arise from the left and right ischiadic arteries, and supply the middle and caudal lobes.

Portal blood supply

The external iliac vein (which brings blood from the hind limb) on entering the kidney, branches into the caudal renal portal vein and the common iliac vein. The common iliac vein gives off the cranial renal portal vein. The right and left common iliac veins unite to form the caudal *vena cava*. The cranial and caudal renal veins drain the kidney into the common iliac vein.

The renal portal valve is a smooth muscle sphincter which lies just peripheral to the junction of the caudal renal vein and the common iliac vein. The degree of contraction of this sphincter controls how much blood is prevented from flowing directly into the caudal *vena cava*. Diverted blood then goes into the cranial and caudal renal portal veins.

Blood flow to the cranial portal vein is from the common iliac vein. However, the blood flow to the caudal renal portal vein is more complex. Caudally, the ischiadic vein flows into it between the caudal and middle divisions of the kidney. Further caudally the left and right caudal renal portal veins anastamose in the midline, and at this point the caudal mesenteric and internal iliac veins also anastomose with the caudal renal veins. Thus the major portal vessels of both kidneys form a vascular ring called the renal portal circle, and so portal blood can enter the kidneys via the external iliac, ischiadic, internal iliac and mesenteric veins.

Ureters

The ureters are found on the ventral surface of the kidneys except in the cranial division where it is partially embedded in the kidney. In males each ureter is closely joined to the ductus deferens by connective tissue. In immature females the left ureter is similarly joined to the oviduct, but this is not so once the female matures. The ureter terminates in the urodeum, and it possesses no valve-like structures or sphincters.

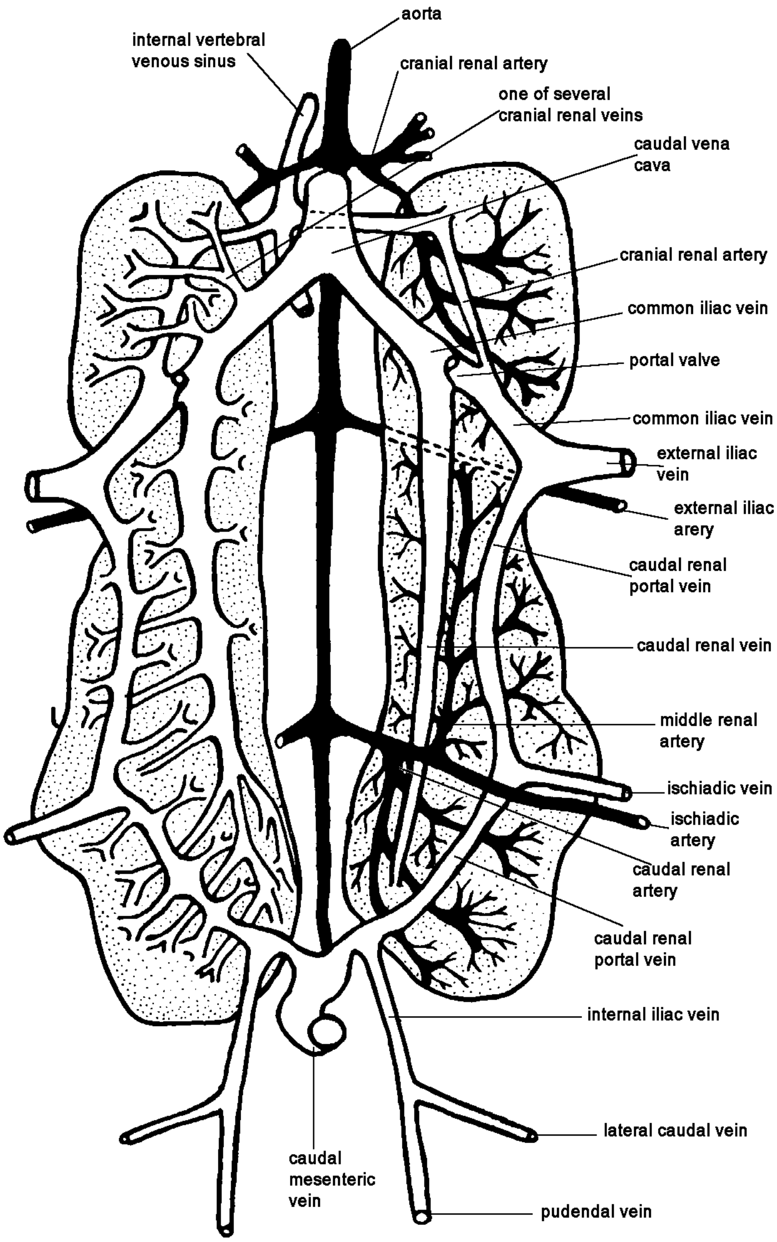

Figure 11: Ventral view of the kidneys of the domestic fowl. The left side shows renal portal and efferent veins; the right side shows arteries (modified from King and McLelland (1979).

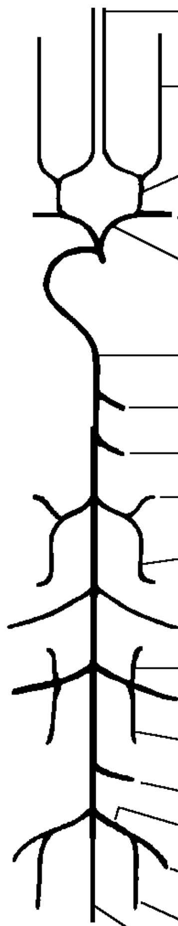

Figure 12: The main arteries of the domestic fowl (modified from King and McLelland (1975).

The Endocrine System

Introduction

When parenchymal cells of endocrine glands are injured, they undergo cell swelling, loss of glycogen, and fatty degeneration, as do other rapidly metabolising cells. Pathologic changes that occur in the endocrine glands are reflected not only in their parenchymal cells but in the target cells stimulated by their secretions. Furthermore, many of the endocrine glands are under trophic control of the pituitary gland, and cell changes can sometimes be detected in this organ. The course of most endocrine disease is made more complex by secondary interacting feedback mechanisms. For example, parathyroid hormone is secreted in response to hypocalcaemia, and calcitonin secreted in response to hypercalcaemia. When blood calcium levels are drastically diminished, multiple cycles of secretion of these two hormones may be required before plasma calcium levels return to normal and stabilise. This may cause the lesions in bone, the target organ, to be difficult to evaluate.

In examining cells taken from animals with endocrine disease, it is imperative to know at what stage of the process the tissue was taken. Hypertrophy and hyperplasia are the response of endocrine glands to stimulation. Their parenchymal cells therefore are expected to be heavily granulated. This is indeed the case after a simple cycle of stimulation-hypertrophy. In the earliest phase, cells may be degranulated although organelles remain small. Endocrine cells tend to discharge their granules explosively as an immediate response, while synthesis of new hormone and regranulation may take several hours. In long-term hyperplasia, the endocrine cells may be heavily granulated or virtually devoid of granules. Prolonged stimulation usually leads to diverse reactivity among the cells of a gland, but it is common to find many cells with few granules and shrunken cytoplasm: evidence of exhaustion and inability to react to further stimulation for hormone release.

