Chapter 11
CLOACA AND VENT

The cloaca: external form

The cloaca is the chamber which receives the terminal parts of the digestive and urogenital systems and opens to the outside at the vent. Its basic organization seems to be fairly uniform throughout birds generally, the main variations being associated with the phallic region of the proctodeum. Externally the cloaca appears as a bell-shaped dilation of the end of the rectum (Figs 6–3, 6–10 and 11–1). In the adult domestic fowl it is about 2.5 cm long and 2.0–2.5 cm wide, although the size varies with the volume of faeces inside it. In the mature male the cloaca is in the midline, but in the mature female the enlarged left oviduct displaces it somewhat to the right; in immature birds the dorsally situated cloacal bursa is larger than the cloaca itself and compresses...
the cloaca on its dorsal aspect. The urogenital ducts traverse the dorsolateral surface of the cloaca and open into it dorsolaterally just caudal to its widest part. The cloaca is divided internally by two mucosal folds into three compartments, the coprodeum, urodeum and proctodeum, but these compartments are not distinguishable externally.

**Coprodeum**

The coprodeum is the most cranial compartment of the cloaca and is usually larger than the other two (Figs 11-1, 11-2, 11-3, 11-5 and 11-6). The internal mucosal junction with the rectum is unmarked except (a) in the Ostrich (and possibly some other ratites) in which there consistently appears to be a true rectocoprodeal fold (Fig 11-3), and (b) in Anatidae in which there is an abrupt and conspicuous ridgelike change in the gross appearance of the mucous membrane caused by a sudden transition to a stratified squamous epithelium in the coprodeum (Figs 11-5 and 11-6). However, in most birds the boundary between the rectum and coprodeum is indicated only by an expansion in calibre at the beginning of the coprodeum. In the domestic fowl the mucosa is lined by villi which are similar to those of the rectum, apart from being somewhat lower and broader. Crypts and simple glands are present. The epithelium is tall columnar with goblet cells. Similar villi occur in some passerines (e.g. the Zebra Finch and Singing Honeyeater); in the Emu the surface area of the coprodeum is further increased by folds which carry villi. The villi and folds may be devices for cloacal reabsorption of water from urine in these desert species. On the other hand, in the xerophilic seed-eating Galah and in the Laughing Kookaburra there are no villi in the coprodeum. Only in the Anatidae among the species explored so far is the coprodeum (and all the rest of the cloaca) lined by stratified squamous epithelium.

**Urodeum**

The urodeum, which is the middle and smallest compartment of the cloaca, is usually partly separated from the other two compartments by two circular mucosal folds (Figs 11-1, 11-2, 11-3, 11-5 and 11-6). The more cranial of these two folds, the coprourodeal fold, is an annular ridge between the coprodeum and urodeum (Figs 11-1, 11-2, 11-3 and 11-5). If the coprodeum is full of faeces this fold becomes a thin diaphragm with a central circular aperture. The presence of the faeces can eventually cause the aperture to be everted through the vent. Thus the faeces may not have to travel through the urodeum and proctodeum during defaecation but instead may be deposited via the everted coprodeum through the vent to the outside. Also, the fold may close during egg-laying, thus preventing simultaneous evacuation of the faeces from the coprodeum due to the increased intra-abdominal pressure. The diaphragm-like coprourodeal fold with its central aperture is also visible externally during defaecation in the male bird, at least in the domestic fowl and turkey (Fig 11-4). The more caudal fold, the uroproctodeal fold, is a semicircular dorsolateral fold between the urodeum and proctodeum which fades out ventrally.
(Figs 11–1, 11–2, 11–3 and 11–5). It is everywhere lower than the coprourodeal fold.

The urogenital ducts open into the urodeum. Their openings are on the dorsolateral mucosal surfaces of the urodeum, the ureters usually being relatively dorsal and the genital ducts relatively lateral in position.

