THE FUNCTIONAL MORPHOLOGY OF THE BRITISH ELLOBIIDAE (GASTROPODA PULMONATA) WITH SPECIAL REFERENCE TO THE DIGESTIVE AND REPRODUCTIVE SYSTEMS

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CONTENTS

The four British members of the primitive pulmonate family Ellobiidae are *Leucophytia bidentata*, living in crevices between tide-marks, *Ovatella myosotis*, inhabiting salt-marshes (with an intertidal subspecies, *denticulata*), and the fully terrestrial *Carychium tridentatum* and *C. minimum*.

The present paper gives an account of the functional morphology of the pallial cavity, alimentary canal and reproductive system, with a description of the developmental stages, for each of the British genera.

In *Leucophytia bidentata*, the arrangement of the organs in the pallial cavity and the distribution of mucus glands upon the foot and pallial margin probably corresponds to the primitive condition of the sub-class Pulmonata. There is an unspecialized supra-anal lobe, representing the adaptive 'gill' of higher Basommatophora, and within the mantle cavity the gill and hypobranchial gland are unrepresented.

There is a small muscular buccal mass, with a broad radula, bearing unspecialized, multiseriate teeth. Into the buccal mass opens a pair of small salivary glands. The oesophagus broadens posteriorly to form a rather more distensible crop-like region. The stomach has lost most of the features of the generalized molluscan condition. The oesophagus opens into a thin-walled ciliated oesophageal atrium, receiving the single digestive diverticulum. The atrium opens backwards into the anterior chamber of the stomach, which is capable of considerable muscular movement, and communicates in turn with a spherical gizzard, lined with cuticle and very strongly muscular. The posterior end of the stomach, corresponding to the posterior caecum, is inversible into the gizzard to form a tongue-like valve whose function is discussed. The digestive gland undergoes a cycle of ingestion, digestion, and fragmentation and excretion. Its histology during each stage is fully described and the nature of the digestive cycle is discussed. The intestine is a short tube, of simple structure, thrown into a single loop, and conveying a mucus-bound faecal string to the anus.

Leucophytia is a protandrous hermaphrodite, showing a sexual succession, which is in evidence both in the condition of the gonad and in the degree of development of the genital ducts. A male phase terminates about December, followed by a stage of egg maturation, terminating with oviposition in May. The gonad leads by a little hermaphrodite duct to the point where male and female ducts

become completely divided. The female portion consists of a fertilization pouch and a posterior and anterior mucus gland, opening close to the aperture of the pallial cavity by a short muscular vagina. A long stalked bursa copulatrix opens into the genital vestibule. The male duct consists of a short posterior vas deferens, continued forward by a glandular prostate. Along the right side of the head proceeds an anterior vas deferens, which passes anteriorly into the haemocoele of the head, to open through a muscular penis which is invaginated into a preputial sac.

An account is given of the egg capsules, and of the embryo, which is operculate, with a shell showing reduced heterostrophy, and with prominent vestiges of a velum. There is no free swimming stage.

Ovatella myosotis shows in the alimentary canal a similar general structural pattern to *Leucophytia*. The chief differences lie in the structure of the stomach which is a good deal more primitive, and perhaps represents an original or basic type in the Ellobiidae. The gizzard is thinner walled but still muscular, and the posterior caecum retains its primitive form, with the posterior diverticulum still represented, opening at the mouth of the caecum into the stomach. Ciliated excurrent grooves run from both anterior and posterior diverticula to the proximal part of the intestine, and this region preserves some features of the structure, but little of the function, of the style sac.

The reproductive system is also more primitive than in *Leucophytia* and probably of a type basal to the family Ellobiidae. The male and female portions of the large hermaphrodite duct, though functionally divided, remain in open communication. The prostate shares a common lumen with the anterior mucus gland. The relations of the anterior vas deferens and the penis are similar to those of *Leucophytia*. The egg capsules and the embryos are described, and show one or two differences from *Leucophytia*.

The mantle cavity in the terrestrial *Carychium* is characterized by a pallial gland, a tubular structure opening outside the cavity in an anterior position. Its structure, homologies and possible functions are discussed.

The alimentary canal agrees in most of its features with a basic ellobiid plan, but the stomach shows a number of differences from other ellobiids studied. In particular, there is no oesophageal atrium, and both of the digestive diverticula open close together into a ciliated, spherical chamber, which also receives the oesophagus, and forms the posterior end of the stomach. The gizzard is strongly muscular and barrel-shaped, lined with cuticle. It opens anteriorly into the narrow intestine, and in the first part of the intestine the ciliary coat shows a rotatory beat reminiscent of that of the style sac. The structure and cycle of activity of the digestive gland is described in detail, with an account of the mode of formation of fragmentation phagocytes.

The reproductive system shows a protandrous sexual succession like that of other ellobiids. The little hermaphrodite duct is dilated into a single pocket forming a seminal vesicle. The albumen gland is small, and opens, with the little hermaphrodite duct, into a cylindrical mucus gland, of simple structure. At the same point opens a very large, strap-shaped shell gland, a structure not represented in other ellobiids, which secretes the tough, leathery egg-capsule, surrounding each of the singly deposited eggs. There is no secretion of a common mucus coat enclosing a cluster of eggs as in marine ellobiids. For a portion of the year, during the female part of the sexual cycle, *Carychium* appears to be aphallic. The penis and the anterior vas deferens were found only in July, the penis being small, and of extremely simple structure.

The evidence on the functional morphology of the Ellobiidae, presented in this paper, is reviewed in a discussion on the position of the family, with relation to the rest of the Pulmonata. The conclusion is reached that the Ellobiidae are by far the most primitive of existing pulmonates, and—in structure and mode of life—cannot be far removed from the earliest members of this sub-class. The alimentary canal and the reproductive system are discussed as they appear in primitive members of the three subclasses Prosobranchia, Pulmonata and Opisthobranchia. The primitive members of each of the three subclasses draw close together in a number of common characters, revealed in both the digestive and the reproductive systems. The relationship of the higher freshwater Basommatophora to the primitive marine pulmonates is dealt with in light of our knowledge of the Ellobiidae, and it is concluded that the Lymnaeidae and the families related to them show fundamental differences setting them apart from the marine pulmonates.

INTRODUCTION

The gastropod subclass Pulmonata falls into two orders, the Basommatophora and the Stylommatophora. The second is by far the larger, and its members are all terrestrial. The Basommatophora, to which belong the snails dealt with in this paper, live—with few exceptions—in the sea between tide-marks and in fresh water. They are grouped by Thiele (1931) in four superfamilies of which, however, only two are represented in the British fauna. Of these, the Hygrophila are entirely confined to inland waters, and the other, the Acto-phila, contains two marine families, the Ellobiidae and the Otinidae, which have long been recognized as very primitive in their organization, and entitled to a place at the foot of any pulmonate classification. The Otinidae consists of one genus with a single species, the British *Otina otis*, already discussed by the writer in a recent paper (Morton 1955 a). The Ellobiidae are a much larger family with a world-wide distribution, comprising twenty genera, of which three are represented in Britain. Two of these genera are marine: *Leucophytia*, with one intertidal species, *L. bidentata*, occurring on most rocky coasts, and *Ovatella*, with one species, *O. myosotis*, restricted to salt-marshes at the supratidal fringe, and its subspecies, *O. m. denticulata*, which is intertidal. The third British genus, *Carychium*, is one of three ellobiid genera which have become terrestrial. Our two species, *C. tri-dentatum* and *C. minimum*, are minute snails with an inland distribution, entirely removed from any apparent connexion with the shore.

The Ellobiidae have a wide interest both to the ecologist and to the malacologist as probably the most primitive surviving members of the Pulmonata. They retain many structural features which betray their prosobranch origin. A study of the evolutionary and ecological aspects of this family is already in the press (Morton 1955 b). It is proposed in this paper to present a more detailed description of the functional morphology, more especially of the digestive and reproductive systems, of the three British genera.

The principal previous contributions to the anatomy of the Ellobiidae form a short list. The most detailed paper is that of Kowslowsky (1933) on the structure of *Melampus boholensis*. Pelseneer (1895 a) had previously written on *Phytia myosotis*; Plate (1897) on *P. scarabaeus*, and Odhner (1924), in the course of a taxonomic paper, made some useful comparative observations on the structure of several of the genera. *Carychium* was the subject of a brief study by Moquin-Tandon (1856). In spite of the incompleteness of our present knowledge of the group, it is clear that, from their systematic position and evo-lutionary level, the Ellobiidae may be expected to provide valuable evidence towards the building up of a broad comparative picture of structure and function in the pulmonates as a whole. Three series of such studies in other gastropods have now appeared: the papers of Yonge (1938, 1947) on the pallial cavity, of Graham (1938, 1949) on the stomach, and of Fretter (1942, 1946) on the genital ducts. In the pallial cavity, the Ellobiidae—like most pulmonates—show perhaps fewer points of comparative interest; in the condition of the alimentary canal and of the genitalia, on the other hand, they are among the most instructive members of the Pulmonata.

Materials and methods

The whole of the material of *Leucophytia bidentata* was collected at Wembury and at other localities in the Plymouth area. The species, which occurs together with *Otina otis*, forms an important member of the intertidal crevice fauna, already described in an ecological paper (Morton 1954 *a*). *Ovatella myosotis* was obtained at the mouth of the River Adur, at Shoreham-by-Sea, Sussex, where it occurs beneath stones and debris among the tangled stems of the succulent herb *Obione portulacoides*, on the narrow strip of salt-marsh to the landward side of the railway-bridge crossing. *Carychium tridentatum* was collected at Box Hill, Surrey, in chalk pits, where its ecology and mode of life has already been briefly described (see Morton 1955 *c*).

In each case, the animals were first examined alive after careful removal of the shell. The ciliary and muscular action of the digestive and reproductive systems were observed and recorded in drawings after exposure of the intact organs in the living animal. The course of the ciliary currents and the nature of the glandular secretions and contents of the lumen were often visible by transparency without further dissection of the organs. For structural details, the stomach and portions of the genital complex were dissected with needles under higher powers of a Cook, Troughton and Sims binocular microscope. Short immersion in dilute solutions of methylene blue was found useful for the better examination of glandular regions as well as for investigating details of the nerve supply. Each dissection was afterwards bulk-stained in Mayer's haemalum, cleared in cedar-wood oil and re-examined in xylol, without mounting, as a transparent object. Fixation was for the most part by aqueous Bouin's fluid at full strength. This was found equally satisfactory to Dubosqu or sea-water Bouin's fluid. Cell distortion appeared to be at a minimum by comparison with excised and macerated fresh material, and the preservation of cytoplasmic and secretory contents was nearly always good. 10 % neutral formalin was at times employed. In *Leucophytia* and *Ovatella* more rapid penetration of the fixative was obtained by gently cracking the shell, while avoiding distortion of the animal, by the pressure of a glass slide. The fragments of shell were entirely dissolved after 12 h fixation in Bouin's fluid after which the transparent shell membrane was carefully picked away with needles to assist more rapid impregnation at a later stage. In all cases, animals were kept 12 h before fixation in a glass dish in order that the alimentary canal might be emptied of hard contents. Clearing of dehydrated material was carried out in cedar-wood oil, which was invariably used when long periods of storage were necessary. Embedding was performed simply by transferring to paraffin wax of m.p. 52° C for 2 h, after a preliminary rinse in xylol of not more than 5 min. No change of paraffin wax was found necessary, and perfectly sectioning blocks could be made by casting the original paraffin wax in watch-glasses. This economy in procedure was found to be a great convenience, especially with the tiny *Carychium*, in eliminating the operation of transferring of material from dish to dish. Fixed animals were examined both by serial sectioning and as cleared intact objects. The latter were either overstained for 24 h with Mayer's haemalum, and differentiated for 3 to 4 days in acid alcohol 70 %, or were examined merely with the aid of the picric acid staining persisting from fixation. Mayer's haemalum was found greatly preferable as a bulk stain to borax carmine or Ehrlich's haematoxylin, both in the contrast obtained of

nuclear detail with the cytoplasm, and in showing up finer points of structure. Animals for examination as whole objects were stored in cedar-wood oil, and examined in watch-glasses in xylol. Permanent mounts were never made, all specimens being kept loose for easy manipulation. Specimens so cleared are easily dissected, the separated systems of organs falling readily apart. Graphical reconstruction of serial sections was found to be necessary only in interpreting the smaller and more difficult details. Accurate shapes and contours were much more rapidly obtained by comparison of living and fixed dissections. Sections were cut at 7μ thickness, which was found convenient for both micro-anatomy and detailed histology. They were stained principally with Heidenhain's azan, as described by Pantin (1946), and also with Mayer's haemalum, which gave a rapid and useful picture of nuclear detail, while subduing the details of cytoplasmic inclusions. Heidenhain's iron haematoxylin was used for the most accurate nuclear detail, together with Pantin's recommended modifications of Masson's trichrome, as an alternative general stain. Special stains used for mucus detection included thionin (counterstained with eosin) and mucicarmine.

1. *LEUCOPHYTIA BIDENTATA*

So far as is known, no previous anatomical description exists of *Leucophytia bidentata*. The ecology of this species has been described by Morton (1954 a); and its abundance at Plymouth made it a convenient form to employ as the example of the Ellobiidae for most detailed morphological study. The shell is well described by both Jeffreys (1869) and Forbes & Hanley (1853). A good figure does not seem to have yet been provided, and a shell is illustrated in outline in figure 2, serving for comparison with *Ovatella myosotis* var. *denticulata*, see figure 17 to which it has often a deceptively close resemblance. As regards nomenclature Winckworth (1949) has pointed out that the generic name *Leucopepla* used in his British List (1932) is elsewhere preoccupied by an insect. He proposed the new generic name *Leucophytia*, which must now remain in use, though it is a little unfortunate that it perpetuates the meaningless mis-spelling, *-phytia*, which has here been abandoned as a generic name in its own right (p. 120). After full consideration it has been decided not to include this species under *Stolidomopsis* as suggested by Watson (1943, p. 17). No other species of *Stolidomopsis* is now living, and since the present species differs rather strongly from all other Ellobiidae investigated, in ways that could not be suspected from conchological characters, it would seem advisable to keep a separate genus available for it. On grounds of euphony, also, the avoidance of *Stolidomopsis* is much to be desired, if respectable reasons can be found for doing so.

The animal of *Leucophytia bidentata* is quite colourless, being frosted white on the exposed parts of the head, mantle and foot. It avoids light. In a moist atmosphere it moves about very actively, and when the foot is extended to its full length the sole is seen to be long and narrow, equal in length to the whole shell. The creeping surface is divided by a shallow transverse groove into an anterior third, semicircular in outline, and longer posterior portion, gently rounded behind. The snout is very short and the mouth is concealed beneath a pair of broad, rounded oral lappets. These are narrowly separated in the mid-line, and reach close to the substratum over the front of the foot. The cephalic tentacles are

short, stout and bluntly tipped, widely diverging near the mid-line of the head; they are triangular in outline as viewed from above, and the eyes are set at their bases at the middle of the upper surface.

The edge of the mantle forms a free skirt, reflected round the rim of the shell. Its inner surface is ciliated and glandular. A short way behind the skirt, the mantle cavity is closed
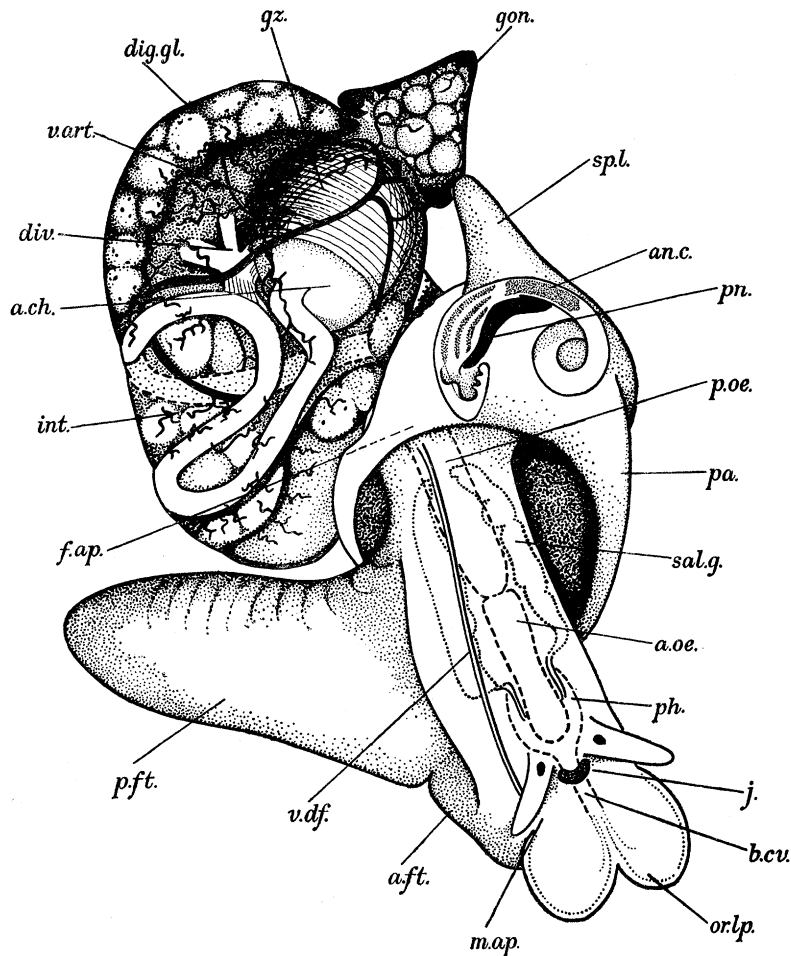

FIGURE 1. *Leucophytia bidentata*. General view of the entire animal after removal of the shell. The visceral mass is slightly dissected to show the relations of the visceral aorta and the origin of the intestine and the digestive diverticula. The buccal mass, salivary glands and anterior oesophagus are indicated in outline through the body wall. *a.ch.*, anterior chamber of stomach; *a.ft.*, anterior division of the foot; *an.c.*, anal canal on the mantle margin; *a.oe.*, anterior oesophagus; *b.cv.*, buccal cavity; *dig.gl.*, digestive gland; *div.*, digestive diverticulum; *f.ap.*, position of female genital aperture; *gon.*, ovotestis; *gz.*, gizzard; *int.*, intestine; *j.*, jaw; *m.ap.*, male aperture; *or.lp.*, oral lappet; *pa.*, mantle; *p.ft.*, posterior division of the foot; *ph.*, buccal mass; *pn.*, pneumostome; *p.oe.*, posterior oesophagus; *sal.g.*, salivary gland; *sp.l.*, supra-anal lobe; *v.art.*, visceral aorta; *v.df.*, position of anterior vas deferens beneath the genital fold.

by a membranous septum, which attaches the mantle to the body wall of the trunk just behind the head. This septum is interrupted only on the right side where the mantle cavity opens to the exterior by the pneumostome, which is circular when widely open. On the right, the terminal part of the rectum encircles the pneumostome, running outwards along

the pallial skirt; the faeces are led from the anus to the edge of the mantle by a narrow anal groove, in which the epithelium is thrown into ciliated longitudinal folds. The edge of the mantle, immediately posterior to the anus and pneumostome, has a different structure from elsewhere. It is covered with thin integument and produced backwards into a tri-angular supra-anal lobe lying along the posterior canal of the shell aperture. The lobe is kept tumid and erect with blood, and its appearance most resembles that of the lateral surfaces of the foot in *Otina* which, it has been suggested (Morton 1955 *a*), may serve a respi-ratory function. The supra-anal lobe in *Leucophytia* is filled with lacunar connective tissue, traversed by a close mesh of muscle fibres and crowded with blood cells. The external epithelium is squamous, without cilia, resembling that of the lateral area of the foot in *Otina*. This part of the mantle shows in ellobiids its simplest development among the
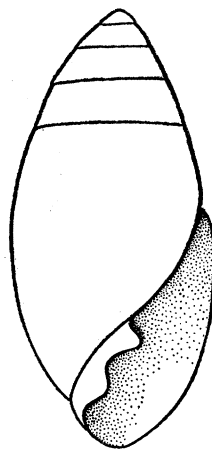

FIGURE 2.   *Leucophytia bidentata*.   Shell.

Basommatophora; it is generally assumed to be a respiratory organ. In the higher aquatic pulmonates, it has become elaborately folded, and gives rise in whole or in part to a secondary 'adaptive gill'.

The arrangement of the organs of the pallial cavity is relatively simple. There is no well-defined hypobranchial gland. The kidney is broader behind, in contact with the pericardium; it narrows in front to form a simple unfolded tube, opening by a small renal pore just inside the pneumostome. Along the right side of the mantle runs the rectum; below it, along the floor of the mantle cavity, bulges a stout, opaque white tube, the pallial portion of the genital duct. To the left of the kidney the mantle is occupied by a thin-walled respiratory area, which is traversed from right to left by a series of narrow blood spaces. The female genital aperture is hidden between the supra-anal lobe and the side of the foot. Along the right side of the head a narrow fold of epithelium runs forward from the female aperture, conveying the vas deferens to the tiny male opening, beneath the right oral lappet.

The two lobes of the foot are structurally very similar, and both are kept on the ground continuously when the animal is crawling. There is no well-marked stepping action as with the divided foot of *Otina*. A supra-pedal gland, as in *Otina*, provides a supply of mucus for compacting the food bolus. A sheet of secretion passes towards the mouth, during the

rasping or plucking action of the radula, driven by cilia beating forward along a median tract of epithelium on the anterior part of the upper surface of the foot. From observation of the anterior edge of the foot while the animal is feeding, it appears that this part of the sole may also have a function in collecting food particles and compacting them with mucus. The anterior lobe of the foot forms a rounded cushion, on to which particles of
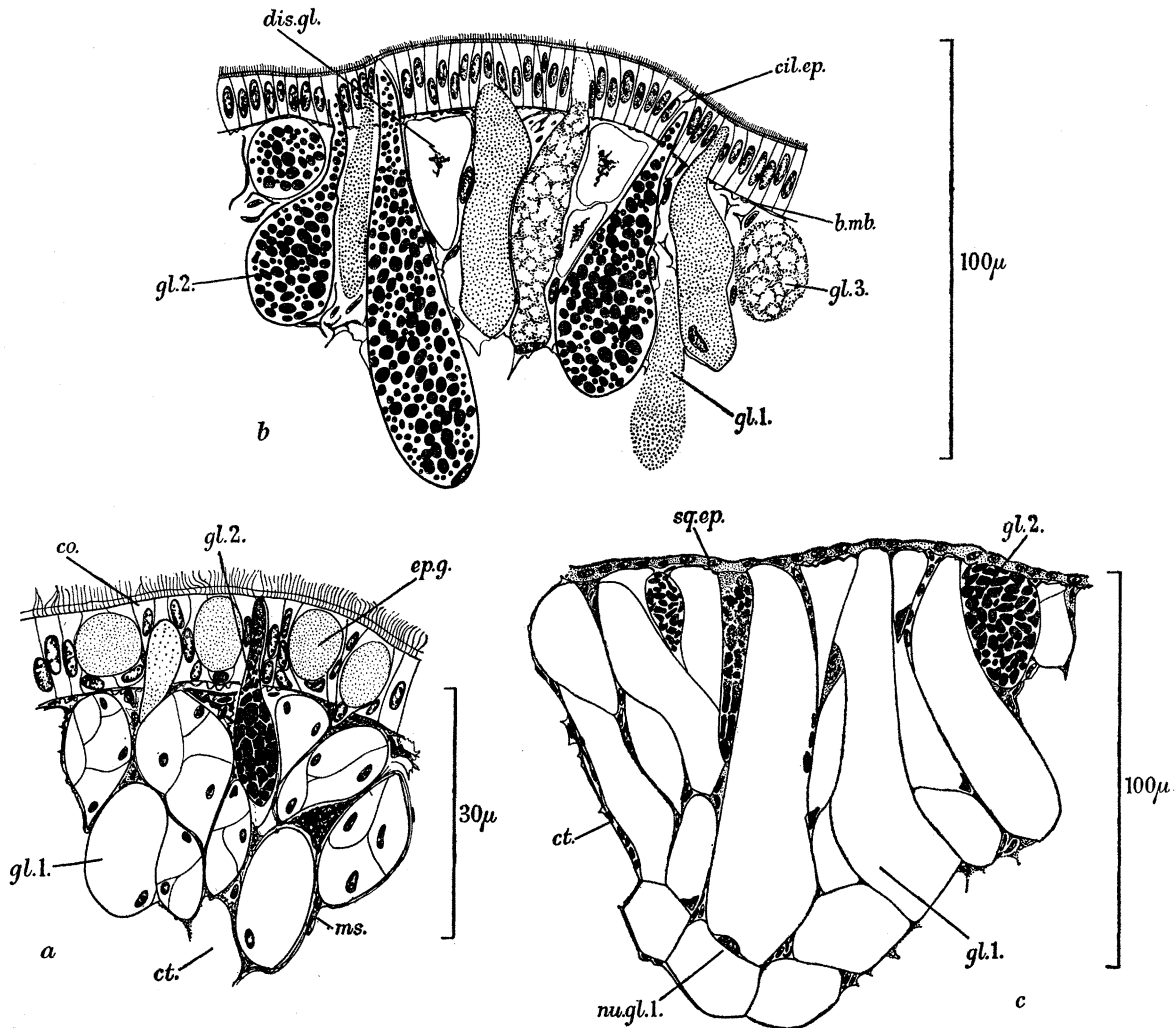

FIGURE 3. *Leucophytia bidentata*. (*a*) Epithelium of the sole of the foot. *co.*, columnar epithelial cell; *ct.*, connective tissue; *ep.g.*, epithelial gland; *gl.* 1, *gl.* 2, two types of glandular cell; *ms.*, muscle fibres. (*b*) Epithelium of the lateral region of the foot. *b.mb.*, basement membrane; *cil.ep.*, ciliated epithelial cells; *dis.gl.*, discharged gland cell; *gl.* 1, *gl.* 2, *gl.* 3, three types of gland cell referred to in text. (*c*) Epithelial of the lining of the pneumostome. *ct.*, connective tissue trabecula between gland cells; *gl.* 1, *gl.* 2, two types of gland cell; *nu.gl.* 1, nucleus of a gland cell; *sq.ep.*, squamous external epithelium.

debris may pass forward along the sole, especially by way of an impermanent groove at the centre of the foot which tends to be flattened out in crawling. The shifting of material forward by cilia may also be in part a cleansing reaction. The thickened edge of the anterior lobe is, however, regularly rolled forward, and its mucus secretion and particles are brushed off on to the under-surfaces of the oral lappets. Meanwhile, mucus reaches the

mouth from the supra-pedal gland, and particles picked up by the radula are liberally surrounded with secretion before being raked into the mouth. The suggested action of the foot in assisting food collecting and supplementing the mucus supply of the gut has several parallels among other gastropods: among pulmonates the lymnaeids are known (Brock-meier 1898) to collect food by the ciliary action and mucus secretion of the sole, and *Ampullarius* also (Whitaker, personal communication) collects material for ingestion along the anterior edge of the foot. In the ellobiids, a pedal mucus supply must be of special advantage, since, apart from the small salivary and buccal glands, sources of mucus in the foregut are quite lacking.

The epithelium of the sole (figure 3a) has a short ciliary coat and a subepithelial layer of plump mucus cells, flask-shaped or spherical and compacted together in ovoid groups of 6 to 10 glands (*gl.* 1). They stain pale blue in azan, pink in mucicarmine. A second type of gland occurs singly; it is narrower and ovoid or fusiform, filled with separate secretion spherules, staining deep wine red in azan and orange after Masson's stain. On the sides and posterior surface of the foot (figure 3b), the ciliary coat is much shorter and the sub-epithelial gland cells are less closely compacted, but individually much larger. The longest (100 to 120μ) are filled with spherules staining red in azan. Of similar shape but shorter are two other types of glands: the first has irregularly reticulate cytoplasm, with no separate secretion spherules and stains light blue after azan. In the second, the cytoplasm is uniform and without visible granules; azan renders it deep wine red.

The inner surface of the free skirt of the mantle is lined with an epithelium similar to that of the sides of the foot; its gland cells are, for the most part, shorter, but in the pneumo-stome, the glandular lining is extremely thick. The bounding epithelium is thin and squamous and not ciliated; the subepithelial gland cells are packed close together and separated only by thin trabeculae of connective tissue. Their contents are mucoid, staining uniformly light green in Masson's stain, pale blue in azan and black with thionin.

