
Bird Anatomy
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First Edition, 2012

ISBN 978-81-323-4095-9

Published by:
White Word Publications
4735/22 Prakashdeep Bldg,
Ansari Road, Darya Ganj,
Delhi - 110002
Email: info@wtbooks.com

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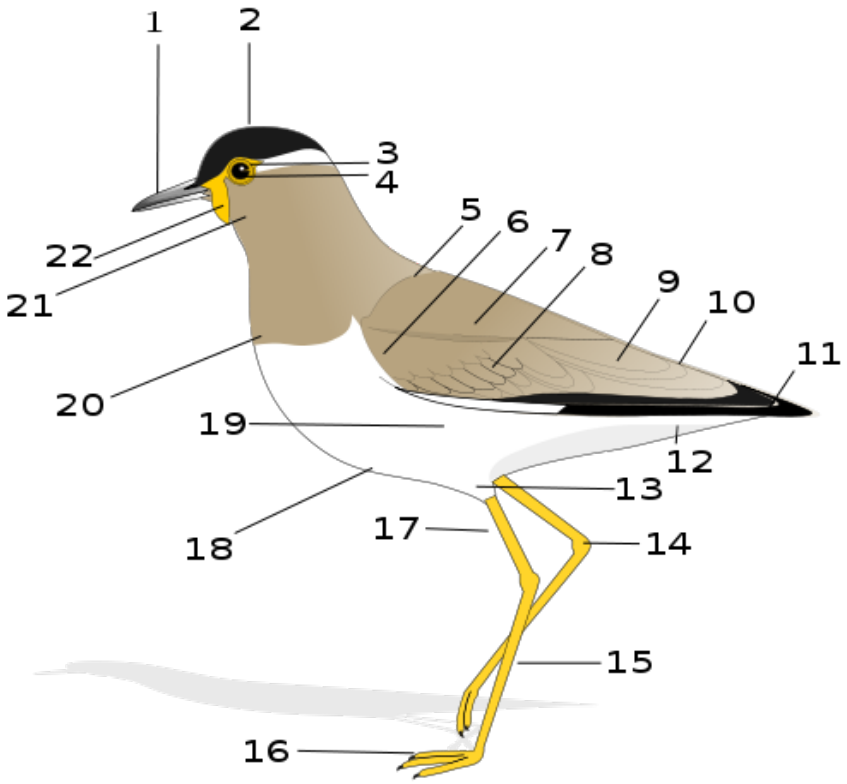
Bird Anatomy

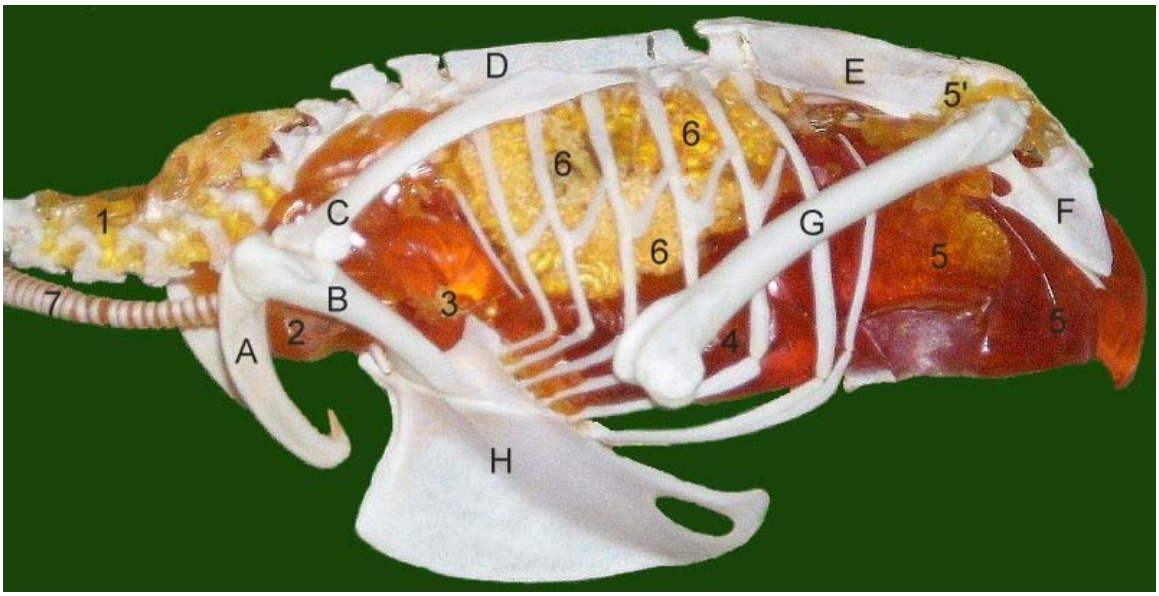


External anatomy (topography) of a typical bird: 1 Beak, 2 Head, 3 Iris, 4 Pupil, 5 Mantle, 6 Lesser coverts, 7 Scapulars, 8 Coverts, 9 Tertials, 10 Rump, 11 Primaries, 12 Vent, 13 Thigh, 14 Tibio-tarsal articulation, 15 Tarsus, 16 Feet, 17 Tibia, 18 Belly, 19 Flanks, 20 Breast, 21 Throat, 22 Wattle

Bird anatomy, or the physiological structure of birds' bodies, shows many unique adaptations, mostly aiding flight. Birds have a light skeletal system and light but powerful musculature which, along with circulatory and respiratory systems capable of very high metabolic rates and oxygen supply, permit the bird to fly. The development of

a beak has led to evolution of a specially adapted digestive system. These anatomical specializations have earned birds their own class in the vertebrate phylum.

Respiratory system

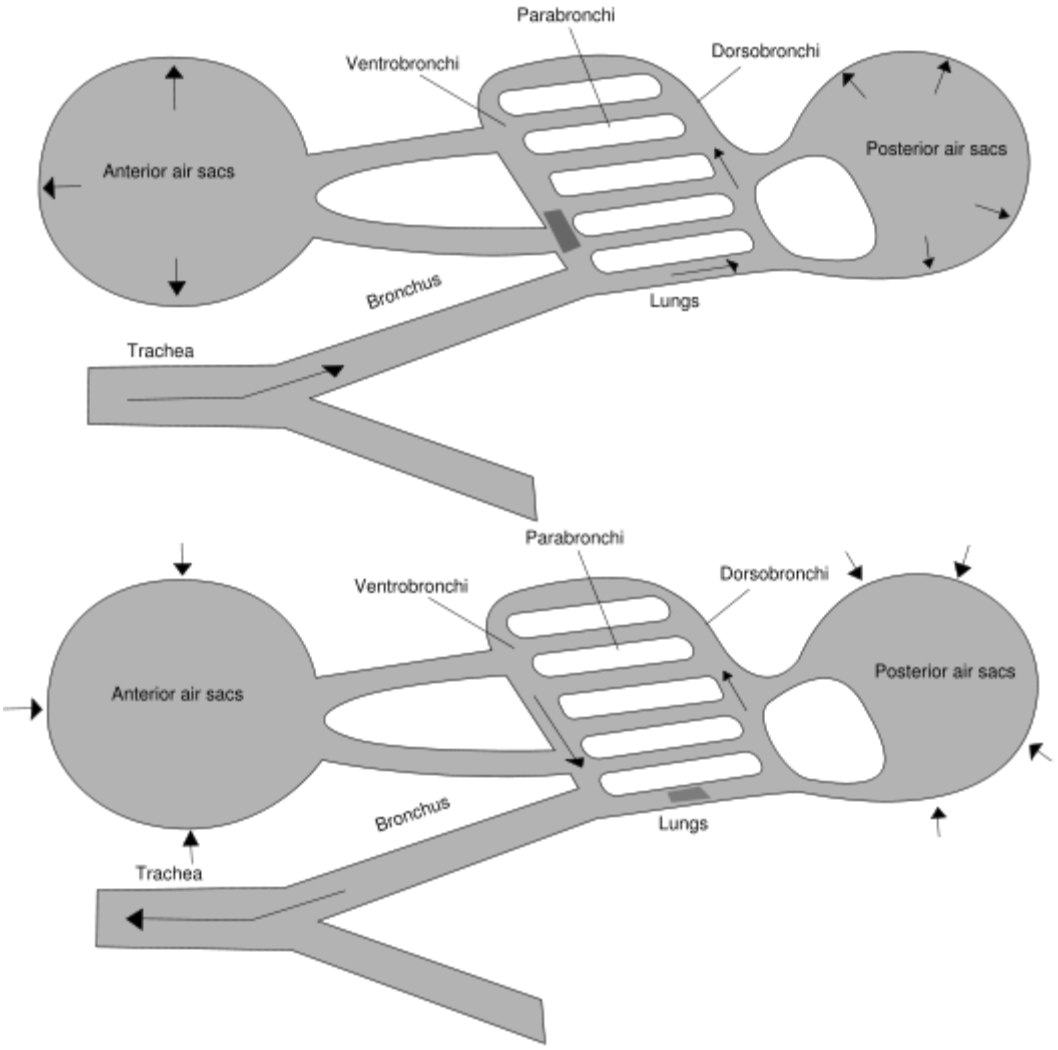


Air always flows from right (posterior) to left (anterior) through a bird's lungs during both inhalation and exhalation. Key to a Common Kestrel's circulatory lung system: 1 cervical air sac, 2 clavicular air sac, 3 cranial thoracic air sac, 4 caudal thoracic air sac, 5 abdominal air sac (5' diverticulus into pelvic girdle), 6 lung, 7 trachea

Due to their high metabolic rate required for flight, birds have a high oxygen demand. Development of an efficient respiratory system enabled the evolution of flight in birds. Birds ventilate their lungs by means of air sacs.

These sacs do not play a direct role in gas exchange, but to store air and act like bellows, allowing the lungs to maintain a fixed volume with fresh air constantly flowing through them.

Three distinct sets of organs perform respiration—the anterior air sacs (interclavicular, cervicals, and anterior thoracics), the lungs, and the posterior air sacs (posterior thoracics and abdominals). The posterior and anterior air sacs, typically nine, expand during inhalation. Air enters the bird via the trachea. Half of the inhaled air enters the posterior air sacs, the other half passes through the lungs and into the anterior air sacs. Air from the anterior air sacs empties directly into the trachea and out the bird's mouth or nares. The posterior air sacs empty their air into the lungs. Air passing through the lungs as the bird exhales is expelled via the trachea. Some taxonomic groups (Passeriformes) possess 7 air sacs, as the clavicular air sacs may interconnect or be fused with the cranial thoracic air sacs.



Birds lungs obtain fresh air during both exhalation and inhalation

As air flows through the air sac system and lungs, there is no mixing of oxygen-rich air and oxygen-poor, carbon dioxide-rich, air as in mammalian lungs. Thus, the partial pressure of oxygen in a bird's lungs is the same as the environment, and so birds have more efficient gas-exchange of both oxygen and carbon dioxide than do mammals. In addition, air passes through the lungs in both exhalation and inspiration, with the air sacs functioning as a reservoir for the next breath of air.

Avian lungs do not have alveoli, as mammalian lungs do, but instead contain millions of tiny passages known as parabronchi, connected at either ends by the dorsobronchi and ventrobronchi. Air flows through the honeycombed walls of the parabronchi into air vesicles, called atria, which project radially from the parabronchi. These atria give rise to

air capillaries, where oxygen and carbon dioxide are traded with cross-flowing blood capillaries by diffusion.

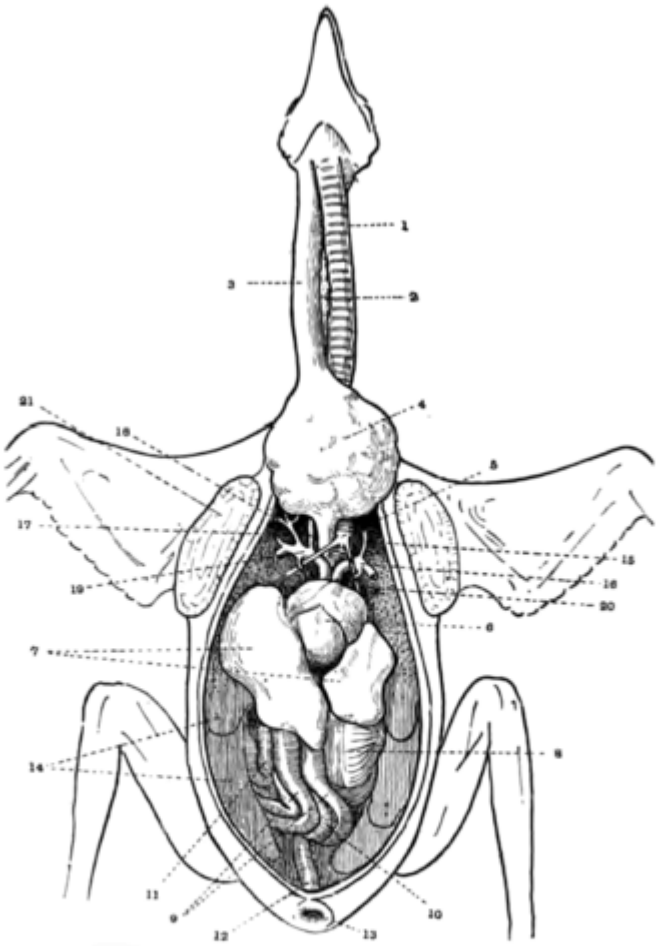
Birds also lack a diaphragm. The entire body cavity acts as a bellows to move air through the lungs. The active phase of respiration in birds is exhalation, requiring muscular contraction.

The syrinx is the sound-producing vocal organ of birds, located at the base of a bird's trachea. As with the mammalian larynx, sound is produced by the vibration of air flowing through the organ. The syrinx enables some species of birds to produce extremely complex vocalizations, even mimicking human speech. In some songbirds, the syrinx can produce more than one sound at a time.

Circulatory system

Birds have a four-chambered heart, in common with humans, most mammals, and some reptiles (namely the crocodilia). This adaptation allows for an efficient nutrient and oxygen transport throughout the body, providing birds with energy to fly and maintain high levels of activity. A Ruby-throated Hummingbird's heart beats up to 1200 times per minute (about 20 beats per second).

Digestive system



The chief Viscera of the Pigeon, *Columba livia*

1. Trachea. 2. Thymus gland. 3. Oesophagus. 4. Crop. 5. Syrinx. 6. Heart. 7. Liver. 8. Gizzard. 9. Duodenum. 10. Pancreas. 11. Small intestine. 12. Rectum. 13. Cloaca. 14. Air-sacs. 15. Left carotid. 16. Left subclavian. 17. Right carotid. 18. Brachial artery. 19. Right subclavian. 20. Muscles of syrinx. 21. Pectoralis major muscle cut across.

Alimentary canal of the bird exposed.

Sharp tooth-like structures in this rooster's mouth called papillae help birds hold and move food around

Many birds possess a muscular pouch along the esophagus called a crop. The crop functions to both soften food and regulate its flow through the system by storing it temporarily. The size and shape of the crop is quite variable among the birds. Members of the order Columbiformes, such as pigeons, produce a nutritious crop milk which is fed to their young by regurgitation. Birds possess a *ventriculus*, or gizzard, composed of four muscular bands that rotate and crush food by shifting the food from one area to the next within the gizzard. The gizzard of some species contains small pieces of grit or stone swallowed by the bird to aid in the grinding process of digestion, serving the function of mammalian or reptilian teeth. The use of gizzard stones is a similarity between birds and dinosaurs, which left gizzard stones called gastroliths as trace fossils.

Drinking behavior

There are four general ways in which birds drink.

Most birds are unable to swallow by the "sucking" or "pumping" action of peristalsis in their esophagus (as humans do), and drink by repeatedly raising their heads after filling their mouths to allow the liquid to flow by gravity, a method usually described as "sipping" or "tipping up". The notable exception is the Columbiformes; in fact, according to Konrad Lorenz in 1939,

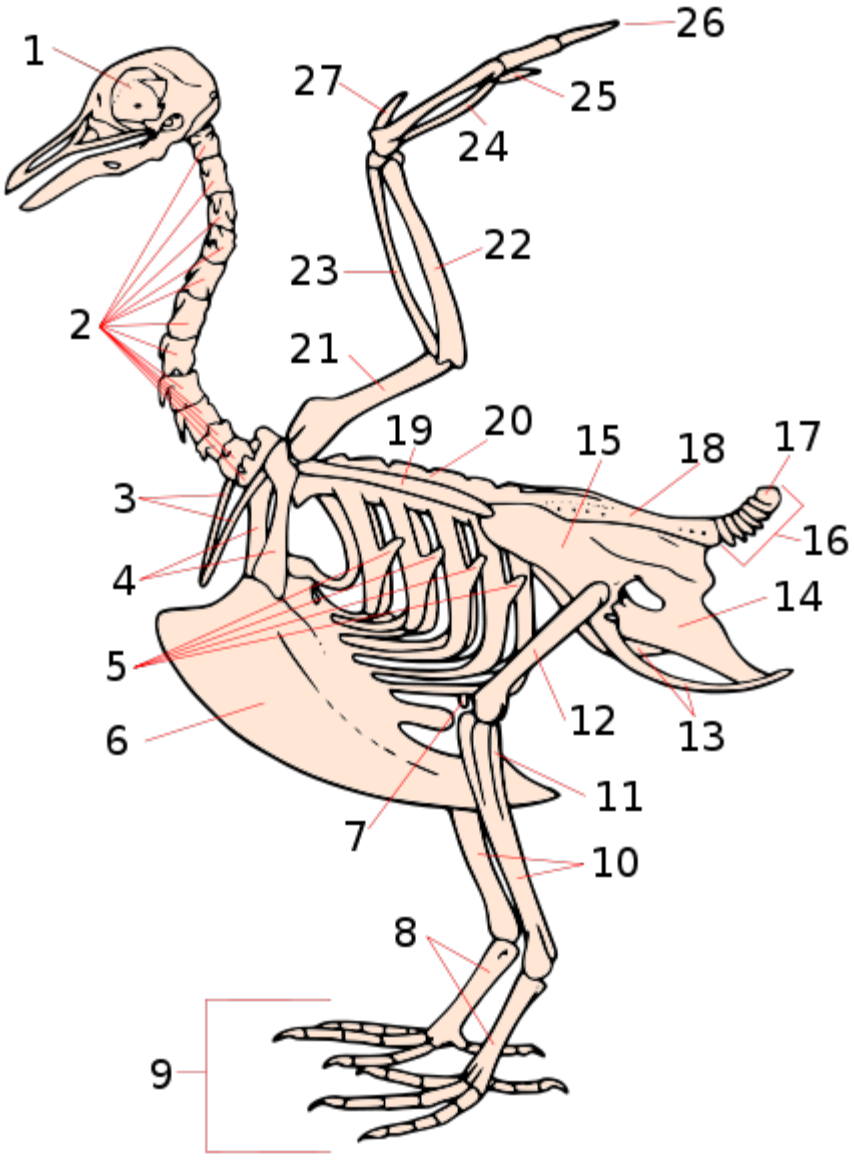
"one recognizes the order by the single behavioral characteristic, namely that in drinking the water is pumped up by peristalsis of the esophagus which occurs without exception within the order. The only other group, however, which shows the same behavior, the Pteroclidae, is placed near the doves just by this doubtlessly very old characteristic."

Although this general rule still stands, since that time, observations have been made of a few exceptions in both directions.

In addition, specialized nectar feeders like sunbirds (Nectariniidae) and hummingbirds (Trochilidae) drink by using protrusible grooved or trough-like tongues, and parrots (Psittacidae) lap up water.

Many seabirds have glands near the eyes that allow them to drink seawater. Excess salt is eliminated from the nostrils. Many desert birds get the water that they need entirely from their food. The elimination of nitrogenous wastes as uric acid reduces the physiological demand for water.

Skeletal system

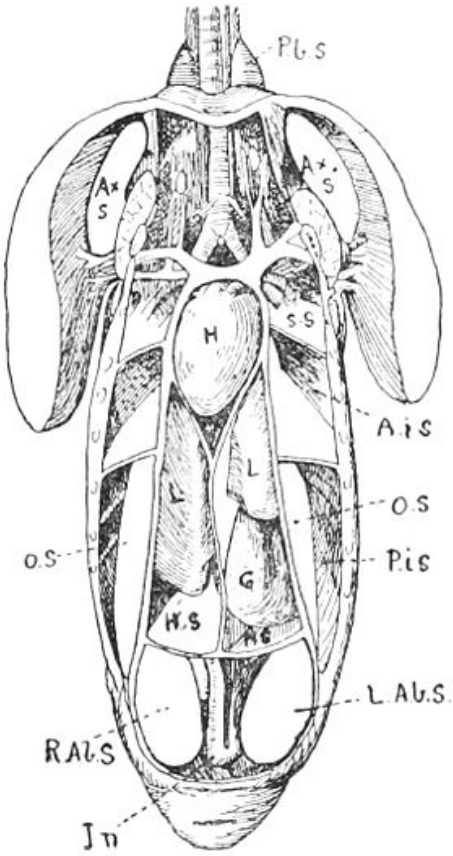


A stylised dove skeleton. Key:
1. skull
2. cervical vertebrae
3. furcula
4. coracoid
5. uncinate processes of ribs
6. keel
7. patella
8. tarsometatarsus
9. digits
10. tibia (tibiotarsus)
11. fibia (tibiotarsus)

12. femur
13. ischium (innominate)
14. pubis (innominate)
15. illium (innominate)
16. caudal vertebrae
17. pygostyle
18. synsacrum
19. scapula
20. lumbar vertebrae
21. humerus
22. ulna
23. radius
24. carpus
25. metacarpus
26. digits
27. alula

The bird skeleton is highly adapted for flight. It is extremely lightweight but strong enough to withstand the stresses of taking off, flying, and landing. One key adaptation is the fusing of bones into single ossifications, such as the pygostyle. Because of this, birds usually have a smaller number of bones than other terrestrial vertebrates. Birds also lack teeth or even a true jaw, instead having evolved a beak, which is far more lightweight. The beaks of many baby birds have a projection called an egg tooth, which facilitates their exit from the amniotic egg.

Birds have many bones that are hollow (pneumatized) with criss-crossing struts or trusses for structural strength. The number of hollow bones varies among species, though large gliding and soaring birds tend to have the most. Respiratory air sacs often form air pockets within the semi-hollow bones of the bird's skeleton. Some flightless birds like penguins and ostriches have only solid bones, further evidencing the link between flight and the adaptation of hollow bones.