Hypophysis (Pituitary Gland)

The hypophysis lies immediately beneath the diencephalon, just caudal to the optic chiasma. It is accommodated within the *fossa hypophysialis* of the *sella turcica*, a part of the basisphenoid bone. The hypophysis consists of two parts:

a) the adenohypophysis, which is derived from the pharyngeal epithelium of the embryonic Rathke's pouch; and

b) the neurohypophysis, which is a downgrowth of the post-optic part of the hypothalamic floor.

The avian adenohypophysis is divided into two parts, the *pars distalis* and the *pars tuberalis*. There is no separate pars intermedia, although in individuals of some species of birds there may be a zone of intermedia-like cells where a small section of the dorsal surface of the *pars distalis* makes contact with the ventral surface of the neural lobe. The pars distalis is connected to the median eminence of the neurohypophysis by the porto-tuberal tract of the *pars tuberalis*. The *pars distalis* is divided into rostral and caudal zones, while the *pars tuberalis* is divided into the *pars tuberalis* proper, the porto-tuberal tract and the *pars tuberalis interna*.

The neurophypophysis consists of three parts: the infundibulum, the median eminence, and the neural lobe (*pars nervosa*). The median eminence is covered by the *pars tuberalis*. The infundibulum is part of the hypothalamic wall. The neural lobe is a saccular structure overlying the caudal end of the *pars distalis*. The *pars tuberalis* proper is the largest of the three subdivisions of the *pars tuberalis*, and consists of a thin sheet of cells lying within the *dura mater* on the ventral surface of the brain. It covers the floor and sides of the median eminence, as well as the sides of the infundibulum. The porto-tuberal tract extends ventrally from the *pars tuberalis* proper and surrounds the hypophyseal portal vessels. The infundibulum, the *pars tuberalis* proper and the median eminence are situated within the dura mater, while the *pars nervosa*, the *pars distalis*, and the remainder of the *pars tuberalis* are situated external to the *dura mater*.

Structure of the adenohypophysis

The *pars distalis* is divided into rostral and caudal zones, the acidophils of the rostral zone being light-staining, whilst those of the caudal zone are more darkly staining. The cell cords of the rostral zone are more closely packed than those of the caudal zone.

The cell types of the pars distalis are as follows:

a) **Protein-containing cells**

i) α cells or caudal acidophils, which secrete somatotrophic hormone, which regulates body growth in immature birds.

ii) η cells or cephalic acidophils, which produce prolactin, a hormone which causes broodiness and in some birds stimulates the production of brood patches.

b) **Glycoprotein-producing cells**

i) β cells or rostral PAS-positive cells, which are basophilic cells and which do not stain with alcian blue. They produce follicle stimulating hormone, which stimulates the development of ovarian follicles and the secretion of ovarian oestrogens, as well as testicular growth and sperm maturation.

ii) δ cells or alcian blue-positive cells. These cells are moderately PAS-positive. They produce thyroid stimulating hormone which controls the activity of the thyroid gland and the secretion of thyroid hormones. These cells are found in both the rostral and caudal zones.

iii) γ cells or glycoprotein-containing acidophils, which occur in the caudal zone and produce luteinising hormone (LH). LH causes ovulation in females and stimulates the production of androgen by the interstitial cells of the testis.

c) **Mixed cell types**

i) ϵ cells, slightly acidophilic and PAS-positive, and which become visible after adrenalectomy in the centre of the rostral zone. They produce adrenocorticotropic hormone, which controls the production of adrenal corticosteroids.

ii) κ cells, basophils, may occur in either or both zones (depending on the species of bird), and secrete melanotropic hormone (the function of which is uncertain).

d) **Chromophobe cells**

These are small spherical cells which are found in small clusters throughout the *pars distalis*. These cells are poorly granulated and appear to be undifferentiated non-secretory cells. The *pars tuberalis* consists of cords of cells surrounded by a basement membrane.

Structure of the Neurophypophysis

The *pars nervosa* consists of three basic layers:

a) the ependymal layer, which lines the lumen of the lobe and sends nerve processes through the other two layers to the external surface;

b) the fibre layer, which is formed by nerve fibres of the supraoptico-hypophysial tract; and

c) the glandular (external) layer, formed by the distal ends of cell processes.

Vasotocin (ADH) and oxytocin are packaged in nerve cell bodies within the hypothalamus and pass to the rostral median eminence and *pars nervosa* via axons. In contrast, the hypothalamic releasing factors which control the glandular portion pass to the pituitary via a special capillary network.

Thyroid Gland

The paired thyroid glands are situated at the base of the neck at the thoracic inlet, one on either side of the midline. They develop as a single median diverticulum of the pharynx which divides to form two separate lobes, each taking up a position on the medial side of the jugular vein immediately cranial to the angle between the subclavian and carotid arteries. Their colour varies from translucent yellow to deep red. The thyroid gland is enclosed by a thin capsule. The gland consists of roughly spherical follicles, each lined by a single layer of endodermal cells, and each containing a colloid (thyroglobulin).

The thyroids synthesize, store and secrete thyroxine. Thyroglobulin is formed in the endoplasmic reticulum of follicular cells then secreted into the lumen of the follicle by exocytosis. Iodine is bound to thyroblobulin at this stage. Thyroxine is formed extra-cellularly in the follicle colloid. Colloid is scavenged back into epithelial cells by endocytosis, then thyroglobulin is degraded down to thyroxine and secreted into adjacent capillaries. In iodine deficiency, thyroxine output is decreased, there is a compensatory rise in pituitary TSH secretion and consequent hyperplasia of thyroid epithelium. This is still a common problem in caged budgerigars. The location of the thyroids is such that hyperplasia (goitre) often causes respiratory distress and coughing. Pressure on the oesophagus may cause regurgitation of food.

The C-cells of the thyroid are formed into a separate gland - the ultimobranchial gland. It is located on the medial side of the bifurcation of the brachycephalic artery. These cells secrete calcitonin, which acts to inhibit bone matrix resorption, thereby lowering blood calcium.

The Parathyroid Glands

The paired parathyroid glands lie on either side of the mid-line at the thoracic inlet, caudal to the thyroid glands, in front of the subclavian artery, and between the common carotid artery medially and the jugular vein laterally. In the domestic fowl they develop from the third, fourth and fifth pharyngeal pouches, and are designated pharathyroid glands III, IV and V.

Parathyroid V is usually enclosed by the ultimobranchial gland. Their colour varies from translucent yellow to brownish-red. They are bounded by the thyroid gland cranially, the subclavian artery caudally, the common carotid artery medially and the jugular vein laterally.

The parenchyma contains a single cell type, the chief cell. No oxyphil cells are present. The cells present a range of profiles according to the angle at which they are cut. The cytoplasm is basophilic and finely granular when full of secretory product, and clear when degranulated.

