ON THE BASIC FORM AND ADAPTATIONS TO HABITAT IN THE LUCINACEA (EULAMELLIBRANCHIA)

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[Plate 18]

CONTENTS

The Lucinacea (Eulamellibranchia) have been studied and particular attention has been paid to the feeding, respiratory and cleansing currents and their relation to the morphology and habits of the group.

The Lucinacea comprise three families, the Ungulinidae, Thyasiridae and Lucinidae, and living specimens of thirteen species were studied; namely, *Diplodonta rotundata*, *D. punctata*, *D. semiaspera* (Ungulinidae); *Thyasira flexuosa* (Thyasiridae); *Lucina pennsylvanica*, *L. chrysostoma*. *Codakia orbicularis*, *C. orbiculata*, *C. costata*, *Loripes lucinalis*, *Phacoides borealis*, *Myrtea spinifera*, *Divaricella quadrisulcata* (Lucinidae).

These species occur on a variety of substrata ranging from coarse sand to fine mud particularly where the associated fauna is sparse. Shallow-water species are often found among the roots of marine grasses such as *Zostera* and *Thalassia*.

The mantle is described, notably the extensive glandular tissue of the mantle margin, also the 'mantle gills' and the unique form of the exhalent siphon both of which are confined to the Lucinidae.

The great development of the glandular tissue at the mantle margin is probably related to large quantities of sediment entering the mantle cavity. While many of the gland cells close to the epithelium show typical basiphilic reactions of mucus-secreting cells, those further from the epithelium show marked eosinophilic-staining reactions. The only visible difference between the cells appears to be a difference in cytoplasmic granule size, those to the inside possessing the larger granules.

'Mantle gills' consist of convoluted folds of the inner mantle epithelium close to the anterior adductor muscle. They occur in *Codakia orbicularis* and *Lucina pennsylvanica*. The folds are parallel

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to the direction of the ciliary currents. There are no gland cells, but there are many blood vessels below the folds and the latter are probably concerned with respiration.

The exhalent siphon in the Lucinidae does not contract into a pallial sinus, but turns inside out and lies in the suprabranchial cavity, a method that appears to be unique.

The anterior adductor muscle is elongate and the greater part of it lies ventral and posterior to the mouth. Its surface epithelium is ciliated and acts as a sorting area for particles entering by the anterior inhalent tube. The Ungulinidae are least specialized in this respect and the Lucinidae the most specialized.

The variations of the ciliary currents on the body are described.

The foot is highly specialized, it is used in burrowing and also forms the anterior inhalent tube. It is typically long and vermiform often with a distinct tip. In the Lucinidae the heel is well developed and may be distinct from the vermiform portion. The latter is chiefly concerned with tube formation and the heel with digging. In some species the foot can extend to more than ten times the length of the shell. The tip of the foot is profusely supplied with glands which supply material for tube formation. An account of this and of burrowing is given.

The morphology and ciliary mechanisms of the gills are described. In the Ungulinidae and Thyasiridae the outer demibranch is reduced and in the Lucinidae this demibranch is absent. All the species studied have homorhabdic gills. In the Thyasiridae and Lucinidae development of the subfilamentar tissue gives a fleshy appearance to the gills.

The palps show progressive reduction in size in the three families. The Ungulinidae and the Thyasiridae retain the typical ciliated folds. The palps of the Lucinidae are slight enlargements of the walls of the oral groove. Vestiges of not more than three folds remain which are still capable of a limited amount of sorting.

The stomach and digestive diverticula are described; the sorting mechanisms are progressively reduced. They are least reduced in the Ungulinidae being essentially the same as those of other Eulamellibranchia. In the Thyasiridae and the Lucinidae there is reduction in the sorting areas of the stomach and the number of ducts of the digestive diverticula. The resulting simplification of the stomach emphasizes the importance of (1) the acceptance tract, (2) the typhlosoles, (3) the left caecum, (4) the dorsal groove, and (5) the tooth on the gastric shield.

The digestive diverticula of the Ungulinidae are of the typical eulamellibranch pattern, those of the Lucinidae and Thyasiridae have much larger ducts and tubules, both in the size of the lumen and of the cells. Tubules only are present in the Thyasiridae.

The excretory, circulatory and nervous systems do not differ significantly from those of other Eulamellibranchia.

The evolution of the group is discussed particularly in relation to the anterior inhalent current and the correlated reduction in sorting mechanisms of the gills, palps and stomach, together with the development of the anterior adductor muscle, foot and exhalent siphon.

Introduction

Despite the superficial similarity of structure throughout the Class, the different groups within the Lamellibranchia are frequently highly specialized for particular habitats. Even within the subclass Eulamellibranchia, which includes the Lucinacea, there is considerable variation in form and habit. The Lucinacea is a well defined group which shows many characteristic features (figure 1). These include an elongate anterior adductor muscle and an anterior inhalent tube formed by the foot, the latter being capable of extending to a remarkable extent (Allen 1953). From the work of Dall (1901), Lamy (1920) and Chavan (1937, 1938) the shell characters are well known, but, apart from the work by Atkins (1937*a*, *b*; 1938*a*, *b*) on the ciliation of the gills, the living animals have not been studied.

Investigations have been made on living specimens of as many species as could be obtained from British, Mediterranean and Caribbean waters. An analysis of the fundamental structure of the group has been made with particular reference to the habits and habitats of the animals. In particular, the feeding, respiratory and cleansing currents have been studied. The scattered observations of previous workers have been brought together and an attempt has been made to give a comprehensive account of the Lucinacea and indicate the probable course of evolution within the group. Later papers will appear on the ligament and on reproduction.

CLASSIFICATION

The Lucinacea is a well-defined group of the Eulamellibranchia but accounts differ as to its subdivision (Pelseneer 1888; Menégaux 1890; Dall 1901). Dall (1901) in his synopsis of the Lucinacea lists five families—the Lucinidae, Corbidae, Thyasiridae, Ungulinidae and Cyrenellidae. Theile (1935) includes the Cyrenellidae in the Stirps Carditacea and he places the Corbidae in the Lucinidae. In addition to this, Theile includes two subfamilies, the Thyasirinae and the Ungulininae, in the family Ungulinidae. The present work shows that the Thyasirinae and the Ungulininae differ from one another so much that they must be regarded as separate families, thus agreeing with the classifications of Winckworth (1932) and Chavan (1937, 1938).

The following living genera are listed by Theile (1935) and Chavan (1937, 1938), species of those genera marked with an asterisk have been examined in the present study:

Ungulinidae: *Diplodonta*,* *Ungulina* and *Joannisiella*.

Thyasiridae: *Thyasira*,* *Leptaxinus* and *Axinopsis*.

Lucinidae: *Phacoides*,* *Miltha*, *Myrtea*,* *Divaricella*,* *Loripes*,* *Megaxinus*, *Lucina*,* ? *Vaticinaria*, *Codakia*,* *Corbis* and ? *Bathycorbis*.

HABITAT

Species of all families of the Lucinacea are to be found on a variety of substrata ranging from coarse sand to fine mud from mid-tide level to depths of over 1500 fm. Members of the group are distributed throughout the seas, but are most commonly found in tropical and subtropical waters. Living specimens of thirteen species were studied at Marine Stations in Britain, France and the Caribbean area (see p. 481).

UNGULINIDAE

Diplodonta rotundata (Montagu) was the largest member of the family studied (maximum length found 21 mm). The species ranges from the south coast of Britain to the Canaries and is also found in the Mediterranean (Forbes & Hanley 1853; Lamy 1920). It is taken from muddy gravel and muddy sand in depths varying from 4 to 35 fm. It is not common and only one living specimen was obtained from Plymouth Sound in muddy gravel at a depth of 4 fm. It was found in association with *Nucula turgida*, *Thyasira flexuosa*, *Abra alba*, *Corbula gibba*, *Cultellus pellucidus*, *Melinna adriatica* and *Nephthys hombergi*.

Diplodonta punctata Say is also large (maximum length found 17·5 mm) and differs from the other species of *Diplodonta* in that it is not globose. It is reported by Dall (1901) as occurring in depths of 14 to 124 fm, and ranges from Cape Hatteras southwards to the Straits of Megellan and northwards up the coast of Chile to Chiloe Island. *Diplodonta punctata* was found to be common in the mangrove swamps of the Palisadoes (Kingston Harbour, Jamaica) in muddy and sandy gravel in depths varying from 1 to 3 ft. particularly

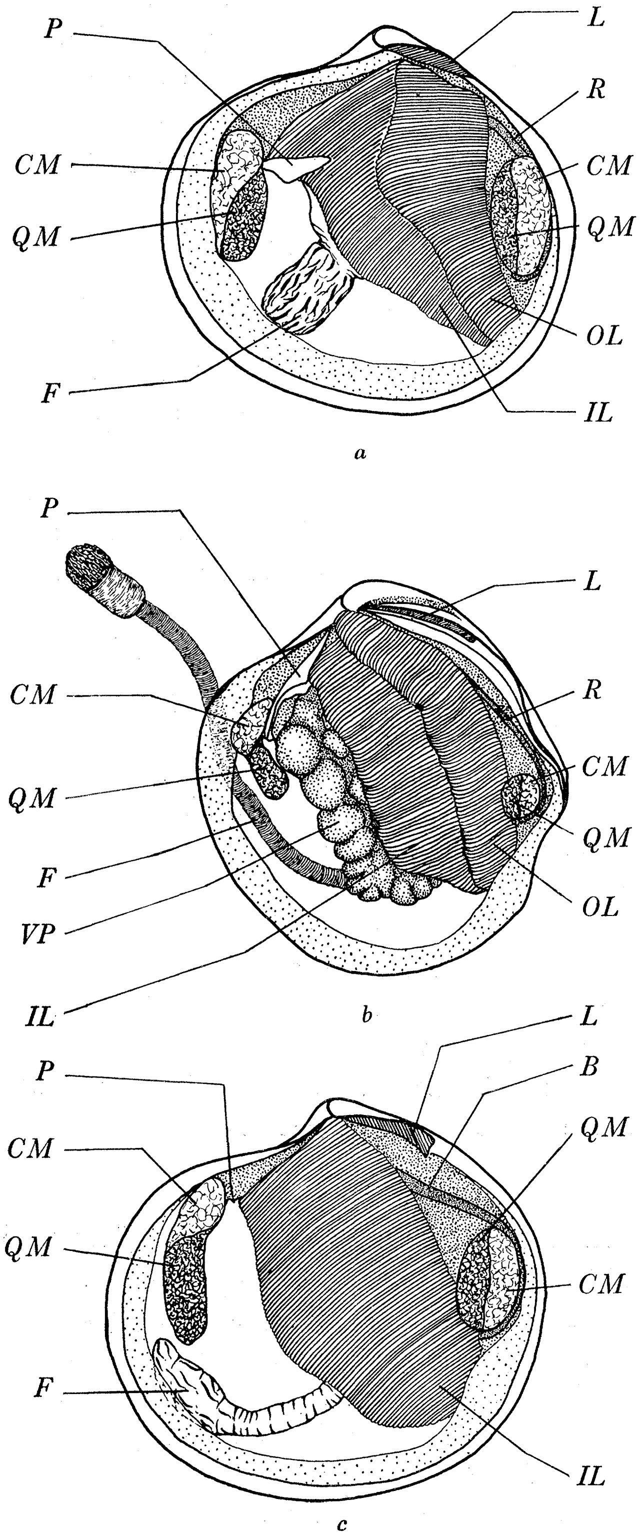


FIGURE 1. Lateral views of representative species of the three families of the Lucinacea. The left shell valve has been removed. *a*, *Diplodonta semiaspera* (Ungulinidae) (magn. × 5); *b*, *Thyasira flexuosa* (Thyasiridae) (magn. × 9); *c*, *Loripes lucinalis* (Lucinidae) (magn. × 3). *CM*, 'catch' muscle; *F*, foot; *IL*, inner demibranch; *L*, ligament; *OL*, outer demibranch; *P*, palp; *QM*, 'quick' muscle; *R*, rectum; *VP*, visceral pouch.

where a current was flowing. It occurred together with *D. semiaspera*, *Codakia orbiculata*, *Crassinella lunulata* and *Semele* sp.