DISSECTION SHOWING THE LUNGS AND AIR-SACS OF A BIRD

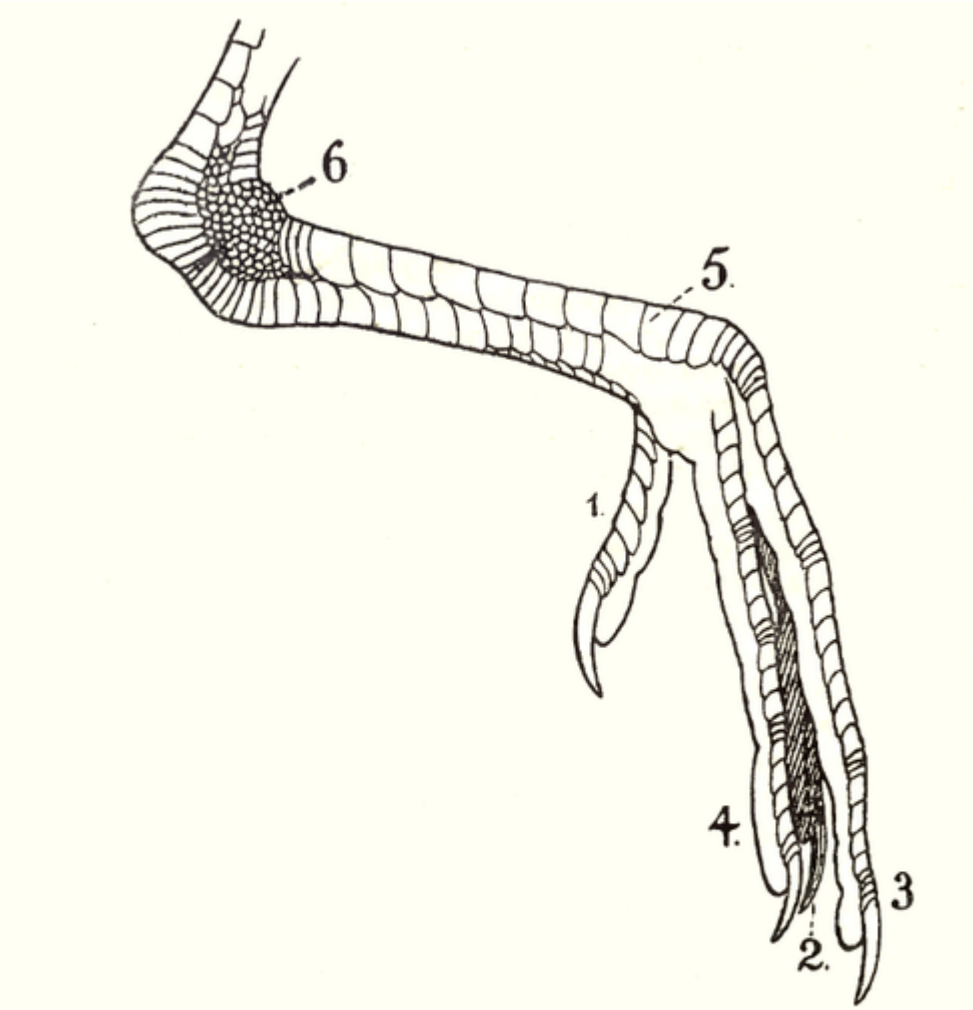
Pb. s. = Pre-bronchial sac. Ax. = Axillary sac bounded externally by the breast-muscles, seen here in section. S. s. = Partition dividing anterior intermediate sac (A.i.s.) from the sub-bronchial sac. P.i.s. = Posterior intermediate sac. O.s. = Oblique septum. H.s. = Horizontal septum. L. Ab. s. = Left abdominal sac. H. = Heart. G. = Gizzard. L. = Liver. In. = Intestine. (After Strasser.)

Air-sacs and their distribution

Birds also have more cervical (neck) vertebrae than many other animals; most have a highly flexible neck consisting of 13-25 vertebrae. Birds are the only vertebrate animals to have a fused collarbone (the furcula or wishbone) or a keeled sternum or breastbone. The keel of the sternum serves as an attachment site for the muscles used for flight, or similarly for swimming in penguins. Again, flightless birds, such as ostriches, which do not have highly developed pectoral muscles, lack a pronounced keel on the sternum. It is noted that swimming birds have a wide sternum, while walking birds had a long or high sternum while flying birds have the width and height nearly equal.

Birds have uncinate processes on the ribs. These are hooked extensions of bone which help to strengthen the rib cage by overlapping with the rib behind them. This feature is also found in the tuatara *Sphenodon*. They also have a greatly elongate tetradiate pelvis as in some reptiles. The hindlimb has an intra-tarsal joint found also in some reptiles. There is extensive fusion of the trunk vertebrae as well as fusion with the pectoral girdle. They have a diapsid skull as in reptiles with a pre-lachrymal fossa (present in some reptiles). The skull has a single occipital condyle.

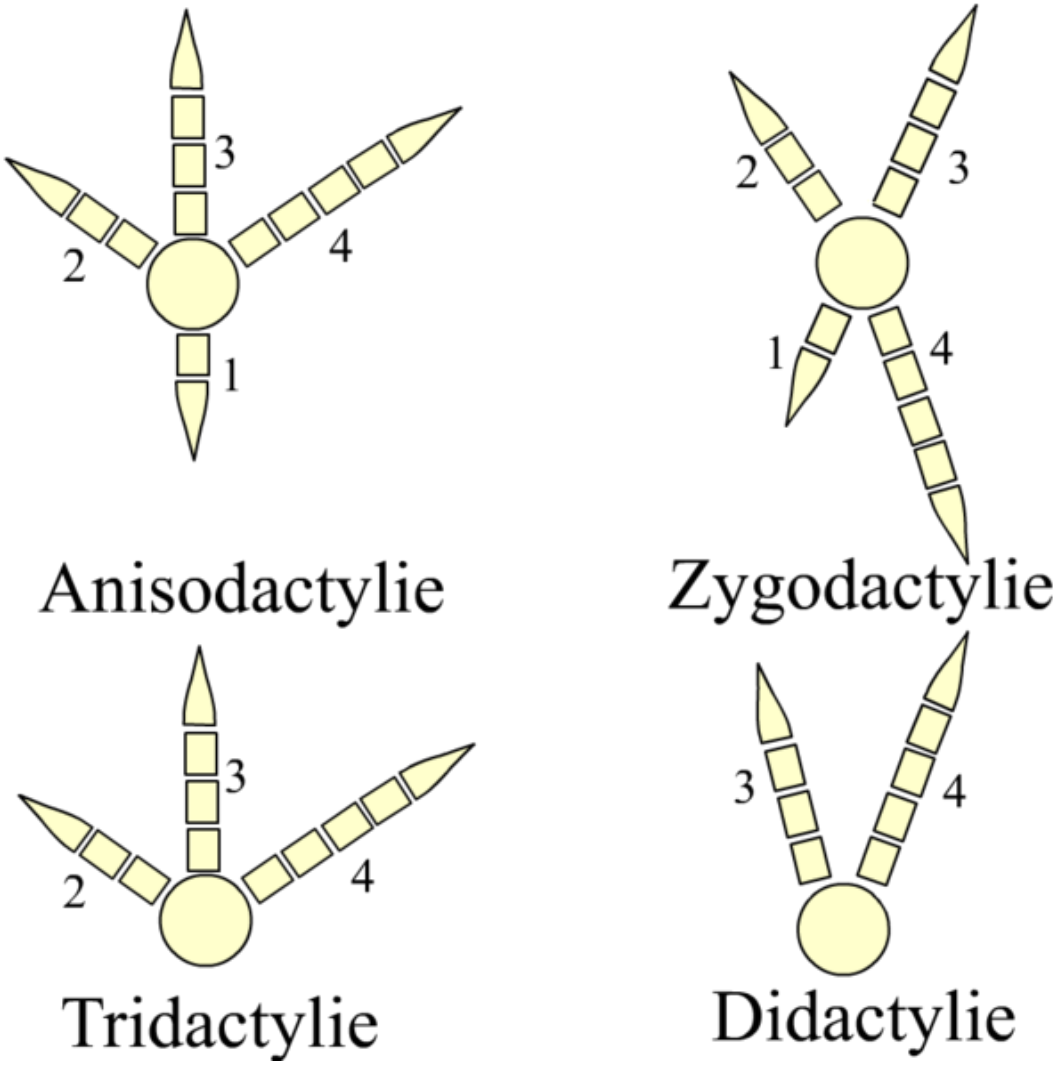
Skeleton



Side view of Right Foot of a Purple Gallinule (*Porphyrio*) to show the composition of the horny covering (*podotheca*).

1. Hallux or hind toe.
2. Inner toe.
3. Middle toe.
4. Outer toe.
5. Scales (*Scutellæ*).
6. Reticulate scales.

Scalation and structure of the leg



Types of bird feet

The skull consists of five major bones: the frontal (top of head), parietal (back of head), premaxillary and nasal (top beak), and the mandible (bottom beak). The skull of a normal bird usually weighs about 1% of the birds total bodyweight.

The vertebral column consists of vertebrae, and is divided into three sections: cervical (13-16) (neck), Synsacrum (fused vertebrae of the back, also fused to the hips (pelvis)), and pygostyle (tail).

The chest consists of the furcula (wishbone) and coracoid (collar bone), which two bones, together with the scapula (see below), form the pectoral girdle. The side of the chest is formed by the ribs, which meet at the sternum (mid-line of the chest).

The shoulder consists of the scapula (shoulder blade), coracoid, and humerus (upper arm). The humerus joins the radius and ulna (forearm) to form the elbow. The carpus and

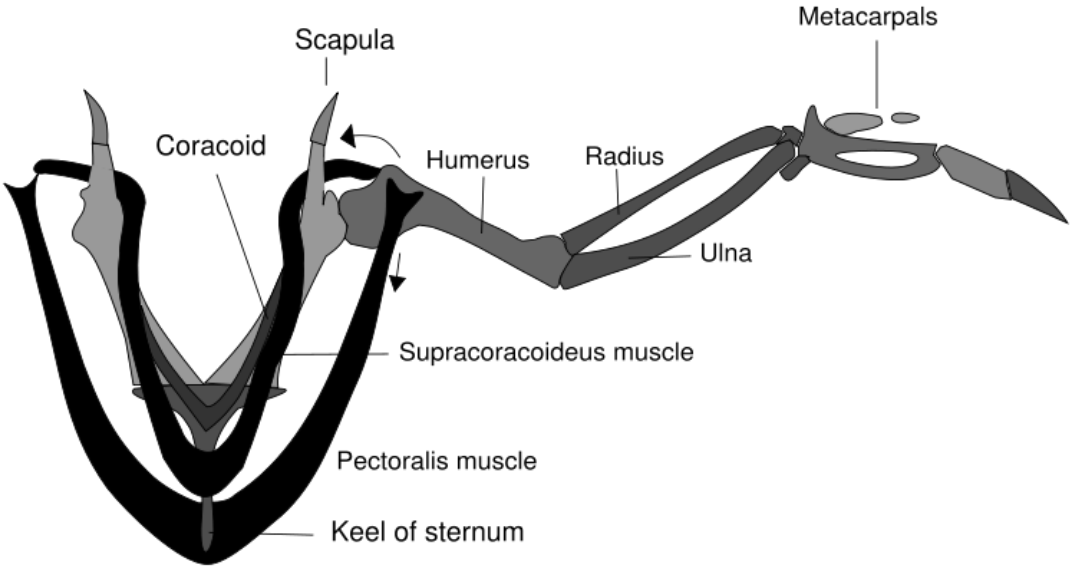
metacarpus form the "wrist" and "hand" of the bird, and the digits (fingers) are fused together. The bones in the wing are extremely light so that the bird can fly more easily.

The hips consist of the pelvis which includes three major bones: Illium (top of the hip), Ischium (sides of hip), and Pubis (front of the hip). These are fused into one (the innominate bone). Innominate bones are evolutionary significant in that they allow birds to lay eggs. They meet at the acetabulum (the hip socket) and articulate with the femur, which is the first bone of the hind limb.

The upper leg consists of the femur. At the knee joint, the femur connects to the tibiotarsus (shin) and fibula (side of lower leg). The tarsometatarsus forms the upper part of the foot, digits make up the toes. The leg bones of birds are the heaviest, contributing to a low center of gravity. This aids in flight. A bird's skeleton comprises only about 5% of its total body weight

Birds feet are classificated as anisodactyl, zygodactyl, heterodactyl, syndactyl or pamprodactyl.

Muscular system



The supracoracoideus works using a pulley like system to lift the wing while the pectorals provide the powerful downstroke

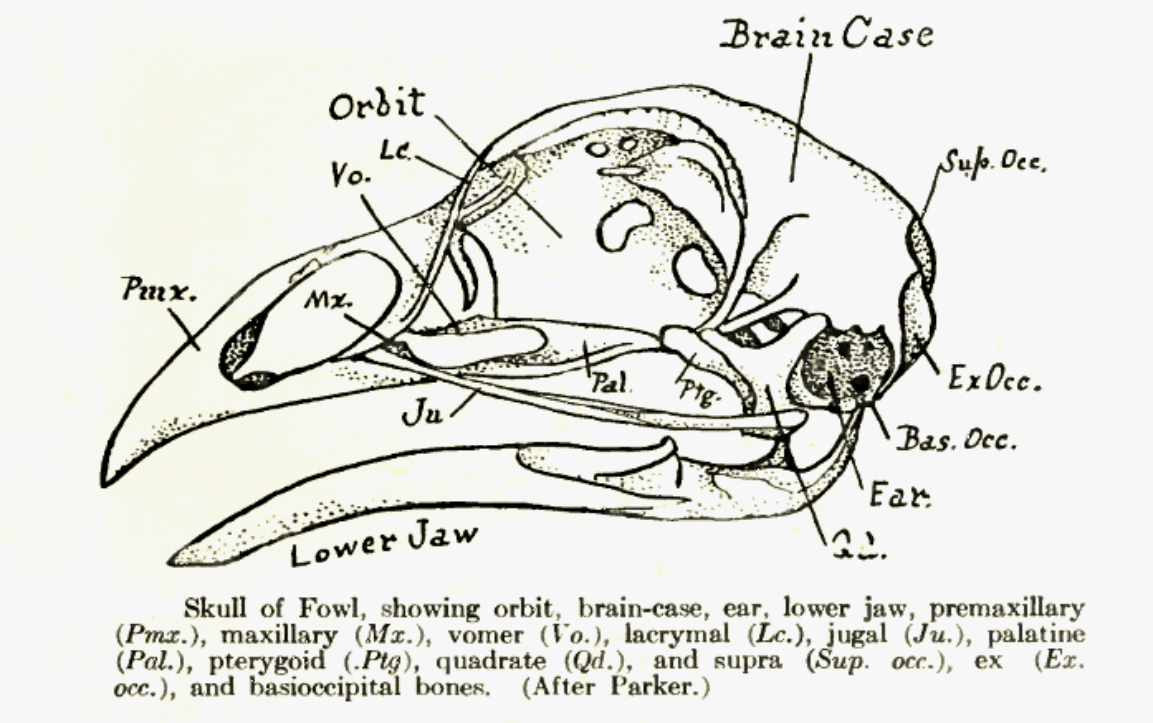
Most birds have approximately 175 different muscles, mainly controlling the wings, skin, and legs. The largest muscles in the bird are the pectorals, or the breast muscles, which control the wings and make up about 15 - 25% of a flighted bird’s body weight. They provide the powerful wing stroke essential for flight. The muscle ventral (underneath) to the pectorals is the supracoracoideus. It raises the wing between wingbeats. The

supracoracoideus and the pectorals together make up about 25 – 35% of the bird's full body weight.

The skin muscles help a bird in its flight by adjusting the feathers, which are attached to the skin muscle and help the bird in its flight maneuvers.

There are only a few muscles in the trunk and the tail, but they are very strong and are essential for the bird. The pygostyle controls all the movement in the tail and controls the feathers in the tail. This gives the tail a larger surface area which helps keep the bird in the air.

Head



Skull of Fowl, showing orbit, brain-case, ear, lower jaw, premaxillary (*Pmx.*), maxillary (*Mx.*), vomer (*Vo.*), lacrymal (*Lc.*), jugal (*Ju.*), palatine (*Pal.*), pterygoid (*.Ptg*), quadrate (*Qd.*), and supra (*Sup. occ.*), ex (*Ex. occ.*), and basioccipital bones. (After Parker.)

Skull of a bird

Birds have acute eyesight - raptors have vision eight times sharper than humans - thanks to higher densities of photoreceptors in the retina (up to 1,000,000 per square mm in *Buteos*, compared to 200,000 for humans), a high number of optic nerves, a second set of eye muscles not found in other animals, and, in some cases, an indented fovea which magnifies the central part of the visual field. Many species, including hummingbirds and albatrosses, have two foveas in each eye. Many birds can detect polarised light. The eye occupies a considerable part of the skull and is surrounded by a sclerotic eye-ring, a ring of tiny bones that surround the eye. This character is also seen in the reptiles.

The bills of many waders have Herbst corpuscles which help them detect prey hidden under wet sand using minute pressure differences in the water. All extant birds can move

the parts of the upper jaw relative to the brain case. However this is more prominent in some birds and can be readily detected in parrots.

Birds have a large brain to body mass ratio. This is reflected in the advanced and complex bird intelligence.

The region between the eye and bill on the side of a bird's head is called the lore. This region is sometimes featherless, and the skin may be tinted, as in many species of the cormorant family.

Reproduction

Fledgling

Although most male birds have no external sex organs, the male does have two testes which become hundreds of times larger during the breeding season to produce sperm. The testes in male birds are generally asymmetric with most birds having a larger left testis. Female birds in many families have only one the left ovary functional and connected to an oviduct although two ovaries are present in their embryonic stage. Although some birds may show two ovaries, the order Apterygiformes always retain both ovaries.

In the males of species without a phallus (see below), sperm is stored in the semenal glomera within the cloacal protuberance prior to copulation. During copulation, the female moves her tail to the side and the male either mounts the female from behind or in

front (in the stitchbird), or moves very close to her. The cloacae then touch, so that the sperm can enter the female's reproductive tract. This can happen very fast, sometimes in less than half a second.

The sperm is stored in the female's sperm storage tubules for a week to more than a 100 days, depending on the species. Then, eggs will be fertilized individually as they leave the ovaries, before being laid by the female. The eggs continue their development outside the female body.

A juvenile Laughing Gull

Many waterfowl and some other birds, such as the ostrich and turkey, possess a phallus. The length is thought to be related to sperm competition. When not copulating, it is hidden within the proctodeum compartment within the cloaca, just inside the vent.

After the eggs hatch, parents provide varying degrees of care in terms of food and protection. Precocial birds can care for themselves independently within minutes of hatching; altricial hatchlings are helpless, blind, and naked, and require extended parental care. The chicks of many ground-nesting birds such as partridges and waders are often able to run virtually immediately after hatching; such birds are referred to as nidifugous. The young of hole-nesters, on the other hand, are often totally incapable of unassisted

survival. The process whereby a chick acquires feathers until it can fly is called "fledging".

Some birds, such as pigeons, geese, and Red-crowned Cranes, remain with their mates for life and may produce offspring on a regular basis.

Scales

The scales of birds are composed of the same keratin as beaks, claws, and spurs. They are found mainly on the toes and metatarsus, but may be found further up on the ankle in some birds. Most bird scales do not overlap significantly, except in the cases of kingfishers and woodpeckers. The scales and scutes of birds are thought to be homologous to those of reptiles and mammals.

Bird embryos begin development with smooth skin. On the feet, the corneum, or outermost layer, of this skin may keratinize, thicken and form scales. These scales can be organized into;

1. Cancella – minute scales which are really just a thickening and hardening of the skin, crisscrossed with shallow grooves.
2. Reticula – small but distinct, separate, scales. Found on the lateral and medial surfaces (sides) of the chicken metatarsus. These are made up of alpha-keratin.
3. Scutella – scales that are not quite as large as scutes, such as those found on the caudal, or hind part, of the chicken metatarsus.
4. Scutes – the largest scales, usually on the anterior surface of the metatarsus and dorsal surface of the toes. These are made up of beta-keratin as in reptilian scales.

The rows of scutes on the anterior of the metatarsus can be called an acrometatarsium or acrotarsium.

Feathers can be intermixed with scales on some birds' feet. Feather follicles can lie between scales or even directly beneath them, in the deeper dermis layer of the skin. In this last case, feathers may emerge directly through scales, and be encircled at the plane of emergence entirely by the keratin of the scale.

Chapter 2

Bird Vision

With forward facing eyes the Bald Eagle has a wide field of binocular vision.

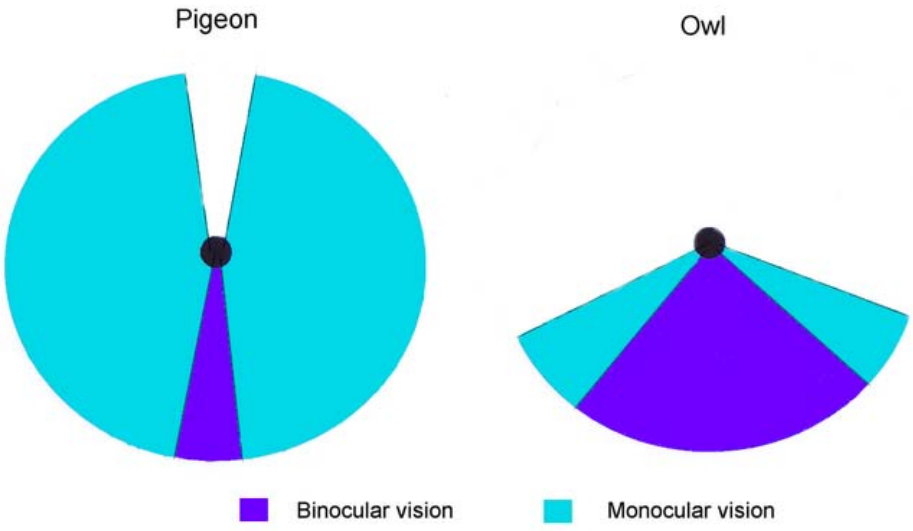
Vision is the most important sense for birds, since good eyesight is essential for safe flight, and this group has a number of adaptations which give visual acuity superior to that of other vertebrate groups; a pigeon has been described as "two eyes with wings". The avian eye resembles that of a reptile, with ciliary muscles that can change the shape of the lens rapidly and to a greater extent than in the mammals. Birds have the largest eyes relative to their size within the animal kingdom, and movement is consequently limited within the eye's bony socket. In addition to the two eyelids usually found in vertebrates, it is protected by a third transparent movable membrane. The eye's internal anatomy is similar to that of other vertebrates, but has a structure, the pecten oculi, unique to birds.

Birds, like fish, amphibians and reptiles, have four types of colour receptors in the eye. Most mammals have two types of receptors, although primates have three. This gives birds the ability to perceive not just the visible range but also the ultraviolet part of the spectrum, and other adaptations allow for the detection of polarised light or magnetic fields. Birds have proportionally more light receptors in the retina than mammals, and more nerve connections between the photoreceptors and the brain.

Some bird groups have specific modifications to their visual system linked to their way of life. Birds of prey have a very high density of receptors and other adaptations that maximise visual acuity. The placement of their eyes gives them good binocular vision enabling accurate judgement of distances. Nocturnal species have tubular eyes, low numbers of colour detectors, but a high density of rod cells which function well in poor light. Terns, gull and albatrosses are amongst the seabirds which have red or yellow oil drops in the colour receptors to improve distance vision especially in hazy conditions.

Extraocular anatomy

The eye of a bird most closely resembles that of the reptiles. Unlike the mammalian eye, it is not spherical, and the flatter shape enables more of its visual field to be in focus. A circle of bony plates, the sclerotic ring, surrounds the eye and hold it rigid, but an improvement over the reptilian eye, also found in mammals, is that the lens is pushed further forward, increasing the size of the image on the retina.



Fields of view for an owl and a pigeon

Most birds cannot move their eyes, although there are exceptions, such as the Great Cormorant. Birds with eyes on the sides of their heads have a wide visual field, useful for detecting predators, while those with eyes on the front of their heads, such as owls, have binocular vision and can estimate distances when hunting. The American Woodcock probably has the largest visual field of any bird, 360^{o} in the horizontal plane, and 180^{o} in the vertical plane.

The nictitating membrane of a Masked Lapwing

The eyelids of a bird are not used in blinking. Instead the eye is lubricated by the nictitating membrane, a third concealed eyelid that sweeps horizontally across the eye like a windscreen wiper. The nictitating membrane also covers the eye and acts as a contact lens in many aquatic birds when they are under water. When sleeping, the lower eyelid rises to cover the eye in most birds, with the exception of the horned owls where the upper eyelid is mobile.

The eye is also cleaned by tear secretions from the lachrymal gland and protected by an oily substance from the Harderian glands which coats the cornea and prevents dryness. The eye of a bird is larger compared to the size of the animal than for any other group of animals, although much of it is concealed in its skull. The Ostrich has the largest eye of any land vertebrate, with an axial length of 50 mm (2 in), twice that of the human eye.

Bird eye size is broadly related to body mass. A study of five orders (parrots, pigeons, petrels, raptors and owls) showed that eye mass is proportional to body mass, but as expected from their habits and visual ecology, raptors and owls have relatively large eyes for their body mass.

