Chapter 8

FEMALE REPRODUCTIVE SYSTEM

Two bilaterally symmetrical gonads and oviducts develop in the avian embryo. In birds generally, however, and in all the domestic species, the left ovary and oviduct soon exceed the right in their development. In the great majority of species in adult life only the female organs on the left side are functional, although rudiments of the right gonad and oviduct sometimes persist. Among the species in which two fully developed ovaries are frequently seen are many birds of prey and the Brown Kiwi, although right and left ovaries have also been observed in birds belonging to at least 16 orders which are usually assumed to have only one ovary. Two oviducts occur much less frequently, but appear to predominate in birds of prey. In the Brown Kiwi which has two functional ovaries, the single left oviduct is reported to be specially positioned to receive oocytes from both the right and left ovaries.

The general form and function of the left ovary and oviduct seem to be remarkably constant in the majority of birds.

THE LEFT OVARY

Growth and form

At an early stage of embryonic growth in the genetic female of the domestic fowl and of several other species, the gonadal region is colonized unequally by the incoming germ cells, more of which arrive at the left gonad than at the right. This initial asymmetry is further augmented by migration of many germ cells from the right to the left gonad. The left gonad therefore becomes larger than the right gonad, even before hatching. The primordial germ cells become incorporated in the so-called germinal epithelium, the other cells of this epithelium being of mesenchymal (peritoneal) origin. During the 6th and 7th days of incubation in the domestic fowl, the germinal epithelium buds off the primary sex cords into the depth of the gonad; these give rise to the ovarian medulla in the genetic female, and to the seminiferous tubules in the genetic male. In the genetic female the germinal epithelium multiplies into a thickened peripheral zone of cells, which is separated from the primary sex cords by a layer of connective tissue called the primary tunica albuginea.
During the 8th to 11th days of incubation this thickened peripheral zone of cells proliferates a second wave of down-growing cells, the *secondary sex cords*; it is these that form the oogonia. An *oogonium* is a germ cell which is actively multiplying. When the oogonia stop multiplying and begin to enlarge they become *primary oocytes*. This occurs at the time of hatching. At this stage they reach the prophase of their first maturation (reduction) division. Most of the yolk material now accumulates and the primary oocyte gradually grows to full size. The avian primary oocyte is the largest cell in the animal kingdom. In the domestic fowl its final weight is about 20 g. One of the largest cells to occur on this planet was the oocyte of the Madagascan Elephant-bird, which achieved a diameter of about 37 cm and a volume of much the same capacity as a bucket; the enormous eggs of this recently extinct bird were probably the basis for the gigantic Roc of ancient mythology. At the end of their period of growth the oocytes can complete their two maturation divisions, the first of which forms the *secondary oocyte* and the second forms the *ovum*. Thus there are three phases of oogenesis, a period of multiplication, a period of growth and a period of maturation.

From hatching until about four months in the domestic fowl the left ovary grows slowly, reaching about 1.5 cm in length and weighing about 0.5 g. During this phase the ovary consists of a cortex and medulla. The cortex encloses the medulla except where the ovary is in contact with the dorsal body wall. The outer surface of the cortex is lined by a tall cuboidal or flattened peritoneal epithelium which persists into maturity. Beneath the epithelium is a layer of dense connective tissue, the *definitive tunica albuginea*. Between 18 and 24 weeks the rate of growth rapidly accelerates, with many oocytes reaching their final size and the distinction between cortex and medulla becoming virtually lost. The cortex is now represented by ill-defined *parenchymatous zones* containing many immature follicles; the medulla is represented by irregular *vascular zones* containing blood vessels, nerves, smooth muscle and interstitial cells. In the final phase of rapid growth the diameter of the maturing primary oocyte increases from about 6 mm to a maximum of about 40 mm in about six days. The ovary now weighs about 60 g and, suspended by the mesovarium, occupies an extensive area on the roof of the coelom, overlapping the kidneys and lungs.

The light breeds of domestic fowl come into lay at five months and the heavy breeds at six to seven months, but modern hybrids can be persuaded to lay at four-and-a-half months. Most seasonal birds breed in the first spring or, in some species, in the second spring after hatching. Some birds, however, become sexually active much later than that. Fulmars, for example, begin breeding when about eight years old. On the other hand, the Australian Zebra Finch can breed when only a few months old, taking advantage of the restricted periods of rainfall, and captive Japanese Quail are sexually active at six weeks of age, a characteristic which enhances their value as laboratory animals.

During sexual activity the left ovary resembles a bunch of grapes because of the many large follicles which hang from it (Fig 8-1). In an actively laying hen about four or five very large follicles, reaching 40 mm in diameter, may be present as well as thousands of smaller ones. During the resting phase the left ovary diminishes in size and in the domestic fowl weighs only 2–6 g. In seasonal birds three phases in the ovary can generally be distinguished, a phase of prenuptial acceleration in which it enlarges, a culmination phase when ovulation and laying occur, and possibly a refractory period when the ovary is much reduced in size. These phases are more or less synchronous with comparable phases in the testes, and, as in the male, are under the control of the neuroendocrine system.

