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OBSERVATIONS ON THE LIFE HISTORY AND FUNCTIONAL MORPHOLOGY OF *CERITHIOPSIS TUBERCULARIS* (MONTAGU) AND *TRIPHORA PERVERSA* (L.)

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(Text-figs. 1–6)

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Introduction

Cerithiopsis tubercularis occurs along the west and south-west coasts of the British Isles. It may be collected from intertidal coralline pools, especially those in which ample sponge growth occurs, or from the sheltered sponge-covered slopes and crevices of rocks, and under boulders, in the lower third of the intertidal zone. It is also dredged in Plymouth Sound and outside where, again, it is associated with sponges. *Triphora perversa* is found in a somewhat similar habitat; inshore, however, *Triphora* is confined to rock crevices and slopes within, or immediately above, the laminarian zone. In their internal anatomy these two prosobranchs have many points of resemblance, and they are placed in consecutive families of the order Mesogastropoda (Thiele, 1929). Both are of approximately the same size, the pointed tuberculate shell attaining a height of 8 mm. in *Triphora*, and 7·5 mm. in *Cerithiopsis*. The former, however, is sinistrally coiled, the latter dextrally: the organs of the mantle cavity of *Triphora* and also the nervous system are, in their arrangement, mirror images of those of the dextrally coiled *Cerithiopsis*. Their anatomy is little known: Fischer (1887) gives a drawing of the radula of *Triphora*, though this is incomplete, and more recently Risbec (1943) gives a brief description of some points in the gross anatomy of the proboscis, oesophagus and nervous system of *Triforis* (= *Triphora*) *montrouzieri*. Pelseneer (1926) describes the eggs and newly hatched larvae of *T. perversa* from the coast of Brittany, and Lebour (1933) describes and figures the external features of these larvae as well as those of two species of *Cerithiopsis*—*C. tubercularis* and *C. barleei*. She is also the first to describe the egg masses of *C. barleei* (1933) and *C. tubercularis* (1936), which are embedded in the tissues of the sponges *Ficulina ficus* and *Hymeniacidon sanguinea* respectively.

CERITHIOPSIS TUBERCULARIS (MONTAGU)

Cerithiopsis tubercularis rests on the surface of sponges, adhering by means of the copious supply of mucus from the foot, or buried in their superficial tissues so that only half the length of the shell, or even less, is visible. The animals are reluctant to feed in captivity, and it is probably for this reason that the feeding mechanism has not been observed, and the correlated structures described. Specimens collected inshore from the south coast of Cornwall show a preference for *Hymeniacidon sanguinea*, and during the late spring and summer months, which is the breeding season, a number of mature individuals may be found on a single cluster of the sponge; in early August as many as twenty have been collected from 12 sq. in. of *Hymeniacidon*. The molluscs feed on the tissues of this sponge as well as laying their eggs therein, and they suck up the tissues through a comparatively long proboscis. The feeding mechanism, however, may be difficult to see. On the few occasions when it has been observed the proboscis has been thrust out of sight through an osculum or into the irregularities of the broken surface of the sponge.

A number of young, immature specimens, averaging 1·25 mm. long, have been found on the shells of *Chlamys opercularis* in dredgings from the Rame-Eddystone Ground. These were collected in early January, presumably developed from summer spawn. In the same dredgings mature individuals 5·5 mm. long were obtained, though not on the bivalves, nor would they, like the younger ones, exploit these shells for their food when given the opportunity. The young will collect diatoms and detritus from the narrow crevices of the shells by means of the proboscis, and if separated from the bivalve will quickly return to it. Although the adult shows a special liking for sponges it will perhaps take other food, for Lebour (1933) states that 'adults were kept for a month in plunger jars and lived quite happily without the sponges, probably feeding on debris or small algae'.

The foot, by which the mollusc keeps a firm hold whilst feeding and when washed by the waves of the ebbing or flowing tide, is truncated in front and tapers to a blunt point posteriorly. It is capable of considerable and rapid distention, and frequently a temporary transverse groove demarcates the anterior half, which is rectangular in shape and contains the opaque white tissues of the anterior pedal mucous gland, from the triangular posterior half with the posterior pedal gland and the operculum. The anterior gland opens by a transverse slit along the anterior margin of the foot and comprises not only mucous glands, but a second type of cell with discrete spherules of a different type of protein filling the cytoplasm. The sole of the foot is covered by a ciliated columnar epithelium with numerous mucous cells and between the ciliated cells run ducts from sub-epithelial mucous glands. The posterior pedal gland, as in other prosobranchs of small size (Fretter, 1948), is too big to be accommodated wholly in the tissues of the foot and spreads into the haemocoel of the head where it lies anterior to, and alongside, the nerve ring. Its opening is near the middle of the sole, just within the posterior half, appearing sometimes in the form of a longitudinal slit, sometimes as a deep pit, and from it a transient, median, longitudinal groove conveys the secretion, augmented by mucus from the surface of the sole, to the posterior tip of the foot. This fluid may be used as a viscid climbing rope which allows the animal to lower itself from its inverted swimming position on the surface film of water in a rock pool, or it may be used to secure the animal on a wave-swept rock. The opening of the posterior gland leads dorsally into a ciliated duct which resembles histologically the surface of the sole, and as the duct passes inwards it bifurcates, branching to each side of the head. Each lateral branch receives two diverticula lined by tall mucous cells; no sub-epithelial glands occur.

The head bears a pair of long, linear tentacles, beset, especially around the distal half, with bristle-like motionless cilia, and as the animal moves along the tentacles are waved as though sensing the pathway. In the base of each is embedded an eye, surrounded by connective tissue and separated from the columnar epithelium by a sparse layer of muscles. No snout is developed, nor a mentum: from the anterior pedal mucous gland the dorsal surface of the foot curves upwards and backwards to the head which is concave in the transverse plane between the eyes, and in the centre of the concavity lies a small inconspicuous opening. This is the opening of the introvert (Fig. 1A, O) at the base of which the mouth (M) is placed.

The introvert is lined by columnar epithelium, slightly cuticularized and rich in mucous cells. Immediately beneath the epithelium is an intrinsic musculature of circular fibres and beneath this lie muscles which form part of the mechanism for the retraction of the proboscis. The retractors run parallel to the length of the introvert and buccal cavity from which they arise, and posteriorly they converge to form a compact, closely knit sheet (Fig. 1 A–C, R), which lies ventral to the oesophagus, alongside the columellar muscle, and so passes up the spiral of the shell to be inserted on the columella itself. Other muscles run from the gut wall directly on to the body wall, passing through the nerve ring when the proboscis is retracted. Of these many from the anterior wall of the introvert to the wall of the head are short (Fig. 1 A, D) and act as dilators, and of the longer ones three bundles are particularly conspicuous (PR)—from the head they traverse the whole length of the introvert and buccal cavity to their insertion on the wall of the anterior oesophagus, and will help in the extension of the proboscis, though this is chiefly brought about by pressure on the blood in the haemocoel exerted by the musculature of the body wall.