Diplodonta (*Phlyctiderma*) *semiaspera* Phillippi was the smallest species of *Diplodonta* studied (maximum length found 11 mm). It is globular in shape and the shell is ornamented with very small pustules, the latter being the distinguishing character of the subgenus. It is reported by Dall (1901) to range along the Atlantic coast of America from Cape Hatteras to Brazil at depths from 14 to 20 fm. It was found commonly among the roots of *Thalassia* grass in coarse coral sand on moderately exposed beaches of the south coast of Jamaica in depths ranging from 3 to 5 ft. A few specimens were found in the same locality as *D. punctata*. The animals that occurred amongst the roots of *Thalassia* had a surprisingly sparse associated fauna and only *Codakia orbiculata* occurred in any numbers.

THYASIRIDAE

Thyasira flexuosa (Montagu) was the only species of this family that was obtained living. This small, fragile shell (maximum length found 6·5 mm) is found in all British waters and ranges from Spitzbergen to the Azores and is found in the Mediterranean (Lamy 1920). It is common in sandy muds in depths of water ranging from 6 to 80 fm. Living specimens were collected from the Clyde, Plymouth Sound and the Bay of Mentone. In the two former localities *Thyasira* was found to be in association with *Nucula tenuis*, *Abra alba*, *Amphiura filiformis* and *Melinna adriatica*, while in the latter locality it was found together with small specimens of *Myrtea spinifera*, *Phacoides borealis* and *Dentalium rubescens*.

LUCINIDAE

Phacoides borealis (Linné) is the largest European member of the Lucinacea (maximum length found 26 mm) and has a similar geographical range to *Thyasira flexuosa*. It is found along the European Atlantic coast and in the Mediterranean and lives in sandy mud at extreme low-water spring-tide level down to 90 fm. It was found living among the roots of *Zostera* at low-water mark at Roscoff, Finistere, but elsewhere it was found in the sublittoral zone (Plymouth Sound, Firth of Clyde and Bay of Mentone). In British waters it was found to be associated with *Abra alba*, *Cardium echinatum*, *Gari ferroensis*, *Dosinia lupinus*, *Pectinaria belgica*, *Lipobranchius jeffreysii*, while in the Bay of Mentone young specimens were found together with those species listed under *Thyasira flexuosa* for the same locality. At Roscoff it was found together with *Cardium edule*, *Dosinia exoleta*, *Leptosynapta gallienna*, *Nephthys hombergi* and *Amphitrite edwardsi*.

Loripes lucinalis Turton has a small fragile shell (maximum length found 18·5 mm) and ranges from the Northumbrian coast and the Isle of Man to the Mediterranean at depths ranging from low-water mark to 80 fm. Living specimens were obtained from sandy beaches at Roscoff, Finistere, where it was most commonly found amongst the roots of *Zostera*. It was found associated with the same species as are listed under *Phacoides borealis*.

Myrtea spinifera (Montagu) has a stout shell and is compressed laterally to a greater extent than any other species examined in this study (maximum length found 18 mm). It is found off the coast of Norway and extends into the Mediterranean (Forbes & Hanley, 1853) at depths varying from 4 to 60 fm. Specimens were taken from soft mud in Loch Sween (Argyll) and from muddy sand in Plymouth Sound and the Bay of Mentone. In

Loch Sween it is associated with *Abra nitida*, *Nucula sulcata*, *Amphiura chiajei* and *Brissopsis lyrifera*. In Plymouth Sound it was obtained from the same locality as *Diplodonta rotundata* and in the Bay of Mentone from the same locality as *Thyasira flexuosa*.

Divaricella quadrisulcata d'Orbigny is a large species of a genus that is characterized by an unusually marked shell (see p. 427 and plate 18; maximum length found 20 mm). It is reported by Dall (1901) to range from Massachusetts to Rio de Janeiro at depths varying from 10 to 50 fm. It was taken occasionally among the roots of *Thalassia* at Miami and Bimini Island, Bahamas, and was found in large numbers in clean coral sand in the lagoon at the latter locality in 5 ft of water. This sand was remarkable for its lack of associated fauna, the only other animals found were *Lucina pennsylvanica* which occurred in moderate numbers and an occasional specimen of *Codakia orbiculata*. The associated fauna of the *Thalassia* beds is given under *Codakia orbicularis*.

Codakia orbicularis Linné was the largest member of the Lucinacea collected (maximum length found 92 mm). It is reported to occur (Dall 1901) at Bermuda, Florida, throughout the Caribbean area and southwards to Brazil. It occurs amongst the roots of *Thalassia* where this grows in course coral sand in fairly sheltered conditions. The animal was taken at depths ranging from 1 to 3 ft. of water. It was found on the north and south coasts of Jamaica, Florida Keys and at Bimini Isle. There is a remarkably sparse infauna in the *Thalassia* beds and this comprised of an occasional lucinid (*Divaricella quadrisulcata*, *Lucina chrysostoma*), *Syndosmya* sp. and *Calocaris* sp.

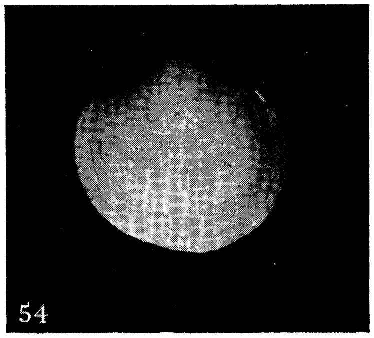
Codakia (*Jagonia*) *orbiculata* Montagu is reported by Dall (1901) to be a very variable species. This was confirmed, shell sculpturing varying with locality (maximum length found 16·5 mm). It ranges along the American Atlantic coast from North Carolina throughout the Caribbean as far as Brazil and is also found in the Azores. It is recorded from depths varying from 8 to 300 fm. Living specimens of this species were found in small numbers in muddy gravel in the mangrove swamps of Kingston Harbour, Jamaica, and in clean coral sand at Bimini Isle. At the former locality this species was found together with *Diplodonta semiaspera* and at the latter locality with *Divaricella quadrisulcata* and *Lucina pennsylvanica*.

Codakia (*Jagonia*) *costata* d'Orbigny was the smallest member of the Lucinidae studied (maximum length found 11 mm). It is reported to occur along the American coast from North Carolina to Rio de Janeiro at depths varying from 13 to 85 fm (Dall 1901). A few living specimens were obtained from the same localities as *C. orbiculata* listed above.

Lucina pennsylvanica Linné is a stout shell that grows to a large size (maximum length found 38 mm). It occurs in shallow water from Cape Hatteras to the Caribbean. It was found to be common in clean coral sand at Bimini Isle where it occurred with *Divaricella quadriculcata*.

Lucina (*Loripinus*) *chrysostoma* (Meuschen) grows to a similar size to *L. pennsylvanica* (maximum length found 35 mm). Dall (1901) records it in moderate depths at Bermuda and the Caribbean area. It was occasionally found among the roots of *Thalassia* at Miami where it was associated with those species given under *Codakia orbicularis*.

The Lucinacea show certain ecological peculiarities. Members of the group tend to occur in substrata that have a very sparse infauna. In addition, several species of the group may occur together in the same habitat. Even in the Clyde and in the Plymouth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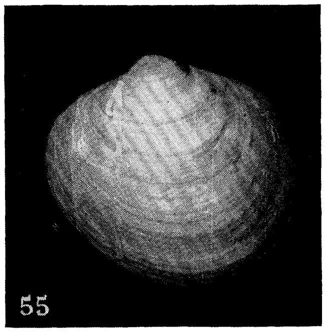
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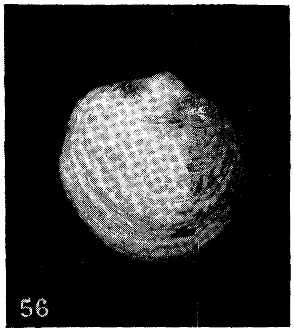
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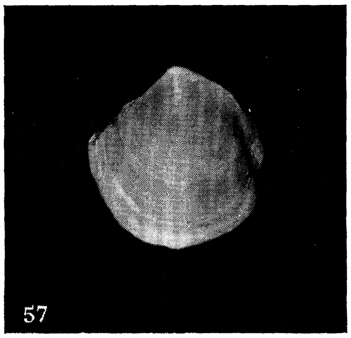
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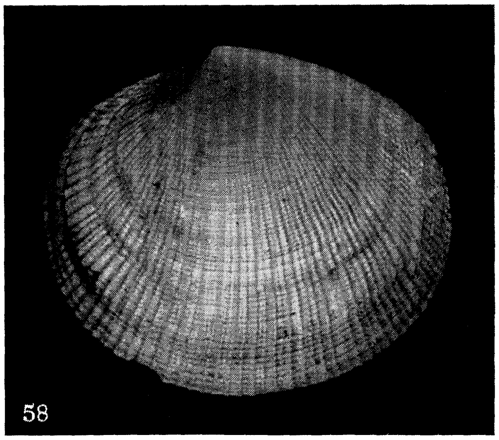
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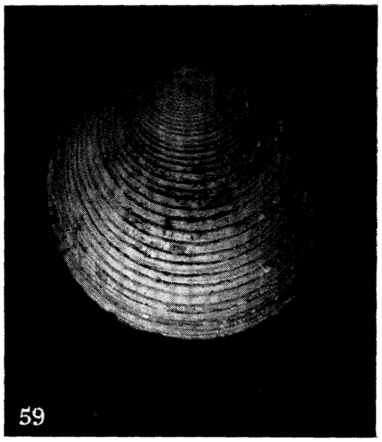
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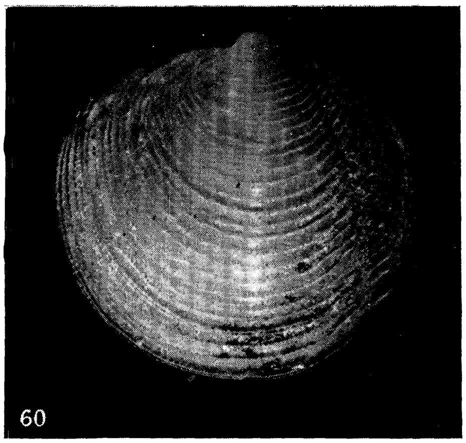
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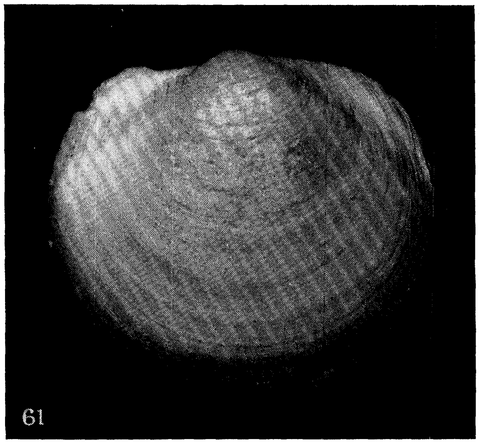
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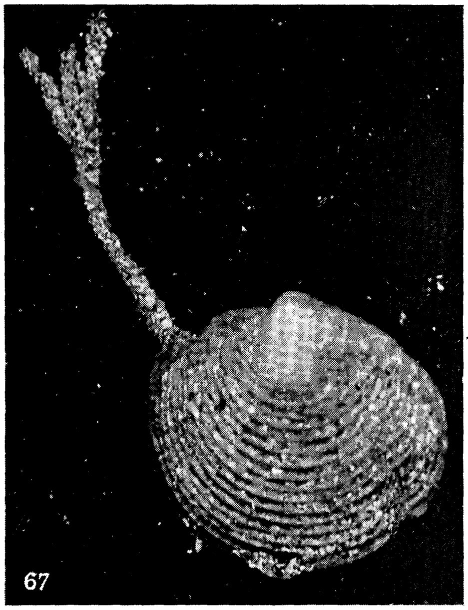
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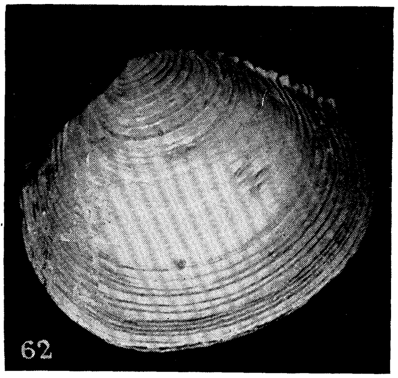
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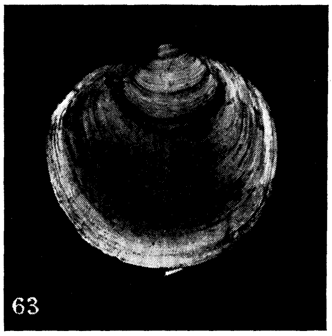
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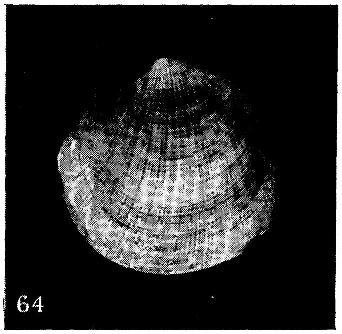
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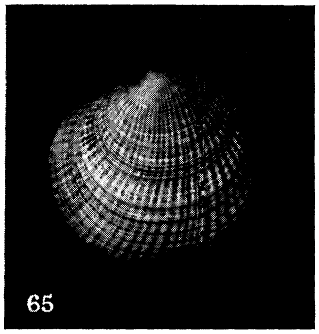
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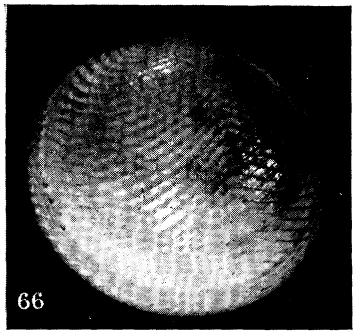
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FIGURES 54 TO 67. Valves of the species of the Lucinacea studied. 54, *Diplodonta semiaspera* (× 3); 55, *D. rotundata* (× 1); 56, *D. punctata* (× 1·5); 57, *Thyasira flexuosa* (× 4); 58, *Codakia orbicularis* (× 1); 59, *Phacoides borealis* (× 1·5); 60, *Lucina pennsylvanica* (× 1·5) 61, *L. chrysostoma* (× 1·5); 62, *Myrtea spinifera* (× 3); 63, *Loripes lucinalis* (× 2); 64, *Codakia costata* (× 3); 65, *C. orbiculata* (× 3); 66, *Divaricella quadrisulcata* (× 1·5). 67, *Lucina pennsylvanica* with the anterior inhalent tube intact showing clearly the repaired end that lies at the surface of the substratum.