In the domestic fowl the ovary is usually supplied with arterial blood via the ovario-oviductal branch of the left cranial renal artery (Fig 13–5). The ovary is drained via two ovarian veins directly into the caudal vena cava. These blood vessels and many nerves enter the broad dorsal surface of the ovary, the ovarian hilus, which is planted on the roof of the coelom.
The follicle

A large follicle is suspended by a stalk (Fig 8-1) which possesses smooth muscle and is abundantly vascularized and innervated. The follicle contains the large primary oocyte. This is enclosed by the wall of the follicle, which consists from inside to outside of the following six layers. (a) A fine inner layer (Fig 8-2), comprising an inner and outer component. The inner one is the zona radiata. This consists of the fine radial processes of the cytolemma of the oocyte, and the secretions and delicate radial processes of the granulosa. It is a transient structure, disappearing shortly before ovulation. The outer component is the perivitelline lamina; this consists of electron dense rods which eventually develop into a meshwork of long fibres. (b) The stratum granulosum (Figs 8-2 and 8-3), a layer of cells with an unusually prominent basal lamina. (c) The theca interna (Fig 8-3), a compact narrow layer of spindle-shaped fibroblast-like cells and collagen fibres. (d) The theca externa (Fig 8-3), a looser, wider layer of flattened elongated fibroblast-like cells and numerous collagen fibres. Groups of interstitial cells usually occur at the boundary between the two thecae. (e) A superficial tunic of connective tissue (Fig 8-3). (f) The superficial epithelium (Fig 8-3) formed by peritoneal mesothelial cells (the so-called germinal epithelium). The wall of the follicle is highly vascular and quite profusely innervated by cholinergic and adrenergic fibres. A white meridional band, the stigma, occurs on all large follicles of most but not all species (Fig 8-1) (an exception is the White-crowned Sparrow). At the stigma the wall of the follicle has no superficial tunic of connective tissue and is less vascular than elsewhere. Contrary to general opinion the stigma seems to be devoid of smooth muscle.

Maturation of the oocyte, ovulation and fertilization

At the end of their period of growth the oocytes continue the process of maturation. As in most mammals, the first maturation division (reduction or meiotic division from the diploid to the haploid number of chromosomes), forming the secondary oocyte and first polar body, is completed while the primary oocyte is still in the follicle (about two hours before ovulation). In contrast to mammals and most other vertebrates, however, it is the female bird which is heterogametous and carries the XY combination, and therefore determines the sex of the progeny.

Ovulation occurs next. Luteinizing hormone (LH) released by the adenohypophysis is clearly involved in this process, but the exact mechanism is not known. LH may induce contraction of the smooth muscle of the stalk of the follicle, causing the stigma to split. Or it may induce ischaemia and hence necrosis of the stigma, but such necrosis has not been demonstrated. The number of ovulations in a reproductive cycle varies greatly with the species. Some birds, such as albatrosses and petrels, lay only one egg. Galliform birds, on the other hand, have clutches containing 8 to 12 eggs. A few birds such as the Budgerigar and crows are determinate layers and lay a fixed number of...
eggs. Many other birds, however, including the Red Jungle Fowl, are indeterminate layers and can quickly replace eggs which are lost from their clutch. This characteristic of the Red Jungle Fowl has been artificially selected by man with the result that the domestic fowl lays almost continuously for a large part of the year. Domestic fowl have laid up to 352 eggs in a year, and a Japanese Quail has managed 365 eggs thereby losing not a single working day. Most wild birds lay only one clutch of eggs each year, while others (e.g. redpolls) lay two or more clutches. A few species which take more than a year to rear their young, such as albatrosses and penguins, do not lay every year.

Ovulation in the domestic fowl usually follows about half an hour after an egg is laid, the integrating mechanism being hormonal or nervous. The newly released secondary oocyte is grasped and finally swallowed by the infundibulum. This catching process is made easier by the left abdominal air sac, which tightly encloses the ovary in the *ovarian pocket* except caudally where the infundibulum opens. Nevertheless, not all ovulated oocytes are successfully captured by the infundibulum. 'Internal laying' occurs quite often, especially when the bird is just going in or out of 'lay'; at these times the oviduct and ovary tend to get out of phase. Some at least of the oocytes which are thus lost in the coelom are believed to be harmlessly absorbed within 24 hours; others become involved in *egg peritonitis*, although it is not known why this happens. Egg peritonitis is one of the most common conditions seen in end of lay hens, turkeys and ducks. In the Brown Kiwi, which normally has a functional ovary on the right side as well as the left, the infundibulum of the left oviduct spreads right across the body and can therefore receive ovulated oocytes from both ovaries.