Pro-parathyroid hormone is made by rough endoplasmic reticulum in the chief cells, and packaged into parathyroid hormone (PTH) by the Golgi apparatus. PTH induces elevations in plasma calcium by increasing osteolysis by osteoclasts and osteocyte enzyme activity. PTH also increases renal excretion of phosphorus and augments intestinal absorption of calcium. PTH is secreted in response to low blood calcium, and parathyroid hypertrophy occurs when the demands for plasma calcium are persistently increased. Laying hens have large parathyroids dominated by active chief cells. Nutritional hyperparathyroidism is common in birds, usually manifest as bone disease. Unsupplemented all-meat diets, or improperly formulated pellets are the usual cause.

The Ultimobranchial Gland

The paired ultimobranchial glands are situated within the angle formed by the brachiocephalic trunk into the subclavian and common carotid arteries, with the common carotid artery lying medial to the gland, and the jugular being lateral to it. The gland is not enclosed by a capsule and so tends to merge gradually with adjacent tissues. The parenchyma of the gland consists of cords of cells and groups of vesicles. The glandular component has four components: C cells, parathyroid nodules, vesicles and lymphoid tissue.

a) C cells. These constitute the major proportion of the ultimobranchial gland. They produce calcitonin and have a variable shape, with a prominent nucleus and a granular cytoplasm.

b) Parathyroid nodules. These are separated from the rest of the ultimobranchial gland by a capsule and represent parathyroid V.

c) Vesicles. These are of variable shape and size and occur throughout the gland. They are lined by an epithelium which may be low columner (simple or stratified), cuboidal or squamous. The vesicles contain colloid-like material, cellular remnants representing desquamated lining cells, and granular material.

d) Lymphoid tissue. The gland contains foci of lymphoid tissue as well as collections of thymus tissue.

The Adrenal Glands

The adrenal glands are small, paired structures, lying in the thoracoabdominal cavity, cranial and medial to the anterior poles of the kidneys and just behind the lungs. In many birds (galliform birds, ducks and pigeons) there are two distinct glands. In some species, such as the greater rhea (*Rhea americana*), the maguari stork (*Ciconia maguari*), the bald eagle (*Haliaeetus leucocephalus*) and the common loon (*Gavia immer*), the two glands are fused into one structure.

The glands vary in colour from greyish-yellow to reddish-yellow. When placed in formol-saline, they discolour the fixative yellow. They are enclosed by a capsule of dense fibro-elastic connective tissue. The parenchyma is composed of two main tissue types: the "cortex" and the "medulla". Although they are termed as such, there is no definite cortex and medulla as in the mammalian gland, and it has been suggested they be termed inter-renal tissue (cortex) and chromaffin tissue (medulla). Cords of cortical and medullary cells interdigitate and mix throughout the gland.

Cortical tissue consists of anastomosing cords of cells. In cross section the cells are arranged radially. There is no central lumen, however, and the basal poles of the cells rest on a basement membrane, outside which lie capillaries.

Medullary tissue consists of irregular strands and masses of basophilic cells scattered throughout the cortical tissue. The cells are larger than cortical cells and have a well-developed nerve supply.

The subcapsular zone of the adrenal gland is associated with mineralocorticoid activity while the central zone is concerned with glucocorticoid production. The two major hormones of the cortex are corticosterone (glucocorticord and mineralo-corticoid) and aldosterone (mineralocorticoid). Aldosterone acts on kidney tubules to increase sodium reabsorption from the glomeruler filtrate, and so increases retention of sodium and water within the body. It also stimulates sodium efflux in the nasal gland of marine birds.

Corticosterone induces lipogenesis, resulting in increased lipaemia and deposition of fat. It also induces hyperglycaemia and deposition of glycogen in the liver.

Acute stress causes an initial marked depletion of glucocorticoid granules from cortical cells. The adrenals become small, buff coloured and haemorrhagic. Acute stress is often seen in injured birds, particularly falcons. In chronic stress, hyperplasia of the cortex develops. Birds exposed to long periods of cold, and a low plane of nutrition may develop massive adrenals, e.g. sea birds. Stress damage is caused by local endothelial cell damage and vasoconstriction, with consequent parenchymal damage. In acute generalized infection, glucocorticoids are elevated; in chronic disease they are depressed.

The adrenal medullary tissue secretes two hormones, adrenaline and noradrenaline. These are synthesized within medullary cells from tyrosine, via dopamine to adrenaline, which form dense granules. Adrenaline-storing cells stain with acid-phosphatase techniques, but do not react with silver or iodine. Noradrenaline-storing cells are auto- fluorescent and stain with silver or iodine, but not acid phosphatase. Adrenaline provides a transient reaction for sudden bursts of muscle power, it makes the heart beat fast and stronger, the spleen contract and blood go to the muscles.

Pineal gland

The pineal gland is dorsal outgrowth of the roof of the diencephalon and lies in the narrow triangular space between the cerebral hemispheres and the cerebellum. It is a narrow conical organ with its base extending dorsally and attached to the dura, and its apex directed ventrally as a slender stalk to the diencephalon.

It is divided into two parts: the narrow basal stalk and the more extensive lobular parenchymal gland itself. In the domestic fowl, the latter consists of a number of large, irregularly polyhedral lobules separated from each other by narrow connective tissue strands. Within the lobules may be found compact rosettes of cells either with or without a lumen. Two types of cells are described. Ependymocytes are tall columnar cells with basal nuclei in the form of rosettes arranged radially around lumina. Hypendocytes are polygonal cells arranged concentrically and peripheral to the ependymocytes. The pineal gland may be involved in control of reproductive function, photo-reception and circadian rhythm.

The Endocrine Pancreas

The pancreas is a long, narrow, grey-white to pinkish gland which lies in the mesentery connecting the two arms of the duodenal loop. It consists of dorsal, ventral and splenic lobes. It is functionally divided into the exocrine, enzyme-secreting portion, and the endocrine, hormone-secreting portion, the islets of Langerhans. The pancreatic islets can be divided into light, dark and mixed cell types. Dark (A or α) islets are largest in the splenic lobe. The borderline between the islets and the exocrine pancreas is indistinct, since the cell types insinuate. They consist of two cell types, α and δ cells. α cells are columnar and contain cytoplasmic granules which stain with phloxine and orange G. δ cells are small and occur singly or in groups near the connective tissue supporting structure of the islets. Light (B or β) islets are rounded or ellipsoidal bodies scattered at random throughout all lobes of the pancreas. They are composed of beta cells and a few delta cells. β cells are polygonal and arranged in strands. The argyrophil reaction of these cells is negative, hence β islets are termed 'light' islets.

Birds have a high percentage of α cells which produce glucagon, and fewer β cells (insulin) and δ cells (gastrin). The duck has separate alpha cell islets. α cell degranulation and release of glucagon is a reaction to hypoglycaemia. Glucagon interacts with liver cell enzymes to increase glycogenolysis, and suppress enzymes, e.g. pyruvate kinase, which normally inhibit glucose formation.