Behavioural studies show that many avian species focus on distant objects preferentially with their lateral and monocular field of vision, and birds will orient themselves sideways to maximise visual resolution. For a pigeon, resolution is twice as good with sideways monocular vision than forward binocular vision, whereas for humans the converse is true.

The European Robin has relatively large eyes, and starts to sing early in the morning.

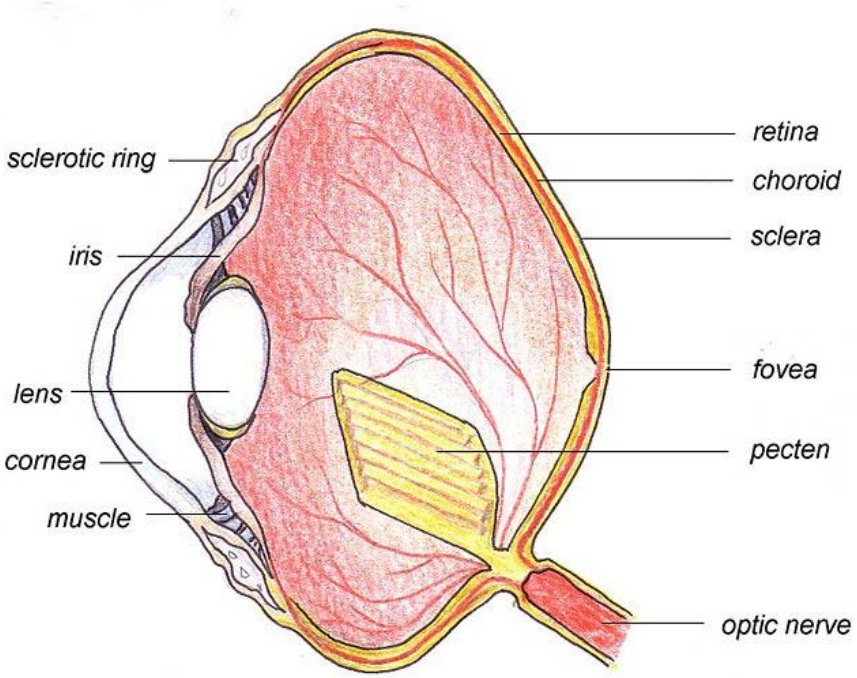
The performance of the eye in low light levels depends on the distance between the lens and the retina, and small birds are effectively forced to be diurnal because their eyes are not large enough to give adequate night vision. Although many species migrate at night, they often collide with even brightly lit objects like lighthouses or oil platforms. Birds of

prey are diurnal because, although their eyes are large, they are optimised to give maximum spatial resolution rather than light gathering, so they also do not function well in poor light. Many birds have an asymmetry in the eye's structure which enables them to keep the horizon and a significant part of the ground in focus simultaneously. The cost of this adaptation is that they have myopia in the lower part of their field of view.

Birds with relatively large eyes compared to their body mass, such as Common Redstarts and European Robins sing earlier at dawn than birds of the same size and smaller body mass. However, if birds have the same eye size but different body masses, the larger species sings later than the smaller. This may be because the smaller bird has to start the day earlier because of weight loss overnight.

Nocturnal birds have eyes optimised for visual sensitivity, with large corneas relative to the eye's length, whereas diurnal birds have longer eyes relative to the corneal diameter to give greater visual acuity. Information about the activities of extinct species can be deduced from measurements of the sclerotic ring and orbit depth. For the latter measurement to be made, the fossil must have retained its three-dimensional shape, so activity pattern cannot be determined with confidence from flattened specimens like *Archaeopteryx*, which has a complete sclerotic ring but no orbit depth measurement.

Anatomy of the eye



Anatomy of the avian eye

The main structures of the bird eye are similar to those of other vertebrates. The outer layer of the eye consists of the transparent cornea at the front, and two layers of sclera – a tough white collagen fibre layer which surrounds the rest of the eye and supports and protects the eye as a whole. The eye is divided internally by the lens into two main segments: the anterior segment and the posterior segment. The anterior chamber is filled with a watery fluid called the aqueous humour, and the posterior chamber contains the vitreous humour, a clear jelly-like substance.

The lens is a transparent convex or 'lens' shaped body with a harder outer layer and a softer inner layer. It focuses the light on the retina. The shape of the lens can be altered by ciliary muscles which are directly attached to lens capsule by means of the zonular fibres. In addition to these muscles, some birds also have a second set, Crampton's muscles, that can change the shape of the cornea, thus giving birds a greater range of accommodation than is possible for mammals. This accommodation can be rapid in some diving water birds such as in the mergansers. The iris is a coloured muscularly operated diaphragm in front of the lens which controls the amount of light entering the eye. At the centre of the iris is the pupil, the variable circular area through which the light passes into the eye.

Hummingbirds are amongst the many birds with two foveae

The retina is a relatively smooth curved multi-layered structure containing the photosensitive rod and cone cells with the associated neurons and blood vessels. The density of the photoreceptors is critical in determining the maximum attainable visual acuity. Humans have about 200,000 receptors per mm^2, but the House Sparrow has 400,000 and the Common Buzzard 1,000,000. The photoreceptors are not all individually

connected to the optic nerve, and the ratio of nerve ganglia to receptors is important in determining resolution. This is very high for birds; the White Wagtail has 100,000 ganglion cells to 120,000 photoreceptors.

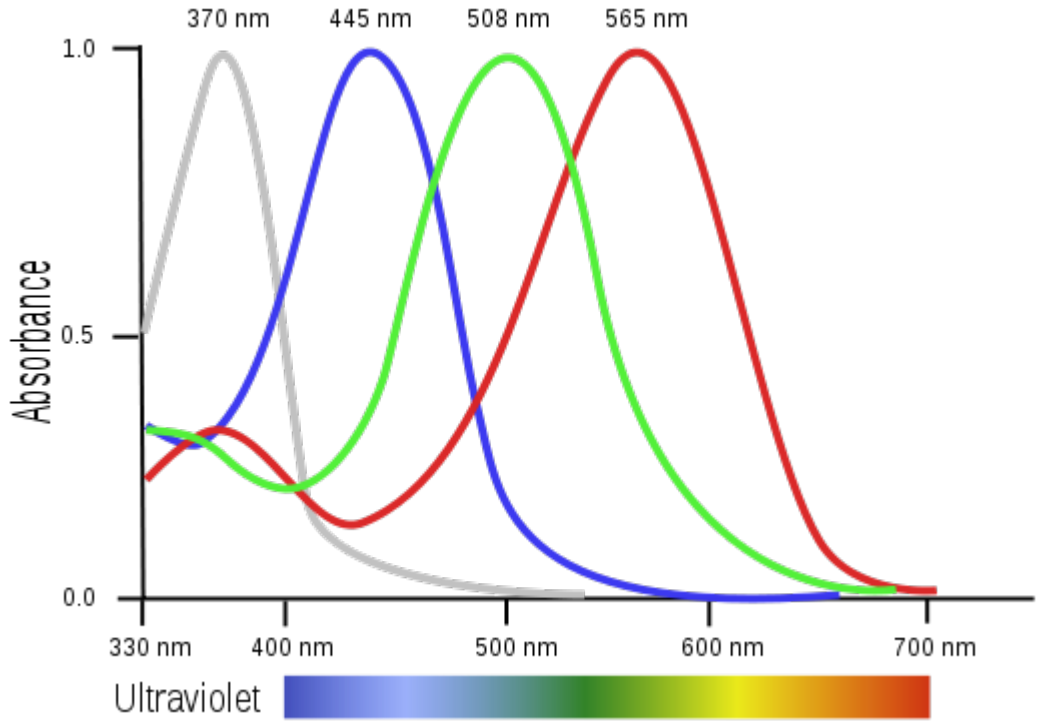
Rods are more sensitive to light, but give no colour information, whereas the less sensitive cones enable colour vision. In diurnal birds, 80% of the receptors may be cones (90% in some swifts) whereas nocturnal owls have almost all rods. As with other vertebrates except placental mammals, some of the cones may be double structures. These can amount to 50% of all cones in some species.

Towards the centre of the retina is the fovea which has a greater density of receptors and is the area of greatest forward visual acuity, i.e. sharpest, clearest detection of objects. In 54% of birds, including birds of prey, kingfishers, hummingbirds and swallows, there is second fovea for enhanced sideways viewing. The optic nerve is a bundle of nerve fibres which carry messages from the eye to the relevant parts of the brain and vice-versa. Like mammals, birds have a small blind spot without photoreceptors at the optic disc, under which the optic nerve and blood vessels join the eye.

The pecten is a poorly understood body consisting of folded tissue which projects from the retina. It is well supplied with blood vessels and appears to keep the retina supplied with nutrients, and may also shade the retina from dazzling light or aid in detecting moving objects.

The choroid is a layer situated behind the retina which contains many small arteries and veins. These provide arterial blood to the retina and drain venous blood. The choroid contains melanin, a pigment which gives the inner eye its dark colour, helping to prevent disruptive reflections.

Light perception



The four pigments in a bird's cones extend the range of colour vision into the ultraviolet.

There are two sorts of light receptors in a bird's eye, rods and cones. Rods, which contain the visual pigment rhodopsin are better for night vision because they are sensitive to small quantities of light. Cones detect specific colours (or wavelengths) of light, so they are more important to colour-oriented animals such as birds. Most birds are tetrachromatic, possessing ultraviolet (UV) sensitive cone cells in the eye as well as those for red, green and blue, but pigeons have an additional pigment and are therefore pentachromatic.

The four spectrally distinct cone pigments are derived from the protein opsin, linked to a small molecule called retinal, which is closely related to vitamin A. When the pigment absorbs light the retinal changes shape and alters the membrane potential of the cone cell affecting neurones in the ganglia layer of the retina. Each neurone in the ganglion layer may processes information from a number of photoreceptor cells, and may in turn trigger a nerve impulse to relay information along the optic nerve for further processing in specialised visual centres in the brain. The more intense a light, the more photons are absorbed by the visual pigments, the greater the excitation of each cone, and the brighter the light appears.

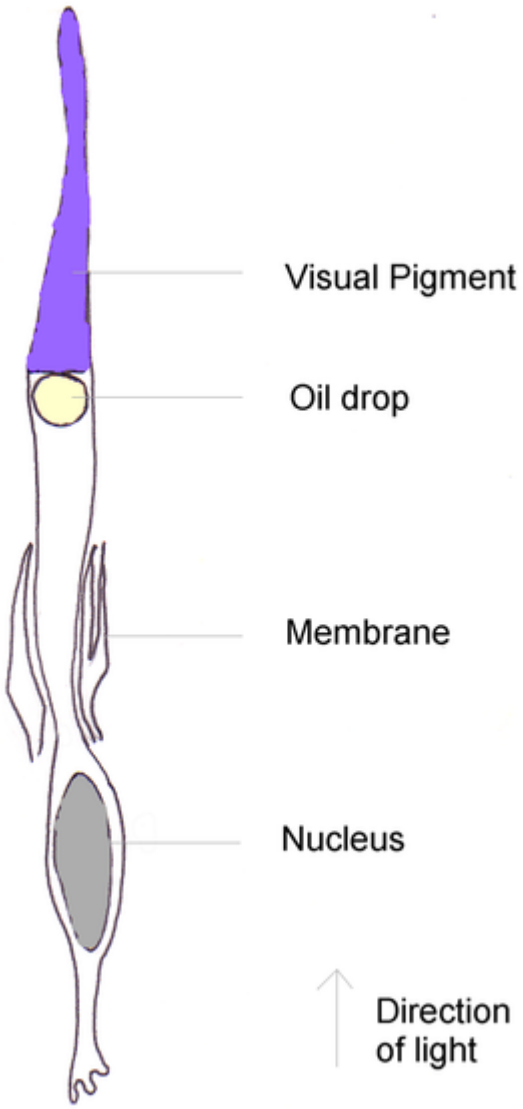


Diagram of a bird cone cell

By far the most abundant cone pigment in every bird species examined is the long-wavelength form of iodopsin, which absorbs at wavelengths near 570 nm. This is roughly the spectral region occupied by the red- and green-sensitive pigments in the primate retina, and this visual pigment dominates the colour sensitivity of birds. In penguins, this pigment appears to have shifted its absorption peak to 543 nm, presumably an adaptation to a blue aquatic environment.

The information conveyed by a single cone is limited: by itself, the cell cannot tell the brain which wavelength of light caused its excitation. A visual pigment may absorb two wavelengths equally, but even though their photons are of different energies, the cone cannot tell them apart, because they both cause the retinal to change shape and thus

trigger the same impulse. For the brain to see colour, it must compare the responses of two or more classes of cones containing different visual pigments, so the four pigments in birds give increased discrimination.

Each cone of a bird or reptile contains a coloured oil droplet; these no longer exist in mammals. The droplets, which contain high concentrations of carotenoids, are placed so that light passes through before reaching the visual pigment. They act as filters, removing some wavelengths and narrowing the absorption spectra of the pigments. This reduces the response overlap between pigments and increases the number of colours that a bird can discern. Six types of cone oil droplets have been identified; five of these have carotenoid mixtures that absorb at different wavelengths and intensities, and the sixth type has no pigments.

The colours and distributions of retinal oil droplets vary considerably among species, and is more dependent on the ecological niche utilised (hunter, fisher, herbivore) than genetic relationships. As examples, diurnal hunters like the Barn Swallow and birds of prey have few coloured droplets, whereas the surface fishing Common Tern has a large number of red and yellow droplets in the dorsal retina. The evidence suggests that oil droplets respond to natural selection faster than the cone's visual pigments. Even within the range of wavelengths that are visible to humans, passerine birds can detect colour differences that humans do not register. This finer discrimination, together with the ability to see ultraviolet light, means that many species show sexual dichromatism that is visible to birds but not humans.

Migratory songbirds use the Earth’s magnetic field, stars, the Sun, and polarised light patterns to determine their migratory direction. An American study showed that migratory Savannah Sparrows used polarised light from an area of sky near the horizon to recalibrate their magnetic navigation system at both sunrise and sunset. This suggested that skylight polarisation patterns are the primary calibration reference for all migratory songbirds. However, it appears that birds may be responding to secondary indicators of the angle of polarisation, and may not be actually capable of directly detecting polarisation direction in the absence of these cues.

Ultraviolet

The Common Kestrel can detect the ultraviolet trail of its vole prey.

Birds can perceive ultraviolet light, which is involved in courtship. Many birds show plumage patterns in ultraviolet that are invisible to the human eye; some birds whose sexes appear similar to the naked eye are distinguished by the presence of ultraviolet reflective patches on their feathers. Male Blue Tits have an ultraviolet reflective crown patch which is displayed in courtship by posturing and raising of their nape feathers. Male Blue Grosbeaks with the most, brightest and most UV-shifted blue in their plumage are larger, hold the most extensive territories with abundant prey, and feed their offspring more frequently than other males do.

The bill's appearance is important in the interactions of the Blackbird. Although the UV component seems unimportant in interactions between territory-holding males, where the degree of orange is the main factor, the female responds more strongly to males with bills with good UV-reflectiveness.

A UV receptor may give an animal an advantage in foraging for food. The waxy surfaces of many fruits and berries reflect UV light that might advertise their presence. Common Kestrels are able to locate the trails of voles visually. These small rodents lay scent trails of urine and faeces that reflect UV light, making them visible to the kestrels, particularly in the spring before the scent marks are covered by vegetation.

Perception

Movement

A hunting Common Kestrel needs a steady visual image

Birds can resolve rapid movements better than humans, for whom flickering at a rate greater than 50 Hz appears as continuous movement. Humans cannot therefore distinguish individual flashes of a fluorescent light bulb oscillating at 60Hz, but Budgerigars and chickens have flicker thresholds of more than 100 Hz. A Cooper's Hawk can pursue agile prey through woodland and avoid branches and other objects at high speed; to humans such a chase would appear as a blur.

Birds can also detect slow moving objects. The movement of the sun and the constellations across the sky is imperceptible to humans, but detected by birds. The ability to detect these movements allows migrating birds to properly orient themselves.

To obtain steady images while flying or when perched on a swaying branch, birds hold the head as steady as possible with compensating reflexes. Maintaining a steady image is especially relevant for birds of prey.

Edges and shapes

When an object is partially blocked by another, humans unconsciously tend to make up for it and complete the shapes. It has however been demonstrated that pigeons do not complete occluded shapes. A study based on altering the grey level of a perch that was coloured differently from the background showed that budgerigars do not detect edges based on colours.

Magnetic fields

The perception of magnetic fields by migratory birds has been suggested to be light dependent. Birds move their head to detect the orientation of the magnetic field, and studies on the neural pathways have suggested that birds may be able to "see" the magnetic fields. The right eye of a migratory bird contains photoreceptive proteins called cryptochromes. Light excites these molecules to produce unpaired electrons that interact with the Earth's magnetic field, thus providing directional information.

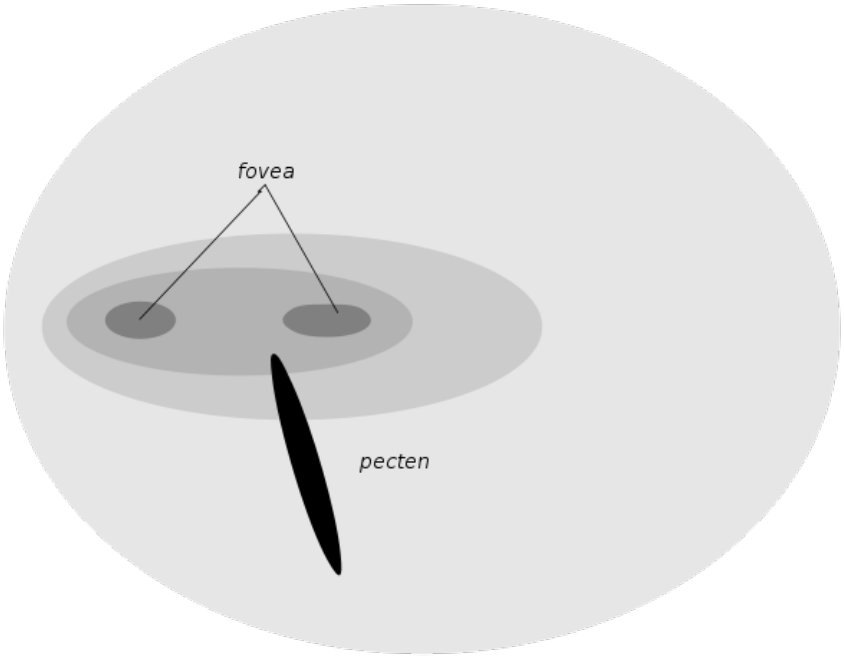
Variations across bird groups

Diurnal birds of prey

"Hawk-eyed" is a byword for visual acuity

The visual ability of birds of prey is legendary, and the keenness of their eyesight is due to a variety of factors. Raptors have large eyes for their size, 1.4 times greater than the average for birds of the same weight, and the eye is tube-shaped to produce a larger retinal image. The retina has a large number of receptors per square millimetre, which determines the degree of visual acuity. The more receptors an animal has, the higher its ability to distinguish individual objects at a distance, especially when, as in raptors, each receptor is typically attached to a single ganglion.

Many raptors have foveas with far more rods and cones than the human fovea (65,000/mm^2 in American Kestrel, 38,000 in humans) and this provides these birds with spectacular long distance vision. The fovea itself can also be lens-shaped, increasing the effective density of receptors further. This combination of factors gives *Buteo* buzzards distance vision 6 to 8 times better than humans.



Each retina of the Black-chested Buzzard-eagle has two fovea

The forward facing eyes of a bird of prey give binocular vision, which is assisted by a double fovea. The raptor's adaptations for optimum visual resolution (an American Kestrel can see a 2–mm insect from the top of an 18–m tree) has a disadvantage in that its vision is poor in low light level, and it must roost at night. Raptors may have to pursue mobile prey in the lower part of their visual field, and therefore do not have the lower field myopia adaptation demonstrated by many other birds. Scavenging birds like vultures do not need such sharp vision, so a condor has only a single fovea with about 35,000 receptors mm^2

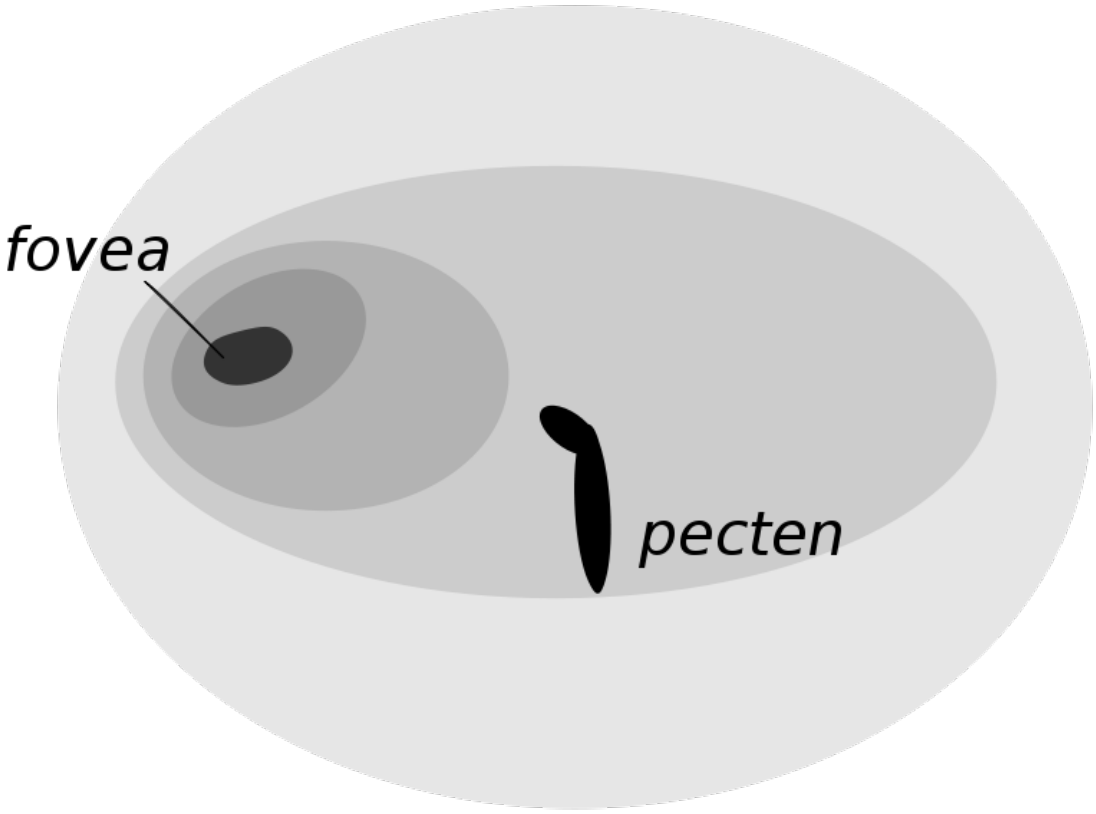
Raptors lack coloured oil drops in the cones, and probably have similar colour perception to humans, and lack the ability to detect polarised light. The generally brown, grey and white plumage of this group, and the absence of colour displays in courtship suggests that colour is relatively unimportant to these birds.

In most raptors a prominent eye ridge and its feathers extends above and in front of the eye. This "eyebrow" gives birds of prey their distinctive stare. The ridge physically protects the eye from wind, dust, and debris and shields it from excessive glare. The Osprey lacks this ridge, although the arrangement of the feathers above its eyes serves a similar function; it also possesses dark feathers in front of the eye which probably serve to reduce the glare from the water surface when the bird is hunting for its staple diet of fish.