In the majority of birds each ureter appears to open by a simple orifice (Figs 11–1, 11–5 and 11–6) which is difficult to see in the fresh cloaca. In some species, however, including the Ostrich and penguins the opening of each ureter is situated on the summit of a small papilla (Fig 11–3). In the male each ductus deferens opens on the end of a slender conical projection, the papilla of the ductus deferens (Figs 11–1, 11–4, 11–5 and 11–6), the length of the papilla in the domestic fowl being about 2.5 mm and the diameter about 2–3 mm in the mature but detumescent bird. Each papilla points medially and caudally in detumescence. If the cloaca of the domestic fowl is laid open the tip of the papilla is about 1 cm from the opening of the related ureter. In the immature female domestic fowl, duck and goose, as well as in penguins, a small conical papilla which is probably the female homologue of the papilla of the ductus deferens is present on each side of the cloaca. In the domestic birds these papillae disappear as the bird matures, but in penguins they appear to persist in the adult. By means of a speculum the presence or absence of papillae has been used to sex mature pigeons and penguins. In penguins the papilla of the ductus deferens (or its homologue in the female) must be distinguished from the more dorsomedially situated ureteric papilla. In males the two papillae are approximately the same size. In females, however, the lateral papilla (the homologue of the ductus deferens) is only one-third the length of the papilla of the ureter.

Embedded in the ventrolateral wall of the urodeum is the paired, egg-shaped paracloacal vascular body (Figs 11–1 and 11–7) about 5 mm in diameter and 7–10 mm long in the domestic fowl. This structure is the source of the lymph which enlarges the lateral phallic bodies and lymphatic folds during detumescence. It is known to occur in the domestic fowl, turkey, duck and goose, and also a few other species; despite the fact that little is known of its occurrence in other species it is almost certainly a characteristic of birds in general. Within the paracloacal vascular body of the domestic fowl a cortex and medulla can be distinguished. The cortex is made up of many reteform tufts of blood capillaries, the glomera, each of which is invaginated into a lymphatic vessel, rather like a ball pressed into the surface of a balloon. The lymph vessels finally empty into subcapsular lymphatic sinuses which drain from the caudal end of the vascular body and join the erectile lymphatic cavities of the phallus. At the cranial end of the vascular body the subcapsular lymphatics open into the lymphatic vessels running with the pudendal artery, thus providing an escape route for lymph during detumescence. The medulla of the vascular body is formed by large blood vessels, and by nerves and connective tissue. In the paracloacal vascular body of the duck the subcapsular lymphatic sinuses are replaced by a large lymphatic (paired) cavity which connects with the lymphatic channels of the vascular body on the one hand and with the erectile tissue of the phallus on the other (Fig 11–7).

In the female, the left oviduct opens ventrally and laterally relative to the left ureter (Figs 8–6 and 11–3). The opening in the domestic fowl and turkey is generally situated on a slight domelike mound which becomes inconspicuous when the cloaca is cut open and flattened out. In young ducks, geese and swans the opening of the left oviduct is closed by a membrane which is not resorbed until the bird attains sexual maturity. In some species of duck this oculding membrane disappears before the bird is one year old; in other species of duck and in geese generally it probably persists until 1½ years of age. The presence or absence of the membrane can be seen with the aid of a speculum and has been used to distinguish immature from mature females. A similar membrane occurs in the domestic fowl and is lost at the beginning of the first breeding season. The disappearance of the membrane is probably under the control of oestrogen. The vestigial right oviduct can quite often be found attached to the right side of the urodeum, but usually lacks a patent cloacal orifice (Fig 8–6). As already mentioned, in immature female Anatidae and domestic fowl a small papilla lies between the orifice of the ureter and the opening of the oviduct on each side of the cloaca, and is believed to be the female homologue of the papilla of the ductus deferens. It is absent in mature birds. The mucosa of the urodeum is smooth apart from a number of irregular folds and furrows. The epithelium in the domestic fowl is tall columnar with goblet cells. A few crypts and glands are present. In other species the epithelium is stratified squamous, and in yet others there is a mixture of epithelia.