DIGESTIVE SYSTEM

The mouth opens as a vertical slit between the two oral lappets and leads directly into the cavity of the buccal mass. This structure forms a short, muscular bulb, and is essentially similar in form and relations to the unspecialized pulmonate buccal mass already described in *Otina*. Along its roof the anterior region of the oesophagus commences to run backwards as a strongly ciliated groove. The floor of the buccal mass is built up of the odontophoral cartilages and their attached muscles, which form rounded prominences at either side. The short, broad radular caecum emerges slightly from the postero-ventral aspect. Immediately within the mouth lies a transverse, crescentic jaw, built up of sharp, chitinous prisms firmly set in cuticle. Behind the mouth, the side walls of the buccal cavity are pierced by the ducts of lateral clusters of subepithelial mucus glands, which resemble in structure and histology the lateral buccal glands of *Otina*, and the glands previously mentioned by Carriker (1946a) in the buccal mass of *Lymnaea*. From their presence in several other Basommatophora examined, the lateral buccal glands would seem to be a regular feature of the lower Pulmonata, providing—with the salivary glands—the chief source of lubricating secretion with which food particles are mixed on introduction into the mouth by the radula.

The dentition of *Leucophytia* is illustrated in figure 4a. The central tooth is broad and equilaterally triangular, with a shallow sinus at the base. It carries anteriorly a small back-pointed cusp, elongate-triangular in shape. The first of the lateral teeth on either side of the central tooth are furnished with a single hook-shaped cusp, broadly triangular when viewed from above. The second and subsequent laterals develop bifid cusps, the outer cusp tending to become longer towards the marginals which are otherwise uniform with the laterals.
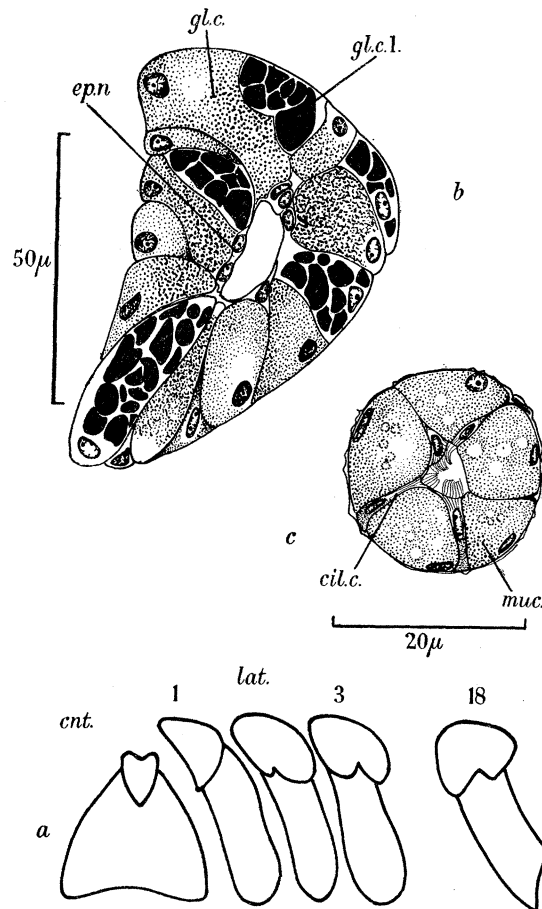

FIGURE 4. *Leucophytia bidentata*. (a) Representative teeth of the radula. *cnt.*, central tooth; *lat.*, lateral teeth. (b), (c) Transverse section of a salivary gland and its duct. *cil.c.*, ciliated cell; *ep.n.*, nucleus of flattened epithelial cell; *gl.c.*, gland cell (blue in azan); *gl.c.* 1, gland cell (red in azan); *muc.*, mucous gland in epithelium of duct.

The salivary glands (figure 1, *sal.g.*) lie alongside the oesophagus, suspended in the haemocoele of the trunk, and attached by fine connective tissue strands to the oesophageal wall. They form a pair of opaque, whitish tubes, often triangular in section or flattened against the oesophagus. The ducts are extremely narrow, and penetrate the roof of the buccal mass at its junction with the oesophagus. Each gland is composed of two types of secreting cell (figure 4b). The first type, usually more numerous, corresponds to the single kind found in the salivary gland of *Otina* and also in the buccal glands of both *Otina* and *Leucophytia*. It is broad-based and cubical or triangular, or sometimes narrower and columnar. The cytoplasm is coarsely granular, staining pale blue in azan, grey green in

Masson's stain, pink in mucicarmine and black in thionin. The second type of cell resembles the glands found occasionally in the oesophagus and more frequently in the intestine. It is filled with ovoid or sometimes polygonal spherules, wine red after azan, orange from Masson's stain and colourless with mucus stains. The lining of the gland is chiefly of flattened cells with occasional patches of long cilia from wedge-shaped triangular cells. The salivary duct (figure 4*b*) has a narrow central lumen surrounded by triangular cells like those of the first type of gland cell. A coat of long cilia is borne by isolated wedge-shaped cells inserted between the free ends of the gland cells.

The ciliated roof of the buccal cavity continues backward above the opening of the radular sac as a cylindrical tube, 300μ in diameter, forming the anterior region of the oesophagus. A short distance behind the buccal mass, the posterior oesophagus is marked off from the anterior portion by a slight constriction which is often best observed in fixed material. The histology of the oesophagus differs somewhat in its two regions. The anterior oesophagus is lined dorsally by a single broad fold of taller epithelium, with six or more smaller ridges on the opposite side formed chiefly by differences in cell height. The ciliary coat is very tall and the individual cilia long and lash-like. Mucus glands are not frequent, and form simple, goblet cells, staining pink in azan, orange in Masson's stain. Muscle fibres run through the underlying connective tissue, and are both circular and longitudinal, especially well developed along the large longitudinal fold. The posterior oesophagus is wider, thinner-walled and more distensible. It dilates at its middle length to form a simple crop tapering towards the stomach. The lining epithelium is shorter than in the anterior oesophagus, and the ciliary coat is of small, close-set cilia. The gland cells tend to be larger, packed with separate secretory spherules, resembling in general the second type of cell in the salivary gland.

The stomach

The stomach is a plump, globular sac, lying in a deep concavity on the left side of the visceral mass. Around its right side it is loosely enclosed by the larger (anterior) lobe of the digestive gland. To the left the little hermaphrodite duct and the albumen gland lie close against it, and it is covered from behind by the apical part of the visceral mass, which is built up of the smaller (posterior) lobe of the digestive gland, and the conical ovotestis. The stomach is divisible into two main regions of about equal size. A thinner walled anterior chamber (figure 5, *a.ch.*) forms its base and gives exit to the intestine, which runs forward close to the entry of the oesophagus. This anterior chamber is widely open behind to a thicker walled posterior chamber. This part is invested by a massive zone of circular muscle and forms a well-marked gizzard (*gz.*). At the apex of the stomach, opening into the gizzard from behind, is a small rounded pouch, the gastric caecum, which forms a small third chamber in the stomach of most other ellobiids (see *Ovatella*, below), though in *Leucophytia* it has become so modified as almost to lose its separate identity (*cm.*). On dissecting the stomach, the gizzard is found to be lined throughout with a tough, transparent cuticle, and its muscular wall is thrown into several stout longitudinal ridges. When the stomach is empty, the lumen of the gizzard is occupied by a long tongue-shaped fold, with a soft, finely ciliated surface. This fold is formed chiefly by the inversion into the stomach of the wall of the caecum, which in these circumstances completely disappears from view

externally. The fold, when it is withdrawn from the gizzard, is partly obliterated by the out-pushing of the caecum (figure 5, inset) at the apex of the stomach; and in part persists as a short ridge lying inside the caecum.

The anterior chamber of the stomach is ciliated throughout. On its left side, a narrow thin-walled tube leads in from the opening of the oesophagus. Some distance forward along this tube, removed from the main portion of the stomach, opens the single digestive diverticulum (*ap.dig.*) by a small transverse slit. Anteriorly to the diverticulum, the wall of
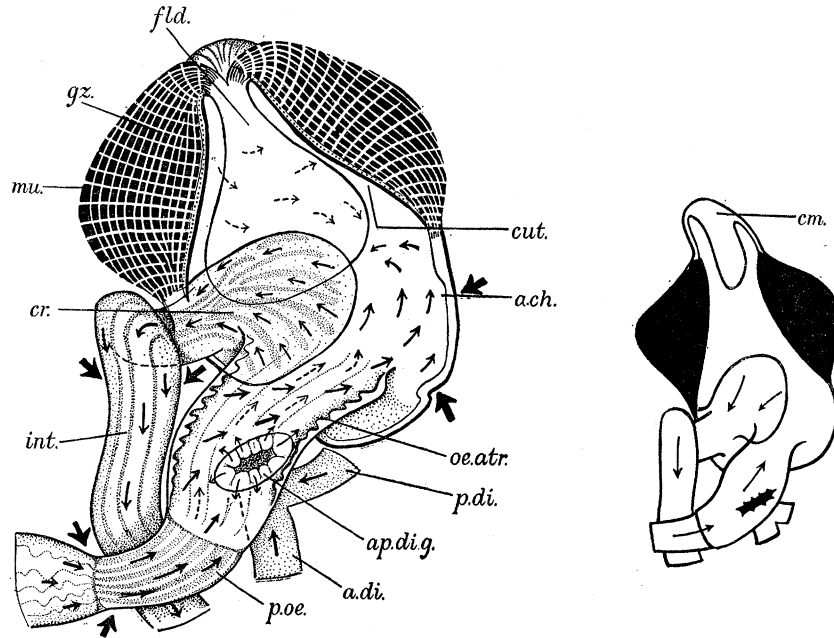

FIGURE 5. *Leucophytia bidentata*. The stomach viewed as a transparent object without dissection, showing the course of the principal ciliary currents. The bold arrows outside the stomach indicate regions of greatest peristaltic action. On the right, a diagram of the stomach with the internal fold of the gizzard retracted and the posterior caecum protruded. *a.ch.*, anterior chamber; *ap.dig.*, aperture of the single digestive diverticulum; *a.di.*, anterior branch of the digestive diverticulum; *cm.*, posterior caecum; *cr.*, ciliated ridges of the anterior chamber; *cut.*, cuticular lining of the gizzard; *fld.*, fold occupying the lumen of the gizzard or retractible into the caecum; *gz.*, gizzard; *int.*, intestine; *mu.*, muscular wall of the gizzard; *oe.atr.*, oesophageal atrium; *p.di.*, posterior branch of the digestive diverticulum; *p.oe.*, posterior region of the oesophagus.

the tube is marked by a slight circular constriction, which delimits the oesophagus, properly speaking, from the stomach. The narrow chamber, containing the opening of the digestive gland, is thus to be looked on as morphologically part of the stomach, and will be referred to here as the 'oesophageal atrium' (*oe.atr.*). The intestine, opening from the right side of the anterior chamber, is a thin-walled tube of rather less width than the atrium. Towards its aperture, the lining epithelium of the stomach is somewhat thickened, and is thrown into a series of grooves and ridges which converge over a funnel-shaped area to enter the intestine (*int.*).

The muscle coat may reach 200μ thick in the empty stomach, and is composed entirely of circular fibres, stouter towards the periphery, more slender and mixed with

collagenous connective tissue towards the epithelial basement membrane. The epithelial lining (*ep.*) is of short columnar cells, with a layer of cuticle, averaging 15μ thick, attached to the epithelium by a zone of short, fine fibrillae (*ct.b.*), tall, superficially like cilia, and inserted in little indentations of the scalloped lower edge of the cuticle (*ct.*). Apart from faint perpendicular striations, the cuticle appears almost structureless. Its substance stains only lightly in azan (pale blue) and in Masson's stain (green); and resembles the cuticle described in other molluscan stomachs, as, for example, Yonge (1926) in lamelli-branchs, Bidder (1950) in cephalopods and Millot (1937) in opisthobranchs.

The epithelium of the anterior chamber is rather featureless. It bears a coat of short, very fine cilia and may be thrown into small undulations by variations in cell height. Gland cells are entirely lacking, and amoebocytes are rather infrequent, wandering at times between the ciliated cells from the subepithelial connective tissue in small numbers. A slender muscle coat is present (8 to 10μ thick), composed mainly of circular fibres inter-
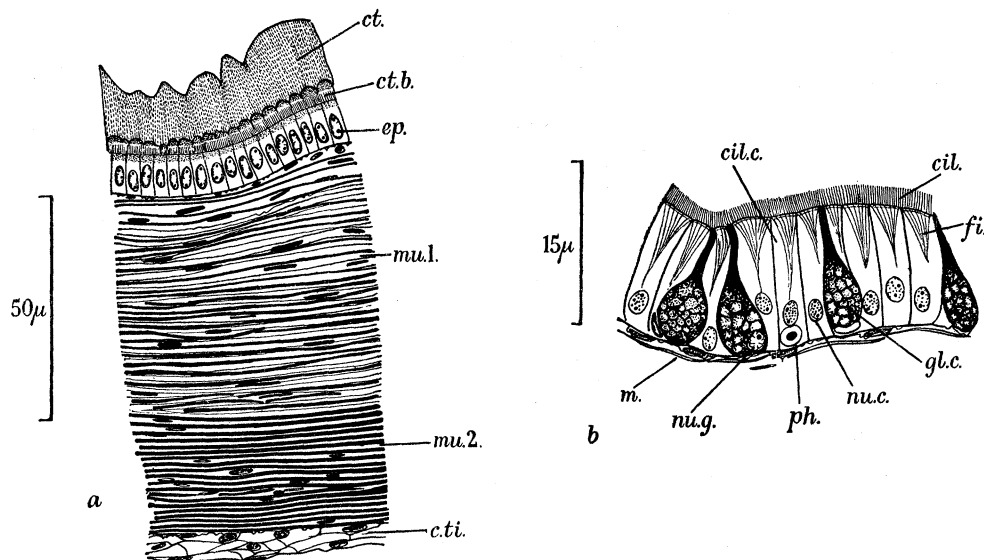

FIGURE 6. *Leucophytia bidentata*. (*a*) Transverse section of the wall of the gizzard. *ct.*, layer of cuticle; *ct.b.*, striations extending from surface of epithelium to base of cuticle; *c.ti.*, connective tissue; *ep.*, epithelial cell; *mu.* 1, inner layer of circular muscle, with connective tissue; *mu.* 2, peripheral layer of circular muscle. (*b*) Epithelium of the ciliated region of the digestive diverticulum. *cil.*, cilia; *cil.c.*, ciliated cell; *fi.*, intracellular fibrillae; *gl.c.*, glandular cell; *m.*, muscle; *nu.c.*, nucleus of ciliated cell; *nu.g.*, nucleus of gland cell; *ph.*, phagocyte.

mixed with a few longitudinal and oblique fibres. On the tongue-shaped posterior fold, the epithelium is, as a rule, smooth, though it may show small, impermanent ridges when the fold is strongly contracted.

The ciliary currents of the stomach (figure 5) are rather weak, and play only a minor role in the movement of its contents. Their action is most prominent along the folds and ridges of the funnel-shaped area of epithelium surrounding the mouth of the intestine. Here, the tracts of rapidly beating cilia extend into the intestine along the close-set folds formed by the entry of the ridges from the stomach. In the rest of the anterior chamber the wall is smoother. Transverse ciliary currents extend over a wide surface, tending to carry particles inwards around the anterior chamber from the oesophageal atrium. The wall of

the atrium is entirely ciliated. The side penetrated by the digestive diverticulum is thrown into weak longitudinal furrows running in the general direction of the anterior chamber. The ciliary currents here are weaker than in the posterior part of the oesophagus proper, but they assist the action of the muscular coat of the atrium, in carrying back to the stomach a stream of material from the diverticulum. On the opposite wall the epithelial ridges with their ciliary currents have a transverse direction, running obliquely round the wall of the atrium and finally merging into the smooth wall of the anterior chamber. The opening of the digestive diverticulum is puckered up 10 to 12 folds, all finely ciliated, with currents leading out of the mouth of the diverticulum. On the tongue-shaped fold projecting into the gizzard, the ciliary currents are very indistinct and irregular. At times weak currents are to be observed in a transverse direction, but it is uncertain what role these cilia play in the movement of stomach contents.

The stomach of *Leucophytia* is thus to be looked upon as much more specialized than that of *Otina*; and it has lost almost all of the landmarks distinctive of the generalized proso-branch stomach. Functionally, the role of mucus and of the ciliary systems is much reduced, and there is much greater reliance on the action of muscle. The wall is highly contractile, not only in the gizzard but in the anterior chamber also. In the left half, regular peristaltic waves pass away from the entry of the oesophagus, and backward along the atrium. On the right there are strong muscular contractions in the direction of the intestine, which play the chief part in the expulsion of faeces. In the gizzard, intermittent contractions of the layer of circular muscle, less frequent than the movements of the anterior chamber, exert a powerful compression on the whole of the stomach contents. The gut has no sorting mechanisms and the mixed mass of food and detritus is only slightly compacted with mucus, most of it probably derived from the supra-pedal gland before ingestion. Coarser particles are continually broken down in the gizzard, and the whole mass thoroughly kneaded and triturated. Finally, fluid material, containing particles sufficiently finely divided for absorption by the digestive gland, is squeezed out from a residual mass of faeces and forced into the digestive diverticulum.

The tongue-like fold (*fld.*, figure 5) within the gizzard seems to act as a valve in con-junction with the muscular movements. The action of the stomach takes place in several rather distinct phases. During the inflow of food and detritus from the crop, the tongue-shaped fold is small and retracted and the caecum projects at the top of the stomach (figure 5, inset). The gizzard is now open to the flow of detritus, and by its contractions semi-fluid contents are expressed and driven into the digestive diverticulum. The closure of the intestine during this phase comes about by the contraction of its circular muscles and the approximation of its close-set lining ridges. Peristaltic waves towards the intestine temporarily cease. Back-flow of contents into the oesophagus is prevented by the large bulk of food and detritus already within the crop. When the atrium and the diverticulum are filled with fluid squeezed out of the food mass, this region can be partly closed off from the rest of the stomach by muscular constriction of its opening, and also by the extension forward of the tongue-shaped fold of the gizzard. At its greatest length this projects into the anterior chamber, where it tends to lie to the left and to close off the oesophageal atrium. Meanwhile, by further contractions of the gizzard, and by the beginning of peristalsis towards the intestine, a rod of faeces begins to be forced out of the stomach. This

usually happens intermittently as the sphincter of the intestine nips off boluses one by one from the detritus in the stomach. Ciliary action also assists in expelling faeces, especially the smaller detached particles. When the faeces have left the stomach, the gizzard remains empty, and the tongue-shaped fold broadens and fills its whole cavity (figure 5), and thus excludes from the gizzard the inflow of the material that presently begins to arrive back from the digestive diverticulum.

TABLE 1. DIGESTIVE EXPERIMENTS WITH *LEUCOPHYTIA*

(1) *Hydrolysis of 1 % ethyl acetate solution*

Four tubes, with 1 ml. ethyl acetate in distilled water, titrated after 24 h with
N/500-NaOH for estimation of free acetic acid.

		vol. N/500-NaOH reqd.
tube A	control	1 drop
tube B	six digestive glands added	1·73 ml.
tube C	six stomachs filled with ingested detritus	0·35 ml.
tube D	six stomachs filled with fluid from the digestive gland	0·35 ml.

(2) *Hydrolysis of 1 % starch solution*

Three tubes, 1 % starch solution, titrated after 24 h with
ammoniacal $AgNO_3$ for reducing sugars.

tube E	control	faint tint of reduced silver
tube F	six digestive glands added	strongly positive result
tube G	three stomachs filled with detritus	less positive but distinct result

(3) *Erosion of gelatin film on a developed photographic plate*

	digestive gland	definite area of complete digestion
H	stomach filled with detritus	little digestion: film softened and at small points eroded
J	stomach filled with fluid from digestive gland	definite area of complete digestion
K	faeces from intestine	no digestion

Much of the egested material from the digestive diverticulum passes directly to the intestine, assisted by peristalsis and ciliary currents. But fragments of digestive gland cells may remain for some time in the stomach, suspended in watery mucus. It appears that they may provide enzymes for extracellular digestion, as is indicated from the following experiments (table 1). An amylase and an esterase (which may be regarded as acting similarly to a lipase) are present in the stomach in smaller concentrations than in the digestive gland; while in stomachs empty of food but filled entirely with extruded material from the digestive cells, the action of a protease is equally strong as in the macerated gland. In the faeces, from the intestine, which incorporate traces of digestive cells, enzymic action no longer persists.

The digestive gland

The digestive diverticulum forks into two equal branches (figure 5, *a.di.*, *p.di.*) just after leaving the oesophageal atrium. The posterior branch passes backwards to the left (posterior) lobe of the digestive gland. The anterior breaks up at once in the larger right lobe. The digestive tubules are stout and bluntly rounded, averaging 0·25 mm in diameter.

They fuse to form a continuous spongy lobe, and into the fissures between them penetrates a loose connective tissue, filled with lacunar blood spaces. These open into the general haemocoele of the visceral mass, and are supplied by fine arterioles that spread around the tubules from the branches of the visceral artery. The wall of the diverticulum, as distinct from the terminal tubules, is thin and membranous but with a sufficient muscular coat to perform distinct peristaltic movements. Its epithelium (figure 6b) is ciliated and, unlike the gastric epithelium, possesses numerous flask-shaped goblet cells. These produce a mucoid secretion staining deep orange with Masson's stain, red with azan, and purplish black in haemalum. The glandular epithelium of the tubules (figure 7) contains cells of two types, digestive and excretory. Its appearance varies a good deal with the state of activity of the gland, and we may recognize a sequence of three phases: (i) 'absorption', (ii) 'digestion' and (iii) 'fragmentation and excretion'. Figure 7a illustrates the digestive epithelium during a period of ingestion of material from the lumen of the tubule after the animal has recently fed. The lumen is now rounded and spacious, distended by the suspension of food material in fluid mucus, which has flowed into the diverticulum on contraction of the stomach. The digestive cells (di.c.) are rather short and columnar, of a uniform height of 25μ. Their nuclei are rounded and somewhat ovoid, pressed closely against the basement membrane by the numerous vacuoles which occupy the middle and basal part of the cell, packed together so as usually to obscure the cell walls. These vacuoles average 5μ across, and lie three or four deep in each cell, a single row of vacuoles occupying the width of the whole cell. With most stains, including haemalum, mucicarmine, azan and Masson's stain, they remain colourless or golden yellow. After thionin staining each vacuole appears to consist of a colourless inner sphere, surrounded by an outer membrane staining deeply blue or black. In places this membrane appears torn or retracted to expose wide areas of the non-staining central substance of the vacuole.

The free surface of the digestive cell is flat and entire, traversed by a row of some ten to twelve fine perpendicular striations (str.) penetrating to a depth of 5μ in each cell. Beneath the striations, the most distal of the vacuoles at the stage figured are beginning to fill with droplets of bluish (azan) material from the lumen; in some cases these run together to form a globule almost filling a vacuole. This is the typical absorption picture; and the vacuoles of the superficial half of the cell gradually take on a colour identical with the contents of the lumen. Continued digestion probably takes place within the food vacuoles of the digestive cells, and these vacuoles are probably formed by the filling of the more superficial of the colourless vacuoles (vac. 2) with droplets of ingested food. If this is so, their thionin reaction is lost after food material is taken up. We may perhaps assume that the basal vacuoles (vac. 2) are the site of enzyme production in the digestive gland; the thin external sheath with its affinity for thionin perhaps represents a zone where enzymes are concentrated. The striated border of the absorbing cell rather strikingly recalls the structure of the free border of the intestinal cell in vertebrates (Baker 1942). In vertebrates, the cell border is traversed by short canaliculi, ca. 2μ long, as compared with striations of as much as 5μ long in Leucophytia. Baker considers these canaliculi to be the pathway of lipoid droplets entering the intestinal epithelium. In Leucophytia they are always lost after the absorbing phase is completed. The present writer (1951) has referred to the same type of striation in the prosobranch Struthiolaria, suggesting they might be connected with cilia,

which are often detectable in living digestive cells in gastropods and lamellibranchs (*Teredo*, Potts 1923), at the absorbing stage in *Jorunna* (Millott 1937), and in *Suterilla* (Mesogastropoda) (present writer, unpublished). Living macerations of the digestive gland of *Leucophytia* did not, however, show cilia at any stage.
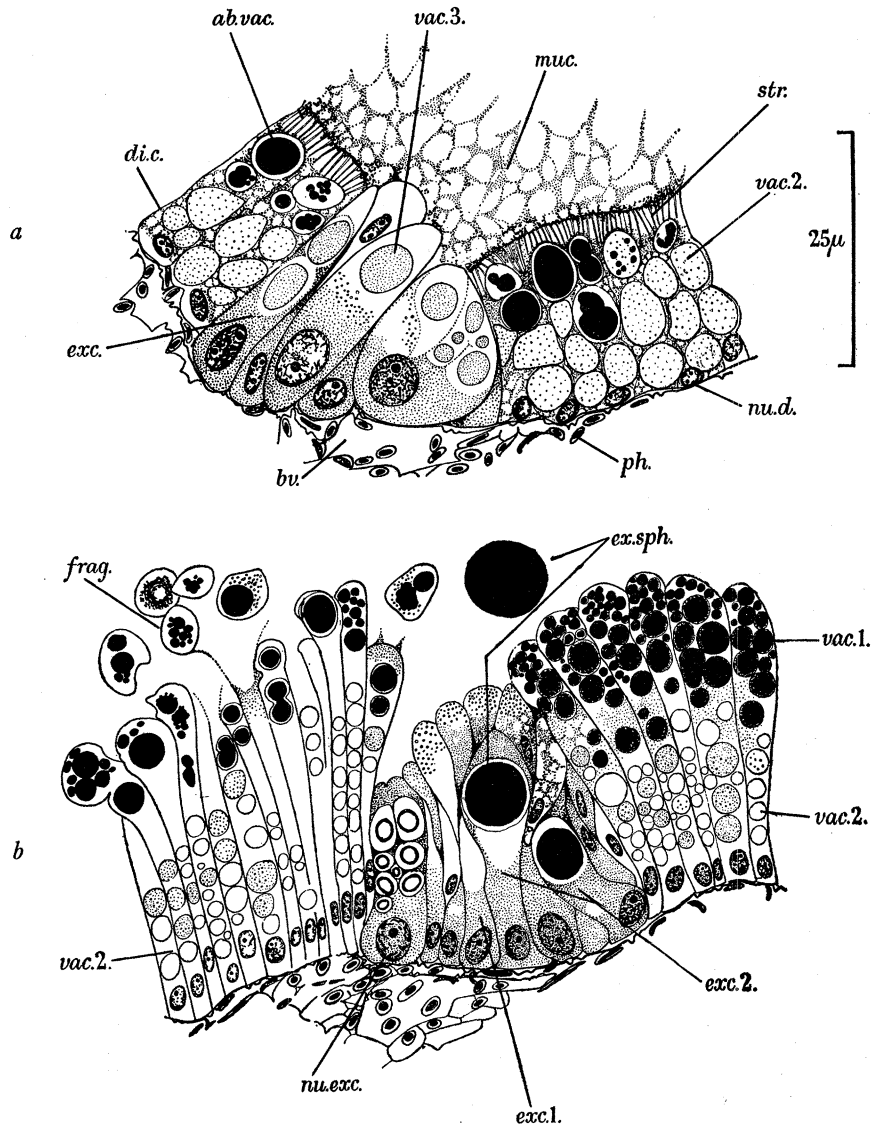

FIGURE 7. *Leucophytia bidentata*. Histology of the digestive gland, illustrating the phases of *absorption* upper figure (*a*), *digestion* (*b*, right) and *fragmentation and excretion* (*b*, left). *ab.vac.*, vacuoles of the digestive cells filled with material absorbed from the lumen; *bv.*, subepithelial blood vessel; *di.c.*, digestive cell; *exc.*, excretory cell as it appears during the absorbing phase of the digestive gland; *exc.* 1, younger excretory cell; *exc.* 2, later stage of an excretory cell; *ex.sph.*, excretory spherules; *frag.*, fragmented tip of a digestive cell, extruded into the lumen; *muc.*, mucoid material with finely divided food material filling the lumen at the absorptive phase; *nu.d.*, nucleus of a digestive cell; *nu.exc.*, nucleus of an excretory cell; *ph.*, amoebocytic blood cell in the subepithelial connective tissue; *str.*, border striations of the digestive cell, resembling fine canaliculi; *vac.* 1, vacuoles within the digestive cell, containing absorbed material; *vac.* 2, clear basal vacuoles of a digestive cell; *vac.* 3, lightly staining vacuoles of an excretory cell, during the absorbing phase of the digestive gland. The scale of (*b*) is considerably smaller than of (*a*).