Beta cells produce insulin and are a well-known model of hormone production, i.e: formation of proinsulin in the endoplasmic reticulum, packaging of insulin granules in the Golgi complex and release by exocytosis. Insulin facilitates the entry of glucose into cells by binding onto membrane sites and accelerating glucose transport systems. Excess blood glucose causes the active exocytosis of β cell granules. δ cells produce gastrin and somatostatin. Diabetes mellitus caused by β cell destruction has been reported in chickens and budgerigars.

The Lymphatic System

Introduction

The lymphatic system of the domestic fowl has been described in detail by Firth (1977), Rose (1981) and Payne and Powell (1984). Lymphatic tissue in general consists of reticulin fibres and fixed cells (macrophages and reticulin cells), as well as free cells (lymphocytes, plasma cells and granulocytes). In loose lymphatic tissue, fixed cells predominate, whereas in dense lymphatic tissue, free cells predominate. The avian lymphatic system may be divided into:

1. primary lymphatic tissue (central), which consists of the **thymus** and **cloacal bursa**. This is antigen dependant, and in it incoming stem cells differentiate into immunologically competent B and T cells, which then migrate to the secondary lymphatic tissue; and

2. secondary lymphatic tissue (peripheral), which consists of the **spleen**, **bone marrow**, **mural lymphoid nodules** and variable aggregations of lymphocytes throughout the body. Secondary lymphatic tissue is antigen dependent "effector" tissue, in which B and T cells mature into respective effector cells.

The stem cells which colonise the embryonic thymus and bursa originate in the *area pellucida* or embryo proper in birds. Late in embryonic development, stem cells may be found in the liver and spleen. In adult life they exist primarily in the bone marrow.

Lymphatic vessels are closely associated by connective tissue to the arteries in the trunk, and to the veins outside the trunk. These drain into the jugular and subclavian veins, the cranial *vena cava*, and the thoracoabdominal trunks (thoracic ducts). In the domestic fowl, the latter extend on either side of the aorta and drain into the cranial *vena cava*. The wall of lymphatic capillaries consists of a layer of flat endothelial cells. As the vessels increase in size they develop a layer of collagen and elastic fibres and a few smooth muscle cells. Along the course of these vessels may be found lymphatic plexuses. Valves are occasionally found in the larger lymphatic vessels.

"Lymphatic hearts" are muscular dilatations of the lymphatic vessels and occur in the embryonic stages of all species but persist into adult life only in ratite birds. They lie at the level of the second coccygeal vertebra between the origins of the *m. flexor cruris medialis* and the dorsal coccygeal muscles. They have three layers: an endothelial layer, a middle muscular layer and an outer fibrous layer.

Primary Lymphoid Tissue

1. **Thymus**

The epithelial portion of the thymus is derived from the 3rd and 4th branchial pouches and in the domestic fowl consists of 4-7 lobes extending from the 3rd cervical vertebra to the thyroid gland within the thoracic cavity. In some instances the thyroid gland may contain thymic tissue.

The thymus is a primary lymphoid organ and contains T cells which are derived from embryonic stem cells which colonise the embryonic thymus. The thymus increases in size to 17 weeks and then slowly regresses.

Each lobe is enclosed by a connective tissue capsule of collagen and elastic fibres. True septa pass inward from the capsule and divide the lobe into lobules, which may be further subdivided by septules into segments. Each lobule is indistinctly divided into cortex and medulla.

The cortex consists of densely packed small lymphocytes and a few medium-sized lymphocytes. Since the lymphocytes in the medulla are much larger and fewer, the medulla stains more lightly than the cortex. Reticular cells in the medulla form small, rounded islands called thymic corpuscles (Hassal's corpuscles). Also within the medulla are myoid cells. These contain myofibrils and are commonly found in the thymus of birds and reptiles, although their function is not known.

Thymic lymphocytes are derived from stem cells from the circulation. The main function of the thymus is as a maturation site in which stem cells differentiate into T lymphocytes which then populate the secondary lymphoid tissues. Endocrine- like cells at the cortico-medullary junction have been described. The thymus also contains B-lymphocytes, and in older birds contains germinal centres. The thymus thus also acts as a peripheral lymphoid organ, and in times of stress may become erythropoietic.

2. **Cloacal Bursa**

The cloacal bursa (bursa of Fabricius, *bursa Fabricii*) is a blind, dorsal diverticulum of the cloacal proctodeum. In the domestic fowl it is largely spherical, and its inner surface is thrown into a number of folds (plicae) which can partly obscure the lumen. It reaches maximum size in the domestic fowl (relative to body weight) at 3-6 weeks of age, and begins to regress at 8-12 weeks of age. It is completely regressed at sexual maturity (18-22 weeks of age), and disappears at 6 months to one year.

The wall of the bursa consists of three layers: a thin serosa, a *muscularis* and the mucosa. The mucosa is thrown into 10-15 folds, each of which contains numerous polyhedral lymphatic follicles (8-12,000 in the domestic fowl). Follicles are separated by a fine interfollicular septum consisting mainly of fibrous tissue. Each follicle consists of a central medulla enclosed by a cortex. In some ratites, cuckoos, and nocturnal raptors, however, the medulla is not enclosed by a cortex but lies between the cortex and the mucosal epithelium.

As in the thymus, the cortex stains more deeply because of its higher concentration of small lymphocytes. However, unlike in the thymus, the cortex and medulla of the follicles of the cloacal bursa are separated by a distinct basement membrane, capillaries and a thin layer of stellate reticular epithelial cells. Reticular epithelial cells form a supporting network for lymphocytes in the follicle. During regression, lymphocytes are lost from the cortex and medulla and the framework of reticular epithelial cells becomes more apparent.

The surface epithelium lining the inner surfaces of the plicae is a tall, columnar, pseudostratified epithelium.

The function of the bursa complements that of the thymus. It is primary lymphoid tissue which oversees the differentiation of B-lymphocytes from stem cells to fully mature plasma cells. The bursa also contains a small number of T cells. The bursa can also be involved in a local immunological response mainly via "cloacal drinking". It has been postulated that the fowl gains part of its immunity to environmental antigens in this way.

Secondary Lymphoid Tissue

In avian species, the secondary (peripheral) lymphoid tissue consists of the spleen, bone marrow, mural lymphoid nodules, lymphoid tissue in the digestive tract and oculonasal region, and the aggregated lymphoid nodules scattered throughout the body.

1. **Spleen**

The spleen in the domestic fowl and turkey is round to egg-shaped, while in aquatic birds it is triangular with a flat dorsal and convex ventral surface. It lies against the dorsal surface of the right lobe of the liver between the proventriculus and gizzard. The spleen functions as a peripheral lymphoid organ and also disposes of effete erythrocytes.

The connective tissue capsule of the spleen contains almost no smooth muscle and is covered by peritoneum. However, unlike the mammalian spleen, the avian spleen is not clearly subdivided by trabeculae arising from the capsule. Some workers claim that trabeculae do not exist in the spleen. The normal spleen is almost equally divided into red pulp (RP) and white pulp (WP). The WP is enclosed by RP and consists of islands of lymphocytes surrounding central arteries.