The *second maturation division*, forming the ovum and second polar body, occurs in the oviduct. Probably penetration by the spermatozoon is needed before this division can be completed, as in vertebrates generally. *Penetration by spermatozoa* occurs about 15 minutes after ovulation. Since penetration must occur before the secondary oocyte becomes covered by albumen, it presumably happens in the funnel of the infundibulum where there are no glandular cells. *Fertilization* is the actual fusion of the male and female pronuclei. Polyspermy is quite common. When present the supernumerary male pronuclei divide and initiate local centres of division, but these nuclei soon stop dividing and then degenerate.

The postovulatory follicle

Immediately after ovulation the follicle shrinks to a thin-walled sac, devoid of blood clots, which then undergoes quite rapid regression and absorption (Fig 8-1). Within two or three days the lumen of the sac has become filled with hypertrophied granulosa cells containing large amounts of lipid. In a few species thecal luteal cells invade the lumen. This luminal mass in the later stages is penetrated by capillaries. By the 10th day after ovulation, regression is virtually complete in the domestic fowl and in most of the other species that have been examined. Thus there is certainly no persistent postovulatory corpus luteum in birds. The likelihood remains, however, that the postovula-

The ovary in the period after laying

After the period of egg laying the bird enters a non-breeding state during which it is involved in incubation and caring for the chicks. In the period of *follicular atresia* any developing oocyte which may be present undergoes resorption. Several different forms of atresia have been observed. These include 'bursting atresia' which is characterized by rupture of the follicle wall and escape of the yolk into the ovary or body cavity, and 'invagination atresia' which is typified by invasion of the oocyte by cells from the granulosa layer or theca and reabsorption of the yolk in situ. Both of these types of atresia occur in the domestic fowl and in many other species. The disappearance of the follicle may or may not leave a scarlike area in the ovary. Following atresia of the follicle the resting ovary enters the *interbreeding period* in which its shrunken appearance is similar to that of the juvenile ovary (Fig 6–10).

The endocrine secretions of the left ovary

There is evidence for secretion of (a) oestrogens, by thecal interstitial cells; (b) androgens, by thecal interstitial cells and by interstitial cells which lie in the ovarian tissue outside the follicles; and (c) progestagens by granulosa cells of the preovulatory follicle and perhaps also from the postovulatory follicle. The term *interstitial cell* refers to the large vacuolated cells of the ovary, all of which are histologically similar whether they lie in the medulla, cortex or the thecal of the follicular wall. It is possible that all these interstitial cells are merely the same endocrine cell at different stages of development. On the other hand, some of them may arise from the embryonic medulla, that is from the primary (medullary) sex cords, and are then the so-called 'medullary interstitial cells'; some of these medullary cells may then migrate into the cortex and become the so-called 'cortical interstitial cells'. Alternatively, the cortical cells may come from the secondary (cortical) sex cords. Finally, some of the cortical interstitial cells may embed themselves in the thecae and become the 'thecal interstitial cells'; another possible source of the thecal interstitial cells is the mesenchyme of the developing gonad, rather than the epithelium of the cortical sex cords. The true origins of the interstitial cells of the ovary remain controversial.

Sex determination by laparoscopy

Laparoscopy is a technique successfully used to determine the sex of wild birds in captivity which do not show sexual dimorphism. The procedure involves incising the body wall between the last two ribs on the left side and introducing the laparoscope into the left caudal thoracic air sac. However, in all but the smallest of birds the left gonad can only be visualized if the
THE LEFT OVIDUCT

In the laying bird the left oviduct fills most of the dorsal and caudal part of the left side of the coelom. In the domestic fowl it weighs about 75 g and is about 65 cm in length. When the bird goes out of lay the size of the oviduct becomes much reduced (to about 5 g weight and 15 cm length, in the domestic fowl). The juvenile oviduct is shown in Fig 6–10. Seasonal growth and differentiation of the oviduct is under the control of the ovarian hormones, oestrogens, progesterone and androgens.

The left oviduct has five parts: infundibulum, magnum, isthmus, uterus (shell gland) and vagina.

Infundibulum

This part has two components, a funnel followed by a tubular region (Fig 8–1). In the domestic fowl their combined length is about 7 cm. The funnel has a thin wall and low mucosal folds. The opening of the funnel into the coelom faces into the 'ovarian pocket'. It is an elongated slit (about 9 cm long in the domestic fowl). The funnel tapers rapidly into the tubular part. The tubular part, also called the chalaziferous region, has a slightly thicker wall and taller mucosal folds with more secondary folds than in the funnel. In the Brown Kiwi the infundibulum extends the whole width of the coelomic cavity and is therefore able to receive oocytes from the left and right ovaries both of which are functional in this species.

Plates of glandular cells occur at the bottom of the grooves in the wall of the funnel region. The tubular part has some convoluted branched tubular glands, but these are confined to the region adjoining the magnum. The cells of these glands differ from those of the magnum: their secretory granules are smaller and do not compress the nuclei so strongly into a flattened form and basal position. Penetration by the spermatozoon presumably occurs in the funnel, before the secondary oocyte is covered by the first coat of albumen.