The excretory cells (*exc.*) lie in small clusters of up to a dozen cells, opening over a rather narrow surface into the lumen. They may be distinguished from the digestive cells by their much larger nuclei, which stain intensely in azan. A typical cluster shows one or two cells, broad-based and triangular, or plumply rounded, others cigar-shaped or columnar, and wedge-shaped cells, presumably younger, with smaller nuclei inserted between the bases or free ends of larger cells. The basal half of the cell is, at the absorbing phase, pale pinkish brown in fresh material, remaining so in azan, and staining bright purple in thionin. The distal half is filled with colourless vacuoles (*vac.* 3) containing spherules staining pale blue in azan. Two or three ovoid spherules may be arranged in a row in a columnar cell, or in a cluster of varying sizes in a triangular cell. Whether these spherules are formed by ingested droplets of the same type as in the digestive cells it is not easy to decide. The free border of the excretory cell is always intact and there is no histological evidence of absorption.

Figure 7*b*, right shows the appearance of the digestive epithelium at the 'digesting phase', 24 h after cessation of feeding. Absorption from the lumen has ceased and the cavity of the tubule is reduced to a narrow triradiate cleft by the bulging from the wall of clusters of digestive cells. These have now become extremely tall, sometimes increasing to as much as 120μ in height, with a narrow basal portion, broadening to a rounded club-shaped tip. In the distal half, the vacuoles are entirely filled with absorbed material from the lumen, in large globules, 6 to 7μ across, or, towards the free surface, in clusters of smaller droplets. The striated border is lost. In the cytoplasm of the excretory cells, the most prominent inclusions are large, black or greenish brown, refringent spherules, up to 20μ across, lying in clear vacuoles, which distend the distal parts of some cells to a club-shape. Most of the excretory cells are now columnar, containing as many as a dozen pale brown or pink spherules, 4 to 5μ across and each in a separate vacuole. These cells usually cluster in groups of two or three on either side of a cell containing a large black spherule. In each nest of excretory cells about a dozen younger cells appear, short and wedge-shaped, inserted between older cells. They have no separate inclusions and their nuclei are smaller (5μ), as in the digestive cells.

At a later stage, generally after starvation for 48 h, the digestive epithelium reaches its 'fragmentation and excretion' phase, which may be taken to mark the end of a cycle of activity (figure 7*b*, left). The digestive cells are now extremely narrow, expanding only at the tips, which are rounded and club-shaped, becoming freely constricted into the lumen. Here they form rounded, non-nucleated fragments, usually about 10μ in diameter, the cytoplasm crammed with droplets of absorbed material. In this form, the fragments are returned to the stomach. Extrusion of nucleated portions containing thionin-staining vacuoles, as found in *Otina*, were not observed in any material of *Leucophytia* examined. It is, however, by no means established that this process does not occur in *Leucophytia*. Such nucleated fragments of the digestive cells are broken off into the lumen in *Carychium* among ellobiids (p. 137, below), and the formation of 'fragmentation phagocytes' might be regarded in general as a fourth and final stage in the cycle of the digestive gland. From the excretory cells, larger spherules now pass into the lumen. The empty cells remain as vesicles which are presumably soon displaced by the growth of the more slender neighbouring cells. An apparent absence of mitotic figures is, however, a feature of all the

sections of the digestive gland examined; and it is remarkable to find no histological evidence of cells in a state of division.

To summarize, we may outline the following course of digestion and excretion in the gut of *Leucophytia*. During trituration in the stomach, the first stages of digestion take place extracellularly. The extruded portions of the digestive cells which are returned to the stomach, evidently contain enzymes, either remaining in traces in the food vacuoles or perhaps present in the basal vacuoles. Many fragments of digestive cells pass unchanged into the intestine, where, especially after starvation, they form a large part of the faeces. By compression of the bolus of detritus in the gizzard, a suspension of finely divided material in fluid mucus is forced into the digestive diverticulum. Solid particles are not separately recognizable. The digestive cells absorb this material over a wide surface. It passes into clear-staining vacuoles in small droplets, and digestion is evidently completed by intracellular enzymes. On completion of digestion, extruded tips of the digestive cells pass back to the stomach, carrying with them the residue of undigestible waste. The darkly staining spherules in the excretory cells probably consist of material extracted from the blood. Small blood vessels underlie each group of excretory cells, and pigmented excretory spherules are built up during the phase of digestion. Fragmentation of digestive cells and rupture of the excretory cells then take place simultaneously.

The intestine

The intestine in *Leucophytia* is a uniform tube of 150μ in average diameter. On leaving the stomach, it takes a sharp, elbow-shaped bend to the left, and passes beneath the oesophagus, running forward at the base of the stomach to reach the surface of the visceral mass. It describes a wide S-shaped loop under the surface of the anterior lobe of the digestive gland, and finally runs forward along the right side of the mantle, as the rectum. The lining epithelium is raised into five to six strong folds, and this portion of the intestine has evidently the function of a 'faeces compressor' of the type described by Carriker (1946) in *Lymnaea*. By muscular compression, the loosely compacted faeces are moulded into a firmer rope. Regular peristaltic waves, assisted by ciliary action, constantly carry smaller particles along the intestine from the stomach to be added to the faecal rope. The ciliated cells of the intestine resemble those of the anterior chamber of the stomach. The cilia are fairly tall, beating strongly in the direction of the anus. Gland cells are abundant, narrow and cigar-shaped, inserted between the tips of the ciliated cells. Their mucoid secretion stains red or pink with azan. In addition, amoebocytic cells are much more abundant in the intestine than in the stomach, thrusting between the epithelial cells from the subepithelial connective tissue and blood vessels. The faecal rope in *Leucophytia* is a continuous, rather friable string of detritus yellowing brown in colour. As well as sand grains, diatom frustules and undigested plant fragments, it contains much material from the digestive gland. This does not follow a separate path into the intestine, and there appears to be distinguishable no well-marked 'liver string' as in the faeces of *Lymnaea*. Firm faecal pellets are never elaborated, as in prosobranchs, since the anus opens outside the pallial cavity, and there is small likelihood of faeces fouling the pallial water current.

The epithelium of the rectum (figure 8*b*) shows few glandular cells, and its cells are shorter. The cilia beat rapidly towards the anus. The most interesting feature of the

rectum in *Leucophytia* is its dense production of amoebocytes, which migrate in immense numbers into the lumen from the spacious underlying blood sinus, separated from the rectum only by the rectal epithelium and muscle coat. The amoebocytes are large and ovoid (5 to 6μ) with densely staining central nuclei. After starvation they aggregate in the rectum in a compact rod, greyish white in colour, and of mucoid appearance, passed slowly backwards by cilia.

Such cells may—as was suggested by the present writer (1951) for the intestinal amoebocytes of *Struthiolaria*—at times perform an excretory function, though it has to be said that in the specimens sectioned there was at no time any trace of particulate material visible in the cytoplasm of these cells.
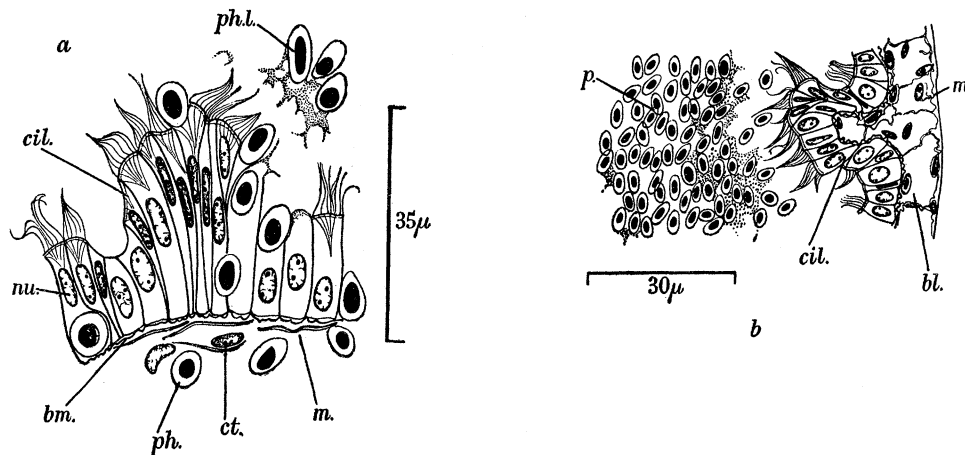

FIGURE 8. *Leucophytia bidentata*. (a) Epithelium of the middle region of the intestine from an animal after 48 h starvation, showing extrusion of phagocytes. Mucus glands were rare in this portion of the intestine in the individual sectioned. They are generally well-developed. *bm.*, basement membrane; *cil.*, ciliated cell; *ct.*, connective tissue nucleus; *nu.*, nucleus of ciliated cell; *m.*, muscle fibre; *ph.*, phagocyte; *ph.l.*, phagocyte in lumen. (b) Epithelium of rectum, showing portion of plug of phagocytes in the lumen. *bl.*, blood space; *bm.*, basement membrane of rectal epithelium; *cil.*, ciliated cell; *m,.* mantle wall; *p.*, plug of phagocytes.

REPRODUCTIVE SYSTEM

Like all other ellobiids, *Leucophytia* is a protandrous hermaphrodite. Though the ovotestis during some portion of the year contains both eggs and sperm together, there are two pronounced phases of sperm production and egg production respectively, taking place at successive seasons. There are corresponding changes in the degree of development of the accessory glands. The hermaphrodite gland or ovotestis forms a cluster of rounded follicles, yellowish white in colour, tucked compactly into a concavity in the posterior lobe of the digestive gland. In the sexually mature adult, the gonad (figure 9, *go.*) enlarges to a conical sac and occupies most of the tip of the visceral spire, covered by the membranous external epithelium, which is densely laden with black pigment. During oogenesis the follicles of the gonad are distended and pressed close together so that their boundaries are indistinct.

Sex products are led from the gonad by the thin-walled little hermaphrodite duct (figure 9, *lhd.*). This tube at first passes deeply between the lobes of the digestive gland as

a straight transparent duct 25μ in diameter. On approaching the glandular part of the genital tract it widens and becomes thrown into close coils, often deeply sacculated, and containing large amounts of stored sperm. It acts thus for the greater part of the year as
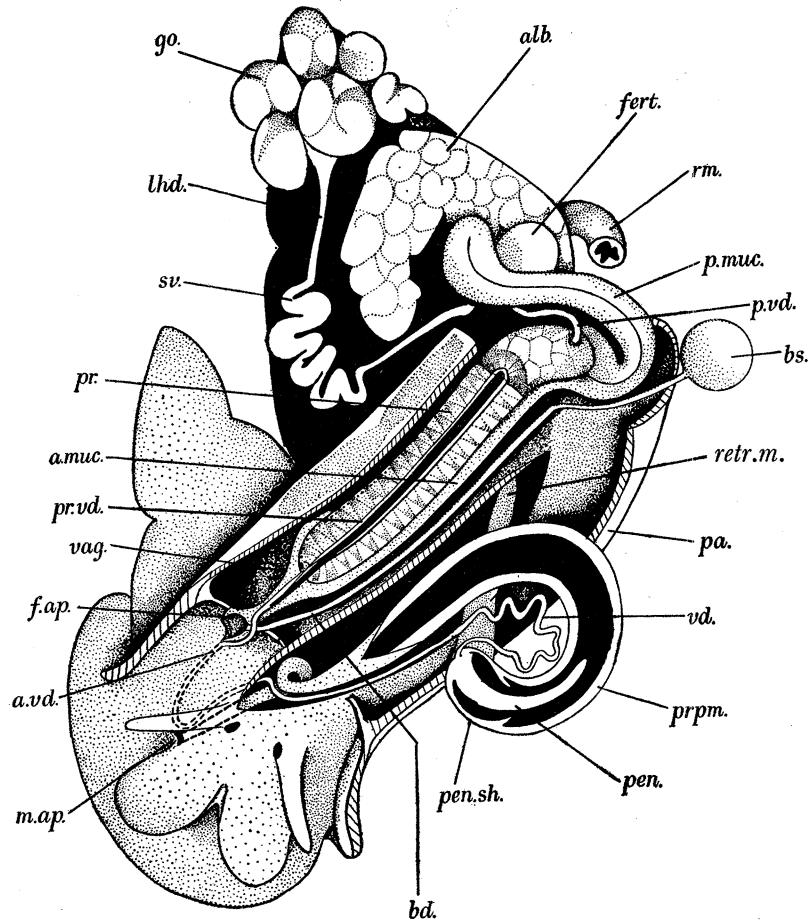

FIGURE 9. *Leucophytia bidentata*. Semi-diagrammatic view of the genital tract, partly dissected. The pallial cavity has been opened to display the prostate and the course of the anterior mucus gland, the prostate having been sectioned longitudinally. The whole of the digestive tract has been removed, except for the rectum. The floor of the mantle cavity has been opened by an incision through the muscular body wall to remove the preputium from the haemocoele, and this organ is opened longitudinally to display the penis. The anterior vas deferens is shown in broken outline beneath the right body wall. *alb.*, albumen gland; *a.muc.*, anterior mucus gland; *a.vd.*, anterior vas deferens; *bd.*, duct of the bursa copulatrix; *bs.*, bursa copulatrix; *f.ap.*, female aperture; *fert.*, fertilization pouch; *go.*, ovotestis; *lhd.*, little hermaphrodite duct; *m.ap.*, male aperture; *pa.*, mantle; *pen.*, penis; *pen.sh.*, penis sheath; *p.muc.*, posterior mucus gland; *pr.*, prostate; *prpm.*, preputium; *pr.vd.*, portion of the vas deferens traversing the prostate; *p.vd.*, posterior vas deferens; *retr.m.*, retractor muscle of the penis; *rm.*, rectum; *sv.*, portion of little hermaphrodite duct serving as a seminal vesicle; *vag.*, vagina; *vd.*, vas deferens.

a seminal vesicle, and appears opaque and pure white in colour. The epithelial cells of the little hermaphrodite duct are short and cubical. Their ciliary coat is often patchy and interrupted as the duct is stretched by distention with sperm. The chief movement of its contents is probably brought about by the elasticity of the connective-tissue wall. The

epithelium is not glandular, and at no time of the year was it observed to show any trace of sperm resorption.

At the base of the albumen gland, the little hermaphrodite duct bifurcates to give rise to male and female ducts which continue forward separately to the common genital aperture. The male duct proceeds first as a straight non-glandular tube (figure 10, *p.vd.*); the female duct enlarges at once, becoming thick-walled and glandular to form the posterior mucus gland (*p.muc.*). It lies side-by-side with the base of the albumen gland on
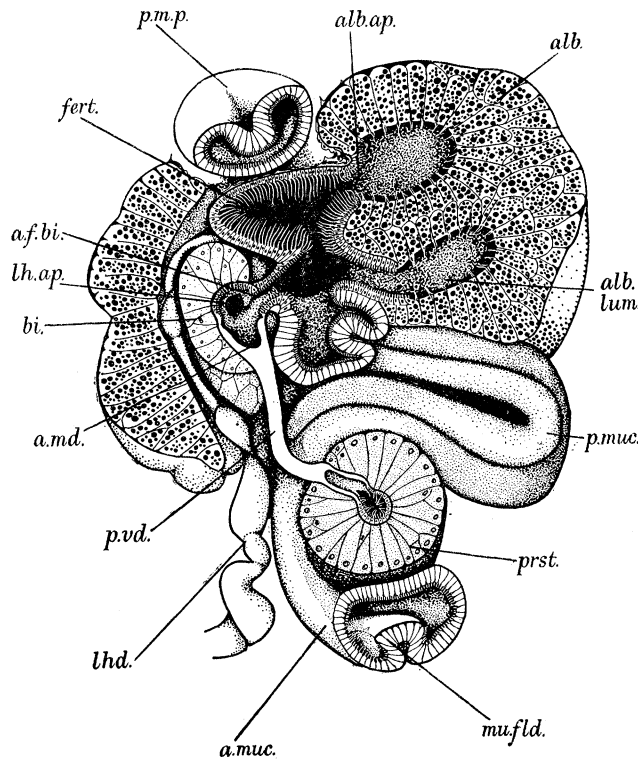

FIGURE 10. *Leucophytia bidentata.* Stereogram illustrating the relations of the genital ducts at the bifurcation of the little hermaphrodite duct and the entry of the albumen gland into the fertilization pouch, with the origin of the posterior mucus gland and the prostate. *alb.*, albumen gland; *alb.ap.*, one of the openings of the albumen gland into the fertilization pouch; *alb.lum.*, fissures forming part of the lumen of the albumen gland; *a.md.*, aperture of the male duct from the bifurcation gland; *a.muc.*, beginning of anterior mucus gland; *a.f.bi.*, aperture of the fertilization pouch from the bifurcation gland; *bi.*, bifurcation gland; *fert.*, fertilization pouch; *lhd.*, little hermaphrodite duct; *lh.ap.*, aperture of the little hermaphrodite duct; *mu.fld.*, internal fold of the mucus gland; *p.m.p.*, terminal pocket of the posterior mucus gland; *p.muc.*, posterior mucus gland; *prst.*, prostate; *p.vd.*, posterior part of the vas deferens.

the left of the visceral mass, extending between the base of the stomach and the anterior lobe of the digestive gland. At its posterior end it receives the secretion of the albumen gland. The whole of the secreting portion of the female genital tract is thus separated from the path of the sperms, and the genital system in *Leucophytia* is completely divided into separate male and female ducts, distally to the bifurcation of the little hermaphrodite duct.

The albumen gland (*alb.*) is stout and tongue-shaped, compact and solid in texture. It is

somewhat laterally compressed, extending within the narrow space between the little hermaphrodite duct, the digestive gland and the wall of the stomach. Its posterior end is slightly recurved, and its whole surface is beset with small acinous projections formed by the tips of the secretory lobules of which the gland is built. In development the albumen gland arises as a pouch-like outgrowth, with thickened walls and a slit-like or crescentic cavity. The lining epithelium (figure 11a) is of stout columnar cells, very long, reaching 50μ in the secreting gland. There are no subepithelial gland cells, and the secreting cells are interspersed with much smaller ciliated cells, at first clavate or tapering narrowly, and soon becoming wedge-shaped or triangular, displaced to the surface of the epithelium as the
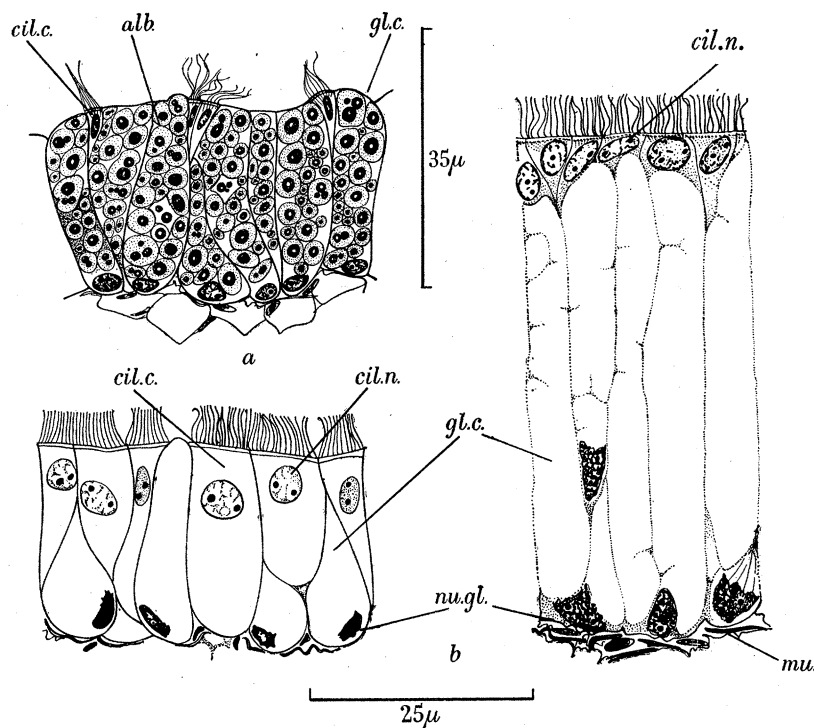

FIGURE 11.. *Leucophytia bidentata.* (*a*) Epithelium of the albumen gland, January. *alb.*, albumen droplets; *cil.c.*, ciliated cell; *gl.c.*, gland cell. (*b*) Epithelium of the posterior mucus gland, (left) in November, before the maturing of the secretory cells, and (right) in June, immediately before oviposition, with mucus cells fully developed. *cil.c.*, ciliated cell; *cil.n.*, nucleus of ciliated cell; *gl.c.*, gland cell; *mu.*, muscle; *nu.gl.*, nucleus of gland cell.

gland cells enlarge. The free surfaces of the gland cells remain flat and entire till the secreting phase, when they rupture and shed their contents into the lumen. Their cytoplasm is tightly packed with secretory spherules, staining lightly blue with azan, green with Masson's stain, and not at all with thionin or mucicarmine. Each spherule is filled with a number of smaller refringent droplets, which stain deep red in azan and golden brown to red in Masson's stain. In some spherules these inclusions may be very tiny and twenty or more in number; in the majority they have coalesced into one or two larger droplets, 2 to 3μ across. Isolated patches of lash-like cilia are borne by smaller distal cells. As the gland cells enlarge, the ciliated cells become widely scattered and their cilia appear to serve little function in the transport of secretion.

Figure 10 illustrates the relations of the male and female genital ducts as the bifurcation of the little hermaphrodite duct. A small, compact gland, referred to here—from its position—as the bifurcation gland, surrounds the little hermaphrodite duct at this point and is itself generally embedded in the base of the albumen gland. The bifurcation gland is ovoid in shape, and, unlike the albumen gland, is built up wholly of subepithelial gland cells, of large size, squarish or triangular in shape, with rounded nuclei; they contain mucin, staining bright pink with mucicarmine, light blue with azan and pale green after Masson's stain. The secretory role of this gland was not ascertained; both eggs and sperm pass through it from the hermaphrodite duct. Towards the anterior end of the bifurcation gland, the female duct emerges as a narrow tube, which opens directly through the wall of the fertilization pouch (*lh.ap.*). A second tube with a narrow circular lumen continues forward to form the most posterior part of the separate male duct.

The fertilization pouch (*fert.*) forms a large thin-walled atrium, opening into the posterior mucus gland, and receiving the secretion of the albumen gland. Its cavity is lined with non-glandular columnar cells, bearing long, dense cilia. Into it extend two wide fissures forming the short ducts of the albumen gland, which at its base is closely fused to the fertilization pouch. The ciliated epithelium of the ducts becomes gradually continuous with the albumen-secreting layer. From the bifurcation gland, the eggs pass into the pouch, which is evidently, as in *Otina*, the site where they are fertilized and receive their albumen layer, before being carried into the mucus gland.

The blind end of the posterior mucus gland forms a short pocket (*p.m.p.*) projecting backwards beyond the fertilization pouch. The rest of the gland consists of a wide tube, averaging 0·5 mm in diameter, which curves twice upon itself and runs forward from the haemocoele to the right side of the mantle cavity. Along one side it is furrowed externally by a narrow groove, which represents the base of a broad fold (*mu.fld.*) dipping into the lumen and partly dividing the cavity of the gland. The fold is lined by ciliated and gland cells (figure 11*b*). At an earlier stage, before the onset of secretion, ciliated cells predominate in the epithelium, and extend to the basement membrane. The ciliary coat is rather long (8 to 9μ). The gland cells stain deeply black with thionin, pink with mucicarmine and remain colourless with Masson's stain or azan. They are at first ovoid in shape, wedged between the bases of the ciliated cells. Their nuclei are spherical and stain deeply with azan. At the secreting phase (figure 11*b*, right) the mucus gland becomes tumid and thick-walled. The lumen narrows and the gland cells elongate. They narrowly compress the ciliated cells which remain as small wedges between the distal ends of the glands. The ciliary coat remains active through the period of secretion; the general direction of beat is forward along the longitudinal fold, upwards over the sides of the fold to the summit, and forwards on the rest of the wall.

The more anterior part of the glandular genital tract, formed by the prostate and the anterior mucus gland, lies immediately beneath the thin epithelium of the pallial floor. Both glands are usually visible externally, on opening the mantle, and follow the curve of the columellar muscle along the whole length of the mantle cavity. The prostate (figure 9, *pr.*), is an opaque cylindrical tube, bulging strongly into the pallial cavity. Posteriorly, it dips back into the haemocoele where the last coil of the posterior mucus gland encircles it, and it is continuous with the narrow posterior vas deferens which emerges from the bifur-

cation gland. This duct perforates the wall of the prostate (figure 10, *prst.*) and continues through it as the narrow prostatic central lumen. The cilia beat actively, lashing the sperms and prostatic secretion forward through this central duct. There is a wide layer of sub-epithelial gland cells, radially arranged. These cells are long and columnar extending through the whole prostatic wall, tapering slightly towards the lumen. The gland nuclei are very large, rounded or sausage-shaped, with darkly staining chromatin. The cytoplasm is sparsely granular, consisting of a mass of secretion staining grey-green with Masson's stain and blue or pinkish-blue after azan. It is not mucoid, remaining colourless after thionin and mucicarmine. Gland ducts are not normally to be seen perforating the epithelium, but at the period of secretion large masses of viscid cell contents make their way into the lumen by displacement of the ciliated lining.

The anterior mucus gland (figure 9, *a.muc.*) forms a translucent or whitish duct, some-times obscured from above by the prostate, which, at the period of greatest development, bulges ventrally against its lumen. Its wall is rather extensible, thrown into longitudinal folds which become obliterated during the passage of the eggs. The cilia are very short, and, as compared with the muscular layer, play little part in the movement of the eggs. The mucus cells of the anterior gland differ from those farther back in staining a deeper blue in azan, and usually reach secretory activity some time before the posterior gland.

At the anterior end of the mantle cavity, the female duct narrows to a small, non-glandular tube (20μ), running forward in the connective tissue of the body wall. From this point to the female aperture, we may refer to it as the vagina. The narrow central duct of the prostate continues as the first part of the anterior vas deferens, and has a strong, forward-beating ciliary coat. The vas deferens and vagina are each surrounded by a narrow circular muscle coat; in addition, there is an investment of circular fibres around both ducts together. The vagina (figure 9, *vag.*) leads in front into a muscular-walled genital vestibule, spherical in shape, which opens to the exterior by the female aperture. This opening corresponds in *Leucophytia* to the original common genital aperture of proso-branchs, and lies concealed beneath the mantle skirt on the right side, just in front of the pallial septum. The cavity of the vestibule contains a broad epithelial fold which separates the vagina from the opening of the bursal duct, leading out of the dorsal side of the vestibule. The vas deferens runs forward along the right side of the head, to the male genital opening, which is a tiny pore concealed beneath the right oral lappet. Its course is marked by a narrow external fold of integument (figure 13 c) which continues forward from the wide upper lip of the female aperture. The male duct is enclosed just beneath the surface in the connective tissue of the fold. The groove below the fold is more strongly ciliated than the rest of the epithelium of the head. The vas deferens is, however, closed throughout; and there is no survival of the open seminal groove which was originally, and is still in *Pythia* (see Morton 1955 *b*) overhung by the fold.