Radiating from these central arteries are the penicillar (penicilliform) arterioles, which, at the periphery of the WP, give rise to six to eight ellipsoidal arterioles (sheathed capillaries), small straight vessels with a cuboidal endothelium. These ellipsoidal arterioles are enclosed by reticular cells, forming the ellipsoid. In longitudinal section, ellipsoidal arterioles may be recognised by their parallel rows of endothelial nuclei. Blood from these vessels flows via "terminal arterioles" and empties directly into erythrocyte- filled spaces between the reticular cells of the RP. Blood from these spaces is collected by small veins arranged in a star-like manner (see Figure 1).

Varying amounts of lymphoid tissue surround the arteries and veins of the spleen. The ellipsoids are on the edge of the WP and lymphocytes surrounding them form the peri-ellipsoidal cuffs (B-lymphocytes). Lymphocytes surrounding arterioles form the peri-arteriolar sheaths and are T-lymphocytes. The latter make up the major part of the WP. The germinal centres (lymphoid follicles) of the WP, and the lymphocytes which surround them, are B-dependent. B-lymphocytes and antigen- bearing dendritic cells migrate from the peri-ellipsoidal cuff along the penicillary arterioles to their point of origin from the central artery, where they form germinal centres. Germinal centres are thus always associated with a central artery and are bordered by collagenous lamellae and crescentic sinuses which are connected with the venous system. Large follicles contain a corona of dark cells surrounding a light centre. Numerous mitoses may be present in germinal centres

2. **Bone Marrow**

The bone marrow functions as secondary lymphoid tissue - a source of B and T lymphocytes. It contains diffuse lymphoid tissue with germinal centres.

3. **Mural Lymphoid Nodules**

These are aggregations of lymphoid tissue associated with lymphatic vessels. They are very numerous and occur in all birds. They are usually confined to one side of a vessel and may protrude into the lumen. These nodules vary from diffuse aggregations of small lymphocytes up to organised tissue containing a number of germinal centres.

4. **Lymph Nodes**

In birds, lymph nodes exist only in certain aquatic birds (ducks and swans). They may be found on the dorsal surface of the jugular vein in the angle formed by the jugular and vertebral veins (cervicothoracic nodes), and on each side of the lumbar aorta (lumbar nodes). The former occur as elongated structures surrounding the end-point of the cervical lymphatic duct.

The centre of the node consists of a sinus which is, in effect, an intranodal lymphatic vessel. This central sinus is surrounded by a zone of dense lymphoid tissue consisting of small lymphocytes. Outside this is a peripheral zone of loose lymphoid tissue containing small and medium lymphocytes. The central sinus opens directly into the peripheral zone, where filtration takes place.

5. **Lymphoid Tissue of the Digestive Tract**

i) **Oral cavity and pharynx**. Lymphoid tissue is abundant in the oral cavity, particularly around the choana and the openings of the auditory tubes.

ii) **Small intestine**. Aggregations of lymphoid tissue occur regularly throughout the small intestine, and are analogous to the Peyer's patches (PP) of mammals. PP can be distinguished from the rest of the intestine by their thickened villi and large subepithelial accumulations of lymphoid cells. The epithelium of normal intestinal villi and crypts consists of tall columnar cells of three types: chief or main cells; goblet cells; and enterochromaffin cells, whereas PP are separated from the intestinal lumen by a flattened epithelium which has a marked absence of goblet cells. PP epithelial cells stain positively for acid phosphatase (AP) whereas the columnar cells of normal epithelium do not. AP has been postulated as a chemotactic agent attracting lymphocytes to specific areas of lymphoid organs. Discontinuities in the epithelium over PP allow lymphocytes and plasma cells to be extruded into the intestinal lumen. The presence of AP in the PP epithelium might act as a mediator in this extension.

Beneath the epithelium the PP consist of dense aggregations of lymphoid cells, either as germinal centres or as diffuse lymphoid tissue. Germinal centres are surrounded by several layers of reticular cells separating them from the diffuse lymphoid tissue.

In *Anas* sp there are four regularly spaced, macroscopically visible, annular bands of lymphoid tissue in the proximal and distal parts of the jejunum and ileum. The bands are about 1 cm wide. The distal jejunal and proximal ileal rings are well defined, whereas the proximal jejunal and distal ileal rings are not. In *Anser* sp there are seven such rings.

iii) **Caeca**. Large aggregations of lymphoid tissue, the "caecal tonsils", occur near the junction of each caecum with the rectum. They may be seen macroscopically as dilatations and thickenings of the necks of the caecae. Small lymphocytes predominate and germinal centres are common. Macrophages, plasma cells, mast cells and reticular cells are also present.

The lymphoid tissue of the digestive tract consists of both B and T cells. The B cells are concerned mainly with the production of IgA.

6. **Oculonasal Lymphoid Tissue**

The amount of lymphoid tissue in the oculonasal region varies between species. It is relatively large in galliform birds but small in aquatic birds and passerines. This lymphoid tissue is found in the gland of the nictitating membrane (Harderian or Harder's gland) and its draining duct, the lacrimal (lachrymal) gland and its duct, and the nasal (salt) gland and its duct.

All these glands have a compound tubuloacinar structure and produce a merocrine secretion. The secretions of the Harderian and lacrimal glands clean and moisten the cornea. In the interstitium of the Harderian gland are accumulations of plasma cells, which secrete antibodies into the exocrine secretion to confer local immunity in the eye and upper respiratory tract. The lacrimal gland is less well developed than the Harderian gland, the reverse of the situation in mammals. The lacrimal gland and its duct contain foci of small lymphocytes and germinal centres, and a few plasma cells. If the Harderian gland is removed, the number of plasma cells in the lacrimal gland increases as a compensatory mechanism. In the domestic fowl the nasal gland and its duct contain sub- epithelial plasma cells. The Harderian gland is necessary for protection against challenge by infectious bronchitis (IB) virus in chicks vaccinated against IB virus by this route.

7. **Aggregations of Lymphoid Tissue in other Organs**

The secondary lymphoid tissue which occurs in the alimentary canal and oculonasal region has been described. In addition, variable amounts of lymphoid tissue may be found in parenchymatous organs, the gall bladder, pancreas, lungs, endocrine glands, gonads, skin and peripheral nerves. Some authors refer to these areas of lymphoid tissue as "ectopic lymphoid areas". It is considered that they function as the equivalent of mammalian lymph nodes. They consist mainly of small lymphocytes with or without germinal centres.