Magnum

The transition into the magnum is abrupt being marked by a sudden great enlargement of the mucosal folds. This is by far the longest and most coiled part of the oviduct (about 34 cm long in the domestic fowl) (Fig 8–1). The great thickness of the wall is caused by the presence of numerous tubular glands which are packed into the massive mucosal folds (Fig 8–4). These folds are taller and thicker than those of any other region of the oviduct, increasing the secretory area of the mucosa by a factor of about three. There are about 22 primary folds, which are seen to be devoid of true secondary folds when examined histologically; the few indentations in the epithelium are due to ducts of the glands.

The branched convoluted tubular glands in the lamina propria reach their greatest development in the magnum. Their cells contain large eosinophilic granules and have small rounded basal nuclei. The ducts open anywhere on the luminal surface, but are difficult to see in ordinary histological sections except after their secretion has been released. Immediately before ovulation the cells of these glands are so bulging with their secretion (which forms the bulk of the egg-white protein) that the lumen of the glands and the inter-glandular connective tissue are almost invisible. Because of the presence of this secretory material the magnum has a milky-white colour. In hens that lay 'watery-white' eggs the secretory cells are abnormal. After discharge of the secretion the lumen and the outlines of the individual glands are more easily distinguished histologically. The stimulus to discharge may be mechanical, arising from the passage of the egg along the magnum. However, some glands seem to remain full even though many others are emptied, and this may indicate that discharge is controlled by more complex factors than simple mechanical influences.

The last few centimetres of the magnum are modified to form the so-called mucous region of the magnum. The folds and tubular glands here are much reduced, and the glandular cells contain relatively abundant mucus.

Isthmus

This region is short (about 8 cm long in the domestic fowl) and reduced in calibre (Fig 8–1). A narrow and sharply distinguished translucent band of tissue (1–3 mm wide in the domestic fowl) marks the exact junction of magnum and isthmus. The folds of the isthmus are less prominent than those of the magnum. Unlike those of the magnum, histologically they carry secondary folds. The translucent region is unusual in having no tubular glands, but the rest of the isthmus does have tubular glands histologically resembling those of
the magnum. However, only the cells of the isthmus glands possess sulphur-containing proteins, which is consistent with the production by the isthmus of shell membranes of a keratinous nature.

**Uterus**

There is no distinct anatomical boundary between the isthmus and uterus (shell gland). The uterus is a relatively short region (about 8 cm long in the domestic fowl) (Fig 8–1). The cranial part is short and relatively narrow (the so-called ‘red region’) through which the egg passes rapidly. The major part is pouchlike and holds the egg during shell formation; it is here that the egg remains during the greater part of its journey through the oviduct. The longitudinal folds of the uterus are intersected by transverse furrows, thus forming numerous leaflike lamellae (about 4 mm tall). When an egg is inside the uterus these lamellae flatten themselves against the shell.

The tubular glands differ from those of the magnum, their cells being less granular and more vacuolated and possessing larger basally or centrally placed nuclei.

**Vagina**

The junction of the uterus with the vagina is marked by the vaginal sphincter which belongs to the beginning of the vagina. The vagina is fixed in a permanent S-shape by smooth muscle and connective tissue (Fig 8–1). When dissected free the vagina is about 8 cm long in the domestic fowl. The powerful muscle of the vaginal wall is thicker than that of any other part of the oviduct. The mucosal folds are relatively thin and low, and possess secondary folds. The mucosa has no secretory tubular glands. In the region of the sphincter the folds carry the tubular spermatic fossulae (sperm-host glands) which are the main site for storage of spermatozoa. The fossulae are lined by tall columnar cells possessing apical microvilli. In the juvenile bird the entrance to the cloaca from the vagina is closed by a membrane, at least in the domestic fowl and in wild anseriform birds; this occluding plate breaks down at sexual maturity, its removal apparently being under hormonal control.

**The general structure of the wall of the oviduct**

The wall of the adult oviduct possesses an epithelial lining, multicellular glands and smooth muscle. The epithelium consists of ciliated cells alternating with unicellular glands which resemble goblet cells, the proportions of the two cell types varying between different regions of the oviduct. This arrangement occurs in all parts of the oviduct in spite of the distinctive contribution made by each region. The unicellular glands are particularly large and numerous in the magnum, where they discharge their contribution to the albumen as each egg goes by, and refill between successive eggs. While the cilia in all regions mainly beat in the direction of the cloaca, the cilia in the magnum in a tract adjacent to the attachment of the dorsal ligament beat towards the infundibulum. The functions of the oviductal cilia have not been agreed, but they probably provide a protective mucociliary carpet, as in the upper respiratory tract. The multicellular glands are of two sorts, tubular glands and glandular grooves. The tubular glands open on the mucosal folds of the tubular part of the infundibulum, the magnum, the isthmus (except in the translucent region) and the uterus. Glandular grooves are found only in the infundibulum.