When the proboscis is fully everted the mouth (M) is carried to its tip and just within the buccal cavity a pair of horn-coloured jaws (J) may be visible dorsally and the tip of the odontophore (OD) ventrally. The jaws are close together, one on either side of the mid-dorsal line, and each is composed of forty or so long spikes packed tightly to form a semicircular pad. Each spike is secreted by a single epithelial cell and has an irregularly blunted tip. When the mollusc is feeding, with the proboscis thrust through an osculum to get at the softer tissues of the sponge, the jaws loosen the tissues which are then raked up into the buccal cavity by the numerous fine radular teeth. The long median teeth of the radula (Fig. 2, M) are spoon-shaped with the free edge produced into a few long spike-like cusps; the teeth lateral to these bear more numerous and shorter cusps (L). The action of both jaws and radula is lubricated by the copious saliva from the salivary glands (Fig. 1 A, RS, LS) which open one behind each jaw (ORS).

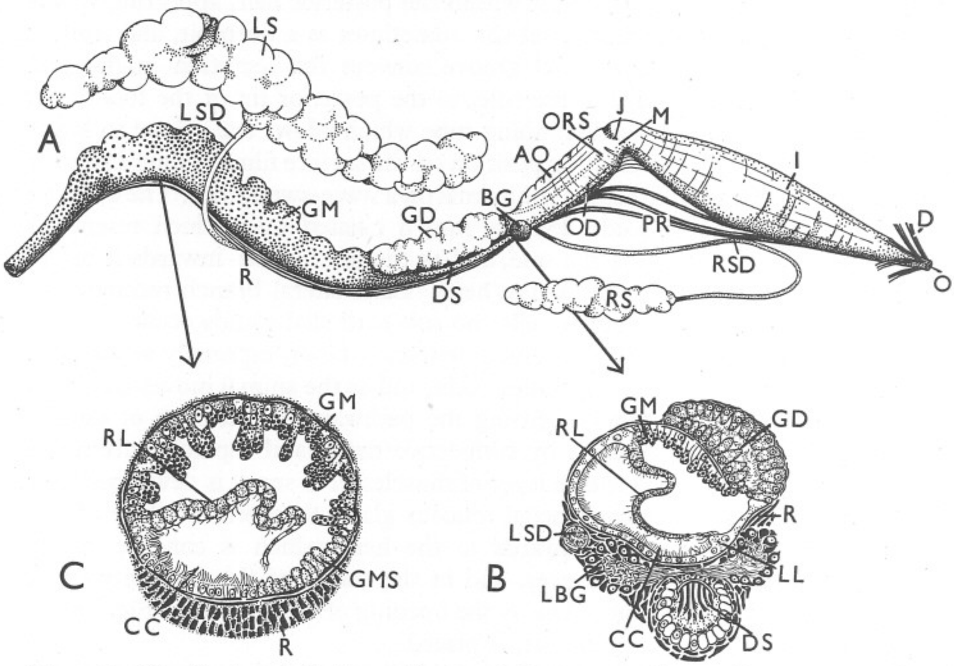

Fig. 1. *Cerithiopsis tubercularis*. A, anterior part of alimentary canal. × 40. B, transverse section at level indicated. × 240. C, transverse section at level indicated. × 170. AO, anterior limit of anterior oesophagus; BG, buccal ganglion; CC, ciliated channel; D, dilator muscles; DS, radular sac; GD, glandular diverticulum of oesophagus; GM, glandular wall of mid-oesophagus; GMS, second type of gland cell of mid-oesophagus; I, introvert; J, right jaw; LBG, left buccal ganglion; LL, left longitudinal fold; LS, left salivary gland; LSD, duct of left salivary gland; M, position of mouth; O, opening of introvert; OD, odontophore; ORS, opening of right salivary duct into buccal cavity; PR, protractor muscles of proboscis; R, retractor muscles of proboscis; RL, right longitudinal fold; RS, right salivary gland; RSD, duct of right salivary gland.

The buccal cavity and the short anterior oesophagus (AO), which lies immediately behind the point where the radular sac separates from the rest of the gut (Graham, 1939), comprise a muscular tube, its posterior limit marked by the large, conspicuous buccal ganglia (BG), the size of which is correlated with the delicate manipulative power of the proboscis. Along the roof is a narrow dorsal food channel bordered by broad, muscular folds. In the buccal cavity the epithelium of the folds has no basement membrane and the intrinsic radial muscles which dilate the dorsal channel to suck in the food penetrate between the epithelial cells; interspersed with these muscles are occasional circular and longitudinal fibres. Posteriorly, in the region of the buccal ganglia, the bases of the longitudinal folds narrow, the left becoming inconspicuous, the right deep and glandular.

The two salivary glands (RS, LS), which appear as opaque white, lobular masses in the living state, are remarkably unequal in size, and their histology is also different. Each has a long, narrow, ciliated duct (RSD, LSD) which from its opening, posterior to the jaw (ORS), runs straight back through the wall of the buccal cavity and anterior oesophagus, and then, as a result of torsion, is twisted around the oesophagus. The right duct curves over the dorsal and then down the left wall of the anterior oesophagus immediately in front of the left buccal ganglion. It then lies freely in the haemocoel and describes, when the proboscis is retracted, a forwardly directed U-shaped bend, running forward as far as the nerve ring, bending ventralwards, and reversing its course to join the small salivary gland which lies ventral to the gut. When the proboscis is protruded the duct will be carried out into the introvert along the oesophagus. The right salivary gland is a simple tube and has only one type of secretory cell, which alternates with ciliated cells and produces mucus.

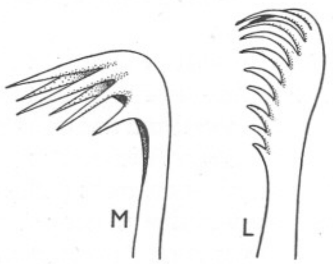

Fig. 2. *Cerithiopsis tubercularis*. Teeth of radula. ×3300. L, lateral tooth; M, median tooth.

The left salivary duct (Fig. 1 A, B, LSD) curves ventrally around the left wall of the oesophagus immediately behind the left buccal ganglion (Fig. 1 B, LBG), passes back through the thickness of the ventral retractor muscles (Fig. 1 A, R), and eventually, freed to the haemocoel, joins the central region of the relatively enormous left salivary gland (LS) which is displaced dorsally. The wall of this gland is deeply folded and, although ciliated cells alternate with gland cells in the main channels which open to the duct, it is difficult to trace ciliated cells in the finer ramifications of the gland. The secreting cells are of two types: some, the minority, produce mucus; the others are filled with small spherules which stain lightly with iron haematoxylin, whereas the surrounding cytoplasm is deep blue-black after this stain. Perhaps this second type of cell produces an enzyme which is mixed with the tissues of the sponge as they are loosened.