Sound the infauna of the substrata in which species of the Lucinacea occur was never rich and other uncommon species were often present, e.g. *Lyonsia norvegica* and *Solecurtus chamasolen*. There is also a marked tendency for the shallow water species to live among the roots of the marine grasses *Zostera* and *Thalassia*. Again, where species of the Lucinacea were found in this latter habitat there was a marked lack of associated fauna. At Roscoff, this lack could be explained in some cases where *Loripes* and *Phacoides* were collected in black sandy mud that smelt strongly of hydrogen sulphide. Presumably the possession of the anterior inhalent tube (see p. 448) enables them to live under these conditions.

Thus, the Lucinacea are found where competition is at a low level and can survive conditions that are not suitable for what are generally regarded as more common species. Such conditions are to be found in sands where the organic content is low (Bimini Isle) or possibly unavailable (roots of sea grasses and mangrove swamps). Yet, where conditions are suitable for a rich fauna they are sparingly distributed.

SHELL

The Lucinacea have characteristically rounded shells with the umbones facing anteriorly (see plate 18). All species examined had white shells, often discoloured anteriorly and posteriorly at the free margins of the valves where the inhalent and exhalent apertures are situated. The Ungulinidae and the Thyasiridae have fragile shells while the Lucinidae usually have strongly built shells. In many species the shell is globose. This is associated with the outpouching of the body (see p. 449) and is not related to the type of substratum that they inhabit (Owen 1953). Apart from growth lines, shell sculpturing was present in *Diplodonta semiaspera* alone of the three species of this genus examined (figure 54, plate 18). This sculpturing takes the from of pustules and is the distinguishing feature of the subgenus *Phlyctiderma*. The Ungulinidae do not show the characteristic indentation of the shell that follows the line of attachment of the gill (*LGA*) with the body, as seen in *Thyasira* and many species of the Lucinidae (plate 18). This distinctive feature appears to be confined to species of the Lucinacea. It is distinct in the more globose members of the Thyasiridae and the Lucinidae, e.g. *T. flexuosa* (figure 57) and *Lucina pennsylvanica* (figure 60), and can just be discerned in the more laterally compressed species such as *Codakia orbicularis* (figure 58). However, it is not present in every globose species as is shown in the case of *Loripes lucinalis* (figure 63).

As in the Ungulinidae, the Thyasiridae, apart from growth lines, show little shell sculpturing. Only in the more heavily built shells of the Lucinidae are the valves decorated. The most common form of sculpturing is that of concentric ridges running parallel to the lines of growth, e.g. *Phacoides borealis* (figure 59), and *Lucina pennsylvanica*. Species of *Codakia* have radiating striae superimposed on the concentric ridges with the result that decussations and characteristic patterns are formed. There is little tendency to produce spines and only in *Myrtea spinifera* (figure 62) are small spines present. These are found at the limit of the concentric ridges on either side of the ligament. Most unusual sculpturing is shown by *Divaricella* (figure 66, plate 18). In this genus the lines of sculpture are at an angle of approximately 45° to the lines of growth. Furthermore, these lines run in opposite directions at opposite ends of the shell, with the lines from each end of the shell meeting one another in an obtuse angle. These points of convergence are set above one another along an imaginary line from the umbo to the free margin of the shell. This line is anterior and therefore does not correspond to an indentation following the line of attachment of the gill. The only other lamellibranch known to the author to have similar sculpturing is *Myllita* pictured by Theile (1935, p. 872).

MANTLE

The mantle edge of the Lucinacea shows no major difference from that of other lamellibranchs. It consists of three parallel lobes (figure 2). The outer lobe (*EL*) is concerned with the secretion of the outer calcareous layers of the shell, while the periostracum (*PE*) is secreted by the cells at the head of a well-defined groove (*PG*) between it and the middle sensory lobe (*CL*). The middle lobe is moderately well developed in the Ungulinidae and the Lucinidae as a thin delicate fringe, tentacles being present only in the region of the posterior inhalent and exhalent apertures. A second fringe (*FM*) is present just to the inside of the middle lobe. In *Phacoides borealis* and *Loripes lucinalis* this second fringe is of a similar size to the first, but in other species it is better developed, particularly in *Divari-*

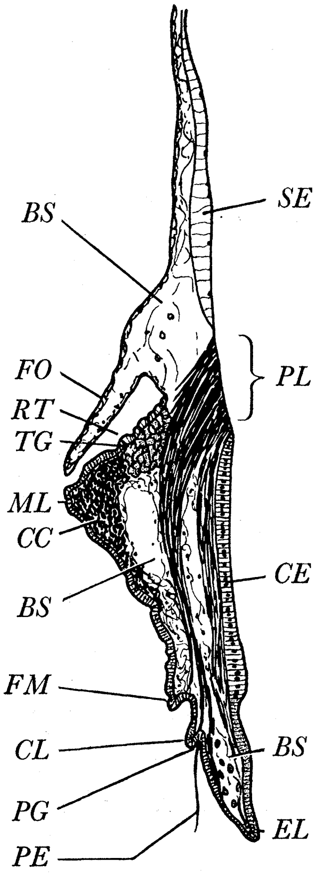


FIGURE 2. Transverse section of the mantle edge of *Phacoides borealis* (magn. × 25). *BS*, blood space; *CC*, concrescent muscle strands; *CE*, mantle epithelium (see text); *CL*, middle lobe; *EL*, outer lobe; *FM*, inner sensory frill; *FO*, mantle fold; *ML*, inner lobe; *PE*, periostracum; *PG*, periostracal groove; *PL*, pallial line; *RT*, main rejection tract of the mantle; *SE*, mantle epithelium (see text); *TG*, gland cells.

cella quadrisulcata. In the Thyasiridae the sensory lobe is not well developed but a fine double fringe is still present, although there are no tentacles in the region of the apertures. The inner muscular lobe (*ML*) is well developed in all three families and on the inside it forms a shelf along which the main rejection tract of the mantle (*RT*) runs. A third delicate fringe at the outer edge of the rejection tract is present in the Lucinidae.

The basic histological details of the mantle are similar in all three families (figure 2). The epithelium facing the mantle cavity is a ciliated pavement type and the cilia beat in the manner described below. Occasional mucus-secreting gland cells are present between or just below, the epithelial cells. The inner blood space (*BS*) varies in width depending on the quantity of blood present at any particular time. The epithelium (*SE*) secreting the shell is typical of that found in other lamellibranchia. The cells are large, columnar and vacuolated with the cytoplasm confined to a thin layer along the cell wall. The thickness of this epithelium varies but in *Codakia orbicularis* it reaches a maximum of $160\,\mu$.

In *Phacoides borealis* and *Codakia orbiculata* there is a mantle fold (*FO*) immediately above the inner lobe (figure 2). This is similar to that found in other lamellibranchs such as *Spisula* (Yonge 1948) and *Pandora* (Allen 1954) and forms a roof over the main rejection tract of the mantle. In *Lucina pennsylvanica*, *L. chrysostoma* and *Divaricella quadrisulcata* this fold is much enlarged. In addition, the latter two species possess a triangular fold (*TF*) immediately posterior to the anterior adductor muscle (see figure 17 and p. 442). In the Lucinacea there is a large blood sinus at the base of the mantle fold (see below).

The musculature of the mantle edge is similar to that of other lamellibranchs. Concrescent muscle strands are present in the muscular lobe below the outer edge of the main rejection tract. To the inside of these strands longitudinal muscles form two main groups, one inserted on the hinge side of the pallial line (*PL*) and connecting with the sensory and outer lobes, and the other inserted on the lower half of the pallial line and connecting with the outer lobe. The space between the two groups of muscles is filled with packing tissue, blood spaces and in some species (see below) glandular tissue. Glandular tissue (*TG*) also may be present between the longitudinal and concrescent muscles below the epithelium of the main rejection tract. This epithelium is the most heavily ciliated surface of the mantle and due to the intercellular ducts from the gland cells appears irregular in cross section.

'*Mantle gills*'

Pelseneer (1911) refers to three species, *Lucina exasperata*, *L. punctata* and *L. tumida*, as having 'pallial gills'. Similar structures were first described by Duvernoy (1853) for *Lucina tigerina*. Semper (1880) describes them in *L. phillipinensis* and states that they are similar in structure to the gills of opisthobranchs and refers to them as 'Mantelkienen'. Both Duvernoy and Semper describe the gill as being composed of seven or eight wrinkles on either side of the mantle close to the palps. Pelseneer describes three types of gill. In *L. exasperata* he found two of these, one consisting of twenty-four to twenty-five lamellae close to the inner lobe of the mantle and antero-ventral in position, and the other forming a long and deep fold extending from the posterior mantle edge to the anterior adductor muscle. In *L. punctata* there is a similar group of five folds antero-ventrally, but in *L. tumida* the gill is close to the anterior adductor muscle and consists of one very convoluted ridge. This is Pelseneer's third type of gill.

