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)

By Vera Fretter, Ph.D.

From the Department of Zoology, Birkbeck College, University of London

(Plate IV and Text-figs. 1–6)

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Introduction

Amongst the more common inhabitants of the seashore are a number of prosobranch molluscs which, owing to the smallness of their size, have escaped investigation. *Skeneopsis planorbis* (Fabricius), *Omalogyra atomus* (Philippi), *Rissoella diaphana* (Alder) and *R. opalina* (Jeffreys) are some of the least known of these: their shells, and so much of their body as is exposed when the animal is creeping, have been described by Forbes & Hanley (1853) and Jeffreys (1867), but the internal anatomy and most of their habits are entirely unknown. The present investigation shows that in many respects these molluscs are highly specialized in correlation with their small size and their habitat. The more important features of structure and life history are described for each animal and, in the discussion, the features which they share because of their minuteness and their adaptation to a rock-pool habitat are dealt with.

Skeneopsis planorbis (Fabricius)

Skeneopsis is found abundantly all around the British Isles and is especially plentiful in coralline pools. The shell is roughly discoidal in shape, having an extremely depressed, blunt and rounded spire which is scarcely visible unless the shell be viewed edge-on (Fig. 1 A, B). There are four rather loosely coiled whorls, with deep sutures, and the umbilicus is open and funnel-shaped. The last whorl is by far the largest. The mouth is almost circular, its lips projecting outwards, thin and entire in young specimens, though somewhat flexuous in older ones looking as if an original entire edge had been clipped. The only sculpture on the shell is due to the lines of growth (LG). The colour varies: typically, as in young specimens, the shell is reddish brown and glossy; older specimens may be dull and either a pale buff or olive green owing to algal

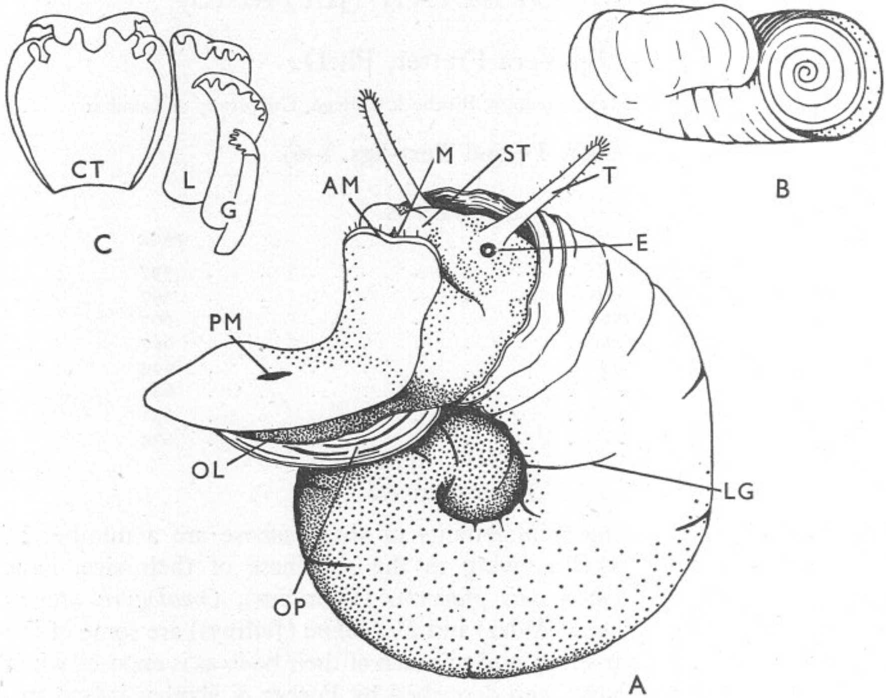


Fig. 1. *Skeneopsis planorbis*. A. Living animal seen from the left and below. ×45. B. Shell from the side. ×30. C. Half row of radula teeth. ×230. AM, opening of anterior pedal gland; CT, central tooth of radula; E, eye; G, marginal tooth of radula; L, lateral tooth of radula; LG, puckered lines of growth; M, mouth; OL, opercular lobe of foot; OP, operculum; PM, opening of posterior pedal gland; ST, snout; T, tentacle.

growth. As the mollusc grows to maturity algal spores gain a holdfast on the surface of the shell. These germinate and the small plants become embedded in a thick layer of mucus which they themselves secrete, and the layer may be added to by diatoms which are scattered in large numbers amongst the algal filaments. Thus in older specimens the shell is completely encased in a mucous covering from which arises a thick woolly coat of algal filaments.

When *Skeneopsis* crawls over weed or rock the shell is not carried erect but tilted sideways and may be rocked from side to side. The exposed parts of the body have a ground colour of greyish white. On the metapodial (opercular) lobes (Fig. 1 and Pl. IV, fig. 1, OL) there is a mottling of deep grey or black, and patches of yellow occur on the body, all due to epithelial pigment granules. Two yellow patches lie between the eyes, each over a similarly pigmented region of the buccal cavity, with another of smaller size behind each eye, and a streak underlies the operculum. The two dorsal patches which lie close together are contiguous with a black streak extending for some distance beneath the shell. The head bears a pair of long cylindrical and widely diverging tentacles which may be waved slowly in the water as the mollusc creeps. Each is scantily covered with motionless cilia (Fig. 1, T), and the eye is situated on the outer side of the swollen base (E). The snout (ST) is broad with a mid-dorsal groove dividing it into two rounded lobes, between which lies ventrally the mouth (M). The foot is relatively short, truncated in front and tapering along the posterior third to a blunt point. Around the anterior edge a deep groove marks the opening of the anterior pedal mucous gland (AM), and a row of stiff cilia arises from the upper lip of the groove. The anterior pedal gland comprises three groups of mucous and mucoid cells set in a transverse row in the anterior tissues of the foot (Pl. IV, fig. 1, MG); the middle group is the most extensive, and the whole appears as a semicircular opaque white mass in the living animal. Gland cells of a similar nature are embedded in the tissues of the sole (GD) and open singly between the cells of the ciliated columnar epithelium. Yet another and still greater supply of mucus comes from a posterior pedal gland which opens as a mid-ventral longitudinal slit about a third of the pedal length from the posterior end (Fig. 1, PM). The opening leads dorsally into a ciliated duct (Pl. IV, fig. 1, D), which soon bifurcates into left and right branches, and each becomes surrounded by glandular tissue which extends into the haemocoel. On each side, at about the level of the pedal ganglia, this tissue then splits into two lobes, one passing dorsally (AL) and the other running back alongside the oesophagus and immediately above the columellar muscle (PL).

The animal is fond of crawling on the surface film of water and may suspend itself from this by means of a viscid thread issuing from the posterior pedal gland. The free end of the thread floats on the surface, and, as the animal slowly descends, it plays out the mucous rope: from the opening of the gland the secretion is directed into a longitudinal groove along the sole, where, in contact with the sea water, it hardens before leaving the posterior end of the foot. In such a manner *Skeneopsis* may finally reach the bottom of a shallow pool, or, if the thread be short, the mollusc may even reverse its course and climb along it to reach the surface again.

The mantle cavity extends along the whole length of the body whorl. On the left side is the well-developed, bipectinate osphradium, and dorsal to this the monopectinate gill, which has only nine finger-like filaments (Pl. IV, fig. 1, F) projecting downwards from a somewhat elongated axis. The hypobranchial gland runs along the right wall of the cavity anteriorly. It passes back parallel to, and just above, the rectum as a single layer of mucous and mucoid cells, but near the level of the posterior end of the ctenidium the gland thickens, occupies a more dorsal position and the mucus is replaced by another type of protein. Posteriorly, the mantle cavity is much reduced in size, and, covered by the hypobranchial gland, pushes back over the kidney (K), which therefore opens on its floor. In the female the large glandular genital duct projects from the right wall of the mantle and partly obliterates the cavity on this side, the rectum running along its median side to open on a prominent papilla anterior to the genital opening. In the male the genital duct is far less conspicuous, and the anal papilla smaller. The penis (PE), which arises behind the right tentacle, is slightly compressed laterally and when fully developed extends the whole length of the mantle cavity.

The Alimentary Canal

The mouth leads dorsally into a short though very dilatable tube, a ventral extension of the buccal cavity which bears a cuticle, and this also spreads on to the floor of the main part of the cavity in which the odontophore lies. At the inner end of the buccal tube the cuticle is thickened to form two jaws laterally placed, each consisting of six transverse rows of teeth with about twenty in each row (Pl. IV, fig. 1, J); each tooth is secreted by a single epithelial cell. When the animal is feeding, the radula (R) works over the surface of the weed or other material to rasp off diatoms and algal cells, the jaws meanwhile gripping the substratum. The radula (Fig. 1 C) is made up of numerous

EXPLANATION OF PLATE IV

Fig. 1.

Skeneopsis planorbis. Right lateral view of whole animal seen as a transparent object. ×80. A, anus; AH, anterior region of stomach; AL, anterior lobe of posterior pedal gland; AM, opening of anterior pedal gland; BU, buccal ganglion; C, columellar muscle; CD, ciliated duct leading from vas deferens to mantle cavity; CE, cerebral ganglion; D, duct of posterior pedal gland; DI, digestive gland; DP, penial duct; E, eye; EX, spherules in excretory cells of digestive gland; F, gill filament; GA, parapedal ganglion; GD, mucous glands opening on sole of foot; H, heart; I, intestine; J, jaw; K, kidney; L, opening of digestive gland into stomach; LI, left salivary gland; MA, mantle; MG, anterior pedal gland; OE, oesophagus; OL, opercular lobe of foot; OP, operculum; P, prostate; PE, penis; PG, pedal ganglion; PH, posterior region of stomach; PL, posterior lobe of posterior pedal gland; PR, pleural ganglion; R, radula; RA, radular sac; RI, right salivary gland; ST, snout; T, tentacle; TE, testis; TO, statocyst; V, vesicula seminalis.

Fig. 2.

Omalogyra atomus. Right lateral view of whole animal seen as a transparent object. ×120. AB, albumen gland; AG, anterior lobe of digestive gland; B, buccal cavity; BC, bursa copulatrix; CG, capsule gland; DA, duct of albumen gland; FC, fertilization chamber; GA, genital aperture; HD, hermaphrodite duct; HL, head lobe; KM, large glands opening into mantle cavity near anus; MG, anterior pedal gland; MU, mucous gland; MT, muscular tube; O, ovarian duct; OD, muscles of odontophore; OM, opening of albumen gland into mucous gland; OPE, opening of sperm sac into prostate; OV, egg in ovary; PD, pallial vas deferens; PM, opening of posterior pedal gland; PO, pallial oviduct; SP, sperm sac; ST, stomach. Other letters as in fig. 1 above.