The oesophagus is divisible into three regions: the anterior and posterior which are short, and the middle region (GM) which is long, glandular and has a continuation of the dorsal food channel (Fig. 1 B, C, CC). The right longitudinal fold from the buccal cavity and anterior oesophagus passes into the mid-oesophagus as a thin, deep sheet of tissue (RL) which stretches across the lumen to the opposite wall, and extends down the length of the mid-oesophagus separating the dorsal glandular section from the ventral ciliated area. The insignificant left fold is difficult to trace beyond the initial region of the mid-oesophagus (Fig. 1 B, LL). The first 90° of torsion occurs in the region of the buccal ganglia, and is an abrupt twist which brings the originally dorsal ciliated area on to the left side (CC), and the right longitudinal fold on to the dorsal wall (RL); to the right of this fold the wall of the oesophagus is glandular. The second 90° of torsion is more gradual and at its completion the glandular region comprises the dorsal and lateral walls; the smaller ciliated area is ventral.

If an animal be dissected the glandular area of the oesophagus is seen to be divisible into two regions: along the whole of its length the gland cells which form the dorsal and dorso-lateral epithelium of the mid-oesophagus are emerald green in colour (Fig. 1, GM) but, in contrast, there is anteriorly a mass of white glands against the right wall. This is a diverticulum (Fig. 1 A, B, GD) of mucous cells alternating with ciliated cells which opens at its anterior end to the anterior oesophagus beneath the small left longitudinal fold, and marks the posterior end of this part of the gut. The diverticulum is involved in the first 90° torsion of the gut so that its free end stretches back along the right wall of the oesophagus. A diverticulum in a corresponding position, though thin-walled and larger, is present in *Lamellaria perspicua* anterior to a large oesophageal pouch which has its secreting area increased by the development of deep septa. Behind it in *Cerithiopsis* there is no swollen pouch: the presence of such would be impracticable, for the mid-oesophagus must be narrow enough to pass through the confined space in the nerve ring when the proboscis is protruded. Thus, although an equivalent amount of secreting area is developed in *Cerithiopsis*, it is not concentrated, but spread along the elongated section of the oesophageal tube, covering three-quarters of the wall. In *Lamellaria* and in *Trivia arctica* and *T. monacha* the right longitudinal fold which borders the dorsal food channel and passes back from the buccal cavity to the oesophagus, is deeper than the left. This discrepancy is much more pronounced in *Cerithiopsis* (Fig. 1 B, C, RL), where the right fold partitions off the glandular area from the ciliated channel (CC), acting, perhaps, as a valve to prevent the suction of the secretion from the oesophageal glands into the proboscis when it is extended. The fold gradually tapers away towards the posterior end of the mid-oesophagus. It is formed of a fold of epithelium with very little connective tissue between the two layers of cells. On one side, that facing the ciliated channel, the epithelium consists of large mucous cells and wedge-shaped ciliated cells between them; on the other side the cells are flattened and bear no cilia.

The common type of gland cell, which is filled with green spherules in the living tissue, is little affected by acid fixatives; with iron haematoxylin the spherules stain lightly and with azan they stain blue. Between these glands and the ciliated cells on the post-torsional right side of the mid-oesophagus, that is, facing the free edge of the longitudinal septum, is a longitudinal strip of another type of epithelial gland (Fig. 1 C, GMS) in which the cytoplasm is filled with globular secretion masses, colourless during life, dissolving readily in acid fixatives. The cytoplasm of these cells stains deeply with iron haematoxylin and red with azan.

The short posterior oesophagus is ciliated throughout; the tube is narrow, of capillary dimensions, and runs straight back immediately above the columellar muscle to open into the antero-ventral wall of the stomach which is a small bag receiving two ducts from the digestive gland—one ventral and not far behind the oesophageal opening, the other dorsal and not far behind the antero-dorsal intestinal opening. The stomach is lined by an epithelium on which the cilia are densely packed and in no part is there a cuticular covering; the musculature is rather poorly developed. After a meal the lumen may be filled with the tissues of *Hymeniacidon* including long monaxon spicules, and nothing but a sheet of mucus shields the gastric wall. This general simplification of structure, in which the stomach is little more than a crop in which the meal lies to undergo digestion and from which the products of digestion are passed to the digestive gland, is paralleled in dorids which have adopted a similar diet. Throughout the gastropods such simplification is mainly correlated with the development of a macrophagous carnivorous habit and extracellular digestive processes (Graham, 1949).

From its origin the intestine passes dorsally over the kidney and forwards along the right side of the mantle cavity to the anus, which lies well within this cavity. It is ciliated throughout. The middle region is distinguished histologically by the large number of gland cells scattered amongst the ciliated cells. Each is filled with colourless spherules which respond readily to stains for protein, and when discharged the secretion droplet swells giving an irregular and indistinct outline, and presumably helps to elaborate the faecal rod around which the secretion can be traced. The rod contains not only sponge spicules but orange concretions pigmented like the sponge on which the mollusc feeds and similar to the concretions in the faeces of *Diodora apertura*, which also feeds on *Hymeniacidon*. Three types of cell occur in the tubules of the digestive gland: two are rather infrequent and confined to the crypts; elsewhere the digestive cell occurs. Fluid contents from the stomach and extremely minute particles of food can be traced to the vacuoles of the digestive cell, where presumably digestion is completed. These vacuoles may occupy a half or two-thirds of the cytoplasm, whilst below them are tightly packed spherules. In a starved individual the spherules fill the entire cell, and sections of an individual which was interrupted at the commencement of a meal suggest that they are secretory: they can be traced into the tubules of the gland and into the ducts where they swell and their identity is ultimately lost. The cells in the crypts of the tubules are highly vacuolated throughout, and the vacuoles contain spherules. In one type of cell, the more numerous, the spherules, apparently colourless at first, may change in consistency and coalesce into brown masses which have the appearance of excretory matter. The second type of cell contains lime spherules.

In *Cerithiopsis* the sexes are separate and in both male and female the glandular pallial section of the genital duct is open along its length to the mantle cavity. As in other mesogastropods in which this duct is open—*Turritella communis* (Fretter, 1946), *Bittium reticulatum* and *Scala communis* (Johansson, 1947)—no penis is present. The transference of sperm to the female was once observed during August when ten individuals, together with the piece of *Hymeniacidon* on which they were found, were kept under observation. The molluscs were clustered together, and from the males sperm mixed with prostatic secretion left the mantle cavity in the exhalant stream and clouded the surrounding water. Little dispersal of the sperm occurred, however, for immediately the fluid was sucked through the short inhalant siphons of the adjacent females—the ultimate destination of the sperm was traced in sections.