The bursa copulatrix (figure 9, *bs.*) leaves the female tract at its extreme anterior end, and runs backwards in the connective tissue of the floor of the pallial cavity. At the posterior end of the prostate, it diverges to run into the haemocoele, where it expands into a spherical sac, 250μ across. Both the duct and its terminal sac appear to store sperm introduced at copulation, at which time the mouth of the vagina is evidently closed by its sphincter, and sperm is injected directly into the bursal duct. The lining of the terminal

sac (figure 13a) is mainly of ciliated columnar cells. These are not all of uniform size, and the epithelium may become locally flattened and squamous. The nuclei are extremely large and rounded, with single central nucleoli and a mass of dark-staining chromatic granules. The cytoplasm is coarsely granular but without secretion spherules. The surface of each cell bulges into the lumen; the superficial cytoplasm becoming nipped off as a clear-staining mass which is constricted from the tip of the cell. At times a whole cell
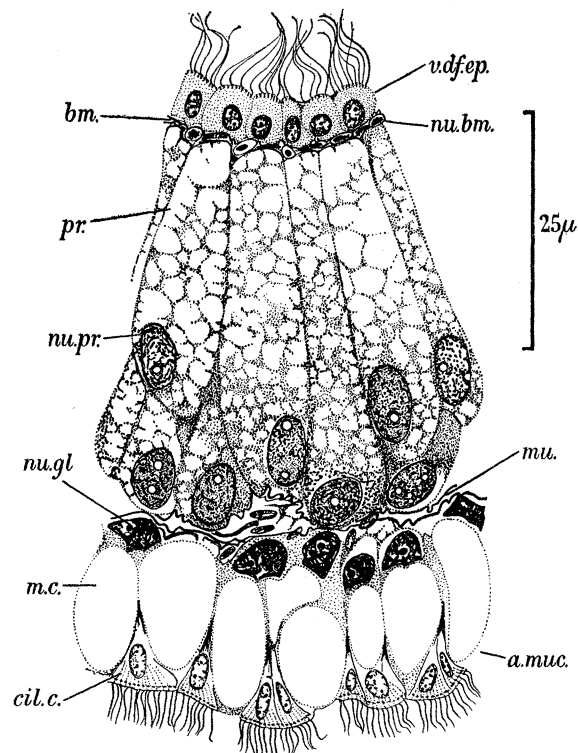

FIGURE 12. *Leucophytia bidentata*. Portions of the adjacent epithelia lining the lumen of the prostate (above) and the anterior mucus gland (below). The material was fixed in January and illustrates the beginning of the increase in size of the cells of the anterior mucus gland, in preparation for the secretory phase (compare with figure 11b for November and June). *a.muc.*, secretory cells of the anterior mucus gland; *bm.*, basement membrane of the prostatic vas deferens; *cil.c.*, ciliated cell; *m.c.*, droplet of secretion filling a single mucus cell; *mu.*, muscle fibre; *nu.bm.*, connective tissue nucleus lying beneath the basement membrane; *nu.pr.*, large nucleus of a prostatic cell; *nu.gl.*, nucleus of a gland cell; *pr.*, prostatic cell; *v.df.ep.*, epithelial cell of the prostatic vas deferens.

may become pseudopodial and project like a villus into the lumen. Sperms do not become oriented on the wall of the bursa. At most times, intact sperms lie near the periphery, and the centre of the lumen is filled with a spherule of disintegrating sperm, mixed with several layers of mucus (staining blue and yellow in azan), prostatic secretion and cell fragments. Like the accessory bursa of *Otina*, this sac appears to serve as a depot for surplus sperm, much of which remains after fertilization.

The preputium (*prpm.*) forms a stout muscular sheath, leading inwards from the male genital pore, and curving backwards within the haemocoele. Crossing above the buccal mass, it terminates in a recurved club-shaped bulb, which is thinner-walled, and consti-

tutes the penis sheath proper. The penis (*pen.*) is a short muscular papilla, pointed at the tip; it springs from the bottom of the penis sheath, and extends forward a short distance into the preputium. At its base, the penis is perforated by the vas deferens, which turns inwards from the body wall at the male aperture, and runs closely along the preputium and
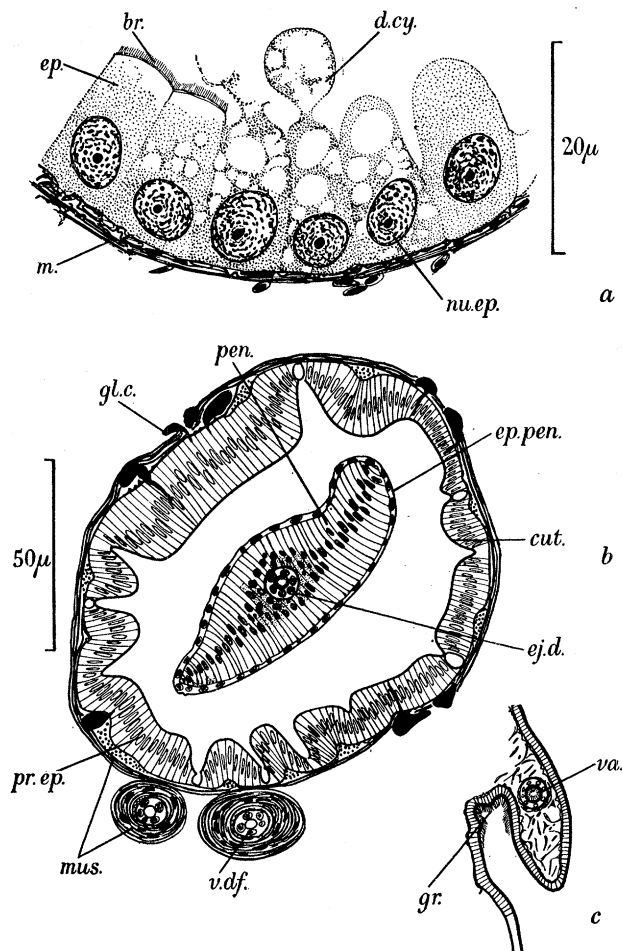

FIGURE 13. *Leucophytia bidentata.* (*a*) Epithelial cells of the bursa copulatrix. *br.*, ciliated or brush border of an epithelial cell; *d.cy.*, distal cytoplasm becoming constricted off from the tip of an epithelial cell; *ep.*, epithelial cell; *m.*, muscle fibre; *nu.ep.*, nucleus of an epithelial cell. (*b*) Transverse section of the penis and the preputium. *cut.*, cuticular lining of the preputium; *ep.pen.*, external epithelium covering the penis; *ej.d.*, ejaculatory duct; *gl.c.*, glandular cell of the preputium; *mus.*, muscular layer of preputium and of vas deferens; *pen.*, penis; *pr.ep.*, epithelium of the preputium; *v.df.*, vas deferens. (*c*) Transverse section across the anterior genital fold, showing the anterior vas deferens, shortly behind the male genital opening. *gr.*, open ciliated groove; *va.*, enclosed vas deferens.

penis sheath. Within the penis, it forms a narrow ejaculatory duct. A retractor penis muscle is attached to the end of the penis sheath, and inserted posteriorly upon the floor of the trunk.

The wall of the preputium (figure 13*b*) is built up of a tall epithelial layer, invested with a muscle coat, consisting of loosely arranged circular fibres, intermixed with longitudinal. The two strongest folds form low and flat-topped ridges running the whole length of the

tube. The epithelial cells are narrowly columnar and there are occasional ovoid gland cells, with non-staining secretion droplets.

A second type of gland is also present, packed in clusters, or more or less solitary, in the connective tissue beneath the basement membrane. The contents stain black or deep purple with haematoxylin, and are discharged by long cigar-shaped ducts which penetrate the columnar epithelium.

The penis (*pen.*) is composed wholly of muscle without vascular spaces. The whole length of the preputium is eversible, but the penis alone appears to form the intromittent organ. Transverse muscle fibres cross its whole width, and the external epithelium of the penis forms a coat of flattened squamous cells with dark-staining nuclei bulging from the free surface.

The egg and embryo

Egg masses of *Leucophytia* were found at Wembury from the third week till the end of June 1951, in crevices in the rocks, with groups of ovipositing snails. Each mass was about 4 mm across, irregular in shape, containing a cluster of from eighteen to twenty-four eggs, produced by a single individual. Each egg was enclosed in a blunt-pointed ovoid capsule, and the whole cluster invested by a viscid, mucoid secretion which formed the matrix of
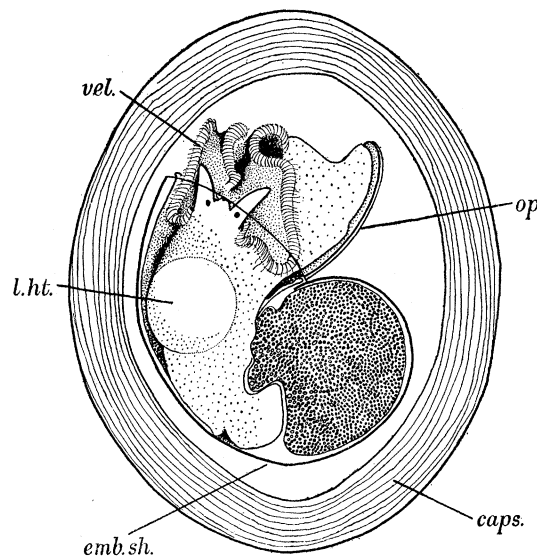

FIGURE 14. *Leucophytia bidentata.* An embryo in the egg capsule, shortly before emerging. *caps.*, concentrically laminated capsule wall; *emb.sh.*, embryonic shell; *l.ht.*, 'thoracic vesicle' or accessory embryonic heat; *op.*, operculum; *vel.*, velum.

the egg mass, and adhered closely to the surface of the rock. This embedding substance stained light blue in azan and black in thionin. It is almost certainly the secretion of the anterior mucus gland. The yolk of the egg is opaque white, surrounded by a thin layer of albumen. The wall of the capsule is finely laminated concentrically, and appears to have the nature of a condensed mucoid secretion. As its site of origin, the posterior mucus gland seems the most reasonable suggestion.

During the first week of their development, while they remain enclosed in the capsule, the embryos of *Leucophytia* are velate and operculate (figure 14). The velum is reduced in

size to two short, rounded lobes, one on either side of the head, and encircled with a thick rim of actively beating velar cilia. The embryos move about within the capsule by the muscular action of both the foot and the lobes of the velum. The operculum is thin and horny, and its sharp edge assists the emergence of the embryo through the capsule membrane. The most interesting feature of the embryo in *Leucophytia* is the disposition of the apical whorl of the shell. This whorl forms a transparent ovoid chamber, its long axis being at right angles to that of the post-embryonic and mature shell. There appears—as in *Pythia*, of which the embryo shell was described by Harry (1951)—to be an initial tendency to a sinistral coil, as is present in *Melampus*, the only member of the Ellobiidae
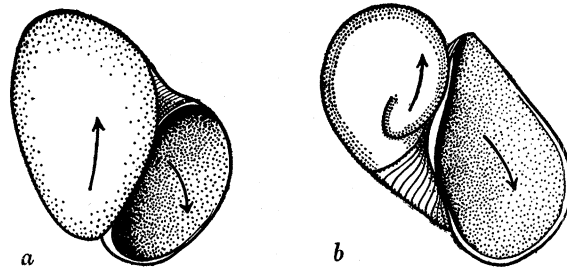

Figure 15. An embryonic shell of *Leucophytia bidentata* (*a*), at the same stage as the embryo in the preceding figure, shown in a different aspect to illustrate the reduced hyperstrophy of the apical whorl. A larval shell of *Akera bullata*, is illustrated (*b*) for comparison of the same condition (modified from Thorson (1946)).

known to retain a free-swimming veliger. The condition known as 'reduced hyperstrophy', as found in *Leucophytia*, is characteristic—in an even more vestigial form—of *Otina*, as recently described by the present writer (1955*a*). Further, the early development of the bullomorph tectibranchs is known to begin upon the same lines, the first benthic stage having a sinistral apex on top of a dextral shell. A sketch of a young benthic stage shell of *Akera bullata*, copied from Thorson's figure (1946), is added here (figure 15) for comparison with *Leucophytia*.

Reproductive cycle

Reproduction in *L. bidentata* was studied at Plymouth from July 1950 to July 1951, and the cycle of changes in the condition of the genitalia was thus observed over one season only. A great deal of work remains to be carried out upon growth rates and their possible variations from year to year; but from the range in size of animals found to be sexually mature, it would appear that there are at least 2 years during which a single individual is normally sexually active. *Leucophytia*, like *Carychium* investigated elsewhere (see below, and Morton 1954*c*), would thus conform to the rule of a biannual life cycle which appears to be rather general (see Boycott 1934) among Basommatophora. Gamete production in *Leucophytia* during a single season is protandrously hermaphroditic. The seasonal changes found to take place in Plymouth material consisted of a phase of development of sperms beginning early in September and finishing at the end of December, followed by a female phase continuing until egg-laying, which was most pronounced at the end of June. The cyclical diagram (figure 16) presents the changes taking place in the gonad and accessory

genital organs of *L. bidentata* during a single breeding season. A fuller discussion of repro-
duction in hermaphroditic Gastropoda it is hoped to present elsewhere; but it may be
remarked here that a similar sequence to that of *Leucophytia* appears to be the general rule
among the more primitive sections of both the Pulmonata Basommatophora and the
Opisthobranchia Tectibranchiata (see, for example, *Otina otis* (Morton 1955 a) and *Limacina*
(*L. retroversa* (Hsiao 1939)) and *L. bulimoides* (Morton 1954 b)).

In sexually mature *Leucophytia* towards the end of the summer the sexual cycle begins
with a male phase, which apparently occurs both in animals becoming for the first time
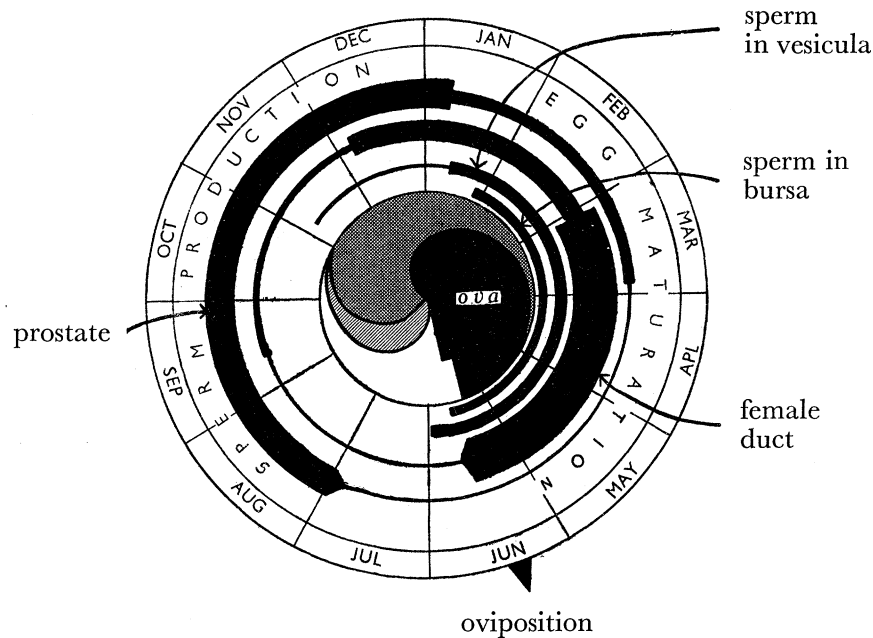

oviposition

FIGURE 16. *Leucophytia bidentata*. Generalized diagram to illustrate the seasonal cycle of the gonad
    and accessory genital organs as observed in Plymouth material. The central area represents the
    condition of the gonad, light stipple showing pre-meiotic stages in spermatogenesis, darker
    stipple later stages in the production of male gametes, and black representing ova. The con-
    centric circular area indicates the presence of sperms in the vesicula seminalis and in the bursa
    copulatrix, and the relative degree of development of the anterior mucus gland of the female
    duct, and of the prostate.

mature and in those which have in the preceding months deposited eggs. Oocytes are
now represented only by small oogonia lying undeveloped in the epithelium of the
gonadial tubules. Towards the end of September, spermatogenesis is well advanced;
clusters of dividing spermatogonia and primary spermatocytes line the walls and fill the
lumen of the ovotestis. Ripe sperm morulae containing post-meiotic spermatocytes with
densely chromatic nuclei are also abundant. At the end of November and in December,
small platelets of mature, tailed sperms begin to fill the gonad.

It is important to note that this stage of sperm development cannot properly speaking be
regarded as a 'pure male' phase. The animal is at present what Hsiao (1939) has called
a 'hermaphrodite male', and the female parts of the genital ducts, though they have not
yet reached their functional condition, are prominent and completely differentiated

throughout. The albumen gland is already prominent. In the anterior and posterior mucus glands, the epithelium is short-celled and predominantly ciliated (see figure 11*b*, left). The gland cells remain small and secretory activity has not yet begun. In the male portion of the genital tract, on the other hand, the prostate now reaches its greatest size. The total diameter of the gland is approximately 250μ, as great or somewhat greater than that of the anterior mucus gland. Sperm is stored in the little hermaphrodite duct; and the bursa copulatrix is either empty or filled with clear mucoid material, no foreign sperms being yet present.

Towards the beginning of December female development in the ovotestis begins to accelerate. The oocytes increase in size (100μ) and the cytoplasm becomes densely granular, staining grey or pink in azan. The earlier formed ova have by now become filled with red-staining yolk droplets, and the egg nuclei themselves reach 12μ across. The majority of the spermatocytes and spermatids have undergone transformation into sperm, and mature sperm crowd the lumen of the gonad near its duct, and fill the little hermaphrodite duct along its whole length. The bursa is still empty, and the prostate large. Development of oocytes continues until March, by which time the gonad is tightly filled with matured ova interspersed with developing oocytes. Sperm are almost all excluded, only a few isolated mother cells and morulae remaining. A large accumulation of sperm is contained in the little hermaphrodite duct. Copulation was never able to be observed, but evidently takes place at least from the end of March onward, since foreign sperm and prostatic secretion then began to appear in the bursa. Changes rapidly follow in the male ducts, the prostate becoming smaller, of less than half the diameter of the now enlarged anterior mucus gland. Mucus-secreting cells now predominate in the epithelium of the anterior and posterior mucus glands, and the wall of this part of the duct becomes tumid with its contained mucous secretion. The contents of the bursa consist of a dense mass of sperm suspended in prostatic secretion. The female ducts are now at their stage of greatest development and oviposition takes place from the beginning to the end of June. The prostate by this time has entirely lost its gland cells, and is represented merely by a narrow vas deferens running along the surface of the anterior mucus gland.

Towards the end of June, and early July, most animals sectioned show empty spaces in the gonad followed by great shrinkage in size of this organ. A few degenerating egg cells and undeveloped oocytes remain. In some individuals sperm mother cells and morulae are already beginning to form again. The little hermaphrodite duct is empty, and the bursa forms a very small sac filled with degenerating sperm. During July the female accessory glands, having shed their secretion, remain very tiny, especially the albumen gland and the posterior mucus gland. The pallial portion of the mucus gland remains always somewhat more prominent.

2. *OVATELLA MYOSOTIS*

The whole of the material of the genus *Ovatella* used during the present investigation belongs to the species most generally referred to as *Phytia myosotis* (Draparnaud). The second British *Phytia*, the species *denticulata* of Montagu, has by later workers usually been regarded as a subspecies of *myosotis*. *Denticulata* is the equivalent of Turon's species *ringens*,

which was first reduced to varietal rank under *myosotis* by Jeffreys (1869). In the most recent list (*Cens. Distr. Brit. Non-Mar. Moll.* 1951), the compiler follows Winckworth in treating *denticulata* as a subspecies. A contrary opinion was held by Monteresato (1906), who claimed that *myosotis* and *denticulata* were in fact representative of different genera; and Wenz (1920) even made *denticulata* the type species of his genus *Nealexia* and *myosotis* the type of a distinct genus *Myosotella*. The question of the separate status of *myosotis* and *denticulata* was recently discussed at length by Watson (1951).

The continued use of the generic name *Phytia* in the family Ellobiidae is unfortunate. Watson (1943) traces its origin to a mis-spelling by Gray (1821) of *Pythia*, one of the four generic names originally in use for ellobiids. The frequent occurrence of the two names close together in print is an obvious source of confusion, and Watson recommends the rejection of *Phytia*, as an evident mis-spelling, under Article 19 of the International Rules. He suggests *Ovatella* Bivona Bernardi, 1832, as available and valid. This opinion is endorsed by Boettger (1949), and the present writer proposes to adopt the name *Ovatella* in this account. It is admittedly a little unfortunate that *Ovatella* has been in the past applied to the group containing the British species *Leucophytia bidentata*, but for convenience in use it is still a great improvement on *Phytia*, and this is one instance where the general zoologist may wholly welcome a change which the systematist urges him to adopt.

The conchological differences between *Leucophytia bidentata* and the two British forms of *Ovatella* are well summed up by Forbes & Hanley (1853, vol. 4, pp. 191 *et seq.*). The distinction in apertural details between *myosotis* and *denticulata* coincides with a well-marked ecological difference. *Myosotis* is an inhabitant of brackish marshes, saltings and strips of salt meadow about the estuaries of rivers. It is almost always supratidal, except at the highest spring tides, but sometimes extends into the intertidal zone above extreme high-water mark of spring tides under driftwood on mud flats. Ellis (1926) gives a series of English localities for *Ovatella myosotis*; it occurs widely on English coasts but, like *denticulatus*, (though it may be locally very abundant) its distribution is discontinuous and patchy.

In external features the animal of *O. myosotis* differs only in colour and in rather small structural details from *Leucophytia bidentata*. The exposed parts of the head and foot are steely grey in colour, becoming lighter and brownish in the midline of the head, where the reddish brown buccal mass shows through. At the sides of the mouth, the head is a lighter ashen grey and the integument delicately rugose. The tentacles are short and stout, bluntly rounded at the tips and widely diverging from near the mid-line, with jet black eyes at their inner bases. They are smooth and darker grey in colour. The sole of the foot is long and narrow, gently rounded behind and squarish along the anterior edge; its under-surface is light grey or white. Though the anterior third of the foot is never divided from the posterior part by a transverse groove as in *Leucophytia*, the front of the sole tends to become rather more expanded. It ripples ahead rather faster in creeping over flat surfaces, the rest of the foot being drawn up upon it from behind. Secretion of the supra-pedal gland is apparently employed in compacting a food bolus as in *Leucophytia*, being admixed with particles rasped from the substratum by the radula. There are no separate oral lappets as in *Leucophytia* or *Otina*. The mouth is protected at either side by a fleshy

pad of integument which is pressed close against the substratum when the radula is at work. The mouth is a simple circular aperture, and a median furrow extends back from its posterior margin to the base of the foot, where the supra-pedal gland opens. Its margins are extremely distensible and the anterior edge supported by a bow-shaped cuticular jaw.

DIGESTIVE SYSTEM

In general plan the alimentary canal of *Ovatella* conforms closely to that of *Leucophytia*. In the following account attention will be focused chiefly on differences of detail, and especially on the structure of the stomach, in which *Ovatella* is much less highly specialized. In some features, the stomach shows resemblances to that of *Otina* as already described; and in general the gut of *Ovatella* may be regarded as very primitive among the ellobiid genera examined (Morton 1955 b). The only existing account of the alimentary canal in *Ovatella* is that of Pelseneer (1901), which is illustrated by simple outline figures but gives no finer details of structure nor any mention of histology or mode of functioning.

The anterior part of the alimentary canal in *Ovatella* presents no features requiring special mention. The buccal mass, the jaw, the odontophore and the salivary gland are all essentially as in *Leucophytia*. A figure is given here (figure 17 b) of the details of the radular teeth. It agrees with that of Odhner (1924) who regards the radula of *Ovatella* as constituting a primitive and basal type among ellobiids. The oesophagus shows the typical division into short anterior oesophagus, and thinner-walled dilated crop, ciliated throughout. The crop is demarcated by slight constriction from the short extension of the stomach, forming the oesophageal atrium.

The stomach (figure 18) is a spacious sac partly surrounded by the digestive gland, lying on the left side of the visceral mass; its transparent lateral portion is prominently visible on the external surface of the animal. It is rather broader than long, kidney-shaped in outline with the convex side facing posteriorly. The thin-walled oesophageal atrium (*oe.at.*) and the intestine are separated from each other by a deep notch at the anterior margin of the stomach. The two halves of the stomach tend to form separate regions, somewhat constricted from each other at the mid-line, but widely communicating. The right half of the stomach, funnelling forward to the intestine, corresponds to the gizzard in *Leucophytia*. Its wall is covered with thin cuticle and surrounded by a strong girdle of circular muscle fibres. The muscular zone extends round to the left side to enclose the oesophageal half of the stomach continuously with the gizzard. On the deep aspect of the left side, the wall, though still muscular, is thinner, and here a smooth tract of ciliated epithelium sweeps across the stomach from the opening of the oesophagus to the margin of the posterior caecum (*cm.*). The caecum forms a small, bluntly rounded pouch projecting from the convex surface of the postero-dorsal aspect of the stomach. At the mouth of the caecum, the posterior digestive diverticulum (*p.div.*) takes its origin, opening directly through the dorsal wall of the stomach.

Unlike *Leucophytia*, *Ovatella* retains both of the digestive diverticula. The duct of the posterior lobe of the digestive gland still opens separately from the posterior end of the stomach as in *Otina*. As in *Leucophytia* the anterior digestive diverticulum (*a.div.*) has moved forward from the main part of the stomach to open from the tubular oesophageal
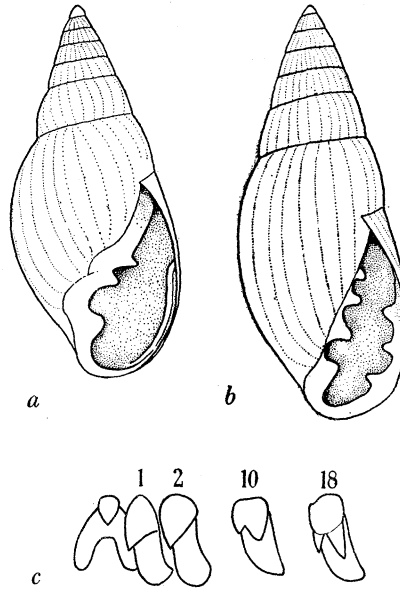
FIGURE 17. (a), (b) Shells of *Ovatella myosotis* (Draparnaud) and *Ovatella myosotis* var. *denticulata* (Montagu). (c) Representative teeth of the radula of *Ovatella myosotis*.
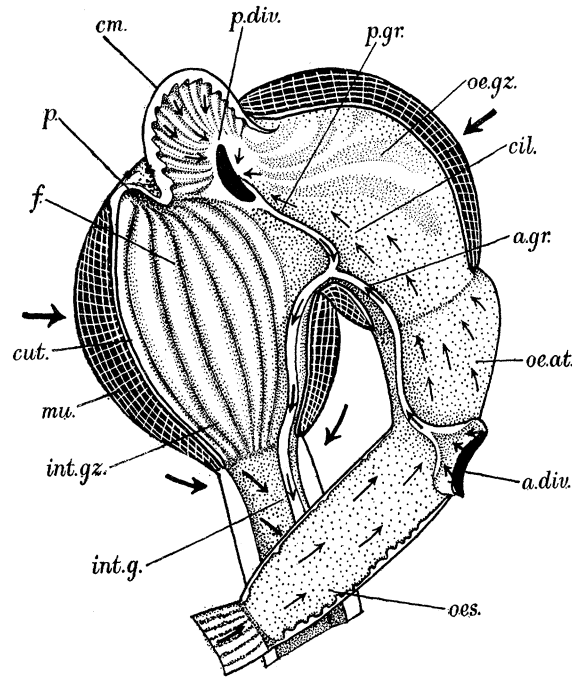

FIGURE 18. *Ovatella myosotis*. The stomach, viewed as a transparent object, without dissection, showing the course of the chief ciliary currents. The heavier arrows outside the stomach represent the regions of the chief muscular movements. *a.div.*, anterior digestive diverticulum; *a.gr.*, anterior excurrent groove; *cm.*, posterior caecum; *cil.*, ciliated tract leading from oesophageal atrium to the posterior caecum; *cut.*, cuticle of the gizzard; *f.*, lining folds of the intestinal half of the gizzard; *int.g.*, intestinal groove; *int.gz.*, intestinal portion of the gizzard; *mu.*, muscular layer of the gizzard wall (viewed in optical section); *oes.*, oesophagus; *oe.at.*, oesophageal atrium; *oe.gz.*, oesophageal portion of the gizzard; *p.*, cuticle-lined pocket mentioned in the text; *p.div.*, posterior digestive diverticulum; *p.gr.*, posterior excurrent groove.

atrium. From each diverticulum, there proceeds, as in *Otina*, a strongly ciliated excurrent groove leading to the intestine. This is bounded by the ridge forming, as in *Otina*, the major typhlosole of Graham (1949). The fold and its groove curve directly forward over the dorsal surface of the stomach to the base of the intestine. Here they are joined by the anterior excurrent groove, running downward into the stomach from the oesophageal atrium. The anterior groove begins widely at the opening of the diverticulum and its margins converge to enclose a narrow tract along which ciliary currents sweep round the neck of the oesophageal atrium, converging with the current of the posterior groove, to run forward into the intestinal groove (*int.g.*) up the left wall of the intestine. The rest of the oesophageal atrium is also lined with ciliated epithelium, which beats backward into the stomach, and along the thinner dorsal wall, towards the caecum.

The ciliated tract (*cil.*) is lined by short cells and is devoid of mucus glands. Towards the caecum, the epithelium becomes raised into a series of nine to twelve small close-set ridges, which by-pass the posterior diverticulum and enter the caecum, running transversely round its left side. Weak ciliary currents run along the ridges and the intervening grooves into the caecum, and the whole lining of this part of the caecum is finely ciliated. The caecum is divided by a strong ridge projecting into the stomach and cutting off on the right side a small pocket lined with thin cuticle, continuous in front with the gizzard. The whole wall of the caecum is appreciably muscular, though much less so than the gizzard. The folds of the cuticle, in the pocket (*p.*) on the right side fan out into the gizzard as strong longitudinal ridges. Of the two sides of the gizzard, the wall of the right, or intestinal, half tends to be the stouter. The histology is in no important respect different from that of *Leucophytia*. The oesophageal half of the gizzard is also strongly muscular, and its wall extends forward to the oesophageal atrium; as distinct from *Leucophytia* there is no clearly marked anterior chamber with a ciliated lining; both oesophagus and intestine communicate directly with the gizzard.