Nocturnal birds

Eurasian Eagle-owl

Owls have very large eyes for their size, 2.2 times greater than the average for birds of the same weight, and positioned at the front of the head. The eyes have a field overlap of 50–70%, giving better binocular vision than for diurnal birds of prey (overlap 30–50%). The Tawny Owl's retina has about 56,000 light-sensitive rods per square millimetre (36 million per square inch); although earlier claims that it could see in the infrared part of the spectrum have been dismissed.



Each owl's retina has a single fovea

Adaptations to night vision include the large size of the eye, its tubular shape, large numbers of closely packed retinal rods, and an absence of cones, since colour vision is unnecessary at night. There are few coloured oil drops, which would reduce the light intensity, but the retina contains a reflective layer, the tapetum lucidum. This increases the amount of light each photosensitive cell receives, allowing the bird to see better in low light conditions. Owls normally have only one fovea, and that is poorly developed except in diurnal hunters like the Short-eared Owl.

Besides owls, bat hawks, frogmouths and nightjars also display good night vision. Some bird species nest deep in cave systems which are too dark for vision, and find their way to the nest with a simple form of echolocation. The Oilbird is the only nocturnal bird to echolocate, but several *Aerodramus* swiftlets also utilise this technique, with one species, Atiu Swiftlet, also using echolocation outside its caves.

Water birds

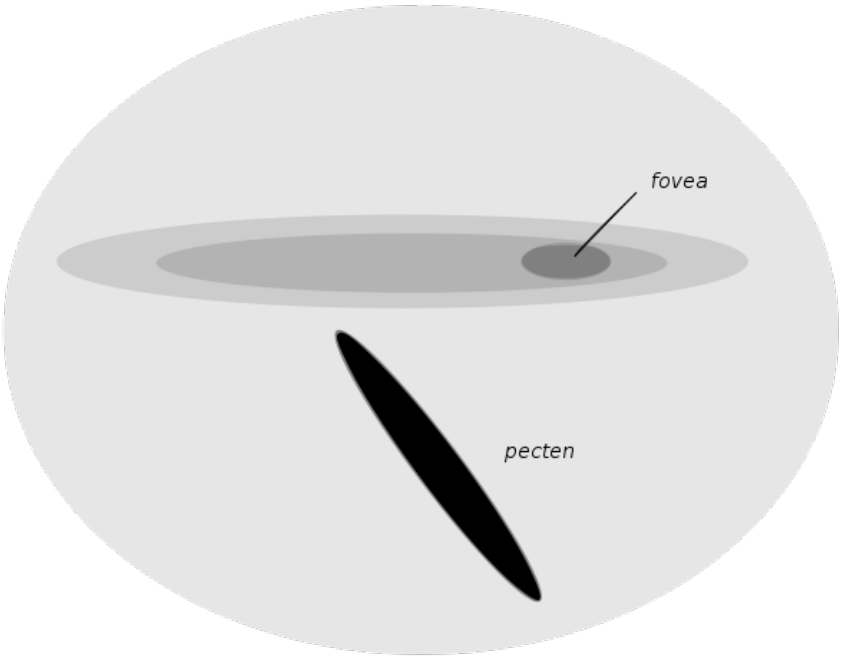
Terns have coloured oil droplets in the cones of the eye to improve distance vision

Seabirds such as terns and gulls that feed at the surface or plunge for food have red oil droplets in the cones of their retinas. This improves contrast and sharpens distance vision, especially in hazy conditions. Birds that have to look through an air/water interface have more deeply coloured carotenoid pigments in the oil drops than other species.

This helps them to locate shoals of fish, although it is uncertain whether they are sighting the phytoplankton on which the fish feed, or other feeding birds.

Birds that fish by stealth from above the water have to correct for refraction particularly when the fish are observed at an angle. Reef Herons and Little Egrets appear to be able to make the corrections needed when capturing fish and are more successful in catching fish when strikes are made at an acute angle and this higher success may be due to the inability of the fish to detect their predators.

Birds that pursue fish under water like auks and divers have far fewer red oil droplets, but they have special flexible lenses and use the nictitating membrane as an additional lens. This allows greater optical accommodation for good vision in air and water. Cormorants have a greater range of visual accommodation, at 50 dioptres, than any other bird, but the kingfishers are considered to have the best all-round (air and water) vision.



Each retina of the Manx Shearwater has one fovea and an elongated strip of high photoreceptor density

Tubenosed seabirds, which come ashore only to breed and spend most of their life wandering close to the surface of the oceans, have a long narrow area of visual sensitivity on the retina This region, the *area giganto cellularis*, has been found in the Manx Shearwater, Kerguelen Petrel, Great Shearwater, Broad-billed Prion and Common Diving-petrel. It is characterised by the presence of ganglion cells which are regularly arrayed and larger than those found in the rest of the retina, and morphologically appear similar to the cells of the retina in cats. The location and cellular morphology of this novel area suggests a function in the detection of items in a small binocular field projecting below and around the bill. It is not concerned primarily with high spatial resolution, but may assist in the detection of prey near the sea surface as a bird flies low over it.

The Manx Shearwater, like many other seabirds, visits its breeding colonies at night to reduce the chances of attack by aerial predators. Two aspects of its optical structure suggest that the eye of this species is adapted to vision at night. In the shearwater's eyes the lens does most of the bending of light necessary to produce a focused image on the retina. The cornea, the outer covering of the eye, is relative flat and so of low refractive power. In a diurnal bird like the pigeon, the reverse is true; the cornea is highly curved and is the principal refractive component. The ration of refraction by the lens to that by

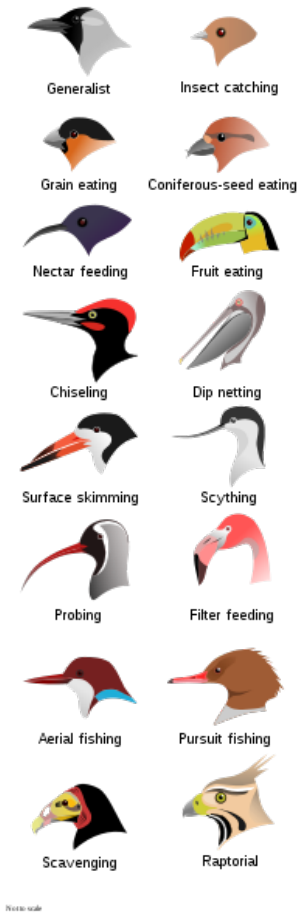
the cornea is 1.6 for the shearwater and 0.4 for the pigeon; the figure for the shearwater is consistent with that for a range of different nocturnal bird and mammal.

The shorter focal length of shearwater eyes give them a smaller, but brighter, image than is the case for pigeons, so the latter has sharper daytime vision. Although the Manx Shearwater has adaptations for night vision, the effect is small, and it is likely that these birds also use smell and hearing to locate their nests.

It used to be thought that penguins were short-sighted on land. Although the cornea is flat and adapted to swimming underwater, the lens is very strong and can compensate for the reduced corneal focusing when out of water. Almost the opposite solution is used by the Hooded Merganser which can bulge part of the lens through the iris when submerged.

Chapter 3

Beak



Comparison of bird beaks, displaying different shapes adapted to different feeding methods. Not to scale.

The **beak**, **bill** or **rostrum** is an external anatomical structure of birds which is used for eating and for grooming, manipulating objects, killing prey, probing for food, courtship and feeding young. The term beak is also used to refer to a similar mouthpart in some

Ornithischian dinosaurs, monotremes, cephalopods, cetaceans, pufferfishes, turtles, Anuran tadpoles and sirens.

Etymology

The terms 'beak' and 'bill' are interchangeable, although the former was formerly restricted to hooked beaks of birds of prey and parrots.

Anatomy

Beaks vary significantly in size and shape from species to species. The beak is composed of an upper jaw, called the maxilla, and a lower jaw, called the mandible. The jaw is made of bone, typically hollow or porous to reduce weight for flying. The outside surface of the beak is covered by a thin horny sheath of keratin called the **rhamphotheca**. Between the hard outer layer and the bone is a vascular layer containing blood vessels and nerve endings. The rhamphotheca can include **knob**, which is found above the beak of some swans, such as the Mute Swan, and some domesticated Chinese geese (*pictured*).

The beak has two holes called **nares** (nostrils) which connect to the hollow inner beak and thence to the respiratory system. The nares are usually at the base of the beak, near the dorsal surface. Kiwi are the only birds with nostrils at the end of their beak. In some birds, the nares are in a fleshy, often waxy structure at the base of the beak called the **cere** (from Latin *cera*, meaning wax). The cere is an indicator of the reproductive cycle of budgerigars.

Petrels and albatrosses have external horny sheaths called naricorns that protect the nares. These are separately placed on either side of the base of the upper mandible in albatrosses, but fused, with an internal septum, on the top of the base of the upper mandible in petrels. In the mallard, and perhaps in other ducks, there is no cere, and the nostrils are in the hard part of the beak, as a soft cere would be liable to injury when the duck dredges for food among submerged debris and stones.

On some birds, the tip of the beak is hard, dead tissue used for heavy-duty tasks such as cracking nuts or killing prey. On other birds, such as ducks, the tip of the bill is sensitive and contains nerves, for locating things by touch. The beak is worn down by use, so it grows continually throughout the bird's life. Some birds such as the Snow Goose have cutting serrations to their bills, these are known as *Tomia*.

Uses of beaks

As noted by Darwin in his observations on Galapagos Finches, birds' beaks have evolved to suit the ecological niche they fill: Raptors have decurved (downward curving) beaks for ripping up meat. Hummingbirds have long thin beaks for reaching nectar. The spoonbills' beaks allow them to filter-feed in shallow water. Unlike jaws with teeth, beaks are not used for chewing. Birds swallow their food whole, and it is broken up in the gizzard. Beaks are also very useful for scrabbling.

Billing

A fledgeling Common Starling shows the interior of its bill.

During courtship, mated pairs of a variety of bird species touch and clasp each other's bills. This is called **billing** and appears to strengthen the pair bond (Terres, 1980). Gannets raise their bills high and repeatedly clatter them (*pictured*); the male puffin nibbles at the female's beak; the male waxwing puts his bill in the female's mouth; and ravens hold each other's beaks in a prolonged "kiss".

Beak gallery

A variety of beaks

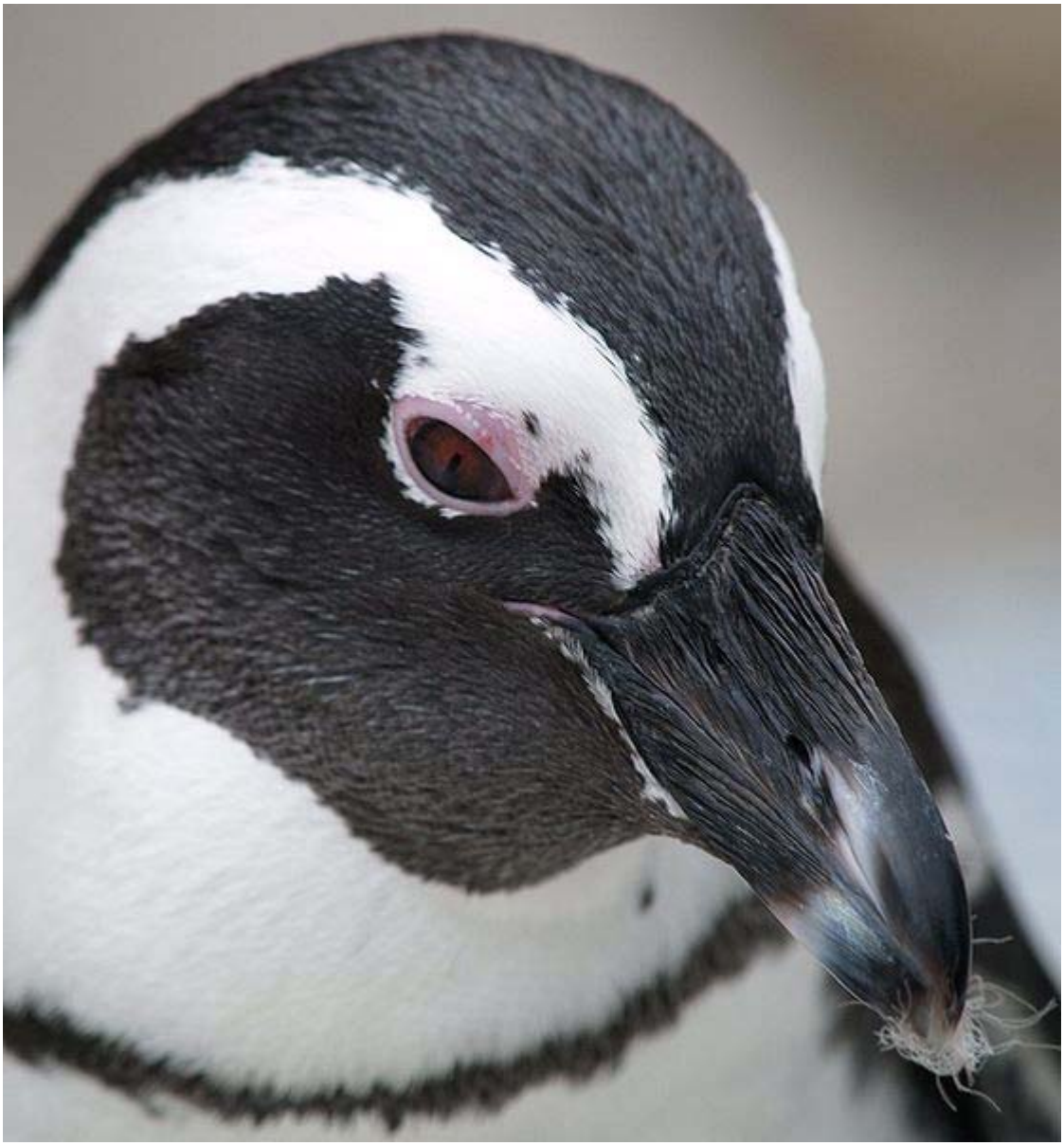
The bill of a scavenger—the Griffon Vulture.

The bill of a domesticated Chinese goose. The knob is highly exaggerated by farm selection.

Northern Gannets billing.

The bill of the Greater Flamingo.

The beak of a Brown Falcon.



The beak of an African Penguin.

The Kea uses its long curved beak to prey on animals as large as sheep.

The beak of a Catalina Macaw

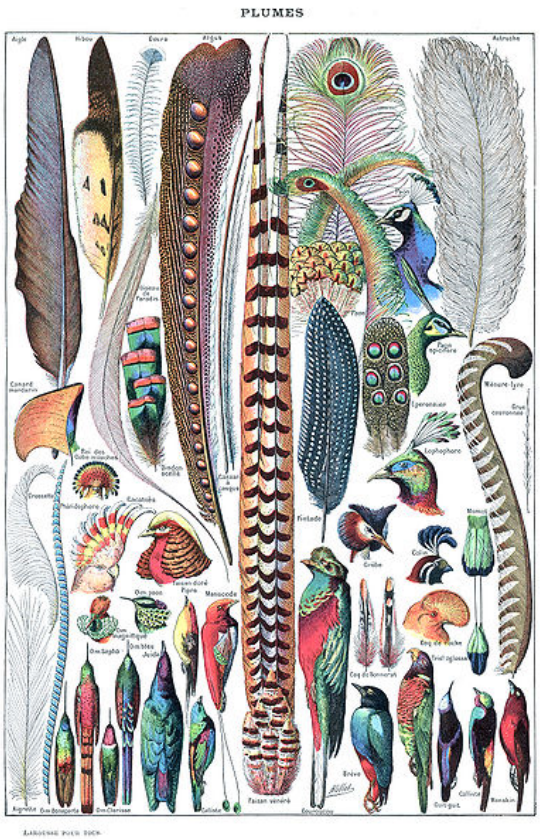
The beak of a malabar grey hornbill

The beak of a golden eagle

Dusky Moorhen, Gallinula tenebrosa

Chapter 4

Feather



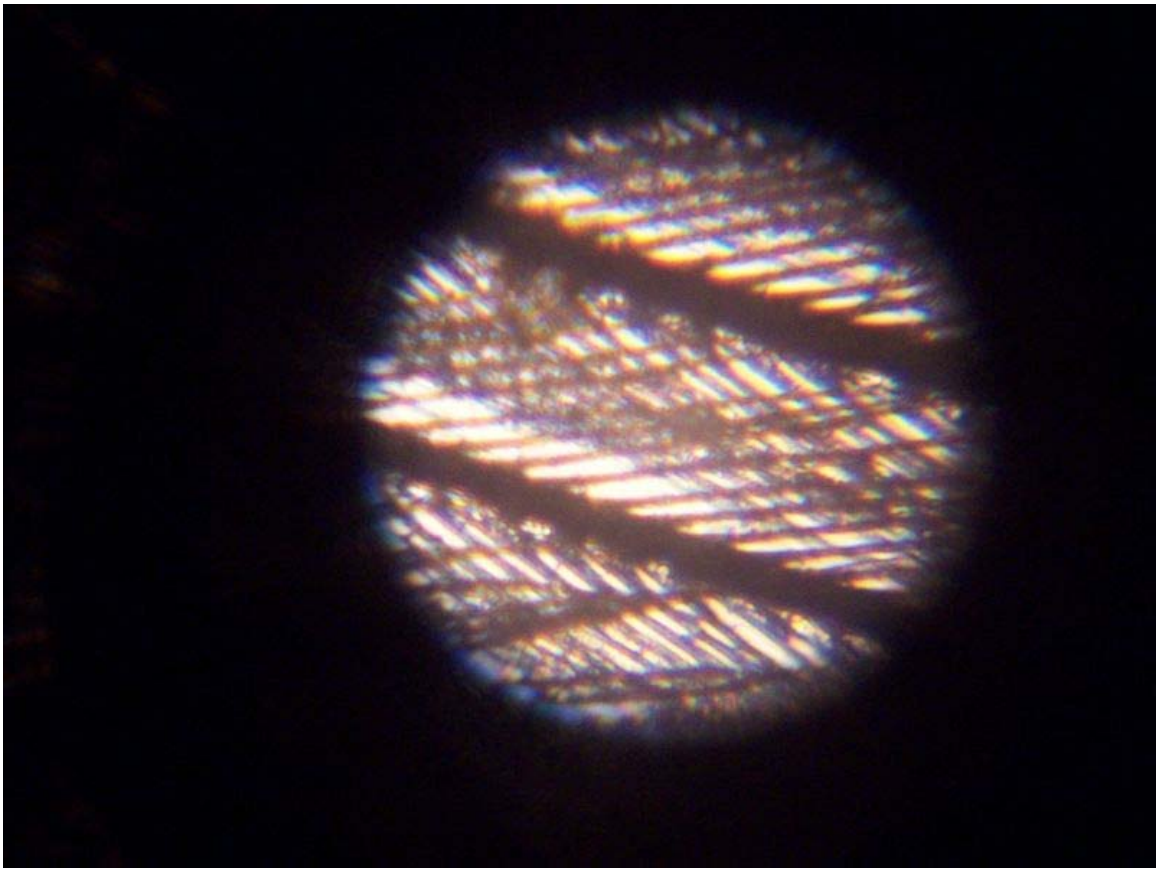
Feather variations

Feathers are one of the epidermal growths that form the distinctive outer covering, or plumage, on birds. They are considered the most complex integumentary structures found in vertebrates, and indeed a premier example of a complex evolutionary novelty. They are among the characteristics that distinguish the extant Aves from other living groups. Feathers have also been noticed in those Theropoda which have been termed feathered dinosaurs. Although feathers cover most parts of the body of birds, they arise only from certain well-defined tracts on the skin. They aid in flight, thermal insulation, waterproofing and coloration that helps in communication and protection.

Structure and characteristics

Parts of a feather:
1. Vane
2. Rachis
3. Barb
4. Afterfeather
5. Hollow shaft, calamus

Featherstructure of a Blue-and-yellow Macaw



Budgerigar feather, magnified, showing interlocking barbules

Feathers are among the most complex integumentary appendages found in vertebrates and are formed in tiny follicles in the epidermis, or outer skin layer, that produce keratin proteins. The β-keratins in feathers, beaks and claws — and the claws, scales and shells of reptiles — are composed of protein strands hydrogen-bonded into β-pleated sheets, which are then further twisted and crosslinked by disulfide bridges into structures even tougher than the α-keratins of mammalian hair, horns and hoof. The exact signals that induce the growth of feathers on the skin are not known but it has been found that the transcription factor cDermo-1 induces the growth of feathers on skin and scales on the leg.

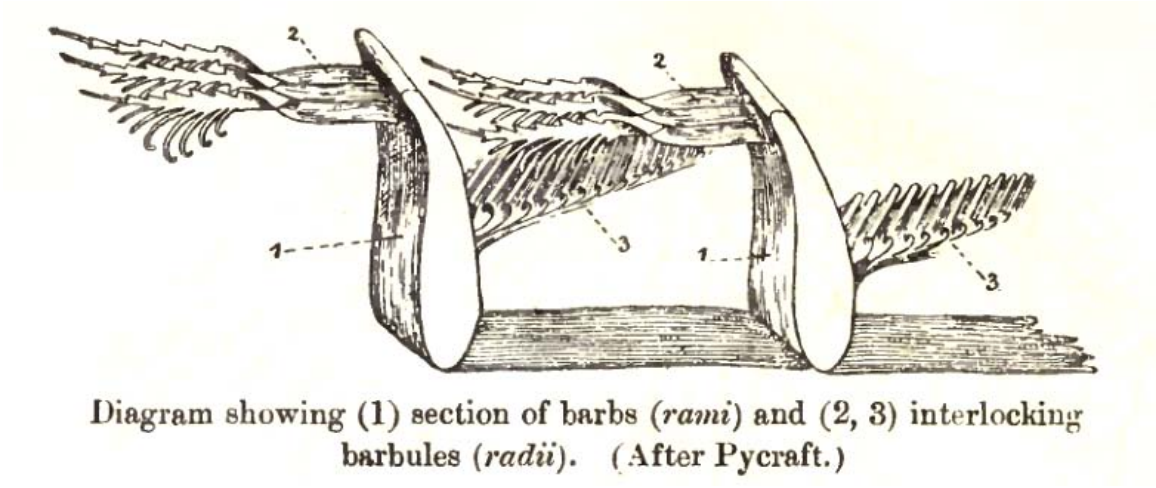


Diagram showing (1) section of barbs (*rami*) and (2, 3) interlocking barbules (*radii*). (After Pycraft.)

Feather microstructure showing interlocking barbules.

Classification

There are two basic types of feather: **vaned feathers** which cover the exterior of the body, and **down feathers** which are underneath the vaned feathers. The pennaceous feathers are vaned feathers. Also called **contour feathers**, pennaceous feathers arise from tracts and cover the whole body. A third rarer type of feathers, **filoplumes**, is hairlike and (if present in a bird) grows along the fluffy down feathers. In some passerines, filoplumes arise exposed beyond the contour feathers on the neck. The remiges, or flight feathers of the wing, and rectrices, the flight feathers of the tail are the most important feathers for flight. A typical vaned feather features a main shaft, called the rachis. Fused to the rachis are a series of branches, or barbs; the *barbs* themselves are also branched and form the *barbules*. These barbules have minute hooks called *barbicels* for cross-attachment. Down feathers are fluffy because they lack barbicels, so the barbules float free of each other, allowing the down to trap much air and provide excellent thermal insulation. At the base of the feather, the rachis expands to form the hollow tubular *calamus* (or quill) which inserts into a follicle in the skin. The basal part of the calamus is without vanes. This part is embedded within the skin follicle and has an opening at the base (proximal umbilicus) and a small opening on the side (distal umbilicus).

Hatchling birds of some species have a special kind of natal down (neossoptiles) and these are pushed out when the normal feathers (teleoptiles) emerge.

Flight feathers are stiffened so as to work against the air in the downstroke but yield in other directions. It is noted that the pattern of orientation of β-keratin fibers in the feathers of flying birds differs from that in flightless birds. The fibers are better aligned in the middle of the feather and less aligned towards the tips.