**Proctodeum**

The proctodeum is a short compartment (about 1.0–1.5 cm in length in the domestic fowl) between the uroproctodeal fold and the lips of the vent (Figs 11–1, 11–2, 11–3, 11–5 and 11–6). In young birds the opening in the dorsal midline (Figs 11–2 and 11–3) leads into the globular cloacal bursa (see Chapter 14). In the midline, immediately caudal to the opening of the cloacal bursa the roof of the cloaca in some galliform birds carries an oval glandular mound about 1 cm long in the domestic fowl, the dorsal proctodeal gland (Figs 8–6 and 11–2). In the domestic fowl it consists of mucous glands invaded by lymphoid tissue. In sexually mature male domestic quail this gland is generally enlarged, reaching a size of about $10 \times 11 \times 12$ cm and causing the dorsal lip of the vent to protrude slightly. The gland in this species has numerous openings, each leading into one of the sac-like glandular cavities which form a layer below the mucosa. The secretion is a white frothy fluid (hence the gland in the quail was formerly known as the 'foam gland') which is transferred to the oviduct during coitus, although no function has been found for it. In many species a number of glands, the lateral proctodeal glands, occur in the lateral wall of the cloaca (Figs 11–5 and 11–6). Again the function of these glands is unknown.

In the domestic cock the paired lymphatic folds lie on the floor of the proctodeum, just inside the ventral lip of the vent (Fig 11–1). In some Anatidae and ratites most of the floor of the proctodeum is taken up by the intermittant phallus. These structures are described below. In females of the species with an
intromittent phallus the floor of the proctodeum has a phallic homologue analogous to the mammalian clitoris (Fig 11–3).

The mucosa of the proctodeum is smooth except for some irregular projections and furrows. The epithelium in most species examined is stratified squamous, but in the domestic fowl it is simple columnar except on the inner aspect of the lips of the vent where it becomes stratified squamous. The absence of stratified squamous epithelium in the proctodeum, as well as in the urodeum, suggests that in these compartments in the domestic fowl resorption of water may occur. In the domestic fowl large numbers of Herbst corpuscles, which are sensitive to vibration, are present under the epithelium of the lips of the vent.

The vent

At rest the vent is usually a transverse slit (Figs 6–3 and 6–10) guarded by dorsal and ventral lips, the lips being inverted into the cavity of the proctodeum (Fig 11–2). When a large mass of faeces is evacuated from the cloaca, the lips are partly everted exposing the orifice of the vent which then assumes a circular shape. In the domestic Anatidae the resting vent is U-shaped. In the domestic fowl the part of the caudal surface of each vent lip that is visible is keratinized and characterized by numerous radial furrows (the furrowed part, Fig 11–2). This is continued by a concealed part which is only slightly furrowed (the smooth part, Fig 11–2). The cranial (inner) surfaces of the lips are lined by stratified squamous epithelium. In many species (but not the Anatidae or the domestic fowl) the vent lips contain numerous mucous glands.

Spontaneous and vigorous sucking movements of the vent ('cloacal drinking') have been observed in domestic fowl chicks at hatching, and material applied to the lips of the vent is carried to both the cloacal bursa and the caeca. The experimental evidence strongly suggests that the domestic fowl acquires part of its basic immunity via this pathway.

Cloacal promontory

The terminal convolutions of the ductus deferens in breeding males of a number of passerine species form a conical projection of the cloacal region, the cloacal promontory. For details see Chapter 9.

Cloacal muscles

There are three striated cloacal muscles. The sphincter muscle of the cloaca surrounds the proctodeum and vent (Fig 11–2). The transverse muscle of the cloaca arises from the caudal part of the pelvic bone or the caudal vertebræ and passes ventral to the proctodeum and vent, its fibres interdigitating with those of the sphincter muscle. In the duck it pulls the proctodeum ventrally during coitus with the result that the tympanumus phallus is directed cranially towards the cloaca of the female. The levator muscle of the cloaca extends from the ventral side of the tail lateroventrally around the proctodeum to insert on its ventral wall. In male birds it attaches to the phallus. In the domestic fowl and duck it acts after copulation, and possibly defaecation, to pull the ventral lip of the vent and the floor of the proctodeum back into the resting position.

The phallus

The ratites have a penislike protrusible intromittent phallus which resembles that of crocodiles, the contemporary reptiles most closely related to birds. The anseriform birds also have a protrusible intromittent phallus, but it is somewhat more advanced in having, for example, a spiral phallic sulcus. In birds generally, however, there may be a small non-protrusible structure on the ventral lip of the vent, as in the domestic fowl and turkey, or it may be absent altogether; there is almost a total lack of reliable anatomical knowledge about this region in the great majority of birds. The similarity between the phallus of ratites and crocodiles led to the suggestion that all ancestral birds had a protrusible phallus and that those which still retain it are relatively primitive forms. However, an alternative hypothesis proposes the opposite, that the phallus in ancestral birds was in fact simple and that only a few groups (ratites, tinamous and anseriforms) have developed a specialized type. It has been suggested that a fully intromittent phallus offers an adaptational advantage in the anseriforms by preventing water from entering the female cloaca during coitus and thus avoiding osmotic damage to the spermatozoa. However, a number of supposedly primitive anseriforms (screamers, Magpie Goose, whistling ducks, Coscoroba Swan and Cereopsis) copulate on land or while standing in shallow water.

