

THE GENITAL DUCTS OF *THEODOXUS*,
LAMELLARIA AND *TRIVIA*, AND A
DISCUSSION ON THEIR EVOLUTION
IN THE PROSOBRANCHS

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INTRODUCTION

The prosobranchiate gastropods are divided into three orders, the Archaeogastropoda, the Mesogastropoda and the Stenoglossa. In the first of these groups the gonad is connected with the right kidney by a duct which is developed from the ovary, and the sex cells escape to the posterior end of the mantle cavity through the right ureter. The eggs are usually shed singly into the sea where fertilization occurs. In the Mesogastropoda and Stenoglossa the right kidney is not developed and the ovarian duct leads to a short and

narrow section of the genital duct which is typically ciliated, and may communicate with the pericardium by a gonopericardial duct and passes anteriorly to a long glandular tract running forwards to the mouth of the mantle cavity. This glandular section is incipient in the archaeogastropod *Calliostoma zizyphinum*. It is probably formed, as Thiele (1935) suggests, by an ectodermal intucking and will be referred to as the *pallial oviduct*, for it lies anterior to the opening of the original right kidney, and must be derived from the ectoderm of the mantle (Bourne, 1908; Giese, 1915). The short duct which links it with the ovarian duct will be termed the *renal oviduct*: in *Paludina* (= *Viviparus*), in which its development has been investigated (Drummond, 1903), it is formed from the vestige of the right kidney, and even in the highly specialized *Stenoglossa* it retains the connexion with the pericardium which is characteristic of the right and left kidneys of the archaeogastropods. Similarly, in the male system of the Mesogastropoda and *Stenoglossa* there can be distinguished a testis duct, which is connected to the posterior end of the mantle cavity by a *renal vas deferens*, and this in turn is followed by a *pallial vas deferens*.

The Neritacea, although grouped among the archaeogastropods, resemble the mesogastropods in the loss of the right kidney and in the development of a pallial oviduct and vas deferens. They also approach this group in that they produce egg capsules within which the young are nourished until they escape as a crawling form resembling the parent.

THEODOXUS FLUVIATILIS (L.)

The male

From the testis, which spreads over the surface of the digestive gland, the testis duct takes a sinuous course along the right side of the visceral mass to the posterior end of the mantle cavity. Except for its initial part this duct contains sperm and acts as a vesicula seminalis, which is much dilated in the coils overlying the posterior end of the prostate. The testis duct is continued into a much narrower ciliated conducting tube—homologous with the renal vas deferens of mesogastropods—which leads forwards beneath the posterior end of the prostate and up its left side to open into the lumen of the gland. The renal vas deferens is heavily loaded with black pigment granules contained in the ciliated cells, and is surrounded by a coat of circular muscles which constrict the lumen except at times when sperm are passed through it. The wall of the distended vesicula seminalis is grey, since its epithelium also contains black pigment granules, though the cells are not ciliated.

The lumen of the prostate is, except at the two ends, U-shaped in transverse section because of a downgrowth from the dorsal wall. Its walls are ciliated throughout, and between the ciliated cells lie gland cells and the ducts of subepithelial glands. There are two principal masses of these subepithelial secreting cells, the more posterior—the 'glande annexe' of Lenssen (1899)—

appearing as a pinkish mass in dissection and consisting of blind tubules. Some of these underlie the vesicula seminalis and open into the posterior wall of the prostate, whilst others spread forwards dorsally between the two limbs of the gutter-shaped lumen and around the left wall to open at the summit of the left limb. The vas deferens penetrates this mass, and its opening into the left wall, also near the summit of the left limb, is surrounded by the openings of these tubules. Where the opening occurs the cavity is slightly enlarged, and this region is referred to by Bourne (1908) as the thalamus—it comprises a larger chamber in other Neritidae. The glands which open into it Bourne terms the prostate, though it seems better to include all the glands opening into the lower or pallial part of the male duct under this name. The histology of the posterior mass is uniform throughout, the tubules being lined by large secreting cells, alternating with wedge-shaped ciliated cells. In the secreting cells the nuclei are round, basal and with a nucleolus, and in the vacuoles of the protoplasm are large spherules which in the fully elaborated state stain rather deeply with iron haematoxylin.

The second large subepithelial glandular mass comprising the prostate fills the gap between the limbs of the gutter anteriorly, projecting downwards as a ridge to invaginate the dorsal wall, though the ridge is free behind and not attached to the concave posterior wall of the duct. About half-way along the length of the prostate this gland ends against the left wall. The cells of which it is composed are filled with small spherules of secretion, protein in nature, and form an opaque white mass in the living tissue. The nuclei are basal, round and nucleolated.

A longitudinal strip of mucous cells, for the most part alternating with ciliated cells, runs parallel with the central glandular area and lines the dorsal edge of the gutter-shaped duct on each side. The wall along the dorsal edge is thrown into slight longitudinal folds, and it is between the folds on the left side that the vas deferens and tubules of the posterior gland open. Ventral to each mucous strip on the outer side is a second longitudinal tract of glands similar histologically to those of the central ridge; posteriorly the two tracts meet one another along the ventral wall. Some of the glands are subepithelial, others lie between the ciliated cells. Otherwise the ventral wall is composed of a simple columnar ciliated epithelium with mucous cells.

Anteriorly the genital duct is gradually reduced in size and rotates through an angle of 90° , so that the ventral concave wall lies to the right, the left edge of the gutter becomes ventral and the right dorsal. The tracts of gland cells filled with protein spherules dwindle and are replaced by mucous cells. Towards the genital aperture, which lies in front of the anus and within the mantle cavity, the lumen of the duct is no longer crescentic in transverse section, but approximately rounded, and the wall has longitudinal folds.

Median to the base of the right tentacle and beneath the anterior edge of the mantle arises the penis which is dorso-ventrally flattened, stout proximally and tapering distally; a deep seminal groove lined by cuticularized epithelium

runs up the outer edge to the tip. The genital aperture is close to the origin of the groove, and in the intervening space there is a pronounced gutter in the overlying mantle. This is lined by mucous cells alternating with ciliated cells which produce a strong forward current and presumably direct the seminal fluid on to the penial groove.

The female

The anus (Fig. 1A, *a*) and oviduct (*oa*) open at the tip of a papilla near the mouth of the mantle cavity on the right side; ventrally and subterminally is the opening of the vagina (*va*). The vagina (*v*) is entirely separate from the oviduct and runs parallel with it and with the rectum (*rm*) along the right side of the mantle cavity. Posteriorly it leads into the bursa copulatrix (*b*), whilst from its right wall arises a receptaculum seminis (*re*) which passes back ventral to the bursa to the limit of the mantle cavity. Not far from its origin the receptaculum gives off a duct (*dr*) which is at first narrow and coiled and then, before opening into the posterior end of the glandular oviduct, broadens into a small vestibule (*ve*). Except for the complete separation of the vagina from the oviduct the female system agrees in its general outlay with that of the mesogastropods—a proximal ovarian duct, with an epithelium resembling that of the ovary, is followed by a narrow thin-walled section—presumably a renal oviduct—which, in turn, leads into a wide glandular pallial oviduct, and into the inner end of this opens a receptaculum seminis. Moreover, as in the mesogastropods, the glandular section, which occupies the length of the mantle cavity, comprises an albumen gland followed by a bilobed capsule gland.

The ovarian duct runs forward from the ovary and passes for a short distance beneath the capsule gland where it joins the narrow, thin-walled, ciliated duct, which leads back to open into the albumen gland. The albumen gland is divided into dorsal (Fig. 1A and B, *d*) and ventral (*av*) lobes, the ventral one forming a small pouch partly embedded in the posterior tip of the right lobe of the capsule gland (*r*). Near the anterior end of this pouch the thin-walled oviduct opens ventrally (Fig. 1B, *o*), and not far from this opening in a dorso-lateral position is a narrow communication with the much larger dorsal lobe of the albumen gland (*vd*). This lobe lies immediately above the ventral one, extending considerably farther forwards, and opens along its length into the capsule gland. At its posterior end the dorsal lobe is C-shaped in transverse section—the ventral wall overlying the right lobe of the capsule gland, and the concavity resting against the dorso-lateral wall of the ventral pouch of the albumen gland. The dorsal wall is at first separated from the left lobe of the capsule gland by a thin sheet of tissue, a forward extension of the posterior wall of the pallial oviduct (Fig. 1A and B, *p*); anteriorly, however, it spreads across to fuse with this lobe, and appears in dissection as the most prominent part of the gland—a yellowish and rather transparent mass which opens ventrally into the capsule gland. Near the anterior end of the albumen

gland the dorsal edges of the two lobes of the capsule gland, which have so far been separated from one another, approach and fuse, causing the lumen of the oviduct to be abruptly constricted at this point (Fig. 1 C).

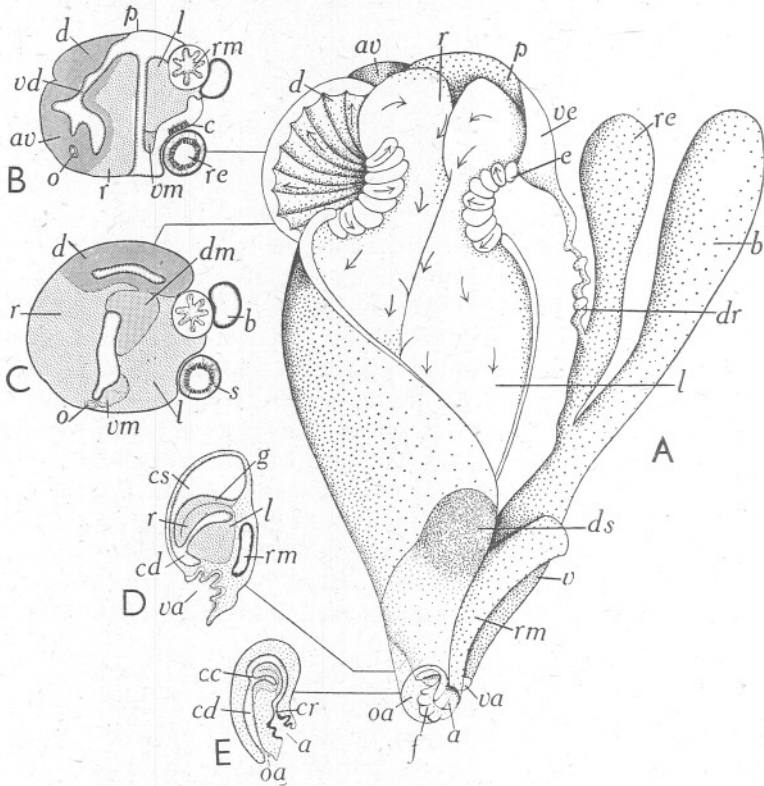


Fig. 1. *Theodoxus fluviatilis*. A, pallial oviduct seen from the dorsal surface, posterior end above. The bursa copulatrix and receptaculum seminis have been dissected away from the glandular oviduct, the dorsal lobe of the albumen gland opened by an incision along its right wall and the two lobes of the capsule gland separated mid-dorsally. Arrows indicate ciliary currents. $\times 43$. B, C, D, E, transverse sections taken at the levels indicated. The bursa copulatrix and spermatheca are in their natural positions. $\times 30$. a, anus; av, ventral lobe of albumen gland; b, bursa copulatrix; c, strip of tall columnar ciliated cells; cc, opening of crystal sac into capsule duct; cd, capsule duct; cr, opening of crystal sac into rectum; cs, crystal sac; d, dorsal lobe of albumen gland; dm, dorsal longitudinal strip of mucoid cells; dr, duct of receptaculum seminis; ds, diatoms and sand grains in posterior end of crystal sac; e, strip of glandular and ciliated epithelium spreading ventrally from albumen gland; f, flap of tissue acting as valve; g, glandular ventral wall of crystal sac; l, left lobe of capsule gland becoming ventral anteriorly; o, renal oviduct; oa, opening of pallial oviduct; p, posterior wall of pallial oviduct; r, right lobe of capsule gland becoming dorsal anteriorly; re, receptaculum seminis; rm, rectum; s, orientated sperm; v, vagina; va, vaginal aperture; vd, opening of ventral into dorsal lobe of albumen gland; ve, vestibule; vm, ventral longitudinal strip of mucoid cells.

The ventral pouch of the albumen gland is strongly ciliated. The epithelial cells are separated by ducts of subepithelial glands. These are unicellular,

grouped in clusters lying at various depths, and bound together by a tenuous layer of connective tissue; from each cluster the ducts run parallel with one another to open into the lumen. Except for the dorsal wall the secreting cells of the pouch are of one type, their secretion spherules are small, stain lightly with iron haematoxylin and blue with azan, though they are unaffected by mucicarmine. Along the dorsal wall and surrounding the opening into the dorsal pouch is a strip of mucous cells, some lying within the epithelium. Around the periphery of this strip are a few cells in which the secretion appears bright yellow after the azan stain.

The epithelium of the dorsal pouch is also ciliated, though the cilia are short. Histologically this part of the gland is divisible into three regions. The largest comprises the dorsal wall in which each group of subepithelial glands contains mucoïd cells alternating with cells filled with minute secretion droplets of a protein nature which stain deeply with iron haematoxylin. Along the right wall is a longitudinal band of mucous cells which is in contact posteriorly with the mucous strip of the ventral pouch through which the two parts of the gland communicate. The third histologically differentiated region consists of subepithelial and epithelial mucoïd cells which, together with strongly ciliated cells, form the wall overlying the left lobe of the capsule gland. The ciliated and glandular epithelium spreads ventrally down this lobe (Fig. 1A, *e*), and together with a similar area on the opposite lobe is responsible for directing the contents of the albumen gland into the capsule gland.