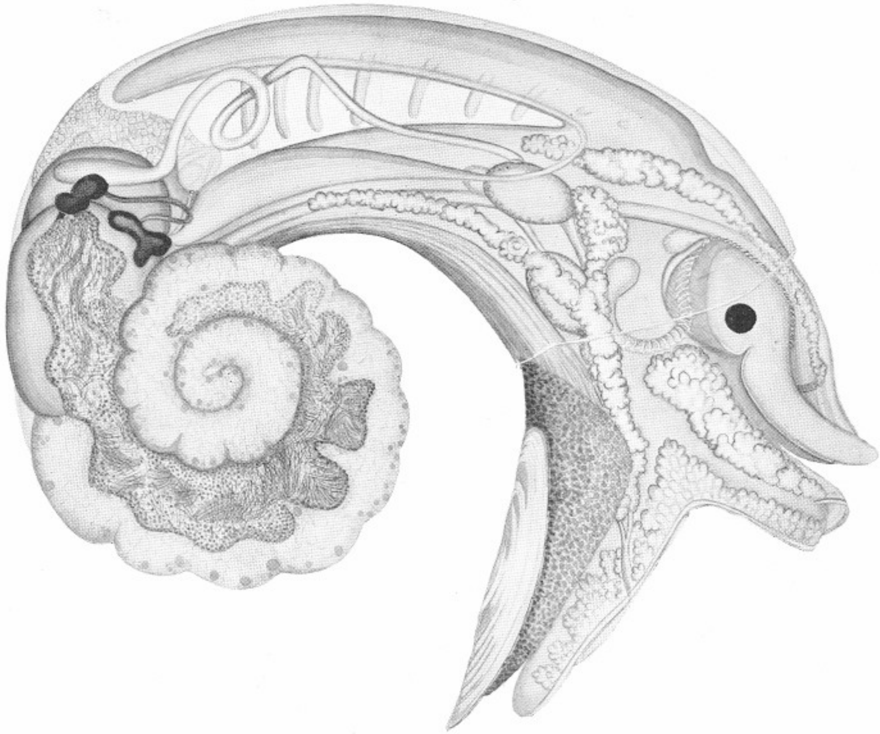
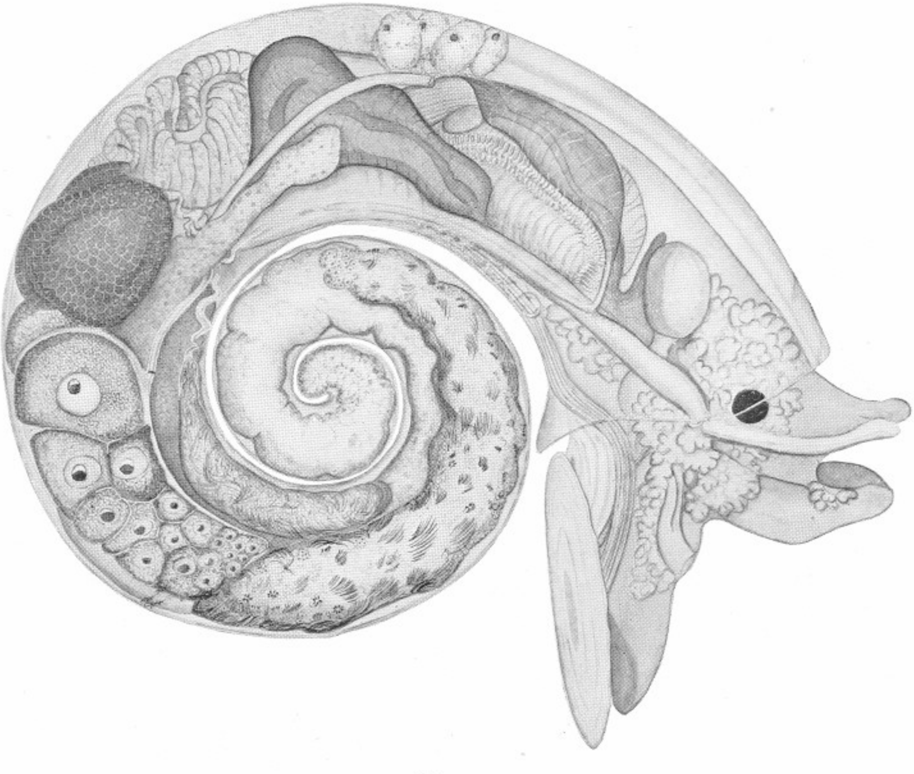


Fig. 1.



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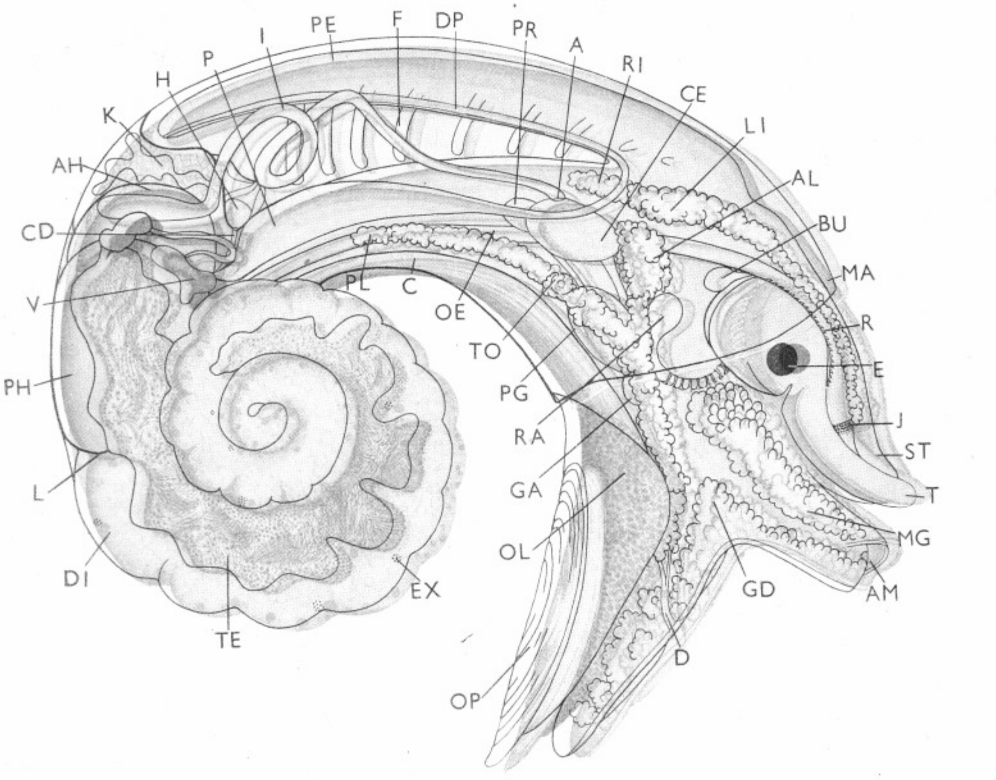
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Fig. 1.

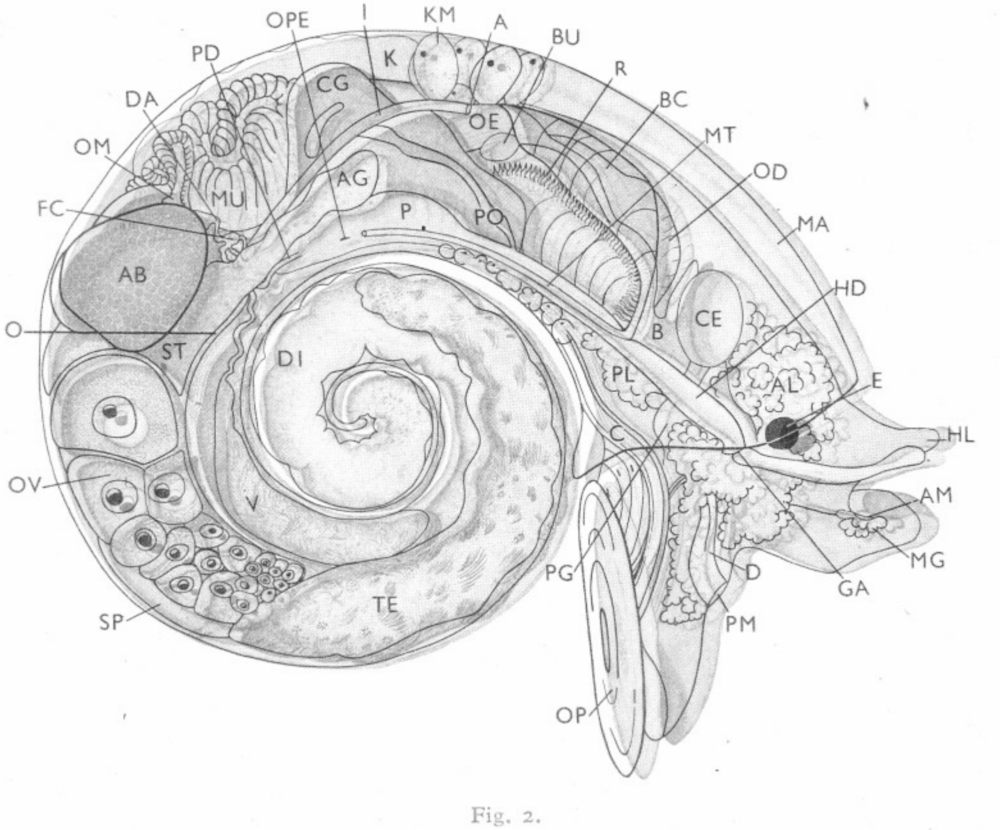
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Fig. 2.

transverse rows of sharply cusped teeth, each row comprising a large central tooth (CT) bordered on each side by one lateral (L) and two marginals (G).

Along the mid-dorsal wall of the buccal cavity is a deep ciliated channel along which the food is directed to the oesophagus. The salivary glands (Pl. IV, fig. 1, RI and LI) open at the extreme anterior end of this channel, one on either side. Their secretion lubricates the action of the radula and entangles the food particles which are drawn in by it. The glands run parallel with the oesophagus as far as the nerve ring, the one on the left side being slightly longer than that on the right. Mucous cells provide the greater part of the saliva. There is, however, a second type of secreting cell filled with protein spherules which swell and dissolve when expelled, probably liberating an enzyme.

The oesophagus (OE) is a straight, narrow, ciliated tube of about the same diameter throughout. From its origin at the posterior end of the buccal cavity it is directed ventrally and slightly to the left of the median line, and traverses the length of the body whorl. There are no glandular pouches along its course, as are common amongst herbivorous prosobranchs, and the only secreting cells are epithelial mucous glands.

The stomach is spacious and lies at the posterior end of the body whorl, at right angles to which it is elongated. It is divided by a transverse constriction into two regions: an anterior (AH), which is dome-shaped and lined by a columnar ciliated epithelium, the cilia being thick and closely set; and a more posterior one (PH), the wall of which is, in the main, cuticularized. The upper, anterior, chamber corresponds to the style sac of style-bearing prosobranchs and the lower, posterior, chamber to the part containing the gastric shield. The anterior wall of the posterior chamber is ciliated where it receives the opening of the oesophagus at the level of the transverse constriction. At the extreme posterior end is the opening of the single lobe of the digestive gland (L). The stomach, especially its anterior compartment, is conspicuous in the living animal since there is a heavy deposit of black spherules in the epithelial cells. The intestine (I) arises from the dorsal wall of the anterior chamber and bends abruptly to pass forward on the right side. For a short distance along its initial length can be traced a longitudinal groove bordered by a fold of epithelium. This gutter, with its accompanying fold, arises on the wall of the duct from the digestive gland, passes forwards to the anterior chamber of the stomach and so reaches the intestine. It affords a path by which waste from the duct may be conveyed to the intestine.

On histological grounds the intestine may be divided into four regions. The initial part, in which the columnar ciliated cells are heavily pigmented with black spherules, and along which the channel from the digestive gland can be traced, passes to a slightly wider and more muscular tube in which mucous cells alternate with ciliated cells. Here the faecal pellets are moulded: the particulate waste from the stomach, which consists of diatom cases, algal cells and detritus, is agglutinated by means of mucus and compacted into oval rods.

These are still further elaborated in the third section of the intestine, the longest of the four, which takes a somewhat sinuous course as it accompanies the genital duct along the right wall of the mantle cavity. In this section the mucous cells are replaced by another type of gland which is scattered somewhat sparingly amongst the ciliated cells—it is conical in shape, with a broad base, and tapering distally, and towards the base is a large round nucleus, with a prominent nucleolus. The cytoplasm is dense and contains small secretion spherules which swell in the lumen of the gut and presumably help to harden the outer rind of the pellet. In the terminal or rectal region the cilia are longer than elsewhere and mucous cells are scattered in the epithelium, increasing in number towards the anus.

The digestive gland (DI), together with the gonad (TE), constitute the visceral mass which occupies the smaller coils of the shell. The gonad, frequently the smaller of the two glands, lies on the right side. The digestive gland has a segmented appearance, since it is made up of a series of lobes which open into one another and increase in size towards the stomach, into which they ultimately open. The epithelium of the gland consists of three types of cells: the most frequent, the digestive cell, is narrow at the base and gradually broadens towards a rounded distal end where there is a dense layer of protoplasm containing innumerable small spherules. These have been seen to be discharged and are probably enzymatic. The rest of the cytoplasm, except around the nucleus, is filled with vacuoles which vary in size, and contain during life either a clear refringent liquid or agglomerations of fine particulate matter sometimes embedded in a mucoid substance. No diatoms, algal cells or any such particulate food has ever been found within the lumen of the digestive tubules. The stomach, however, may often be seen filled with such objects, and since only empty cases of diatoms and the walls of broken cells are to be found in the intestine, it may be assumed that the bulk of the digestive process occurs in the stomach and that only the resulting solution, with perhaps minute particles, enters the liver, and is taken up by the digestive cells for further treatment.