In the testis both eupyrene and apyrene spermatozoa are developed and are stored in the large vesicula seminalis which constitutes the initial part of the vas deferens. The apyrene sperm have not been traced farther forwards in the duct, nor have they been seen in the female. From the vesicula seminalis a short vas deferens, closed by a sphincter except during copulation, passes forwards over the columellar muscle on the right side of the visceral mass and opens to the prostate, the pallial vas deferens, which lies along the junction of body wall with mantle skirt on the right side. The prostate has deep lateral walls joined by a narrow dorsal wall, and is open ventrally. Its epithelium consists of tall gland cells alternating with ciliated cells: proximally the glands respond to stains specific for mucus, whilst anteriorly, throughout the greater length of the duct, only an occasional cell secretes mucus, and there is a second type of gland in which the cytoplasm is uniformly vacuolated and the vacuoles contain spherules staining lightly with iron haematoxylin. The pallial duct extends along the mantle cavity as far as the level of the anus.

The disposition of the female genital duct is similar to that of the male. From the ovary a short ovarian duct, with an epithelium similar to that of the gonad, passes forwards along the right side of the visceral mass, just above the columellar muscle, to the renal oviduct. This is short and ciliated, leading to the postero-ventral limit of the pallial duct. The pallial duct is better developed than the homologous region, the prostate, in the male, though, like it, it has deep lateral walls joined by a narrow dorsal wall, and, except at the extreme posterior end where there is a small cul-de-sac, it is open along its ventral edge. The cul-de-sac receives ventrally the renal oviduct and dorsally it accommodates spermatozoa received from the male by way of the inhalant water current. If a female be fixed immediately after taking up a supply of spermatozoa, sections

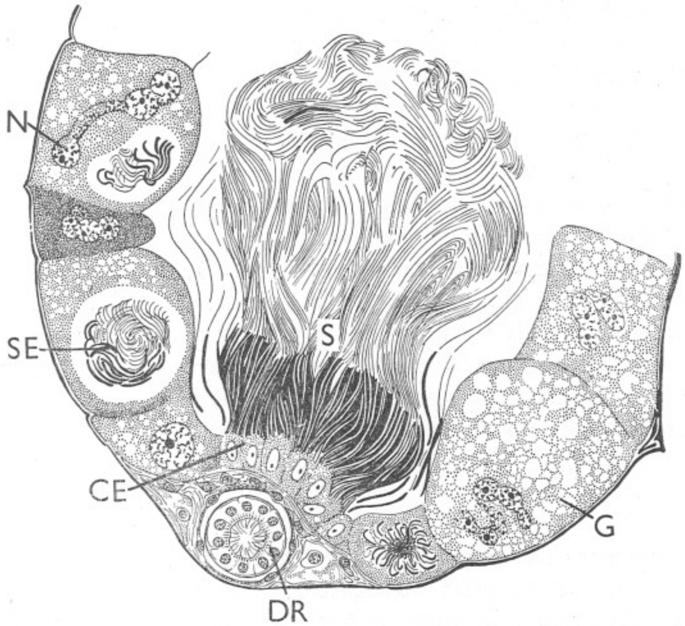

Fig. 3. *Cerithiopsis tubercularis*. Part of a transverse section through a receptaculum seminis. × 357. CE, columnar epithelium surrounding entrance to receptaculum; DR, duct leading to receptaculum; G, gland cells; N, nucleus; S, orientated spermatozoa; SE, spermatozoa in vacuoles of epithelial cells.

show that many of the sperm are concentrated in a limited region of the pallial duct, along the dorsal wall, at the entrance to the cul-de-sac. Here there is a small, shallow pouch, lined only by ciliated cells, where the sperm may be orientated. Still other spermatozoa have travelled up a muscular and ciliated duct which leads dorsally from this pouch and bifurcates at its distal end. Each bifurcation (Fig. 3, DR) opens to a receptaculum, the two receptacula lying one above the other on the right side of the rectum. They are approximately spherical sacs lined, except around the entrance, by relatively enormous cells (G) in which the long nuclei (N), each with a number of nucleoli, may be twisted into a variety of shapes. The cytoplasm of these cells is vacuolated and contains spherules which dissolve in acid fixatives. Around the entrance to the receptaculum is a circular patch of low, columnar epithelium (CE) and in its distal cytoplasm the heads of spermatozoa (S) are embedded. Not all the sperm are thus accommodated: others lie in tangled balls in vacuoles of the giant epithelial cells (SE) and here they appear to undergo digestion.

The gland cells of the pallial duct alternate with ciliated cells and are especially tall in the lateral walls. The cul-de-sac has mucous cells only. Anteriorly, the spherules which fill the secreting cells are of uniform size and are colourless in living tissue: near the cul-de-sac they respond slightly to mucicarmine and celestine blue; elsewhere they stain lightly with iron haematoxylin and the cytoplasm in which they are embedded stains deeply. These anterior glands produce a colourless fibrillar secretion which forms the resistant coat of the egg capsule, the posterior part of the pallial duct giving the albumen in which the eggs are embedded.

At the level of the anus the gland cells of the pallial duct are replaced by ciliated cells, and the duct is reduced in diameter. It extends beyond the anus as a shallow, ciliated groove leading towards the mouth of the mantle cavity, and ends a short distance from this opening.

Within the mantle cavity alongside the posterior third of the pallial duct and extending back to the kidney aperture is a ventral gutter which is lined by mucous glands and cells with exceptionally long cilia. It runs between the body wall and the median wall of the oviduct, providing a pathway by which sperm are directed first to the proximal part of the pallial oviduct and then to the receptaculum. It has no homologue in the male.

TRIPHORA PERVERSA (L.)

Triphora perversa is the only British member of the family Triphoridae and consequently the only British mesogastropod which is typically sinistrally coiled. This direction of coiling, determined by a reversal of the normal cleavage pattern, brings about a reversal of the arrangement of the organs in the mantle cavity: the osphradium and ctenidium are on the right side, which receives the inhalant stream of water by way of a short siphon, and the rectum and genital duct are on the left. The visceral loop of the nervous system shows, moreover, that the direction of torsion is also reversed, for the left pleuro-visceral connective with its parietal ganglion is supra-oesophageal. The ganglion is thus close to the osphradium which it innervates, and the right connective runs ventral to the gut bringing the right parietal ganglion beneath the oesophagus. The pleuro-parietal connectives are short as in the Cerithiidae, concentrating the parietal ganglia in the head. The visceral ganglia, however, lie posteriorly, near the stomach, and their long fine connectives with the parietals, lengthened on account of the development of the introvert, are difficult to trace.

When the animal is crawling the exposed parts of the body, opaque white in colour, can be seen to resemble those of *Cerithiopsis*, and this resemblance extends to feeding habits as well.