The posterior wall of the pallial oviduct (*p*), thin and somewhat muscular, encloses a small pouch, the 'poche de confluence' of Lensen (1899). Into this on the left side opens the duct from the receptaculum (*dr*), on the right the posterior end of the dorsal lobe of the albumen gland, whilst anteriorly it communicates with the capsule gland. Eggs passed from the ovarian duct and embedded in albumen from the albumen gland are directed into the posterior end of the pallial oviduct, and here they are fertilized. On the ventral wall of the vestibule (*ve*) which terminates the duct from the receptaculum is a strip of tall columnar ciliated cells (Fig. 1B, *c*) which is continued along the ventral wall of the 'poche de confluence' and up the median side of the right lobe of the capsule gland towards the albumen gland. To the opening of this gland the cilia direct the sperm. The tip of the left lobe of the capsule gland (*l*) overlies the opening of the vestibule into the oviduct, and its posterior and ventral edges are free to act as a valve which can regulate the flow of seminal fluid.

From its point of constriction at the anterior end of the albumen gland the lumen of the capsule gland gradually deepens as it passes forwards, and becomes crescentic in transverse section, with the concave inner surface of the right lobe (*r*) enveloping the convex inner surface of the left (*l*). The two lobes are separated dorsally and ventrally by a narrow strip of wall almost without glands. Anteriorly the lobes taper so that the lumen narrows again and the whole gland rotates through 45°, the original right lobe becoming dorsal, the

left ventral, and the intervening strips lateral. They both extend to the genital aperture near which the dorsal one is very thin (Fig. 1 D, *r*).

The capsule gland is lined by a columnar ciliated epithelium resting upon a basement membrane, beneath which in localized areas muscle fibres are developed. Over the thick lobes of the gland the membrane is pierced by ducts of the underlying secreting cells which are grouped as in the albumen gland. The typical secreting cells which comprise the two lobes, except at their anterior ends, produce a white or yellowish viscid fluid which in contact with water hardens to a horny substance. Within the gland cells the secretion is in the form of spherules which give the gland an opaque white appearance in living tissue; they stain a vermilion red with azan and deeply with iron haematoxylin, displaying the same staining reactions as similar spherules in the capsule gland of the *Stenoglossa* (Fretter, 1941). Only the left lobe of the gland has mucoid cells, and these constitute, first, a ventral longitudinal strip of epithelial and subepithelial glands (Fig. 1 B and C, *vm*) which extends from the posterior tip of the left lobe to half-way along its length, and, secondly, a much shorter though deeper area situated dorsally (Fig. 1 C, *dm*) immediately in front of the albumen gland. The cilia on the walls of the gland beat towards the genital aperture and mix the two types of secretion from the left lobe of the capsule gland; the effect of this mixing can be traced in the structure of the egg capsule. Anteriorly, as the lobes of the gland narrow, the typical secreting cell is replaced by another type of gland; the replacing cells in the ventral lobe are filled with large droplets, irregular in outline, which stain more deeply with iron haematoxylin and are purple-red after azan; the replacing cells in the dorsal lobe are similar to this, but their spherules are minute. The secretion from this anterior region of the capsule gland is more fluid than that produced posteriorly though of a similar nature.

The muscles of the gland are responsible for moulding the egg capsule. They are developed not only beneath the ciliated lining, but also in the connective tissue which separates the groups of underlying glands. Two especially pronounced bands of circular muscles underlie the epithelium, one around the narrow lumen anterior to the albumen gland enabling this space to be still further reduced, the other towards the tapering end of the gland near the point at which the histology of the lobes is changed. The intervening portion of the gland is about as long as it is deep, and it is probably here that the capsule is, for the most part, constructed. Beneath the narrow strips of epithelium which separate the two lobes of the capsule gland are circular muscles, and radial fibres from these narrow walls penetrate the connective tissue between the nearby groups of glands; a few also occur elsewhere in the thickness of the lobes.

The most unusual feature in the reproductive system of female *Neritidae* is the crystal sac, the function of which has been described by Andrews (1935). It lies at the anterior end of the oviduct, the blind posterior part resting against the left side of the dorsal lobe of the capsule gland just above the

rectum (Fig. 1A, *ds*). Anteriorly the sac spreads over the convex surface of this lobe and so envelops its outer wall. At the anus the crystal sac opens into the dorsal wall of the rectum (Fig. 1E, *cr*) from which it collects faecal scraps. In *Theodoxus* these consist of diatom cases, small sand grains and sponge spicules; in *Nerita* Andrews (1935) states that the sac collects spherules which have come from the liver. The contents of the sac are used to reinforce the wall of the egg capsule and for this purpose are passed into the oviduct.

Towards the female aperture, and level with the opening of the vagina, the thin right wall of the capsule gland gradually expands outwards and ventrally to form the short terminal region of the oviduct, which may be termed the capsule duct (Fig. 1D and E, *cd*). The crystal sac spreads over the dorsal lobe to its right side and opens along the length of the dorsal wall of the capsule duct (Fig. 1E, *cc*); anteriorly the sac is open to the exterior. In *Theodoxus* the crystal sac always has a supply of diatoms and sand grains stored in its posterior end, where the wall is muscular and not ciliated (Fig. 1A, *ds*). The anterior part does not appear to be used for storage, but to conduct particles from the rectum to the blind end of the sac and thence to the oviduct; for this purpose the epithelium is ciliated. The anterior part of the ventral wall which overlies the dorsal lobe of the capsule gland is also glandular (Fig. 1D, *g*). The gland cells, which resemble those of the underlying lobe of the capsule gland, secrete a sticky fluid in which the particles are entrapped as they leave the crystal sac and are conducted to the capsule duct (*cd*). The capsule duct is very muscular and is lubricated by mucous cells scattered between the ciliated columnar cells which direct the capsule towards the genital opening. This opening is separated from the anus by a projecting flap of tissue (Fig. 1A, *f*), a downgrowth from the anterior tip of the ventral lobe of the capsule gland, which can be folded over the anus and the adjacent opening of the rectum into the crystal sac, acting as a valve which directs contents of the rectum into the sac.

Only a few structural and histological details need be mentioned in connexion with the copulatory ducts of the female system. The epithelium of the bursa copulatrix (*b*) and the vagina (*v*) is ciliated and glandular. The gland cells, which are club-shaped with rounded distal ends and spherical basal nuclei, have large irregularly shaped secretion spherules, colourless in the living state, staining blue with azan and lightly with iron haematoxylin. Beneath the epithelium is a considerable layer of circular muscles, which, in the vagina, penetrate the characteristic longitudinal folds of the wall. After copulation the bursa contains large numbers of unorientated sperm, which are transferred later to the receptaculum seminis, though there is usually a surplus retained in the bursa. No gland cells occur in the receptaculum (Fig. 1A and B, *re*); to its walls are attached orientated sperm with their tails embedded in the epithelium (Fig. 1C, *s*). The passages from the receptaculum into the vagina, and into the receptacular duct (Fig. 1A, *dr*), are each surrounded by a sphincter and strongly ciliated. The sperm are passed along the

duct by peristalsis as well as by the action of cilia. Towards the distal end of the duct originates the ventral strip of tall columnar cells (Fig. 1B, *c*) which passes through the vestibule (Fig. 1A, *ve*) to the 'poche de confluence'. Except for its ventral wall the vestibule has a covering of squamous epithelium.

The egg capsule

An account of the egg capsules of the Neritidae is given by Andrews (1935) who studied their structure in eight species including *Theodoxus fluviatilis*. He found that all conformed to the generalized plan (Fig. 2A) in which the shape is that of a flattened spheroid made up of two approximately equal halves sutured together (*s*) around the equator; one half, the base, is fixed to the substrate and rises up to form part of the side wall of the capsule, the other, the lid (*l*), is strengthened by particles from the crystal sac (Fig. 2B, *p*) and is lifted off when the young escape—the base of the used capsule remains attached to the substrate for some time (Fig. 2A, *b*). The walls are of tough conchiolin, white to straw colour, lined internally by a homogeneous membrane enclosing an albuminous fluid in which the eggs float. Andrews states that the capsule is produced by the lower part of the oviduct, but he did not study the structure of this and consequently can give no suggestions as to the local manufacture of the various parts of the egg case.

Sections of the egg capsule of *Theodoxus* suggest that the thick outer wall is formed by secretion from the bilobed capsule gland, since both have the same composition and staining properties. The lid of the capsule is homogeneous in texture, and so differs from the base, in the substance of which there are vesicles filled with mucus (Fig. 2B, *vm*). It may be assumed that since the capsule is made up of two approximately equal parts, and since the capsule gland is bilobed, we have, as in the *Stenoglossa* (Fretter, 1941), one lobe of the gland responsible for forming one-half of the capsule. In *Theodoxus* these lobes differ histologically: in the left there are patches of mucous cells, the secretion from which is mixed with the conchiolin secretion. It follows that probably this left lobe secretes the base of the capsule, whilst the right produces the uniform secretion for the lid.

The periphery of the egg capsule is approximately circular in outline, and here the lid and the base are fused together. The diameter is roughly equal

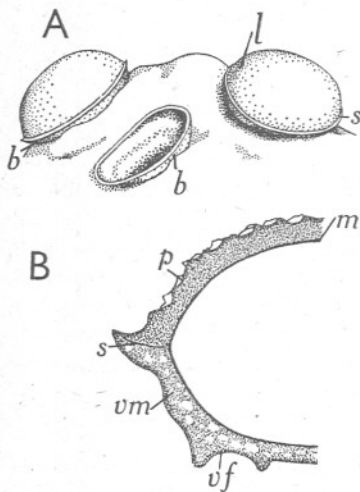


Fig. 2. *Theodoxus fluviatilis*. A, egg capsules on a stone. The young animal has escaped from one capsule and the base remains. $\times 25$. B, part of a V.S. through a capsule. $\times 96$. *b*, base; *l*, lid; *m*, membrane; *p*, particles from crystal sac; *s*, suture; *vf*, viscous outer layer; *vm*, vesicles filled with mucus.

to the length of the oviduct between its constriction at the anterior end of the albumen gland (Fig. 1C), and the tapering anterior end at the locus of the band of circular muscles which underlies the ciliated epithelium; the depth of the oviduct between these two points is equivalent to its length. It seems probable that the wall of the capsule is secreted within these limits, whilst the fertilized eggs embedded in albumen are detained here. If this be so then the suturing of the two sections, produced by the right and left lobes, is brought about by the anterior and posterior limiting bands of subepithelial circular muscles, and by the muscles underlying the narrow dorsal and ventral walls.

Microscopic examination of the capsule wall shows that on the outer surface is a very thin layer of secretion which has a slightly different staining property from the rest of the wall (Fig. 2B, *vf*), and is similar to the viscid fluid produced by the anterior tips of the capsule gland. This would be coated around the capsule as it passes anteriorly, and here, with the rotation of the oviduct, the future lid of the capsule would be dorsal and the base ventral. Towards the genital aperture the capsule projects laterally into the terminal capsule duct, and on to its upper wall are poured the contents of the crystal sac which are then pressed to the sticky outer covering (*p*). This similar covering over the ventral wall serves for attachment to the substrate. The method by which fixation is accomplished has not been observed. In female animals a semicircular muscular flap of tissue projects from the body wall immediately beneath the genital opening, and this may act as an ovipositor. No such structure has previously been described in any of the Neritidae. When the capsule is laid it contains over seventy eggs, but of these only one attains full development and comes to occupy the entire space within the capsule walls, hatching as a miniature of the adult.

LAMELLARIA PERSPICUA (L.)

The male

The male genital duct of *Lamellaria perspicua* closely resembles that of the stenoglossan *Nassarius reticulatus*. A short distance from the gonad the testis duct is thrown into deep coils and acts as a vesicula seminalis, which is distended with sperm throughout the year. The wall is composed of a columnar ciliated epithelium, and beneath the basement membrane circular muscles are developed. The vesicula seminalis leads forwards immediately beneath the body wall on the right side of the viscera, and on approaching the mantle cavity is delimited by a sphincter which surrounds the very short renal vas deferens. Anteriorly the histology of the genital duct changes abruptly, and throughout the rest of its course the epithelium is ciliated and glandular; the glandular part subserves the function of a prostate. The gland cells, alternating with wedge-shaped ciliated cells, contain colourless spherules which dissolve readily on fixation. Their nuclei are round and basal, whilst those of the ciliated cells are elongated and lie in the mid-region of the cytoplasm. The

cilia arise from basal granules and to these are connected intracellular fibrillae. The tubular prostate traverses the mantle cavity on the right side and reaches the base of the penis. Posteriorly, near its origin, it gives off a short duct which opens into the right posterior corner of the mantle cavity; a corresponding structure has been figured for *Buccinum* (Fretter, 1941). In this duct the cilia are longer than elsewhere; the opening into the mantle cavity is surrounded by a sphincter. As in *Nassarius reticulatus* and *Buccinum undatum* it is probable that the duct functions as a safety valve which allows the escape of sperm and secretion into the mantle cavity. At the base of the penis which lies behind the right tentacle the genital duct enters the haemocoel and, turning abruptly back on its course, it passes towards the posterior end of the mantle cavity, and then leads forwards again by a circuitous route and runs through the penis. These coils lie on the right side of the oesophagus, just beneath the body wall; they are surrounded by a layer of circular muscles which may attain considerable thickness.