The two other types of cell, neither of which attains the height of that already described, occur in the crypts of the tubules. In one, which appears to be excretory in function, the protoplasm may be highly vacuolated and an irregular clump of brown or black granules be contained in each vacuole. A more frequent appearance is when the cell contains only one large vacuole filled with a single spherical mass of such granules. These can be seen through the shell of a living animal (EX). They have never been found in the lumen of the gland. Somewhat similar cells of undoubted excretory function are described in the digestive gland of tectibranchs (Fretter, 1939), and it is probable that, as in that group, waste matter is absorbed from the blood through the broad bases of the cells. This, however, has not been tested owing to the difficulty of injecting such small molluscs.

The third type of cell may be grouped in small numbers around the excretory cell, though sometimes it occurs alone in larger numbers. In longitudinal section it is triangular in outline with a broad base resting on the basement membrane and a tapering distal end which hardly reaches the surface of the epithelium. The spherical nucleus lies towards the base and has a large nucleolus. The protoplasm stains deeply with iron haematoxylin and is vacuolated. Each vacuole contains a colourless refringent spherule which gives a positive reaction for lime. The probable function of these cells is either to act as a storage of lime for shell formation, or for the purpose of controlling the reaction of the secretion from the digestive gland.

The Reproductive System

The male. The testis (Pl. IV, fig. 1, TE), situated on the right side of the visceral mass, consists of a linear series of lobes which open broadly into one another and lead finally to the gonadial duct. This acts as a vesicula seminalis (V) which is dilated with sperm from the onset of sexual maturity. It coils on the right side of the stomach and then leads into a short narrow tube with a straight course, conducting the sperm from the vesicula seminalis to the prostate (P). This tube, the renal vas deferens, is surrounded by a layer of circular muscles which closes the lumen except when spermatozoa are actually passing through it during copulation. It opens into the prostate gland on a small papilla. Alongside this is a ciliated duct (CD) which leaves the prostate and runs dorsally to open into the mantle cavity. Such an outlet to the mantle cavity has been described in certain Stenoglossa and in *Lamellaria*, and provides an escape for unwanted sperm (Fretter, 1941).

For the rest of its course the male duct runs straight along the right side of the mantle cavity to the penis (PE)—this section comprises the pallial vas deferens and along the posterior half the epithelium is tall and glandular and constitutes the prostate (P). The gland cells, which rest upon a basement membrane, are broad at the base and each tapers slightly towards the distal end. Wedged between the distal ends are ciliated cells which drive the prostatic secretion forward along the duct. The prostate is surrounded by a thin layer of connective tissue in which both circular and longitudinal muscle fibres occur. Anteriorly it ends abruptly, the duct narrows and is lined only by a ciliated columnar epithelium. The musculature, however, is greatly increased, for the circular muscle forms a layer which in thickness exceeds twice the height of the epithelial cells. Here, and along the penial duct, the histology of which is similar, the spermatozoa are conducted by peristaltic action.

The penis is somewhat compressed laterally and tapers to a point, the duct through it (DP) running near its ventral surface to open at the tip. Externally it is covered by a slightly cuticularized epithelium, except along the narrow dorsal and ventral walls where longitudinal strips of epithelial mucous glands occur, the secretion from which assists the passage of the penis through the pallial groove of the female to reach the opening of the receptaculum seminis (Fig. 2, RE). Beneath the epithelium is a layer of circular and longitudinal muscle fibres, and through the thickness of the organ oblique and dorso-ventral fibres separate numerous blood spaces. These, when gorged with blood during copulation, so enlarge the penis that if the copulating partners be separated it is only after some minutes that the penis can regain its position of rest along the length of the mantle cavity.

The female. The ovary, on the right side of the visceral mass, occupies a position similar to that of the testis and extends as far as the posterior chamber of the stomach. From here a narrow ovarian duct (Fig. 2, O) passes towards the posterior end of the mantle cavity where it opens into the fertilization chamber (FC), placed at the posterior end of the pallial oviduct, and receiving a duct from the receptaculum seminis (DR), and another from the albumen gland (DA). Its walls are ciliated and muscular.

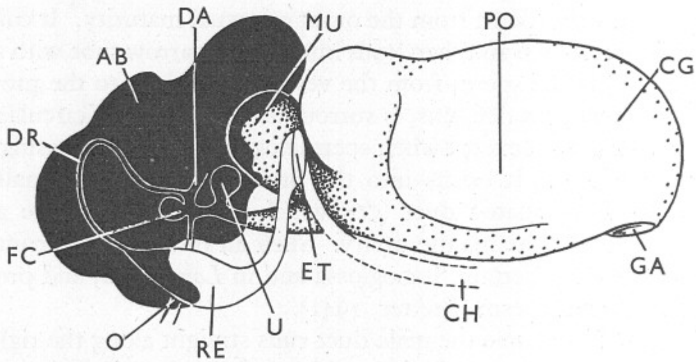

Fig. 2. *Skeneopsis planorbis*. Diagrammatic reconstruction of female genital duct. × 100. AB, albumen gland; CG, capsule gland; CH, channel along outer surface of mantle; DA, duct of albumen gland; DR, duct from receptaculum seminis; ET, entrance to receptaculum seminis; FC, fertilization chamber; GA, genital aperture; MU, mucous gland; O, ovarian duct; PO, lateral pouch of capsule gland; RE, receptaculum seminis; U, muscular sac.

The albumen gland is of considerable size (AB), and completely surrounds the fertilization chamber and the various ducts leading to it. The walls are thrown into a few deep folds, so that the gland has a lobed appearance, and they are lined throughout by a single type of cell in which the cytoplasm, except towards the base, takes up stains specific for mucus and contains somewhat large and irregularly shaped secretion masses of a protein nature, presumably albumen.

The oviduct extends along the right side of the mantle cavity. At first it is narrow and lined by ciliated cells, and, a short distance from the fertilization chamber, a muscular sac (U) opens into its dorsal wall. This sac is in the usual position for a receptaculum seminis, and might be its homologue, but it no longer functions as such and its use is unknown. The only point of interest concerning it is the enormous length of the cilia on the walls—at least five times the height of the cells. The pallial oviduct then thickens, and, for the rest of its course, except for a narrow strip along the ventral wall, the plan of the epithelium is essentially the same: gland cells alternating with ciliated cells. The initial part of this glandular section is narrow and both mucous and mucoid cells occur. It then opens into the ventral wall of a mucous gland (MU) which produces the inner mucous layer of the wall of the egg capsule, and here the lumen is elongated dorso-ventrally, the lateral walls being thick and the dorsal and ventral ones moderately thin. The ventral is composed of a low ciliated epithelium with occasional mucous cells, and a similar thin ventral wall extends as far as the genital aperture; it corresponds to the ventral channel of the pallial oviduct of other prosobranchs. Anteriorly, the mucous gland leads into the final and largest section of the pallial oviduct, the capsule gland (CG), where the egg capsule is retained whilst the main thickness of its wall is deposited. Here the lumen on each side is extended laterally to form a pouch of considerable dimensions (PO), though towards the genital aperture the duct gradually narrows. Three types of gland cells occur in the epithelium. Around the opening from the mucous gland there is a ring of cells in which the cytoplasm is filled with small protein spherules of uniform size. Mucous cells occur at the posterior limit of each lateral pouch and a considerable number lie around the genital aperture (GA). Elsewhere, that is, over the main area of the wall, the cytoplasm of the gland cells produces a fluid which has the appearance and consistency of conchiolin. Within the cells the secretion droplets stain lightly with iron haematoxylin and pale blue with azan.

Perhaps the most interesting point in the female genital system is the structure of the receptaculum seminis (RE). Between the pallial oviduct and the underlying columellar muscle the outer surface of the mantle—that is, directly under the inner surface of the shell—is folded to give a fairly deep longitudinal groove, the mouth of which faces outwards. The anterior end of the groove is about one-third of the length of the pallial duct behind the genital aperture. As it passes back the groove deepens and is subdivided longitudinally by a fold of epithelium to give an upper channel (CH) which leads to the receptaculum seminis, and a lower or ventral one which eventually narrows and disappears. The upper or dorsal channel is lined by tall columnar ciliated cells, the lower one by a squamous epithelium. The former passes postero-dorsally up the side of the mantle, and therefore parallel to and alongside the genital duct, and, meanwhile, twists through 90° so that it now lies more towards the dorsal side of the duct, the mouth of the groove pointing in that direction too. At the level of the middle of the mucous lobe of the pallial duct the lips of the groove fuse to form the entrance (ET) to a ciliated tube which leaves the surface of the body and passes deeper to enter the receptaculum seminis (RE). The receptaculum is an elongated pouch on the right of the genital duct and its posterior end is surrounded, except on the median side, by the albumen gland. Within it, the spermatozoa become orientated with their heads embedded in the epithelium. A narrow muscular duct (DR) leads from the posterior end of the receptaculum and takes a somewhat circuitous course to reach the fertilization chamber. The duct is surrounded by a thick layer of circular muscle, and only on rare occasions has sperm been seen in it. It would appear that during copulation the penis of the male is inserted between the shell and the mantle of the female on the right side, and directed along the course of the longitudinal groove. Its passage would be facilitated by the slight flattening of the penis and by the secretion from the mucous glands situated on its dorsal and ventral walls. The tip of the penis would then reach to the opening of the duct leading down to the receptaculum seminis. Sections of a female fixed immediately after copulation showed the receptaculum and the duct leading to it filled with spermatozoa. Such a specialized method of copulation is not known elsewhere in the Mollusca.

Reproduction and Life History

The egg capsule of *Skeneopsis* is described by Linke (1933). It is approximately spherical or ovate (0·45 mm. long, 0·35 mm. broad), though flattened along the surface by which it is attached to an algal filament. It contains one or two heavily yolked eggs which pass through a veliger stage within the capsule and hatch as miniatures of the adult. Each egg is surrounded by a layer of albumen which gradually diminishes as development proceeds, and the young molluscs come to occupy most of the space within the capsule. The wall consists of two layers, a fairly thin mucous lining, and a much thicker fibrous coat. The former is secreted by the posterior mucous lobe of the capsule gland, the latter by the anterior larger section of the pallial duct. Linke (1933) states that the full development takes from 3 to 4 weeks in sea water at a temperature of 12–15° C. At a slightly higher temperature (approximately 14·5–17·5° C.) eggs which were laid on weed in a finger bowl developed in 2½ weeks. The young rasp their way through the wall of the capsule by means of the radula.

Lebour (1937) states that *Skeneopsis planorbis* breeds throughout the year at Plymouth. This statement, however, requires amplification. From an examination of animals in rock pools around Cawsand, Plymouth, it is found that the majority are spawning during spring. These adult individuals measure at their broadest diameter 1·55 mm. on the average, which is also about the maximum size to which they grow in this locality. By the first week in June innumerable young are present, exceeding, in most rock pools, the number of adults, and the average breadth of these is 0·48 mm. Egg laying continues throughout the summer months, though by September it is decreasing and only a few animals are spawning as late as the end of October. By the new year the typical individual found in the rock pools has a diameter of 0·85 mm. and is sexually immature. A few perhaps exceed a millimetre. The older generation has by this time died out—only one or two individuals have ever been found—

so that it is in the main an immature population which tides over the winter, a population produced by the late spawners.

It would thus appear that *Skeneopsis* is an 'annual' with a normal breeding season during the spring or summer. This, however, may be extended in two directions: (1) to the earlier months of the year if the weather be suitable, by precocious ripening of the snails which have survived from the previous year; or (2) it may be prolonged into late autumn, again if the weather is kind, by the arrival at maturity of young which were hatched during the summer months and which would otherwise have to wait for the coming of the next spring.

OMALOGYRA ATOMUS (PHILIPPI)

Omalogyra is one of the most minute of British molluscs, as is suggested by its specific name. The shell (Fig. 3), which resembles that of a miniature *Planorbis*, measures only about 1 mm. at its broadest diameter. It is reddish brown in colour, coiled in a plane spiral, and, since the umbilicus is widely open, the interior of the spire is exposed. The shell is thus concave on both sides and has a bilateral symmetry about the sagittal plane. There are three whorls, compactly coiled, with the outer one, the largest, enwrapping the others which are exceedingly small and diminish in size towards the apex. Each is rounded on the outside, but somewhat flattened on the inside; the sutures are strongly impressed and deep. The mouth, approximately circular in outline, projects slightly outwards and has a sharp and even edge. The surface of the shell is glossy and smooth except for fine striae marking the lines of growth. The operculum (Pl. IV, fig. 2, and Fig. 3, OP) is white, circular and flat, with a slightly thickened spiral line which coils outwards from the centre to give three or four turns of increasing diameter.