Specimens of *Triphora perversa* collected from the laminarian zone of south Cornwall have frequently large numbers of monaxon, siliceous sponge spicules in their stomachs, and with these diatoms may occur. In captivity, the animals rarely feed though supplied with fresh *Hymeniacidon* and *Halichondria*—the sponges with which they are associated on the shore and in the substance of which the shell may be partly or completely hidden. On two occasions only has the protrusion of the proboscis been observed; on one of these tissues of *Halichondria panicea* were sucked into the gut. The proboscis was thrust out of sight through an osculum of the sponge, seeking presumably the softer tissues. The surface of the proboscis is covered by an epithelium containing two types of glands: the more numerous is a mucous cell; in the second the secretion appears as minute discrete granules which are colourless in the living tissue and

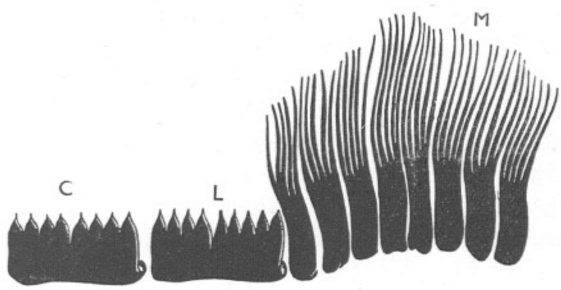

Fig. 4. *Triphora perversa*. Half row of radular teeth. × 1700. C, central tooth; L, lateral tooth; M, marginal tooth.

so numerous that they obscure the large basal nucleus. The epithelium is surrounded by its intrinsic layer of circular muscle fibres and external to these are the muscles of the proboscis which run back to their insertion on the columella.

When the proboscis is fully everted a pair of dorso-lateral jaws is brought to its tip, and ventral to them lie the teeth of the radula. The jaws form two large triangular plates which surround the buccal cavity anterior to the odontophore, the broad bases of the triangles meeting mid-dorsally. Their blunt spikes, each comprising the secretion from a single cell and providing a flattened plate slightly raised in the centre, are firmly sutured together, the sutures being slightly wavy. The superficial appearance of these jaws is reminiscent of the jaws of a skate. The radula consists of numerous rows of minute teeth. In each row the single central tooth (Fig. 4, C), attaining 10μ broad and 5μ high, has eight equal cusps, short and broad, and arranged in two groups which are separated from one another by a fissure. This tooth is bordered on each side by a single lateral (L) differing from it only in the number of cusps, nine, and these are again arranged in two groups separated by a fissure; the number of lateral cusps varies from five to six, and in the median group there are either four or three. The numerous marginal teeth (M) are each about one-third the breadth of the central or lateral, and the longest may attain four times the height; the distal end is frayed out into fine pliable processes which sweep into the buccal cavity the tissues loosened by the jaws and by the biting teeth of the radula. Dorsal to the odontophore the buccal cavity is cuticularized.

Within the extended proboscis is the narrow, muscular oesophagus, which passes back from the buccal cavity, and the large salivary glands. The saliva is poured into the oesophagus, not far from its origin, by a single glandular duct which is divided histologically into two regions and is formed by the union of two short ducts from a pair of glands. These glands are enormous and unequal in size; when the proboscis is retracted the larger extends anteriorly as far as the nerve ring and posteriorly as far as the stomach; the smaller lies wholly behind the introvert, mainly ventral to the oesophageal tube and to the larger gland. It is a simple tubular gland, whereas the walls of the dorsal one are folded and its lumen insignificant. Three types of secreting cells occur in the salivary glands, and all of them are large with conspicuous nuclei. In both glands there are mucous cells, relatively more numerous in the ventral one, where they comprise more than half the epithelium. In the dorsal gland there is a second type of cell with spherules of irregular shape and size which stain with mucicarmine and also, deeply, with iron haematoxylin: the abundance of this kind of cell would appear to vary, for it may comprise about half the gland or only a small fraction; the frequency is inversely proportional to the third type of secreting cell which, although of constant occurrence and abundance in the ventral salivary gland, may be exceedingly infrequent in the dorsal. In this third type the cytoplasm is filled with spherules of uniform size which stain lightly with iron haematoxylin; the cytoplasm stains even lighter. A few of these cells may be found in the initial region of the duct from each gland, scattered amongst the mucous cells which comprise most of the epithelium. Along each duct, however, is a longitudinal strip of low cubical cells and after the ducts have united this non-glandular tract persists for a while together with the mucous epithelium. About half-way along its course the duct broadens and there is an abrupt histological change, and for the rest of its course—to its junction with the oesophagus—the most common type of cell is one filled with protein spherules which are not mucous and are unlike any in the gland. This cell makes up the whole of the secretory epithelium, except for a narrow longitudinal strip of mucous cells which continues to the oesophagus.

When the proboscis is withdrawn into the haemocoel, it passes through the confines of the nerve ring, which necessarily restricts its diameter, and comes to lie in the first two coils of the tightly spiralled shell: the mouth is now at its base; the long connectives between the cerebral and large buccal ganglia are directed posteriorly, the ganglia lying between the anterior end of the oesophagus and the ventral radular sac; the oesophagus is thrown into deep coils.

The oesophagus is a narrow muscular tube of uniform structure throughout the greater part of its length, surrounded by the retractor muscles of the proboscis. It is lined by a ciliated, columnar epithelium with only an occasional mucous cell; no dorsal folds can be traced along its length revealing the position of torsion. In *Triphora* the glandular areas are separated from the oesophageal tube. Not far from the stomach a pouch lies over the oesophagus and communicates with it dorsally at its posterior end (Fig. 5, GP). The dorsal and lateral epithelia of the pouch are thrown into numerous, deep, transverse folds (TF) which subdivide the lumen; radial muscles penetrate the folds and circular muscles form a thin outer coat. The epithelial cells are all secretory and they are of small size; the majority of the cells are filled with spherules which give