The mucosal folds (Fig 8–4) are more or less continuous throughout the oviduct, though varying in height and thickness. They are slightly spiral and thus rotate the egg as it goes down the oviduct.

The smooth muscle layers (inner circular and outer longitudinal) are thickest in the vagina and uterus and thinnest in the infundibulum. One function is to transport spermatozoa rapidly up the oviduct by oviducal retroperistalsis. Another is to drive the egg down the oviduct by peristaltic waves.

**Ligaments of the oviduct**

The oviduct is suspended from the roof of the coelomic cavity by a double-layered sheet of peritoneum forming the dorsal and ventral ligaments of the oviduct (Fig 8–1). The dorsal ligament extends from the roof of the coelomic cavity to the oviduct. The ventral ligament extends ventrally from the oviduct and has a free border. Both the dorsal and ventral ligaments contain much smooth muscle which is continuous with the outer longitudinal layer of muscle in the wall of the oviduct. Caudally, the smooth muscle of the ventral ligament condenses into a massive muscular cord about 5 mm in diameter in the domestic fowl, which fuses with the ventral surface of the uterus and vagina (Fig 8–1). The smooth muscle of the oviductal ligaments may help to move the egg along the oviduct, especially in the magnum where the intrinsic musculature appears too feeble to perform this function unaided.

**The blood and nerve supply of the oviduct**

In the domestic fowl the arterial supply to the oviduct (Fig 13–5) is generally derived from three oviductal arteries, the cranial, middle and caudal oviductal arteries, which are branches of the left cranial renal artery, the left ischiadic artery, and the left pudendal artery respectively. Sometimes in the domestic fowl there is a fourth oviductal artery, the cranial accessory oviductal artery, arising from the left external iliac artery; in some species, such as the domestic duck, this vessel is constantly present. The oviductal arteries form a series of longitudinal anastomosing arterial arcades along the dorsal and ventral surfaces of the oviduct in the dorsal and ventral ligaments. Within the wall of the oviduct the arteries form plexuses between the muscle layers and in the lamina propria, arterioles from the plexuses ending in a capillary network around the tubular glands. The uterus is especially vascular, as would be expected from the fact that in the domestic fowl calcium is deposited in the shell during the last 15 hours of shell formation at a rate of 100–150 mg/h. The veins draining the cranial part of the oviduct empty into the caudal vena cava,
while those draining the caudal part empty into the hepatic portal or renal portal systems. The oviduct is innervated by both sympathetic and parasympathetic nerves, although the precise origin of these nerves does not appear to have been established. The most densely innervated region of the oviduct is the uterus and its junction with the vagina.

**Storage of spermatozoa in the oviduct**

Spermatozoa must be stored somewhere in the oviduct. This is evident from the fact that, in the domestic fowl and several other species, the capacity for fertilization is retained for several weeks after a single insemination; this characteristic is likely to be common to birds in general. Within minutes of insemination sperm reach the top of the oviduct, but within 24 hours they disappear, only to reappear in the lumen in small numbers at the time of each subsequent laying or ovulation. In the domestic fowl the spermatic fossulae in the vagina (the sperm-host glands) are the main sites of residence, but it is not known how the sperm enter the fossulae, how they survive and what causes them to be released at the time of laying or ovulation; mechanical, nervous and vascular factors have been considered. Some sperm may also be stored in the glandular grooves and tubular glands of the infundibulum.

**FORMATION OF THE EGG**

The egg traverses the oviduct in about 25 hours. The raw materials of the yolk (protein and lipids) are synthesized in the liver and travel in the blood plasma to the granulosa cells, which then pass them to the oocyte (vitellogenesis). The oocyte reorganizes them into yolk spheres and fluid. There is no biochemical synthesis of yolk in the oocyte itself.

The egg passes through the infundibulum in about 15 minutes. The chalaziferous layer of the albumen (Fig 8–5) is laid down by the tubular glands there. It consists of only a thin layer of dense albumen, immediately surrounding the yolk. The tubular part of the infundibulum forms the chalaza (Fig 8–5) at each end of the egg. The chalaza at the sharp end is a double strand, while that at the blunt end is a single strand. The chalazae appear to suspend the yolk between the two ends of the egg. They become twisted, probably from the rotation of the egg as it travels down the oviduct.

The egg takes about three hours to traverse the magnum. During this time it acquires albumen (Fig 8–5) secreted by the tubular glands, with a contribution also from the unicellular glands. Sodium, magnesium and calcium are added mainly in the magnum.

Movement through the isthmus is slow, taking about 75 minutes in all. The inner and outer shell membranes (Fig 8–5), lining the shell, are the main components which are formed here (from the tubular glands). Before these are laid down, however, a small amount of protein (about 10 per cent of the total) is added to the albumen. Calcification of the shell appears to be initiated in the isthmus.