The body is a uniform yellowish white, though little is exposed as the animal creeps along; the shell is then held erect with the mouth parallel to the substratum. The mollusc has a steady gait and the shell is rarely tossed to and fro as in *Skeneopsis*. Projecting anteriorly from the mouth of the shell is the broad, flat, flexible snout which is notched medially so as to form on each side a flat semicircular lobe (HL); the two lobes are joined by a straight and thin intermediate membrane beneath which is the mouth. Around the outer edge of each lobe and along the intermediate membrane is a row of stiff cilia which are presumably sensory in function: when the animal moves about it frequently waves the lobes in the water or presses them against the weed or rock as though sensing its environment. The lateral and posterior margin of each lobe is thickly ciliated. On the upper surface towards the posterior extremity is the eye (Pl. IV, fig. 2, E), which is large for the size of the snail; it is only just exposed when the animal creeps. No tentacles are present; functionally they are replaced by the lateral head lobes.

The foot, with sides approximately parallel, is rounded or slightly bilobed in front and rounded posteriorly. It is short in proportion to the length of the shell, beyond the posterior end of which it does not project, and rarely is it seen to protrude beyond the snout anteriorly. Its epithelium is thickly ciliated except for a cuticularized band at the junction of the foot with the body. Projecting from this cuticular surface, immediately beneath the head lobe on each side, and on a level with the eye, is a small tuft of tall ciliated cells. Fibres from the pedal nerves pass to them, and they may therefore be epipodial sense organs. There are two pedal glands. The anterior one (MG) opens on the upper surface of the propodium, where, directly in front of the mouth, there is a median ciliated depression (AM). The gland consists of unicellular mucous cells which are embedded in the substance of the foot beneath this depression and open singly between the ciliated cells. The posterior gland, which is much more extensive, has a longitudinal slit-like opening at about a third of the pedal length from the posterior end of the foot (PM). The ciliated duct (D), which passes dorsally from the opening, soon bifurcates into left and right branches and each of these, as in *Skeneopsis*, drains the secretion from two main glandular masses: one lies in front of the nerve ring and extends forwards between the eyes (AL), whilst the other (PL), lateral and more posterior, runs back beneath the genital duct on the right side, and, on the left, extends up the side of the odontophore. The posterior part of the gland is composed entirely of mucous cells, except for a few large cells at its extreme posterior end. These are filled with spherules which are readily dissolved on fixation leaving an inconsiderable amount of vacuolated cytoplasm. In the anterior part of the gland a different type of secreting cell accompanies the mucous cell, with spherules staining lightly with iron haematoxylin and deep red with azan. All the cells of the posterior pedal gland are arranged in groups, and each group has its own individual duct which leads to one main branch of the collecting duct. The gland is a useful possession for animals inhabiting rock pools; for *Omalogyra* often creeps on the surface film of water and can employ a thread of secretion to lower itself gradually into the water should it be disturbed, in exactly the same way as *Skeneopsis*. Also, when the mollusc is creeping over weed, or occasionally over rocks, its path is lubricated by the viscid secretion, and this gives the firm anchorage which is so necessary on a wave-washed shore, and which in the larger rock-clinging gastropods may be given by the more muscular type of foot.

The mantle cavity extends to the posterior end of the body whorl. Anteriorly, for a short distance, it completely surrounds the body, as the left and right lobes of the mantle fuse with one another beneath the columellar muscle. Farther back, near the anterior end of the odontophore, and between this and the anus (A), it is restricted mainly to the right side, but also extends over the dorsal surface of the body. On the left, where in other prosobranchs the ctenidium hangs down from the roof of the cavity, the body wall is fused with the over-lying mantle: in *Omalogyra* there is neither ctenidium nor osphradium. Posterior to the anus the presence of the genital ducts, and of the kidney, confines the mantle cavity to the left of the median line so that it comes to overlie the oesophagus. The anus opens far back on the right side, a position which is probably secondary. From it, two longitudinal strips of ciliated columnar cells, extensions of the rectal epithelium, pass forwards to the mouth of the mantle cavity (omitted, for simplicity, from Pl. IV, fig. 2). The dorsal strip, which is the longer, runs along the roof to its edge, the ventral one along the body wall, ending on a level with the nerve ring. This appears to constitute a tract along which faecal matter is led to the mouth of the mantle cavity. In a living animal faecal matter can be seen through the transparent shell to leave the anus and to be directed forwards in this way, apparently rotating on its route. Below each strip lie mucous glands which discharge into the mantle cavity, some between the ciliated cells. The dorsal layer of glands is broader than the ventral and extends towards the median line; it represents the hypobranchial gland. At its posterior limit, in the vicinity of the anus, the mucous cells are replaced by a group of about a dozen enormous cells of another type, the openings of which lie close together (KM). It is these large glands which have been mistaken for eggs by Jeffreys (1867) and Lebour (1937). Each is broadly elliptical in longitudinal section, with the nucleus, near the base, surrounded by a dense layer of cytoplasm. Elsewhere the cytoplasm is vacuolated. There may be one vacuole which fills the greater part of the cell or several smaller ones; in living material each contains a colourless fluid. The secretion of these glands appears to be concerned as much in the elaboration of faecal pellets as in lubrication, and thus compensates for the absence of glands in the intestine. The pellets are rod-shaped, often with rounded ends, and are not so compacted as in *Skeneopsis*.

The kidney (K), which lies in the mantle, extends back from the level of the anus to the heart, which is directed obliquely across its posterior wall, with the auricle in front of the ventricle. The kidney is a simple vesicle in which the epithelium is not folded, as is typical of other molluscs, to increase the excretory area. Along its left wall runs the main pallial vein which branches anteriorly over the mantle and leads posteriorly to the auricle. The inner wall of the mantle is covered for the most part by squamous epithelium which separates the blood vessels from the flow of water in the underlying cavity. This water current is presumably set up by the cilia on the longitudinal strips of epithelium passing forwards from the anus, which are constantly beating towards the mouth of the mantle cavity. The gaseous exchange which occurs through the wall of the mantle is apparently adequate for the respiratory needs of a gastropod of such small size, and so explains the absence of any specialized respiratory organ.

The Alimentary Canal

The lateral walls of the extreme anterior end of the buccal cavity are thickened by an epithelium of considerable height bearing a cuticle. These thickenings act as jaws which grasp the weed as the radula plays over its surface. The odontophore is far removed from the mouth owing to the elongation of the buccal cavity in an anterior direction to form a proboscis-like tube. This tube is very distensible and is also cuticularized. *Omalogyra* is a pendulum feeder (Ankel, 1938) with *Ulva* as its favourite food: as it creeps slowly over the surface of a thallus the head is swayed to and fro whilst the surface cells of the alga are rasped by the radular teeth. The animal thus leaves behind it a zig-zag feeding trail (Fig. 3, FT). During the spring, summer and autumn months the stomach, and especially the cells of the digestive gland, are coloured green with chlorophyll from the weed. The contents of the plant cells which are rasped by the radula, and perhaps some severed pieces of alga, are mixed with mucus from the anterior pedal gland, sucked up into the buccal cavity and passed along the dorsal ciliated channel which lies above the odontophore. At the extreme posterior end of this channel the salivary ducts open, one on each side; they are extremely narrow tubes and each passes back to a compact group of a few large secretory cells. The dorsal channel leads imperceptibly into the oesophagus (Pl. IV, fig. 2 OE) which is about the same diameter throughout its length.

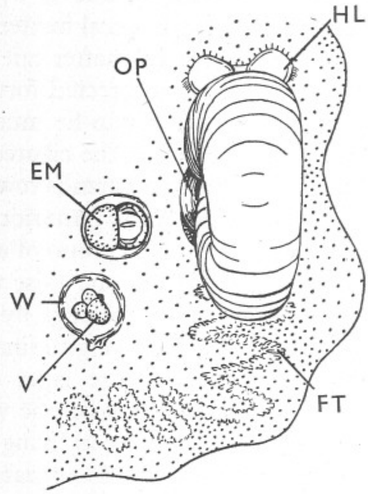

Fig. 3. *Omalogyra atomus*. Living animal feeding on *Ulva*. Two egg capsules are attached to the weed. ×45. EM, embryo at time of hatching; FT, feeding trail; HL, head lobe; OP, operculum; V, veliger; W, wall of egg capsule.

In animals which are collected during the summer, when food is plentiful, the oesophagus is broader than in the winter and spring. Moreover, there is a histological difference between them: in *Omalogyra* which live through the winter the oesophagus is ciliated at its extreme anterior end, along the whole length of its dorsal wall and for a narrow longitudinal strip along the mid-ventral wall. Laterally, however, in a region comparable to the oesophageal pouches of other prosobranchs, it is lined by digestive epithelium which is identical with the digestive cells of the liver, and also comprises the lining of the stomach. In animals which develop and breed during the summer, the longitudinal glandular tracts of the oesophagus are not present, though the stomach has the lining of digestive cells, reminiscent of the embryonic condition of gastropods in which the liver cells cover the wall of the stomach only to be constricted off at a later stage. In these forms, too, the salivary glands are relatively larger. The unusual distribution of the digestive epithelium in the adult is correlated with the type of food: the principal, perhaps exclusive, food is plant sap, and since this needs no mechanical treatment prior to digestion, the stomach is no longer necessary for this and can act as an extension of the digestive gland. Presumably in winter, when food is most scarce and when the animals are immature and undergoing slow development, the spreading of the digestive epithelium along the oesophagus enables a more thorough absorption of any food which may be obtained, or if the cells are capable of secreting enzymes it may permit a fuller utilization of the material. As the oesophagus passes back through the body whorl it is directed to the left and consequently gives ample space for the development of the voluminous genital glands on the right side; it opens at the extreme left of the antero-dorsal wall of the stomach. The stomach (ST), in proportion to the animal's size, is smaller than in *Skeneopsis*. The anterior wall not only receives the oesophagus, but the intestine (I) and anterior lobe of the digestive gland (AG) also open here. The intestinal aperture is median to that of the oesophagus, and a strip of ciliated epithelium, continuous with that of the oesophagus, runs across the stomach wall from oesophagus to intestine. The small anterior lobe of the digestive gland (AG) enters the stomach to the right of the intestinal opening. This lobe is not present in *Skeneopsis*, but only the much larger posterior one (DI), which leads from the posterior wall of the stomach and occupies the coils of the visceral mass. It would correspond with the left lobe of the digestive gland of other gastropods. This is always the larger of the two, since the right lobe—anterior in *Omalogyra*—is reduced as a result of torsion, and may be lost entirely. Each lobe in *Omalogyra* is a blind tube, constricted at regular intervals along its length, and the epithelium does not form the ramifications which are typical of the more solid construction of the liver of other gastropods. The digestive epithelium consists of two types of cells—digestive cells and rather infrequent lime cells. In the digestive cells the cytoplasm is vacuolated and the vacuoles seem to contain ingested food; no particulate matter has ever been found within them. The lime cells arise from a broad base and taper at the distal end; the cytoplasm is filled with large colourless spherules of calcareous matter.

The intestine is a short, straight tube which runs along the right side of the genital duct. Rather unusually there are no gland cells along its course. The cilia of the epithelium are so long that their tips meet across the tube and beneath the epithelium are a few circular and longitudinal muscle fibres embedded in a thin layer of connective tissue.

The Reproductive System

The gonad (Pl. IV, fig. 2, OV, TE) spreads over the surface of the digestive gland on the right side of the visceral mass. It is composed of two lobes lying alongside one another, one a testis and the other an ovary. In animals which have been collected in the spring and which have developed slowly from late summer or autumn eggs the genital system is in the male condition; the female organs are developed, but are not as yet functional. The anatomy of such an individual is shown in Pl. IV, fig. 2, and its reproductive system will now be described. The testicular duct (V) acts as a vesicula seminalis. It leads, by a somewhat sinuous course, to the posterior end of the body whorl, on approaching which it narrows and is surrounded by a sphincter. The duct opens into the fertilization chamber (FC), a muscular pouch lined by ciliated epithelium, and into this there also passes (i) the ovarian duct (O) which at this stage is retarded in its development, (ii) the duct of the albumen gland (DA) and (iii) the pallial vas deferens (PD). The pallial vas deferens passes along the right side of the mantle cavity and is initially narrow and ciliated. Soon, however, it broadens and is surrounded, except on its ventral side, by numerous gland cells. The outer ends of these pass between the circular muscle fibres beneath the epithelium and form a thick subepithelial layer. In sections stained with iron haematoxylin and counterstained with mucicarmine, the differences between the epithelial and subepithelial parts of the cell are most pronounced. In the latter the cytoplasm stains rather deeply with iron haematoxylin, and spherules in the cytoplasm may be either a very pale grey, and slightly affected with mucicarmine, or a few small ones may be stained black. In the distal region the cytoplasm stains pink and the spherules may be either a deep pink or black. The latter occur towards the free tips of the cells and probably represent the final stage in the elaboration of the secretion. These glands constitute the prostate (P) and surround the pallial duct for about a third of its course.