In its general topography the stomach of *Ovatella* thus retains much of the generalized prosobranch plan (see p. 151). The excurrent grooves from the digestive diverticula survive as in *Otina*, and the posterior caecum still appears. On the oesophageal side, the ciliated tract (*cil.*) is probably a remnant of the sorting area, as is shown also in *Otina*. Though most of the wall of the stomach has become muscular and gizzard-like, there is no separation, as in *Leucophytia*, of the massive posterior gizzard from the rest of the stomach, and the relative thickness of the muscular coat remains much less. We may well imagine the stomach in *Ovatella* to be derived from the simple *Otina* type by the ballooning out of its posterior muscular pocket to constitute the spacious gizzard forming most of the stomach. The posterior digestive diverticulum is carried posteriorly by the growth of the gizzard. In all primitive ellobiids genera it remains present, together with its excurrent groove. In advanced genera, both the diverticulum and the excurrent groove disappear.

In function, the stomach of *Ovatella* already resembles that of *Leucophytia*. There seems to be little reliance at all on cilia, which must obviously be ineffective in moving the heavy mass of detritus lying within the stomach. The caecum, likewise, appears to retain little function; it is short and seldom filled with detritus. Lighter particles, presumably squeezed from the food mass, are carried by cilia into the caecum, which appears to serve as an annexe receiving finely divided material which will presently enter the posterior diverti-

culum. The oesophageal atrium, as well as being ciliated, is strongly contractile (like the anterior chamber in *Leucophytia*), and detritus is forced tightly into both right and left halves of the stomach. There is only slight evidence of functional difference in the right and left halves, but muscular contractions usually appear to be stronger in the right half and peristaltic movements appear to be directed towards concentrating detritus on this side. Strong triturating and squeezing movements are supplied by the contraction of the gizzard. Semi-fluid material is squeezed out from the bolus and tends to collect in the left half of the stomach and to flow into the oesophageal atrium. Backflow of bulkier food into the oesophagus is evidently prevented by muscular contractions towards the gizzard. Finer particles suspended in fluid material are squeezed into the apertures of the diverticula, and the residual mass of indigestible waste eventually comes to lie wholly in the right half of the stomach. From here, intermittent muscular contractions direct boluses of faeces into the intestine. The functional separation of the gizzard from the rest of the stomach is much less efficient than in *Leucophytia*, but it is easy to see how the stomach in higher ellobiids, with well-marked functional regions, must have been derived from the generalized stomach of *Ovatella*.

Digestive gland

In *O. myosotis* the two lobes of the digestive gland are about equally large. The posterior lobe is conical, and occupies the whole apex of the visceral mass. The anterior lobe in part surrounds the stomach in the first whorl of the visceral mass. It is encircled by the last loop of the intestine, which then runs forward along the mantle as the rectum. On leaving the stomach, the two digestive diverticula are thin-walled and membranous. They are lined with fine cilia, which beat rapidly towards the stomach. There is also a considerable power of peristalsis, by the action of the thin coat of muscle lying beneath the basement membrane. The structure and the phases of activity of the digestive gland are in general very similar to those of *Leucophytia*, and there are few points that require separate mention.

Intestine

The proximal limb of the intestine runs straight forward from the gizzard. There is no elbow bend at its origin, as in *Leucophytia*, and the first part of the intestine resembles in histological structure the simplified 'style sac' of *Otina*. The intestinal groove is lined with cilia bearing aborally. In the rest of the lining epithelium the cilia are not of the strong, dense, style-sac type, but short and fine. The direction of their beat is difficult to observe in dissected material, but appears to be transverse, or obliquely backwards, into the more distal part of the intestine. The histology of the proximal limb of the intestine may be regarded as a further relic of the prosobranch alimentary canal, though few of the functions of the style sac appear to persist, and this part of the intestine has already become strongly peristaltic. Farther back, the course of the intestine resembles exactly that of *Leucophytia*, with small fusiform gland cells. They occupy about half the height of the ciliated epithelial cells and their secretion, staining reddish in azan, is evidently not mucoid. In the rectum the epithelium is shorter and the wall less folded. The cilia are more strongly developed and beat very rapidly towards the anus. The faeces with the added secretion of the intestinal glands are soft and very little compacted as compared with those of prosobranchs.

Reproductive system

Just as in the digestive system, *Ovatella* as compared with *Leucophytia* shows many features in the genitalia at once recognizable as primitive among ellobiids, and in some ways reminiscent of *Otina*. In general, the reproductive organs show a close homology, region by region, with those of *Leucophytia*, and the present account will direct attention chiefly to differences in detail between the two genera.

The ovotestis consists of a spacious, light-coloured sac, which may give rise to a series of short blunt tubules interpenetrating among the lobules of the digestive gland. In contrast with its location in *Leucophytia*, the gonad in *Ovatella* does not occupy the apex of the visceral spire, and is hardly at all visible externally. It is closely invested behind by the posterior lobe of the digestive gland, and comes into contact anteriorly with the anterior digestive lobe and the stomach. The cavity of the ovotestis is cut up by short trabeculae of connective tissue, over which spreads the germinal epithelium. The sequence of spermatogenesis and oogenesis throughout the year was not followed in detail; such observations as were made indicate a sexual cycle not unlike that of *Leucophytia*.

The little hermaphrodite duct (figure 19, *g*) is a ciliated tube, functioning as a seminal vesicle as in *Leucophytia*. Its coils are for most of the year strongly distended, and appear to contain sperms long after spermatogenesis has ceased in the ovotestis. Sperms were never found oriented upon the surface of the epithelium, nor was resorption found to occur.

In *Ovatella* the glandular portion of the genital tract remains structurally hermaphrodite as far forward as the common genital aperture. The large (or glandular) hermaphrodite duct, into which the little hermaphrodite duct leads from the ovotestis, is divided into a proximal region, the posterior mucus gland (*p.mu.*) and a distal region comprising the anterior mucus gland (*a.mu.*) and the prostate (*pr.*). The posterior mucus gland, together with the albumen gland, lies within the haemocoele as in *Otina* and *Leucophytia*; the rest of the glandular hermaphrodite duct is superficial, in position, running forward, just beneath the thin lining epithelium of the right side of the floor of the pallial cavity. This anterior part of the glandular duct forms a single tube, with two secretory tracts, muciparous and prostatic, discharging their secretions into a common lumen.

As in *Leucophytia*, the albumen gland opens into a rounded thin-walled sac, the fertilization pouch (*ft.*), which leads into the posterior mucus gland, close to the opening of the little hermaphrodite duct. The fertilization pouch is lined with very long cilia reaching almost to the centre of the lumen. In both *Leucophytia* and *Ovatella*, the fertilization pouch may be looked upon morphologically as a vestibule formed by the enlargement of the duct of the albumen gland, at the point where this duct opens into the posterior mucus gland. This is usually held to be the fertilization site of the female tract, and is the region occupied in prosobranchs by the receptaculum seminis (see Fretter 1946), a sperm-storing sac which remains undeveloped as such in the Pulmonata. In *Ovatella*, the gland is opaque white and solid in appearance, with its surface raised into fine acini. It is built up of a pair of massive lobes which in dissection appear to be closely fused together at their bases. In section, however, their separate origins are still recognizable. The anterior lobe (*a.alb.*) is compact and rounded, enclosed, together with the fertilization pouch, between the two arms of the posterior mucus gland. The posterior lobe (*p.alb.*) extend farther backwards,

pressed close against the wall of, and posterior to, the blind limb of the mucus gland. The two lobes open close together into the fertilization pouch, around the base of which they spread widely. They evidently correspond with the two entirely separate lobes of the
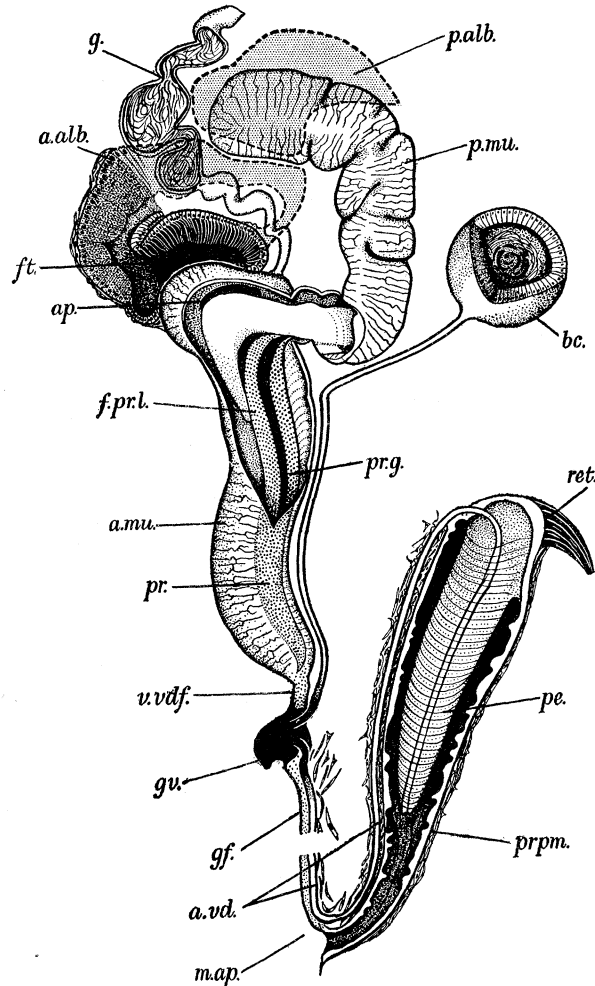

FIGURE 19. *Ovatella myosotis.* Stereogram showing the structure and arrangement of the genital ducts. The fertilization pouch has been opened to show the entry of the duct leading from the anterior lobe of the albumen gland. Most of the anterior, and the whole of the posterior, lobe of this gland are indicated merely by broken outlines. The final part of the posterior mucus gland and the beginning of the anterior mucus gland has been opened to show the dividing fold, together with the openings of the little hermaphrodite duct and the fertilization pouch, and the commencement of the prostate. Portion of the wall of the bursal sac has been removed and the preputium has been sectioned longitudinally to show the retracted penis. *a.alb.*, anterior lobe of the albumen gland; *a.mu.*, anterior mucus gland; *ap.*, aperture of the fertilization pouch into the posterior mucus gland; *a.vd.*, anterior vas deferens; *bc.*, bursa copulatrix; *f.pr.* 1, fold bounding the first part of the prostatic canal; *ft.*, fertilization pouch; *g.*, little hermaphrodite duct, distended to form vesicula seminalis; *gf.*, external genital fold, beneath which runs the vas deferens; *gv.*, genital vestibule; *m.ap.*, male aperture; *p.alb.*, posterior lobe of the albumen gland; *p.mu.*, posterior mucus gland; *pr.*, prostate; *pr.g.*, prostatic channel; *prpm.*, preputium; *ret.*, retractor muscle of penis and preputium; *v.vdf.*, combined channel of vagina and vas deferens, leading forward from the anterior mucus gland and the prostate.

albumen gland, which were described by Plate (1897) in the very primitive ellobiid *Pythia scarabaeus*.

In histology the albumen gland rather closely resembles that of *Leucophytia*, figure 20*b*. There are no subepithelial gland cells, the whole of the secretion being produced by the tall columnar epithelium. Between the tips of the gland cells occur small wedge-shaped ciliated cells. The tips of the glandular cells are strongly convex and break down during secretion when the cell contents flow out freely. The nuclei are large and ovoid, with dark nucleoli and dense chromatin granules. The contents of the gland cells consist of a crowded mass of spherules, staining uniformly bluish grey in azan. There are also smaller spherules filled with tiny refringent particles that are present also in a free state in the general cytoplasm, especially distally, by the breakdown of the spherules.

The posterior mucus gland (*p.mu.*) is a wide, laterally compressed tube, delicate and translucent in appearance. It follows a broadly U-shaped course, extending around three sides of the compact mass formed by the fertilization pouch and the base of the albumen gland. Its walls are for the most part smooth, but may be thrown into shallow saccules, demarcated by narrow furrows on the external surface. The lumen is occupied by a broad fold, rounded or triangular in section, formed by the involution of the wall along the convex side of the U, and running the entire length of the mucus gland. The cavity of the posterior mucus gland consists chiefly of two narrow fissures communicating across the summit of this fold. Both the fold and the side channels are covered by a thick glandular lining, consisting of a columnar ciliated epithelium with a dense zone of subepithelial glands, up to 70 to 100 μ deep. The gland cells are rounded or flask-shaped, and are grouped together in ovoid lobules, each lobule sparsely surrounded by connective tissue. The cell ducts are stout and round-tipped, penetrating thickly between the columnar epithelial cells. The secretion of the posterior mucus gland, as in *Leucophytia*, stains bright pink with mucicarmine, black in thionin, and pale blue or not at all with azan.

Around the concave margin of the U, above the summit of the longitudinal ridge, the wall of the posterior mucus gland is thin and non-secreting. Through this wall open anteriorly, near the junction of the U-shaped tube with the anterior mucus gland, the little hermaphrodite duct and the slit-like aperture of the fertilization pouch (*ap.*). The greater part of the posterior mucus gland thus projects backwards as a stout diverticulum, lying behind the opening of the little hermaphrodite duct. This region is traversed by the eggs alone, and the successive layers of the egg capsule, and probably some part of the mucus of the egg mass, are evidently secreted here. The path of the egg through the mucus gland in relation to the lining fold is not quite clear, though it may be assumed that the eggs pass from the little hermaphrodite duct along one of the lateral grooves to the blind tip of the diverticulum, and return along the opposite groove which is so placed as to lead directly into the female portion of the pallial genital tract. Muscular movement as well as ciliary action evidently plays an important part in the passage of the eggs through the posterior mucus gland. From the opening of the little hermaphrodite duct, the sperm are able to by-pass the diverticulum formed by the mucus gland and to pass directly across the dividing fold into the prostatic side of the common duct (*pr.g.*). Sections of this duct in animals fixed in June, when sperm was passing forward from the vesicula seminalis, revealed large accumulations of sperm near the summit of the dividing fold and along the

posterior part of the prostatic channel. Sperms were never found in the mucus-secreting parts of the genital tract.

At the posterior end of the mantle cavity, the glandular hermaphrodite duct leaves the haemocoele and turns sharply forward. Its dividing ridge dwindles and disappears and the duct, as it runs along the pallial floor, develops a tract of the much more opaque secretory epithelium which forms the prostate. This tract is at first horseshoe-shaped in section and is clearly distinguishable in life from the more translucent mucus cells. It arises posteriorly as a narrow wedge of cells reaching into the anteriormost part of the U-shaped posterior mucus gland. The rest of the wall of the pallial genital duct is lined with mucus cells, and constitutes the anterior mucus gland.

The prostatic epithelium (figure 20a) is somewhat like that of *Leucophytia*, where, however, this gland is separated from the female duct as a distinct tube. In *Ovatella*, the sub-
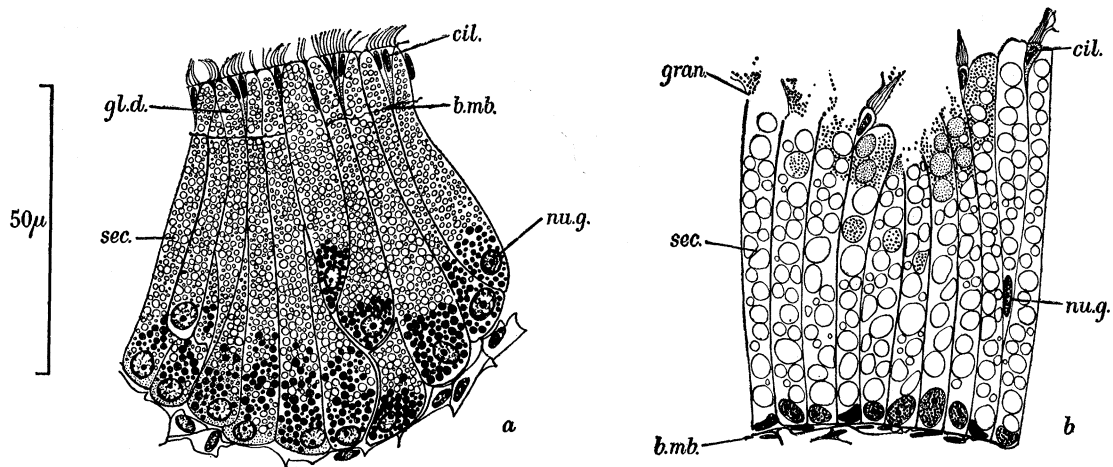

FIGURE 20. *Ovatella myosotis*. Epithelium of the prostate (a) and of the albumen gland (b). b.mb., basement membrane; cil., ciliated cell; gl.d., duct of gland cell of prostate; gran., finer secretory granules liberated from the prostate; nu.g., nucleus of a gland cell; sec., droplets of secretion.

epithelial gland cells are tall, columnar or cigar-shaped, their bases projecting in clusters through the surrounding connective tissue. The nuclei are large, rounded and basal. The cytoplasm is crowded with small spherules that stain for the most part light blue in azan, lightly pink in haemalum, and remain colourless in mucus-detecting stains. They are more densely clustered towards the base of the cell, where the residual cytoplasm stains bright pink with azan. The overlying ciliated epithelium is separated from the glands by a strong basement membrane of connective tissue, through which the stout ducts of the glands penetrate between the columnar cells. The latter are small, with compressed rod-shaped nuclei. They are clustered together in short triangular wedges, of some five or six cells.

The anterior mucus gland and the prostate terminate just behind the septum which closes the pallial cavity, and the hermaphrodite duct continues forward, just beneath the surface of the body wall, as a narrow tube (figure 19, v.vdf.) without gland cells, which corresponds to the separate vagina and vas deferens of *Leucophytia*. It leads into a muscular genital vestibule (gv.), ciliated throughout, from which the common genital aperture opens

ventrally, hidden beneath the pallial skirt on the right side. A thin lip of the integument overlies the female aperture, and continues towards the head as a narrow fold, enclosing the anterior vas deferens (*a.vd.*), which, from the female aperture forwards, forms a closed duct like that of *Leucophytia*. An open ciliated groove remains, overhung as in *Leucophytia* by the fold of the integument, but the vas deferens itself has sunken below the surface and is surrounded by its own coat of connective tissue and muscle fibres.

The bursa copulatrix (*bc.*) opens directly from the genital vestibule, dorsally to the common duct, and immediately within the female aperture. Its narrow duct is muscular and distensible and the penis is evidently able to enter it directly in copulation. In the haemocoele, the bursal duct expands into a spherical sac, which, as in *Leucophytia*, is clear-walled and contains a dark bolus of disintegrating sperm and prostatic secretion at its centre. Living sperm lie near the periphery.

The penis forms a stout conical papilla, pointed at the tip and attached at its base to the bottom of the preputium. It is circular in transverse section and is built up entirely of circular muscle fibres, arranged concentrically around the vas deferens. This duct enters the base of the penis close to the attachment of the retractor muscle and runs forward through the papilla as the strongly ciliated ejaculatory duct. The preputium into which the penis is withdrawn forms a thin-walled sheath (*prpm.*) opening narrowly by the male aperture upon the right side of the head. Into one side of the preputium projects the vas deferens, enclosed in a strong muscular ridge, which surrounds it from the level of the male aperture, along the preputial wall, as far as the base of the penis. The deeper part of the preputium is expanded to form a thin-walled transparent sac, through which the penis is easily visible externally, bulging upwards against the floor of the pallial cavity immediately behind the head. The lining of the preputium is thrown into close-set circular ridges. Its epithelium, like the external covering of the penis, consists of short, unciliated columnar cells, 5 to 6 μ in height. In contrast with *Leucophytia*, there are no secretory cells.

The egg and embryo

The egg masses of *Ovatella myosotis* were examined from material collected at Littlehampton, Sussex, in May 1954, and the writer is grateful to Dr H. E. Quick for making available an abundance of fixed and living material taken on several occasions. Clusters of from thirty-five to fifty eggs, enclosed in a tough protective investing mass, are attached securely to stones, pieces of grass stems and dead twigs, in the moist environment generally frequented by the adult animals. The egg capsules and their arrangement in the investing mass in a general way resemble those of *Leucophytia bidentata*, as described above, but there are many differences in detail. First, the capsules themselves lie in close contact, oriented side-by-side in approximately the same direction, and there is relatively little intervening substance between them. This extracapsular material is colourless and for the most part extremely fluid, while over the whole surface of the egg mass lies a much tougher binding membrane, by which the mass is fastened to the substratum, and which can only with difficulty be teased away with needles. The eggs near the surface of the cluster tend to bulge prominently against the investing layer and the surface is thus ornamented with tiny rounded prominences marking the positions of individual capsules.

The egg yolk is pure white, the investing membranes and the albuminous contents of the capsule, as well as the embedding substance, quite transparent. The whole cluster somewhat resembles a miniature mass of frog-spawn.

Each egg capsule is ovoid in shape, approximately twice as long as wide, and its two ends are easily distinguishable, one being narrower and bluntly pointed, the other broader and gently rounded. The capsular wall is very massive, and difficult to rupture; it is perfectly transparent, and on critical illumination may be seen—like that of *Leucophytia*—to be built up of a large number of fine, concentric laminae. The fluid-filled albumen space has one end sharper than the other, produced into a tiny dome-shaped mamilla.
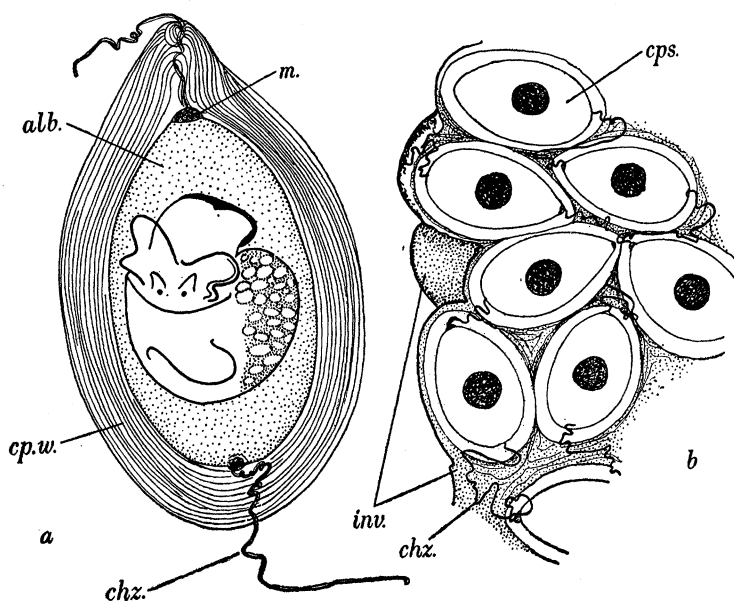

FIGURE 21. *Ovatella myosotis.* (*a*) A single egg capsule, containing an embryo with shell and velum, removed from an egg mass. (*b*) Portion of an egg mass showing a group of eggs at an earlier stage than (*a*) joined together by their chalaziform filaments. *alb.*, albumen enclosed within egg capsule; *cp.w.*, capsule wall; *cps.*, egg capsule; *chz.*, chalaziform filament; *inv.*, investing secretion, surrounding egg capsules in the egg mass; *m.*, dome-like protuberance at insertion of chalaziform filament in the wall of the egg capsule.

From either end of the albumen space proceeds a long filament, irregularly and loosely convoluted, forming a chalaziform process by which each egg capsule is successively attached as part of an egg chain, with the capsule in front of and behind it. The sharp end of one capsule is in this way attached to the blunt end of the next, and a chalaziform filament appears to wind loosely through the investing substance between one capsule and the next, uniting all of the capsules in an egg mass into a single string. At the sharp end of the egg capsule the chalaziform filament continues through the laminated capsular membrane to be secured in the tiny mamilla of the albuminous region, and within this mamilla it is usually seen to be finely convoluted. At the rounded end of the capsule the chalaziform filament runs through the capsular membrane, and is attached directly to the albuminous region, after describing one or two more widely spaced convolutions. The presence of a chalaziform filament in the egg mass of *Ovatella* is the more interesting in that

no trace of it was detected in the material of *Leucophytia* examined; here the egg capsules lie quite separately in the investing substance, with no apparent inter-connexion.

As they issue from the female genital duct the eggs are apparently linked in a continuous string by the chalaziform filament. The capsular substance must be given its final shape by the rotation of the egg during the laying down of the successive layers, and at the pointed end the capsular substance frequently terminates in a blunt 'twist' following the direction of winding of the chalazal filament which runs through it.

A single embryo, within an egg capsule, is illustrated in figure 21*a*, and in most of its features it greatly resembles that of *Leucophytia*. A thin, horny operculum, transversely elongate, covers the upper posterior surface of the foot; and the velum consists of a pair of simple, rounded lobes, dark grey or black pigmented around the margin. By slight muscular movements of the velum, the embryo at this stage moves about within the capsule, but no signs of velar cilia could be identified. The embryonic shell, with its trace of very reduced hyperstrophy, resembles in all respects that of *Leucophytia*.

3. *CARYCHIUM TRIDENTATUM*

Carychium tridentatum in Britain is at present known almost entirely from the characters of the shell. Good conchological descriptions are provided by Jeffreys (1867), Ellis (1926) and the most recent and detailed by Watson & Verdcourt (1953), in which the authors deal at length with the taxonomic separation of the two species *tridentatum* and *minimum*. The present writer (1955*c*) has figured the embryonic and immature shells of *C. tridentatum*. *Carychium* agrees in the shell with the ellobiids in general in the resorption of the apical part of the columella and a large part of the inter partitioning. This trend has not, however, proceeded so far as in *Leucophytia* or *Ovatella*, and a distinct spiral lamella still runs around the line of the suture in the interior of the shell. This lamella cuts a spiral groove around the visceral mass, which otherwise forms a single compact unit, having become axially solid with the disappearance of the columella. The columella muscle, which has now lost its central attachment to the columella, spreads outwards into a wide sheet which is inserted upon the portion of the internal spiral lamella lying within the body whorl. The visceral mass thus tends to become cut off, as a separate unit, from the trunk and pallial region, by the development of a 'diaphragm' formed by the internal lamella and the spread of the columellar muscle.

The animal of *Carychium* is of delicate appearance, its exposed parts translucent and frosted white, flushed with pink where the buccal mass is visible through the body wall of the head. The body may be clearly seen by transparency through the fragile shell. The digestive gland, at the apex of the visceral mass, is yellowish brown, and the stomach and intestine deep brown when filled with food or faeces. The foot is long and narrow, tapering to a sharp point behind. It is broader in front with a rounded anterior lobe, thicker than the rest of the foot, but never marked off by a well-defined furrow as in *Leucophytia*. A supra-pedal gland opens below the mouth as in other ellobiids, and there is a pair of rounded oral lappets like those of *Leucophytia*. The tentacles are short and blunt-tipped, diverging in the living animal at right angles from near the mid-line of the head. The bases are rather expanded and bulbous, and bear the eyes at their inner sides.