Unfortunately, none of the species referred to above was obtained during the course of this work, but similar mantle folds (*GM*) were found in two of the species examined (figures 3 and 4), *Codakia orbicularis* and *Lucina pennsylvanica*. The condition in *Codakia orbicularis* (figure 3) closely resembles that in *Lucina exasperata*. The gills consist of a varying number of ridged folds that stretch from the posterior end of the anterior adductor muscle (*AA*) backwards and downwards towards the siphons and the mantle edge. The fold that lies immediately to the inside of the inner mantle lobe extends along the outside of the anterior adductor almost as far as the point of anterior mantle fusion. Close to the posterior end of the anterior adductor there is a complex 'knot' of tissue (*KF*) formed at the junction of three folds. Two of the latter are anterior to the 'knot' one on each side of the anterior adductor. The third fold runs posteriorly parallel to the remainder of the gill. As in *L. exasperata* there is a non-ridged fold (*NGM*) to the inside of the folded area and this extends from the palps to the posterior limit of the other folds. In *L. pennsylvanica* the folds are much finer than those of *Codakia orbicularis* and do not project so far into the mantle cavity (figures 4 and 5). They are situated on either side of the pallial blood vessel (*PBV*) and at right angles to it and extend from the inner lobe to the junction of the mantle with the gill lamella. There is no 'knot' at the posterior end of the anterior adductor muscle.

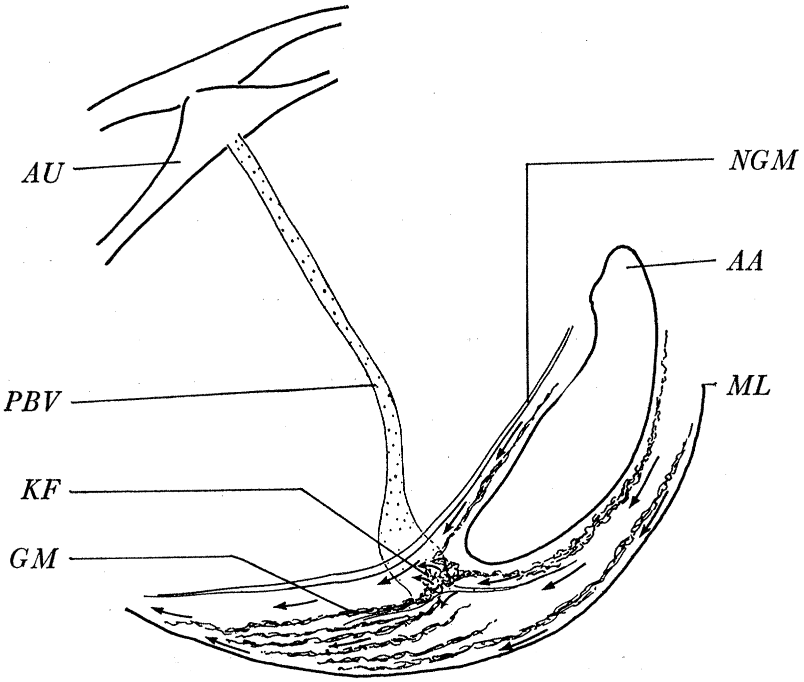


FIGURE 3. *Codakia orbicularis* (magn. × 2). The left mantle showing the disposition of the mantle 'gills' and the pallial blood vessel. *AA*, anterior adductor muscle; *AU*, auricle; *GM*, mantle gill; *KF*, 'knot'; *NGM*, non-ridged fold; *PBV*, pallial blood vessel. Other lettering as before.

The folds in the two species are similar histologically (figure 5). In transverse section they appear as convoluted folds of the inner mantle epithelium (*IME*). Internally they are composed of blood spaces surrounded by a parenchymatous packing tissue. As noted by Pelseneer (1911), few gland cells occur. The epithelium is more strongly ciliated than the general mantle epithelium.

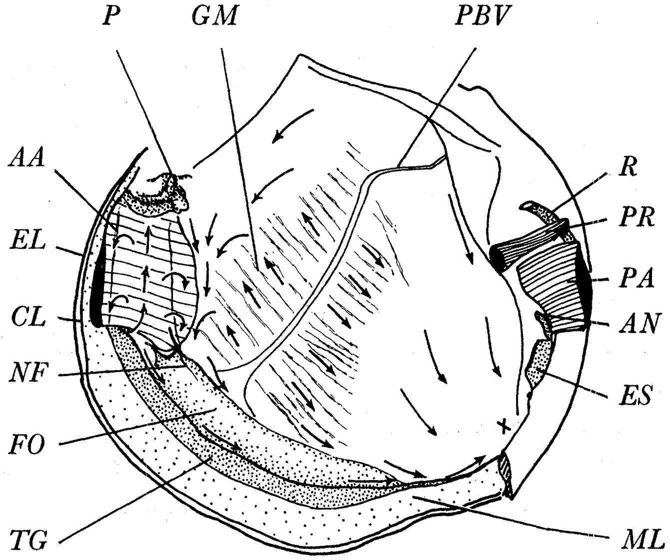


FIGURE 4. *Lucina pennsylvanica* (magn. × 3). The right mantle showing the position of the mantle 'gills', the pallial blood vessel and the direction of the ciliary currents. *AN*, anus, *ES*, exhalent siphon; *NF*, anterior pallial nerve; *PA*, posterior adductor muscle; *PR*, posterior retractor muscle. Other lettering as before.

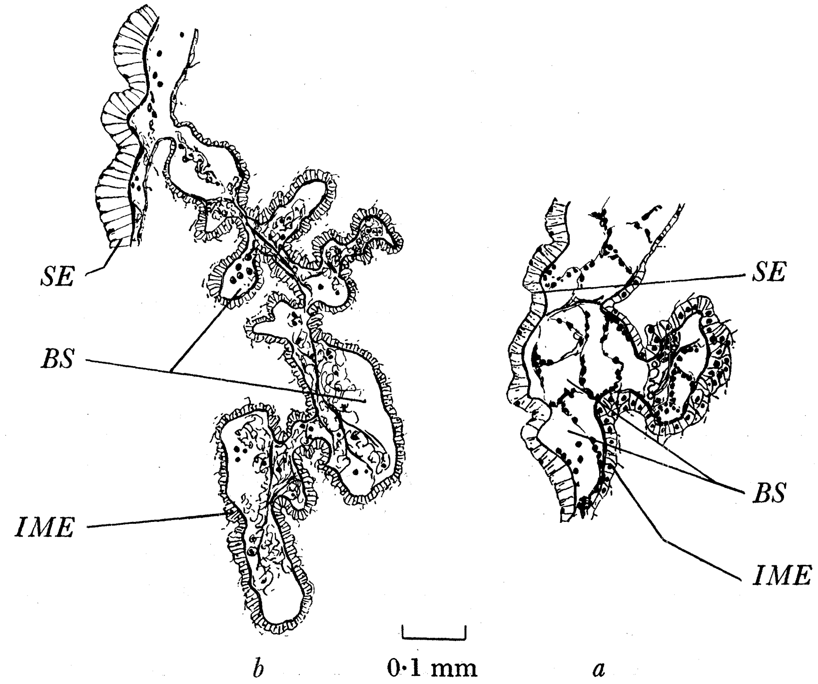


FIGURE 5. Transverse sections through the mantle gills of *a*, *Lucina pennsylvanica* and *b*, *Codakia orbicularis*. *IME*, inner mantle epithelium. Other lettering as before.

It seems probable that these 'gills' are respiratory in function as was suggested by Pelseneer. Not only are all the pallial blood spaces greatly extended but a large pallial blood vessel is present. This vessel is largest in those species with mantle gills (figures 3 and 4). A large blood sinus lies immediately posterior to the anterior adductor muscle and beneath the 'knot' when this is present. Blood enters from two large vessels that lie parallel to the mantle edge, one anterior to the sinus and the other posterior, and which receive blood from the blood spaces in the mantle. From the sinus blood is transported directly to the auricle by means of the large pallial vessel. Oxygen is probably absorbed through the mantle in all lamellibranchs, but the Lucinacea appear to be unique by increasing the pallial surface for this purpose.

Mantle glands

All species of *Diplodonta* examined, *Thyasira flexuosa*, *Lucina pennsylvanica*, *Divaricella quadrisulcata* and *Codakia orbicularis* show a marked concentration of glandular cells on the upper edge of the inner mantle lobe below the main rejection tract (figure 2). The glands are most concentrated at the posterior end of the anterior adductor muscle, just anterior to the posterior inhalent aperture in the region where the pseudofaeces are formed and also, in the Lucinidae, at the base of the exhalent siphon.

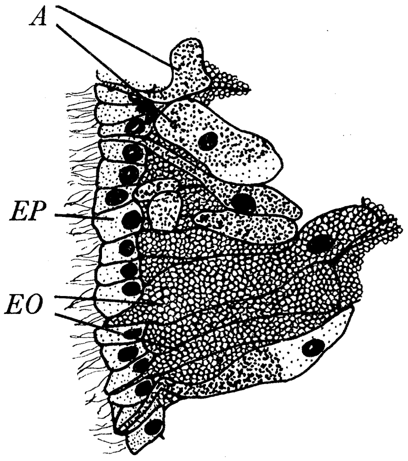
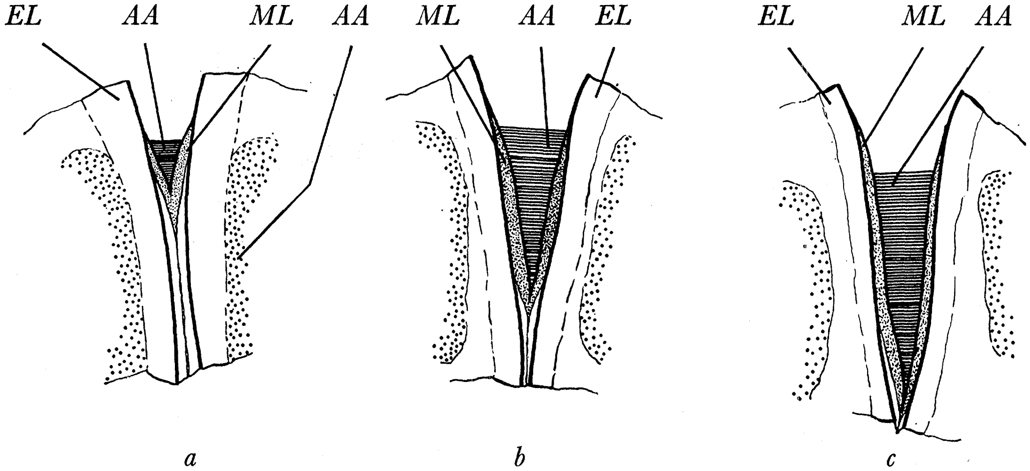


FIGURE 6. Transverse section of the glands cells of the inner mantle lobe below the rejection tract (magn. × 200). *A*, Alcian blue staining cells; *EO*, eosinophils; *EP*, epithelium.

The cells are large, up to 30 μ long, and regular in shape (figure 6). They are packed with large granules and open to the surface by a narrow neck between the epithelial cells. Staining distinguished two types of gland cell. One stained well with Alcian blue (*A*) and the other very markedly with eosin (*EO*) in the Alcian blue-haematoxylin-eosin technique of Steedman (1950). The only apparent difference between the two types of cells, was that the eosinophils had large spherical granules of a similar size, while the Alcian blue staining cells had smaller granules of a varying size. The latter were found closer to the mantle epithelium than the eosinophils. In some specimens all the gland cells stained with Alcian blue. Typically, a mucus-secreting cell stains heavily with basic dyes (Alcian blue), but Steedman, in a personal communication, confirms that eosinophilic glands are found in the Mollusca and suggests that such glands produce a mucin that is a carrier for another product. This product may be in sufficient concentration to mask or inhibit the mucin staining reaction. The function of these glands in the Lucinacea is probably related to the rejection of unwanted material from the mantle. They appear to be similar to those described by Hunter (1949) in *Hiatella*.