Normally, in the mesogastropods, the pallial vas deferens leads to a penis which lies on the right side of the head, a muscular organ which is distended with blood during copulation. *Omalogyra*, however, has no such penis, and its method of copulation would appear to be unique amongst the molluscs.

Lying in the lumen of the prostate, and projecting back from an anterior origin, is a muscular tube (MT) which is open at its distal end to the prostatic cavity. Around the opening the walls are ciliated. Elsewhere, inside and out, the epithelium of the tube is covered by a thin cuticle; beneath the outer epithelium is a layer of circular muscles, and a layer of longitudinal muscles underlies the inner epithelium. The tube passes forwards beyond the anterior limit of the prostate, where the genital duct narrows, and it comes to occupy the greater part of the lumen of this part of the duct. Here the epithelium of the genital duct is also cuticularized and surrounded by circular muscles of considerable thickness. At some distance from the genital aperture the tube originates from the wall of the vas deferens. Closer investigation of this region shows that it actually passes through the dorsal wall of the duct, and enlarges into a muscular sac (BC) which lies in the haemocoel, and spreads over the right wall of the odontophore on to its dorsal surface. It is as though the lips of the opening of this sac had been pulled out to form a long tube which lies in the duct to which the pouch connects, pointing towards the visceral mass. The histology of the sac is similar to that of the tube except that it lacks an outer epithelium. It is homologous with the bursa copulatrix of other forms. Strictly, the origin of the bursa is from an hermaphrodite duct (HD), since posterior to that point the pallial oviduct (PO) joins the vas deferens by way of an extremely minute opening surrounded by a sphincter. But obviously at this stage the oviduct is not functional and the main channel is, in effect, a male one. The hermaphrodite duct, which is extremely muscular, appears as a forward continuation of the vas deferens and opens anteriorly on the right side of the head (GA), just within the shelter of the mantle. It is lined by a slightly cuticularized epithelium in which there are a few mucous glands.

One other structure which is associated with the male genital system and which, like the elongated neck of the bursa, is only present in animals collected during the spring months, has yet to be described. It is a sac which lies against the left wall of the ovary (SP), and is connected to the posterior end of the prostate (OPE) by a narrow ciliated duct. The duct passes antero-dorsally on the left side of the stomach, and over the posterior end of the oesophagus to reach the thickly ciliated ventral wall of the prostate. The sac, which will be referred to as the sperm sac, is lined by an epithelium in which the protoplasm is highly vacuolated, and the nuclei are large with prominent nucleoli. In fixed material many vacuoles appear to contain a loose coagulum, and in the living state a somewhat watery fluid. The sac, and sometimes also the duct, may be distended with sperm and a mucoid secretion, presumably derived from the prostate.

The suggested mode of functioning of these male reproductive ducts is as follows. Animals collected in spring show the vas deferens as the principal pallial genital duct, and at this stage the opening of the pallial oviduct into the hermaphrodite duct is far too small to allow the passage of an egg capsule—in other words, the animal is purely male. Since the tube which extends from the opening of the bursa is an extremely muscular organ, and blocks the passage through the anterior end of the vas deferens, and since the bursa itself is also at this time extremely distensible, it may be assumed that, with the absence of the normal type of penis, these structures are concerned in copulation. The only means by which this seems possible is for the tube to suck up, by peristaltic action, sperm liberated from the vesicula seminalis, and prostatic secretion. These would then fill the bursa. The direction of the penial tube might then be reversed and it could be protruded through the muscular hermaphrodite duct so as to project from the genital aperture and pass into the duct of the copulating partner. Into this the sperm from the bursa would then be passed by muscular action. However, during the male phase no contents have been found in the bursa or in the penis. I do not know what part of the genital system receives spermatozoa, and have been unable to discover whether there is a mutual cross-fertilization or not.

The function of the sperm sac, which, it will be recalled, is found in the male phase only, is probably to clear the pallial vas deferens of sperm and prostatic secretion which have failed to enter the copulatory organ. Sections suggest that here the spermatozoa undergo disintegration: they appear to be digested and the final products absorbed by the vacuolated epithelial cells.

For the investigation of the female genital system it is necessary to examine animals collected in the months June to September. The eggs (Pl. IV, fig. 2, OV) in the ovary are relatively enormous even before the female system is functional, and appear to be out of all proportion to the size of the ovarian duct (O) along which they pass to the fertilization chamber (FC). From there the eggs are carried to the albumen gland (AB), which is divided approximately into two lobes lying side by side and communicating with one another along their adjacent walls. The short ciliated duct (DA) from the fertilization chamber opens into the anterior end of the right lobe, whilst at the anterior end of the left a narrow though muscular passage (OM) leads into the mucous gland (MU). Along this route the eggs are conducted. The epithelium of the albumen gland is composed of a single type of secreting cell. The mucous gland is of a rather irregular shape owing to the folding of its walls; the epithelium is high and the gland cells alternate with ciliated cells which are wedged between their distal ends.

The capsule gland (CG) is the next and last section of the pallial duct, and receives the eggs from the mucous gland; it lies on the right side of the pallial vas deferens and not above it as in the male phase (Pl. IV, fig. 2). Its secreting cells have a mucoid cytoplasm which is vacuolated and in the vacuoles are irregularly shaped protein spherules. Wedge-shaped cells, which lie between the distal ends of the secretory cells, are covered with closely set short cilia. The basement membrane is surrounded by a layer of circular muscles which thickens at the entrance to the hermaphrodite duct.

In all animals which have been collected in June and the succeeding months of the summer, that is, during the height of the breeding season, the reproductive system in all stages of maturity shows certain fundamental differences from the male phase: no tube extends from the lips of the bursa and no sperm sac is present; the capsule gland, now more voluminous, lies on the right side of the vas deferens, and not above it, and is broadly open to the hermaphrodite duct anteriorly; the pallial vas deferens is glandular along its whole length and its junction with the left wall of the oviduct, to form the hermaphrodite duct, is by way of a minute aperture surrounded by a sphincter. Certain changes have occurred in the structure of the bursa. It now opens by way of a muscular ciliated duct which is of considerable length, so that the sac itself appears to occupy a more posterior position and often lies behind the odontophore, between the oesophagus on the left and the male duct on the right. Its musculature is insignificant—in fact it is only with difficulty that any muscle fibres can be seen at all—and its epithelium is no longer cuticularized. The cells are larger, with vacuolated protoplasm and the nuclei are spherical and have prominent nucleoli. The histology of the bursa in the female phase resembles that of the sperm sac in the male phase, and the function of these two structures appears to be similar, for within the bursa waste secretion from the genital ducts may accumulate and later be disposed of; the accumulation is greatest after an egg capsule has been deposited. On histological grounds the hermaphrodite duct may be divided into two distinct regions. The first is lined by a ciliated and glandular epithelium in which mucous cells alternate with ciliated cells, and there are a few subepithelial mucous glands. In the second, which leads to the genital aperture, the epithelium is low, cuticularized and thrown into slight longitudinal folds. Below it lies a thick coat of circular and longitudinal muscles, and a sphincter surrounds the genital opening.

Originally it was thought that every animal passed through a functional male phase with the genital structure as shown in Pl. IV, fig. 2, and later the reproductive system underwent certain changes associated with the adoption of the female phase—this would account for the differences noted above. This may indeed be true for the animals which survive the winter and are the early spring spawners. Although the transition has not been followed in any detail, some individuals collected in mid-April do show the capsule gland enlarging around the right wall of the vas deferens, and a reduction in the size of the sperm sac and of the penial tube. It is now known, however, that individuals which hatch from eggs of summer spawners fail to develop the full anatomical characteristics of the male, and pass directly into a state anatomically comparable with the completely feminized individual. This anatomical femaleness, however, does not prevent the formation of apparently ripe spermatozoa in the testis and their passage into such parts of the male system as are present, and although the lack of a penis and associated structures would appear inevitably to preclude copulation and cross-fertilization, it may not be incompatible with successful self-fertilization.

Reproduction and Life History

No description of the egg capsule of *Omalogyra* is known. Jeffreys (1867) states that capsules 'are occasionally found in the upper cavity of the last whorl in dried specimens', and Lebour (1937) regarded the large glands which open near the anus as egg capsules, and assumed, from the very young crawling stages she observed, that direct development occurred.

The capsules are laid during the spring, summer and early autumn. They are irregularly spherical or ovoid (Fig. 3), and only slightly flattened along the surface which anchors them to weed (*Ulva* and *Enteromorpha*). Each measures 0·2 mm. in diameter, or 0·17 × 0·20 mm., and contains one or occasionally two eggs surrounded by albumen and encased in a wall (W) which consists of two layers. The inner is a mucous layer, and the outer is thick, rather adhesive and of a composite texture which gives a fibrous appearance and a somewhat wrinkled surface.

The eggs are fertilized either in the fertilization chamber or in the albumen gland: in a ripe female spermatozoa have been found in both of these. From the albumen gland the egg and albuminous secretion pass into the mucous gland, and here the inner layer of the capsule wall is added. The outer wall is manufactured by the capsule gland, to which the egg and its coverings is next transferred, and where it is detained for a much longer period. On two occasions a capsule has been found here, distending the duct to apparently abnormal proportions. The capsule is finally fixed to the weed, on which the adults are living, by pressure applied by the foot.

The development of the egg was studied during the month of August when the temperature of the sea water was high (15·0–18·5° C. day temperatures). A typical veliger (V) occurs, though the young develop to the crawling stage (EM) before they emerge. At this stage the individual practically fills the entire space within the wall of the capsule, the albumen being apparently used as food, and often it may be seen moving around the confined space with difficulty. Pressure thus exerted against the wall, together with the action of the radula, may assist hatching. The development is very rapid and is completed in about 10 days at the above temperature. On hatching, the small active molluscs, which measure about 0·16 mm. in diameter, begin to feed on *Ulva* and *Enteromorpha*, and appear to feed continuously. Their growth rate is rapid. In a week the size is doubled, after 17 days the average length is about 0·55 mm., and by the end of 5½ weeks the reproductive organs appear to be functional.

Throughout the summer numbers of individuals of all sizes are abundant; during the autumn the numbers fall until in December and January it is frequently difficult to find more than half a dozen specimens in a rock pool which in summer contained hundreds. The specimens which have been collected during the winter months are immature, of an average length of 0·57 mm., and are apparently hatched from the eggs of late spawners; by March the average length of the individual is 0·77 mm. This would suggest that, as in *Skeneopsis*, animals which have bred do not survive the winter. There is no indication that they migrate elsewhere or choose another habitat. Thus immature individuals tide over the winter and their growth rate is exceedingly slow. In spring they attain maturity, copulation occurs, and egg capsules are produced. The rate of reproduction increases with the rise in temperature and prolific growth of weed in the early weeks of summer. From the anatomy of adult individuals in summer it would appear that self-fertilization may then be practised. Some indication of the rate of increase in numbers during August was obtained from sixty individuals which were kept in a finger bowl and supplied with *Ulva*: after 3 weeks 156 young were produced and there were 21 embryos.

RISSOELLA DIAPHANA (ALDER)

The two species of *Rissoella*, *R. diaphana* (Alder) and *R. opalina* (Jeffreys) occur in intertidal coralline pools, together with the two genera which have been described. Externally the species are readily distinguishable by the shape of the shell and by the tentacles and snout (Figs. 4 and 6), but on the whole their internal anatomy is similar.