Functions

Feathers insulate birds from water and cold temperatures. They may also be plucked to line the nest and provide insulation to the eggs and young. The individual feathers in the wings and tail play important roles in controlling flight. Some species have a crest of feathers on their heads. Although feathers are light, a bird's plumage weighs two or three times more than its skeleton, since many bones are hollow and contain air sacs. Color patterns serve as camouflage against predators for birds in their habitats, and by predators looking for a meal. As with fish, the top and bottom colors may be different to provide camouflage during flight. Striking differences in feather patterns and colors are part of the sexual dimorphism of many bird species and are particularly important in selection of mating pairs. In some cases there are differences in the UV reflectivity of feathers across sexes even though no differences in color are noted in the visible range. The wing feathers of male Club-winged Manakins *Machaeropterus deliciosus* have special structures that are used to produce sounds by stridulation.

A contour feather from a Guinea fowl.

Some birds have a supply of powder down feathers which grow continuously, with small particles regularly breaking off from the ends of the barbules. These particles produce a powder that sifts through the feathers on the bird's body and acts as a waterproofing agent and a feather conditioner. Powder down has evolved independently in several taxa and can be found in down as well as pennaceous feathers. They may be scattered in plumage in the pigeons and parrots or in localized patches on the breast, belly or flanks as in herons and frogmouths. Herons use their bill to break the feathers and to spread them while cockatoos may use their head as a powder puff to apply the powder. Waterproofing can be lost by exposure to emulsifying agents due to human pollution. Feathers can become waterlogged and birds may sink. It is also very difficult to clean and rescue birds

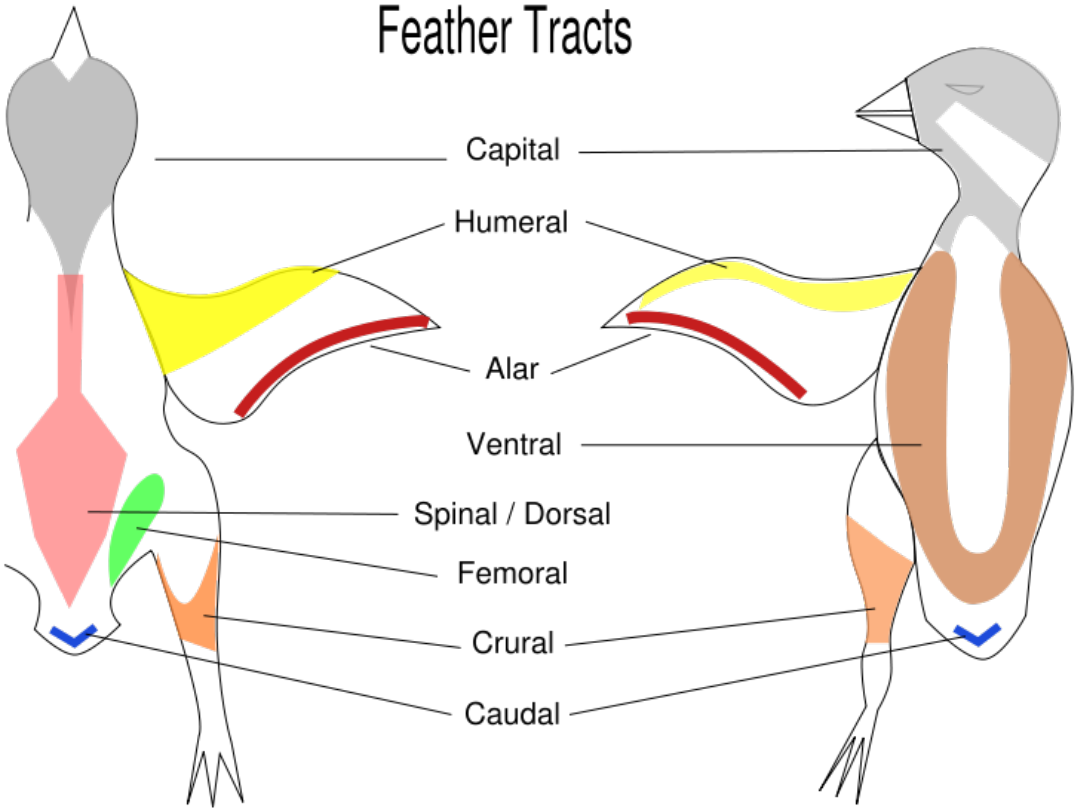
whose feathers have been fouled by oil spills. The feathers of cormorants soak up water and help in reducing buoyancy and thereby allowing the birds to swim submerged.

Rictal bristles of a White-cheeked Barbet

Bristles are stiff, tapering feathers with a large rachis but few barbs. **Rictal bristles** are bristles found around the eyes and bill. They may serve a similar purpose to eyelashes and vibrissae in mammals. It has been suggested that they may aid insectivorous birds in prey capture or that it may have sensory functions, however there is no clear evidence. In one study, Willow Flycatchers (*Empidonax traillii*) were found to catch insects equally well before and after removal of the rictal bristles.

Grebes are peculiar in their habit of ingesting their own feathers and also feeding them to their young. Observations on the diet and feather eating frequency suggest that ingesting feathers particularly down from their flanks aids in forming easily ejectable pellets along with their diet of fish.

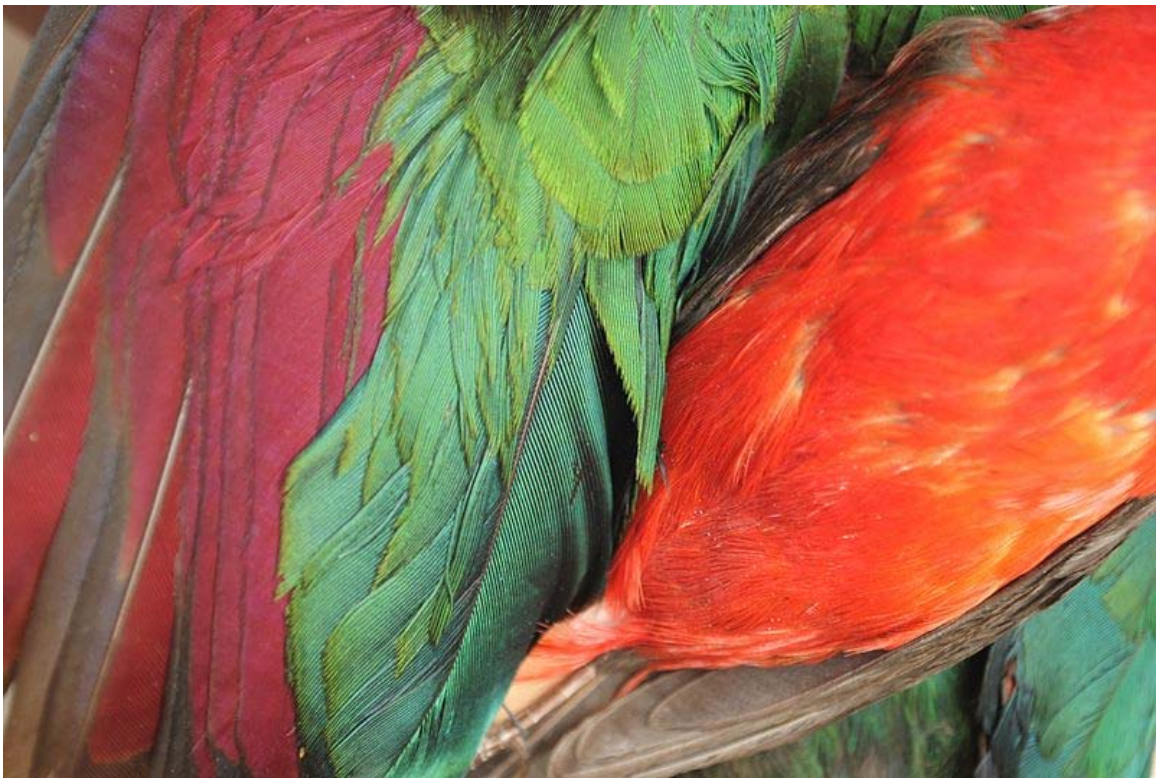
Distribution



Feather tracts or pterylae and their naming

Contour feathers are not uniformly distributed on the skin of the bird except in some groups such as the Penguins, ratites and screamers. In most birds the feathers grow from specific tracts of skin called pterylae while there are regions which are free of feathers called apterylae. Filoplumes and down may arise from the apteriae, regions between the pterylae. The arrangement of these feather tracts, pterylosis or pterylography, varies across bird families and has been used in the past as a means for determining the evolutionary relationships of bird families.

Coloration



Colors resulting from different feather pigments **Left:** turacin (red) and turacoverdin (green, with some structural blue iridescence at lower end) on the wing of *Tauraco bannermani* **Right:** carotenoids (red) and melanins (dark) on belly/wings of *Ramphocelus bresilius*

The colors of feathers are produced by the presence of pigments, or by microscopic refractive structures, or by a combination of both.

Most feather pigments are melanins (brown and beige pheomelanins, black and grey eumelanins) and carotenoids (red, yellow, orange); other pigments occur only in certain taxa – the yellow to red psittacofulvins (found in some parrots) and the red turacin and green turacoverdin (porphyrin pigments found only in turacos). Structural coloration is involved in the production of blue colors, iridescence, most ultraviolet reflectance and in the enhancement of pigmentary colors; structural iridescence has been reported in fossil feathers dating back 40 million years. White feathers lack pigment and scatter light diffusely; albinism in birds is caused by defective pigment production, though structural coloration will not be affected (as can be seen e.g. in blue-and-white budgerigars).

A feather with no pigment

For example, the blues and bright greens of many parrots are produced by constructive interference of light reflecting from different layers of the structures in feathers, in the case of green plumage in addition to the yellow pigments; the specific feather structure involved is sometimes called the Dyck texture. Melanin is often involved in the absorption of some of the light; in combination with yellow pigment it produces dull olive-greens.

In some birds, the feather colors may be created or altered by uropygial gland secretions. The yellow bill colors of many hornbills are produced by preen gland secretions. Other differences that may only be visible in the ultraviolet region have been suggested but

studies have failed to find evidence. Uropygial oil secretion may also have an inhibitory effect on feather bacteria.

A bird's feathers undergo wear and tear and are replaced periodically during its life through molting. New feathers, known as blood, or pin feathers (depending on the stage of growth) when developing, are formed through the same follicle from which the old ones were fledged. The presence of melanin in feathers increases their resistance to abrasion. One study notes that melanin based feathers were observed to degrade more quickly under bacterial action, even compared to unpigmented feathers from the same species, than those unpigmented or with carotenoid pigments. However, another study the same year compared the action of bacteria on pigmentations of two song sparrow species and observed that the darker pigmented feathers were more resistant and they cited other research also published in 2004 that stated increased melanin provided greater resistance. They observed that the greater resistance of the darker birds confirmed Gloger's rule. The evolution of coloration is based on sexual selection and it has been suggested that carotenoid-based pigments may have evolved since they are likely to be more honest signals of fitness because they are derived from special diets, or because carotenoids are also required for immune function.

Parasites

The feather surface is the home for some ectoparasites, notably feather lice (Phthiraptera) and feather mites. Feather lice typically live on a single host and can move only from parents to chicks or mating birds and occasionally by phoresy. This life history has resulted in most of the species being specific to the host and coevolving with the host, making them of interest in phylogenetic studies.

Feather holes are chewing traces of lice (most probably *Brueelia* spp. lice) on the wing and tail feathers. They were described on barn swallows, and because of easy countability, many evolutionary, ecological, and behavioral publications use them to quantify the intensity of infestation.

Interestingly, parasitic cuckoos which grow up in the nests of other species also have host specific feather lice and these seem to be transmitted only after they leave the host nest.

Birds maintain their feather condition by bathing in water, dust bathing and preening. A peculiar behavior of birds, anting, where ants are introduced into the plumage was suggested to help in reducing parasites but no supporting evidence has been found.

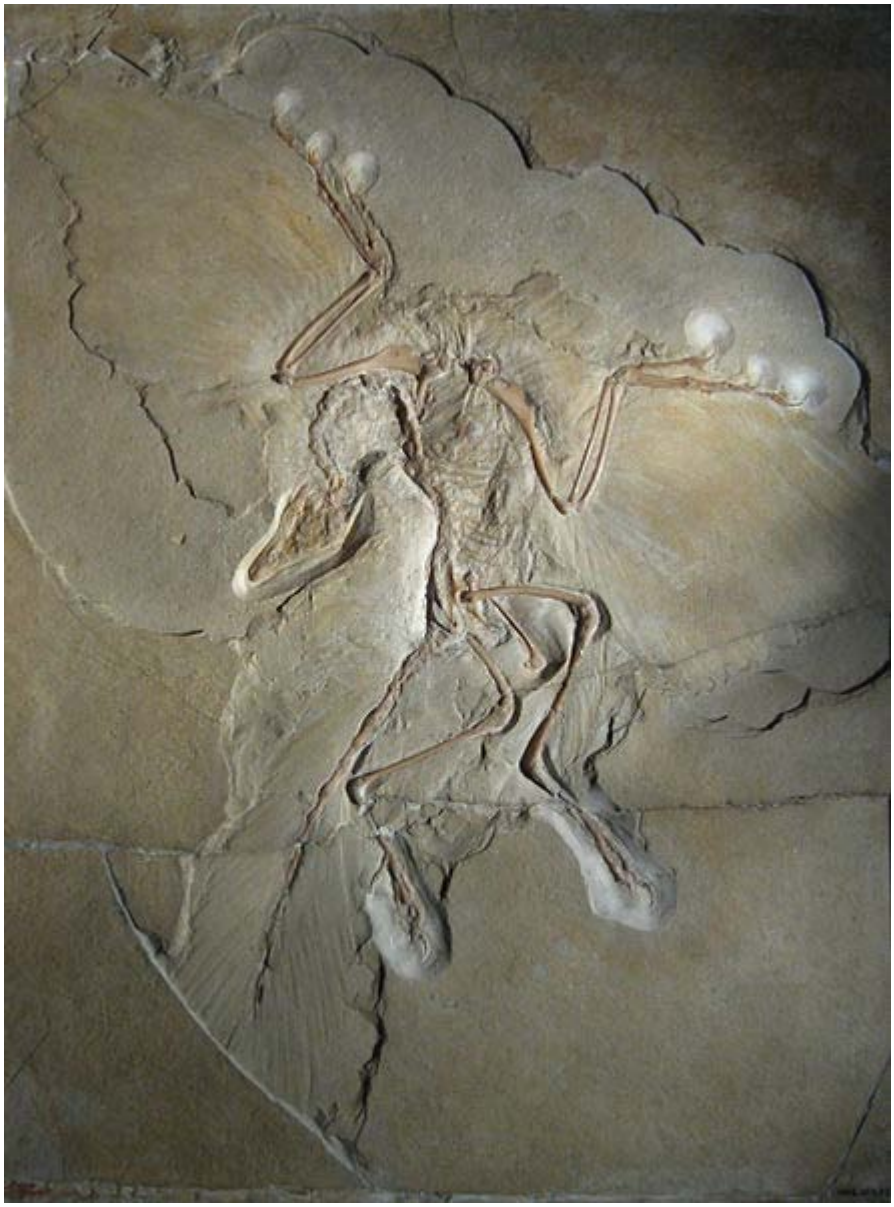
Evolution

Fossil feather of Archaeopteryx

The functional view on the evolution of feathers has traditionally focused on insulation, flight and display. Discoveries of non-flying Late Cretaceous feathered dinosaurs in China however suggest that flight could not have been the original primary function. There have been suggestions that feathers may have had their original function in thermoregulation, waterproofing or even as sinks for metabolic wastes such as sulphur. While feathers have been suggested as having evolved from reptilian scales, there are numerous objections, and more recent explanations have arisen from the paradigm of evolutionary developmental biology. Theories of the scale-based origins of feathers suggest that the planar scale structure was modified for their development into feathers by splitting to form the webbing; however, the developmental process involves a tubular

structure arising from a follicle and the tube splitting longitudinally to form the webbing. The number of feathers per unit area of skin is higher in smaller birds than in larger birds, and this trend indicates their important role in thermal insulation, since smaller birds lose more heat due to the relatively larger surface area in proportion to their body weight. The coloration of feathers is believed to be primarily evolved in response to sexual selection. In many cases the physiological condition of the birds (especially males) is indicated by the quality of their feathers and this is used (by the females) in mate choice.

Feathered dinosaurs



Archaeopteryx lithographica (Berlin specimen)

Several non-avian dinosaurs had feathers on their limbs that would not have functioned for flight. One theory is that feathers originally evolved on dinosaurs as a result of

insulation properties; those small dinosaurs that then grew longer feathers may have found them helpful in gliding leading to the evolution of proto-birds like *Archaeopteryx* and *Microraptor zhaoianus*. Dinosaurs that had feathers or protofeathers include *Pedopenna daohugouensis*, and *Dilong paradoxus*, a tyrannosauroid which is 60 to 70 million years older than *Tyrannosaurus rex*.

The majority of dinosaurs known to have had feathers or protofeathers are saurischians, however featherlike "filamentous integumentary structures" are also known from the ornithischians *Tianyulong* and *Psittacosaurus*. The exact nature of these structures is still under study.

Since the 1990s, dozens of feathered dinosaurs have been discovered in the clade Maniraptora, which includes the clade Avialae and the recent common ancestors of birds, Oviraptorosauria and Deinonychosauria. In 1998, the discovery of a feathered oviraptorosaurian, *Caudipteryx zoui*, challenged the notion that feathers were an exclusive structure of Avialae. Buried in the Yixian Formation in Liaoning, China, *C. zoui* lived during the Early Cretaceous Period. Present on the forelimbs and tails, their integumentary structure has been accepted as pennaceous vaned feathers based on the rachis and herringbone pattern of the barbs. In the clade Deinonychosauria, the continued divergence of feathers is also apparent in the families Troodontidae and Dromaeosauridae. Branched feathers with ranchis, barbs, and barbules were discovered in many members including *Sinornithosaurus millenii*, a dromaeosaurid found in the Yixian formation (124.6 MYA).

Previously, a temporal paradox existed in the evolution of feathers - theropods with highly derived bird-like characteristics occurred at a later time than *Archaeopteryx*, suggesting that the descendants of birds arose before the ancestor. However, this paradox was resolved in 2009 with the discovery of *Anchiornis huxleyi*, found in the Late Jurassic Tiaojishan Formation (160 MYA) in western Liaoning. By predating *Archaeopteryx*, *Anchornis* proves the existence of a modernly feathered theropod ancestor, providing insight into the dinosaur-bird transition. The specimen shows distribution of large pennaceous feathers on the forelimbs and tail, implying that pennaceous feathers spread to the rest of the body at a earlier stage in theropod evolution.

Chapter 5

Arcopallium, Brood Patch and Comb (Anatomy)

Arcopallium

The **arcopallium** refers to regions of the avian brain which partially overlap regions homologous to the amygdala of mammals. These regions have formerly been referred to as **archistriatum**, and before this **epistriatum** or **amygdaloid complex**, and a recent change of nomenclature has divided the region into the **arcopallium** and **posterior pallial amygdala**. The new nomenclature, adopted in 2004, reflects a modern understanding that the avian brain is broadly similar to the mammalian brain, containing large regions homologous to the mammalian neocortex, claustrum, and pallial amygdala. The outdated nomenclature it replaced perceived the avian brain as consisting almost entirely of enlarged basal ganglia, to which more complex outer layers had been added during a progress toward mammalian intelligence.

Reassignments

Specific reassignments of terminology were made with consideration of retaining abbreviations, and include:

- Archistriatum: Arcopallium (A)
- Nucleus archistriatalis anterior: Anterior arcopallium (AA)
- Archistriatum, pars dorsalis: Dorsal arcopallium (AD)
- Upper part of Archistriatum, pars ventralis: Intermediate arcopallium (AI)
- Medial part of Archistriatum, pars ventralis: Medial arcopallium (AM)
- Robust nucleus of archistriatum in male songbirds: Robust nucleus of arcopallium (RA)
- Central nucleus of anterior archistriatum in parrots: Central nucleus of anterior arcopallium (AAC)
- Ventral part of Archistriatum, pars ventralis plus caudal part of Archistriatum: Posterior nucleus of the pallial amygdala (PoA)

- Nucleus taeniae: Nucleus taeniae of the amygdala (Tn/TnA)
- Region below paleostriatum primitivum posterior to anterior commissure: Subpallial amygdaloid area (PA/SpA)

Brood patch

Brood patch of Sand Martin

A **brood patch** is a patch of featherless skin that is visible on the underside of birds during the nesting season. This patch of skin is well supplied with blood vessels at the surface making it possible for the birds to transfer heat to their eggs when incubating. In most species the feathers in the region are shed automatically but ducks and geese may pluck the feathers and use them to line the nest. The feathers of the region regrow soon after the eggs hatch in the case of precocial birds but may be delayed in those birds having altricial young.

The positions of brood patches can vary with many having a single brood patch in the middle of the belly while some shorebirds have one patch on each side of the belly. Gulls and galliformes may have three brood patches. Pelicans, boobies and gannets do not develop brood patches, but instead cradle the eggs on their feet when incubating. Brood

parasitic cuckoos do not develop brood patches. In species where both parents incubate, brood patches may develop in both sexes.

Comb (anatomy)

A rooster with a large red comb.

Anatomically, a **comb** is a fleshy growth, caruncle, or crest on the top of the head of gallinaceous birds, most notably turkeys, pheasants, and domestic chickens. Its alternative name **cockscomb** (spelling variations abound) is because combs are generally larger on males than on females (a male gallinaceous bird is called a cock).

Rooster cockscombs are red, but in other species the color may vary from light grey to deep blue or red; turkey cockscombs can vary in colour from bright red to blue.

In cookery

Cockscombs are used in cookery, often in combination with wattles or chicken kidneys.

Cockscombs were formerly used in French cuisine as garnishes. They were also used to prepare salpicons served in vol au vents, profiteroles, and so on; in that case, they were often combined with other luxury ingredients such as truffles, sweetbreads, or morels in a cream sauce.

In Italian cuisine, cockscombs are an important ingredient in the famous sauce called *Cibreo*, which also includes chicken livers, wattles, and unlaid eggs. It is used as a sauce for tagliatelle and in the molded potato-ricotta ring *Cimabella con cibreo*.

Cockscombs are prepared by parboiling and skinning, then cooking in court-bouillon. After preparation, they are greyish.

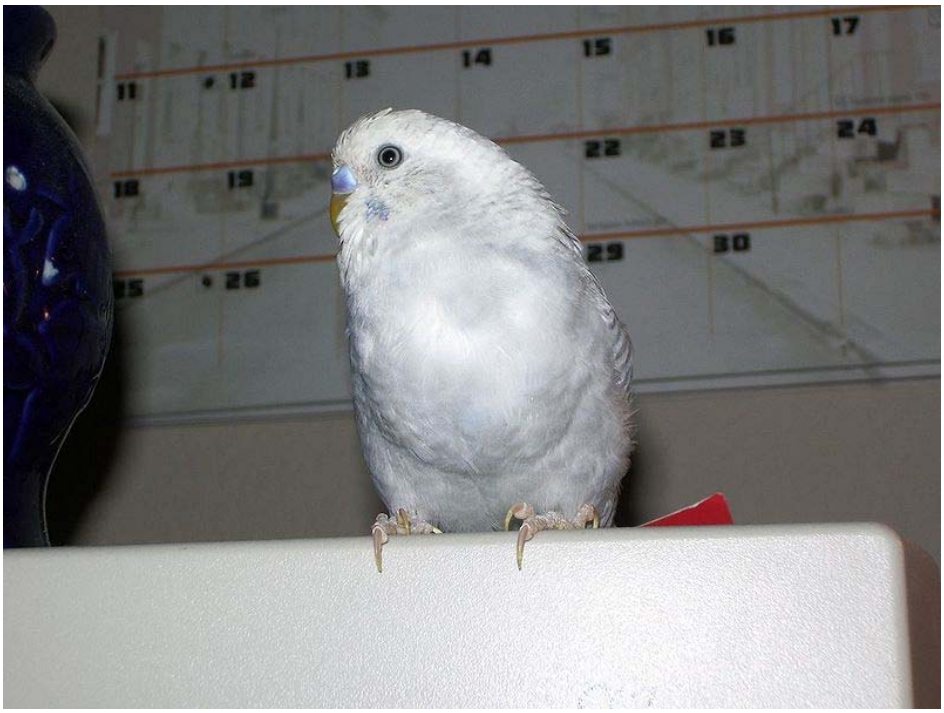
Other

Because of its bright color and distinctive shape, 'cockscomb' also describes various plants, including the florists' plant *Celosia cristata*, the meadow weed yellow rattle, sainfoin, wild poppy, lousewort, *Erythronium* and *Erythrina crista-galli*; the characteristic jester's cap; a shape of pasta (*creste di galli*); and so on.