The pallial organs are relatively simple in arrangement. There appear to be no respiratory blood vessels on the pallial roof, and it seems likely that respiration takes place chiefly in the dilated marginal sinus, which runs round the edge of the free pallial skirt. The kidney is a tubular sac of the simplest structure, its lining wall unfolded. It opens by a small pore just behind the pneumostome. Along the right side of the mantle cavity, just mesially to the rectum, runs a hypobranchial gland. Farther towards the mid-line a second
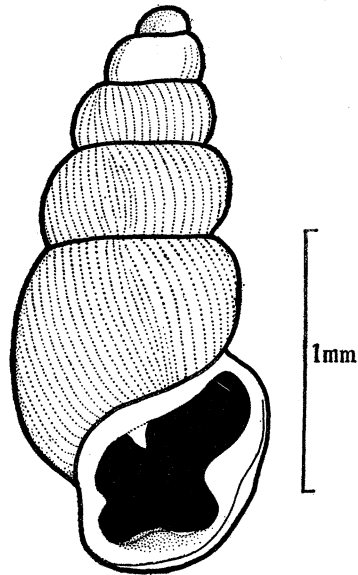
FIGURE 22. *Carychium tridentatum.* Shell.
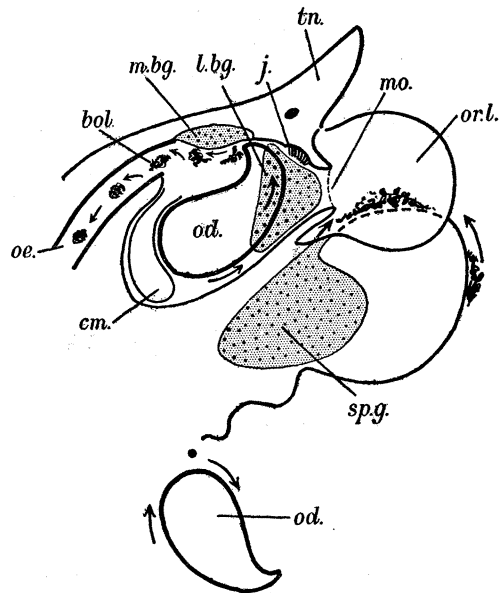
FIGURE 23. *Carychium tridentatum.* Schematic longitudinal section through the head, buccal mass and foot to show the relations of the foot, oral lappets and odontophore during feeding. (Below) odontophore in protruded position. *bol.*, food boluses; *cm.*, radular caecum; *l.bg.*, lateral buccal gland; *j.*, jaw; *mo.*, mouth; *m.bg.*, median buccal gland; *od.*, odontophore; *oe.*, oesophagus; *or.l.*, oral lappet; *sp.g.*, suprapedal gland; *tn.*, tentacle.

glandular structure runs along the pallial roof. It forms a narrow, muscular tube, about as wide as the rectum (60μ), bulging strongly into the mantle cavity and covered ventrally by an expansion of the epithelium of the hypobranchial gland. It opens outside the mantle cavity, being somewhat expanded at the anterior end, and discharging its secretion beneath the free pallial skirt.

The histology of the pallial gland is illustrated in figure 24a. The lumen is surrounded by no more than twelve to fifteen gland cells, 15μ in height. These cells are of two apparent types, both probably stages in the growth of a single kind of gland. They are usually stout and squarish, with a flat or rounded free surface. The first type (gl.c. 1) are sometimes compressed by the enlargement of cells of the second type, which alternate with them. They stain uniformly deep purple with haemalum and deep blue with azan. The second type
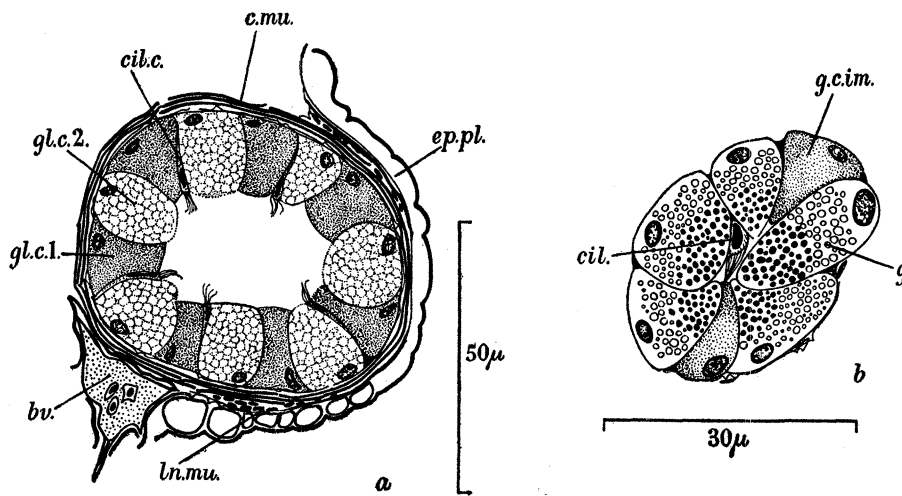

FIGURE 24. Carychium tridentatum. (a) Transverse section of the pallial mucus gland. cil.c., ciliary cell; bv., blood vessel; c.mu., circular muscle layer; ep.pl., pallial lining epithelium; gl.c. 1, gl.c. 2, first and second types of gland cell; ln.mu., longitudinal muscle layer. (b) Transverse section of a salivary gland. cil., ciliated cell; g., glandular cell; g.c.im., immature glandular cell.

(gl.c. 2) are lighter blue or colourless with azan, with a dense cytoplasmic reticulum; they appear to be a more mature stage, and they alone discharge secretion into the lumen. The nuclei of the gland cells are flattened, basal or parietal. Cilia are borne only in isolated tufts on occasional compressed, rod-like cells, wedged in near the free surface of the epithelium. There is a strong circular muscle coat, rather unevenly developed and in places constricting the lumen by a series of annular ridges. Outside the circular muscle run bundles of longitudinal fibres, and between the two layers of muscle, small blood vessels are frequently enclosed.

The function of the pallial gland in Carychium has not been determined. It appears to have no counterpart in the marine ellobiids, although a corresponding structure has been described by Plate (1897), and figured by Morton (1955 b) in the mantle of the terrestrial ellobiid Pythia scarabaeus. Here the gland is longer and has the form of a narrow U, with the side limbs evidently thick-walled and secretory and the connecting narrower isthmus. It takes its shape by the reflexion forwards of the blind posterior end—present in Carychium

—to lie alongside the anterior limb as far forward as the edge of the mantle. It is likely that the development of a pallial gland in both *Pythia* and *Carychium* is to be looked upon as an example of parallel adaptation, probably to some condition of terrestrial life. Plate suggested that the gland might have some connexion with reproduction, as an additional source of protective secretion for the eggs. In *Carychium*, however, it appears to contribute nothing to the covering of the egg, and shows secretory activity not only during oviposition but at all times of the year. A further suggestion is that it may secrete a mucoid substance conferring protection against desiccation when the animal is withdrawn into its shell. This would seem the less likely in view of the known inability of *Carychium* to tolerate dry places, or to live for long in atmospheres not saturated with water vapour. Finally, such a gland might produce a secretion with properties obnoxious to predators or bacteria that might attack the soft parts of the snail by way of the unguarded aperture of the shell.

DIGESTIVE SYSTEM

Carychium like *Leucophytia* and *Ovatella* is a rather unselective feeder, ingesting particles of plant origin scraped with the radula from the substratum. The stomach contents consist of a closely compacted mass of plant material picked up from the surface of leaves and decaying wood. Fragments of leaves, pteridophyte hairs and sporangia, fungal mycelia and particles of soil figure prominently. Before ingestion the food is bound into small mucous boluses, and as in *Leucophytia* the supra-pedal gland probably plays its chief role in supplying mucus for the compacting of the food. The sources of mucous secretion within the gut, which are restricted to the small salivary gland and to the lateral and median buccal glands, probably provide no more than a lubrication for the passage of food boluses along the oesophagus. When the animal is stationary, the anterior margin of the foot is able to be withdrawn from the substratum and rolled upwards to form a rounded cushion lying in front of the mouth. This comes into contact with under-surfaces of the oral lappets which overhang the mouth below the bases of the tentacles, in much the same fashion as in *Leucophytia*. Ciliary currents pass round the edge of the foot, and a sheet of secreted mucus with entrapped particles picked up from the substratum is carried to the uppermost portion of the anterior lobes and lodged beneath the lappets. This secretion is regularly wiped on to the lappets, and added to by mucus extruded from the supra-pedal gland which opens just beneath the mouth, behind the anterior margin of the foot. Although the animal often picks up particles directly from the substratum by the plucking action of the radular teeth, ingested food appears often to be collected from the front of the foot and carried forward in the manner described by ciliary currents to the mouth. The animal frequently ingests portions of its faecal string which may be extruded from the anus on to the foot. It is probable, especially when the gut is filled with food, that a good deal of material passes from the anus while still retaining some nutritive value. *Lymnaea adpressa* has been observed (Carriker 1946) to practise ingestion of its faeces in the same way, and this habit may prove to be not uncommon among snails with a generalized diet of particles of plant detritus.

The action of the odontophore and radula within the buccal bulb can easily be observed in the intact animal by examination through the translucent body wall (figure 25). The

buccal mass agrees in all essential features with that of *Leucophytia* and *Ovatella*; indeed, few variations in this region of the gut seem likely to be met with among the ellobiids. The odontophore (*od.*) is small and comma-shaped, attached at its broad base to the floor of the buccal cavity, and with the radular ribbon curved as a broad sheet around its upper surface. The odontophore is supported by a cartilage of much the same shape as in *Leucophytia*, and between the cellular elements of the odontophoral cartilage extend large transverse and oblique muscle fibres, so that a good deal of intrinsic muscular movement is possible. The free end of the odontophore is slightly upcurved to form a small scoop as the organ rotates upon its attached base. The odontophore is moved very actively and describes periodic darting movements; the tip is pointed down and thrust out of the mouth, between the side walls of the buccal cavity, which are covered with a thin soft cuticle. The teeth project backwards and their fine cusps rake in mucus-bound food in minute boluses. The extruded odontophore is immediately rotated backwards so that the recurved tip is drawn upward towards the roof of the buccal cavity. The collected food material is thrust back into the oesophageal food tract and is carried along the roof of the buccal cavity by the aid of aborally beating cilia. The odontophore has also some power of lateral movement; in rotating forward it is often thrust to one side or other of the buccal cavity as if to collect mucus expressed from the two lateral buccal glands. These glands form clusters of subepithelial mucous cells, staining pink in mucicarmine, light blue in azan, and prolonged into narrow ducts which penetrate the lining cuticle of the buccal cavity. Along the roof of the buccal bulb runs a third strip of glandular tissue, the median buccal gland, dipping downward towards the radula in the mid-line, so that a further supply of mucus is provided as the food travels into the oesophagus. A succession of tiny mucous boluses is thus carried rapidly into the oesophagus, and rolled backwards by the ciliary beat towards the stomach.

The median jaw (*j.*) is represented by a thickening of cuticle, staining blue in azan, and lying across the dorsal wall of the buccal cavity. Minute yellow-staining rods of cuticle are embedded in its substance. In normal food collecting, the jaw appears to play little part; its chief function may be to assist the action of the radula when this is scraped against the substratum, providing a hard surface against which the radular teeth work on upward thrust. Watson & Verdcourt (1953) have clearly figured the radular teeth for both *Carychium minimum* and *C. tridentatum*, and there is good agreement with Odhner's drawing (1924) of the dentition of *minimum* (in the wide sense). The teeth are excessively small; the width of the radular sac itself is only 20 to 25μ and of the central and lateral teeth not much more than 3μ. Specific differences in the dentition are almost impossible to detect from the published figures, and when allowance is made for the changes in proportion which must be brought about by even the slightest differences in the attitude of the mounted teeth, the taxonomic value of the radula in *Carychium* is seen to be of a subtle order indeed. Specific distinction must surely rest upon conchological characters, and on the reported ecological separation of the two British forms.

At the origin of the oesophagus a simple pair of tubular salivary glands (figure 24*a*) open into the buccal mass. A single transverse section of a salivary gland shows some six to nine rounded or triangular cells, surrounding a narrow lumen, and with wedge-shaped ciliated cells interspersed. The secretion consists of small spherules filling the cell and depressing

the rounded nucleus to the base; these spherules stain blue in azan, light pink in haemalum. Occasional cells with denser cytoplasm and containing no recognizable spherules, probably represent developmental stages of secreting cells.

The oesophagus in *Carychium* is of exceedingly simple structure. It is a narrow tube of uniform diameter (50μ) passing directly back to the posterior end of the stomach. No crop is differentiated in its posterior part as in the larger-sized ellobiids *Leucophytia* and *Ovatella*, and the food is carried rapidly to the stomach.
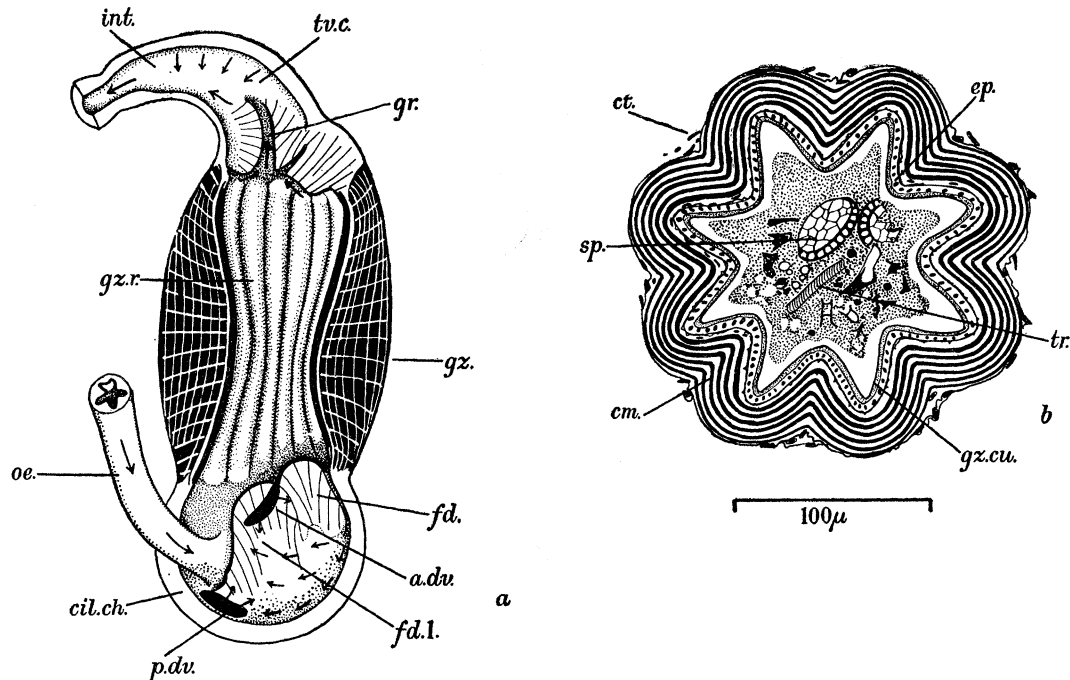

FIGURE 25. *Carychium tridentatum*. The stomach, viewed in longitudinal section as a transparent object (*a*) and in transverse section through the gizzard region (*b*). *a.dv.*, anterior digestive diverticulum; *cil.ch.*, posterior ciliated chamber; *cm.*, circular muscle zone; *ct.*, connective tissue; *ep.*, lining epithelium of the stomach; *fd.*, *fd.* 1, folds within posterior ciliated chamber; *gr.*, intestinal groove; *gz.*, muscular layer of the gizzard wall; *gz.r.*, longitudinal ridges of the gizzard lining; *gz.cu.*, lining cuticle of the gizzard; *int.*, intestine; *oe.*, oesophagus; *p.dv.*, posterior digestive diverticulum; *tv.c.*, area of transverse ciliary beat in the first part of the intestine; *sp.*, fern sporangium among food contents of the stomach; *tr.*, portion of decayed woody tissues among food contents of the stomach.

The stomach

The stomach (figure 25) forms a small elongate sac, 0·5 to 0·75 mm in length. It is built up of a muscular barrel-shaped gizzard (*gz.*), giving rise to the intestine at its anterior end, and a thinner-walled spherical chamber (*cil.ch.*) which receives the oesophagus together with a pair of digestive diverticula at the posterior end. The anterior diverticulum (*a.dv*) is the smaller of the two, and breaks up into a cluster of tubules upon the right side of the visceral mass. The posterior diverticulum (*p.dv.*) arises close alongside the anterior and widens to give rise to digestive tubules lying to the left of the stomach, and forming the whole of that part of the digestive gland lying in the whorls behind the stomach. The structural plan of the stomach in *Carychium* is upon first examination somewhat unlike that of *Leucophytia* or

Ovatella. The oesophagus, with the anterior digestive diverticulum opening—as in the previous genera—very close to it, enter the stomach at the intestinal end, but is separated from the intestinal aperture by the whole length of the gizzard. The two digestive diverticula thus open close together; and the anterior one is not removed from the main portion of the stomach into an oesophageal atrium as in *Leucophytia*, but opens directly into the posterior chamber beside the aperture of the posterior diverticulum. In the vicinity of the opening of the oesophagus, the spherical posterior chamber of the stomach is lined with low-celled columnar epithelium. The lining epithelium of the gizzard is of cubical cells, secreting a thin cuticle. When the stomach is contracted the wall of the gizzard is thrown into ten or twelve strong triangular folds and the circular muscle fibres take on a wavy contour. In the posterior chamber of the stomach the muscular zone is much narrower. There is in *Carychium* no trace of ciliated grooves leading from the diverticula. Phagocytes are never apparent in the wall of the stomach and the epithelium has no gland cells.

The mode of action of the stomach is very straightforward, and muscular contractions play the predominant part. The wall of the posterior chamber, when distended with food, is capable of strong contractions, and, in addition to being rotated, the food mass is gradually compressed and forced forward into the gizzard. Here the regular contractions of the muscular wall thoroughly knead and triturate the food mass. Many of the particles are finely broken up, probably in part by free enzymes which flow into the stomach from the digestive gland. Larger particles may, however, pass forward unbroken into the intestine. The contents of the whole stomach soon become compressed into a stout, drumstick-shaped rod, the rounded end filling the posterior chamber. Semi-fluid mucus, containing in suspension the finest particles, sufficiently divided to be able to pass into the digestive cells, is in this region squeezed out of the food mass. The digestive diverticula themselves appear to have little power of peristalsis. They are entirely glandular, and their contents are introduced chiefly by the muscular action of the stomach, which forces fluid material into the openings of the diverticula. The oesophagus is meanwhile kept closed against the backflow of stomach contents by the contraction of its circular muscle fibres.

Digestive gland

The digestive gland in *Carychium* agrees in its essential structure with that of *Leucophytia*. Its tubules are rounded in section, and average 100μ in diameter. The height of the lining epithelium varies greatly at the ingesting and the excreting phases. At ingestion, the lumen is widely distended, becoming afterwards rounded and narrow. The most numerous cells are the columnar digestive cells, which are shown at the ingesting stage (figure 26, lower right). The superficial fourth of each is filled with droplets of absorbed material (*abs.*) taken up from the lumen, in an extremely finely divided form. Along the free surface of the cell runs a narrow striated border (*str.*); longer vertical striations or canaliculi are obscured at this stage by the filling of the cytoplasm with absorbed material. They appear more clearly at the later stage of excretion. At a somewhat deeper level, the food droplets increase in size and flow together. The middle portion of the cytoplasm is occupied chiefly by large rounded masses of ingested material, clumped together and sur-

rounded by clear vacuoles (*abs.v.*). They stain blue in azan and green in Masson's stain. Towards the base of the cell lie a series of large, clear-staining vacuoles (*b.vc.*), three or four in each cell, resembling the basal vacuoles in *Otina* and *Leucophytia*. These were never observed to contain blue-staining absorbed material.

At the phase of the digestive gland illustrated in figure 26 (upper), blue-staining absorbed material is much more scarce. In the superficial layer of the digestive cells the
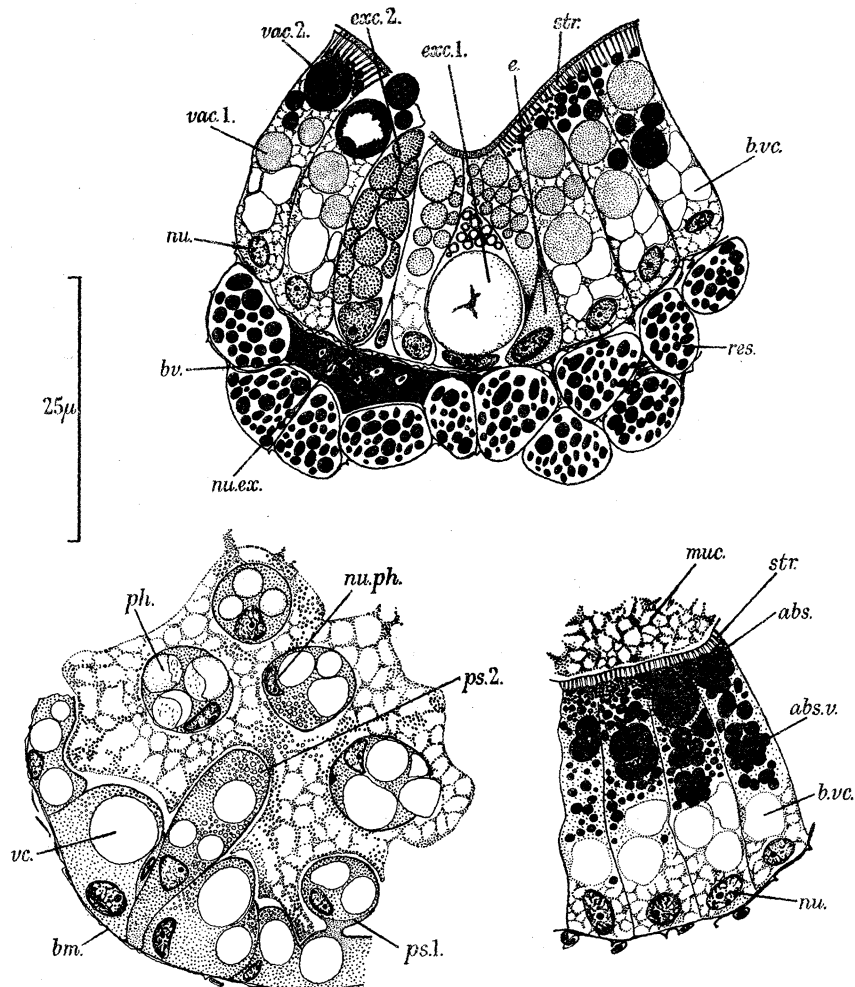

FIGURE 26. *Carychium tridentatum*. The histology of the digestive gland, showing (above) portion of the epithelium of a tubule, with the underlying connective tissue, at the stage of excretion; (below, right) four cells of the epithelium at its absorbing phase; and (below, left) portion of the wall of a tubule during the formation of 'fragmentation phagocytes', together with a group of phagocytes within the lumen. *abs.*, droplets of absorbed material immediately beneath the free surface of a digestive cell; *abs.v.*, vacuole of absorbed material (staining blue in azan); *bm.*, basement membrane; *bv.*, blood vessel; *b.vc.*, basal vacuole of digestive cell; *e.*, young excretory cell; *exc.* 1, *exc.* 2, two types of excretory cell; *muc.*, finely divided material, suspended in mucus, in the lumen, during absorptive phase; *nu.*, nucleus of digestive cell; *nu.ex.*, nucleus of an excretory cell; *nu.ph.*, nucleus of a phagocyte; *ph.*, 'fragmentation phagocyte' set free in lumen; *ps.* 1, *ps.* 2, two stages in the formation of a 'fragmentation phagocyte' as a pseudopodial outgrowth of the epithelial layer; *res.*, reserve material in connective tissue, staining red in azan; *str.*, striated free border of digestive cells; *vac.* 1, *vac.* 2, *vc*, vacuoles within the digestive cell staining reddish brown and blue, respectively, in azan.

row of fine canaliculi is now visible, with a layer of minute blue droplets lying immediately beneath it. A few large, blue-staining vacuoles (*abs.v.*) are present deeper in the cells. The majority of vacuoles stain now, however, uniformly reddish brown in azan, and fill the distal half of the cell (*vac.* 1), below which the colourless basal vacuoles are still present. Occasionally red-brown vacuoles, as well as larger blue ones, are seen to pass into the lumen by the rupture of the free border of the cell. This process evidently represents the return to the stomach of indigestible and excretory material remaining after digestion of the contents of the food vacuoles.

The excretory cells are distinguished by their larger nuclei (*nu.ex.*), and lie in groups in which the central cell is most commonly broad-based and triangular. This cell generally contains a colourless or brown vacuole (*exc.* 1) of very large size, and may in addition be crowded distally with small spherules staining blue in azan. Larger blue spherules often fill the cytoplasm of two or three excretory cells of columnar or fusiform type (*exc.* 2). Whether this blue material has been previously absorbed from the lumen is not clear; it is often replaced in the same position by brown spherules of the same diameter, and in both types of spherules are destined to be returned to the lumen by the rupture of the narrow tips of the cells.

The distal parts of the digestive cells in *Carychium* were not observed to become constricted off into the lumen of the tubule as in *Otina* and in *Leucophytia* (p. 105). Both the blue and the brown spherules are liberated separately by the rupture of the surface of the cell. A prominent feature of the digestive gland of *Carychium*, is, however, the budding off from the digestive cells of 'fragmentation phagocytes' of the kind found also in *Otina* and in the nudibranch *Jorunna* (Millot 1937). At the stage of fragmentation (figure 26, lower left), the lumen of both the digestive gland and of the stomach was filled with semi-fluid mucoid material. The contents of the upper parts of the cells, forming bluish or brown food vacuoles, had already been extruded, and the bases of the cells alone remained. The nuclei were retained here, together with a single row of basal colourless vacuoles. These vacuoles showed a refractile surface layer, in most cases split and retracted after fixation. In a number of cells the cytoplasm was observed to project into the lumen in the form of a blunt pseudopodium, which became narrowly constricted from the body of the cell. In more advanced stages three or four colourless vacuoles flowed into this distal portion of the cell. Several of these 'pseudopodial' lobes had already come from the cells, and the lumen of the stomach contained spherical 'phagocytes' (10 to 20μ across) (*ph.*), suspended in mucoid material. The vacuoles within the phagocytes remained colourless, but the rest of the cytoplasm appeared to contain granular material absorbed from the lumen. The colourless vacuoles themselves may contain enzymes that will later be freed within the stomach, though many of these vacuoles probably pass intact into the faeces, as was at times actually observed in *Ovatella*.

These detached nucleated fragments of the digestive cells precisely resemble the 'fragmentation phagocytes' described by the present writer (1955 *a*) in *Otina* and previously observed by Millott (1937) in *Jorunna*, and by Forrest (1951) in a number of nudibranchs. They were shown to possess a digestive action in opisthobranchs, and in the pulmonates also they probably have the same function with the combined role of liberating enzymes in the stomach and of absorbing finely divided particles for intracellular digestion.

The digestive gland in *Carychium*, like the rest of the organs of the visceral spire, is embedded in a loose meshwork of connective tissue that evidently subserves a storage function. The connective tissue forms rounded or hexagonal spaces which are packed tightly with small, rounded or ovoid spherules (*res.*). These measure 1 to 2μ across and stain bright red with azan, and lightly or not at all with Masson's stain or haemalum. They are evidently protein in nature, and may best be compared with the protein granules found by Fretter (1937) in the connective tissue surrounding the blood vessels of chitons.

The intestine, as it leaves the stomach, develops two or three tall ciliated folds, which may be brought together by the contractions of circular muscle fibres to form a sphincter. Periodically a plug of compacted faeces is released into the intestine by the opening of its exit from the stomach; farther backwards in the intestine this material becomes continuous with the posterior end of the loose faecal string. Immediately behind the stomach, the intestine shows an interesting feature in the arrangement of its ciliary currents. In addition to a well-marked longitudinal current along one side of the lumen, there is a field of transversely beating cilia covering the rest of the intestinal wall. Though the action of these cilia is weak as compared with the action of the muscle coat, it evidently plays some part in rotating the faecal plugs into a more compact rod. *Carychium*, like *Ovatella*, thus preserves in the first part of the intestine a relic of the primitive 'style sac' of the prosobranchs, though the cilia in this region never bring about the rotation of a protostyle or rod of faeces within the stomach itself.

Nearer the anus the intestine narrows to a uniform diameter of 50μ. Its cilia beat strongly aborally. The rope of faeces is carried back by short, strong peristaltic waves combined with more continuous ciliary action. The epithelium is equipped with mucus cells while towards the anus the ciliation becomes especially strong and the epithelial cells shorter and the gland cells fewer.

REPRODUCTIVE SYSTEM

Moquin-Tandon's short account (1856) has remained the only published description of the genital system of *Carychium*. He demonstrated that the sexes are united as in the rest of the Pulmonata, contrary to some of the older statements, and the chief glands of the genital tract are fairly accurately figured in outline, but without exact demarcation of the limits of the shell gland and albumen gland. The breeding habits, the nature of the egg and the sexual cycle have been recently discussed in a short paper by the present writer (1955c). In general, *Carychium* corresponds fairly closely to other ellobiids in the structure of the reproductive system, but there are certain features, such as in the glands secreting the projective layers of the egg, in which it differs from the maritime genera. The eggs are relatively much larger, and few in number, enclosed singly in tough leathery capsules after the manner of the Stylommatophora.

The ovotestis (figure 27, *ovt.*) retains its primitive position, buried beneath the tubules of the digestive gland in the second whorl of the visceral mass; it never acquires an apical position as in *Leucophytia*. From July to September, the ovotestis produces sperm, and its cavity is broken up by trabeculae of connective tissue into several rounded follicles. For the rest of the year it is filled almost wholly with developing oocytes, its partitions breaking down to leave a single spacious pouch, light yellow in colour in contrast with the brown digestive gland.