The penis is relatively enormous and is equivalent in length to the pallial oviduct, through which it is inserted during copulation. It is laterally compressed like the lumen of the oviduct, and from the ventral surface, at about a quarter of its length from the extreme tip, there arises a flagellum which is traversed by the genital duct. The flagellum extends well beyond the tip of the penis, the ventral edge of which is deeply grooved anterior to its origin. The free edges of this groove, lubricated by the secretion of epithelial gland cells, may embrace the base of the flagellum and steady its position when, during copulation, seminal fluid is being passed from its filamentous tip into the fine ducts of the spermatheca of the female. As the genital duct passes through the penis its lumen decreases in size until in the flagellum it has the dimensions of a fine capillary tube through which the sperm are conveyed by peristalsis assisted by cilia. Near the genital opening the epithelial gland cells of the duct are gradually replaced by ciliated cells.

Lebour (1937) states that the echinospira larvae of *Lamellaria perspicua* are found in the plankton in all stages of development throughout the year, which suggests that breeding may occur in any month. This is supported by the fact that there is no marked seasonal reduction in the glands of the genital ducts. The maximal breeding occurs in spring and summer.

The female

From the ovary, which spreads over the visceral mass, the ovarian duct, with an epithelium resembling that of the gonad, leads forwards on the right side of the viscera to the posterior end of the mantle cavity. Here the epithelium changes and becomes columnar and ciliated and the duct turns abruptly dorsalwards to open into the glandular oviduct. The ciliated section is the renal oviduct (Fig. 3, *ro*); its walls are folded longitudinally and are surrounded by a coat of circular and longitudinal muscles.

The pallial oviduct, in which the egg capsule is formed, extends along the right side of the mantle cavity and comprises an albumen gland (*ag*) which receives the renal oviduct, a capsule gland (*pc*, *dc*, *vc*, *ac*), and a capsule duct (*cd*) which opens anteriorly on a papilla (*ga*). The albumen gland lies ventral to the posterior lobe of the capsule gland, and along its posterior wall open the ducts of six diverticula which constitute the receptaculum seminis (*s*, *dr*), their openings closely approximated. Each duct, lined by columnar ciliated epithelium and surrounded by a sphincter, leads to a small sac (*s*) which is not ciliated and contains throughout the year unorientated sperm. During copulation the sperm are deposited directly into the receptaculum by the

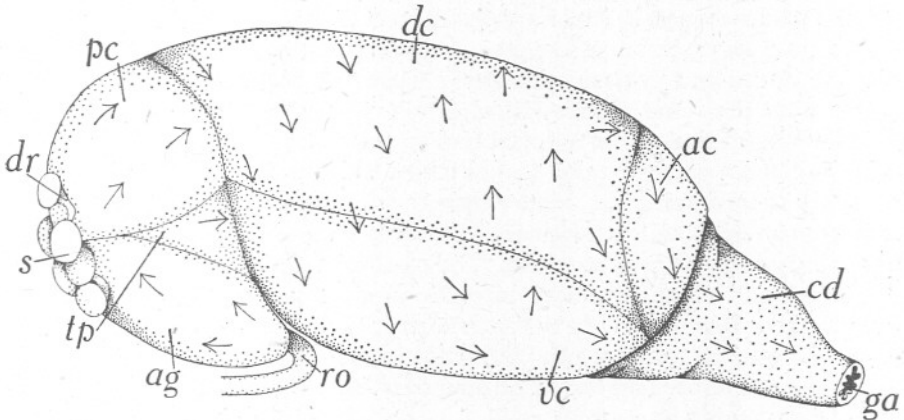


Fig. 3. *Lamellaria perspicua*. Oviduct seen from the right side. Arrows indicate ciliary currents on the inner side of the wall of the right lobe of the pallial section; those on the left are similar. $\times 13$. *ac*, mucoid cells forming anterior tip of capsule gland; *ag*, albumen gland; *cd*, capsule duct; *dc*, subepithelial mucoid cells; *dr*, duct of diverticulum of receptaculum seminis; *ga*, genital aperture; *pc*, posterior lobe of capsule gland; *ro*, renal oviduct; *s*, end sac of diverticulum of receptaculum seminis; *tp*, triangular patch of gland cells; *vc*, ventral region of capsule gland with uniform secreting cells.

flagellum of the penis: the penis flattened from side to side, passes through the lumen of the capsule gland, which is also laterally compressed, and because of the ventral insertion of the flagellum this comes into contact with and may penetrate the ducts of the diverticula to discharge the seminal fluid.

The albumen gland and the capsule gland are lined by columnar ciliated cells, and their walls, especially laterally, are thickened by subepithelial gland cells. These are arranged in tightly packed bundles lying at various depths, and the long ducts run parallel with one another to open between the ciliated cells. A fairly precise indication of the main groups of gland cells can be made out from a study of living material, and is indicated in Fig. 3. In a transverse section of the albumen gland nearest the renal oviduct two types of secreting cells may be recognized though the boundaries between the areas which they occupy are not visible externally. One type constitutes the dorsal

half of the gland, which underlies the ventral wall of the capsule gland, and the other the ventral half. In the former the secretion spherules stain lightly with iron haematoxylin; in the latter they are smaller and stain more deeply. This second type spreads up the posterior wall of the pallial oviduct to beyond the point of entry of the receptaculum and comes into contact with the posterior lobe of the capsule gland (*pc*). In living material this lobe is distinguished by its pink colour. Its cells are filled with small droplets which are purple after methylene blue intra-vital staining, are slightly affected by mucicarmine and stain lightly with iron haematoxylin. Ventral to this pigmented lobe, and wedged between it and the albumen and capsule glands, is a small triangular patch of gland cells (*tp*), which is distinguished by its opaque whiteness and in which spherules stain deeply with iron haematoxylin.

In a transverse section of the capsule gland the lumen appears as a vertical slit, the dorsal and ventral walls being narrow and comparatively thin, the lateral ones deep and thick. Histologically the main part of the gland is divided longitudinally into a dorsal region composed of subepithelial mucoid cells (*dc*), and a ventral region (*vc*) in which the secreting cells are filled with regularly shaped spherules, longer than they are broad, staining deeply with iron haematoxylin and red with azan, the cells resembling histologically those of the capsule gland of *Stenoglossa*. The two types of secretion are passed into the lumen and mixed by ciliary currents, producing a viscid fluid which can be drawn out into fibrils. At the anterior tips of the right and left lobes of the gland the mucoid cells are of a different character and respond more readily to the mucicarmine stain (*ac*). The boundary between capsule gland and duct (*cd*) is surrounded by mucous cells.

In the thickness of the wall of the albumen and capsule glands there are muscle fibres developed in the connective tissue binding together the groups of gland cells; they are especially numerous dorsally and ventrally. Circular muscles are also present in the layer of connective tissue which surrounds this part of the oviduct. By means of these muscles the lumen may be enlarged and become tubular.

The capsule duct is lined by columnar ciliated cells and surrounded by a very thick layer of circular muscles; no gland cells are present.

The egg capsule

The egg capsules of *Lamellaria perspicua* which are sunk in the tissues of compound ascidians (*Leptoclinum*, *Polyclinum*, etc.) are common between tidemarks around our coasts. The capsule is described and figured by Ankel (1935). Each is pot-shaped, with a rounded base, and measures approximately 2 mm. high and 3 mm. across the broadest diameter, and tapers slightly towards the circular opening which is filled with a plug made of concentric layers of a rather transparent material. Only the plug, surrounded by a low rim of capsule wall, is exposed at the surface of the ascidian, and it is frequently so transparent that through it may be seen the contents of the capsule

—many unshelled eggs, yellow in colour, floating in an albuminous fluid. The wall of the capsule is divided into approximately equal halves by a suture which runs down its length and is continuous through the substance of the plug bisecting its concentric layers. Externally the wall has a fibrillar appearance, the fibrillae running in a circular direction. There is also a thin inner layer to the wall which completely surrounds the albumen, and so is continuous beneath the substance of the plug. The dimensions of the capsule correspond to those of the lumen of the capsule gland. In its general lay-out the egg capsule thus resembles those of *Nucella* (Ankel, 1937; Fretter, 1941). Since there is a fairly close resemblance between the female genital ducts of these two molluscs it is probable that the method of formation of the egg capsules is similar. I have never observed a capsule in the process of manufacture in *Lamellaria*, but the following conjecture seems most probable. The eggs are passed down the ovarian duct in considerable numbers—according to Ankel 1000–3000 are contained in one capsule—and in the albumen gland they are embedded in a nutritive fluid. On to the eggs are poured sperm from the receptaculum seminis and fertilization occurs. The eggs embedded in albumen are then directed into the capsule gland and retained there whilst the capsule wall is secreted. The thin inner layer of this wall, which is continuous round the egg mass, may be derived from secretion poured into the lumen of the gland prior to the entry of the egg mass and invaginated by this mass as it passes into the capsule gland. Around this layer is then deposited the outer coat, the thicker part of the capsule wall. One half of this is produced by each lobe of the gland and the dividing suture lines correspond to the thin dorsal and ventral walls of the gland. The transverse fibrillar appearance of this outer layer is undoubtedly due to the blending of the protein secretion from the ventral half of the capsule gland with the mucoid secretion of the dorsal half, the mixing being effected by the action of the predominantly transverse ciliary currents of the epithelium. In *Nucella* the plug is produced by the posterior lobes of the capsule gland, and this probably occurs in *Lamellaria* too, since the plug is of a different consistency from the rest of the wall. The substance for the plug would be driven into the open end of the capsule by cilia and muscular action. At the opposite end of the capsule gland whilst the case is being formed the lumen is closed off from that of the duct by the sphincter which surrounds this part.

Lamellaria, unlike the *Stenoglossa*, possesses no ventral pedal gland for the final moulding and deposition of the egg case. With the aid of the radula the mollusc bites small round holes in the compound ascidian and places therein a capsule, but the exact method by which this is accomplished is unknown: it may be a function of the foot aided by the anterior pedal mucous gland. The capsule is embedded vertically in the test of the ascidian so that only the plug projects slightly from the surface, and around this the test thickens to form a protecting rim.

TRIVIA MONACHA (DA COSTA) AND *T. ARCTICA* (MONTAGU)*The male*

Fig. 4 displays the essential features of the male genital ducts of *Trivia monacha*. The testis duct leads from the gonad, which is situated on the columellar side of the visceral mass, towards the right posterior corner of the mantle cavity. Except in its initial part it forms a deeply coiled vesicula seminalis (*vs*) of which the epithelium is ciliated. The cilia are often difficult to detect in sections. Beneath their basal granules the cytoplasm contains spherules which stain blue with azan and deeply with iron haematoxylin. Frequently a number of amoebocytes are seen between the epithelial cells and among the sperm, but it is uncertain as to whether they absorb effete sex cells as in the oviduct of the female. The vesicula seminalis passes into the renal vas deferens (*rd*), a short, narrow and more muscular duct which communicates with the prostate by a papilla. Sperm are only contained in the renal vas deferens during copulation, and then they are passed rapidly through the duct by peristalsis aided by the action of the thick coat of cilia which covers its walls. The prostate (*pr*) is a roomy pouch extending along the right side as far as the opening of the mantle cavity; in transverse section its lumen appears as a deep dorso-ventral slit. The epithelium is glandular and ciliated cells are wedged between the distal ends of the gland cells, alternating regularly with them. The gland cells are tall, particularly in the lateral walls, and are of two kinds. In the more plentiful, which is also the larger of the two, the cytoplasm is filled with secretion spherules of a considerable size, which tend to dissolve in acid fixatives; both they and the rather fibrillar cytoplasm stain blue with azan and lightly with iron haematoxylin. The nuclei are large, lying towards the bases of the cells, and each contains two or three prominent nucleoli. In the second type of gland the spherules are small and so numerous that there appears to be little intervening cytoplasm, and the nucleus is hidden; these spherules stain bright red with azan and black with iron haematoxylin. Such glands are most common in the anterior edge of the prostate; some occur in the epithelium of the posterior wall, and fewer laterally. The epithelium rests upon a basement membrane beneath which is a layer of connective tissue containing muscle fibres.

The papilla through which the sperm are emitted from the vas deferens opens at the posterior end of the ventral wall of the prostate. Immediately in front of its opening the gland communicates with the mantle cavity by a longitudinal slit (*ls*)—an opening which in *Lamellaria* lies at the end of a short duct. Cilia direct the sperm through the gland, but they beat away from the slit; the lateral lips which border it are covered by a columnar ciliated epithelium, and normally embrace one another to keep the prostate closed.