The non-intromittent phallus. In the absence of information about wild birds the following account describes the domestic fowl. In this species the phallus is mounted on the crest of the ventral lip of the vent (Fig 11–1). It consists of the white median phallic body which in the detumescent male is about 1.5–3.5 mm in diameter, and a pair of flesh-coloured lateral phallic bodies which are 2 × 4 mm in the detumescent male, the larger measurement being mediolateral. In the classical method of sexing day-old chicks, which depends on observing the presence or absence of a phallus of male dimensions (the female has a smaller one), the ventral lip of the vent is everted by digital pressure to expose the phallic region on the crest of the lip. The paired spindle-shaped reddish lymphatic folds lie on the ventrolateral floor of the proctodeum, rather than on its crest. The median and lateral phallic bodies and the lymphatic folds consist of connective tissue and interconnecting lymphatic channels.

Tumescence is mainly due to the flow of lymph from the paired paracloacal vascular bodies to the phallic bodies and lymphatic folds. The lymphatic folds become greatly enlarged and merge with the less enlarged lateral phallic bodies from which they are now separated only by indistinct grooves (Fig 11–4A); the lymphatic folds are believed to contribute lymphlike fluid to the
semens (p. 171). The median phallic body enlarges least (Fig 11-4A). These enlargements evert the ventral lip of the vent and adjacent proctodeal floor and thus extrude the phallus as a whole. The meeting in the midline of the right and left lymphatic folds and the right and left lateral phallic bodies forms a median groove with the median phallic body at its ventral tip (Fig 11-4A). Contraction of the levator and sphincter cloacal muscles just before ejaculation compresses the lymphatic channels carrying lymph to the phallus and causes the phallus to protrude still further. At this stage the urodeum and proctodeum are both more or less everted, so that the coprourodeal fold becomes visible like a diaphragm (Fig 11-4A). At the moment of ejaculation the protrusion of the phallus occurs with darting rapidity. Semen is discharged from the deferent papilla into the median groove, and at the same moment the ventral tip of the phallus is applied to the protruded oviduct of the female. Detumescence occurs in a few seconds and is due to the drainage of lymph into the general lymphatic system.

The phallus of the turkey is essentially similar to that of the domestic fowl, but the median phallic body although still small has a double apex, and the lateral phallic bodies are longer dorsoventrally and therefore protrude further from the vent in tumescence (Fig 11-4B).

The phallus in the female is a reduced structure consisting of a pair of folds separated by a shallow median groove.

**Fig 11-4** A, The erect phallus of the male domestic fowl as seen during collection of semen by manually-induced ejaculation. The degree of eversion of the floor of the cloaca is probably exaggerated by the squeezing of the cloaca between the finger and thumb. B, The erect phallus of the male domestic turkey as observed during collection of semen by manually-induced ejaculation. The degree of eversion of the cloaca is probably exaggerated by pressure from the fingers. From King (1981b), with kind permission of the publisher. These drawings are based on photographs by P.E. Lake and colleagues, Poultry Research Centre, Edinburgh.

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**Fig 11-5** Longitudinal section of the cloaca of an immature male domestic goose viewed from the left side. The left wall of the cloaca has been removed showing the interior of the right side. The phallus is in the resting position. From Komarek (1969), with kind permission of the editor of *Acta Veterinaria Brno*.

**The intromittent phallus.** The anseriforms, tinamous and ratites possess a truly intromittent type of phallus of which two forms can be distinguished depending on whether or not it contains a blind tubular cavity.