The shell of *R. diaphana* has the appearance of a rather short oblique cone, whitish in colour, smooth except for the faint markings of the lines of growth (Fig. 4, LG). It is extremely thin and transparent so that the cream, brown and orange coloration of the underlying viscera are exposed to view. There are four and a half convex whorls separated by fine though well-defined sutures: the apical one is blunt and rounded, and they gradually enlarge towards the mouth, the last occupying three-fifths of the entire spire. The mouth of the shell is large with an outer lip which is incurved and somewhat expanded below. The inner lip is sinuate—it follows the curve of the pillar of the shell and is slightly reflected. The exposed parts of the body of *R. diaphana* are yellowish white with brown pigment patches occurring on the opercular lobes of the foot (OL), an isolated streak on each side of the foot anterior to these, and on the head, between the eyes, a narrow median longitudinal streak which expands anteriorly to the middle of the upper lip, and posteriorly along the neck. In some specimens the pigmentation is more intense, of a purple-brown colour, and covers all the exposed surfaces of the body. Through the transparent colourless shell, on the dorsal surface of the body whorl, wavy streaks of light brown pigment in the underlying mantle are conspicuous against a general background of deep cream. On the right a deep brown blotch, the outer pigmented covering of a group of glands, marks, approximately, the position of the anus. Through the coils of the spire may be seen the deep brown digestive gland, accompanied on the columellar side by the gonad, which is of an orange colour. The transparency of the shell is so great that even the different types of cells in the digestive gland can be distinguished: the excretory cells as black dots scattered throughout the gland, the lime cells with their colourless refringent spherules and, most frequently, the brown digestive cells.

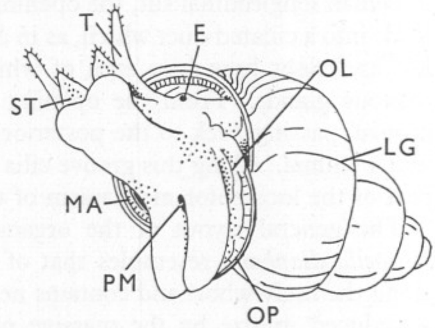

Fig. 4. *Rissoella diaphana*. Living animal. ×50. MA, mantle. Other letters as in Fig. 1.

The snout (ST) is bifid and forms two triangular lobes which diverge from one another at an angle of about 45°. These lobes are shorter and stouter than the tentacles (T) which arise one at the base of each, and the tentacles are cylindrical and taper slightly towards a blunt tip. Each is covered, at least around the distal half, by stiff cilia, and these also fringe the margins of the snout. The eyes (E) are small and placed on slight protuberances far back on the neck, so that when the animal is creeping they lie beneath the shell and never emerge from its shelter.

The foot is more or less lanceolate, somewhat bilobed in front and rounded or bluntly pointed behind; the opercular lobe on each side projects beyond the lateral margins of the sole, which is covered by short thick cilia. Between the ciliated cells open the ducts of subepithelial mucous and mucoid glands. The pedal mucous gland opens on a ciliated V-shaped depression on the upper surface of the foot just in front of the mouth, the angle of the V being directed posteriorly. At about half the pedal length from the anterior end of the sole is a median longitudinal slit, the opening of the posterior pedal gland (PM). This leads into a ciliated duct which, as in *Skeneopsis* and *Omalogyra*, bifurcates into left and right branches, each of which receives the openings of unicellular mucous glands. From the opening of the gland a temporary longitudinal groove, passing back to the posterior tip of the foot, may be observed in the living animal. Along this groove cilia direct the secretion which is an essential part of the locomotor mechanism of the animal.

The general layout of the organs associated with the mantle cavity of *Rissoella diaphana* resembles that of *Omalogyra atomus*. The cavity extends along the body whorl and contains neither gill nor osphradium. Posteriorly it is reduced in size by the massive pallial section of the female duct which projects dorsally from the body wall. The anus is far back on the right side, and from it the dorsal and ventral walls of the rectum are produced anteriorly towards the head as two longitudinal strips of columnar ciliated cells—one along the roof and the other along the floor of the mantle cavity. The former extends farther forwards than the latter. Below each is a broad band of secreting cells which open in, and on either side of, the ciliated strip; the dorsal band is the broader and is composed entirely of mucous cells. It represents the hypobranchial gland. The ventral one is composed of mucous and mucoid cells, the former opening on the median and the latter on the lateral side of the ciliated epithelium. Faecal matter—diatom cases, pieces of algal filaments and detritus—is directed forwards between these ciliated strips and agglutinated by the secretion from the adjacent glands. Broad, oval pellets are thus expelled from the mantle cavity. Near the anus, and on its median side, is a group of large gland cells, about six in number, which open into the mantle cavity. They are surrounded by a thin coat of connective tissue in which dark brown pigment granules occur, and they constitute the conspicuous blotch which is always seen through the transparent shell. In each cell the cytoplasm is filled with very large vacuoles which contain secretion spherules: these dissolve rapidly in acid fixatives. On the median side of the ventral longitudinal strip of gland cells is a deep gutter into which the female duct opens at the summit of a long papilla, and at the anterior end of which is placed the penis. The latter, when at rest, is folded back along the groove so that its tip lies immediately in front of the female aperture.

As in *Omalogyra* the kidney spreads forwards into the thickness of the mantle and opens near the anus. It is a simple sac lined by glandular tissue except for the dorsal wall where squamous cells occur. The glandular tissue is supplied by blood capillaries which are separated from the water current in the mantle cavity only by the squamous epithelium of the floor of the mantle. Through these capillaries the blood is filtered on its way to the efferent pallial vessel which passes along the left wall of the kidney.

Owing to the absence of a ctenidium, which is normally responsible for the setting up of a water current through the mantle cavity, *Rissoella* must depend upon other ciliated tracts for this purpose. Of these the longitudinal strips running forwards from the anus are the most powerful and maintain an exhalant stream. On the right side of the mantle is a band of columnar ciliated cells—a vestige, perhaps, of the ctenidium—where the direction of the effective beat of the cilia has not been determined, but together with a strip of similar epithelium on the underlying body wall they probably produce an inhalant current. Around the inhalant opening of the mantle cavity is a prominent tuft of ciliated cells which beat to the exterior and, as in other prosobranchs, they may expel the largest and heaviest particles which are drawn into the cavity with the stream of water.

The Alimentary Canal

The food of *R. diaphana* consists of diatoms, detritus and small algal filaments. These are collected by the radula whilst the object on which they occur may be held by the jaws. These comprise numerous teeth on the lateral walls of the buccal cavity, each secreted by a single cell and having a finely serrated edge. Anteriorly the buccal cavity is protected by a cuticle, and in the epithelium are a few mucous cells. The secretion from the anterior pedal gland, which opens immediately beneath the mouth, may assist in lubricating the action of the radula and agglutinating the small food particles. The radula is similar to that of *R. opalina* (Thiele, 1929) in that there is one central and two intermediate teeth, the lateral or marginals being absent.

The dorsal food channel, above the radula, conveys the food into the oesophagus. From its origin the oesophagus curves abruptly ventrally and to the left of the radula sac. Its displacement is due to the enormous growth of the reproductive ducts which fill the haemocoel dorsally; immediately behind the odontophore they cross to the right side to open into the mantle cavity. For the same reason the salivary glands, which open into the posterior end of the buccal cavity, are displaced; they are ventral in position, the left slightly anterior to the right. Each gland is a small tubular structure consisting of a comparatively few large cells which are of two types occurring in about equal numbers. There are mucoid cells and glands which, perhaps, produce an enzyme. The oesophagus is lined throughout its length by a ciliated epithelium. It passes beneath the albumen gland to open ventrally into the anterior wall of the stomach.

The stomach, approximately spherical in shape, lies at the posterior end of the body whorl. Dorsally, along its anterior wall, it receives the opening of the intestine, and ventrally the opening of the oesophagus. There are two liver ducts, one dorsal, well behind the origin of the intestine, the other ventral and posterior to the oesophageal opening. The epithelium lining the anterior half of the stomach is ciliated, but posteriorly is an extensive gastric shield. The stomach usually contains a large quantity of food, apparently mixed with fluid from the digestive gland, and compressed into a bolus by the cuticle of the gastric shield.

The two lobes of the digestive gland are unequal in size. That opening into the dorsal wall of the stomach is the smaller and spreads forwards to the posterior end of the albumen and capsule glands. It corresponds to the smaller right lobe of the gland of other prosobranchs. The second lobe, which opens ventrally, constitutes the greater part of the gland and spreads through the smaller coils of the visceral mass with the hermaphrodite gland. The digestive epithelium consists of three types of cells: one, which may be termed the digestive cell, arises from the basement membrane to a broad club-shaped distal end. The cytoplasm is vacuolated and in the upper half of the cell lie spherules which are probably enzymatic and are frequently seen in the digestive tubules. In the lower half of the cytoplasm are greenish brown masses, circular or irregular in outline, which may be absorbed food. No particulate matter has ever been seen in the tubules of the liver, only the same greenish brown fluid as occurs in the stomach. Another irregularly scattered type of cell of varying shape is excretory in function and contains spherules usually of a deep brown colour. Frequently their base is broad and the cytoplasm contains numerous small spherules, those near the base staining moderately intensely with iron haematoxylin, whilst the more distal ones are unaffected. At what appears to be a later stage in their development, these fuse to give a brown homogeneous mass. None of these masses has been traced in the faecal matter. It may be that, since the mollusc is an annual, waste matter, extracted from the blood, is rendered harmless within these cells and accumulates throughout its life. The third type of cell in the digestive gland is of large size and contains spherules of calcareous matter.

The intestine is a short tube which from its origin passes posteriorly for a short distance and then runs abruptly forwards along the right side of the genital duct to the anus. It is lined by columnar ciliated epithelium in which there appear to be no gland cells.

The Reproductive System

The gonad, which lies on the columellar side of the visceral mass, is a hermaphrodite gland with sperm and ova developed in the same tubules. A single and very distensible gonadial duct leads to the posterior end of the body whorl. Proximally it acts as a vesicula seminalis which contains sperm even when eggs are passing through it. Simultaneous hermaphroditism occurs,

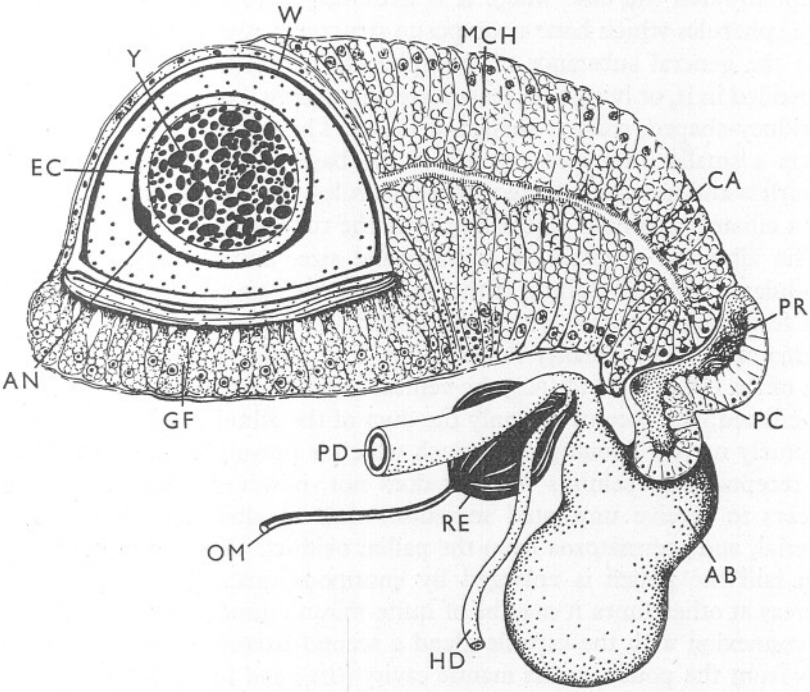

Fig. 5. *Rissoella diaphana.* Section through capsule gland and a reconstruction of the associated parts of the reproductive system. × 150. AB, albumen gland; AN, albumen; CA, gland cells producing a secretion similar to that of the albumen gland; EC, egg covering; GF, glands which thicken the floor of the egg capsule; HD, hermaphrodite duct; MCH, glands producing a mucoid-conchiolin fluid; OM, opening to mantle cavity; PC, posterior lobe of capsule gland; PD, pallial vas deferens; PR, spermatozoa; RE, modified receptaculum seminis; W, outer wall of egg capsule; Y, yolk granules of egg.

though, as is the usual rule, the male system is more precocious in its development than the female. The distal end of the gonadial duct (Fig. 5, HD) is lined by columnar ciliated epithelium, and on reaching the posterior end of the body whorl it divides into two branches which diverge from one another, one of these leading to the pallial vas deferens (PD) and the other to the albumen gland (AB).