Mantle fusion and siphon formation

Fusion of the mantle edges is not extensive in the Lucinacea. In the Ungulinidae the anterior fusion of the inner muscular lobe commences just anterior to the posterior limit of the anterior adductor muscle, so that only a small amount of muscle is seen when the valves are relaxed (figure 7). In the Thyasiridae the extent of this anterior fusion is not so great, with two-thirds of the anterior adductor exposed, while in the Lucinidae the



a *b* *c*

FIGURE 7. To show the variation in the extent of anterior mantle fusion in the three families of the Lucinacea. The mantle edges, as seen externally, of *a*, *Diplodonta semiaspera* (Ungulinidae) (magn. × 7); *b*, *Thyasira flexuosa* (Thyasiridae) (magn. × 15); *c*, *Myrtea spinifera* (Lucinidae) (magn. × 7). Other lettering as before.

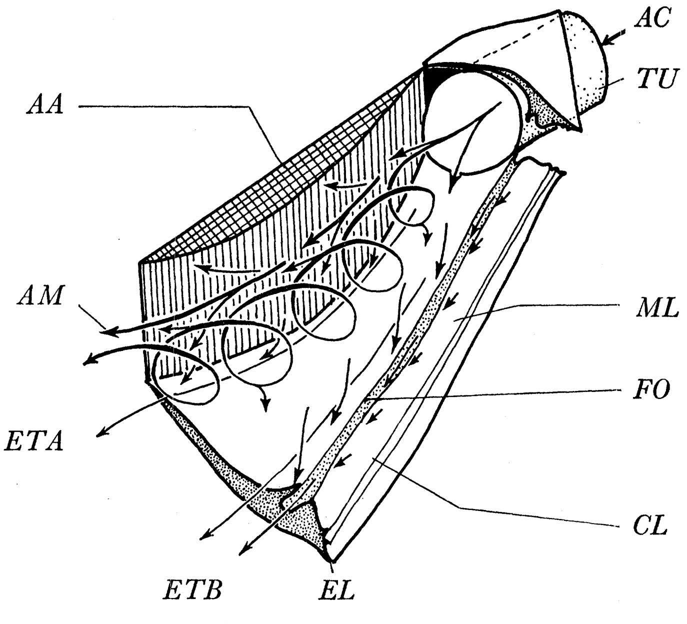


FIGURE 8. Diagram of the outer face of the anterior adductor muscle of a member of the Lucinidae, to show the position of the anterior inhalent tube and the ciliary currents in the channel extending from the aperture of the tube to the posterior end of the adductor muscle. *AC*, anterior inhalent current; *AM*, main current to the mouth; *ETA* and *ETB* rejection tracts (see text); *TU*, anterior inhalent tube. Other lettering as before.

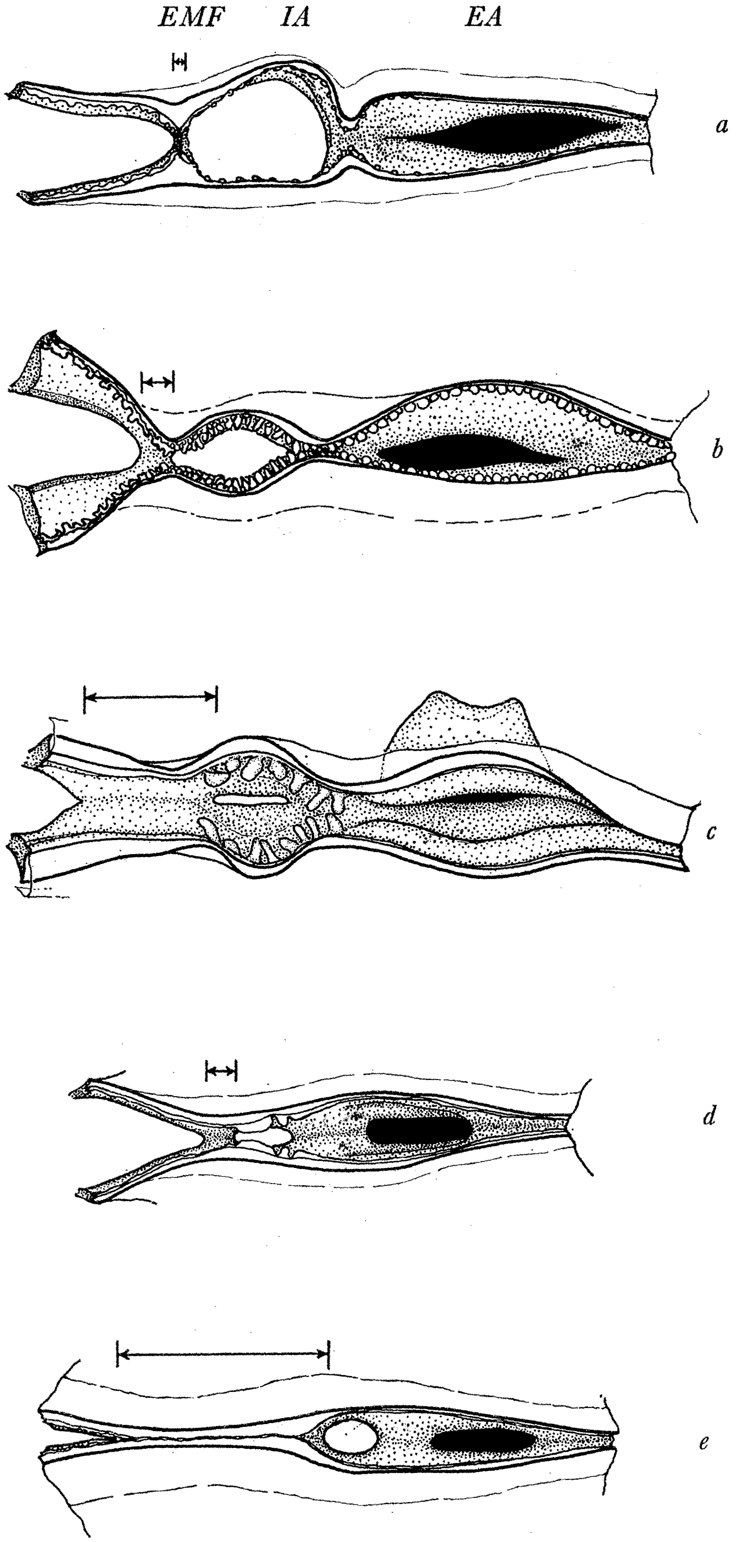


FIGURE 9. External views of the region of the posterior inhalent and exhalent apertures of *a*, *Codakia orbiculata* (magn. × 15); *b*, *C. orbicularis* (magn. × 7); *c*, *Phacoides borealis* (magn. × 20); *d*, *Lucina pennsylvanica* (magn. × 10); *e*, *L. chrysostoma* (magn. × 10). *EA*, exhalent aperture; *EMF*, extent of mantle fusion; *IA*, inhalent aperture.

fusion of the inner lobes commences so far anterior that the outer face of the anterior adductor muscle is completely visible. This is a secondary progressive reduction in the amount of anterior mantle fusion which is correlated with the degree to which the anterior inhalent tube (*TU*) and its sorting mechanisms have been developed (p. 440). In the Lucinidae where mantle fusion is at its minimum anteriorly, a channel connecting the anterior inhalent tube with the mantle cavity is formed and is bounded by the mantle and its inner lobes and the outer wall of the anterior adductor muscle (figure 8).

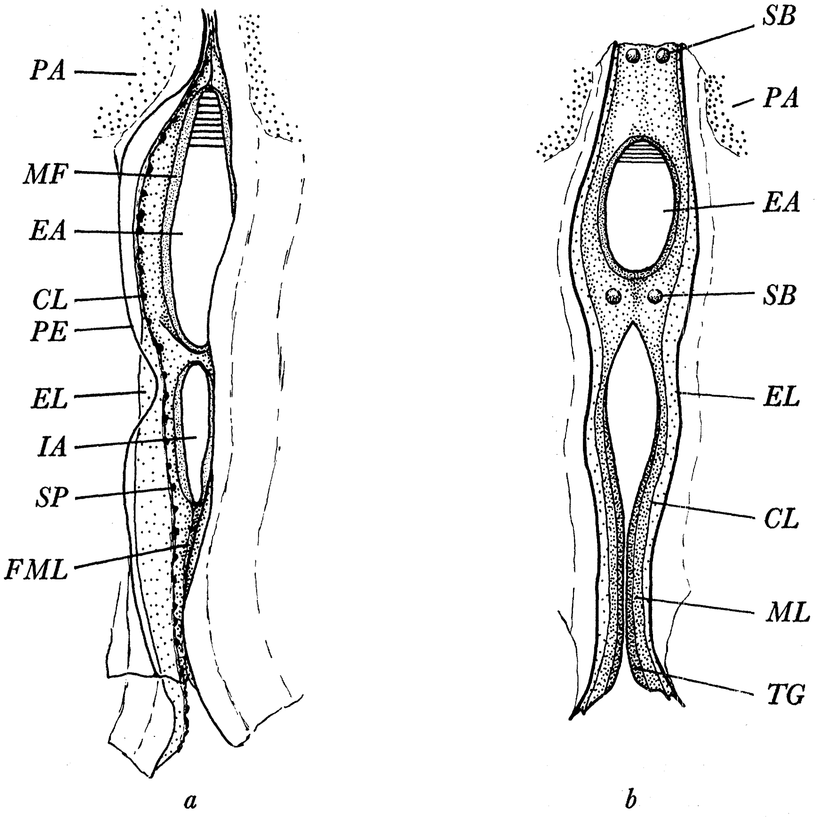


FIGURE 10. *a*, *Diplodonta punctata* (magn. × 18). External view of the posterior inhalent and exhalent apertures. *b*, *Thyasira flexuosa* (magn. × 30). External view of the posterior exhalent aperture. *FML*, fused inner lobes; *MF*, membrane lining the apertures; *SB*, sensory 'button'; *SP*, sensory papillae. Other lettering as before.

Although there is some variation in the amount of fusion between the inhalent aperture and the pedal gape (*EMF*) (figure 9), the mantle is not fused to any great extent posteriorly. The inner fold of the mantle only is concerned.† In most species only the innermost pallial muscles cross connect.

No siphons are present in the Ungulinidae. In the three species of *Diplodonta* examined, the inhalent aperture (*IA*) (figure 10) is approximately one-third the size of the exhalent (*EA*). The apertures are slit-like, surrounded by a thin narrow membrane (*MF*) which is an extension of the inner mantle lobe. On either side of the apertures there are a number of sensory papillae (*SP*). These are modifications of the inner fringe of the middle or sensory

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† This is true in so far as mantle fusion, here, refers to the encroachment of the pedal gape and siphon formation. Below the ligament mantle fusion involves much more of the mantle edge.

lobe (p. 428). The outer fringe continues unmodified around the apertures. The number of papillae varies from species to species, but in large specimens of *D. punctata* there may be as many as twenty-five on either side of the apertures. They are small, simple structures extending no further than the inner fringe and showing no histological difference from it.