The little hermaphrodite duct (*lhd.*) is a tiny transparent tube 20 to 30μ across. It is straight or only slightly convoluted, and passes forwards in the visceral mass deep to the shell gland and the digestive lobules, running closely alongside the oesophagus. A transverse section shows eight or nine cubical or triangular cells, clear-staining, surrounding a circular lumen. The epithelium bears a dense coat of cilia, which beat rapidly forward. The wall of the duct is not muscular and becomes temporarily much distended by the
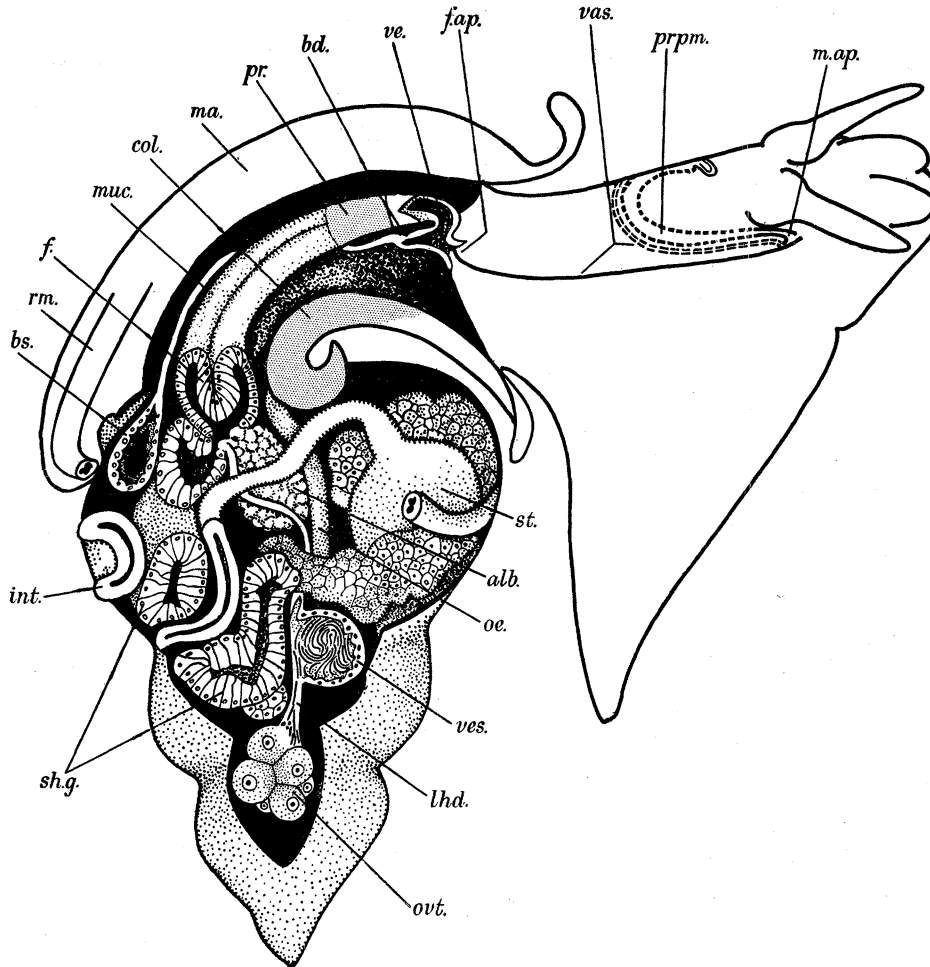

FIGURE 27. *Carychium tridentatum*. Stereogram showing the structure and arrangement of the genital system, viewed within the outline of the complete animal, and with relation to the position of the stomach and intestine. The pallial cavity is represented as being opened along the right side to show the mucus gland; the course of the bursal duct is shown as by transparency; and the visceral mass is incised by a tangential longitudinal section, which has passed at several points through the wall of the genital tract to show its internal structure. The anterior vas deferens and the preputium are not in fact present at the (female) stage of the gonad shown in the figure. Their position is however indicated by dotted lines. *alb.*, albumen gland; *bd.*, opening of the bursal duct into the genital vestibule; *bs.*, bursa copulatrix; *col.*, columellar muscle; *f.*, fold of epithelium within the mucus gland; *f.ap.*, female genital aperture; *int.*, intestine; *lhd.*, little hermaphrodite duct; *ma.*, mantle; *m.ap.*, male genital aperture; *muc.*, mucus gland; *oe.*, oesophagus; *ovt.*, ovotestis or hermaphrodite gland; *pr.*, prostate; *prpm.*, preputium; *rm.*, rectum; *sh.g.*, shell gland; *st.*, stomach; *vas.*, vas deferens; *ve.*, genital vestibule; *ves.*, dilated part of the little hermaphrodite duct, serving as a vesicula seminalis.

passage of egg cells. Storage of sperm occurs during most of the year in a single seminal vesicle (*ves.*), which is formed as a spherical pocket in the wall of one side of the little hermaphrodite duct, half-way along its course. The epithelium of the vesicle resembles that of the duct itself, and the sperm are not oriented upon it but lie massed together in bundles with their tails curved around the periphery of the vesicle. Occasional sperm heads appear to find their way into the distal cytoplasm, but extensive resorption of sperm was never observed.

The little hermaphrodite duct opens in front into the glandular hermaphrodite duct, which remains undivided and is traversed in common by both male and female sexual products as far as the female aperture. By far the greater of this duct consists in *Carychium* of a cylindrical mucus gland (*muc.*). This tube extends deeply into the haemocoele behind, and tapers slightly as it passes forwards along the right side of the pallial cavity, medioventrally to the rectum. In this ellobiid, much the largest of the accessory glands is the shell gland (*sh.g.*); this forms a thick, lobulated strap, encircling the visceral mass and opening into the posterior end of the mucus gland, closely alongside the openings of the little hermaphrodite duct and the albumen gland.

The rounded posterior end of the mucus gland, into which the albumen and the shell substance are secreted, is lined with long cilia. It is the equivalent of the fertilization pouch in other ellobiids, but it is not, as in *Ovatella* and *Leucophytia*, marked off as a separate sac. It consists merely of an enlargement of the mucus gland, where the egg cells are presumably fertilized and receive their albumen coat and their first layer of protective secretion. The material of the leathery 'shell' appears to be carried some distance forward within the mucus gland, and to become applied in a uniform sheet to the egg as it is rotated by cilia, and pressed forward within the duct by slight muscular contractions.

The albumen gland (*alb.*) is relatively small in *Carychium* and situated rather far forward. It is not easy to find in dissections, lying close against the rounded posterior end of the mucus gland. It consists of two lobules, closely fused at the base, but generally opening separately into the fertilization pouch. Each lobule contains a narrow fissure, lined with sparse, carrying a sheet of albumen into the lumen of the mucus gland. The secreting cells are tall and columnar with rounded basal nuclei, staining deep red in azan. The droplets of secretion are packed into the upper two-thirds of the cell, and stain bluish in azan. Towards the middle of the cell they may be pinkish or colourless, while at the base of the cell, towards the nucleus, the cytoplasm is without obvious inclusions and stains uniformly pinkish brown. These cells stain hardly at all with haematoxylin or mucus stains. Their free surfaces bulge into the lumen so that the wedge-shaped ciliated cells are almost displaced from the edge of the epithelium. The more anterior lobe of the albumen gland sometimes sends forward a tract of albumen-secreting tissue some distance along the wall of the mucus gland. Secretion is then discharged directly into the mucus gland.

The shell gland (figure 27, *sh.g.*) forms a long, thick-walled diverticulum of the genital tract. It has the form of a broad flattened tube, 100μ in width, and when fully developed it occupies, together with the stomach, the whole of the last whorl of the visceral mass. Extending backwards from the mucus gland on the left side of the animal, it passes beneath

a loop of the intestine, and then turns transversely across the visceral mass, overlying and concealing the seminal vesicle and the posterior end of the stomach. Its distal end reaches forward and passes across the superficial aspect of the stomach, ending in an irregular strap which breaks up into lobules around the origin of the intestine. In the living animal the shell gland is transparent and jelly-like; its outline is irregular and its cavity is increased by distension into small round saccules. The lumen is elsewhere narrow and slit-like. The epithelium is composed of tall columnar cells of a uniform height of 40μ and 6 to 8μ wide. The droplets of secretion stain bright blue with azan, green with Masson's stain and their colour with haemalum varies from light pink in the younger cells to densely blue or black when the secretion is ready to be discharged. The secretion remains in separate droplets in the cytoplasm, which are packed closely together so that their spherical shape is sometimes distorted. Occasionally two or more droplets are surrounded by a clear-staining vacuole, within which they may be discharged together from the cell. The cell walls are very distinct, sometimes wavy in outline, and the basal nuclei very large (7μ). Ciliary cells are rather few in number, squeezed narrowly between two gland cells, or small and triangular, inserted between the tips of the gland cells. The cilia are short, and form isolated tufts, playing little part in the transport of secretion.

As the mucus gland passes along the pallial cavity, it takes on a superficial position, lying just beneath the thin body wall, curving around the right side of the trunk with the columellar muscle below (figure 27, *muc.*). It forms a stout tube, smooth-walled and trans-lucent. Along its convex curve runs a narrow fissure which underlies a thick fold of epithelium, triangular or semicircular in section, occupying most of the lumen. The secreting cells of the mucus gland are cigar-shaped, and very long, tending to become clavate and narrow-based upon the fold. Their cytoplasm is finely reticulate, non-staining or light yellow in azan and sometimes faintly granular. It remains pale with haema-toxylin, but shows a strong affinity for mucicarmine and thionin. At their free surfaces the gland cells bulge strongly into the lumen. Ciliated cells alternate regularly with them, and are extremely long and narrow, widening slightly at their distal ends which bear tufts of long cilia. Along the summit of the lining fold the cilia beat upwards out of the lateral grooves towards the centre of the duct. Movement of the contents of the mucus gland is evidently brought about chiefly by cilia, while in addition the wall possesses a slight power of muscular contraction.

The prostate (figure 27, *pr.*) is represented in *Carychium* by the narrower anterior fourth of the glandular hermaphrodite duct, which is formed by the tapered continuation of the mucus gland towards the anterior end of the pallial cavity. The lumen now becomes cylindrical or slit-shaped, the longitudinal fold is lost and the character of the secretion changes. The cytoplasm is filled with separate and minute granules staining deep red or orange brown in azan. They are freely dispersed into the lumen by the rupture of the tips of the cells. The cytoplasm appears light blue after haematoxylin, and unlike those of the mucus gland, the prostatic cells have no staining reaction with thionin or mucicarmine. The mucus gland continues forward towards the female aperture merely as a narrow strip of translucent epithelium, interrupting the opaque wall of the prostate along the ventral side. The reduction in the extent of mucus-secreting tissue in the distal part of the genital duct must be correlated with the lack of a common investment of jelly round the eggs. The

capsules are deposited separately, and the mucus secretion of the genital tract forms merely a thin pellicle around the tough envelope from the shell gland.

In front of the prostate, the common genital duct becomes narrow and rounded, 40 to 50μ in diameter, and loses its gland cells. It is surrounded by a stout coat of circular muscle and lined throughout with long cilia. The duct runs forward through the lateral wall of a wider, conical genital vestibule (figure 27, ve.), which opens directly by the female aperture just beneath the free pallial skirt. The vestibule has strong muscular walls, and its cilia beat outwards, probably assisting the muscular action of the common duct during the laying of eggs. From the apex of the vestibule, a bursa copulatrix continues
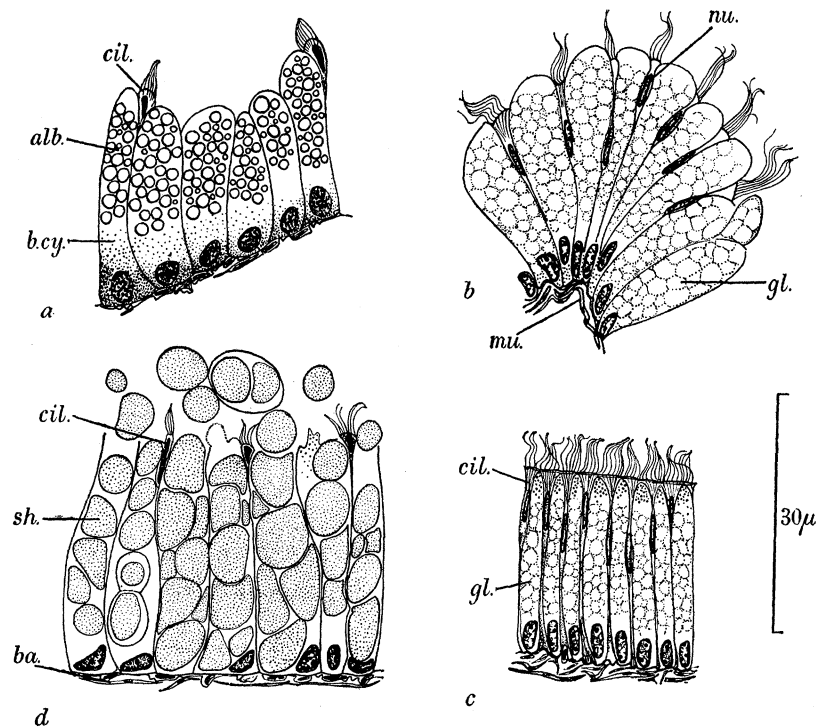

FIGURE 28. *Carychium tridentatum.* Epithelium of the albumen gland (a), the mucus gland (b), the prostate (c), the shell gland (d). alb., granules of albumen cell; ba., basement membrane; b.cy., basal cytoplasm; cil., ciliated cell; gl., gland cell; mu., muscle; nu., nucleus of ciliated cell; sh., secretory material of shell gland.

backwards expanding in the haemocoele into a tiny ovoid sac, lying closely against the shell gland near its junction with the mucus gland. The lining epithelium of the bursa is of small, unciliated cubical cells, with dark-staining nuclei and denser cytoplasm near the free surface. The terminal sac is apparently not always developed and in some specimens is difficult to trace in sections. From April onwards it was at times found to be filled with sperms, which are evidently received at copulation, and pass directly from the vestibule into the bursa, while the common duct is kept closed. These sperms were never found to be oriented on the epithelium and are suspended in a semi-fluid secretion, staining pinkish, or which would appear to be the contribution of the prostatic cells.

Many specimens of *Carychium tridentatum* were found to be aphallic, showing no trace of either vas deferens or penis. In phallate individuals the male organs showed the relations

already described in *Leucophytia* and *Ovatella*. The vas deferens (*vas.*) is an exceedingly narrow tube, not more than 8 μ in diameter. It proceeds forward from the female aperture, enclosed beneath a ridge of epithelium of the body wall. The preputium is extremely slender in relation to the size of the animal, and extends backwards within the haemocoele of the head, to run across the roof of the anterior part of the buccal mass, deep to the cerebral ganglia and commissure. Its blind inner end is slightly expanded and the lining
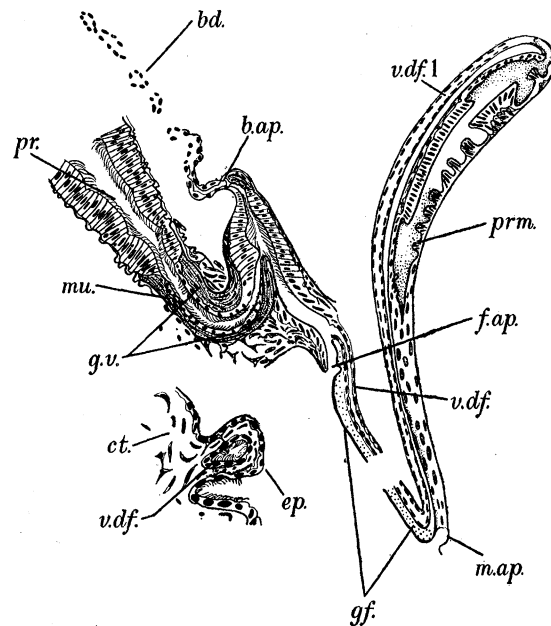
FIGURE 29. *Carychium tridentatum*. A general view of the anterior part of the genital tract, showing the relations of the genital vestibule, vas deferens and penis, as developed in July material. The structures illustrated have been drawn partly by reconstruction of serial transverse sections, and partly by transparency in stained whole mounted specimens. The genital and the ducts opening into it are represented as in longitudinal section; the vas deferens as it runs along the head is for the most part omitted. Inset is shown a transverse section of the external genital fold which is traversed by the closed vas deferens. *b.ap.*, aperture of the bursal duct into the vestibule; *bd.*, bursal duct; *ct.*, connective tissue of body wall; *ep.*, external epithelium; *f.ap.*, female genital opening; *gf.*, external genital fold; *g.v.*, genital vestibule; *m.ap.*, male genital aperture; *mu.*, muscular wall of genital vestibule; *pr.*, anteriormost portion of prostate; *prm.*, preputium invaginated in the haemocoele, shown for part of its length in longitudinal section; *v.df.*, vas deferens traversing external genital furrow; *v.df.* 1, vas deferens running alongside preputium, within the haemocoele.

epithelium, which is not ciliated, is raised into three or four longitudinal folds by increase in the height of the cells. No retractible penis could be found within the preputium. The vas deferens evidently opens simply into the blind end of the tube, which may itself be evaginated to form a copulatory organ.

It is not intended to discuss more fully here the occurrence or significance of aphallism in *Carychium*. The account by the present writer (1955 *c*) of the annual cycle of *C. tridentatum* deals with this phenomenon as it has been observed at Box Hill; and a forthcoming paper by Dr H. W. Harry will record some findings on the distribution of phallate and aphallate individuals in populations of the North American species, *C. exiguum*.

DISCUSSION

In the present paper we have throughout regarded the Ellobiidae as primitive pulmonates. In the following discussion, it is not intended to deal in detail with the interrelations of the various genera included within this family. Though, in general, it has been recognized that *Ovatella* occupies a primitive position with respect to the more advanced *Leucophytia* and *Carychium*, a full discussion of ellobiid phylogeny has been made the subject of a separate paper (Morton 1955 b). That account dealt also with the wider question of pulmonate origins, and the conclusions reached there may be summarized in the following way:

(i) In common with the most primitive prosobranchs (Archaeogastropoda) and the earliest of the tectibranchs (actaeonids) the first pulmonates are among the oldest of the gastropods. They are both generalized in morphology and ancient in origin.

(ii) The two subclasses Opisthobranchia and Pulmonata had probably a common origin among early prosobranchs, and diverged almost at the outset along very different lines.

(iii) It is almost certainly incorrect to think of the early pulmonates and the tectibranchs as being derived either one from the other, or from an advanced level in the Prosobranchiata. Their point of offshoot was probably at the outset of the evolution of the Monotocardia. This becomes clear from their structural features as well as from the early representation of pulmonates and opisthobranchs in geological time.

(iv) Although the Ellobiidae were not in fact the earliest of the pulmonates to appear, being not met with till the Jurassic, they must nevertheless in their anatomical features resemble closely the first of the Pulmonata; and if we were to reconstruct a type embodying the ancestral features needed in any ideal forerunner of both the Basommatophora and the Stylommatophora, it would certainly be an ellobiid that this mollusc would most resemble.

In this section we may review the results recorded in the previous pages on the morphology of the ellobiids and inquire in what respects these snails combine features common to both the prosobranchs and the more advanced pulmonates, and also—to a lesser extent—to the very anciently specialized tectibranchs. As has been stated by the writer (1955 b) the Ellobiidae appear to stand near the point at which the three great divisions of the Gastropoda—the Prosobranchia, the Opisthobranchia and the Pulmonata—draw closest together.

Figure 30 a illustrates in diagrammatic form some of the features that must have been possessed by a primitive prosobranch that had become 'monotocardian' by the suppression of the right half of the pallio-pericardial complex. In some features, though not in others, the trochids may perhaps be taken to represent this type most closely among gastropods living to-day. The external features must have included a broad creeping foot, bearing posteriorly a large operculum, and a short snout with two diverging cephalic tentacles with eyes at their bases. The feeding habit was microphagous, by the rasping and fine comminution of plant detritus with a broad, multiseriate radula. The mantle complex— already reduced on the right side—consisted of a single ctenidium (in earlier forms

bi-pectinate, soon to become monopectinate as in the example figured), and a single osphradium and hypobranchial gland. There is a single functional auricle (left), in *Trochus* itself the right auricle being still present but vestigial. The alimentary canal consisted of a muscular buccal mass, small mucus-producing salivary glands, a narrow anterior oesophagus in front of the region of torsion, a middle oesophagus with glandular oesophageal pouches behind the point of torsion, leading back by a narrow posterior oesophagus to the stomach. The stomach must have possessed all those generalized structural landmarks which were regarded by Graham (1949) as being primitive in gastropods, and which are still best exhibited in the modern Trochidae. A style sac was present, forming the first part of the intestine, and from this sac a rod of compacted faeces known as the 'protostyle' (Morton 1952 *a*) projected into the stomach and was constantly rotated by cilia, winding in a food string from the oesophagus and stirring the contents of the stomach in concert with the action of the ciliary sorting area. The posterior caecum of the stomach was formed as a prolongation of the sorting area, where absorption by amoebocytes, further rejection of coarse particles and compaction of faeces were presumably carried out. In the intestine was formed a long rope of mucus-bound faeces.

The idealized primitive monotocardian has one important difference from the trochids: in any gastropod ancestral to the pulmonates, as well as to later prosobranchs, a pallial genital duct and a penis must have been developed, making provision for internal fertilization in a manner unknown among archaeogastropods but almost universal among higher prosobranchs. As Fretter has earlier stressed (1946) the emancipation of the genital duct from the right kidney, and the introduction of copulation, must have been one of the most fruitful steps in gastropod evolution.

With the freedom from reproductive dependence on the waters of the shallow sea, a great variety of new habitats was at once opened to the gastropods. Evolutionary potentialities seem to have been released on one of those productive bursts that have been noticed in the radiation of so many other groups. The Gastropoda at this level seem to provide on a large scale an example of the type of 'explosive evolution' discussed by Simpson (1944). The 'eruptive evolution' of Cloud (1948) is a description of the same phenomenon, which he regards as an evolutionary 'breaking forth from restraint'. At the very outset of Monotocardian evolution, in the Neritacea, the land and fresh-water habitats were seized upon; and in marine habitats a great number of separate phyletic lines were established, some of them apparently very early specialized, as in the case of the highly adapted Xenophoridae, Vermiculariidae, Epitoniidae and Capulidae, which—according to Zittell (1927) —were all in existence before the close of the Palaeozoic era. The Littorinidae appear also to be a Palaezoic line; from a point near to them the land operculates must have been derived (see Morton 1952 *b*). In the Cyclophoridae, in particular, the anatomy is highly archaic, though the earliest geological record is of Cretaceous age only. Here, as in many other cases, we must be on guard against the tendency to equate primitiveness of structure with necessary antiquity of origin.

With the evolution of the Mesogastropoda we are at present not further concerned. Their chief distinguishing characters are the narrow taenioglossate radula, with the tooth row reduced to five in number; the invariably monopectinate condition of the gill; the concentration of the cerebral, pleural and pedal centres into compact ganglia; and, in the
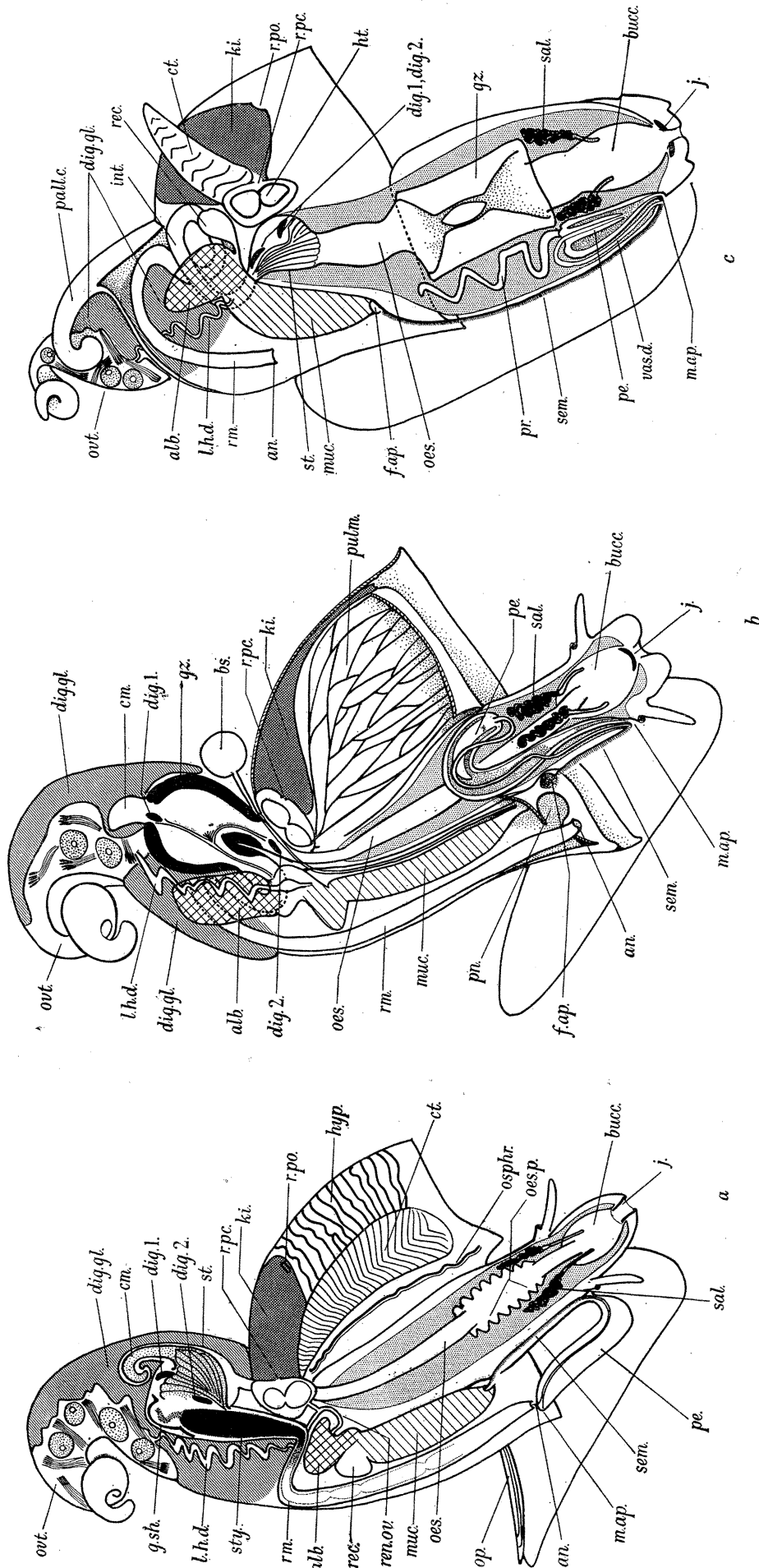
FIGURE 30. Idealized diagrams of primitive members of (a) the Prosobranchia, (b) the Pulmonata, and (c) the Opisthobranchia, as discussed in the text. The prosobranch diagram combines the primitive features of a trochid alimentary canal, with the condition of the genital tract achieved in the earliest mesogastropods; the opisthobranch is based chiefly on *Scaphander*, and the pulmonate on a primitive member of the Ellobiidae. In each case the haemocoele of the head and trunk is shown as if opened (lightly stippled) to display the anterior part of the alimentary canal, and the other structures lying in it. *an.*, anus; *alb.*, albumen gland; *bs.*, bursa copulatrix; *bucc.*, buccal mass; *cm.*, gastric caecum; *ct.*, ctenidium; *dig.gl.*, digestive gland; *dig.* 1, *dig.* 2. openings of the digestive diverticula; *f.ap.*, female genital aperture; *g.sh.*, gastric shield; *gz.*, gizzard; *ht.*, heart; *hyp.*, hypobranchial gland; *int.*, intestine; *j.*, jaw; *ki.*, kidney; *l.h.d.*, little hermaphrodite duct; *m.ap.*, male genital aperture; *muc.*, mucus gland; *oes.*, oesophagus; *oes.p.*, oesophageal glandular pouches; *op.*, operculum; *osphr.*, osphradium; *ovt.*, ovotestis or hermaphrodite gland; *pall.c.*, pallial caecum; *pe.*, penis; *pn.*, pneumostome; *pr.*, prostate; *pulm.*, lung; *rec.*, receptaculum seminis; *ren.ov.*, 'renal oviduct' of Fretter (1946); *rm.*, rectum; *r.pc.*, renopericardial aperture; *r.po.*, renal pore; *sal.*, salivary gland; *sem.*, seminal groove; *st.*, stomach; *stu.*, style sac; *vas.d.*, vas deferens.

gut, the tendency for the protostyle to give rise to a crystalline style in ciliary or micro-phagous feeders, or towards the simplification and reduction of the stomach in the development of a carnivorous habit. In the Mesogastropoda and the Stenoglossa, with a number of exceptions in the former order, separation of the sexes appears to be a characteristic feature. The present writer (1955 b) has previously reviewed the evidence for believing the primitive archaeogastropod stock to have been originally protandrously hermaphroditic, and that the higher prosobranchs represents a departure from the primitive state. At all events, the hermaphroditic condition is present in the opisthobranchs and pulmonates, without exceptions.