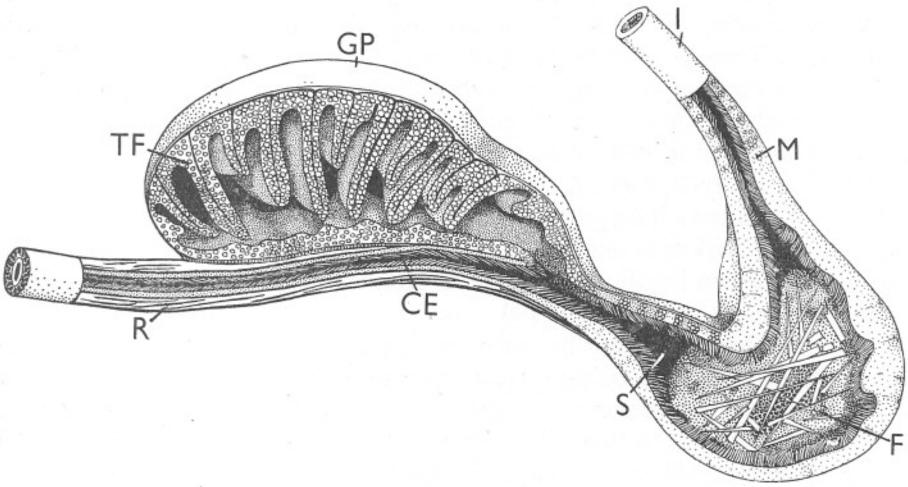

Fig. 5. *Triphora perversa*. Diagrammatic longitudinal section through the posterior oesophageal region, stomach and part of the intestine. × 140. CE, ciliated epithelium of oesophagus; F, food in stomach; GP, glandular pouch; I, intestine; M, mucous cells of mid-intestine; R, retractor muscle of proboscis; S, stomach; TF, transverse folds of epithelium.

the gland a yellowish appearance in the living state and are resistant to acid fixatives. With iron haematoxylin the spherules may all stain lightly, or some very deeply, and this difference in staining would appear to indicate stages in the elaboration of the final secretion—the lightly staining spherules being the precursors of the deeply staining ones. A considerable number of mucous cells also occurs in the epithelium; this is contrary to the typical condition in the lateral glandular pouches of the mid-oesophagus of gastropods for their function is to secrete enzymes, and only on rare occasions do they possess even a few cells secreting mucus or other lubricants (Graham, 1941).

At the posterior end of the oesophagus, between the opening of the gland and the stomach, the epithelium has exceptionally long cilia which direct a current posteriorly; along the dorsal wall are numerous mucous cells.

The plan of the rest of the digestive system is similar to that of *Cerithiopsis*: the stomach (S), a simple ciliated sac receiving anteriorly the opening of the oesophagus and above that the opening of the intestine; the intestine (I), a practically straight tube which leads over the kidney to the mantle cavity where, however, it runs along the *left* side to open towards the anterior end. The main duct from the digestive gland opens to the posterior wall of the stomach and anteriorly there is a small lobe of the gland which opens behind the opening of the intestine. The epithelium of the gland consists of tall club-shaped digestive cells, and excretory cells confined to the crypts of the tubules. The cytoplasm of the digestive cell is always vacuolated, although the details of its appearance depend upon the exact physiological state in which it is examined. In a starved individual the vacuoles appear to contain a uniform type of spherule, homogeneous in consistency and presumably containing a zymogen. There is only slight evidence that these are secretory for I have seen a few spherules freed into the lumen of the gland only on rare occasions. Sometime after a meal the distal ends of many of the digestive cells contain food vacuoles with ingested matter, fluid and minutely particulate; and much later yellow spherules, which can be traced to the faeces, occur in the same position. The stomach frequently contains numerous siliceous sponge spicules (F), and these appear to constitute the greater bulk of the faecal pellets; they are wrapped around with mucus which is secreted in large quantities from the epithelium of the mid-intestine (M).

The reproductive system in both sexes of *Triphora perversa* has an open pallial duct without sub-epithelial glands, and in the male there is no penis. It may be assumed from their close similarity in structure that the functioning of these ducts is similar to that of *Cerithiopsis*. There is, however, a difference in the receptaculum seminis which in *Triphora*, although lined by gland cells, shows no evidence of sperm absorption.

Discussion

Amongst the carnivorous gastropods there are several which browse on the tissues of sponges: *Diodora apertura* and some dorids may live exclusively on siliceous forms, rasping the surface tissues and taking relatively large mouthfuls into the gut. *Cerithiopsis tubercularis* and *Triphora perversa* are also sponge feeders, but they have adopted a different feeding habit. The acrembolic proboscis characteristic of many families of the mesogastropods has been lengthened in these two small animals so that it is long enough to pass through an osculum and reach the inner tissues of the sponge. In this way the spicular cortex which protects the sponge externally is avoided, and the softer parts sucked into the oesophagus; nevertheless, some spicules are taken up. The development of a long proboscis demands some modifications of the anterior part of the gut since this must move forwards through the narrow gap in the nerve ring when the animal is about to feed and be withdrawn later. This involves an increase in length and a removal of projections which might obstruct its movement.

The oesophagus of the primitive gastropod is divisible into three regions: the anterior oesophagus which begins at the point where the radular sac separates from the gut; the mid-oesophagus with the dorsal food channel along its roof, and on each side a glandular region from which digestive enzymes are secreted; and behind this the posterior oesophagus. In this original condition the mid-oesophagus is swollen. The oesophageal glands are lost in some mesogastropods and the diameter of the tube then becomes uniform. This, however, occurs mainly in herbivorous forms, especially those with a constant stream of food into the gut, and the pouches are then replaced by a crystalline style in the stomach producing an amylase. In carnivores (Graham, 1939) where the next meal is unpredictable, the extracellular enzymes are better supplied by a gland under nervous control than by an automatic crystalline style; moreover, the demand is much more likely to be for a free proteolytic enzyme. In *Cerithiopsis tubercularis* the modifications of this region are met by the modification of the mid-oesophagus which is lengthened, with a consequent narrowing of its total diameter, and the glands are no longer concentrated in lateral areas as in the primitive prosobranch, but spread along the morphologically ventral and lateral walls; all trace of their paired origin is lost. The ciliated food channel covers the remaining wall and is separated from the glands by a longitudinal septum: this is the right dorsal fold which originates in the buccal cavity, bordering the dorsal channel, and remains normal in size until it reaches the posterior end of the anterior oesophagus when it rapidly enlarges and extends across the lumen to reach the opposite wall, even when the oesophagus is dilated. It not only provides mucus to lubricate the ciliated food channel where mucous cells are lacking, but also acts as a valve to prevent the sucking forwards of secretion from the oesophageal glands when the proboscis is extended during feeding.

The mid-oesophagus is, in all prosobranchs, involved in torsion; in *Cerithiopsis* this twisting of the gut includes also the posterior end of the anterior oesophagus. Into this posterior end opens a mucous pouch, attached ventro-laterally, but rotated on to the right side. There is no evidence that food is taken into the pouch: its epithelium is tall and glandular and the lumen relatively small; its opening beneath the small left dorsal fold may be covered by the free edge of the right fold. A ventral diverticulum from the oesophagus, immediately anterior to the oesophageal gland, is described by Amaudrut (1898) in *Cypraea arabica* and occurs in *Lamellaria perspicua*; in these molluscs, however, the diverticulum is larger, thin-walled and not differentiated histologically from the surrounding tissue: it may merely provide extra space in the oesophagus. The diverticulum in *Cerithiopsis* secretes a lubricant to augment the secretion from the right dorsal fold; the left fold has no mucous cells and cannot be traced beyond the anterior oesophagus.