The vas deferens passes forward beneath the pallial oviduct, that is, on the left of the median line, and during this part of its course it is ciliated and a few circular muscles underlie the epithelium. Near the posterior end of the buccal mass the duct becomes glandular and turns at an obtuse angle across the dorsal surface of the body to the right side. It ends in a relatively short tubular penis, which, when at rest, lies folded back along the groove in the body wall. The glandular section of the duct constitutes the prostate. Here ciliated cells alternate with gland cells, one type of gland occurring posteriorly, and another along the anterior part of the duct. In the posterior glands the cytoplasm is vacuolated except towards the base where it is extremely dense. The vacuoles contain large spherules which have a composite structure; after the iron haematoxylin stain the general substance of the spherule is a rather yellowish grey, and embedded in it, or lying over its surface, are deeply staining bodies which may be kidney-shaped, comma-shaped or linear. The second type of gland, which covers a smaller area and extends to the base of the penis, contains small colourless and homogenous secretory spherules. No glands occur in the penis, and a ciliated columnar epithelium lines the tube.

The albumen gland is of considerable size, and is composed of a tall glandular ciliated epithelium of the usual type for this situation. It is probable that fertilization occurs within the gland, for during the breeding season spermatozoa are frequently found there. The gland opens into the posterior lobe of the capsule gland (PC), the ventral and anterior walls of which are thin and ciliated, and receive not only the duct of the albumen gland, but also the extremely narrow opening of a pouch which is presumably homologous with the receptaculum seminis (RE). It does not, however, function as such: it appears to receive unwanted secretion, such as albumen and excess shell material, and spermatozoa from the pallial oviduct. After an egg capsule has been laid the pouch is enlarged by enormous quantities of this material, whereas at other times it may be of quite minute dimensions. In addition to the connexion with the capsule gland a second narrow and thin-walled duct leads from the pouch to the mantle cavity (OM), and through this the surplus secretion and spermatozoa are passed to the exterior—there is no indication that the mollusc puts it to any profitable use. The glandular walls of the posterior lobe of the capsule gland (PC) produce a secretion of conchiolin-like consistency impregnated with mucus. Anteriorly the capsule gland leads forwards above the oesophagus and slightly to the right of the mid-dorsal line; it is a comparatively voluminous structure and projects from the dorsal body wall as an opaque white mass. It opens into the right side of the mantle cavity by way of a muscular papilla which is posterior to the root of the penis and well behind the tentacles.

Except in the region of the papilla, the walls of the capsule gland are thickened by tall epithelial secreting cells which alternate with wedge-shaped ciliated cells. In transverse section the lumen is approximately semilunar in shape, with the concavity directed ventro-medially. There are thus two longitudinal grooves along the duct: the outer or right one is the more pronounced, is thin-walled, not glandular, and folds beneath the glandular tissue of the floor. It originates along the wall of the genital papilla and passes back to the posterior lobe of the capsule gland, near the opening of the albumen gland. On several occasions spermatozoa have been found along its posterior end, not orientated, but scattered in irregular masses, and it would therefore seem to be the path along which these travel to the site of fertilization. On a histological as well as a functional basis the secreting part of the duct, anterior to the posterior lobe of the capsule gland, may be divided into three regions. In the most posterior of these the gland cells form a complete band around the duct, and are similar in many respects to those of the albumen gland, though they stain deeper with mucicarmine and purple with toluidin blue (CA). The succeeding glandular belt resembles the posterior lobe in producing a mucoid conchiolin fluid (MCH). The final glandular section comprises, dorsally and laterally, only a very narrow band of cells, though along the floor it thickens and spreads towards the genital papilla. The glands produce a basophil secretion which is added chiefly to the floor of the capsule (GF). The muscular papilla is separated from the glandular duct by a sphincter; it is lined by ciliated cells and a few mucous cells.

Reproduction and Life History

The egg capsules are manufactured one at a time in the pallial oviduct. They are described by Lebour (1936). Each is hemispherical in shape and attached by the flattened base to green or red algae, the base measuring 0·48 mm. long and about 0·25 mm. broad. The capsule contains one or two eggs (Fig. 5, Y), each covered by a thin membrane, albuminous layer (AN) and egg covering (EC), and floating in a fluid which fills the capsule. The outer wall (W) is thick and semi-transparent. During early summer several individuals of *R. diaphana*, with capsules still in the process of formation, have been fixed and sectioned (Fig. 5), and from these the functions of the various parts of the capsule gland have been calculated. The egg is presumably fertilized and receives its supply of albuminous fluid as it passes through the albumen gland (AB), and in the posterior lobe of the capsule gland (PC), where excess spermatozoa are frequently found (PR), the egg covering is deposited. The staining properties of this covering, which isolates each egg from its neighbour, and those of the glands of the posterior lobe are identical. The fluid which fills the capsule is derived from the next section of the duct (CA) as the egg passes forward, and the outer wall (W) from the two ultimate glandular regions. The more posterior of these forms a substantial layer of conchiolin impregnated with mucus (MCH), and this is covered, especially along the base of the capsule, by secretion from the last glandular region (GF)—this stains with iron haematoxylin and is not mucus. It will be remembered that the glands of this last region are thick along the floor and few occur laterally and dorsally. Here the capsule appears to be retained for some time, and its floor is thickened, before it is passed into the lumen of the genital papilla and finally deposited on the weed by the foot. Within the capsule the embryo passes through a veliger stage and hatches as a miniature of the adult.

The young at all stages of development are to be found with the adults in spring, summer and early autumn. During the winter the species is far from its summer abundance and the specimens which have then been collected are not fully grown, their reproductive organs being immature. It would thus appear that, as in the other two genera which have been described, *R. diaphana* is an annual. Its rapid development, which is completed within a fortnight, and its rapid rate of growth, enable it to take advantage of favourable climatic conditions, so that during the spring and summer several generations may be co-existent.

Rissoella opalina (Jeffreys)

The semi-transparent and highly glossy shell of *R. opalina* is globular in form (Fig. 6 A). There are three and a half whorls separated by broad deep sutures; from the first, which is low, the shell expands abruptly. The body whorl is rounded and its length is approximately twice that of the short, blunt spire. The mouth is broadly rounded anteriorly and gradually contracts posteriorly; the outer lip is sharp and thin, the inner flexuous and thickened on the lower part of the columella. The empty shell is a pale yellowish brown, though in the living animal it appears darker owing to pigmentation in the underlying tissues. When the animal is expanded, the short, tubular snout (ST) projects from under the anterior edge of the shell; above it, and on each side, is a deeply bifid tentacle (T) which is thickly ciliated. The upper surface of the body is mottled with purplish brown or black except for the tentacles, the V-shaped depression which lies immediately below the mouth and is the opening of the anterior pedal gland, and the periphery of the foot—these three regions are colourless. The eyes (E) are situated on slight protuberances and lie close together beneath the shell from which they are never extended. Each is surrounded by an unpigmented ring of tissue. In the living animal the brown pigment of the mantle can be seen through the shell, varied here and there by lighter wavy streaks and by cells filled with orange spherules. Three dark blotches lying within the mantle constitute one of the most characteristic features of the species and mark the position of groups of glands (PI), which are similar to the single group found near the anus in *R. diaphana*. In the upper coils of the spire the excretory cells of the digestive gland (P) can also be seen through the shell as scattered dark spots. The foot is large and triangular, slightly notched in front with the two anterior angles rounded, and bluntly pointed behind (PF). There are two pedal mucous glands resembling those of *R. diaphana*; the V-shaped depression on the propodium which marks the opening of the anterior one is, however, more pronounced.

The organs associated with the mantle cavity differ in some detail from those which have been described for *R. diaphana*. On the left of the mantle, and in the anterior position, is the rudiment of a ctenidium in the form of a few strongly ciliated folds of epithelium; these help to maintain the pallial water current, though they are of little importance in respiration. To the left of this, and washed by the inhalant stream, are the openings of two large multicellular glands, one at the edge of the mantle, and the other just within the mantle cavity, around them stretching a patch of epithelial mucous cells. Each opening leads back through a ciliated and glandular duct to the more posterior gland which lies where the mantle separates from the rest of the body. The gland which opens at the edge of the mantle is composed of mucous cells; the second, opening just within the mantle cavity, is surrounded by minute black pigment granules, and these may also be scattered between the large gland cells.

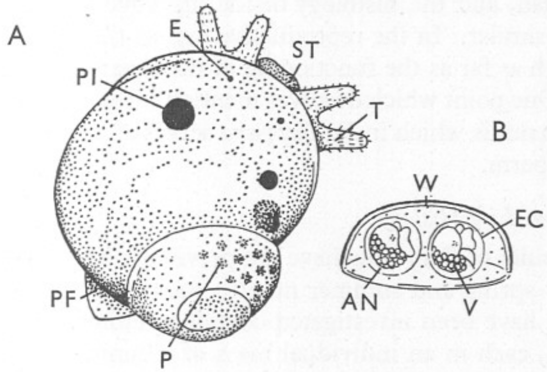

Fig. 6. *Rissoella opalina*. A. Living animal, ×40. B. Egg capsule, ×37. P, spherules in excretory cells of digestive gland; PF, posterior tip of foot; PI, pigmented group of gland cells; V, veliger. Other letters as in Figs. 1 and 5.

This gland is one of the three dark blotches which are conspicuous through the transparent shell. Median to the rudiment of the ctenidium is the anterior limit of the kidney which lies within the mantle, and is separated from the mantle cavity by a layer of squamous epithelium. This part of the mantle, within which lies the kidney with its rich vascular supply, is presumably the chief respiratory surface. The hypobranchial gland is, as in *Omalogyra* and *Rissoella diaphana*, displaced to the right owing to the interpolation of the kidney between the ctenidium and the gland. It stretches back from the opening of the mantle cavity to about the level of the anus—on the median side it abuts against the right wall of the kidney, and laterally against the columnar ciliated epithelium which lines the exhalant opening. Anterior to the anus opens the second of the three groups of large gland cells. This one, embedded in the mantle, is smaller and in a position comparable to the similar gland in *R. diaphana*. From just posterior to the anus a tongue-like projection of the mantle wall juts forwards ventral to the opening, so that the faeces are discharged into a special compartment of the mantle cavity lying between this on the left side and the mantle itself on the right. Along each side of the compartment, on the surfaces facing one another, is a short strip of ciliated epithelium which drives the faecal matter forwards. Unlike *R. diaphana* the strips are short, since the anus is farther forward, and they do not enter the rectum itself. Embedded in the projection, and opening on its ventral surface posterior to the anus, is the third group of large pigmented glands. The only apparent function of these glands is to compensate for the reduced size of the hypobranchial gland and the lack of intestinal glands to consolidate the faeces. Posteriorly the mantle cavity is filled by the pallial oviduct, which projects from the dorsal wall of the body.

The internal anatomy of *R. opalina* is sufficiently similar to that of *R. diaphana* for a description to be unwarranted. The alimentary canal is built on the same plan, and the histology of the digestive gland, and its mode of functioning, is similar. In the reproductive organs there are some differences in detail, though as far as the functioning of the organs is concerned these are insignificant. One point which deserves mention is the absence of the modified receptaculum seminis which in *R. diaphana* serves as a reservoir for unwanted secretion and sperm.

Reproduction and Life History

The egg capsules of *R. opalina* have not previously been described. They are laid during the spring and summer months on green and red algae. The ten capsules which have been investigated contained either two, or rarely (twice) three, embryos, each in an individual mass of albumen which is surrounded by an egg covering. The embryos, with these protective layers, float in a common fluid which fills the capsule. The capsule is hemispherical, with the flattened surface, attached to the weed, measuring approximately 0·65 × 0·4 mm.; the height is about 0·5 mm. The wall is thick, semi-transparent and of a fibrous texture, being composed of conchiolin threads in a mucoid substrate. It is produced by the composite secretion from the capsule gland. The method by which the capsule is manufactured in the pallial oviduct is similar to that of *R. diaphana*.

The embryos pass through a veliger stage and develop to a replica of the parent before they hatch. The full development in the summer months takes about a fortnight. During this time the embryo comes to occupy the entire space within the egg covering, which appears to be stretched during its growth; the covering is not broken until the young are ready to escape from the capsule. The veligers can be recognized by the early appearance of the groups of large pigmented gland cells which lie in the mantle. Also through the mantle, at a later stage in embryonic life, the kidney tissue can be seen.

Young, which hatched from capsules during August, ranged from 0·18 to 0·27 mm. long. They adopt the same feeding habits as their parents and within a fortnight their size is more than doubled (0·43–0·68 mm.). Breeding is continuous throughout the warmer months when individuals at all stages of maturity can be found in the rock pools in comparative abundance. The adults with very few exceptions do not survive the winter, when the number of the species is low, and an immature, slow-growing population is characteristic.