Chapter 6

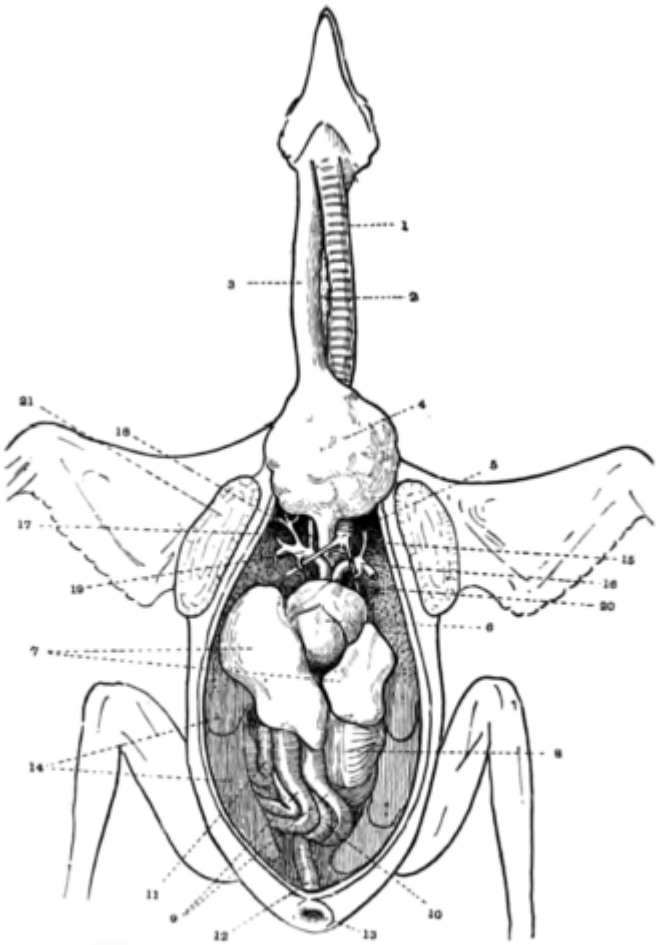
Crop (Anatomy), Culmen (Bird) and Furcula

Crop (anatomy)



A male Budgerigar with a full crop after feeding.

One Greater Flamingo-chick in Zoo Basel is fed on crop milk.



The chief Viscera of the Pigeon, *Columba livia*

1. Trachea. 2. Thymus gland. 3. Oesophagus. 4. Crop. 5. Syrinx. 6. Heart. 7. Liver. 8. Gizzard. 9. Duodenum. 10. Pancreas. 11. Small intestine. 12. Rectum. 13. Cloaca. 14. Air-sacs. 15. Left carotid. 16. Left subclavian. 17. Right carotid. 18. Brachial artery. 19. Right subclavian. 20. Muscles of syrinx. 21. Pectoralis major muscle cut across.

The crop (serial 4) prominently seen at the beginning of the alimentary canal.

A **crop** (or **croup**) is a thin-walled expanded portion of the alimentary tract used for the storage of food prior to digestion that is found in many animals, including gastropods, earthworms, leeches, insects, birds, and even some dinosaurs.

Bees

Cropping is used by bees to temporarily store nectar of flowers. When bees "suck" nectar, it is stored in their crop.

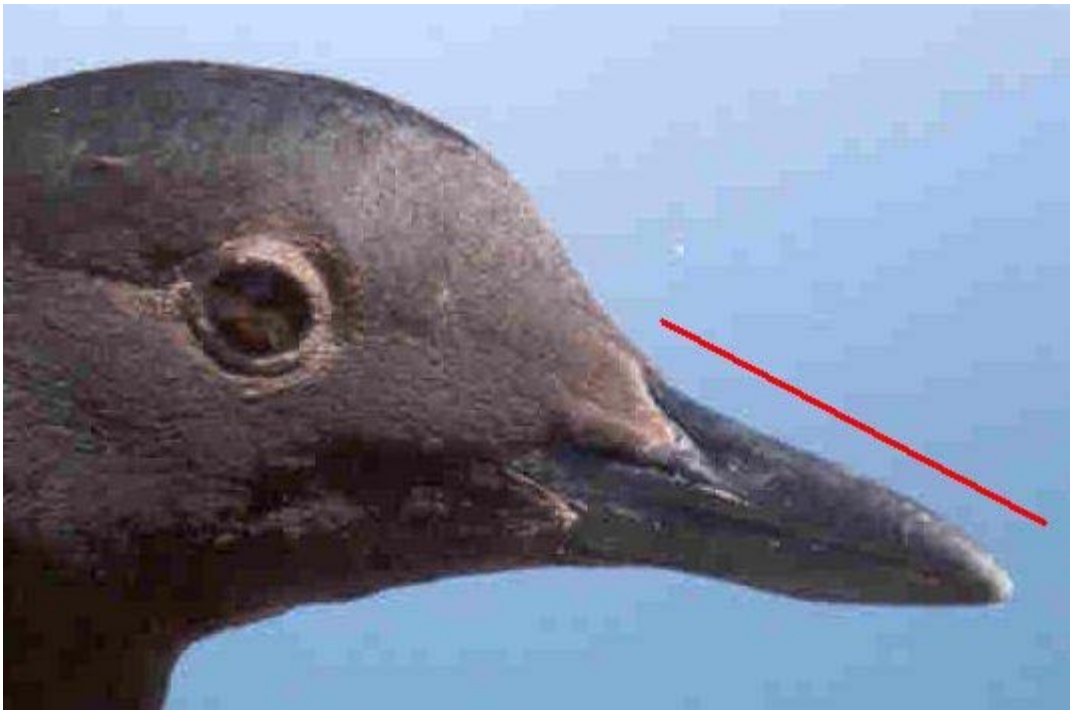
Birds

In a bird's digestive system, the crop is an expanded, muscular pouch near the gullet or throat. It is a part of the digestive tract, essentially an enlarged part of the esophagus. As with most other organisms that have a crop, the crop is used to temporarily store food. Not all birds have a crop. In adult doves and pigeons, the crop can produce crop milk to feed newly hatched birds.

Scavenging birds, such as vultures, will gorge themselves when prey is abundant, causing their crop to bulge. They subsequently sit, sleepy or half torpid, to digest their food.

Most raptors have one; like falcons, hawks, eagles and vultures (as stated above) but owls do not.

Culmen (bird)

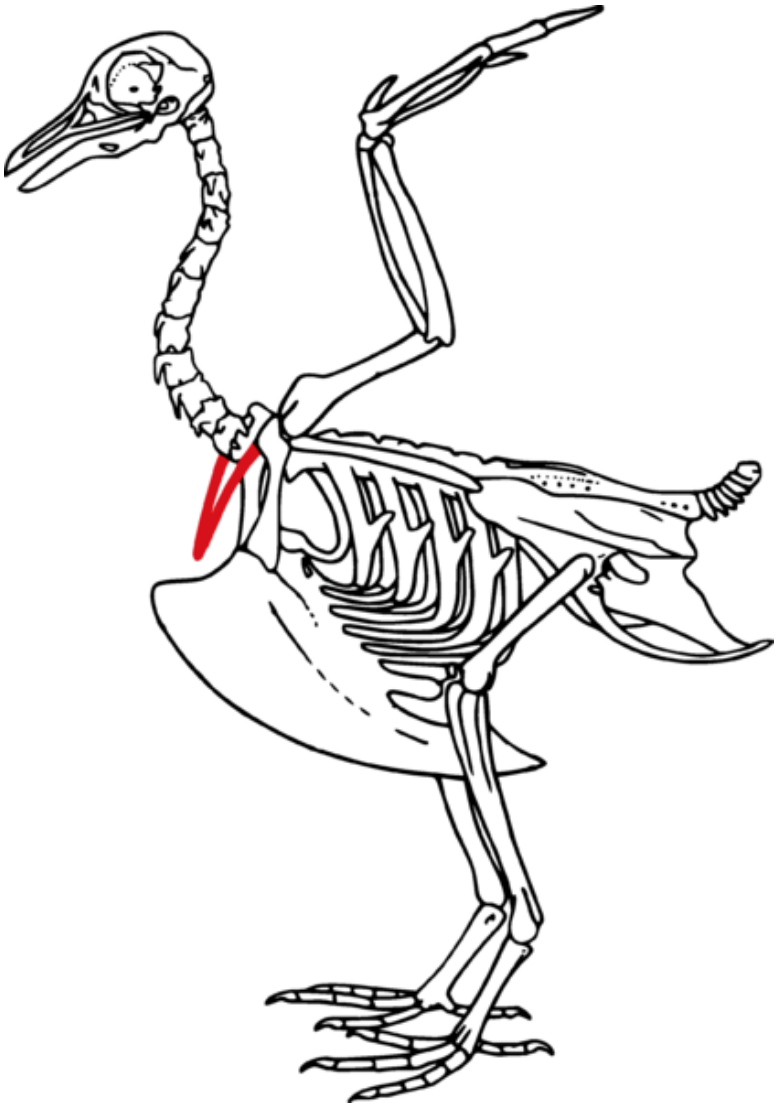


Pigeon Guillemot showing length of Culmen

The **culmen** or **culmen ridge** is a part of a bird's bill. It is the external ridge along the outer part of the centre of the upper mandible, formed where the two halves of the mandible join.

The shape of the culmen can be a useful identification feature. For example, the shape of the culmen differs markedly between the Common Guillemot (evenly, shallowly curved) and the Brünnich's Guillemot, which has a more abrupt angle to its culmen. The same can apply to the colour or patterning — White-billed Diver has a completely pale culmen, whereas on the similar Great Northern Diver this area is dark.

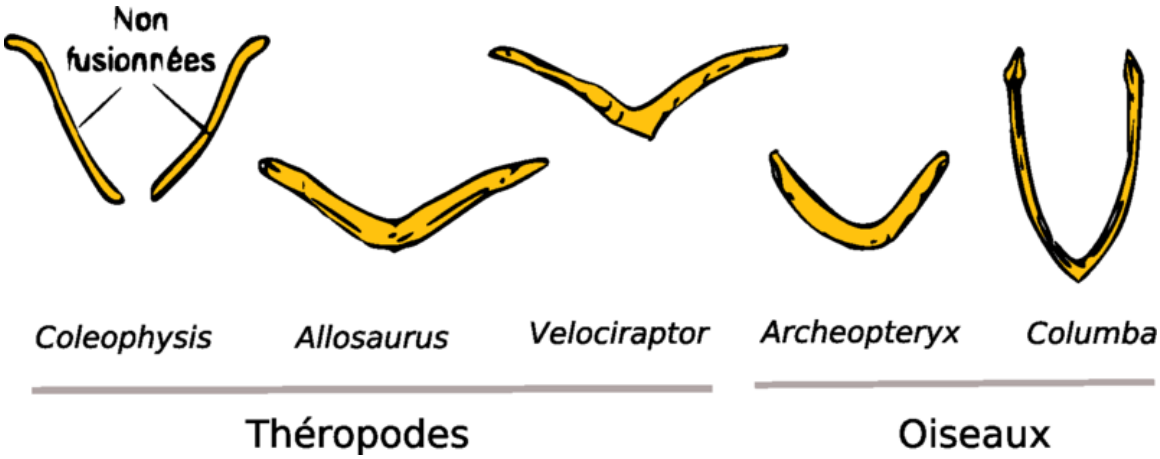
Furcula



This stylised bird skeleton highlights the furcula

The **furcula** is a forked bone found in birds and thecodonts, formed by the fusion of the two clavicles. In birds, its function is the strengthening of the thoracic skeleton to withstand the rigors of flight.

The following theropods have been found to have furculae: dromaeosaurids (including a new North American species of Velociraptor), Oviraptorids, Tyrannosaurids, Troodontids, Coelophysids and Allosauroids.



Evolution of the furcula

Chapter 7

Gape, Gular Skin and Keel (Bird Anatomy)

Gape

A young starling with a bright yellow gape

In bird anatomy, the **gape** is the interior of the open mouth of a bird and the **gape flange** is the region where the two mandibles join together, at the base of the beak. The width of the gape can be factor in the choice of food.

The gape flange on this juvenile House Sparrow is the yellowish region at the base of the beak.

Gapes of juvenile altricial birds are often brightly colored, sometimes with contrasting spots or other patterns, and these are believed to be an indication of their health, fitness and competitive ability. Based on this, the parents decide how to distribute food among the chicks in the nest. Some species especially in the families Viduidae and Estrildidae have bright spots on the gape known as gape tubercles or gape papillae. These nodular spots are conspicuous even in low light. A study examining the nestling gapes of eight passerine species found that the gapes were conspicuous in the ultraviolet spectrum (visible to birds but not to humans). Parents may however not rely solely on the gape coloration, and other factors influencing their decision remain unknown.

Red gape color has been shown in several experiments to induce feeding. An experiment in manipulating brood size and immune system with Barn Swallow nestlings showed the vividness of the gape was positively correlated with T-cell–mediated immunocompetence, and that larger brood size and injection with an antigen led to a less vivid gape. Conversely, the red gape of the Common Cuckoo (*Cuculus canorus*) did not induce extra feeding in host parents. Some brood parasites such as the Hodgson's Hawk-cuckoo (*C. fugax*) have colored patches on the wing that mimic the gape color of the parasitized species.

When born, the chick's gape flanges are fleshy. As it grows into a fledgling, the gape flanges remain somewhat swollen and can thus be used to recognize that a particular bird is young. By the time it reaches adulthood, the gape flanges will no longer be visible.

Gular skin

Male sage grouse have two gular sacs that they inflate two attract mates. And the female selects the right mate by veiwing its gular sacs to see if it's healthy to bare healthy offspring.

Gular skin (throat skin), in ornithology, is an area of featherless skin on birds that joins the lower mandible of the beak (or *bill*) to the bird's neck.

Gular skin can be very prominent, for example in members of the order Phalacrocoraciformes as well as in pelicans (which likely share a common ancestor). In many species, the gular skin forms a flap, or **gular pouch**, which is generally used to store fish and other prey while hunting.

In cormorants, the gular skin is often colored, contrasting with the otherwise plain black or black-and-white appearance of the bird. This presumably serves some function in social signalling, since the colors become more pronounced in breeding adults.

In frigatebirds, the gular skin (or **gular sac** or **throat sac**) is used dramatically. During courtship display, the male forces air into the sac, causing it to inflate over a period of 20 minutes into a startling huge red balloon.

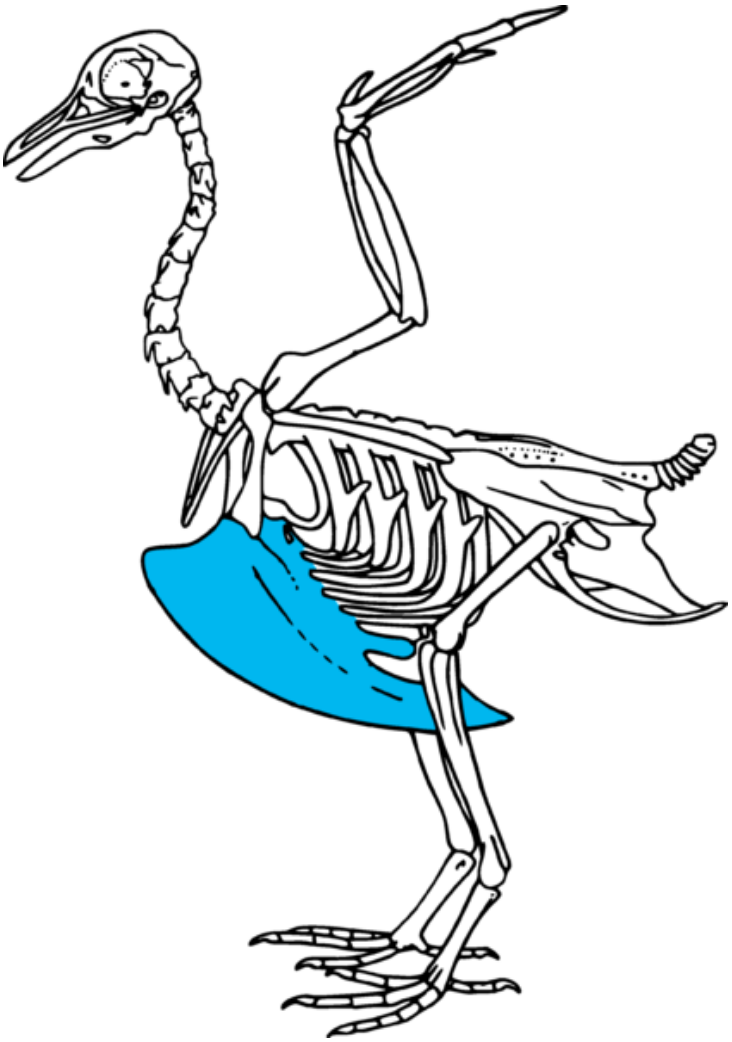
Because cormorants are closer relatives of gannets and anhingas (which have no prominent gular pouch) than of frigatebirds or pelicans, it can be seen that the gular pouch is either plesiomorphic or was acquired by parallel evolution.

In other animals

The walrus, some species of gibbon apes, the conus snail, and fictional species like the snow goblin in *Dungeons & Dragons* and the great oopik in *Star Wars* have a throat sac. Many amphibians will inflate their gular sac to create certain vocalizations to communicate, scare off rivals (to proclaim territory or dominance), and locating and

attracting a mate by using their vocal sac to amplify their voice to be heard louder and closer. And some species of lizards may also have a gular fold (and gular scales).

Keel (bird anatomy)



This stylised bird skeleton highlights the keel bone

A **keel** in bird anatomy is an extension of the sternum (breastbone) which runs axially along the midline of the sternum and extends outward, perpendicular to the plane of the ribs. The keel provides an anchor to which a bird's wing muscles attach, thereby providing adequate leverage for flight. Keels do not exist on all birds; in particular, some flightless birds lack a keel structure.

Historically, the presence or absence of a pronounced keel structure was used as a broad classification of birds into two classes: Carinatae (from *carina*, "keel"), having a pronounced keel; and ratites (from *ratis*, "raft" — referring to the flatness of the sternum), having a subtle keel structure or lacking one entirely. However, this classification has fallen into disuse as evolutionary studies have shown that many flightless birds have evolved from flighted birds. The current definition of Carinatae now includes all extant birds.

Chapter 8

Plumage and Pygostyle

Plumage

The differences in plumage of a Blue Grosbeak, from top to bottom, between a breeding male (alternate plumage) a non-breeding male (basic plumage), a female and a related Indigo Bunting

Plumage refers both to the layer of feathers that cover a bird and the pattern, colour, and arrangement of those feathers. The pattern and colours of plumage vary between species and subspecies and can also vary between different age classes, sexes, and season. Within

species there can also be a number of different colour morphs. Differences in plumage are used by ornithologists and birdwatchers in order to distinguish between species and collect other species specific information.

Humphrey-Parkes (H-P) moult and plumage terminology

Almost all species of birds moult at least annually, usually after the breeding season, known as the **pre-basic moult**. This resulting covering of feathers, which will last either until the next breeding season or until the next annual moult, is known as the **basic plumage**. Many species undertake another moult prior to the breeding season known as the **pre-alternate moult**, the resulting breeding plumage being known as the **alternate plumage** or **nuptial plumage**. The alternate plumage is often brighter than the basic plumage, for the purposes of sexual display, but may also be cryptic in order to hide incubating birds that might be vulnerable on the nest.

The Humphrey-Parkes terminology requires some attention to detail to name moults and plumages correctly.

Eclipse plumage

Many ducks have bright, colourful plumage, exhibiting strong sexual dimorphism to attract the females. However, they moult into a dull plumage in the non-breeding season. This drab female-like appearance is the **eclipse plumage**. When they shed feathers to go into eclipse, the ducks become flightless for a short period of time. Some duck species remain in eclipse for one to three months in the summer, while other would retain the cryptic plumage until the next spring when they undergo another moult to return to their breeding plumage. Although mainly found in the Anatidae, a few other species (for example the Red Junglefowl) also have an eclipse plumage.

Abnormal plumages

Axanthic budgerigar

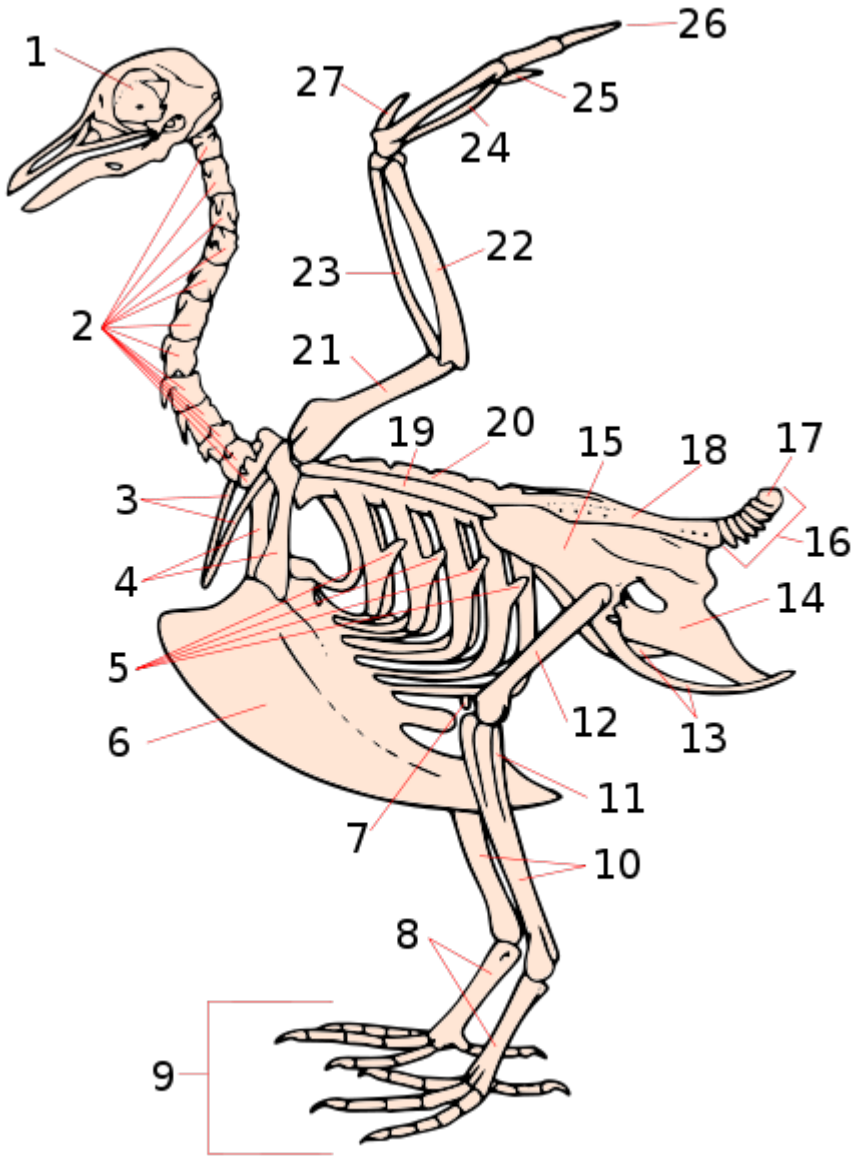
There are hereditary as well as non-hereditary variations in plumage that are rare and termed as abnormal or aberrant plumages. Albinism involves loss of colour in all parts including the iris of the eyes, bills, skin, legs and feet. It is usually the result of a genetic mutation causing the absence of tyrosinase, an enzyme essential for melanin synthesis. Albino adults are rare in the wild because their eyesight is poor resulting in greater risk of predation. Leucism (which includes what used to be termed as "partial albinism") refers to loss of pigments in some or all parts of feathers. Melanism refers to an excess of black or dark colours. Erythromelanism or erythrism is the result of excessive reddish brown erythromelanin deposition in feathers that normally lack melanin. Melanin of different forms combine with xanthophylls to produce colour mixtures and when this combination is imbalanced it produces colour shifts that are termed as schizochroisms (including xanthochromism – overabundance of yellow – and axanthism – lack of yellow – which are commonly bred in cagebirds such as budgerigars). A reduction in eumelanin leads to non-eumelanin schizochroism with an overall fawn plumage while a lack of

phaeomelanin results in grey coloured non-phaeomelanin schizochroism. Carotenism refers to abnormal distribution of carotenoid pigments.