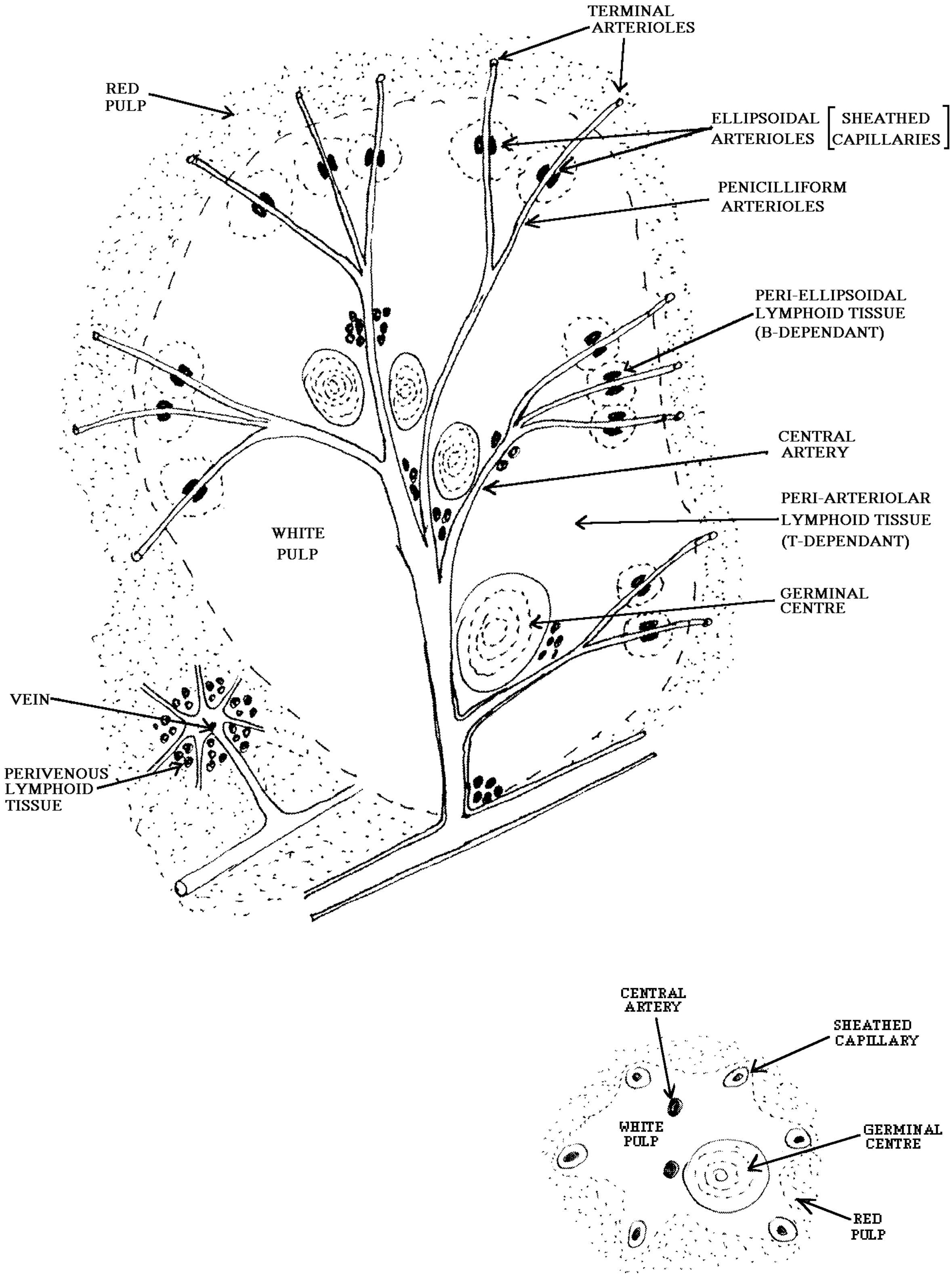

Figure 13: Structure of the avian spleen

The Nervous System

Introduction

The avian nervous system consists of the central nervous system (CNS - brain and spinal cord) and the peripheral nervous system.

The avian brain (encephalon) is divided into the following regions, rostrally to caudally:

a) the forebrain or prosencephalon, consisting of the telencephalon and the diencephalon;
b) the midbrain, or mesencephalon; and
c) the hindbrain or rhombencephalon, consisting of the cerebellum (metencephalon) and medulla oblongata (myelencephalon).

The hindbrain and midbrain have evolved similarly in mammals and birds. However, the forebrain has evolved divergently, and it is difficult to recognise homologous structures.

The olfactory bulb projects from the rostral end of the brain. A median fissure separates right and left hemispheres dorsally, but the surface is almost smooth.

The diencephalon is interposed between the midbrain and forebrain. It is covered by the cerebral hemispheres dorsally. The thalamus forms its lateral walls and contains numerous nuclei. The floor is termed the hypothalamus, the roof the epithalamus. just anterior to the hypothalamic stalk is the optic chiasma. Dorsally, the diencephalon carries a stalk, which extends to the meninges, where the pineal gland may be found.

The mesencephalon is the integration site of optic, acoustic, vestibular and protopathic stimuli. The tectum bulges out between the cerebrum and cerebellum as the rounded optic lobe. The cerebellum lies over the mesencephalon. A median section through it reveals the dark cortical layer and the inner white medullary layer. The cortex consists of three layers from outwards inwards: the molecular layer, the Purkinje cell layer and the granular layer. The molecular layer contains many thinly myelinated neurons originating from nerve cells within this layer as well as the dendrites of the Purkinje cells in the layer below. The axons of the Purkinje cells traverse the granular layer below and enter the white medullary substance where they end in cerebellar nuclei. The granular layer contains a large number of claw-like granule cells. The dendrites of these cells ascend into the molecular layer.

Meninges

The meninges are the protective membranes which separate the CNS from the bones of the cranium and vertebral column. The meninges consist of the *dura mater*, arachnoid and *pia mater*. Some workers claim that birds have no arachnoid, while others describe a thin avascular membrane on the inner surface of the *dura mater* as the arachnoid.

The *ligamentum denticulatum* arises from the spinal pia mater and suspends the spinal cord within the dural tube. Figure 14 shows a lateral view, and Figure 15 shows a ventral view, of an avian brain.