The egg occupies the uterus for about 20 hours, during which time the shell (i.e. the testa, cuticle and pigment) is formed (Fig 8–5). Plumping occurs here. This consists of the rapid addition of watery solutions (probably from the glands of the relatively short and narrow cranial part of the uterus) into the egg, mainly during the first eight hours, doubling the weight of the albumen. During plumping, calcification of the shell is slow, but during the last 15 hours it is rapid. Every 15 minutes the uterus withdraws from the blood a weight of calcium equalling the total amount circulating at any one moment; the extreme vascularity of the uterus presumably contributes to this remarkable activity. Potassium is added mainly in the uterus. Usually, in the domestic fowl the egg lies in the uterus with its sharp end pointing caudally, and the egg is laid with this orientation. In some species (e.g. gulls and ducks) the egg in the uterus turns round just before oviposition, so that the blunt end comes out first. The biological significance of this rotation of the egg, and the way the muscles of the oviduct and its ligaments achieve it, are not known.

The egg travels through the vagina in a matter of seconds. **Obstruction** of the oviduct is relatively common in both domestic and wild birds. The most usual causes include the presence in the oviduct of necrotic egg material, a broken-shelled egg, a normal soft-shelled egg or localized infection. Amongst wild species a common factor associated with obstruction of the oviduct is senility.

**STRUCTURE OF THE EGG**

The egg consists of a germinal disc, yolk, the membranes surrounding the yolk, albumen and a shell (Fig 8–5).

The germinal disc

The germinal disc (blastoderm if fertilized, blastodisc if unfertilized) is a small disc of cytoplasm (Fig 8–5) containing the remnant of the nucleus. It can be seen on the surface of the yolk of a fresh egg as a circular, opaque white spot, which in the domestic fowl is 3–4 mm in diameter.

The yolk

The yolk is a thick viscous material containing about 50 per cent solids of which 99 per cent are proteins (30 per cent of yolk is lipo- and phospho-proteins). As in reptiles it forms the main source of nutrition for the embryo. There are two kinds, white and yellow yolk (Fig 8–5). The white yolk is about two-thirds protein and one-third fat. It consists of a small spherical mass (the centre of the latebra), joined by a slender column (the neck of the latebra) to a conical disc (the disc of the latebra) which lies beneath the germinal disc. The yellow yolk, which is about two-thirds fat and one-third protein, is often organized in the domestic fowl into alternating yellow and white strata. However, this stratification is an artefact depending on the diet, the pale
strata being deficient in carotenoid pigments. When the diet is well balanced these strata disappear. Another kind of stratification of the yellow yolk can be discerned, although only by means of special techniques. These strata do reflect the real form of the yolk, but little is known about their structural basis.

The 'yolk membranes'

These membranes form a barrier (in the domestic fowl probably about 24 μm thick in the fresh state) between the yolk and albumen, which has great mechanical strength but is permeable to water and salts (Fig 8-5). The electron microscope shows that the membranes consist of four layers. The two next to the yolk, i.e. (1) the oocyte cytolemma and (2) the meshwork of coarse fibres known as the perivitelline lamina, are derived from the follicle of the ovary; they are the same structures as those which are shown in Fig 8-2, and are described on page 148 under layer (a) of the wall of the follicle. While the fertilized ovum is in the infundibulum the gaps in the meshwork of the perivitelline lamina are wide enough to admit the head of a spermatozoon, but further down the oviduct the gaps become obliterated. The two outer layers of the yolk membrane are laid down by the oviduct soon after the egg has entered. One of them, (3) the continuous lamina, is a very thin granular layer; the outermost, (4) the extravitelline lamina, consists of delicate lattice-works of fine fibres in concentric layers and forms about two-thirds of the total thickness of all these four membranes together.

The albumen

The albumen is much less viscous than the yolk. The solid component is composed almost entirely of protein (ovomucin). Dense albumen contains a relatively large amount of ovomucin and possibly some mucin fibres; thin albumen is more watery and contains less ovomucin and almost no mucin fibres. The chalaziferous layer is a thin layer of dense albumen which encloses the yolk membranes (Fig 8-5). The two chalazae are twisted strands (absent in reptilian eggs) of fine ovomucin fibres, which are formed from the chalaziferous layer (Fig 8-5). The chalaza at the sharp end is a twisted strand, while that at the blunt end is a single strand. The chalazae are continuous at one end with the chalaziferous layer, and at the other end with the middle layer of dense albumen which is connected to the shell membranes at each end of the egg by the so-called albumen ligament (or polar albumen). Thus the chalazae suspend the yolk more or less in the centre of the egg. They become twisted by the rotation of the egg as it passes down the oviduct. The inner layer is a layer of thin albumen which is almost devoid of mucin fibres (Fig 8-5). The middle layer is a layer of dense albumen, which at each end of the egg attaches by fibres to the inner shell membrane forming the two albumen ligaments (Fig 8-5). The outer layer of thin albumen surrounds the dense layer except at the albumen ligaments (Fig 8-5). The albumen contributes to the aqueous environment of the embryo, has anti-bacterial properties, and in many if not all birds is a source of nutrition for the embryo.