From the anterior end of the ventral wall of the prostate arises the narrow ciliated tube (*cd*) which runs up the right side of the head to the penis (*p*). It is of uniform diameter throughout. Among the ciliated cells which line it are

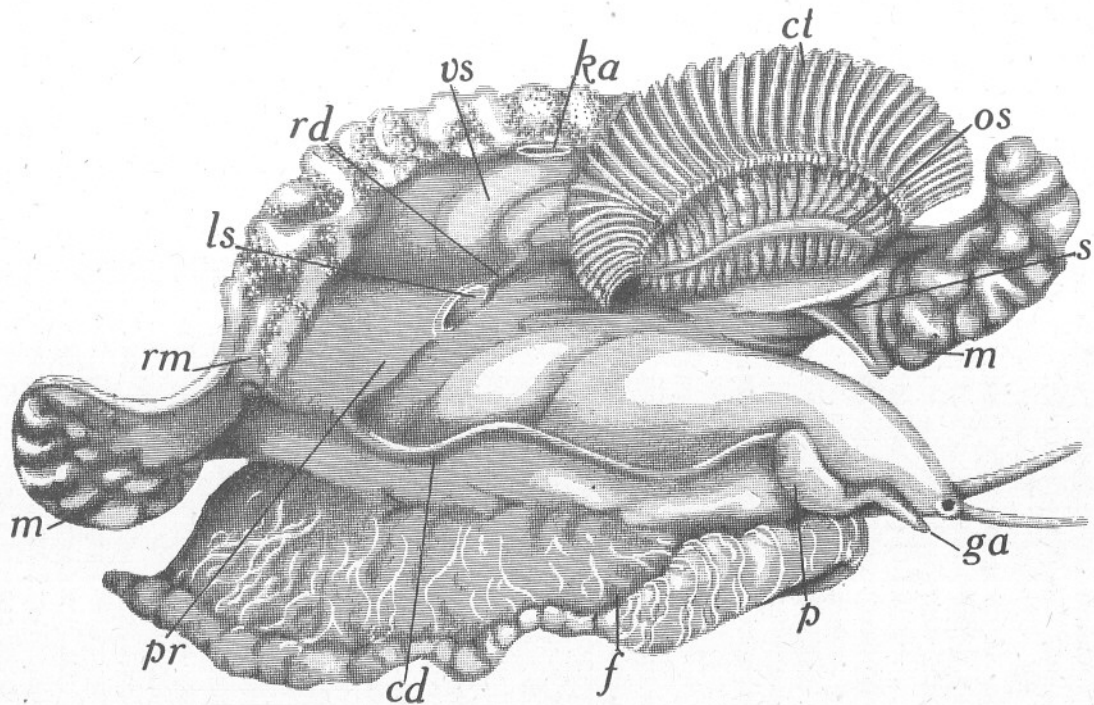


Fig. 4. *Trivia monacha*. Dissection to display the male genital duct; the mantle cavity has been opened along the right side. $\times 10$. *cd*, ciliated duct leading from prostate to penis arising from antero-ventral corner of gland; *ct*, ctenidium; *f*, foot; *ga*, genital aperture; *ka*, kidney aperture; *ls*, longitudinal slit in ventral wall of prostate; *m*, mantle; *os*, osphradium; *p*, penis; *pr*, prostate; *rd*, renal vas deferens; *rm*, rectum with overlying hypo-branchial gland; *s*, siphon; *vs*, vesicula seminalis.

scattered gland cells of a different nature from those already described—the cytoplasm, which is filled with minute spherules, stains blue with azan, whilst the spherules are purple; the glands are unaffected by mucicarmine and stain but lightly with haematoxylin. In the ciliated cells the cytoplasm contains small yellowish granules which are most numerous beneath the basal granules from which the long cilia arise; these cilia may attain a length exceeding twice the height of the epithelium. The duct is surrounded by a thick layer of circular muscles which assist in the transmission of the spermatozoa to the penis. The duct through the thin cylindrical penis is similar in histological detail, except that towards the genital aperture (*ga*) gland cells are lacking. Here the duct is reduced to the dimensions of a fine capillary tube.

The male reproductive system of *Trivia arctica* is constructed on the same plan as that of *T. monacha*, and between the two there is close correspondence in histological detail. The outstanding point of difference, and the only one that need be mentioned, is in the size and shape of the penis—in *T. arctica* it is larger and assumes a broad leaf-like shape.

The female

The ovarian tubules, which lie between the lobes of the digestive gland, converge towards the anterior ventral surface of the visceral mass on the right side, and here join one another to form a short ovarian duct with an epithelium resembling the gonad. The epithelium becomes ciliated as the duct merges into the renal oviduct (Figs. 5A and B, *ro*), which is a muscular tube lined by thickly ciliated columnar cells. The renal oviduct opens into the albumen gland (*ag*), which is a differentiation of the posterior end of the pallial oviduct and is connected to the receptaculum seminis. Anterior to this gland is the bilobed capsule gland (*rc*, *lc*) constituting the anterior part of the pallial oviduct and possessing, as in most mesogastropods, deep and thick lateral walls, and narrow and thin dorsal and ventral walls. The genital aperture is not terminal, but is a longitudinal slit along the greater length of the ventral wall (*f*).

The relationship between the albumen gland and the receptaculum seminis is the chief point of difference between the two species of *Trivia*. In *T. arctica* the receptaculum takes the form of six large diverticula which open separately into the albumen gland (Fig. 5B, *dr*), so that the arrangement corresponds with that of *Lamellaria perspicua*, except that in *Trivia* the albumen gland is constricted off from the capsule gland along the dorsal part of its anterior wall. In *T. monacha* the receptaculum is a spherical sac (Fig. 5A, *rs*) lying above the albumen gland, which has the appearance of a thick duct leading from the receptaculum to the capsule gland.

Trivia monacha (da Costa)

The epithelium of the renal oviduct is folded longitudinally and surrounded by a coat of circular muscles. The muscles increase in thickness to form a

sphincter around the papilla by which the duct opens into the pallial oviduct. Proximal to this opening a bunch of branching diverticula (Fig. 5A, *bd*) leads from the renal oviduct to end blindly in the tissues of the digestive gland. The diverticula contain sperm which are orientated in the lower proximal parts

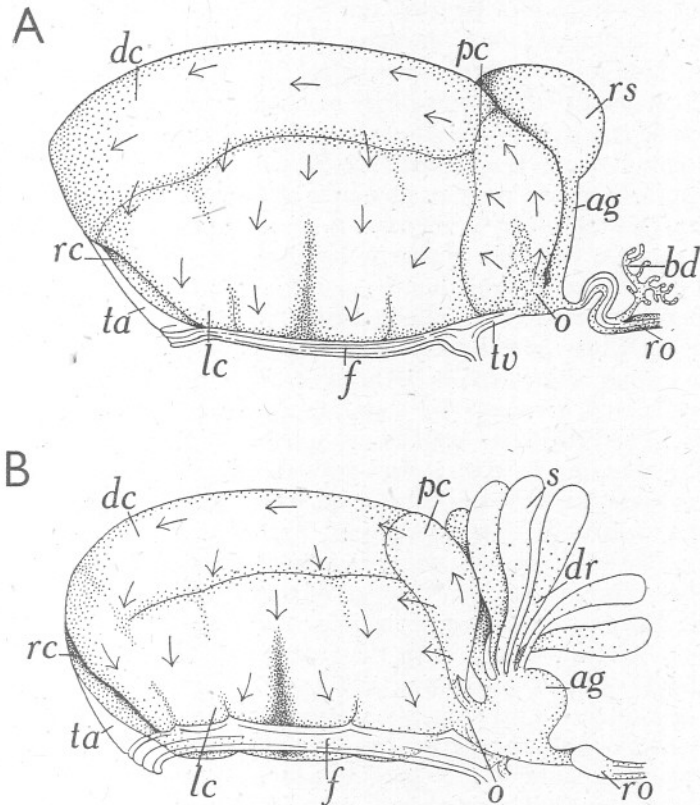


Fig. 5. A, *Trivia monacha*. Oviduct from the left side. $\times 24$. B, *Trivia arctica*. Oviduct from the left side. $\times 30$. Arrows indicate ciliary currents on the inner side of the wall of the left lobe of the pallial section; those on the right are similar. *bd*, branching diverticula from renal oviduct; *f*, ventral wall forming flange over genital aperture; *lc*, left lobe of capsule gland; *o*, position of opening of albumen into capsule gland; *rc*, right lobe of capsule gland; *rs*, receptaculum seminis; *ta*, thin anterior wall of capsule gland; *tv*, thin ventral wall of capsule gland. Other letters as in Fig. 3.

of the tubules, their heads embedded in the ciliated epithelium, whilst in the distal ends the sperm lose their orientation and their heads appear shorter. Their ultimate fate is ingestion by amoebocytes, which invade the blind ends of the tubules in large numbers and there devour and digest the effete sex cells. It is probable that these sperm enter the renal oviduct when ripe eggs are liberated from the ovary. The excess sperm which are not used in

fertilization are trapped here and lodge in the diverticula, in which they orientate themselves and remain healthy for some days.

The epithelium which lines the receptaculum seminis is thrown into deep and somewhat irregular folds. It is composed of ciliated cells, the cilia arising from basal granules from which intracellular fibrillae run through the superficial layer of cytoplasm. Beneath the fibrillae the cytoplasm is vacuolated, the vacuoles containing small granules. If animals be dissected immediately after copulation it is found that the seminal fluid fills the receptaculum, which suggests that the tip of the penis may reach as far as the base of this pouch. This is made possible by the position and size of the female aperture. The sperm orientate themselves immediately after deposition, pushing their heads into the epithelium, and perhaps obtaining nourishment from it. Occasionally a few may become totally embedded in the cytoplasm, when they are contained in vacuoles and later appear to be digested.

In the epithelium of the albumen gland tall secreting cells alternate with wedge-shaped ciliated cells. The secreting cells are of two kinds—mucous cells and unicellular gland cells filled with colourless spherules of protein, which are contained in vacuoles in the cytoplasm, tend to dissolve on fixation, and after the iron haematoxylin stain are a dense blue-black, as is also the cytoplasm. This glandular epithelium spreads around the opening to the receptaculum and up its ventral wall for a short distance.

In the capsule gland the thickness of the wall is due to tightly packed groups of secreting cells underlying the ciliated epithelium, which is penetrated by their ducts. Various types of glands are present and their secretions are mixed by the ciliary currents to form the wall of the egg capsule. The posterior tip (*pc*) of the gland is opaque white in living material, and is distinctly marked off from the anterior part. Along the ventral wall is the opening of the albumen gland (*o*), and the secreting cells from this extend dorsally for a short distance as a tongue separating two different groups of glands, one anterior and one posterior, which together constitute the posterior tip. The posterior group of glands is composed of cells containing spherules which are a bright crimson after azan and stain deeply with iron haematoxylin, whilst in the anterior group the spherules are very small, stain pale blue with azan and lightly with mucicarmine and iron haematoxylin. It is probable that these posterior tips, as in the *Stenoglossa*, form the plug of the egg capsule. If this be so then the rest of the gland must be responsible for forming the capsule wall. In fresh tissue the capsule gland is characteristically pigmented—from the genital aperture a strip of deep brown runs dorsally up each lateral lobe, and on either side of this strip the walls are yellow in colour. The grouping of the various types of subepithelial gland cells is as follows. The thin dorsal and anterior walls of the capsule gland are bordered on each side by mucous or mucoid cells, the former running forwards for a short distance from the posterior tip and also surrounding the anterior end of each lobe, the latter occupying the intervening area. Ventrally two other types of gland cells occur.

In one of these the secretion spherules stain very faintly with haematoxylin and pale blue with azan. These cells spread dorsally from the genital aperture to occupy a semicircular area; among them are a few epithelial and sub-epithelial mucoid cells. This area is surrounded on the side away from the genital aperture by the second type of gland which, except for mucoid cells, constitutes the remainder of each lobe, and in histological detail appears to be identical with the secreting cells of the ventral half of each lobe of the capsule gland of *Lamellaria*. The mucoid cells along the dorsal border run ventrally between these secreting cells in two areas, one towards the anterior and the other towards the posterior end of the genital aperture.

Beneath the epithelium of the ventral wall of the capsule gland no glands occur. Posterior to the genital aperture the wall unites the two lobes and is pouched beneath each, so forming a ventral channel which is surrounded externally by a layer of circular muscles, and along which the penis is inserted during copulation. The passage is lubricated by intra-epithelial gland cells which are similar to those of the albumen gland, and are very numerous near the junctions of the ventral and lateral walls. In the region of the genital aperture the ventral wall forms a flange which is attached to the left lobe of the capsule gland and embraces the free ventral edge of the right lobe so as to close the opening. Anteriorly the lobes are separated by an epithelium which is composed almost entirely of mucous cells.

The musculature of the capsule wall consists of a circular layer which is developed in the connective tissue surrounding the gland externally, and of radial and circular fibres in the connective tissue which binds together the groups of glands in the neighbourhood of the dorsal wall.

Trivia arctica (Montagu)

The renal oviduct (Fig. 5B, *ro*) is lined by a columnar ciliated epithelium which is folded longitudinally. The duct opens by a papilla into the pallial oviduct and possesses no branching diverticula for the accommodation of sperm—a feature which appears to be peculiar to *T. monacha*. The epithelium of the receptaculum seminis is similar in both species: ciliated, and with spherules in the cytoplasm which may provide nourishment for the spermatozoa. In *T. arctica* each diverticulum of the receptaculum is surrounded by a thick layer of circular muscle which forms a sphincter around the duct, and which will eject the sperm lying orientated in the terminal sac on contraction. Only very infrequently do sperm become embedded in the cytoplasm of the epithelial cells.

The albumen gland is in the form of a spherical sac (*ag*), the ventral wall of which is produced posteriorly to meet the renal oviduct and anteriorly to the opening of the capsule gland. The epithelium of the dorsal part of the sac is thrown into deep folds as in *T. monacha*, and within the lumen unorientated sperm, an excess from the receptaculum, are present during the winter months when copulation occurs and egg capsules are produced. The epithelium

consists of ciliated cells, similar to those of the receptaculum except that the spherules in the cytoplasm are more resistant to fixatives, and two types of gland cells which resemble those of the albumen gland of *T. monacha*. The secreting cells are very numerous in the ventral part of the gland, especially near the opening of the renal oviduct and the capsule gland, but are sparse dorsally; a few may extend to the ducts of the receptaculum.

The capsule gland is built on the same plan as that of *T. monacha*, and since the histology is very similar no detailed account need be given. An essential difference between the two species is in the size of the genital aperture which in *T. arctica* extends as far back as the albumen gland—this may be correlated with the larger size of the penis in this species.