The modifications in the oesophagus in *Triphora perversa* are more difficult to interpret. This region of the gut shows several anomalies: it consists of a muscular and ciliated tube which is elongated so that it must be looped within the haemocoel when the proboscis is withdrawn; it receives anteriorly the secretion from the salivary glands by a median glandular duct which is divided histologically into a proximal and distal part; the gland which opens into its dorsal wall posteriorly has a secreting epithelium which differs from that of the typical oesophageal glands in that it includes an appreciable number of mucous cells. From the structure of the oesophagus it is impossible to deduce the site of torsion. The fusion of the two ducts of the salivary glands to a single broad channel where, in the distal part, the common type of secreting cell is unlike any in the glands, and the fact that they discharge into the oesophagus,

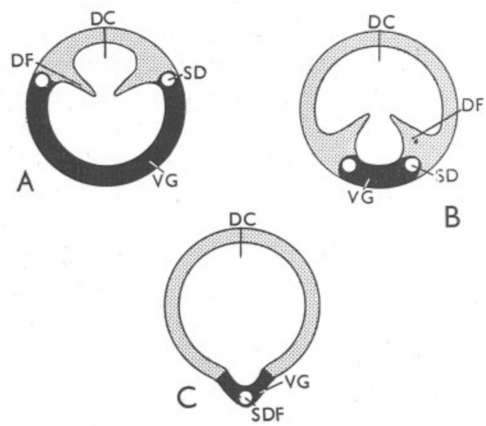

Fig. 6. A–C. Diagrams to illustrate the suggested relations of the dorsal food channel, ventral glandular region of the oesophagus and salivary ducts described on p. 578. DC, dorsal channel; DF, dorsal fold; SD, salivary duct; SDF, fused salivary ducts; VG, ventral glandular part of mid-oesophagus.

are, it would seem, conditions unparalleled in the gastropods. Typically, as in *Cerithiopsis*, the salivary ducts open into the buccal cavity, one on the outer side of each dorsal fold, and they (Fig. 6A, SD) may run back through the connective tissue of the anterior oesophagus along the base of the folds (DF) before passing to the haemocoel. Now the dorsal channel (DC) may be expanded and the ventral glandular part (VG) of the mid-oesophagus correspondingly reduced by the dorsal folds migrating ventrally (Fig. 6B), as has happened for example in the Stenoglossa (Graham, 1941), and when this takes place the salivary ducts (SD) migrate with them so that they come to lie side by side under the reduced ventral part of the oesophagus (VG). They may eventually fuse with one another and by losing their anterior sections open into the oesophagus here instead of into the buccal cavity (Fig. 6C). Now suppose that the ventral glandular part of the oesophagus, into which the single median salivary duct now opens, is stripped off the remainder of the oesophagus from the anterior end backwards, then the conditions which obtain in *Triphora perversa* have been accurately reproduced—the oesophageal tube representing the dorsal food channel, the median glandular duct the oesophageal gland which has fused along its length with the proximal end of the salivary duct so that this opens into its posterior part, the line of fusion being represented by a longitudinal strip of mucous cells.

This interpretation of the oesophagus of *Triphora* does not account for the presence of a posterior dorsal gland which is constricted from the oesophagus not far from its junction with the stomach. The gland may represent a novel structure. That the oesophagus of the gastropod does give rise to such new parts is evident in the Buccinacea, the only family of the Stenoglossa with a dorsal caecum on the posterior oesophagus. The gland in *Triphora* agrees with this caecum in position, in the deep folding of its walls, and in possessing a number of goblet cells; but it differs from it in having an epithelium which, except for mucous cells, is histologically distinct from any other in the oesophagus. Brock (1936) suggests that the caecum in *Buccinum undatum* is merely an enlargement of the oesophagus to provide extra accommodation, and food with digestive enzymes enter it from the oesophagus; in *Triphora* there is no evidence that food is taken into the gland.

An open pallial genital duct in both sexes is known to occur in a number of families of the mesogastropods (Johansson, 1947) and is associated with the absence of a penis. It was described in *Turritella communis* (Fretter, 1946), a ciliary feeder living in a muddy situation, and was thought to be associated with the precautions which prevent excessive sediment entering the mantle cavity. To account for the open duct in such forms as *Bittium reticulatum*, *Scala communis* (= *Clathrus clathrus*) (Johansson, 1947), *Cerithiopsis tubercularis* and *Triphora perversa* seems perhaps at first sight more difficult; it is undoubtedly secondary and presumably advantageous.

It is well known that the mantle cavity of gastropods has to subserve a variety of functions mainly effected by a stream of water through it. In gastropods with a helicoid spiral shell the shape of this cavity varies considerably and is reflected in the form of the shell. This may be a close spiral with a small apical angle (e.g. *Cerithiopsis* and *Triphora*) or a rapidly expanding spiral with a large apical angle (e.g. *Lamellaria*); in the former case the mantle cavity is narrow and deep, in the latter broad and comparatively shallow. In the second group of gastropods the swelling of the pallial oviduct in the female, which occurs during the breeding season, and the presence of the penis in the male with its insertion into the pallial oviduct during copulation, would not interfere with the efficient functioning of the mantle cavity—in fact in viviparous forms like *Littorina saxatilis* there is sufficient space for the pallial oviduct to form a brood pouch accommodating a large number of embryos. The deep mantle cavity of *Turritella*, *Bittium*, *Cerithiopsis*, *Triphora* and *Clathrus*, which contains a large gill following the course of the tight spiral of the shell, may have reached the minimal breadth for maintaining a proper ventilation of the whole cavity, and should it be still further restricted by the presence of a penis or a swelling genital duct its breadth might be brought below the limit for efficiency. Perhaps it is for this reason that the penis is lost and the sperm transferred to the female by a method involving an open pallial duct; moreover, in these molluscs the duct is long and thin without sub-epithelial gland cells. To test this hypothesis the examination of the shells of a series of mesogastropods was made.

The general appearance of a helicoid spiral shell depends upon (i) the angle of the equiangular spiral α, and (ii) the angle β which a tangent to the whorls makes with the axis of the shell—the half apical angle (Thompson, 1942).