An **intromittent phallus with no cavity** occurs in the Ostrich, kiwis and tinamous. In the Ostrich the base and body of the phallus consist essentially of right and left erectile fibrolymphatic bodies, the left body being larger than the right. On the dorsal surface of the phallus between the fibrolymphatic bodies, is the **phallic sulcus** into which the two deferent ducts eject semen. Along the ventral surface of the caudal free half of the phallus there is an elastic vascular body consisting of an outer layer of elastic tissue and an inner layer of erectile tissue. At rest the phallus lies bent in a pocket in the floor of the proctodeum. Since it takes up so much space in the cloaca it has to be partially protruded before micturition and defaecation can occur. Tumescence of the phallus occurs by lymphatic engorgement. The fully erect phallus is bright red and about 40 cm long in the mature Ostrich. It is directed ventrally and cranially, and because of the asymmetry of its fibrolymphatic bodies, is bent slightly to the left. This type of phallus resembles that of chelonian and crocodilian reptiles.

An **intromittent phallus with a cavity** occurs in the Emu, cassowaries, rheas...
and the anseriforms (Figs 11-5, 11-6 and 11-7). In the domestic duck and goose the resting phallus is a long blind-ending tube which lies coiled in a sac lined with peritoneum along the ventrolateral wall of the cloaca, like the invaginated finger of a glove (Fig 11-5). The deep blind-ending portion of the tube secretes mucus and is non-erectile. It is not everted in tumescence. The more superficial portion of the tube (i.e. in the resting phallus the part that opens on the cloacal floor) is lined internally by a keratinized stratified squamous epithelium. This portion of the tube is everted and protruded in tumescence (Fig 11-6). At the tip of the protruded phallus there is an opening which leads into the deep, non-everted blind end of the tube (Figs 11-6 and 11-7). The erectile mechanism is based on the right and left lymphatic cavities which surround the right and left paracloacal vascular bodies (Fig 11-7). Tumescence of the phallus is by engorgement with lymph which is pumped into the lymphatic cavities by the paracloacal vascular bodies. This forces the phallus out of its resting invaginated form. The right and left lymphatic cavities open directly into the cavities of the right and left fibrolymphatic bodies at the base of the erect phallus (Fig 11-7). There, the paired fibrolymphatic bodies become continuous with each other internally, forming a common erectile lymphatic cavity; on the surface, however, they are still divided by a groove housing the beginning of the phallic sulcus. The left and right fibrolymphatic bodies twist spirally round each other, with the phallic sulcus between them (Figs 11-6 and 11-7), the left body being much greater in diameter than the right; this asymmetry of the fibrolymphatic bodies occurs in all birds with a protrusible phallus. The bases of the fibrolymphatic bodies are supported by the trough-shaped fibrocartilaginous body which strengthens the ventral and lateral walls of the urodeum and proctodeum (Fig 11-7). An elastic ligament extends through the phallus from the fibrocartilaginous body to the apex. The erect phallus is about 8 cm long in the domestic drake (only about 4 cm long in the wild Mallard), is greyish yellow in colour and is directed cranially.

The process of tumescence involves (a) eversion of the proctodeum so that the base of the phallus is brought to the vent opening; (b) contraction of the transverse cloacal muscle, turning the orifice of the vent cranially towards the female cloaca; (c) distension of the lymphatic cavities of the fibrolymphatic bodies with lymph (aided by peristaltic contraction of the cloacal sphincter muscle); and (d) sudden eversion of the engorged base and shaft of the phallus. In the fully erect phallus the phallic sulcus can become a closed tube. During manually induced ejaculation, however, semen drips from the base of the phallus not the tip, so that the sulcus is not then a functional seminal groove; whether or not it serves as a seminal groove in natural coition is not known. Detumescence results from draining of the lymphatic spaces of the phallus into the general lymphatic system. As the pressure falls, the tip of the phallus is...
pulled back by the elastic ligament and invaginates into its base, much as the finger of a glove can be pushed into the hand. In geese venereal infection transmitted at coitus can involve the phallus and cloaca, and may lead to infertility and reduced egg production.

Because of the elongated form of the erect phallus and its cranioventral direction, true intromission into the female cloaca occurs in anseriforms and ratites. The phallus in these birds is thus fully analogous to the mammalian penis. It is not, however, homologous to the mammalian penis: its erectile mechanism is lymphatic, whereas that of the mammal is vascular; the seminal fluid travels via the external surface, as opposed to the internal urethra of the mammalian penis, finally, the avian phallus is solely reproductive in function, while the mammalian penis is both reproductive and urinary.

Further reading