The Thyasiridae differ markedly from the Ungulinidae. Only the exhalent aperture is formed by tissue fusion, the inhalent aperture being formed by a cuticular fusion of the inner mantle lobe similar to that described by Atkins (1937*c*) (figures 10 and 11). *Thyasira* further differs from *Diplodonta* in the absence of sensory papillae on either side of the apertures. There are, however, two pairs of sense organs (*SB*), one pair at the anterior and the other pair at the posterior limit of the exhalent aperture (figure 10). These are small cushions, approximately 60 μ in diameter, which are made up of a series of long-radiating ciliated cells (figure 12). The cilia (60 to 70 μ) are longer than the cells (50 to 60 μ) and very dense. They connect with basal granules just below the surface of the cells, and the granules are connected in their turn to a narrow cone of fibres that terminate at the base of the cell. The nucleus is large and lies alongside the cone of fibres. The cell walls are difficult to distinguish. In some sections nerve fibres could be seen passing into the base of the cushion. There seems little doubt that the cushions have a sensory function.

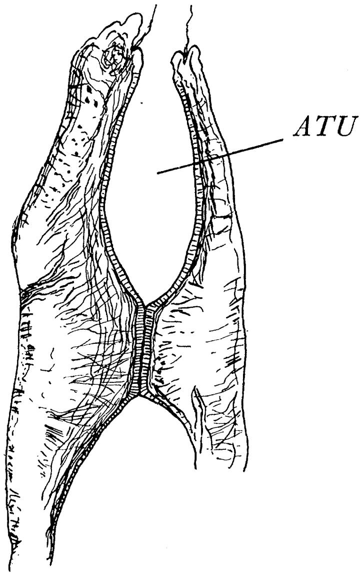


FIGURE 11. Transverse section of *Thyasira flexuosa* showing cuticular fusion of the mantle adjacent to the anterior adductor muscle (magn. ×40). The aperture (*ATU*) so formed encloses the base of the anterior inhalent tube.

The Lucinidae show variation in the form of the sensory lobe in the region of the posterior apertures. Papillae are present in all species except *Lucina chrysostoma* and *L. pennsylvanica*. In *L. chrysostoma* the sensory lobe remains unmodified, but in *L. pennsylvanica* there is a small bilobed flap in place of the usual papillae (figure 9*d*). In other species the papillae always occur on either side of the inhalent aperture, but only in *Codakia orbicularis* and *C. orbiculata* do they border the exhalent aperture. The papillae are similar to those of the Ungulinidae. They vary in number from as few as six on each side of the aperture in *Loripes lucinalis* to over a hundred in *Codakia orbicularis*. The latter species was the only one taken in which both fringes of the sensory lobe are modified forming a double row of papillae. In other species of the Lucinidae, as in the Ungulinidae, they are confined to the inner fringe.

The Lucinidae differ from the Ungulinidae and the Thyasiridae in possessing an exhalent siphon (*ES*). No member of the Lucinacea examined had a posterior inhalent

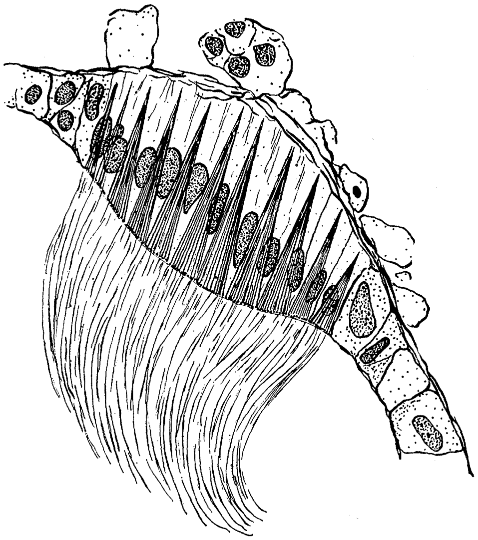


FIGURE 12. Vertical section through a posterior sense organ of *Thyasira flexuosa* (magn. × 500). For explanation see text.

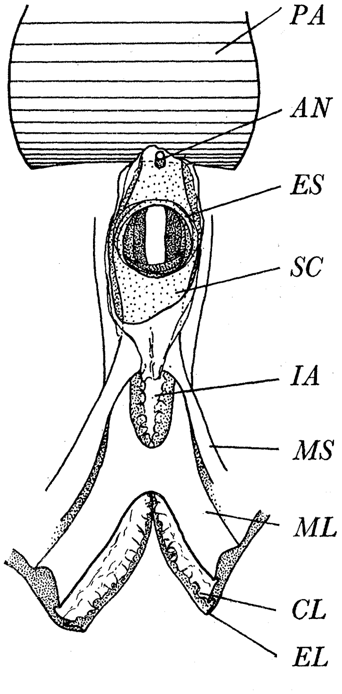


FIGURE 13. The region of the posterior apertures in *Codakia orbicularis* as seen from the inside of the mantle (magn. × 2). The retracted exhalent siphon lies in the posterior end of the suprabranchial chamber. The ctenidia have been removed. *MS*, muscles to the exhalent siphon; *SC*, suprabranchial cavity. Other lettering as before.

siphon. The exhalent siphon is developed solely from the inner muscular lobe of the mantle and is of a type unique in the Lamellibranchia.

No siphonal retractors of the normal type are present and no pallial sinus is formed. The retracted siphon is turned inside out and lies in the suprabranchial cavity (*SC*) (figure 13). It can extend at least six times the length of the shell, i.e. to the same extent as the foot (p. 443). Retraction involves a shortening of the extended siphon which then inverts in the manner shown in figure 14. When it is extended the reverse procedure takes place. A small pair of muscles (*MS*) that originate just anterior to the posterior inhalent aperture to the inside of the inner mantle lobe extend into the base of the siphon and along its length. In addition, muscle fibres from the fused inner lobes pass into the base of the siphon and form part of the longitudinal musculature. Beneath both inner and outer epithelia of the siphon there is a scattered layer of circular muscle fibres and to the inside of these there is a layer of longitudinal fibres. There are no marked nerve cords of the type found in the Tellinacea (Yonge 1949).

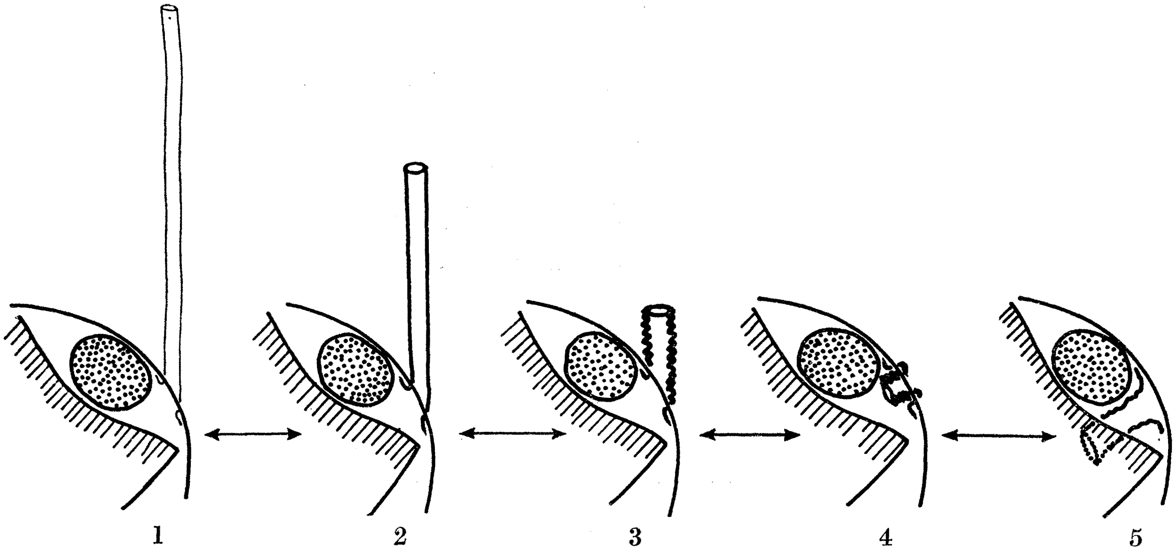


FIGURE 14. To illustrate the method of contraction and expansion of the posterior exhalent siphon of the Lucinidae.

The absence of an inhalent siphon and the very slight posterior inhalent current supports the conclusion that the main function of this aperture is the disposal of pseudofaeces. The main feeding and respiratory current enters by way of the anterior inhalent tube. This conclusion is supported by other morphological features and will be discussed later (p. 480).

Adductor muscles

In the Lucinacea the anterior adductor muscle is elongate and its degree of development is associated with the ability of the animal to form an anterior inhalent tube. The muscle lies parallel to the mantle edge and the greater part of it is ventral and posterior to the mouth (figure 15). The three families form an evolutionary series (figure 1). In the Ungulinidae, the least specialized, the anterior adductor is slightly elongate and lies close to the inner lobe of the mantle. The Thyasiridae and the Lucinidae show progressive elongation of the muscle and the distance between the inner lobe and the ventral end of the adductor muscle increases with the formation of the channel connecting the end of the inhalent tube with the mantle cavity. Thus, the anterior adductor forms a shelf across the mantle cavity ventral to the mouth. The secondary displacement anteriorly of the point of mantle fusion has been referred to already (p. 433) (figure 7).

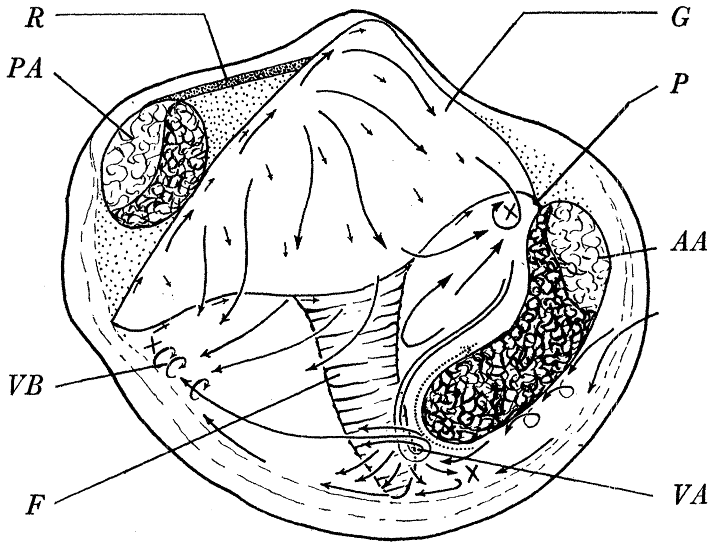


FIGURE 15. *Phacoides borealis* (magn. × 4). To show the direction of the ciliary currents on the mantle (large arrows) and gills (small arrows). *G*, gill; *VA* and *VB*, vortex. The symbols *X* indicate accumulation of rejected material on the mantle. Other lettering as before.

The epithelium covering the muscle is ciliated and acts as the major sorting area for particles entering by the anterior inhalent current. This sorting mechanism is described below.

The nearest approach to this condition in other lamellibranchs, appears to be that of the Montacutidae, the morphology and ciliary currents of which have been described in detail by Popham (1940). All members of the Erycinacea have an anterior inhalent current; but only in the Montacutidae is the anterior adductor noticeably elongate, but never to the same extent as in the Lucinacea. It is not stated whether the epithelium covering the muscle is ciliated.

The posterior adductor in the Lucinacea is unmodified.

Ciliary currents of the mantle

With the aid of carmine, fine carborundum, Ankolok scarlet Y and normal suspended material in sea water, the ciliary mechanisms of the mantle were plotted. All members of the Lucinacea have two inhalent currents, anterior (*AC*) and posterior. The former is weakest in the Ungulinidae and strongest in the Lucinidae, but in all three families it is the main feeding current. Incoming particles undergo similar methods of sorting. On entering the mantle cavity they are first controlled by the cilia on the adductor muscle and on the mantle adjoining the muscle. Fine particles are accepted by a narrow tract of cilia (*AM*) in the centre of the adductor muscle and conveyed towards the mouth (figures 8 and 16).