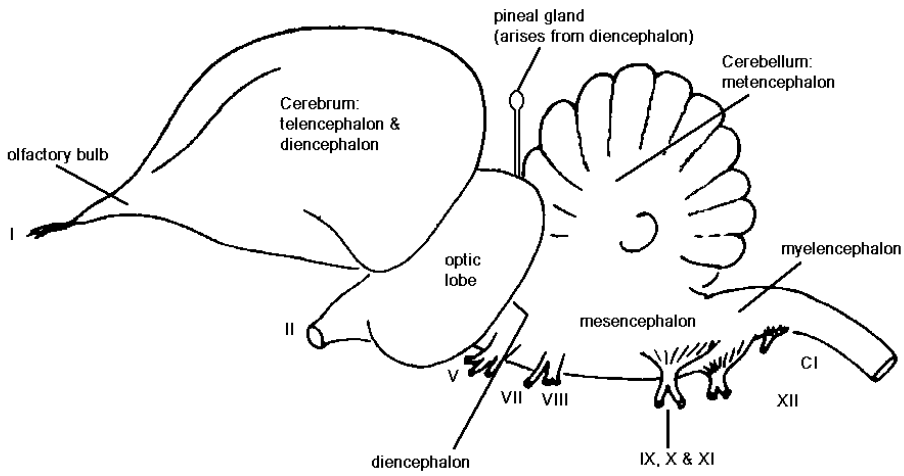

Figure 14: Lateral view of an avian brain

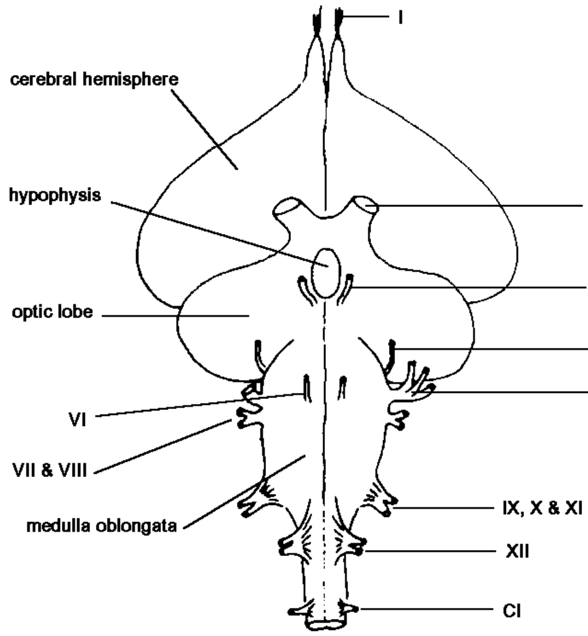

Figure 15: Ventral view of an avian brain

Spinal Cord

The spinal cord of birds has only a slight *cauda equina* and there is no *conus medullaris*. Along its length, it varies in diameter, and there are two distinct enlargements: cervical (*intumescentia cervicalis*) and lumbosacral (*intumescentia lumbosacralis*), which are respectively associated with the innervation of the wings and legs. The cervical enlargement is largest in birds of flight; the lumbosacral enlargement is largest in predominantly terrestrial birds.

In the region of the lumbosacral enlargement the dorsal surface of the spinal cord forms a fossa, the fossa rhomboidalis. This fossa contains a glial structure called the gelatinous (or glycogen) body (*corpus gelatinosum*). The ventral part of the gelatinous body surrounds the central canal (Figure 16).

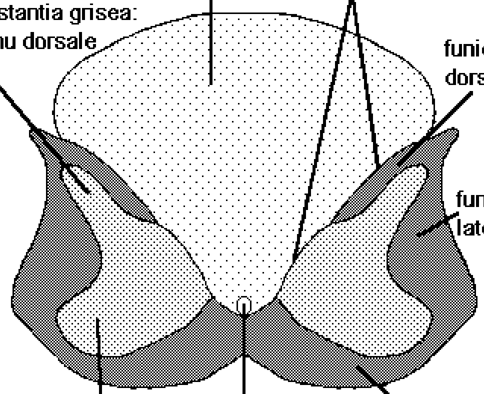

Figure 16: Transverse section of the synsacral part of an avian spinal cord, at the level of the widest part of the *sinus rhomboidalis*. Note that the dorsal parts of the cord are not united, and are separated by the gelatinous body, which enfolds the central canal.

Special Senses

The Eye

The largest eye of any land vertebrate is that of the ostrich. Its bulbar axial length (line passing from the centre of the cornea and lens to the retina) is 49-54 mm. On the other hand, the eyes of the kiwis (*Apterygidae*) have a bulbar axial length of ≈8 mm, which is similar to that of most passeriform birds. The kiwis are nocturnal and thus there is no advantage to having a large eye if you are not going to use it much. It is interesting that the extremes of eye size are in the ratite bird group.

Birds' eyes are so large that in some they meet on their medial sides and are separated only by thin transparent bone. Birds with eyes of small bulbar axial length (5-8 mm) can function adequately only during daylight. Once the light level falls, they must roost, since their eyes cannot extract enough environmental information to allow safe flight.

The eye may be divided into six parts: the cornea, the anterior chamber, the lens, the iris, the posterior chamber, and the sclera-choroid-retina.

The cornea is the transparent, non-vascular membrane forming the front of the eye and acting as one of its principal refractive components, the other being the lens.

The anterior chamber contains the aqueous humour, a thin, watery fluid. It has little refractive power.

The lens consists of:

a. a central body which contains concentric layers of fibres ('lens fibres') which decrease in density from the core; and

b. an annular pad, which surrounds the central part. In the annular pad, fibres are arranged radially rather than concentrically.

The whole lens is surrounded by a capsule. There may be a vesicular space containing albuminous fluid between the body of the lens and the annular pad. The relative size of the annular pad and the body of the lens varies considerably between species.

The iris is a muscular, pigmented diaphragm which controls the aperture of the pupil. It is thin at its ciliary border where it is attached at the ciliary body at the iridocorneal angle. It thickens to its mid-point and then thins again to its pupillary border, where it is in contact with the anterior surface of the lens. The anterior surface of the iris is lined by a single layer of non-pigmented epithelial cells, covered by pigment. Beneath this layer are two layers of striated muscle fibres (sphincter and dilator). Some avian species have a second dilator muscle which is non-striated. The posterior surface of the iris (adjacent to the lens) is lined by a layer of pigmented epithelial cells. These cells contain pigment granules.

The posterior chamber has a wall which is lined by the sclera (continuous with the cornea), the choroid (continuous with the ciliary body), and the retina. The vitreous humour fills the posterior chamber of the eye - it is gel-like in the anterior of the posterior chamber, and watery just above the retina. The sclera consists of outer fibrous and inner hyaline cartilage layers. The cartilaginous layer terminates under the scleral ossicles. The scleral ossicles are a group of bones which number 10 to 18, and which form a complete ring of overlapping plates around the corneo-conjunctival junction. The choroid is a thick, pigmented, highly vascular layer lying between the sclera and retina and terminates in the base of the ciliary body.

The retina may be divided into two main layers, an outer pigmented cell layer and an inner nervous layer. Compared to the mammalian retina, the avian retina is thick and much more ordered in its structure.

The Pecten is a vascular, thin, heavily-pigmented lamina which projects from the retina into the vitreous humour. It lacks muscular and nervous tissue, consisting of capillaries, pigmented stromal cells, and a superficial covering membrane. Three main types of pecten may be seen: conical (found in kiwis); vaned (ostrich, rhea, and tinamons); and pleated (all other birds).

The pecten is considered to be involved in supplying nutrition via the vitreous to the inner layers of the retina, which in birds are avascular.

Vision

Because birds travel at speed in three dimensions, one expects them to have good eyesight, in order to perceive instantaneously the position of objects around them. The size of their eyeballs is an indication of the importance of vision in the lives of birds: hawks and owls have eyeballs as large as the human eye and, in some birds, the eyeballs meet in the middle of the skull, dwarfing the brain. Because of their size, the eyeballs cannot rotate much in their sockets, and so we see the fixed stare of hawks and owls (their eyes are not so immovable as many have reported). Thus many birds have flexible necks and can turn their heads to look around them - owls can turn their heads almost 270°, they rapidly swivel round in the opposite direction and continue the scan.