The egg capsule

The egg capsule of *T. monacha* is figured by Lebour (1931), and specimens laid in the tissues of the compound ascidian *Polyclinum* have been collected at Port Erin, dissected from the ascidian, sectioned and examined microscopically. The capsule is an erect vase-shaped structure, circular in transverse section, rounded at the base, and above the constricted neck at the opposite end it broadens to a tall funnel. A plug at the base of the funnel blocks the entrance and closes off the sac in which the eggs float in an albuminous fluid. The capsule is approximately 5 mm. high, the funnel accounting for two-thirds of this measurement, and 2.5 mm. is the diameter of the egg sac in its broadest region. The breadth corresponds to that of the capsule gland, though the height exceeds that of the gland; this, however, may be accounted for by the fact that the funnel is moulded to its final dimensions after the capsule has left the gland. The wall is of a light straw colour, somewhat transparent so that the orange-coloured eggs can be seen through it, and has a fibrillar texture; in all these features it resembles the secretion from the capsule gland. The fibrillae are for the main part circular in direction corresponding to the transverse nature of the ciliary currents which determine their alinement within the capsule gland. Two longitudinal lines of thickening can be traced over the smooth surface of the capsule wall, and these are placed so as to divide the capsule into approximately equal halves; the suture is continuous across the plug at the base of the funnel. Ankel (1935) states that neither the plug nor the longitudinal suture is present, and the latter was not figured by Lebour (1931): its presence shows that as in *Lamellaria* and the *Stenoglossa* (Fretter, 1941), the structure of the capsule reflects the nature of the capsule gland, within which one-half of the wall is secreted by each of the two lobes. The suture which divides the plug into two demarcates the limit of secretion produced by each posterior tip of the capsule gland.

Female individuals of *Trivia* may be distinguished from the male by the presence of a ventral pedal gland which appears as a pit in the mid-ventral

region of the sole, a short distance behind the anterior pedal mucous gland. If the animals be anaesthetized a small papilla surrounded by a deep groove is protruded from the pit. In *T. monacha* the gland is lined by columnar ciliated epithelium in which mucous and mucoïd cells occur; these, however, are much fewer than in the surrounding epithelium of the foot. A layer of large unicellular glands underlies the epithelium, their long ducts opening between the ciliated cells. The secretion within the cells is in the form of spherules which stain lightly with haematoxylin. Beneath and between the subepithelial glands are groups of longitudinal muscle fibres which cause the protrusion and withdrawal of the papilla; when protruded the papilla is kept turgid by blood in the nearby sinuses. Since the gland is present only in females it is probably homologous with the ventral pedal gland of the *Stenoglossa* (Fretter, 1941) and is concerned with the deposition of the egg capsules. In the *Stenoglossa* the capsule is moulded within the gland, which then fixes it to the substratum. In *T. monacha* the capsule is sunk in a hole in the test of compound ascidians, the hole being excavated by the radula, and the funnel-shaped end projects from the surface of the test. The size and structure of the ventral pedal gland suggests that it is responsible for moulding this projecting part. After the capsule has been placed in the tissues of the ascidian the gland would then drive it into the hole, at the same time gripping the pliable projecting portion of the capsule wall and would fashion it into its final form. The size of the funnel thus formed is equal to that of the papilla which is protruded from the gland, and the characteristic out-turned rim of the funnel is of the same dimensions as the deep groove around the papilla. In *Lamellaria* no ventral pedal gland is to be found, and in connexion with this it is of interest to note that the capsule has no prominent rim projecting around the plug. The latter is surrounded by a thickening of the test of the ascidian—an attempt on the part of this animal to close the hole.

The embryos of *Trivia* develop to echinospira larvae before they leave the capsule. Their escape has not been observed, but empty capsules opened by the loss of the plug have been found. Perhaps the larvae produce an enzyme which loosens the plug and so enables them to quit the embryonic nursery and take up a planktonic life in the coastal waters.

The egg capsules of *T. arctica* are unknown though the larvae have been described by Lebour (1933). Since, however, the female genital duct and the ventral pedal gland are similar in both species, it is probable that there is a close resemblance in the structure of the capsules.

The glandular tissue of the female reproductive system—and this also applies to the male—is greatly reduced between the breeding seasons, that is, during autumn and winter for *T. monacha*, which has a more southerly distribution and which produces egg capsules in spring and summer, and during the summer for *T. arctica*, in which the breeding season extends from late autumn to early spring.

DISCUSSION

Archaeogastropoda

In the archaeogastropods both right and left kidneys are developed: each opens into the posterior end of the mantle cavity by a short ureter, and communicates with the pericardial cavity by a narrow, ciliated renopericardial duct which arises near the base of the ureter. There is a single gonad which discharges into the right kidney by way of a gonadial duct, so that the genital products reach the mantle cavity through the kidney opening. The point of connexion between the gonadial duct and the kidney varies: in *Diodora*, *Puncturella* and the trochids (Fig. 7A) the gonadial duct (*gd*) opens into the renopericardial duct (*rp*), in *Patella* and *Haliotis* it opens into the kidney, and in the other Docoglossa into the ureter (for diagrams see Linke, 1933). In all cases the course taken by the genital products in passing from gonad to mantle cavity is through a composite duct, the proximal part of which is derived from the gonad and the distal part from the kidney, the latter varying somewhat in its constitution. The sperm and ova are directed through the mantle cavity by the exhalant pallial current, and fertilization is external.

The majority of the archaeogastropods are littoral. They either shed their eggs singly, and development to a free trochosphere or veliger stage takes place in the plankton, or embed them in a common gelatinous secretion forming egg masses or ribbons. From data given by Lebour (1937) it appears that in the latter forms the young may develop to a crawling stage within the protection of the common gelatinous covering. If the eggs are liberated singly each is surrounded by one or more protective coats described by Lebour as an inner albuminous layer and an outer jelly layer. Observations show that, at least in certain species, these investments are formed in the ovary and the oviduct can have little or nothing to do with their production. If ova be removed from ripe females of *Patella*, *Patina*, *Gibbula cineraria*, *G. umbilicalis* or *Monodonta* and placed in sea water, each is seen to be provided with an outer gelatinous layer which swells in contact with water, and, except in the two Docoglossa, a thin inner layer of albumen; in fact, the appearance of these eggs seems identical with those which have been obtained from the plankton and described and figured by Lebour (1937).

In *Gibbula* and *Monodonta* the female urinogenital aperture is, unlike that of the left kidney, provided with glandular rosette-shaped lips which are yellow or bright orange in the living animals (*l*). They are not developed in the male. There is some controversy concerning these glandular lips around the opening of the right kidney in the female: Randles (1904) describes them for *Gibbula* spp., and Frank (1914) for *Monodonta turbinata*, though Robert (1902) and Lamy (1928) state that in trochids which lay their eggs singly the glandular appendage is missing, and according to Gersch (1936) 'die Mündung des Ureters in die Mantelhöhle ist bei *Gibbula cineraria* und *G. tumida* durch eine in beiden Geschlechtern gleichmassig ausgebildete Ampulle

kenntlich'. Since the investments of the egg appear to be a product of the ovary or of the egg itself, the secretion from this gland in *G. cineraria*, *G. umbilicalis* and *Monodonta lineata* may merely be responsible for hardening the outer jelly coat, or, more probably, since it is wholly mucous, may augment the secretion from the hypobranchial gland and so assist in the entanglement of the egg stream within the mantle cavity. According to Gersch (1936) the hypobranchial gland secretes most actively during the breeding season, and he concludes that in *Gibbula tumida* it also produces the jelly in which the eggs are embedded, since in this species he finds no glandular appendage around the genital aperture. In *Pleurotomaria Beyrichii* an accessory gland around the female urinogenital aperture, similar to that of trochids, has been described by Woodward (1901).

Diodora apertura and *Calliostoma zizyphinum* exemplify two methods by which gelatinous egg masses may be produced in the archaeogastropods. If eggs be removed from the ripe ovary of *Diodora* they are seen to possess both albuminous and jelly coats. Around the urinogenital aperture there are no glandular lips which might produce a secretion for cementing the eggs together as they are laid, but, according to Boutan (1885), this is accomplished by secretion from a 'glande annexe' developed on the wall of the female genital duct. The eggs coated with a thin layer of this secretion leave the urinogenital aperture and pass to the anterior end of the mantle cavity in a continuous stream; they are spread, usually on the under-surface of a stone, by means of the foot. The outer surface of each egg adheres to that of its neighbours and to the substratum, and an egg mass commonly one cell thick is thus formed. On the other hand, sperm from the male are passed through the apical opening of the mantle and shell and are discharged near the eggs when these are laid.

Calliostoma zizyphinum shows a more marked sexual dimorphism than any other gastropod so far mentioned. In the male the left and right kidney apertures lie level with one another at the posterior end of the mantle cavity, but in the female the right one is considerably farther forwards, since a glandular section is added which is assumedly derived from a closed off portion of the mantle and is built on the same plan as the pallial oviduct of the mesogastropods—lined by columnar ciliated epithelium, the lateral walls deep and thickened by tightly packed bundles of subepithelial gland cells, the dorsal and ventral walls narrow and comparatively thin. The secretion from this glandular section is of a uniform mucoid nature, and as the eggs are passed through it, each covered by an albuminous and gelatinous coat from the ovary, a further fluid of gelatinous consistency is poured over them and binds them into an egg ribbon. Thus in *Calliostoma* the oviduct is made up of (a) the ovarian duct, (b) part of the right kidney and its duct, and (c) a glandular duct derived from the mantle. This triple origin of the genital duct is the general plan on which that of higher gastropods, both male and female, is built. The more advanced nature of the genital duct in *Calliostoma* supports

Lebour's (1937) suggestion, based on the character of the spawn, that in the classification of the Trochidae the genus *Gibbula* should be regarded as more primitive than *Calliostoma* and not as more advanced as in Winckworth's classification (1932).

The aberrant freshwater *Theodoxus fluviatilis* is an archaeogastropod which approaches the mesogastropods not only in the loss of the right kidney and the right ctenidium, but also in the possession of genital ducts which are as complex as in any prosobranch, and which open alongside the anus at the mouth of the mantle cavity. Bourne (1908) suggests that the loss of the ctenidium in the Neritidae is correlated with the development of these accessory genital organs which occupy all the space on the right side of the mantle cavity. This, as in the mesogastropods, probably accounts for the loss of the right kidney. It seems more profitable to discuss the condition of the genital ducts of this genus with the mesogastropods.

Mesogastropoda and Stenoglossa

In the archaeogastropods the anal papilla is well back in the mantle cavity, though in front of the kidney openings. The faeces, bulky in such herbivorous forms, are elaborated in long coils of intestine, in the epithelium of which there are special glands for cementing together the discrete faecal particles (Graham, 1932). Here there is little fear of the compacted pellets disintegrating and fouling the mantle cavity as they are passed to the exterior by the exhalant pallial current. In the mesogastropods the rectum runs across the right side of the mantle cavity to open at its mouth, so that the faeces are discharged directly to the exterior and their elaboration need not be so complete. This new terminal section of the intestine, which brings the anus far forward to a more advantageous position, is probably derived from a folding over of the mantle wall. Running parallel with it is the oviduct which is longer than in *Calliostoma* and extends to the anus. This section of the oviduct which crosses the mantle cavity and frees the eggs directly to the exterior, must be comparable to the terminal part of the intestine and derived from the mantle. It is therefore referred to as the pallial oviduct, as distinct from the renal oviduct which precedes it. Most probably it first arose as a longitudinal groove with a ciliated epithelium similar to that of the mantle, in which case secreting cells producing a lubricant would be present. In no living gastropod does it persist in so simple a form, but the glandular element has been exploited, the walls thickened by addition of subepithelial secreting cells of various kinds, and the lips of the groove have fused to form a more or less spacious tube. From the genital aperture the egg mass, spawn or capsule may be directed on to an ovipositor as in *Littorina littorea* (Linke, 1933) or come under the manipulation of the foot by which it is deposited as in *Bithynia tentaculata* (Ankel, 1936), *Trivia* and the *Stenoglossa* (Fretter, 1941).

The forward migration of the anus and oviduct is not followed by that of the left kidney opening, except in specialized cases, e.g. the freshwater

genera *Viviparus* and *Valvata* which possess a long ureter opening at the mantle edge. The functional right kidney of the archaeogastropod is lost except for the vestige which forms that part of the genital tract linking the ovarian or testis duct with the mantle cavity; the original communication between the ureter and the pericardial cavity may persist.

The gonadial duct sometimes retains an epithelium resembling that of the gonad (Linke, 1933); its musculature is feebly developed as compared with that of the renal genital duct. In the male its lower part is coiled and functions as a vesicula seminalis, the epithelium of which may absorb effete sperm (*Littorina*, Linke, 1933; *Stenoglossa*, Fretter, 1941). The renal oviduct and vas deferens are for conduction: the epithelium is strongly ciliated and surrounded by a thick coat of circular muscles. In the female a gonopericardial duct may be present, and, if so, it arises between the ovarian duct and the renal oviduct resembling the latter histologically. This connexion with the pericardial cavity has never been described for the male, though in some genera in which it is well developed in the female it is represented in the male by dense strands of connective tissue passing from the origin of the vas deferens to the pericardium (*Littorina*, Linke, 1933; *Cremnoconchus*, Linke, 1935; *Ocenebra erinacea* and *Nassarjusz reticulatus*, Fretter, 1941). As such it first makes its appearance when the protandrous hermaphrodites *Calyptraea* and *Crepidula* develop female organs (Giese, 1915). The persistence of the gonopericardial duct in the female proves that it is at least no handicap in the functioning of the genital system, and its appearance in the female stage of *Calyptraea* and *Crepidula* may indicate that it serves some essential role. Its occurrence, however, in the male might be a serious disadvantage in allowing the escape of sperm into the pericardial cavity.