Much of the material that enters by the anterior current never reaches the gills and sorting is carried out by the cilia of the adductor muscle and the palps, and in the Lucinidae and the Thyrasiridae, by the cilia of the mantle between the adductor and the inner mantle lobe. In the Ungulinidae the acceptance current on the adductor muscle is not strong and many particles do get swept on to the gills and are sorted in the normal way. In the other two families the acceptance tract on the muscle is more definite and few particles escape its influence. Particles that are not accepted on to the tract are swept to the sides of the muscle where they join the main rejection tract (*RT*). The latter runs from the palps, along the inner junction of the adductor muscle with the mantle to the inside of the inner lobe, as far as the posterior inhalent opening.

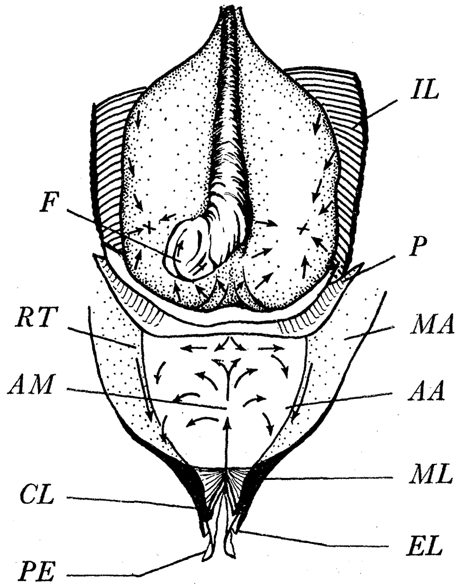


FIGURE 16. *Diplodonta semiaspera* (magn. × 4). Ventral view to show the direction of the ciliary currents on the anterior adductor muscle and the body. *MA*, mantle. The symbols *X* indicate accumulation of rejected material on the body. Other lettering as before.

In the Thyasiridae and the Lucinidae the portion of the mantle that lies between the adductor and the inner lobe, i.e. the sides of the channel connecting the inhalent tube with the mantle cavity, plays an important part in the sorting of the incoming particles. In this region the ciliary beat on the inner lobe and the mantle, together with that on the adductor muscle, produces a spiral movement of the water (figure 8). Particles, fine ones in particular, progress down this channel in a corkscrew fashion and tend to be carried on to the acceptance tract. Heavy particles fall away from the swirl and are carried along either a rejection tract (*ETA*) close to the edge of the muscle or a rejection tract (*ETB*) on the inner lobe.

At the posterior limit of the anterior adductor muscle the ciliary currents are complex. The rejections tracts (*RT*, *ETA*, *ETB*) from either side of the adductor meet at this point and continue towards the posterior inhalent aperture, while the acceptance tract curves round the muscle towards the mouth. This results in a vortex (*VA*) immediately posterior to the anterior adductor. Rejected material from the vortex is passed posteriorly on either side of the mantle fold if this is present (figure 15). The vortex tends to compact the rejected material into small masses bound in mucus which accumulate at the point *X* opposite the posterior limit of the anterior adductor. These masses may fall out of the mantle cavity when the valves gape, but more usually are passed to the posterior inhalent aperture. There is a second vortex (*VB*) at the base of the aperture which compacts the rejected material into peudofaeces.

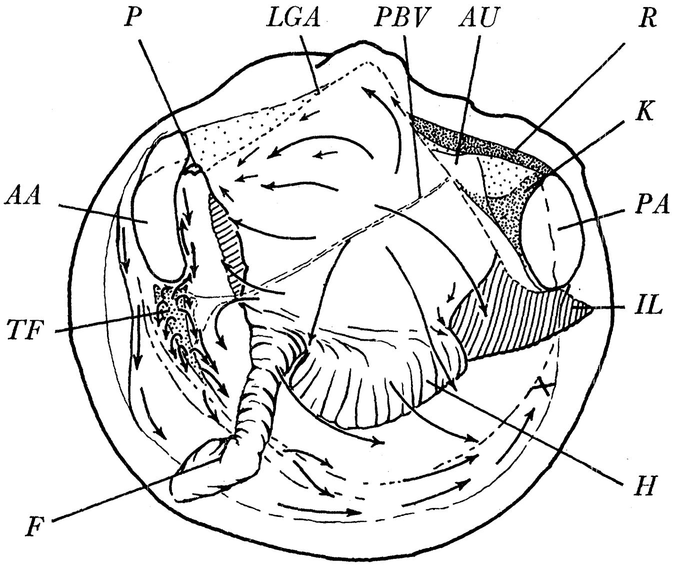


FIGURE 17. *Divaricella quadrisulcata* (magn. × 5). Lateral view with the left demibranch removed to show the direction of the ciliary currents on the mantle (large arrows) and on the body (small arrows). *H*, heel; *K*, kidney; *LGA*, line of attachment of the left demibranch; *TF*, triangular fold. The symbol *X* indicates accumulation of rejected material on the mantle. Other lettering as before.

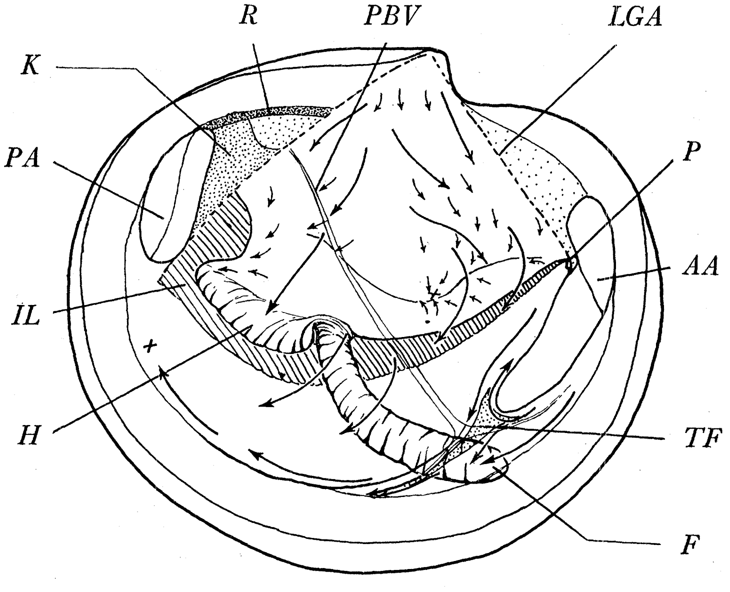


FIGURE 18. *Lucina chrysostoma* (magn. × 3). Lateral view with the right demibranch removed to show the direction of the ciliary currents on the mantle (large arrows) and on the body (small arrows). The symbols *X* indicate accumulation of rejected material on the body and mantle. Lettering as before.

In *Divaricella quadrisulcata* and *Lucina chrysostoma* (figures 17 and 18) the mantle fold forms a raised triangle (*TF*) posterior to the adductor muscle. This acts in a similar fashion to a traffic island. Rejected particles from each side of the anterior adductor are carried posteriorly along the corresponding sides of the triangle. Accepted particles are separated from those to be rejected and are guided round the posterior end of the anterior adductor. Thus the first vortex (*VA*) is lost. The cilia on the triangle beat outwards and in the direction of those of the nearest ciliated tract.

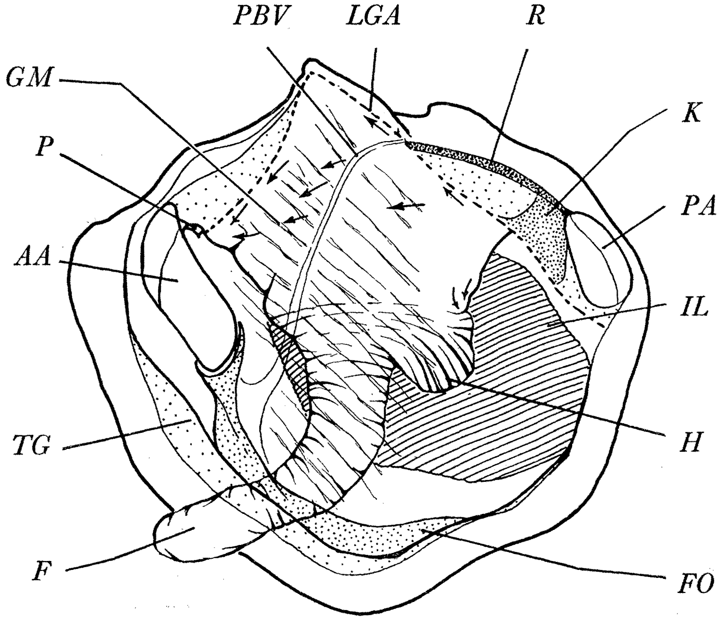


FIGURE 19. *Lucina pennsylvanica* (magn. × 4). Lateral view with the left demibranch removed to show the direction of the ciliary currents on the body. Lettering as before.

In *Codakia orbicularis* the ciliary currents are parallel to the mantle gills (figure 3). Particles are conveyed off the folds and transported in the channels between. The 'knot' corresponds to the position of the first vortex. In *Lucina pennsylvanica* (figures 4 and 19) the well-developed mantle fold posterior to the anterior adductor functions in the way described above, but the mantle folds forming the 'gill' are not parallel to the main rejection tracts, but fit into the pattern of the ciliation on the remainder of the mantle surface.

In all species the ciliary currents internal to the main rejection tracts resolve into two general directions. Those anterior to a line between the posterior end of the anterior adductor muscle and the heart carry particles from the region of the junction of the gill and mantle towards the mouth, while posterior to this line the particles are carried ventrally and posteriorly towards the point *X* where the pseudofaeces accumulate (figure 15). The anterior currents carry particles ventrally until they are opposite the gill edge and then towards the mouth, i.e. they follow the general direction of particles on the gills. Particles on the innermost part of the rejection tracts may be swept back towards the mouth. This anterior current towards the mouth is not so marked in *Diplodonta*, where particles are carried downwards and slightly forward past the palps to the rejection tract (figure 20).

In *Lucina pennsylvanica* ciliary currents anterior to the pallial blood vessel carry particles anteriorly parallel to the mantle gills. Particles posterior to the vessel are carried posteriorly parallel to the folds. The demarcation between the two regions is sharply defined and as in *Codakia orbicularis* the particles move between the folds. Anteriorly directed particles reaching the anterior limit of the mantle gills are carried downwards past the palps to the main rejection tract. Particles reaching the posterior limit of the folds are carried to the posterior inhalent aperture (figures 4 and 19).

All species have a weak anteriorly directed current at the junction of the mantle and gill.

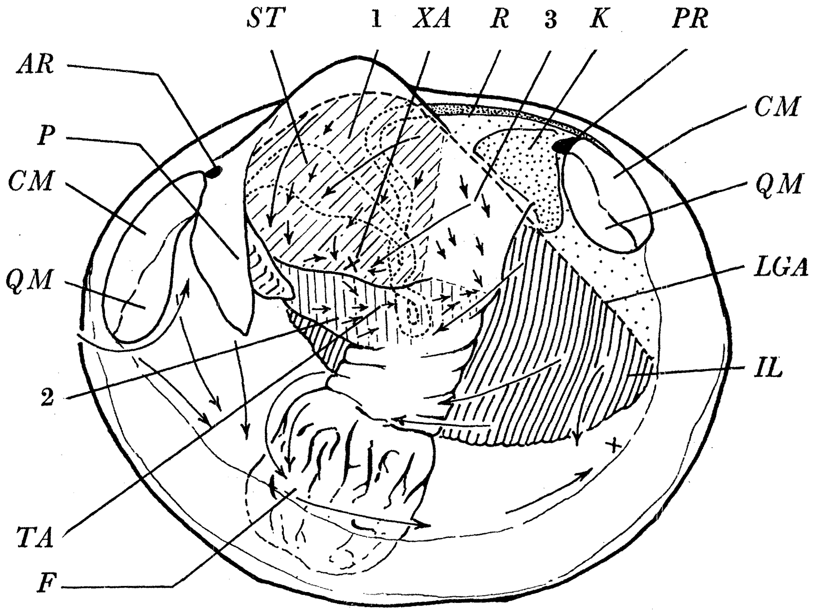


FIGURE 20. *Diplodonta punctata* (magn. × 4). Lateral view with the left demibranchs removed to show the direction of the ciliary currents on the mantle (large arrows) and on the body (small arrows). The course of the alimentary canal is indicated. *AR*, anterior retractor muscle; *ST*, stomach; *TA*, ciliated tract; *XA*, point of accumulation of rejected material on the body; 1, 2 and 3, ciliated areas of the body. The symbol *X* indicates the accumulation of rejected material on the mantle. Other lettering as before.