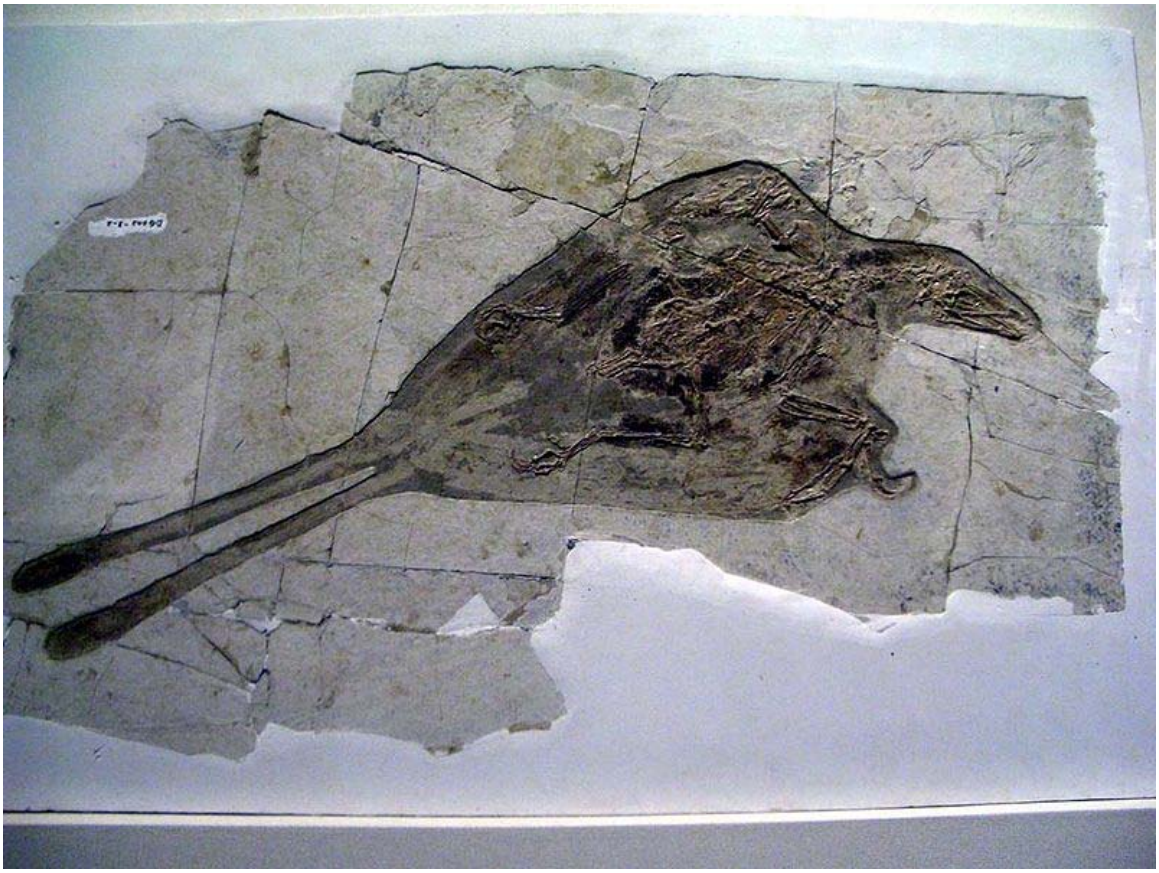
The term "dilution" is used for situations where the colour is of a lower intensity overall; it is caused by decreased deposition of pigment in the developing feather, and can thus not occur in structural coloration (i.e. "dilute blue" does not exist); pale structural colors are instead achieved by shifting the peak wavelength at which light is refracted. Dilution regularly occurs in normal plumage (grey, buff, pink and cream colours are usually produced by this process), but may in addition occur as an aberration (e.g. all normally black plumage becoming grey).

In some birds – many true owls (Strigidae), some nightjars (Caprimulgidae) and a few cuckoos (*Cuculus* and relatives) being widely known examples – there is colour polymorphism. This means that two or more colour variants are numerous within their populations during all or at least most seasons and plumages; in the above-mentioned examples a brown (phaeomelanin) and grey (eumelanin) morph exist, termed "hepatic form" particularly in the cuckoos. Other cases of natural polymorphism are of various kinds; many are melanic/nonmelanic (some paradise-flycatchers, *Terpsiphone*, for example), but more unusual types of polymorphism exist – the face colour of the Gouldian Finch (*Erythrura gouldiae*) or the courtship types of male Ruffs (*Philomachus pugnax*).

Pygostyle



Pigeon skeleton with "plowshare"-type pygostyle (number 17)



Confuciusornis sanctus with "rod"-type pygostyle and the two central tail feathers

Pygostyle refers to a number of the final few caudal vertebrae fused into a single ossification, supporting the tail feathers and musculature. In modern birds, the rectrices attach to these.

The pygostyle is the main component of the structure colloquially known as **Pope's nose**, **parson's nose** or **sultan's nose**. This is the fleshy protuberance visible at the posterior end of a bird (most commonly a chicken or turkey) that has been dressed for cooking. It has a swollen appearance because it also contains the uropygial gland that produces preen oil. Some people consider it to be a sweet and tender delicacy when cooked, whilst others might consider it rather greasy.

Evolution

Pygostyles probably started to evolve very early in the Cretaceous, maybe 140-130 million years ago. The earliest known species to have evolved a pygostyle were members of the Confuciusornithidae. The structure provided an evolutionary advantage, as a completely mobile tail like in *Archaeopteryx* is detrimental to its use for flight control. Modern birds still develop longer caudal vertebrae in their embryonal state, which later fuse to form a pygostyle.

There are two main types of pygostyle: one, found in Confuciusornithidae, Enantiornithes, and some other Mesozoic birds, as well as in some oviraptorosaurs like *Nomingia*, is long and rod- or dagger blade-like. None of the known fossils with such pygostyles show traces of well-developed rectrices. The tail feathers in these animals consisted of downy fuzz and sometimes 2-4 central "streamers" such as those found in some specimens of *Confuciusornis* or in *Paraprotopteryx*.

By contrast, the function of the pygostyle in the terrestrial *Nomingia* is not known. It is notable however that its older relative *Caudipteryx* had no pygostyle but a "fan" of symmetrical feathers which were probably used in social display. Perhaps such ornaments were widespread in Caenagnathoidea and their relatives, and ultimately the oviraptorosaurian pygostyle evolved to help support them. The related *Similicaudipteryx*, described in 2008, also had a rod-like pygostyle, associated with a fan of tail feathers.

Yixianornis grabaui, one of the oldest known species with a pygostyle like in living birds

The other pygostyle type is plowshare-shaped. It is found in Ornithurae (living birds and their closest relatives), and in almost all flying species is associated with an array of well-developed rectrices used in maneuvring. The central pair of these attach directly to the pygostyle, just as in *Confuciusornis*. The other rectrices of Ornithurae are held in place and moved by structures called ***bulbi rectricium*** (**rectricial bulbs**), a complex feature of fat and muscles located on either side of the pygostyle. The oldest known species with such a pygostyle is *Hongshanornis longicresta*.

As evidenced by the oviraptorosaurian cases, the pygostyle evolved at least twice, and rod-shaped pygostyles seem to have evolved several times, in association with shortening of the tail but not necessarily with a retractable fan of tail feathers. In other words, the pygostyles of oviraptorosaurs and *Confuciusornis* were likely weight-saving measures, and the specialized "true" pygostyles of ornithurans were adapted from these later to improve flight performance.

The bird clade Pygostylia was named in 1996, by Luis Chiappe, for the presence of this feature and roughly corresponds to its appearance in the bird family tree, though the feature itself is not included in its definition. In 2001, Jacques Gauthier and Kevin de Queiroz (2001) re-defined Pygostylia to refer specifically to the apomorphy of a short tail bearing an avian pygostyle.

Etymology

"Pygostyle" is of Ancient Greek origin, literally meaning "rump pillar".

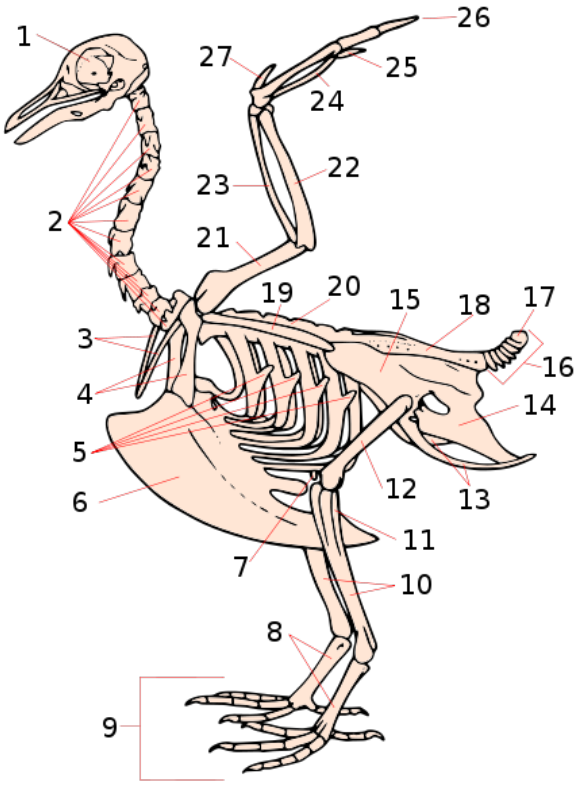
The phrase "parson's nose", from the notion that an English parson may 'have his nose in the air', upturned like the chicken's rear end. The term must have been known as early as around 1400 AD, when a carpenter had been contracted to provide new choir stalls for St Mary's Church, Nantwich. The vicar was either slow to pay the artisan, or did not pay at all. In retaliation, on the last misericord in the stalls, the carpenter carved a bird with an image of that Vicar's face with protuberant nose as rump. The carving is still visible today and featured on a postcard on sale at the church.

A similar derivation applies to the phrase "Pope's nose", which may have originated as a derogatory term meant to demean Catholics in England during the late 17th century.

Chapter 9

Tarsometatarsus and Uropygial Gland

Tarsometatarsus



Pigeon skeleton; number 8 indicates the right tarsometatarsus

The **tarsometatarsus** is a bone that is found in the lower leg of certain tetrapods, namely birds.

It is formed from the fusion of several bones found in other types of animals, and homologous to the mammalian tarsal (ankle) and metatarsal (foot) bones. Despite this, the tarsometatarsus of birds is often referred to as just the tarsus or metatarsus.

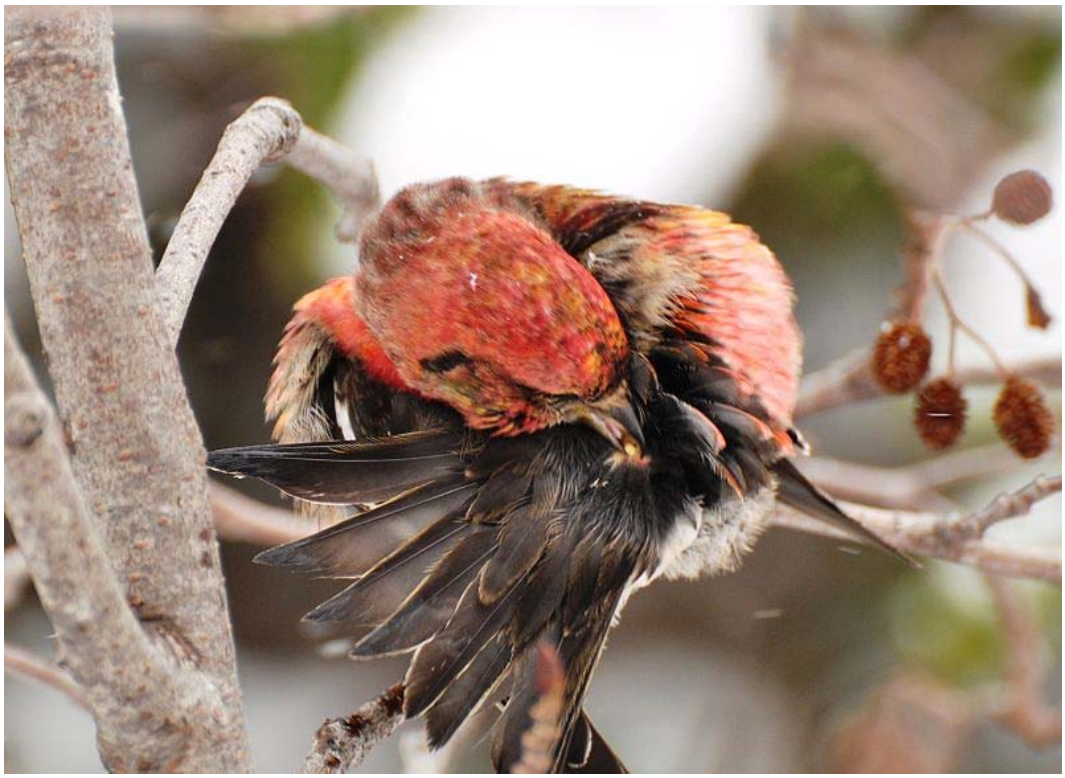
There are several ways and extents in which the tarsometatarsal fusion is accomplished throughout bird evolution. Namely, in Neornithes (modern birds) the fusion is most thorough at the distal (metatarsal) end though present along the entire length of the bone. In the Enantiornithes, a group of Mesozoic birds, the fusion was complete at the proximal (tarsal) end but the distal metatarsi still were somewhat separate.

Cast of the type specimen of *Heterodontosaurus tucki*. Left tarsometatarsus is clearly visible.

While birds are the best-known animals with this fused bone, they were not the only group and not even the first to have it: in a remarkable case of parallel evolution, a tarsometatarsus was also present in the Heterodontosauridae, a group of tiny ornithopod dinosaurs quite unrelated to birds. Their oldest remains date from the Late Triassic more than 200 million years ago, and predate the first birds with a tarsometatarsus by nearly 100 million years.

Uropygial gland

Herring gulls, the bird on the right uncovers its uropygial gland to distribute its oil through the plumage by means of preening. The bird on the left is pushing its head to the gland.



White-winged Crossbill (Loxia leucoptera) extracting preen oil from its uropygial gland.

Hoopoes host symbiotic bacteria in their uropygial glands whose excretions act against feather-degrading bacteria.

The **uropygial gland**, or, more informally, the **preen gland** is a gland found in the large majority of birds that secretes an oil (**preen oil**) that birds use for preening. The chief compounds of preen oil are diester waxes called uropygiols.

The gland is found near the base of the tail and is shaped into two symmetric parts. The oil of each part of the gland is secreted through the surface of the skin through a grease nipple-like nub. A bird will typically transfer this oil to its feathers by rubbing its head against the oil and then around the rest of the body. Tailward areas are usually preened utilizing the beak. Not all birds have a uropygial gland. Exceptions include the emu,

ostrich, and bustards. These typically find other means to stay clean and dry, such as taking a dust bath.

Waterproofing effect

The uropygial gland is strongly developed in many waterbirds, such as ducks (but not in cormorants which are also highly aquatic). It appears that the waterproofing effect is not primarily by the uropygiols – although they are hydrophobic – but by applying an electrostatic charge to the oiled feather through the mechanical action of preening.

Antiparasitic effect

An in vitro study suggests that the preen oils are effective against lice. Furthermore, the taxonomic richness of avian louse burdens covaries positively with preen gland size (relative to body size) across avian taxa suggesting coevolution between gland size and parasite biodiversity. Moreover, hoopoe preen gland harbours symbiotic bacteria whose excretions reduce the activity of feather-degrading bacteria and thus help to preserve the plumage.

Chapter 10

Cloaca and Gizzard

Cloaca

An avian cloaca or vent; in this example, a red-tailed hawk (*Buteo jamaicensis*).

In zoological anatomy, a **cloaca** is the posterior opening that serves as the only such opening for the intestinal, reproductive, and urinary tracts of certain animal species. The

word comes from Latin, and means *sewer*. All birds, reptiles, and amphibians possess this orifice, from which they excrete both urine and feces, unlike placental mammals, which possess two (or three) separate orifices for evacuation.

The cloacal region is also often associated with a secretory organ, the cloacal gland, which has been implicated in the scent marking behavior of some reptiles, amphibians and monotremes.

In birds

In birds the cloaca is also referred to as the *vent*, and among falconers the word *vent* is also a verb meaning "to defecate". Excretory systems with analogous purpose in certain invertebrates are also sometimes referred to as "cloacae".

Birds also reproduce with this organ; this is known as a cloacal kiss. Birds that mate using this method touch their cloacae together, in some species for only a few seconds, sufficient time for sperm to be transferred from the male to the female. The reproductive system must be re-engorged prior to the mating season of each species. Such regeneration usually takes about a month. Birds generally produce one batch of eggs per year, but they will produce another if the first is taken away. For some birds, such as some species of swans and ducks, the males do not use the cloaca for reproduction but have a phallus.

One study has looked into birds that use their cloaca for cooling.

In fish

Among fish, a true cloaca is present only in elasmobranchs (sharks and rays) and lobe-finned fishes. In lampreys and in some ray-finned fishes, part of the cloaca remains in the adult to receive the urinary and reproductive ducts, although the anus always opens separately. In chimaeras and most teleosts, however, all three openings are entirely separate.

In mammals

The only mammals to possess a true cloaca are the monotremes (egg laying mammals). Even in these animals, the cloaca is partially sub-divided into separate regions for the anus and urethra. In marsupials (and a few birds), the genital tract is separate, but a trace of original cloaca does remain externally. This is one of the features of marsupials and monotremes which suggest their basal nature, as the amniotes from which mammals evolved possessed a cloaca, and the earliest animals to diverge into the mammalian class would likely have had this feature too.

Adult placental mammals have no remaining trace of the cloaca. In the embryo, the embryonic cloaca divides into a posterior region that becomes part of the anus, and an anterior region that has different fates depending on the sex of the individual. In females,

it develops into the vestibule that receives the urethra and vagina, while in males it forms the entirety of the penile urethra.

Cloacal respiration

Some turtles, especially those specialized in diving, are highly reliant on cloacal respiration during dives. They accomplish this by having a pair of accessory air bladders connected to the cloaca which can absorb oxygen from the water. There are also a variety of fishes, as well as polychaete worms and even crabs, that are specialized to take advantage of the constant flow of water through the cloacal respiratory tree of sea cucumbers while simultaneously gaining the protection of living within the sea cucumber itself. At night many of these species emerge from the anus of the sea cucumber in search of food.

Gizzard

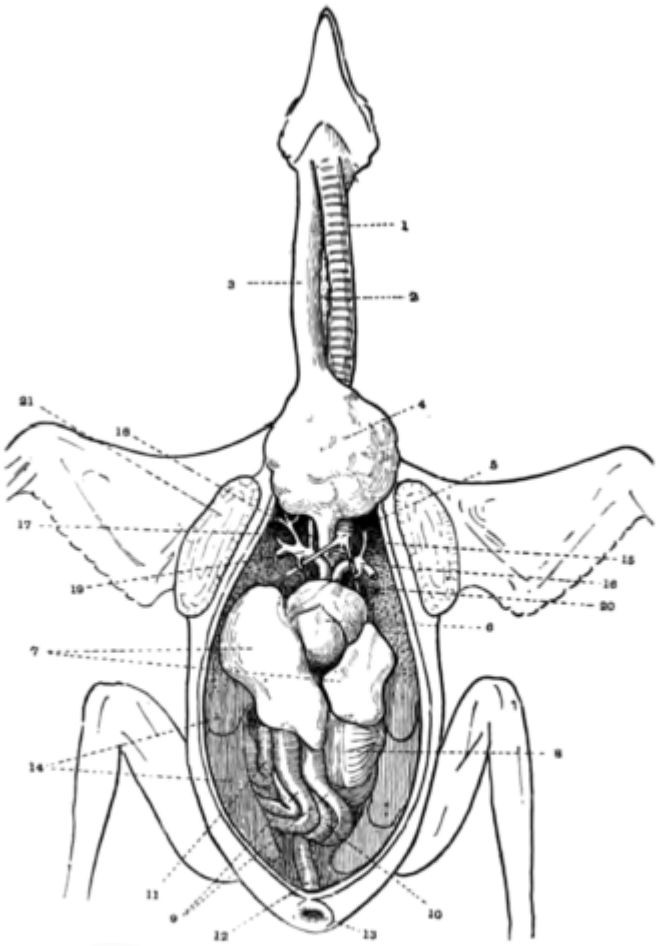
Duck gizzards

The **gizzard**, also referred to as the **ventriculus**, **gastric mill**, and **gigerium**, is an organ found in the digestive tract of some animals, including birds, reptiles, earthworms and some fish. This specialized stomach constructed of thick, muscular walls is used for grinding up food; often rocks are also instrumental in this process. In certain insects and mollusks, the gizzard features chitinous plates or teeth.

Etymology

The word "gizzard" comes from the Middle English *giser*, which derives from a similar word in Old French, which itself evolved from the Latin *gigeria*, meaning giblets. The Latin word probably derives from a common Proto-Indo-European source with the Persian word for liver, which is "jigar".

Structure



The chief Viscera of the Pigeon, *Columba livia*

1. Trachea. 2. Thymus gland. 3. Oesophagus. 4. Crop. 5. Syrinx. 6. Heart. 7. Liver. 8. Gizzard. 9. Duodenum. 10. Pancreas. 11. Small intestine. 12. Rectum. 13. Cloaca. 14. Air-sacs. 15. Left carotid. 16. Left subclavian. 17. Right carotid. 18. Brachial artery. 19. Right subclavian. 20. Muscles of syrinx. 21. Pectoralis major muscle cut across.

The gizzard (serial 8) of a pigeon, seen at the right of the duodenum between the legs.

Birds swallow food and store it in their crop if necessary. Then the food passes into their glandular stomach, also called the proventriculus, which is also sometimes referred to as the true stomach. This is the secretory part of the stomach. Then the food passes into the ventriculus (also known as the *muscular stomach* or *gizzard*). The gizzard can grind the food with previously-swallowed stones and pass it back to the true stomach, and vice versa. Bird gizzards are lined with a tough layer made of the carbohydrate-protein complex koilin, to protect the muscles in the gizzard and to aid in digestion.

Gizzard stones

Some animals that lack teeth will swallow stones or grit to aid in digestion. All birds have gizzards, but not all will swallow stones or grit. The birds that do, employ the following method of 'mastication':

"*A bird swallows small bits of gravel that act as 'teeth' in the gizzard, breaking down hard food such as seeds and thus helping digestion.*" (Solomon et al., 2002).