Most birds' eyeballs are flattened antero-posteriorly, but raptors, owls and others with increased visual acuity have globular or tubular eyes, which increases the distance between the lens and retina. Birds obtain additional focusing power with their cornea, which acts as a convexoconcave lens. Most species have twice the focusing power of human eyes. This allows them to focus on food at very close range, but also gives them the accurate distance and spatial vision necessary for flight. The refractive index of corneal tissue has is about the same as that of water, so there is very little refraction when the eye is underwater. As soon as a bird puts its head underwater, its eyes lose much of their focusing power and so it becomes longsighted. To compensate, diving birds need some extra focusing power, and the solution of the hooded merganser, a diving duck, is for part of the lens to bulge through the rigid iris on submergence, thereby increasing its focusing power. Other diving birds (ducks, auks and divers) increase the refractive power of the eye by covering it with the transparent nictitating membrane.

Many people thought that the eyes of penguins were highly adapted for underwater vision, because they appear to look myopically when on land. Their cornea is flat, so that there is little difference in its refractive power in land or water. Their lens, however, is very strong and can compensate for the lack of focusing by the flat cornea.

The bird's retina is composed of cone and rod cells as mammals. Rods are sensitive to low light levels and predominate in owls; cones are sensitive to colours and are used for resolving fine detail in good light. Diurnal birds of prey have a concentration of rods and cones in the upper half of the retina, which presumably is the area on which images of the ground will fall when they are in flight. Thus when perching, they turn their heads upside down to look at objects overhead.

The ability of nocturnal birds to see in dim light has always been exaggerated. The light-collecting power of the eye depends on the aperture of the iris - the wider the pupil, the more light will fall on the retina. Human eyes have an F-value of 2.1, while those of owls have a value of 1.3, which means that their light-collecting power is two and a half times brighter. This is not significant, and so one concludes that owl and human eyes have similar light-collecting powers.

Birds' eyes, like those of mammals, have a fovea, which is packed with cone cells. Nearly all birds have a central fovea which receives light on the plane of the eye, and also a second "temporal" fovea set in the rear part of the retina to enable them to look forward. Temporal foveas are present in high-speed hunting birds such as raptors, kingfishers, terns and swallows, which need good forward vision for catching their prey. The fovea is thus highly important for sensitive daytime vision, and owls usually have no central fovea. In addition, the temporal fovea is not well developed, except in daytime hunters such as the short-eared owl.

All birds have both monocular vision (seeing independently with each eye) and binocular vision. Monocular vision is used when a bird turns its head to peer closely at the ground, or when it cocks its head to look at objects in the sky above. They are directing their view onto the central fovea of the eye to get the sharpest image. Most birds have their eyes on the side of the head, which gives them good all-round vision to spot danger. Thus pigeons have a 340° field of view (humans 200°), and can see all round except immediately behind them, but the fields of their eyes overlap by only 24° to give a small binocular field to the front. The woodcock, which feeds by thrusting its long bill deep into the soil, has eyes set high on the head, and their fields overlap both anteriorly and posteriorly. Thus, it has binocular vision behind and in front, so it can spot danger when feeding. Some birds raise the angle of their head and look under the their beak to get a better view ahead.

Hunting birds usually have their eyes placed to the front of the head in order to give increased binocular vision. Hawks have overlapping fields of 30-50°, while the fields of owls' eyes overlap 60-70°. So far as is known, owls are the only birds with true stereoscopic, or three-dimensional, vision. Humans and other mammals experience stereoscopic vision because the slight differences between the position of the image on each retina can be compared. In order to do this, nerve fibres from both eyes must link up on each side of the brain, instead of all fibres from one eye going only to the opposite side of the brain. Among birds, only owls have nerve fibres decussating.

Birds other than owls have to judge distances by using perspective and the relative size of images. Bobbing the head gives views from different angles and makes objects appear to move in relation to the background so their position can be judged. When some birds walk, they nod their heads to and fro, but this has a different function from head bobbing. They are stabilising the head, throwing it forward then keeping it steady while the body moves up. With the head steady, the eyes are better able to pick out tiny objects and slight movements. Head stabilising can be demonstrated by holding a bird by its body and gently tilting or rolling it: the head remains fixed in space. Hovering birds, such as kestrels, also need to keep their heads steady, and when a waterbird whiffles, turning onto its back, its neck twists so that the head remains the right way up.

Birds have well-developed colour vision that is similar to our own and plays an equally important role in their lives, but there are some basic differences. Like amphibians and reptiles, but unlike any mammals, birds have coloured droplets of oil in their cone cells, and these droplets are mostly red, orange-red or yellow. These colours have long wavelengths, and it is assumed that they act as selective filters, blocking shorter wavelengths and transmitting longer wavelengths of light.

The colour discrimination of plant-eating species has been tested. That part of the pigeon retina on which images fall when the bird is aiming its pecking is particularly rich in red droplets, which will heighten this sensitivity. Green is the colour of chlorophyll, and the subsidiary leaf pigments are red and yellow (causing autumn colours when the chlorophyll has broken down), so the sensitivity of the pigeon retina matches the colours of its food.

A second property of red, orange and yellow filters is to cut through haze. This is probably the function of droplets in the eyes of waterbirds which hunt above the sea. Cutting out blues makes the sky darker, so white-bodied gulls, gannets, albatrosses and terns are able to see each other at greater distances because they are strongly contrasted against the background of sky or sea.

On the other hand, shags, auks and shearwaters, which pursue their prey underwater, do not want this filtering effect. Such birds have few red and orange droplets and so see better in an blue-green light environment. These droplets reduce the total amount of light reaching the retina, and so are a disadvantage in dim light, and so nocturnal birds of prey have few droplets. Filters that darken the sky would also be disadvantageous to birds which catch dark insects on the wing: there is much less coloured oil in the cones of swifts, swallows and martins.

The Ear

The outer ear of birds consists only of the short *meatus acusticus externus*. The external ears of owls are asymmetric. There is no cartilaginous external ear, or pinna. The avian inner ear is enclosed within the skull and consists of a membranous labyrinth enclosed by a bony labyrinth. The former is filled with endolymph, while the spaces between the membranous and bony labyrinths are filled with perilymph.

Owls use sound localisation to find prey, and some can pounce on prey accurately in pitch darkness. The owl's hearing system has features not found in other birds. There is a circular ruff of very fine feathers around each eye that funnels sound to the ear opening, which is hidden under a flap of skin. The ear openings are asymmetrically placed on the head as a further aid to localisation. The left external ear is placed higher and its opening is tilted downwards. Comparison between the ears gives a very good measurement of the angle of elevation of a sound source, so the owl can judge the position of a mouse on the ground below.

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