The male system

The evolution of the male genital ducts of the mesogastropods is parallel with that of the female. Since when the eggs leave the female aperture they are embedded at least in a thick gelatinous secretion or contained in a capsule, their fertilization must take place within the oviduct. For this purpose a pedal penis is developed behind the right cephalic tentacle of the male, and the male orifice is secondarily removed to the tip of the penis. In some the opening of the vas deferens is still at the posterior end of the mantle cavity, and the seminal fluid is directed forwards along a ciliated groove which runs across the floor of the cavity and up the right side of the head to the tip of the penis. Such a sperm-conducting groove, which functions as a closed tube, is present in *Littorina* (Linke, 1933) *Calyptraea chinensis*, *Crepidula unguiformis*, *Capulus ungaricus* (Giese, 1915) and species of *Cypraea* (Rau, 1934). In *Littorina* that section of the groove lying within the mantle cavity is bordered on each side by a glandular strip of tissue, the secretion from which is mixed with the sperm during copulation. This glandular area therefore functions as a prostate; its origin is similar to that of the pallial oviduct. Such

an open prostate is also present in *Turritella communis* in which the seminal groove ends at the opening of the mantle cavity and no penis is developed; the entry of seminal fluid into the female is probably effected by the inhalant pallial water current. In other mesogastropods and in the *Stenoglossa* the seminal groove is closed throughout its length. The prostate may form a wide sac-like portion of the duct lying within the mantle cavity, with subepithelial gland cells thickening the deep lateral walls and the narrow dorsal and ventral walls remaining thin. Or the prostate may be a narrow tube of about the same diameter as the rest of the male duct, with epithelial gland cells only; in either case the walls are ciliated. The former type of prostate occurs in the hydrobiids, *Assemania grayana* (Krull, 1935), *Trivia monacha*, *T. arctica*, *Ocenebra erinacea*, *Nucella lapillus* (Fretter, 1941) and *Cremnoconchus* (Linke, 1935); the latter in *Lamellaria perspicua* and *Nassarius reticulatus* (Fretter, 1941). *Ocenebra erinacea* and *Nucella lapillus* demonstrate the formation of a closed prostate from the open type of *Littorina*, for the ventral lips of the groove which fuse to form the tube retain the double layer of epithelium at the point of fusion. Moreover, the closure is incomplete at the posterior end so that a ventral slit-like communication with the mantle cavity is retained. A similar opening is also present in the prostate of *Trivia arctica* and *T. monacha*, whereas in forms in which the prostate is a rather narrow tube it may communicate with the posterior end of the mantle cavity by a short duct as in *Nassarius reticulatus*, *Buccinum undatum* and *Lamellaria perspicua*. The presence of this opening in the higher mesogastropods as well as in the *Stenoglossa* offers further support for the suggestion that it plays some important role, probably in providing a means of escape for seminal fluid, and so preventing the possible rupture of the genital duct which might occur if an animal were forced to withdraw into its shell during copulation when the duct is filled with seminal fluid.

The closure of the seminal groove and also the development of the prostate appear to have occurred independently in different genera. In the Hydrobiidae, which are among the more primitive mesogastropods, the vas deferens is closed throughout its length and a sac-like prostate lies within the mantle cavity (Krull, 1935), whereas in the more highly organized cypraeids the duct may be represented by an open groove and Rau (1934) describes no prostate along its course.

The male genital duct of *Theodoxus* follows the same general plan as that of the mesogastropods in so far as there is a testis duct, which stores sperm in its distal coils, a short renal vas deferens, a closed prostate extending the length of the mantle cavity and a penis. The arrangement of the glands in the prostate is, however, more elaborate. With a closed prostate it is customary to have a closed genital duct leading forwards up the side of the head to the male opening at the tip of the penis, but in *Theodoxus*, and in other Neritidae, the male opening is at the anterior end of the prostate. In the short space intervening between genital aperture and penis, in *Theodoxus fluviatilis*, the

flow of seminal fluid appears to be guided by a furrow in the overlying mantle.

In *Lamellaria* the portion of the male duct which lies anterior to the prostate has sunk into the haemocoel and lengthened so that it is thrown into deep coils. These lead to a large penis which is folded beneath the mantle when not in use, and through which the duct pursues a straight course to open at the tip of a flagellum. The reserve coils of the genital duct, which lie within the haemocoel, are drawn upon during copulation when the penis and the anterior end of the body are distended. This condition contrasts with that of the closely allied genus *Trivia* in which, as in other mesogastropods and the *Stenoglossa*, the genital duct remains embedded in the body wall—it is distended with it during copulation and retracts with it when the animal withdraws into its shell—and at the same time the duct through the penis shows a zigzag course which is straightened on the expansion of this organ. In the opisthobranchs and the pulmonates at least part of the vas deferens has separated from the body wall and lies within the haemocoel, so that the condition in *Lamellaria* approaches this.

The female system

The pallial oviduct of the mesogastropod and stenoglossan is elaborated for the reception and storage of sperm and for the production of secretions, both nutritive and protective, in which the eggs are embedded before they leave the genital duct. The glandular elements are fairly constant in their disposition—subepithelial gland cells are invariably grouped in clusters beneath the deep lateral walls of the duct, leaving the narrow dorsal and ventral walls relatively thin. This arrangement is similar to that which is common in the prostate. The glands surrounding the posterior end of the pallial oviduct constitute an albumen gland, whilst, anteriorly, around the greater length of the duct they form either a jelly gland, as in *Littorina* and *Lacuna*, which embed their eggs in a gelatinous secretion, or a capsule gland as in the majority of the mesogastropods and in the *Stenoglossa*, all of which produce egg capsules. In the viviparous prosobranchs—*Littorina rudis* (Linke, 1933), *Paludestrina jenkinsi* (Krull, 1935) and *Viviparus viviparus*—the jelly gland or capsule gland forms a thin-walled brood pouch. The capsule gland may be composed of various types of secreting cells and their secretions mixed by ciliary currents on the walls of the duct. A composite fluid thus produced comprises the wall of the egg capsule in *Calyptrea chinensis*, *Trivia*, *Lamellaria* and the *Stenoglossa*. In *Littorina* (Linke, 1933), in which each egg is shelled after it has received its albuminous coat, a shell gland lies between the albumen and jelly glands.

In *Littorina* and the *Stenoglossa* a bursa copulatrix (Fig. 7B, *b*) at the distal end of the pallial oviduct receives the seminal fluid from the penis. Fertilization takes place at the innermost end of the duct where there is a second pouch, the receptaculum seminis (*rs*), serving as a more permanent

storage place for the sperm. The spermatozoa reach the receptaculum by a channel along the ventral wall of the oviduct (*vc*), arched over by longitudinal folds of epithelium. In the *Stenoglossa* the receptaculum is produced into glandular diverticula which form an absorptive organ for unwanted sperm. The position of the bursa varies. In certain hydrobiids (Krull, 1935) it lies close to the receptaculum at the inner end of the ventral channel and the latter functions as a vagina into which the penis is passed. In *Paludestrina jenkinsi* the ventral vaginal channel is closed off from the oviduct giving two openings to the exterior, a vaginal pore and a birth pore. A somewhat similar condition is found in *Theodoxus* in which the vagina with its associated bursa and receptaculum is cut off from the pallial oviduct in an antero-posterior direction, the receptaculum retaining connexion with the innermost end of the pallial oviduct by a narrow, coiled fertilization duct. A further complication in the female genital system of these highly specialized Neritidae is found in the fresh water *Septaria* and *Paranerita* where there are three external openings, the additional one being that of the 'ductus enigmaticus' which lies between the vaginal pore and the birth pore. This duct would appear to be formed by a subdivision of the vagina, and Bourne (1908) suggests that it may serve to admit water into the sperm sac (= bursa copulatrix), or it may be a means of expelling waste matter.

In a number of mesogastropods only the receptaculum is developed: it is a dorsal outgrowth of the initial part of the pallial oviduct where the eggs are fertilized, and seminal fluid is either deposited directly into it by the penis or close to its opening. The receptaculum may be a simple sac as in *Capulus* (Giese, 1915) and *Trivia monacha*, or subdivided to form diverticula, six in *Calyptraea* (Giese, 1915), *Lamellaria* and *Trivia arctica*, three in *Crepidula* (Giese, 1915). The duct of each diverticulum is muscular and helps the uptake of sperm during copulation and their later ejection for fertilization. Since the penis is long enough to reach the receptaculum no longitudinal sperm-conducting channel is developed. Sections of *Calyptraea* show that along the ventral wall of the pallial oviduct, against which the penis lies during copulation, there is a narrow longitudinal strip of cubical cells which are neither ciliated like the epithelium elsewhere, nor underlaid by glands. It would seem that this line represents the point of closure of the pallial gonoduct in the transformation from the male stage with an open seminal groove to the female stage in which the lips of the groove have fused to form a closed duct.

The temporary storage of sperm in diverticula of the renal oviduct of *Trivia monacha* is an unusual phenomenon, though in *Cremnoconchus* (Linke, 1935) the receptaculum itself is a longitudinal tract along the renal oviduct, stretching from the gonopericardial duct to the pallial oviduct.

In *Turritella communis* the pallial oviduct is open along its entire length. It resembles the prostate of the male in that the lateral walls of the channel are deep, thickened by subepithelial gland cells, joined together dorsally and open to the mantle cavity ventrally. Along the free edge of the left wall is a

thin flange (Fig. 6, *f*) which may lie under the free ventral edge of the right wall and so form a functionally closed duct with an anterior aperture near the mouth of the mantle cavity. At the inner end of the pallial oviduct there are two pouches one on either side of the longitudinal glandular tract. The pouch lying against the right wall, near the columellar muscle, is the smaller of the two and acts as a receptaculum seminis (*rs*) which appears to receive sperm from the inhalant, pallial water current, the principal use of which is as a feeding current (Graham, 1938). The left pouch is embedded in the thickness of

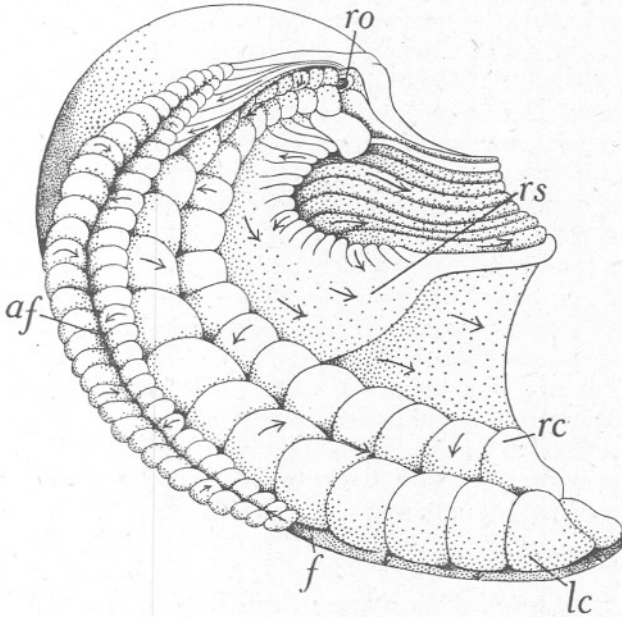


Fig. 6. *Turritella communis*. Upper part of the pallial oviduct. Arrows indicate ciliary currents. $\times 24$. *af*, albumen gland and fertilization pouch; *f*, flange bordering ventral edge of left wall of pallial oviduct; *lc*, left wall of capsule gland; *rc*, right wall of capsule gland; *ro*, opening of renal into pallial oviduct; *rs*, receptaculum seminis.

the left wall (*af*), on the ventral edge of which it has a fairly extensive opening; anteriorly the lips of this opening fuse and are continuous with the flange bordering the free edge of the wall. In this second pouch the eggs appear to be fertilized and surrounded by an albuminous fluid. The lips of the pouch are mobile and may envelop the opening of the receptaculum for the collection of sperm and approach that of the renal oviduct to receive the eggs; both sperm and eggs have been found within it.

The open condition of the pallial oviduct of *T. communis* is certainly secondary and associated with the rigours of a ciliary food-collecting habit in a muddy situation. The mantle cavity must be isolated from the environment in order to avoid clogging of the gills, and this is effected by a curtain of tentacles

which surrounds the pallial opening (Graham, 1938). Should copulation be practised the introduction of the penis into the female aperture would impair this isolation. With an open pallial oviduct exposing the receptaculum the sperm may be transferred to the female by the inhalant water current obviating the necessity for a penis. The route by which the spermatozoa reach the receptaculum remains obscure. The animals are gregarious, and the spawning of large numbers will probably occur simultaneously. So far as is known no other living mesogastropod has a fully open pallial oviduct, and although the open condition in *Turritella* is secondary it represents the condition of an open glandular groove which in the course of evolution must have preceded a closed pallial duct. In the prostate of male mesogastropods, though not in the pallial oviduct of females, there is evidence of the method by which a closed duct has evolved from an open groove, first by the fusion of the epithelial of the free ventral edges of the groove (*Ocenebra*, *Nucella*) and then by the loss of these epithelia so that no trace of the line of closure can be found. It is no unreasonable assumption that the history of the pallial oviduct is similar, and, if so, then the reopening in *Turritella* has occurred along the same line as the original closure took place. In *Trivia* the female genital opening, which is ventral and not terminal as in other mesogastropods, and also the opening of the prostate in the male, probably represent points of incomplete closure of the duct. Posterior to the female opening there is a thin-walled channel along which the penis passes during copulation. This, and also the equivalent ventral channel leading to the receptaculum in other gastropods, correspond in position to the thin marginal strips which would border the free edges of a glandular channel as in *Turritella*, and are probably formed by the fusion of these lips.