TABLE I

Species with an open pallial genital duct in both sexes	No. examined	Average value for β
Turritella communis	10	8·5°
Bittium reticulatum	5	5·25°
Cerithiopsis tubercularis	6	3·25°
Triphora perversa	5	5·5°
Clathrus clathrus	8	7·5°
Species with a closed pallial genital duct in both sexes		
Littorina littorea	12	40·6°
Littorina saxatilis	12	39·0°
Rissoa parva	8	16·0°
Natica poliana	6	47·3°

These two values may change with age. A mean low value for the half apical angle β indicates a tall spire which, with tightly packed whorls, would have a high value for the spiral angle α, as in *Tenebra triseriata* where the spiral angle is 89·2° (Moore, 1936); on a flattened shell it would be impossible to pack the whorls so tightly. A flattened spire has a high value of β, e.g. *Velutina*, *Lamellaria* and *Planorbis*, the extreme case being in the pulmonate with a half apical angle of 90°; the two members of the Lamellariidae have a lower value of α, for their shells are rapidly expanding spirals. The difference in the magnitude of the spiral angle of such diverse shells as *Turritella* and *Natica* may only be 2° (Thompson, 1942), and since such a very small change in α may be associated with such disparity in shape it is clear that it is upon the angle β that the difference in their form mainly depends. Consequently, β is taken as the value of importance in the present consideration, and has been measured as the angle between the tangent to the last two whorls of the shell of mature individuals and the axis of the shell. The last two whorls were selected as they enclose the mantle cavity (Table I).

In all the British mesogastropods in which an open genital duct has been described in both sexes and there is no penis, β does not on the average exceed

8·5°, and in these species the mouth of the shell is small, about one-fifth of the height or less; the ctenidium is well developed and occupies a large part of the mantle cavity. In such tightly coiled spirals there will be a greater degree of shortening of the right side of the body and so less space for the right half of the pallial complex, which is, in the mesogastropod, the genital duct and rectum.

In some other mesogastropods the penis is lost and the pallial genital duct is open at least in one sex. From the description of a female *Cerithium telescopium* by Berkeley & Hoffman (1835) one may conclude that the pallial duct is open; the shell of this species is tightly coiled, with a small value for β (11·5°) and a very restricted opening. The pallial duct is also open in *Fagotia esperi* (Soós, 1936), in the male of *Cerithium vulgatum* (Johansson, 1947) and in the female of *Melanopsis dufourei* (Sunderbrink, 1929), but in these the body whorl of the shell is deep, though compressed, and its opening long, suggesting the presence of a more spacious mantle cavity. It may be that the specialized condition in these three molluscs is to be related to some unknown factor in their mode of life rather than to the shape of the shell. An alteration in shell shape may be recent and the structure of the genital duct not yet changed from the ancestral condition to conform to the new type of shell.

Summary

Cerithiopsis tubercularis and *Triphora perversa* feed on siliceous sponges: a long proboscis is thrust through an osculum of the sponge, or into breaks in the surface, to reach the softer parts. These are loosened by jaws, entangled in saliva and swept into the buccal cavity by the radula.

The formation of a long introvert, which must be withdrawn through the narrow space in the nerve ring and narrow enough to go through an osculum, has brought about (i) a lengthening of the mid-oesophagus in *Cerithiopsis*, with a narrowing of its diameter, and a spreading of the oesophageal glands along its length, (ii) in *Triphora*, a reduction of the ventral glandular part of the mid-oesophagus, its stripping from the food channel and a displacement of the salivary ducts so that they open into the glandular part of the oesophagus. In *Triphora* there is a dorsal gland of unknown function on the posterior oesophagus.

The stomach in both species is a simple ciliated sac: the oesophagus opens anteriorly and ventrally, and the intestine originates above this opening; there are two ducts from the digestive gland.

The pallial region of the male and female genital duct is open; and there is no penis. It is suggested that the open condition of the duct and the absence of a penis in the mesogastropods is correlated with a long, narrow mantle cavity which contains a relatively large ctenidium.

REFERENCES

AMAUDRUT, A., 1898. La partie antérieure du tube digestif et la torsion chez les mollusques gastéropodes. *Ann. Sci. Nat. Zool.*, Sér. 7, Vol. VIII, pp. 1–291.

BERKELEY, M. J. & HOFFMAN, G. H., 1835. A description of the anatomical structure of *Cerithium telescopium* Brug. *Zool. Journ.*, Vol. V., pp. 431–9.

BROCK, F., 1936. Suche, Aufnahme und enzymatische Spaltung der Nahrung durch die Wellhornschnecke *Buccinum undatum* L. *Zoologica, Stuttgart*, Vol. XXXIV, pp. 1–136.

FISCHER, P., 1887. *Manuel de Conchyliologie*. Paris.

FRETTER, V., 1946. The genital ducts of *Theodoxus*, *Lamellaria* and *Trivia*, and a discussion on their evolution in the prosobranchs. *Journ. Mar. Biol. Assoc.*, Vol. XXVI, pp. 312–51.

—— 1948. The structure and life history of some minute prosobranchs of rock pools: *Skeneopsis planorbis* (Fabricius), *Omalogyra atomus* (Philippi), *Rissoella diaphana* (Alder) and *Rissoella opalina* (Jeffreys). *Journ. Mar. Biol. Assoc.*, Vol. XXVII, pp. 597–632.

GRAHAM, A., 1939. On the structure of the alimentary canal of style-bearing prosobranchs. *Proc. Zool. Soc. London*, B, Vol. CIX, pp. 75–112.

—— 1941. The oesophagus of the stenoglossan prosobranchs. *Proc. Roy. Soc. Edin.*, B, Vol. LXI, pp. 1–23.

—— 1949. The molluscan stomach. *Trans. Roy. Soc. Edin.* Vol. LXI, pp. 737–78.

JOHANSSON, J., 1947. Über den offenen Uterus bei einigen Monotocardiern ohne Kopulationsorgan. *Zool. Bidrag, Uppsala* Vol. XXV, pp. 102–10.

LEBOUR, M. V., 1933. The life-histories of *Cerithiopsis tubercularis* (Montagu), *C. barleei* Jeffreys and *Triphora perversa* (L). *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 491–8.

—— 1936. Notes on the eggs and larvae of some Plymouth prosobranchs. *Journ. Mar. Biol. Assoc.*, Vol. XX, pp. 547–65.

MOORE, H. B., 1936. The biology of *Purpura lapillus*. I. Shell variation in relation to environment. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 61–89.

PELSENEER, P., 1926. Notes d'embryologie malacologiques. *Bull. Biol. France Belgique*, Vol. LX, pp. 88–112.

RISBEC, J., 1943. Recherches anatomiques sur les Prosobranches de Nouvelle-Calédonie. *Ann. Sci. Nat. Zool.*, Vol. V, pp. 89–112.

SOÓS, L., 1936. Zur Anatomie der ungarischen Melaniiden. *Állatt. Közlem.*, Vol. XXXIII, pp. 103–28.

SUNDERBRINK, O., 1929. Zur Frage der Verwandtschaft zwischen Melaniiden und Cerithiiden. *Z. Morph. Ökol. Tiere*, Vol. XIV, pp. 261–337.

THIELE, J., 1929. *Handbuch der systematischen Weichtierkunde*. Teil I. Jena.

THOMPSON, D'A. W., 1942. *On Growth and Form*. Cambridge.