The shell

The shell consists of the shell membranes, the testa and the cuticle.

The outer and inner shell membranes (together about 70 μm thick in the domestic fowl) are each composed of several layers of fibres (Fig 8-5). At the blunt end of the egg the outer and inner membranes separate from each other as the egg cools immediately after hatching, forming the air cell (Fig 8-5). The head of the embryo comes to lie close beneath this space, which is absent in reptiles. The outer shell membrane is firmly attached to the testa. At each end of the egg the inner shell membrane is fused to the albumen ligament of the dense layer of albumen.

The major part of the shell is formed by the testa (270–370 μm thick in the domestic fowl) which contributes most of the thickness of the shell. Shell thickness varies greatly between species but the eggs of large birds in general have proportionately thicker shells, being about 2 mm thick in the Ostrich but only paper thin in hummingbirds. The testa consists of an organic matrix of fine fibres, and a far more bulky (98 per cent of the total) solid inorganic component consisting mainly of calcite (a crystalline form of calcium carbonate).

The fibrous organic matrix of the testa is arranged into a relatively thin inner mamillary layer (about one-third of the thickness of the testa) and a thicker outer spongy layer (the remaining two-thirds of the testa). The mamillary layer consists of conical-shaped knobs, the apices of which are embedded in the outer shell membrane. The fibres of the spongy layer are arranged parallel to the surface of the egg. The crystalline inorganic component of the testa is arranged into a thin inner layer (the layer of cones and...
basal caps) corresponding to the mamillary layer of the organic matrix, and a thicker outer layer (the palisade layer) corresponding to the spongy layer of the organic matrix. During the calcification of the testa, the crystals appear first in the mamillary layer (thus forming the layer of cones and basal caps), and then accumulate in columns in the spongy layer gradually growing towards the surface of the shell (thus forming the palisade layer). In most species of birds thousands of fine pores open on the surface of the shell, and extend between the crystals right through to the shell membranes. In the domestic fowl the pores are frequently more closely grouped at the blunt end of the egg near the air cell, and hence near the head of the chick. The pores are covered by the cuticle, but because of radial cracks in the cuticle here the pores still remain permeable to gases.

Overlying the testa and pores is a continuous organic layer, the cuticle, 90 per cent of which is peptide (Fig 8-5). Although extremely thin (10 μm thick in the domestic fowl) the cuticle is water repellant, reduces water loss and acts as a barrier to bacteria.

Pigmentation is frequently present in the shell, in contrast to the eggs of reptiles which are almost always white. Most of the pigmentation occurs in the inorganic palisade layer and sometimes in the cuticle. Rarely is it present in the mamillary layer.

Near the end of incubation the beak of the embryo penetrates the inner shell membrane where it forms the inner wall of the air cell, and at about this time the lungs usually become functional. The embryo breathes into the air cell for several hours and then cracks or 'pips' the shell, in the process of which the outer shell membrane is usually ruptured. In the domestic fowl a period of about 20 hours elapses between pipping and hatching.

**OVIPPOSITION**

At the onset of oviposition the muscle of the uterus drives the egg through the relaxed vaginal sphincter. The presence of the egg in the vagina then initiates the 'bearing down' reflex which forces the egg through the cloaca (the vagina is not capable by itself of expelling the egg from the body). The duration of oviposition varies greatly. In the Cuckoo it lasts only a few seconds since speed is essential to avoid upsetting the host, but in the domestic turkey and goose it takes several hours. The time of oviposition varies greatly between species. Songbirds tend to lay in the early morning. The domestic fowl usually lays in the morning, but may do it in the afternoon. Pigeons utilize the afternoon and pheasants the evening, while the American Coot operates very privately at about midnight. The rate of oviposition in the domestic fowl, and probably in birds generally, usually reflects the rate of ovulation. In most birds the average laying interval ranges from 24 hours (as in most passerines and the domestic fowl) to four or five days (as in the Andean Condor), but it may be much longer as in the Brown Kiwi where the interval may extend to 44 days.

**PHYSICAL CHARACTERISTICS OF THE EGG**

Eggs of different species show an enormous range of external appearance.

Size. Egg size in general is related to the size of the parent, although the relative weight of the egg usually diminishes as body weight increases. Also the eggs of precocial species, such as the domestic fowl of which the young are very active immediately after hatching, are relatively larger than those of altricial birds such as passerines whose young are helpless after hatching. Among living birds the largest egg (1400 g) belongs to the Ostrich, whilst the smallest (0.5 g) is that of the Vervain Hummingbird. The small size of the egg of the Cuckoo relative to body weight (3 per cent of the body weight compared to 7 to 11 per cent in a large number of birds) is possibly due to the fact that the parent bird parasitizes the nests of much smaller species. The largest egg relative to body weight (25 per cent) occurs in the Brown Kiwi.