These stones are called *gizzard stones* or *gastroliths* and are usually round and smooth from the polishing action in the animal's stomach. When too smooth to do their required work, they may be passed or regurgitated.

Animals with gizzards

Birds

All birds have gizzards. The gizzards of emus, turkeys, chickens and ducks are most notable in cuisine (see below).

Reptiles

Alligators and crocodiles also have gizzards.

Invertebrates

Most invertebrates also have gizzards. The gizzard is used to grind up food, and it is part of the digestive system.

Dinosaurs

Dinosaurs which are believed to have had gizzards based on the discovery of gizzard stones recovered near fossils include:

- *Psittacosaurus*
- *Massospondylus*
- *Sellosaurus*
- *Omeisaurus*
- *Apatosaurus*
- *Barosaurus*
- *Dicraeosaurus*
- *Seismosaurus*

Chapter 11

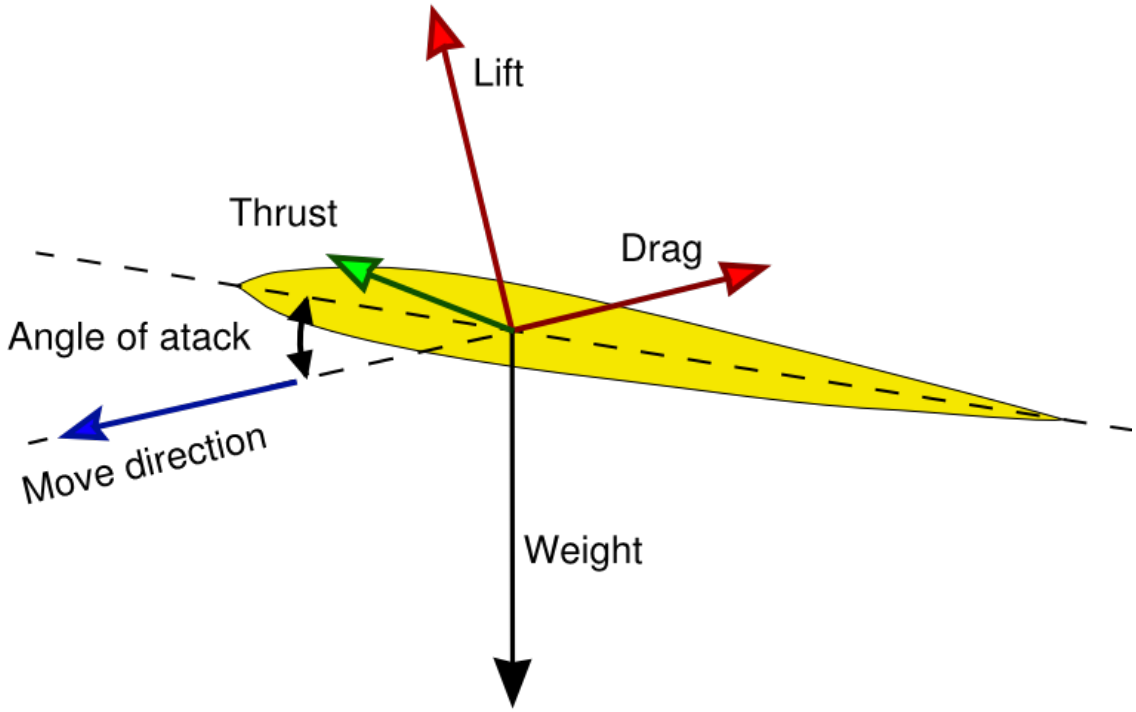
Bird Flight

A magpie-goose taking off

Flight is the main mode of locomotion used by most of the world's bird species. Flight assists birds while feeding, breeding and avoiding predators.

Here we, discusses the mechanics of **bird flight**, with emphasis on the varied forms of bird's wings. The specifics of hovering, take-off and landing are also examined. Additional adaptations of bird's bodies relating to their flying ability are covered. Finally, theories on the evolution of bird flight.

Basic mechanics of bird flight



Forces acting on a wing. The lift force has both a forward and a vertical component.

Lift

The fundamentals of bird flight are similar to those of aircraft. Lift force is produced by the action of air flow on the wing, which is an airfoil. The lift force occurs because the air has a lower pressure just above the wing and higher pressure below.

Gliding

When gliding, both birds and gliders obtain both a vertical and a forward force from their wings. This is possible because the lift force is generated at right angles to the air flow, which in gliding flight comes from slightly below the horizontal (because the bird is descending). The lift force, therefore, has a forward component that counteracts drag.

A flock of domestic pigeons each in a different phase of its flap.

Flapping

When a bird flaps, as opposed to gliding, its wings continue to develop lift as before, but the lift is rotated forward to provide thrust, which counteracts drag and increases its speed, which has the effect of also increasing lift to counteract its weight, allowing it to maintain height or to climb. Flapping involves two stages: the down-stroke, which provides the majority of the thrust, and the up-stroke, which can also (depending on the bird's wings) provide some thrust. At each up-stroke the wing is slightly folded inwards to reduce upward resistance. Birds change the angle of attack between the up-stroke and the down-stroke of their wings. During the down-stroke the angle of attack is increased, and is decreased during the up-stroke.

Drag

Apart from its weight, there are three major drag forces that impede a bird's aerial flight: frictional drag (caused by the friction of air and body surfaces), form drag (due to frontal area of the bird, also known as pressure drag), and lift-induced drag (caused by the wingtip vortices). These forces are reduced by streamlining the bird's body and wings.

Wing

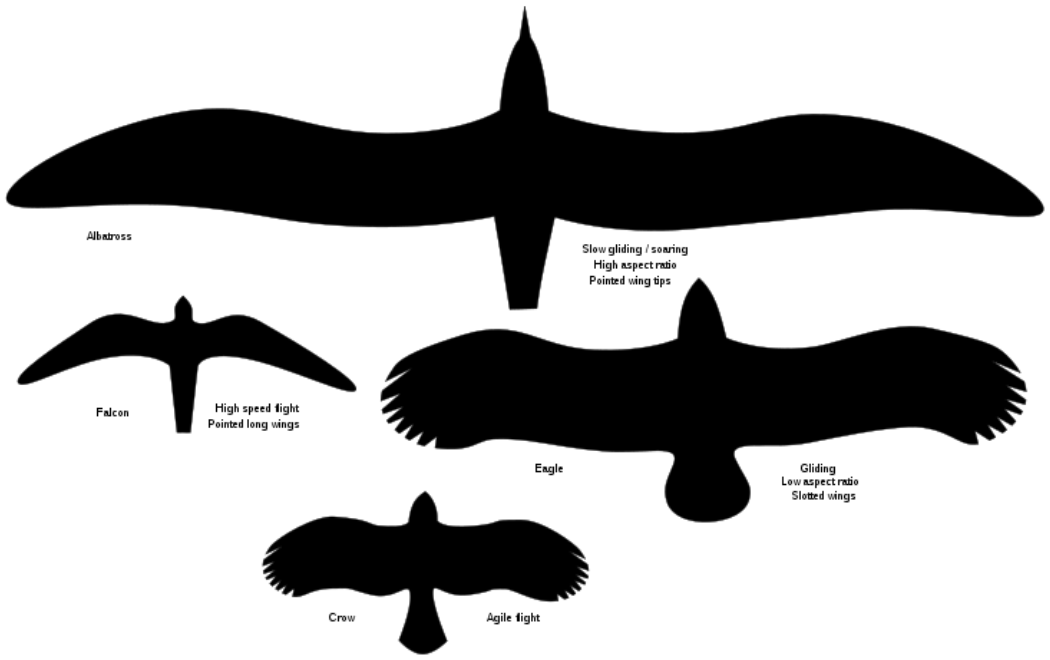
A kea in flight

The bird's forelimbs, the wings, are the key to bird flight. Each wing has a central vane to hit the wind, composed of three limb bones, the humerus, ulna and radius. The hand, or manus, which ancestrally was composed of five digits, is reduced to three digits (digit II, III and IV or I, II, III depending on the scheme followed), which serves as an anchor for the primaries, one of two groups of flight feathers responsible for the wing's airfoil shape. The other set of flight feathers, behind the carpal joint on the ulna, are called the secondaries. The remaining feathers on the wing are known as coverts, of which there are three sets. The wing sometimes has vestigial claws. In most species these are lost by the time the bird is adult (such as the highly visible ones used for active climbing by Hoatzin chicks), but claws are retained into adulthood by the Secretary Bird, screamers, finfoots, ostriches, several swifts and numerous others, as a local trait, in a few specimens. The claws of the Jurassic theropod-like Archaeopteryx are quite similar to those of the Hoatzin nestlings.

Albatrosses have locking mechanism in the wing joints that reduce the strain on the muscles during soaring flight.

Female birds exposed to predators during ovulation produce chicks which grow their wings faster than chicks produced by predator-free females. Their wings are also longer. Both adaptations may make them better at avoiding avian predators.

Wing shape and flight



Wing shapes

The shape of the wing is an important factor in determining the types of flight of which the bird is capable. Different shapes correspond to different trade-offs between beneficial characteristics, such as speed, low energy use, and maneuverability. The planform of the wing (the shape of the wing as seen from below) can be described in terms of two parameters, aspect ratio and wing loading. Aspect ratio is the ratio of wingspan to the mean of its chord (or the square of the wingspan divided by wing area). Wing loading is the ratio of weight to wing area.

Most kinds of bird wing can be grouped into four types, with some falling between two of these types. These types of wings are elliptical wings, high speed wings, high aspect ratio wings and soaring wings with slots.

Elliptical wings

Elliptical wings are short and rounded, having a low aspect ratio, allowing for tight maneuvering in confined spaces such as might be found in dense vegetation. As such they are common in forest raptors (such as *Accipiter* hawks), and many passerines, particularly non-migratory ones (migratory species have longer wings). They are also common in species that use a rapid take off to evade predators, such as pheasants and partridges.

High speed wings

High speed wings are short, pointed wings that when combined with a heavy wing loading and rapid wingbeats provide an energetically expensive high speed. This type of flight is used by the bird with the fastest wing speed, the peregrine falcon, as well as by most of the ducks. The same wing shape is used by the auks for a different purpose; auks use their wings to "fly" underwater. The Peregrine Falcon has the highest recorded dive speed of 175 mph (282 km/h). The fastest straight, powered flight is the Spine-tailed Swift at 105 mph (170 km/h).

A Roseate Tern uses its low wing loading and high aspect ratio to achieve low speed flight

High aspect ratio wings

High aspect ratio wings, which usually have low wing loading and are far longer than they are wide, are used for slower flight, almost hovering (as used by kestrels, terns and nightjars) or alternatively by birds that specialize in soaring and gliding flight, particularly that used by seabirds, dynamic soaring, which use different wind speeds at different heights (wind shear) above the waves in the ocean to provide lift. Low speed flight is important for birds that plunge dive for fish.

Soaring wings with deep slots

These are the wings favored by the larger species of inland birds, such as eagles, vultures, pelicans, and storks. The slots at the end of the wings, between the primaries, reduce the induced drag and wingtip vortices by "capturing" the energy in air flowing from the lower to upper wing surface at the tips, whilst the shorter size of the wings aids in takeoff (high aspect ratio wings require a long taxi in order to get airborne).

Hovering

Hovering is used by several species of birds (and specialized in by one family). True hovering, which is generating lift through flapping alone rather than as a product of the bird's passage through the air, demands a lot of energy. This means that it is confined to smaller birds; the largest bird able to truly hover is the pied kingfisher, although larger birds can hover for short periods of time. Larger birds that hover for prolonged periods do so by flying into a headwind, allowing them to remain stationary relative to the ground (or water). Kestrels, terns and even hawks use this windhovering.

The ruby-throated Hummingbird can beat its wings 52 times a second

Most birds that hover have high aspect ratio wings that are suited to low speed flying. One major exception to this are the hummingbirds, which are the most accomplished hoverers of all the birds. Hummingbird flight is different from other bird flight in that the wing is extended throughout the whole stroke, the stroke being a symmetrical figure of eight, with the wing producing lift on both the up- and down-stroke. Some hummingbirds can beat their wings 52 times a second, though others do so less frequently.

Take-off and landing

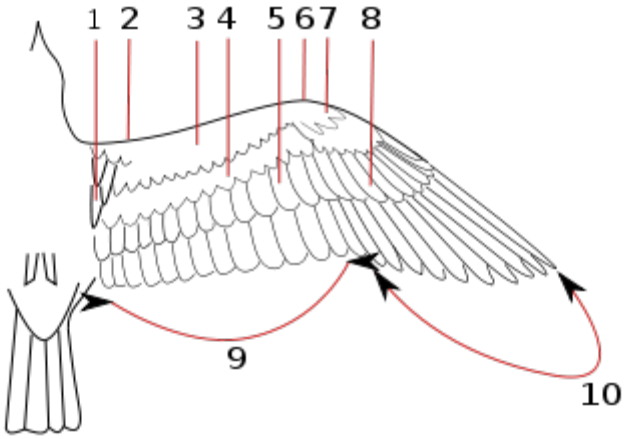
A male bufflehead runs atop the water while taking off

Take-off is one of the most energetically demanding aspects of flight, as the bird needs to generate enough airflow across the wing to create lift. With small birds a jump up will suffice, while for larger birds this is not possible. In this situation, birds need to take a run up in order to generate the airflow to take off. Large birds take off by facing into the wind, or, if they can, by perching on a branch or cliff so that all they need to do is drop off into the air.

Landing is also a problem for large birds with high wing loadings. This problem is dealt with in some species by aiming for a point below the intended landing area (such as a nest on a cliff) then pulling up beforehand. If timed correctly, the airspeed once the target is reached is virtually nil. Landing on water is simpler, and the larger waterfowl species prefer to do so whenever possible, landing into wind and using their feet as skids. In order to lose height rapidly prior to landing, some large birds such as geese indulge in a rapid alternating series of sideslips in a maneuver termed as *whiffling*.

Mute Swan *Cygnus olor*

Adaptations for flight



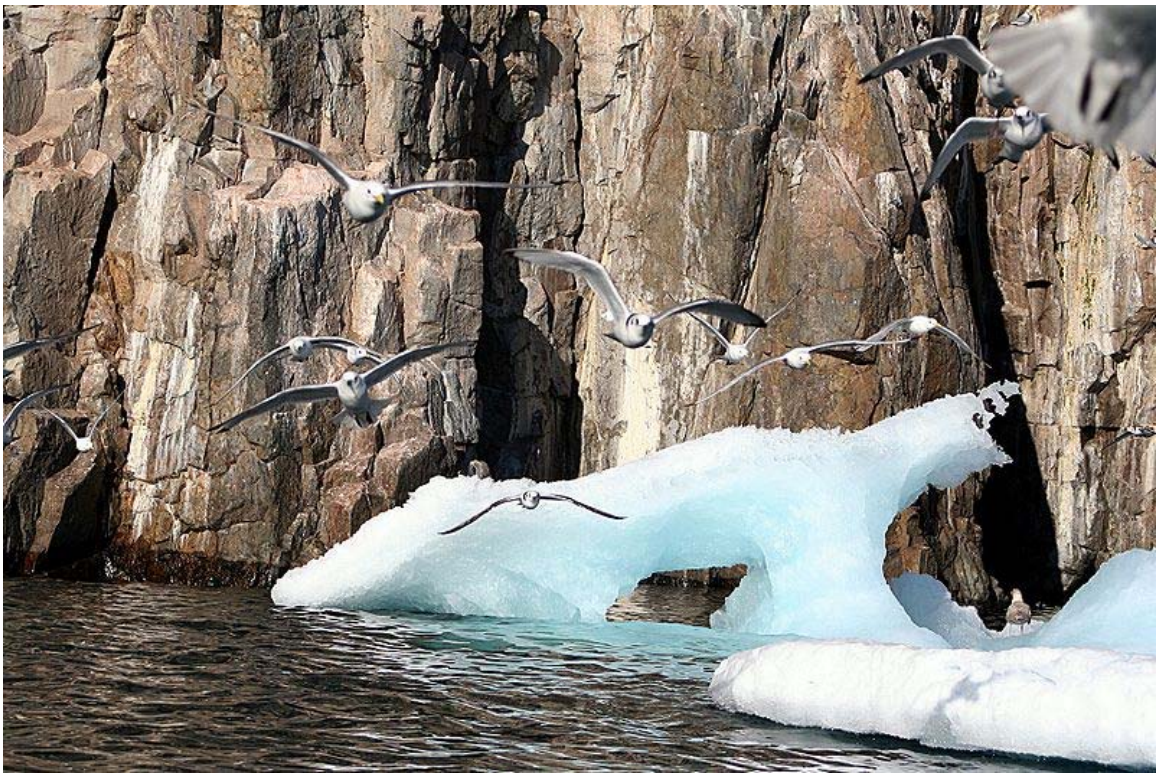
1 Axillaries; 2 Margin (Marginal underwing coverts); 3 Lesser underwing coverts; 4 Median underwing coverts (Secondary coverts); 5 Greater underwing coverts (Secondary

coverts); 6 Carpal joint; 7 Lesser underwing primary coverts; 8 Greater undering primary coverts; 9 Secondaries; 10 Primaries

The most obvious adaptation to flight is the wing, but because flight is so energetically demanding birds have evolved several other adaptations to improve efficiency when flying. Birds' bodies are streamlined to help overcome air-resistance. Also, the bird skeleton is hollow to reduce weight, and many unnecessary bones have been lost (such as the bony tail of the early bird *Archaeopteryx*), along with the toothed jaw of early birds, which has been replaced with a lightweight beak. The skeleton's breastbone has also adapted into a large keel, suitable for the attachment of large, powerful flight muscles. The vanes of the feathers have hooklets called barbules that zip them together, giving the feathers the strength needed to hold the airfoil (these are often lost in flightless birds).

The large amounts of energy required for flight have led to the evolution of a unidirectional pulmonary system to provide the large quantities of oxygen required for their high respiratory rates. This high metabolic rate produces large quantities of radicals in the cells that can damage DNA and lead to tumours. Birds, however, do not suffer from an otherwise expected shortened lifespan as their cells have evolved a more efficient antioxidant system than those found in other animals.

Evolution of bird flight



Marine birds fly at Cape Hay in the High Arctic

Most paleontologists agree that birds evolved from small theropod dinosaurs, but the origin of bird flight is one of the oldest and most hotly contested debates in paleontology. The four main hypotheses are: "from the trees down", that birds' ancestors first glided down from trees and then acquired other modifications that enabled true powered flight; "from the ground up", that birds' ancestors were small, fast predatory dinosaurs in which feathers developed for other reasons and then evolved further to provide first lift and then true powered flight; and "wing-assisted incline running" (WAIR), a version of "from the ground up" in which birds' wings originated from forelimb modifications that provided *downforce*, enabling the proto-birds to run up extremely steep slopes such as the trunks of trees; and "Pouncing Proavis", which posits that flight evolved by modification from arboreal ambush tactics.

There has also been debate about whether the earliest known bird, *Archaeopteryx*, could fly. It appears that *Archaeopteryx* had the brain structures and inner-ear balance sensors that birds use to control their flight. *Archaeopteryx* also had a wing feather arrangement like that of modern birds and similarly asymmetrical flight feathers on its wings and tail. But *Archaeopteryx* lacked the shoulder mechanism by which modern birds' wings produce swift, powerful upstrokes; this may mean that it and other early birds were incapable of flapping flight and could only glide. The presence of most fossils in marine sediments in habitats devoid of vegetation has led to the hypothesis that they may have used their wings as aids to run across the water surface in the manner of the basilisk lizards.

From the trees down

This was the earliest hypothesis, encouraged by the examples of gliding vertebrates such as flying squirrels. It suggests that proto-birds like *Archaeopteryx* used their claws to clamber up trees and glided off from the tops.

Some recent research undermines the "trees down" hypothesis by suggesting that the earliest birds and their immediate ancestors did not climb trees. Modern birds that forage in trees have much more curved toe-claws than those that forage on the ground. The toe-claws of Mesozoic birds and of closely-related non-avian theropod dinosaurs are like those of modern ground-foraging birds.

From the ground up

Feathers are very common in coelurosaurid dinosaurs (including the early tyrannosauroid Dilong). Modern birds are classified as coelurosaurs by nearly all palaeontologists, though not by a few ornithologists. The original functions of feathers may have included thermal insulation and competitive displays. The most common version of the "from the ground up" hypothesis argues that bird's ancestors were small ground-running predators (rather like roadrunners) that used their forelimbs for balance while pursuing prey and that the forelimbs and feathers later evolved in ways that provided gliding and then powered flight. Another "ground upwards" theory argues the evolution of flight was initially driven by competitive displays and fighting: displays required longer feathers

and longer, stronger forelimbs; many modern birds use their wings as weapons, and downward blows have a similar action to that of flapping flight. Many of the *Archaeopteryx* fossils come from marine sediments and it has been suggested that wings may have helped the birds run over water in the manner of the *Jesus Christ Lizard* (Common basilisk).

Most recent attacks on the "from the ground up" hypothesis attempt to refute its assumption that birds are modified coelurosaurid dinosaurs. The strongest attacks are based on embryological analyses, which conclude that birds' wings are formed from digits 2, 3 and 4 (corresponding to the index, middle and ring fingers in humans; the first of a bird's 3 digits forms the alula, which they use to avoid stalling on low-speed flight, for example when landing); but the hands of coelurosaurs are formed by digits 1, 2 and 3 (thumb and first 2 fingers in humans). However these embryological analyses were immediately challenged on the embryological grounds that the "hand" often develops differently in clades that have lost some digits in the course of their evolution, and therefore bird's hands do develop from digits 1, 2 and 3.

Wing-assisted incline running

The WAIR hypothesis was prompted by observation of young chukar chicks, and proposes that wings developed their aerodynamic functions as a result of the need to run quickly up very steep slopes such as tree trunks, for example to escape from predators. Note that in this scenario birds need *downforce* to give their feet increased grip. But early birds, including *Archaeopteryx*, lacked the shoulder mechanism by which modern birds' wings produce swift, powerful upstrokes; since the downforce on which WAIR depends is generated by upstrokes, it seems that early birds were incapable of WAIR.

Pouncing Proavis model

This theory was first proposed by Garner, Taylor, and Thomas in 1999:

We propose that birds evolved from predators that specialized in ambush from elevated sites, using their raptorial hindlimbs in a leaping attack. Drag–based, and later lift-based, mechanisms evolved under selection for improved control of body position and locomotion during the aerial part of the attack. Selection for enhanced lift-based control led to improved lift coefficients, incidentally turning a pounce into a swoop as lift production increased. Selection for greater swooping range would finally lead to the origin of true flight.

The authors believed that this theory had four main virtues:

- It predicts the observed sequence of character acquisition in avian evolution.
- It predicts an Archaeopteryx-like animal, with a skeleton more or less identical to terrestrial theropods, with few adaptations to flapping, but very advanced aerodynamic asymmetrical feathers.

- It explains that primitive pouncers (perhaps like Microraptor) could coexist with more advanced fliers (like Confuciusornis or Sapeornis) since they did not compete for flying niches.
- It explains that the evolution of elongated rachis-bearing feathers began with simple forms that produced a benefit by increasing drag. Later, more refined feather shapes could begin to also provide lift.

Uses and loss of flight in modern birds

Birds use flight to obtain prey on the wing, for foraging, to commute to feeding grounds, and to migrate between the seasons. It is also used by some species to display during the breeding season and to reach safe isolated places for nesting.

Flight is more energetically expensive in larger birds, and many of the largest species fly by soaring and gliding (without flapping their wings) as much as possible. Many physiological adaptations have evolved that make flight more efficient.

Birds that settle on isolated oceanic islands that lack ground-based predators often lose the ability to fly. This illustrates both flight's importance in avoiding predators and its extreme demand for energy.