Discussion

Skeneopsis planorbis, *Omalogyra atomus*, *Rissoella diaphana* and *R. opalina* are amongst the smallest British marine molluscs and are inhabitants of rock pools below the level of mid-tide, especially those which have an abundant growth of algae. They are rarely found elsewhere on the shore. As compared with the more familiar and larger intertidal prosobranchs these small forms show in some respects a simplicity of structure, and in many others a high degree of specialization. The latter may be correlated both with their habitat and their smallness.

All four species are herbivorous, feeding on diatoms, algal filaments and some detritus, and during the warmer and lighter months of the year, when conditions favour plant growth, they feed continuously, even at low tide when other herbivores, uncovered by water, are less active. There appears to be no cellulase in the digestive system, since uninjured plant cells pass through the gut undigested, and add to the abundant faecal matter. Nevertheless, unlike other herbivorous intertidal prosobranchs, the intestine is extremely short: in *Omalogyra* the length is one-third the length of that part of the gut lying anterior to the ducts of the digestive gland, whereas in the limpet the corresponding proportion is 8:1. The limpet is uncovered by the tide for a considerable number of hours each day, and the faecal matter must then be stored in the long glandular intestine where it is elaborated to prevent fouling of the mantle cavity later (Graham, 1932). Molluscs like *Skeneopsis*, *Omalogyra* and *Rissoella*, which live predominantly in rock pools, need none of these precautions, since there is a continuous flow of water through the mantle cavity to carry away the faeces, and a short and histologically simple intestine suffices when its function is simply one of transport. The intestine does not enter the coils of the visceral mass, but, from the anterior region of the stomach, at the posterior end of the body whorl, it passes directly along the right side of the mantle to the anus. Moreover, in *Omalogyra* and *Rissoella diaphana*, and to a lesser extent in *R. opalina* and *Skeneopsis*, it becomes shorter still because of the posterior position of the anus, which lies deep in the mantle cavity instead of at its opening.

It is a well-known fact that certain prosobranchs lose their ctenidium. In *Pomatias elegans*, and perhaps also in *Acicula lineata*, this is associated with a change from an aquatic to a terrestrial habitat. It would seem that smallness is a factor leading to the same result, since in the Omalogyridae, Rissoellidae and Pyramidellidae there is no gill. The loss of a special respiratory surface in the minute representatives of a phylum is, of course, a common occurrence. It is probable that a certain amount of respiratory activity is normally carried out by the mantle in any mollusc, and it would appear that this is adequate for the respiratory needs of animals of such small size as those which are mentioned above. Three of the four species which have been described show other changes in the organs associated with the mantle cavity, which may accompany this loss. *Skeneopsis*, which is larger than the others, retains to a greater extent the typical arrangement of organs in the pallial cavity: it still possesses a ctenidium, though the number of filaments is reduced to nine, the kidney lies near the posterior end of the mantle cavity and the hypobranchial gland extends far back along the right side. In *Rissoella diaphana* and *R. opalina* the ctenidium is represented only by a patch of ciliated columnar cells, and in *Omalogyra* it is lost entirely. In these three the kidney has grown forwards mid-dorsally into the mantle, and brings with it a rich vascular network, which is separated from the water current in the mantle cavity only by a squamous epithelium. This, perhaps, increases the chances for the oxygenation of the blood. It is tempting to imagine that the similar forward thrust of the kidney in the other gastropods without a gill—the pulmonates and *Pomatias elegans*—may confer a similar benefit upon the animal. In *Omalogyra* and *Rissoella* the hypobranchial gland does not spread far beyond the anus, but its small area may perhaps be compensated for by the relatively enormous size of some individual cells. Accompanying the gland are longitudinal strips of columnar ciliated epithelium which pass forwards from the anus and produce a strong exhalant current. This current induces the inhalant flow of water along the right side of the mantle cavity, which is normally maintained by the ctenidium.

The ability of these gastropods to produce vast quantities of mucus from the foot would appear to be associated with their habitat. In the calm waters of a rock pool at low tide, they can utilize the mucous rope played out from the posterior pedal gland to lower themselves through the water in a caterpillar-like fashion. When the tide is high, and the water more turbulent, the viscid secretion from the gland, as well as from the general surface of the sole, helps them to maintain a firm hold. The posterior pedal gland has already been described in the rissoids (Johansson, 1939), and it occurs in other small, intertidal gastropods such as *Bittium*, *Cerithiopsis* and *Triphora* (personal observation). As a result of this excessive demand for mucus the glandular tissue has become too extensive to be accommodated entirely within the foot, and spreads into the haemocoel along each side of the buccal cavity and the anterior oesophagus.

As far as the internal anatomy is concerned there are two main points worthy of notice: the simplicity of the gut, and the complexity of the reproductive organs. The oesophagus differs from that of the typical prosobranch in being devoid of oesophageal glands. In the related Rissoidae the explanation of this seems to be the presence of a crystalline style in the stomach. None of the creatures under consideration possesses such a structure, so that the simplification of the oesophagus must be due to something else. Now this part of the alimentary canal runs through the connexion between head, foot and visceral hump, where space has to be made for large and complex reproductive ducts which spread into all available corners, and it is probable that the presence of these limits the size of the oesophagus. Digestive tissue is, therefore, confined to the digestive gland which completely fills the visceral hump, except for the gonad, and its extent in *Omalogyra* is increased by spreading on to the gastric wall, and in the winter form—a particularly small animal—on to the lateral walls of the oesophagus as well. The epithelium in the digestive gland is composed of (*a*) digestive cells, (*b*) lime cells, and, except in *Omalogyra*, (*c*) cells which appear to act as deposits for excretory material. I have never observed this to be eliminated, and it would appear that these cells act as a kidney of accumulation, which is a perfectly feasible arrangement in an annual mollusc. This would also have the effect of relieving the kidney itself of a great deal of its normal work, leading to a simple sac-like structure, suggesting, in fact, that the organ has become more important from the respiratory than the excretory point of view. It may still, however, be required for osmoregulatory purposes, which may, at times, be a matter of prime importance to an inhabitant of a rock pool.

The survival of these rock-pool prosobranchs depends upon their ability to take advantage of conditions which favour their rapid growth and reproduction. These are fulfilled during the warmer months of the year by the high temperatures and ample food supply. The population is then at a maximum, and several generations of each species may be co-existent. With the fall in temperature during the autumn both growth and reproduction are retarded, and the mature population gradually dies out, so that only perhaps an occasional individual will survive into the winter. The population is then at a minimum: it is typically immature, having been derived from eggs laid by late spawners, and the growth of the individual is extremely slow compared with that during the summer. The necessity for a rapid increase in numbers is reflected in the hypertrophy and complexity of the reproductive organs to provide for the protection and feeding of the embryos. Relatively large egg capsules are produced; each is fixed to the weed on which the animals live and contains one to three heavily yolked eggs, surrounded by albumen, and protected by a thick wall. The development takes about a fortnight during a favourable summer and the young hatch as miniatures of the adult. If conditions are good, they grow rapidly, mature, and reproduce in the same season—*Omalogyra* may develop from the egg and reproduce in about 7 weeks. The life of such individuals is short and may be reduced to less than 6 months.

A similar maximum of numbers during the summer is found in *Rissoa parva* (da Costa), and probably many other rissoids. In these, however, some mature animals may live through the winter, spawning the while.

Rissoella and *Omalogyra* are hermaphrodite and ripe spermatozoa and ova occur simultaneously. Simultaneous hermaphroditism is a fairly common phenomenon within the prosobranchs, and is found in quite unrelated forms—*Valvata*, *Velutina*, *Cerithiopsis* (personal observation) and in all the Pyramidellidae. Little is known of the extent to which self-fertilization is practised. It seems likely that it takes place in *Omalogyra*, and there is no morphological bar to its accomplishment in *Rissoella*. In *Omalogyra* there does not appear to be anything which could act as a copulatory organ in the summer population, in which the development of the reproductive organs is different from that of winter forms, yet, despite this, reproduction goes on rapidly, and the explanation may be self-fertilization or parthenogenesis, but the latter seems far less probable. In individuals which develop slowly during the winter months and which come to maturity in the spring, the male system is the first to become functional, and it seems likely that copulation will then occur, but, as I have never seen this taking place, I do not know whether it is a reciprocal act or not.

If the hermaphrodite reproductive system be neglected, it would appear that the anatomy and life history of the molluscs under discussion indicate a relationship with the Rissoidae. Many of the rissoids are intertidal, or inhabit shallow waters, and they also possess a posterior pedal gland which extends from the foot into the haemocoel of the head; to them such a gland is as useful an aid to locomotion as it is to *Skeneopsis* and *Rissoella* and enables them to exploit the surface film as well as the substratum. The food and feeding habits are also similar—except in *Omalogyra*. The food consists of algal filaments, diatoms and detritus. It is passed down a simple oesophagus, which lacks glandular pouches, and is partly digested in the capacious stomach. Amongst the rissoids several species (Graham, 1939; Johansson, 1939) possess a crystalline style, which, however, is not present in *Skeneopsis* and *Rissoella*. In *Omalogyra* the radula is reduced to three teeth in each row (Ankel, 1936) which puncture the algal cells from which the sap is sucked. Pruvot-Fol (1926) points out the similarities between the structure and function of this radula and that of the ascoglossan nudibranchs, and even goes so far as to suggest the presence of an ascus sac for used teeth in *Omalogyra*, though I have never seen anything of this nature. Her final conclusion is that the similarity is entirely due to convergence. The egg capsules of the rissoids are fixed on weed and are similar in most respects to those of *Skeneopsis*, though they contain relatively smaller and more numerous eggs which escape as free veligers (Lebour, 1934). Thus in the rissoids the general parallelism is maintained between lack of specialization in bodily structure and simplicity of larval history. Related to the rissoids are the hydrobiids amongst which *Hydrobia jenkinsi* Smith is peculiar in practising parthenogenesis. In other species of *Hydrobia* the sexes are separate, so that parthenogenesis in *H. jenkinsi* would appear to have arisen by the loss of the male. *Omalogyra* may indicate a different way in which a purely parthenogenetic species may evolve—that is by the reduction and final loss of the male stage in the reproductive activities of a hermaphrodite.

Summary

The external features of *Skeneopsis planorbis* (Fabricius) are described and compared with those of *Omalogyra atomus* (Philippi), *Rissoella diaphana* (Alder) and *R. opalina* (Jeffreys).

The foot has a large posterior mucous gland (Figs. 1 and 4, PM; Pl. IV, figs. 1 and 2, AL, PL), its secretion forming a thread on which the mollusc can climb from one level to another.

Correlated with their small size are modifications of the pallial organs. *Skeneopsis*, the largest and least specialized, has a bipectinate osphradium, but the gill is reduced to nine filaments; the anus lies well within the mantle cavity. In the other genera osphradium and ctenidium are lost, though the latter may be represented in *Rissoella* by a small tract of ciliated epithelium. In the absence of a ctenidium the animals depend entirely upon pallial respiration and the stream of water through the mantle cavity is maintained by other means: from the anus strips of ciliated epithelium pass forward to the mouth of the mantle cavity, causing a strong exhalant stream and carrying away the faecal pellets. There is a compensating inhalant flow. The kidney (Pl. IV, figs. 1 and 2, K), with its rich vascular supply, has migrated into the tissues of the mantle, increasing its respiratory efficiency.

In the internal anatomy the simplicity of the gut and the complexity of the reproductive organs are the most outstanding features. One may be the cause of the other (pp. 628–29).

The animals are abundant during the warmer months and scarce in winter, when an immature slow-growing population is found. The opportunity for rapid increase in numbers during spring and summer is given by the hypertrophy and complexity of the reproductive organs which provide for the protection and feeding of the embryos.

Omalogyra and *Rissoella* are hermaphrodite. It seems likely that self-fertilization may occur in the summer animals of *Omalogyra* in which there appears to be no copulatory organ. Summer individuals differ in other structural details from the winter animals. In *Rissoella* there is no morphological bar to self-fertilization, but it has never been observed.

Egg capsules (Figs. 1 and 6) are fixed to weed and contain from one to three eggs, which hatch in about a fortnight at summer temperatures. The young escape in the crawling stage, and, if conditions are favourable, become mature in 6 weeks or less and reproduce in the same season. Thus one generation follows rapidly upon another.

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