Shape. The shape of birds' eggs varies greatly—conical, spherical, oval, and cylindrical forms being common. Many adaptive reasons have been suggested for these variations, for example that conical eggs are laid by birds which nest on cliff ledges since this prevents the eggs from rolling off, but few of these explanations survive close examination. On the other hand, the shape of the egg does seem to be related to the shape of the bony pelvis, spherical eggs occurring when the pelvis is deep dorsoventrally and elongated eggs when the pelvis is narrow dorsoventrally.

Colour. The coloration of egg shells ranges over a broad spectrum from pure white, through blues, greens, browns and brick-red, to a near black colour. This range of colour is produced by two main pigments, porphyrins (red-brown) and biliverdin (blue-green), which are deposited as crystals throughout the calcified part of the testa though more densely near the surface. Commonly superimposed on the ground colour are markings such as scribbling, streaking or spotting, these markings being caused by the presence of the pigments on the surface of the cuticle. In some plovers and falcons the pigment is so superficial that it can be easily rubbed off. The egg of the Cuckoo is remarkable in mimicking the egg-colour of the host species. Despite much speculation, the functional significance of the different colours and markings of birds' eggs does not appear to be known.

Surface texture. The outer surface of the shell in most species is smooth with a slight sheen. However, in some birds the shell may be highly glossy (woodpeckers), greasy (ducks and geese), chalky (cormorants), powdery (flamingos), ridged (the Emu) and pitted (the Ostrich). The significance of these variations is not known.
THE REPRODUCTIVE ORGANS ON THE RIGHT SIDE OF THE GENETIC FEMALE

The right gonad of the genetic female

In the genetic female in birds generally, the growth of the right gonad is normally arrested at a testis-like stage of development, when the primary sex cords have been formed giving rise to a medulla with testicular potential, and only a few secondary sex cords have arisen (which would tend to form a cortex and give rise to oogonia). Although very small, the right gonad subsequently persists in the adult as wrinkled strands of tissue along the ventral side of the caudal vena cava (about 5 mm long in the domestic fowl). If the left ovary is destroyed surgically or by natural disease, the right gonad enlarges to a length of about 2 cm. In the domestic fowl about 90 per cent of such enlarged right gonads are testis-like, but areas of active spermatogenesis are scarce and occur only in birds in which the left gonad was removed within a month of hatching (the primordial germ cells disappear from the primary sex cords about three weeks after hatching). Of the remaining enlarged right gonads, some not only develop their primary sex cords but also form scattered, or more rarely, quite extensive areas of secondary sex cords. These gonads are therefore bipotential and develop into an ovotestis and even occasionally into a more or less active ovary.

In only one species, the Brown Kiwi, is it established that paired functional ovaries normally occur. While both ovaries in falconiforms are often reported to be fully formed it seems to be relatively rare for the right ovary in these birds to be functional. As stated at the beginning of this chapter, paired ovaries have been reported in at least 16 orders. Despite the obvious suggestion that the characteristic reduction of the right ovary and oviduct is an adaptation to flight because it saves weight, no really convincing adaptational advantage from this avian modification has been established.

The right mesonephros and right mesonephric duct

These persist in normal adult genetic females. After removal of the left ovary they enlarge and become associated with the right gonad to form an epididymis and ductus deferens. Thus the right side of the adult genetic female can produce a fully functional male system.

Two natural cases are known of a hen which laid eggs and then turned into a cock and sired two chicks, but this has never been accomplished after surgical removal of the left ovary in spite of many attempts. Natural events of this kind have long been a source of superstition and awe, and at least one such unfortunate 'cock' was tried and duly burnt at the stake as a creature possessed of Satan. 'A whistling maid and a crowing hen are fit for neither God nor men.'

The right oviduct

After a normal start, the development of the right oviduct of the genetic female is totally arrested very early in embryonic life. However, in the domestic fowl, a small remnant of the right oviduct can nearly always be found joining the cloaca. Large cystic vestiges (up to 10 cm in diameter), containing fluid derived from the blood plasma, are not uncommon. Very large cysts (up to 20 cm in diameter) cause difficulty in breathing and circulation. Histologically the tissue forming the wall of these cysts is equivalent to that of the magnum or infundibulum, but not the uterus or vagina. Rarely, a fully developed oviduct occurs on both the left and right sides of the domestic fowl, complete with the left ovary or even with functional ovaries on both sides. In such birds, the longitudinal suspension of the rectum from the roof of the abdominal cavity makes it very difficult for ovulated oocytes to cross from the right ovary to the left oviduct (or vice versa), but isolated reports have demonstrated that this really can happen.

Vestiges of the right oviduct have been reported, although somewhat infrequently, in more than 30 other species from many different orders. A fully developed right oviduct is rarely found, except in the domestic fowl. In hawks in which both gonads become fully functional, the right oviduct still remains vestigial. This applies also to the Brown Kiwi, even though both ovaries are regularly present and fully functional in this species.
Further reading