The egg masses

The eggs of the mesogastropod and stenoglossan are rarely shed singly into the sea. They are always embedded in albumen provided by the initial part of the pallial oviduct, and then surrounded by a protective outer covering of varying thickness and consistency. Within these coverings the egg develops to a veliger or crawling stage; in no species is there a trochosphere. A great variety of spawn occurs reflecting variations in the histology of the glandular oviduct, and in the manipulation of the egg mass both within the duct and after it has left the genital aperture. In the spawn of *Littorina* and *Lacuna* (Hertling & Ankel, 1927) each egg is surrounded by albumen and is isolated from any companions first by a shell and then by a common mass of jelly in which all are embedded. From the pelagic capsules of *Littorina littorea* and *L. neritoides* veliger larvae are hatched, and from the fixed egg masses which are laid on weed either veligers, as in *Lacuna vincta*, emerge, or the young develop to the crawling stage and escape by biting their way through the jelly as in *Littorina littoralis* and *Lacuna pallidula*.

In other mesogastropods and in the Stenoglossa it is customary for the eggs

which are laid within any one capsule to share a common albuminous fluid and for the capsules to be attached. The thickness and composition of the capsule wall varies with the size of the capsule and the exposure to which it is submitted. In the rissoids (Lebour, 1937) the capsules are usually lens-shaped, little more than 0.5 mm. in diameter and with a wall which is tough, of inconsiderable thickness, and frequently quite transparent. Each is attached to the substrate by the flattened surface, and through a thin area in the centre of the upper surface the young break through on hatching. The eggs are individually enclosed in a delicate membrane and float together in an albuminous fluid. In most species the larvae hatch as veligers, but in *Cingula cingillus* and *C. semicostata*, which lay only one egg in each capsule, the young emerge in the crawling stage (Lebour, 1937). *Turritella* lays grape-like clusters of capsules each with a thread which fastens it to the substratum. The thread is a prolongation of the spherical wall of the capsule, which measures 0.6 mm. in diameter and is secreted around a group of eggs, in their albuminous covering, as it passes down the pallial oviduct. About ten or more capsules are laid in one cluster and their walls are thin and transparent so that the pinkish eggs are visible. In *Crepidula* and *Calyptraea* the delicate capsules are also stalked and fastened to a stone in clusters of about a dozen. Additional protection is given to the developing embryos by the parent covering the capsules with her body. Sections of the capsules of *Calyptraea* show that the outer covering is a composite secretion with an alveolar texture. A suture divides the wall into two equal halves, reflecting the bilobed nature of the capsule gland and demarcating the limit of secretion produced by each of its thick lateral lobes. Such a suture is a common feature of the egg capsules of prosobranchs being more pronounced in those with thicker walls. In the flattened spheroidal capsule of *Theodoxus* it is the line along which the wall breaks when the young mollusc escapes. The comparatively thick conchiolin wall of this capsule protects the embryo against the adversities associated with life in shallow streams and, as in all freshwater molluscs, the larval stage is suppressed.

Trivia monacha and *Lamellaria perspicua* lay spawn cases which are built on the same plan as those of the *Stenoglossa*, though they are less robust and not subjected to the same degree of exposure since the mollusc sinks them in the tissues of the compound ascidian on which it feeds. Each capsule is pot-shaped with a plug of mucoïd material blocking the opening. The wall displays a fibrillar texture and is divided longitudinally into two equal halves by a suture, which also passes through the substance of the plug. As in the *Stenoglossa* the latter would appear to be secreted by the posterior tips of the capsule gland, a region of the pallial oviduct homologous with the shell gland of *Littorina*. In *Trivia* the rim of the capsule which projects above the surface of the ascidian is moulded by the ventral pedal gland of the female. Such a gland is also present in the *Stenoglossa* and serves to mould the egg case to its final form, harden it and fix it to the substrate.

The practice of embryonic cannibalism in the *Stenoglossa* has been described by Portmann (1925) for *Buccinum undatum* and *Nucella lapillus* and by Thorson (1935) for *Colus islandicus*. In these three species the most precocious embryos within a capsule devour their fellows and, thus supplied with nourishment, they develop to the crawling stage. Such cannibalism is permitted through the absence of a protective shell which in the Lacunidae encloses the egg together with its individual supply of albumen. According to Giard (1875) and Pelseener (1911) nurse cells are also present in *Lamellaria perspicua*, though Ankel (1935) finds no evidence of such.

Although in the majority of prosobranchs the sexes are separate hermaphroditism occurs amongst the archaeogastropods and the mesogastropods. The hermaphrodite form may be protandrous, as in *Acmaea fragilis* (Willcox, 1898), *Crepidula fornicata* and *Capulus ungaricus* (Giese, 1915), the Scalidae (Ankel, 1926) and perhaps *Patella* (Orton, 1928), or it may be simultaneously male and female as in *Valvata*, *Pelseeneria stylifera*, *Velutina* and in all the Pyramidellidae (Ankel, 1936). In those groups which have evolved from the prosobranchs, the pulmonates and the opisthobranchs, the latter is the rule—the pallial genital duct is divided into sperm-conducting and egg-conducting regions, the former leading to the penis by which internal fertilization is accomplished, the latter being associated with massive glandular tracts which provide the albuminous and gelatinous coverings for the spawn. Egg capsules are not produced, but typically a number of eggs, each surrounded by its own portion of albumen, are embedded in a mass of jelly which is fastened to the substratum. The spawn may contain a large number of eggs which hatch as veligers, as in most tectibranchs and nudibranchs, or fewer and larger eggs which hatch as miniatures of the adult as in the Onchidiidae and pulmonates.

The pallial genital duct of the tectibranchs and pulmonates has separated from the mantle and comes to lie within the haemocoel. Apart from minor variations its fundamental plan, for such typical members of these as *Actaeon*, *Aplysia* and *Helix*, agrees remarkably with what has been described for the female genital duct of *Littorina* and the otherwise highly specialized *Stenoglossa*. To this same plan also conforms the hermaphrodite genital system of *Onchidella celtica*, a member of the Onchidiidae which may be regarded as an early offshoot from the main stem of the opisthobranchs (Fretter, 1943). In *Littorina* and the *Stenoglossa* (Fig. 7B) the pallial oviduct of the female is incompletely divided by internal longitudinal folds to give a spacious glandular channel (*c*), for the conduction of eggs and the manufacture of their protective coverings, and a narrow, ventral, thin-walled channel (*vc*) for the conduction of sperm from the bursa copulatrix (*b*) to the receptaculum seminis (*rs*); the short terminal part of the duct between the genital aperture and the opening of the bursa acts as a vagina (*v*). In *Actaeon tornatilis* (Fig. 7C), which is hermaphrodite, the pallial genital duct is similarly subdivided (Guiart, 1901). The sperm-conducting channel (*vc*, *vd*), separated from the oviduct by two

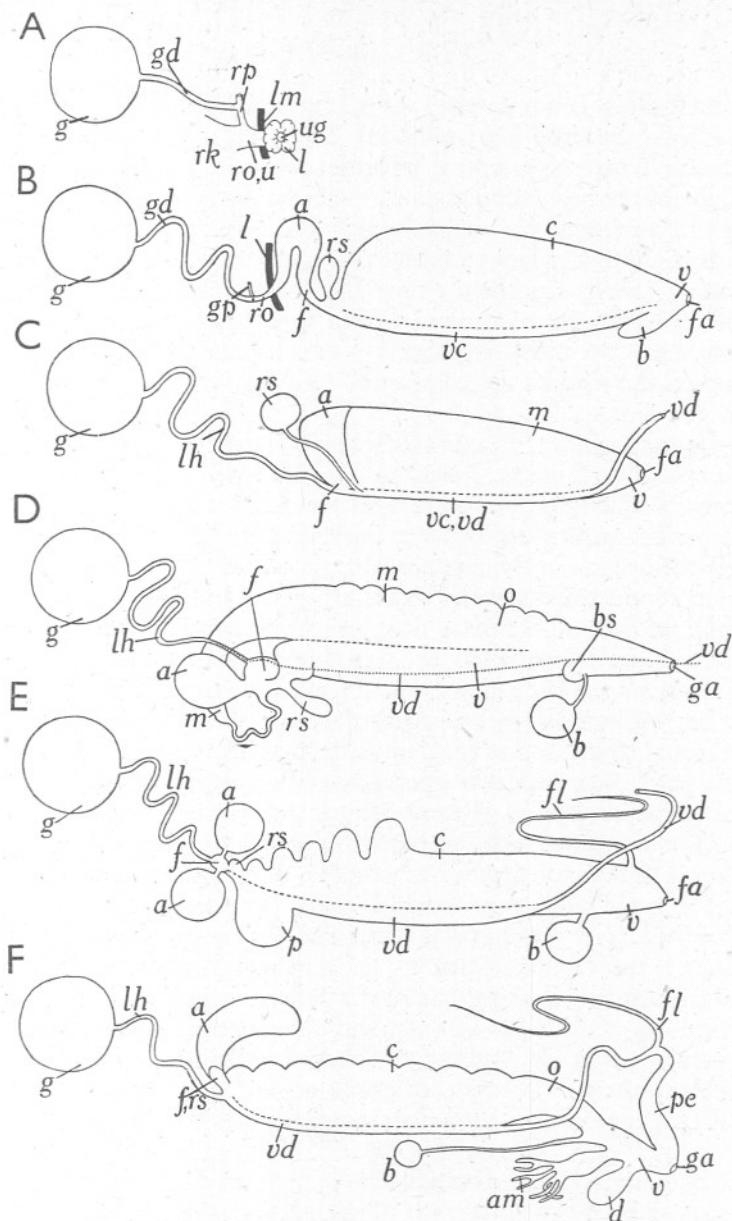


Fig. 7. Comparative diagrams of the genital ducts of: A, the Trochidae ♀; B, *Nucella* ♀; C, *Actaeon* ♂; D, *Aplysia* ♀ (after Eales); E, *Onchidella* ♂; F, *Helix* ♂. Broken lines represent incomplete separations between channels; the dotted line the vas deferens, an open groove throughout. a, albumen gland; in D, E and F a definite fertilization chamber; d, dart sac; f, site of fertilization, in D, E and F a definite fertilization chamber; fa, female aperture; fl, flagellum; g, gonad; ga, common genital aperture; gd, gonadial duct; gp, gonopericardial duct; l, glandular lips; lh, little hermaphrodite duct of gonadial and renal origin; lm, inner limit of mantle cavity; m, mucous gland; o, oviduct; p, prostate; pe, penis; rk, right kidney; ro, renal oviduct; rp, renopericardial duct; rs, receptaculum seminis; u, ureter; ug, urino-genital aperture; v, vagina; vc, ventral sperm channel; vd, vas deferens.

longitudinal folds, communicates at its upper end with the receptaculum (*rs*) and also with the little hermaphrodite duct (*lh*); at its lower end, as it approaches the female aperture, it separates from the pallial genital duct, runs up the side of the head and passes through the penis to its tip. This tube (*vd*) has the sole function of a vas deferens, whilst the channel along the pallial genital duct appears to have a double role, that of a vas deferens and of a path for incoming sperm, since at the time of copulation sperm are introduced into it by the penis of the partner and from there they make their way to the receptaculum. No bursa copulatrix is developed. The subepithelial glands surrounding the oviduct are compacted to form an albumen gland (*a*) and a mucous gland (*m*).

In *Aplysia punctata* (Fig. 7D) the vaginal channel (*v*) and the vas deferens (*vd*) are two distinct tracts (Eales, 1921). The latter is the smaller of the two and arises as a longitudinal groove in the wall of the little hermaphrodite duct (*lh*), and runs forwards between the vagina on the one side and the mucous gland on the other. At their upper end the glandular oviduct separates from the sperm-conducting channels and is elongated and coiled, whilst along the mid-region of the pallial genital duct the three channels, oviduct, vagina and vas deferens, are incompletely separated from one another—three channels sharing a common wall. Towards the female aperture the vaginal channel and oviduct become completely one whilst the vas deferens retains its identity and passes through the aperture (*ga*), up the right side of the head and along the retractile penis. The vagina is associated with a receptaculum seminis (*rs*) at its inner end, and distally, where it merges with the oviduct, there is a second pouch (*b*) homologous with the bursa copulatrix of other gastropods. Eales refers to this second pouch as a spermotheca. It communicates with the vagina by a narrow canal, and at the junction of the two there is a glandular sac, the bursa seminalis (*bs*). Eales (1921) states that during copulation the penis may pass through the vagina so that its tip approximates to the base of the receptaculum, into which the sperm pass. 'There is always a certain amount of debris introduced with the sperms, and this, agglutinated by the secretion of the glands lining the wall of the bursa seminalis, is drawn up into the spermotheca, where it is either absorbed or discharged through the external aperture. No satisfactory evidence, however, has been obtained on this point.'

In the prosobranchs the albumen gland (Fig. 7B, *a*) comprises subepithelial glands surrounding the initial part of the pallial oviduct which is frequently the site of fertilization (*f*). In *Aplysia* and *Onchidella* these glandular elements are separated from the wall of the duct (Fig. 7D and E, *a*), the initial part of which is termed the fertilization chamber (*f*), and receives eggs from the little hermaphrodite duct (*lh*), sperm from the receptaculum (*rs*) and albumen from the associated gland.