The group which formed the opisthobranch-pulmonate common stock almost certainly arose during the same 'burst of evolution' that produced the radiations of the meso-gastropod stock. The emergence of opisthobranchs and pulmonates took place very early; by the Carboniferous times representatives of both groups were distinct. Many of the resemblances between the basal members of the two groups may be ascribed to a common lack of specialized features; yet there are a number of features common to early Basom-matophora and early Tectibranchia which carry the stamp of phylogenetic affinity. In both groups the radula is strikingly similar at an early level, being multiseriate and com-posed of small uniform teeth, and having avoided the specializations characteristic of the later Prosobranchia. A more important resemblance which can be scarcely attributable to adaptive parallelism is the heterostrophic apex, with the sinistrally coiled embryonic shell. This occurs with great regularity in the earlier members of both the Tectibranchia and the Basommatophora. It is a distinguishing mark which has led to a realization of the deeper-seated structural resemblances in gastropods so unlike as the actaeonids, the ellobiids and the pyramidellids (see Harry 1951).

A further evolutionary burst must have taken place early in the history of the Tecti-branchia, with the production of such specialized branches as the Pyramidellidae (Fretter & Graham 1949) and the thecosomatous pteropods (Morton 1954 b), as well as the series of highly adapted bullomorphs, and the first families of the higher opisthobranch phyla. The Opisthobranchia remained entirely marine; and among the most fundamental changes introduced by them were those of reversal of torsion, loss of the ctenidium and pallial cavity and reduction of the shell. The Pulmonata were a much more conservative group. They were evidently of estuarine origin, and for some time confined to the upper shore. Perhaps the single distinguishing character of the group as a whole is the invariable loss of the gill and the closure of the pallial cavity to form a lung. A number of other characters usually occurring in pulmonates are listed by Fretter (1943) in her discussion on the position of the problematic *Onchidella*. Not all of these characters, however, are exclusive to, or invariably found in pulmonates. Like all larger taxonomic groups, the Pulmonates can best be characterized by considering the total direction of their evolu-tionary trends rather than by the possession or absence of particular key characters. Some genera are obvious taxonomic misfits, satisfactorily conforming to the definition of neither pulmonates nor opisthobranchs. The Siphonariidae is one such family, that, like the Onchidellidae, seems to have proceeded from an early date, independently of either of the main stocks.

We may look in somewhat more detail at the nature of the divergence of the pulmonate

and opisthobranch stocks from the prosobranchs, with particular reference to the alimentary and reproductive systems.*

Alimentary canal

In the buccal mass of the prosobranchs, there are paired lateral jaws; in pulmonates the fixed pattern of one median jaw of crescentic shape overlying the buccal cavity in front seems never to be varied. The presence of lateral and median buccal glands—as in ellobiids —seems, as well, to be typical of all the rest of the Basommatophora investigated. The radula, in archaeogastropods, in primitive bullomorphs and in ellobiids is in each case of the broad multiseriate type, adapted to a scraping microphagous habit. There is a well-differentiated median tooth, a rather small number of laterals and a large, but indefinite number of marginals. This generalized central type of gastropod radula has already undergone specializations in the living Trochidae, by the greater elaboration of the lateral and marginal teeth for rasping the tissues of algae. In the Actaeonidae and the Ellobiidae, to take the two earliest opisthobranch and pulmonate families, the numerous simple teeth are almost wholly unspecialized; Pelseneer (1895) has long ago drawn attention to such a similarity between these two families. The specializations in the radula of 'later' prosobranchs such as the Docoglossa, the Taenioglossa and the Stenoglossa are well known; and, moreover, in representatives of both the Pulmonata and the Tectibranchia carnivorous habits have later appeared, involving a reduction in tooth number and elaboration of cutting and rasping surfaces. The salivary glands in the earliest representatives of the three subclasses remain rather unspecialized, although in each case there is more than one type of secreting cell (see Fretter 1939; this paper (p. 98); and Morton (unpublished) for Trochacea). But it is doubtful if the original function of these glands was the secretion of more than a mucous or mucoid binding substance added to the food in the buccal mass. Salivary enzymes have not yet been demonstrated for any gastropod at the present unspecialized level. The oesophageal pouches, which form a series of paired enzyme-secreting pockets along either side of the middle oesophagus, immediately behind the region of torsion, would appear to be a feature of the primitive prosobranchs alone among gastropods. Their appearance, however, in the Polyplacaphora (Fretter 1937) as well as in all the Archaeogastropoda is strong evidence of their antiquity in the Mollusca. Graham (1941), as well as Fretter (1951), has shown the modifications and subsequent history of these pouches in the carnivorous prosobranchs. In very few mesogastropods do these pouches appear in their primitive form, and the majority of the phytophagous forms have lost them altogether. The Littorinidae, however, retain them, and the writer has recently (unpublished results) observed oesophageal pouches of the primitive sort in *Rissellopsis*, a member of the littorinid-like Bembiciidae.

* Since the completion of the manuscript of this paper, I have had the great advantage of reading the recent account by Fretter & Graham (*J. Mar. biol. Ass. U.K.* (3) **33**, 565) of the functional morphology and evolution of the primitive opisthobranch *Actaeon tornatilis*. The views expressed in the present pages on the origin and evolution of the pulmonates and opisthobranchs seem to be in broad agreement throughout with the conclusions reached by Fretter & Graham from the opisthobranch standpoint. It is also particularly encouraging to find a large measure of agreement with what I ventured to say about *Actaeon* in my own recent paper (Morton 1955 *b*).

The stomach with its digestive diverticula is both structurally and functionally the most complicated and important part of the molluscan gut. We have now an adequate knowledge of the structure and homologies of the parts of the stomach throughout the Gastropoda, chiefly as the result of the work of Graham (1938, 1949). Further, the present writer (1953) has given a brief review of the functions of the stomach of the Gastropoda, in which the following summary is given of the mode of action of the stomach in a hypothetical primitive archaeogastropod:

'The stomach showed three regions, a ciliary sorting area, with folds and narrow grooves converging on the intestinal groove; an area of cuticle raised into a stout gastric shield, serving to prevent abrasion by sharper particles; and, adjacent to the intestinal groove, and freely opening to it, a style sac, lined with strong cilia beating transversely, and rotating the mucous string spirally forward from the stomach through the intestine. The portion of the food string within the style sac early became compacted into a 'protostyle' a rod of stiff, viscid mucus, studded with faeces derived both from waste material of the digestive gland, and from larger particles rejected by the stomach. Distally this rod became continuous with the faecal string in the intestine; and where its head projected from the style sac into the stomach, it remained attached to the food string issuing from the oesophagus. Within the stomach the food string became wound into a close-coiled spiral, and the rotating protostyle served as a capstan, with three chief functions, to draw the food string into the stomach from the oesophagus by the gradual coiling and shortening of its length; to slow down the passage of light particles within the stomach to a gradual progress within the mucous string; and to sweep the loose particles in the stomach repeatedly across the surface of the ciliary sorting area.'

In the majority of living archaeogastropods and probably in the early monotocardian stock from which the pulmonates proceeded, a prominent, sometimes spirally coiled posterior caecum was developed, receiving the posterior end of the major typhlosole together with a long salient of the sorting epithelium and phagocytic subepithelial tissue carried back from the general chamber of the stomach.

In the earliest of the pulmonates, there is a very recognizable resemblance to the architecture of this primitive type of gastropod stomach. In an ellobiid such as *Ovatella* (see review in Morton 1955 b) the stomach retains such early landmarks as a remnant of the style sac, with an intestinal groove in the first part of the intestine; paired digestive diverticula with ciliated excurrent grooves leading to the intestinal groove; a posterior caecum receiving the major typhlosole; and a cuticularized area clearly corresponding to the gastric shield. In the primitive pulmonate *Otina otis* (Morton 1955 a) an even more detailed resemblance exists with the early prosobranchs. This is in *Otina* made more diagrammatic by the lack of a highly developed muscular gizzard which has elsewhere become an important diagnostic feature of pulmonates. For a comparison with an early opisthobranch stomach, reference may best be made to Fretter's account (1939) of *Haminea hydatis*, which —in spite of its much greater size—bears a striking resemblance to *Otina* in the arrangement and degree of development of the parts of the stomach.

There is never in the Ellobiidae a rotating protostyle with its old function of drawing in a string of stomach contents and sweeping particles across the sorting area. The ciliary and mucous system of the stomach is in the Pulmonata reduced at the outset in favour of the

development of a muscular gizzard, serving as a pumping and triturating mechanism. There is, further, a complete loss of the ciliary sorting function of the stomach, and with it a loss of the function of amoebocytic cells in the uptake of food particles. Whether the development of fragmentation phagocytes from the epithelium of the digestive gland, reported in both primitive pulmonates (see p. 138, and Morton (1955 a) in *Otina*), and in opisthobranchs (Millott 1937; Forrest 1951), is a device which has in general replaced the role of the amoebocytes from the blood system, we have not yet enough information to decide. The various genera of the Ellobiidae show a number of successive stages in the specialization of the stomach, with the formation of a muscular gizzard (see Morton (1955 b) and compare the above accounts of *Leucophytia* and *Ovatella*). In every case the same functional pattern seems to be well-marked, even in the more primitive genera which have not acquired the whole set of morphological features of the higher ellobiid stomach. In the most advanced genera, the gizzard is highly specialized, and the relationship of a stomach like that of *Leucophytia* to the predominantly ciliated stomach of a prosobranch might quite be lost sight of were we not able to turn to such pulmonates as *Ovatella* and *Otina* to illustrate the transition.

The gizzard in the Ellobiidae is identical in *function* with that of the higher fresh-water Basommatophora, as an example of which *Lymnaea* was selected by Carriker (1946, 1946 a) for a study of the digestive system. Further, Graham (1949) has studied the structure and mode of action of the stomach in *Planorbis*, which, he states, agrees with that of *Lymnaea* at almost every point. It is therefore very necessary to stress that—in the ellobiids on the one hand and in the higher limnic Basommatophora on the other—the stomach follows a radically different structural plan, that appears—with other features—to mark a deep line of cleavage between two sections of the order. In the lymnaeids, the oesophagus merges directly into the anterior end of the gizzard, and at the posterior end the paired digestive diverticula arise close together, alongside the intestine and a small caecum of unknown origin, from a smaller chamber called by Carriker the 'hepatic vestibule'. This forms a ciliated division of the stomach, separate from and posterior to the gizzard. None of the limnic Basommatophora show the tubular oesophageal atrium, by way of which—in most ellobiids—the anterior (and often sole) digestive diverticulum opens into the stomach.

From its relations with the typhlosolar ridges and the position at its mouth of the posterior digestive diverticulum, the posterior caecum of the ellobiids appears to be homologous with the gastric caecum which occurs in the Rhipidoglossa and in many lamellibranchs, and which was held by Graham (1949) to be a basic feature of the primitive molluscan stomach. From a consideration of such evidence as is available, the present writer (1955 b) has concluded that the same caecum has its equivalent in the limnic Basommatophora, such as *Lymnaea*, in the small tubular caecum, opening from the 'hepatic vestibule'.

In his review of the molluscan stomach, Graham (1949) suggests that the gizzards of the Tectibranchia and the Basommatophora (of which *Lymnaea* and *Planorbis* were the only forms then investigated) are homologous. The pulmonate gizzard is thus regarded as forming a part of the oesophagus, and it is stated that 'the true gastric region forms what Carriker (1946 a) calls the "hepatic vestibule" and the caecum'. The study of the ellobiid

stomach makes this view less tenable. Here the anterior digestive diverticulum leaves the stomach anteriorly to the gizzard, very close to the entry of the oesophagus, and in the primitive ellobiids the excurrent groove and the branch of the typhlosole from the posterior diverticulum, traverse the gizzard to continue directly into the intestine (see diagrams in Morton 1955 b). The anterior morphological limit of the pulmonate stomach must thus be moved forward to include the narrow oesophageal atrium with its diverticulum, and the ellobiid stomach must be regarded as being composed of the oesophageal atrium, gizzard and caecum together. Since there can be no reason to doubt the homology of the whole stomach in the lymnaeids with its counterpart in the ellobiids, the gizzard must be held to represent a part of the true stomach in the lymnaeids and the planorbids.

In the primitive opisthobranchs, the evolution of the gut has followed lines quite divergent from those of the pulmonates; and, indeed, one of the chief characters in which the two groups stand in contrast is in the structure and homologies of the gizzard. In all of the Bullomorpha, with the single exception of that most instructive genus *Actaeon*, a very large gizzard is developed as a dilation of the posterior part of the oesophagus, lined with heavily toothed, stout calcareous plates. The gizzard is never developed from the gastric region, and the chief trend of the stomach is towards a reduction of its primitive prosobranch structure, until in an example such as *Philine* (Fretter 1939) it serves as little more than an annexe placed between the oesophagus and the intestine, to receive the openings of the digestive diverticula. It is in the structure of the stomach, with a gastric gizzard, that *Onchidella* as discussed by Fretter (1943) fits least well into its proposed tectibranch location.

Reproductive system

Fretter (1946) has outlined the evolution of the genital ducts in those gastropods derived from the prosobranchs, that is, in the opisthobranchs and pulmonates. The present results shed further light on the transition from the prosobranch to the pulmonate condition of the genital system. A brief investigation was also made of *Actaeon*, from serial sections kindly lent by Dr Fretter, and the statements of Guiart (1901) were in general confirmed.

In both of the 'higher' subclasses of gastropods, the glandular portion of the hermaphrodite genital duct is derived from the pallial genital tract of the female prosobranch. This part of the genital duct—in almost all the monotacardian prosobranchs—lies anteriorly to the point of opening of the primitive genital aperture as represented in the Archaeogastropoda. This aperture corresponds morphologically to the renal pore of the right kidney, which at an early stage became non-excretory, and served for the passage of genital products from the gonad. The pallial portion of the duct was added as a later contribution from a glandular tract along the right side of the mantle, primitively a ventrally open groove, and finally a closed tube, whose glandular walls secreted nutritive and protective layers around the egg, and provided also for the storage and maintenance of sperms received in copulation. Its proximal portion formed an albumen gland, the distal part a capsule gland, and a pouch or a series of diverticula located at the junction of these two glands constituted the receptaculum seminis. Adjacent to this pocket lay the region of fertilization. A longitudinal ventral channel the capsule gland had the function of carrying sperm, received from the male, back to the receptaculum seminis.

There seldom appears in the prosobranch female any trace of a bursa copulatrix, which is a distally opening sac into which sperm is received from the vagina immediately after copulation. This, however, forms the principal sac for the storage of foreign sperm in both the Opisthobranchia and the Pulmonata.

In reconstructing the history of the pallial genital duct in the earliest pulmonates, we find that, though this group must have branched off from the prosobranchs at a very early stage after the acquisition of a pallial genital duct, the early pulmonate genital tract has evolved along lines closely parallel to what have already been described by Fretter in the prosobranchs. Whether in fact the genital ducts in the two stocks, mesogastropod and the combined opisthobranch-pulmonate, have developed parallel from the beginning, or whether these two stocks branched from a common ancestor soon after the formation of a pallial extension of the genital duct, is a question it is not at this day possible—or even very important—to find an answer to. At all events, the innovation of a glandular genital duct, making provision for internal fertilization, is, as has been stressed above, one of the improvements necessary to further evolutionary diversity in these two advancing stocks of gastropods.

As has been previously pointed out, there are grounds for thinking that the primitive monotocardian from which the higher gastropods proceeded, retained a condition of primitive hermaphroditism, and that this condition has been abandoned in favour of separation of the sexes in most of the monotocardians living to-day. All the known opisthobranchs and pulmonates are without exception hermaphroditic; and in the earliest members of both classes, as no doubt in their primitive prosobranch ancestor, hermaphroditism is of a successive protandrous type.

In *Actaeon*, the earliest of the surviving opisthobranchs, we find the most primitive condition of the pallial genital duct, which must now be known as the large, or glandular, hermaphrodite duct. The ventral longitudinal channel, as well as having the function of conducting foreign sperm backwards to the receptaculum, serves also as a vas deferens to conduct home sperm forward to the male aperture. The original female opening, at the distal end of the capsule gland, now becomes the common or hermaphrodite genital aperture. It serves as the terminal aperture of the female system, while from this point the male channel continues forward from the female duct, and runs independently along the right side of the trunk to the head, in the form of a closed tube immediately beneath the integument. The occurrences of a closed anterior vas deferens is, it would appear, unique in *Actaeon* among the tectibranchs. In all other genera an open, ciliated seminal groove, beneath a narrow ridge of the integument, runs forward to the base of the grooved penis. Such a ciliated anterior genital groove is not confined to the opisthobranchs: many families of the more primitive Mesogastropoda show it also (e.g. Struthiolariidae, Aporrhaidae, Strombidae, Vermetidae), and in these the groove is present also in the female for the conduct of the egg string to the foot.

In *Actaeon*, the whole of the glandular portion of the genital duct still keeps its original pallial position. None of it has yet come to lie within the haemocoele. The albumen gland, however, unlike its counterpart in most of the prosobranchs, now forms a spacious, thick-walled outgrowth from the conducting channel of the female tract, and the genital products do not traverse it. They appear to pass through only the most proximal part of the

wide duct of the albumen gland, which at its confluence with the capsule gland is dilated to form the fertilization pouch. No vaginal bursa copulatrix is developed in *Actaeon*, and the single-sperm storage chamber appears to be the short-stalked receptaculum seminalis, lying immediately beneath the floor of the posterior end of the mantle cavity. It opens, as in prosobranchs, from the fertilization site, at the junction of the albumen and capsule glands.

In the earliest of the pulmonates, as typified by *Ovatella* and also by *Pythia* (Plate 1897), the condition of the genital duct is at essentially the same level as in *Actaeon*, though there are one or two features that must be considered more advanced. Thus, the pallial genital duct may be divided on topographical grounds into two sections. The posterior part consists of the albumen gland and fertilization pouch, and the more proximal portion of the mucus gland, described here as the posterior mucus gland. This part of the genital tract has thrust its way backwards into the visceral mass, and, together with the terminal sac of the bursa copulatrix, has lost its primitive pallial location and has become haemo-coelic in position. A more anterior portion, consisting of the anterior mucus gland together with the prostate, remains pallial in position, bulging into the mantle cavity on the right side and being visible externally through the very thin overlying integument. In none of the Stylommatophora or in the limnic Basommatophora (the Lymnaeidae, Planorbidae, Ancylidae and Physidae) does the pallial genital duct remain visible externally in this way; it has there assumed its later position within the haemocoele of the trunk, lying internally to the thick, muscular body wall.

Following the closure of the pallial cavity in the Pulmonata, the female genital aperture has moved forward to lie beside the anus, just in front of the constricted pallial opening, or pneumostome. The secondarily established male aperture lies much farther forward, on the right side of the head, connected with the female opening by a ciliated groove in *Pythia* (as in the opisthobranchs) and by a closed anterior vas deferens in all the rest of the pulmonates. In all the pulmonates, as in the opisthobranchs, with one or two exceptions (*Actaeon* among them) the penis is retracted into an invaginated preputium, or penial sac, lying within the haemocoele of the head and opening to the exterior by the male genital aperture. The invagination of the penis is probably to be correlated in pulmonates with the loss of an open mantle cavity, which in prosobranchs is sufficient to protect from injury the bulky external penis, which, when out of use, extends back into it. In the opistho-branchs, invagination of the penis has come about in a similar way, probably as the result of the posterior migration and eventual loss of the mantle cavity, which still, however, retains its primitive relations in *Actaeon*, where the penis remains external.

In some primitive pulmonates, especially those in which the animal is of minute size, such as *Carychium* (see p. 145) and *Otina* Morton (1955 a), the preputium contains no retractible penis, and the intromittent organ is formed by the simple eversion of the sheath itself.

In none of the Ellobiidae, nor apparently in any described pulmonate, does there persist a receptaculum seminis of the type found in *Actaeon* and the prosobranchs, at the junction of the albumen and capsule glands. In all the ellobiids, the organ of sperm storage is a bursa copulatrix arising from the vagina, just within the female aperture. This diverticulum serves to store sperm received in copulation, both within the duct and the

dilated terminal vesicle. A degenerating mass of sperm with prostatic secretion is generally found at the centre of the lumen. Of the two sperm storage sacs mentioned in *Otina* by Morton (1955*a*), the anterior bursa copulatrix, opening from the vagina, is evidently the homologue of the organ of the same name in the ellobiids. The accessory bursa in *Otina* is evidently a special development; from its position it appears not to be homologous with the receptaculum seminis, which is very constant in its position, between the albumen gland and the receptaculum seminis.

Thus, to summarize, the main trends in which the genital tract of the lowest pulmonates is different from, or advanced upon, that of the prosobranchs include:

(i)   The universal presence of hermaphroditism;

(ii) The separation of the albumen gland from the conducting channel to form a distinct outgrowth of the genital tract;

(iii) The adoption of a haemocoelic position by the albumen gland and the posterior mucus gland;

(iv) The migration forward of the female genital aperture to lie outside the limits of the closed pallial cavity;

(v)   The development of a long-stalked bursa copulatrix opening from the vagina; and

(vi) The retraction of the penis into an invaginable preputium lying within the haemocoele of the head.

Nervous system

The nervous system in all pulmonates is characterized by the tendency to concentration of its central ganglia into a compact perioesophageal ring of nine (later becoming fewer by fusion), formed by the shortening of the connectives and the drawing forward of the out-lying parietal and abdominal ganglia. By this process, all obvious traces of chiastoneury are lost, with the return of the suboesophageal ganglion to its original (left) side, and the supraoesophageal ganglion to the right, by the shortening of the pleuroparietal connectives. It is in this way that the Pulmonata have become euthyneurous; none of them has under-gone the reversal of torsion in the structures of the pallial complex, and in this the Pulmonata differ from the other branch of the so-called subclass 'Euthyneura', the Opisthobranchia. While the opisthobranchs and pulmonates probably arose by a common origin from a prosobranch stock, nothing illustrates their early divergence better than the condition arrived at by the nervous system. In the Prosobranchia, too, constituting the 'Streptoneura', the condition of euthyneury is often found in the higher members of the Mesogastropoda and the Stenoglossa, though the abdominal ganglia are themselves never incorporated in the nerve ring.

The primary interest of the nerve ring in the Ellobiidae is in its indication of the primitive phylogenetic position of these pulmonates. The arrangement and degree of concentration of the nerve ganglia in the Basommatophora and Stylommatophora have been well described in the older text-books, and have been most fully and recently reviewed by Bargmann (1930). It is to be doubted whether further descriptive accounts of the nervous system are greatly needed until more progress has been made with func-tional studies. In the Ellobiidae, Pelseneer (1901) first gave an account of the nerve ring of *Ovatella myosotis*, and Simroth (1928) figures that of *Carychium minimum*. To neither of these

accounts has the present writer any details to add. A figure is provided, however, of the nerve ring of *Leucophytia bidentata* (figure 31) which has not been previously mentioned in the literature. The writer would express his gratitude to Dr J. S. Alexandrowicz for assistance in the methylene-blue staining of the nervous system of *Leucophytia* and other pulmonates. The typically 'basommatophoran' condition of the survival of five ganglia in the visceral loop is well illustrated by *Leucophytia*. In only one pulmonate so far known,
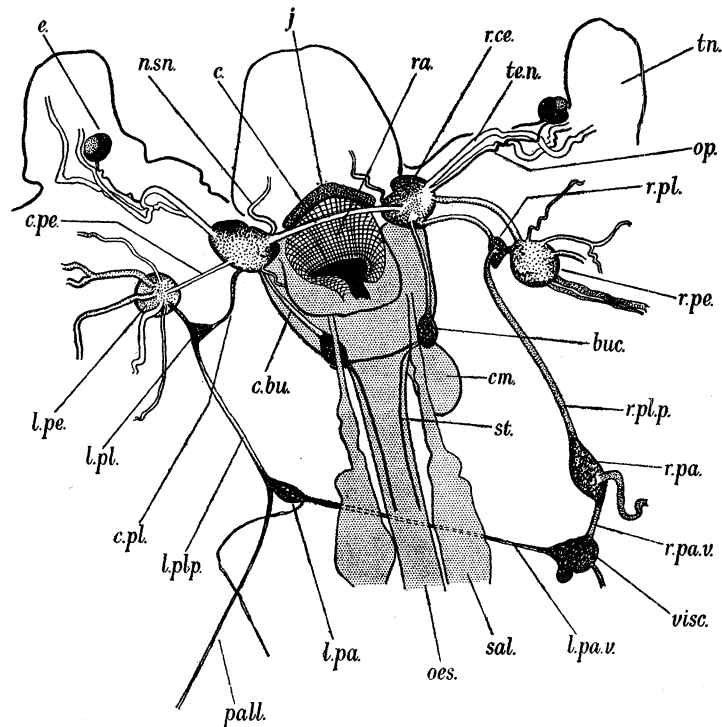

FIGURE 31. *Leucophytia bidentata*. Diagrammatic view of a dissection of the central nervous system, shown in relation to the outline of the head, snout and tentacles, and to the anterior part of the alimentary canal (shaded). *buc.*, buccal ganglion; *c.*, cerebral commissure; *c.bu.*, cerebro-buccal connective; *cm.*, radula caecum; *c.pe.*, left cerebro-pedal connective; *c.pl.*, cerebro-pleural connective; *e.*, eye; *j.*, jaw; *l.pa.*, left parietal ganglion ('subintestinal ganglion'); *l.pa.v.*, left pleural ganglion; *l.pe.*, left pedal ganglion; *l.pl.*, left pleural ganglion; *l.pl.p.*, left pleuroparietal connective; *n.sn.*, nerve to the snout; *oes.*, oesophagus; *op.*, optic nerve; *pall.*, pallial nerve; *ra.*, radula; *r.ce.*, right cerebral ganglion; *r.pa.*, right parietal ganglion ('supra-intestinal ganglion'); *r.pa.v.*, right parietovisceral connective; *r.pe.*, right pedal ganglion; *r.pl.*, right pleural ganglion; *r.pl.p.*, right pleuroparietal connective; *te.n.*, tentacular nerve; *visc.*, visceral ganglion; *sal.*, salivary gland.

Chilina dombeyana (Plate 1895), do traces of chiastoneury survive in the arrangement of these ganglia. In all the Ellobiidae hitherto examined, the subintestinal ganglion has moved underneath the right parietovisceral connective, and lies to the left of the single abdominal ganglion, in what is probably its original (pretorsional) position. Only in the crossing over of the visceral nerves running to the right and left sides, immediately behind these ganglia, does a hint of the former chiastoneurous arrangement show itself. In *Leucophytia bidentata*, the visceral loop is a great deal longer than Pelseneer's drawing would imply for *Ovatella myosotis*, where the loop is indeed shorter than the cerebrobuccal con-

nectives. The left pleuroparietal connective is in *Leucophytia* especially long for a pulmonate, and the left parietovisceral connective is somewhat longer. The single visceral or abdominal ganglion lies to the right side of the oesophagus, and the right parietovisceral connective is short. The right pleuroparietal connective is longer than the left, and the right parietal ganglion gives off the stout nerve that in *Ovatella*—according to Pelseneer—forms the connective to an osphradial ganglion. This ganglion could not be identified in the preparations of *Leucophytia*.

As in previous papers on the Pulmonata, it is a pleasure to record my indebtedness to Professor A. Graham, for his kindness and helpful criticism while I was a research student at Birkbeck College, University of London. I am also greatly obliged to Professor C. M. Yonge, C.B.E., F.R.S., and to Dr Vera Fretter, who have both assisted me in many ways during this work. The whole of the results described in this paper were obtained at Birkbeck College, or at the Plymouth Laboratory of the Marine Biological Association, and I am grateful both for the use of the London University Table at Plymouth, and for the kindness of the Director, Mr F. S. Russell, F.R.S., and the scientific staff.

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