In *Onchidella celtica* the little hermaphrodite duct (Fig. 7E, *lh*) is also functionally divided into two channels at its distal end. On approaching the

pallial genital duct the female channel separates from the male and opens into the fertilization chamber (*f*), whilst the male opens into the pallial vas deferens (*vd*). This separation is only for a microscopic distance. The oviduct and vas deferens unite again to form two relatively deep, parallel and glandular passages sharing a narrow, ciliated dorsal wall. Near its origin the vas deferens is dilated to form a pouch, the prostate (*p*), and the oviduct is produced into six diverticula along each of which the eggs must travel on their way to the genital aperture. The first, the smallest diverticulum, is the receptaculum seminis (*rs*) which overhangs the fertilization chamber. The sperm reach the receptaculum from the bursa (*b*), which is at the opposite end of the oviduct, by way of a ciliated tract along the thin and narrow wall which overlies the male and female passages. Thus, as in *Aplysia*, the incoming and outgoing sperm have separate tracts. Towards the distal end of the pallial genital duct, which owing to complete detorsion of the visceral mass is directed posteriorly, the vas deferens and the oviduct become separate tubes. The latter opens, by way of a vagina (*v*), into the much-reduced mantle cavity which is at the posterior end of the body between mantle and foot. The former is narrow, ciliated and non-glandular. It passes forwards along the right side of the body to reach the retractile penis which lies on that side of the head. The penis cannot be affected by the detorsion which brought the female opening to its posterior position; hence detorsion must be accompanied by the lengthening of the male duct. A flagellum (*fl*) which arises from the vagina, not far from the opening of the bursa, has glandular walls: it may be functionally equivalent to the bursa seminalis of *Aplysia*, the secretion from which is said to agglutinate waste matter from the genital tract. Such waste is frequently found in the bursa copulatrix giving it, as in *Aplysia*, a purple or pinkish hue.

In *Helix pomatia* the receptaculum seminis which receives the little hermaphrodite duct is also the fertilization chamber (Fig. 7F, *f*, *rs*). It is partly embedded in the albumen gland (*a*) from which it receives secretion. The pallial oviduct (*c*) and vas deferens (*vd*) are initially two channels along a single duct; distally they separate. The vas deferens passes to the retractile penis (*pe*) near which it is produced into a fine flagellum (*fl*) where spermatophores are formed. The glandular oviduct, which provides the calcareous coats for the eggs, passes to the vagina (*v*). From this there arises not only the bursa copulatrix (*b*) with its long connecting duct, but accessory structures specifically characteristic of snails—the dart sac (*d*) and mucous gland (*am*). The vagina and the penis open into a common genital atrium (*ga*), with an opening to the exterior far forwards on the right side.

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SUMMARY

General mesogastropod structure

The reproductive ducts of male and female mesogastropods conform to the same plan. They may be divided into the following sections:

- (1) a gonadial region forming in the male a seminal vesicle;
- (2) a renal region which conveys the eggs and sperm over a very short distance to reach the posterior end of the mantle cavity;
- (3) a glandular pallial region which passes to the mouth of the mantle cavity, and comprises an albumen gland, a capsule or jelly gland, a receptaculum seminis and a bursa copulatrix in the female; and a prostate in the male from which a narrow duct, also developed from a fold of epidermis, runs up the right side of the head to the penis.

Details of Trivia and Lamellaria

In *Trivia* and *Lamellaria* no bursa copulatrix is developed on the female duct. Owing to the lateral position of the female genital aperture in *Trivia*, and to the large size of the penis and its possession of a flagellum in *Lamellaria*, the sperm is deposited in contact with the receptaculum seminis which opens into the albumen gland at the inner end of the pallial oviduct. This is the site of fertilization. The egg capsules are the product of the pallial duct, each is basin or vase-shaped, filled with albumen in which numerous eggs float, and sealed with a plug at the external opening; their mode of formation would appear to be similar to that of the *Stenoglossa*. In both species of *Trivia* a ventral pedal gland moulds the capsule into its definitive shape and deposits it in the tissues of a compound ascidian.

Details of Turritella

In *Turritella communis*, a specialized mesogastropod, the male and female pallial ducts are open, bilobed tracts. No penis is developed in the male and the sperm are collected in the spermotheca of the female from the inhalant pallial water current. This open condition of the duct is secondary and is associated with the rigours of a ciliary feeding habit carried out in a muddy situation.

Details of Theodoxus

Theodoxus fluviatilis, although grouped amongst the archaeogastropods, has male and female genital ducts resembling those of the mesogastropods both in structure and function. In the female, however, the vagina is separate from the oviduct communicating with it only indirectly through a narrow tube which conducts sperm from the bursa copulatrix to the posterior end of the pallial oviduct. In the latter the lens-shaped capsules are produced, each with several eggs encased in a tough, resistant conchiolin wall. The lid of the egg case is reinforced with diatom cases and sand grains from the crystal sac, which collects these from the rectum and transfers them to the oviduct. From

each capsule only one individual emerges. In the male the prostate is of complex structure and extends to the genital aperture at the opening of the mantle cavity. Between the genital opening and the penis the seminal fluid passes along a gutter in the overlying mantle.

General archaeogastropod structure

In archaeogastropods in general the course of the eggs from the gonad to the mantle cavity is through a gonadial duct and the duct of the functional right kidney. The eggs are shed singly, their protective coats being a secretion either of the ovary or of the egg itself. Although a pallial section is normally absent, indications of its formation are found in *Gibbula* and *Monodonta* in the form of glandular lips surrounding the genital aperture and providing lubrication for the passage of the eggs, and in *Calliostoma* in the form of a short bilobed glandular tube which provides the gelatinous ribbon in which the eggs are embedded.

Comparison of mesogastropods, opisthobranchs and pulmonates

The evolution of the hermaphrodite genital ducts of the pulmonates and opisthobranchs from the female genital duct of their prosobranch ancestors would necessitate little structural modification: the development of sperm as well as ova in the gonad; the use of the ventral sperm channel of the pallial oviduct as a vas deferens, as well as a vaginal channel, and its extension forwards to a penis. Such a condition is found in *Actaeon*, *Aplysia*, and the aberrant opisthobranch *Onchidella celtica* and, with the addition of certain structures peculiar to snails, in *Helix*.

REFERENCES

- ANDREWS, E. A., 1935. The egg capsules of certain Neritidae. *Journ. Morph.*, Vol. LVII, pp. 31-59.
- ANKEL, W. E., 1926. Spermiozeugmenbildung durch atypische (apyrene) und typische Spermien bei *Scala* und *Janthina*. *Verh. Dtsch. zool. Ges.*, Bd. XXXI, *Zool. Anz.*, suppl. II, pp. 193-202.
- 1935. Das Gelege von *Lamellaria perspicua* L. *Zeitschr. Morphol. Ökologie Tiere*, Bd. xxx, pp. 635-47.
- 1936. Prosobranchiata, in *Der Tierwelt der Nord- und Ostsee*, Teil IX. Leipzig: Akademische Verlagsgesellschaft.
- 1937. Der feinere Bau des Kokons der Purpurschnecke *Nucella lapillus* (L.) und seine Bedeutung für das Laichleben. *Verh. Dtsch. zool. Ges.*, Bd. XXXIX, *Zool. Anz.*, suppl. x, pp. 77-86.
- BOURNE, G. C., 1908. Contributions to the morphology of the group Neritacea of Aspidobranch Gastropods. Part I. The Neritidae. *Proc. Zool. Soc. London*, pp. 810-87.
- BOUTAN, L., 1885. Recherches sur l'anatomie et le développement de la Fissurelle. *Arch. Zool. exp. gén.*, 2 sér., T. III bis, suppl. pp. 1-173.

- DRUMMOND, I. M., 1903. Notes on the development of *Paludina vivipara*, with special reference to the urinogenital organs and theories of gastropod torsion. *Quart. Journ. Micr. Sci.*, Vol. XLVI, pp. 97-143.
- EALES, N. B., 1921. *Aplysia*. L.M.B.C. Memoir, No. xxiv, pp. 1-84.
- FRANK, E. J., 1914. Beiträge zur Anatomie der Trochiden. *Jena. Zeitschr. Naturw.*, Bd. LI, pp. 377-486.
- FRETTER, V., 1941. The genital ducts of some British stenoglossan prosobranchs. *Journ. Mar. Biol. Assoc.*, Vol. xxv, pp. 173-211.
- 1943. Studies in the functional morphology and embryology of *Onchidella celtica* (Forbes & Hanley) and their bearings on its relationships. *Journ. Mar. Biol. Assoc.*, Vol. xxv, pp. 685-720.
- GERSCH, M., 1936. Der Genitalapparat und die Sexualbiologie der Nordseetrochiden. *Zeitschr. Morphol. Ökologie Tiere*, Bd. xxxi, pp. 106-50.
- GIARD, A., 1875. Sur l'embryologie du *Lamellaria perspicua*. *C.R. Acad. Sci., Paris*, T. LXXX, pp. 736-9.
- GIESE, M., 1915. Der Genitalapparat von *Calyptrea sinensis* Linn., *Crepidula unguiformis* Lam. und *Capulus hungaricus* Lam. *Zeitschr. wiss. Zool.*, Bd. CXIV, pp. 169-231.
- GRAHAM, A., 1932. On the structure and function of the alimentary canal of the limpet. *Trans. Roy. Soc. Edinb.*, Vol. LVII, pp. 287-308.
- 1938. On a ciliary process of food-collecting in the gastropod *Turritella communis* Risso. *Proc. Zool. Soc. London*, pp. 453-63.
- GUIART, J., 1901. Contribution à l'étude des Gastéropodes Opisthobranches et en particulier des Céphalaspides. *Mém. Soc. Zool. France*, T. xiv, pp. 5-219.
- HERTLING, H. & ANKEL, W. E., 1927. Bemerkungen über Laich und Jugendformen von *Littorina* und *Lacuna*. *Wiss. Meeres. Komm. Unt. Deutsch. Meere*, N.F., Abt. Helgoland, Bd. xvi, 7, 13 pp.
- KRULL, H., 1935. Anatomische Untersuchungen an einheimischen Prosobranchiern und Beiträge zur Phylogenie der Gastropoden. *Zool. Jahrb. (Anatomie)*, Bd. LX, pp. 399-464.
- LAMY, E., 1928. La ponte chez les Gastéropodes prosobranches. *Journ. Conchyliologie*, T. LXXII, pp. 25-196.
- LEBOUR, M. V., 1931. The larval stages of *Trivia europea*. *Journ. Mar. Biol. Assoc.*, Vol. xvii, pp. 819-32.
- 1933. The British species of *Trivia*: *T. arctica* and *T. monacha*. *Journ. Mar. Biol. Assoc.*, Vol. xviii, pp. 477-84.
- 1937. The eggs and larvae of the British Prosobranchs with special reference to those living in the plankton. *Journ. Mar. Biol. Assoc.*, Vol. xxii, pp. 105-66.
- LENSSEN, J., 1899. Système digestif et système génital de la *Neritina fluviatilis*. *La Cellule*, T. xvi, pp. 179-232.
- LINKE, O., 1933. Morphologie und Physiologie des Genitalapparates der Nordseelittorinen. *Wiss. Meeres. Komm. Unt. Deutsch. Meere*, N.F., Abt. Helgoland, Bd. xix, 5, 60 pp.
- 1935. Zur Morphologie und Physiologie des Genitalapparates der Süßwasserlittorinide *Cremnoconchus syhadrensis* Blandford. *Arch. Naturgesch.* N.F., Bd. iv, Heft 1, pp. 72-87.
- ORTON, J. H., 1928. Observations on *Patella vulgata*. Part I. Sex phenomena, breeding and shell-growth. *Journ. Mar. Biol. Assoc.*, Vol. xv, pp. 851-74.
- PELSENEER, P., 1911. Recherches sur l'embryologie des Gastéropodes. *Mém. Acad. Royale Belgique*, 2^e Sér., T. III, pp. 1-167.
- PORTMANN, A., 1925. Der Einfluss des Nahrerier auf die Larvenentwicklung von *Buccinum* und *Purpura*. *Zeitschr. Morphol. Ökologie Tiere*, Bd. III, pp. 526-41.

- RANDLES, W. B., 1904. Some observations on the anatomy and affinities of the Trochidae. *Quart. Journ. Micr. Sci.*, Vol. XLVIII, pp. 32-78.
- RAU, A., 1934. Anatomisch-histologische Untersuchungen an Cypraeen. *Jena. Zeitschr. Naturw.*, Bd. LXIX, pp. 83-168.
- ROBERT, A., 1902. Recherches sur le développement des Troques. *Arch. Zool. exp. gén.*, 3^e Ser., T. x, pp. 269-538.
- THIELE, J., 1935. *Handbuch der systematischen Weichtierkunde*. 4. Teil. Jena, Fischer.
- THORSON, G., 1935. Studies of the egg capsules and development of Arctic marine prosobranchs. *Medd. om Grønland*, Bd. c, pp. 1-71.
- WILLCOX, M. A., 1898. Zur Anatomie von *Acmaea fragilis*. *Jena. Zeitschr. Naturw.*, Bd. xxxii, pp. 411-56.
- WINCKWORTH, R., 1932. The British marine Mollusca. *Journ. Conch.*, Vol. xix pp. 211-52.
- WOODWARD, M. F., 1901. The anatomy of *Pleurotomaria Beyrichii* Hilg. *Quart. Journ. Micr. Sci.*, Vol. XLIV, pp. 215-68.