FOOT

In the Lucinacea the foot (*F*), in addition to its burrowing and locomotory functions, is responsible for forming an anterior inhalent tube (figure 67, plate 18). In the Lucinidae, particularly in *Divaricella quadrisulcata*, *Lucina chrysostoma* and *L. pennsylvanica* (figures 17, 18 and 19), there is a division into a spade-like heel (*H*) and a typically long vermiform foot. Thus, some division of labour is achieved, the heel being concerned with the movement of the animal and the foot with tube building.

In the Ungulinidae the foot is not as markedly vermiform as in the other families, but is somewhat laterally flattened. The tip is distinct and much wider than the proximal part. The corrugations of the tip run lengthways, while those of the proximal part run transversely (figure 20). These corrugations reflect the form of the expansion, the proximal part increasing in length while the distal part becomes very bulbous. The expansion in the Ungulinidae is not as marked as in the other families, but even so, the foot may expand to more than three times the length of the shell. The heel in *Diplodonta* is not well marked, yet it can expand considerably and acts in the same manner as that of the Lucinidae.

In the Thyasiridae, the foot reaches its maximum length relative to the size of the animal but is correspondingly much thinner, even when contracted it lies slightly coiled in the mantle cavity (figure 21). The foot is tubular and the tip is bulbous and distinct from the proximal part. The tip differs from that in the Ungulinidae in that it is divided into two parts, the proximal part with transverse corrugations and the distal part with longitudinal corrugations (figure 1). The foot of *Thyasira* can expand to a remarkable extent, to more than ten times the length of the shell. There is no heel.

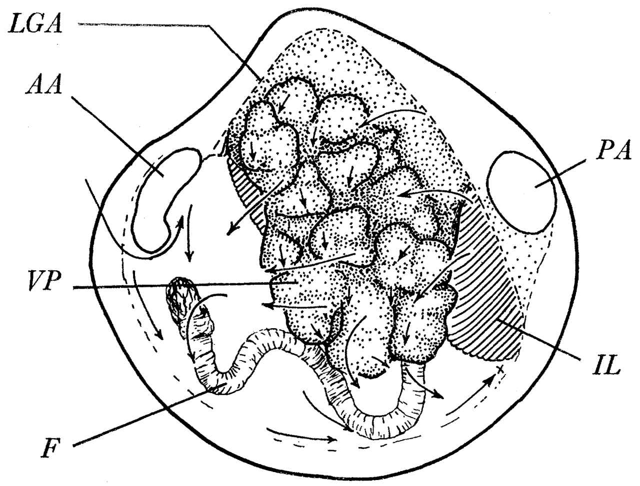


FIGURE 21. Lateral view of *Thyasira flexuosa* with the left demibranchs removed to show the ciliary currents on the mantle (large arrows) and on the visceral pouches (small arrows) (magn. × 15). The symbol X indicates the accumulation of rejected material on the mantle. Lettering as before.

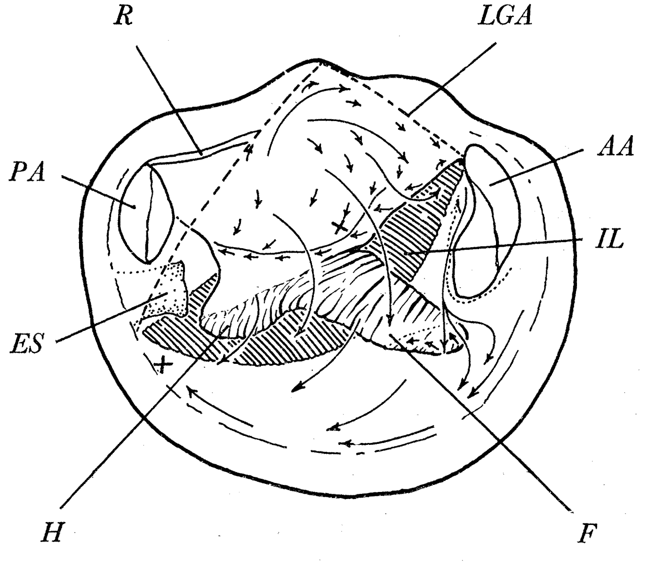


FIGURE 22. *Codakia costata* (magn. × 10). Lateral view with the right demibranch removed to show the direction of the ciliary currents on the mantle (large arrows) and on the body (small arrows). The course of the alimentary canal is indicated. The symbols X indicate the accumulation of rejected material on the mantle and body. Other lettering as before.

The Lucinidae also have a long vermiform foot that can expand to more than six times the length of the shell. Only *Loripes lucinalis*, *Divaricella quadrisulcata* and *Lucina chrysostoma* have a distinct bulbous tip to the foot (figures 1, 17 and 19). Other species have pointed tips which can become bulbous (figures 15 and 22). Longitudinal corrugations of the tip are not marked in the Lucinidae. In contrast to the other families the heel is very well developed, particularly so in those species with a well-defined tip.

The anatomy of the foot is similar in all the Lucinacea and has been generally described by Barrois (1885) and by Menégaux (1890) but more detailed description is justified now that the true functions of the foot in the Lucinacea are known (Allen 1953). The epidermis of the heel and the tip of the foot is heavily ciliated (*CEC*) and the cilia are very regular in length. Immediately below the epidermis there is a narrow layer of circular muscles (*MC*) (figure 23), and to the inside of the latter there is a thin layer of longitudinal musles (*ALM*) which follows the contours of the transverse corrugations. These fibres are short and appear to extend from the summit of one fold to that of the next so that in the contracted foot they are U-shaped. These are derived from the outer elements of the pedal retractor muscles which also form the next muscular layer. This inner layer of longitudinal muscles (*BLM*) extends the length of the foot, although not well marked in the tip. Between the two longitudinal layers there is a scattering of connective tissue, circular muscle fibres and a few mucus-secreting gland cells of the type present in the tip (see below). Inside the inner longitudinal muscle fibres there are more circular muscle fibres and connective tissue. There is no distinct lining to the central blood space (*CBS*) that runs the whole length of the foot. Throughout the foot secondary lateral blood spaces connect with the central

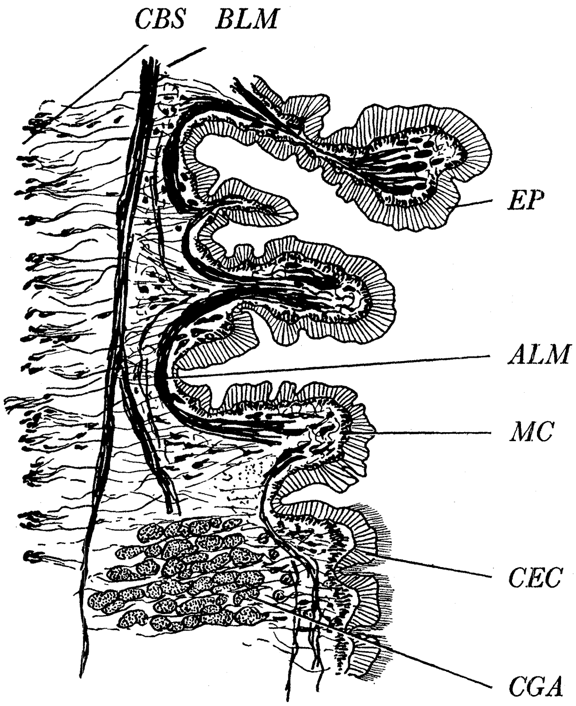


FIGURE 23. Sagittal section through the foot of *Divaricella quadrisulcata* at the junction of the tip with the proximal part (magn. × 70). *ALM*, longitudinal muscle; *BLM*, inner longitudinal muscle; *CBS*, central blood space; *CEC*, ciliated epidermal cells; *CGA*, gland cells; *EP*, epidermis; *MC*, circular muscle.

sinus giving a sponge-like structure. A number of transverse muscle fibres cross the central sinus.

The tip of the foot has become specialized for the construction of the inhalent tube. The epidermis is ciliated and longitudinal muscles are much reduced, while there is great development of the circular muscles and gland cells (*CGA*). These cells, although smaller, are similar to those in the inner mantle lobe. They are present in great numbers below the epidermis and, like those of the mantle, the cells closest to the epithelium stain with Alcian blue while those to the inside stain with acid dyes. Barrois (1885) does not distinguish two types of cell. He describes the cells as being shaped like Prince Rupert's drops with the fine tip opening between the epithelial cells. The description is accurate and it is these glands that lay down the mucus for the building of the inhalent tube.

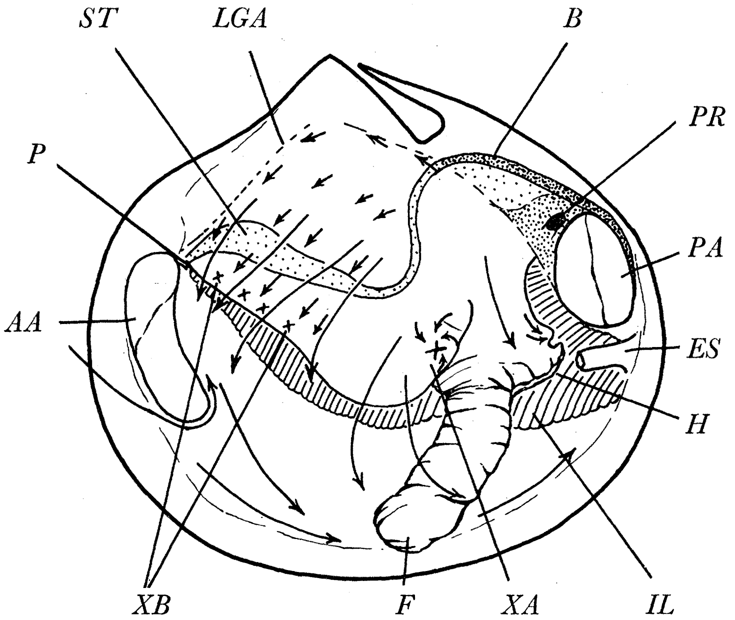


FIGURE 24. *Loripes lucinalis* (magn. × 4). Lateral view with the left demibranch removed to show the direction of the ciliary currents on the mantle (large arrows) and on the body (small arrows). The course of the alimentary canal is indicated. *XB*, accumulation of rejected material. Other lettering as before.

The heel of the foot is also ciliated. Below the epidermis there is a thin layer of muscle fibres lying in an anterior-posterior direction and below this layer, and at right angles to it, there is a thick layer of retractor muscles. There are central and accessory blood spaces and the heel can expand considerably. When contracted the heel is grooved in the sagittal plane (figure 24). No byssus gland is found in the adult.

Burrowing

A short account of burrowing in *Phacoides borealis* has been given by Stoll (1938) and a brief description in other species of the Lucinacea has been given by Allen (1953) since when further observations have provided information mainly on the use of the heel in burrowing and the method of construction of the tube.

In the Ungulinidae and the Thyasiridae where the heel is little developed the method of burrowing is as follows (figure 25). An animal placed on its side on the surface of the substratum will eventually extend its foot mid-ventrally and push it vertically down through

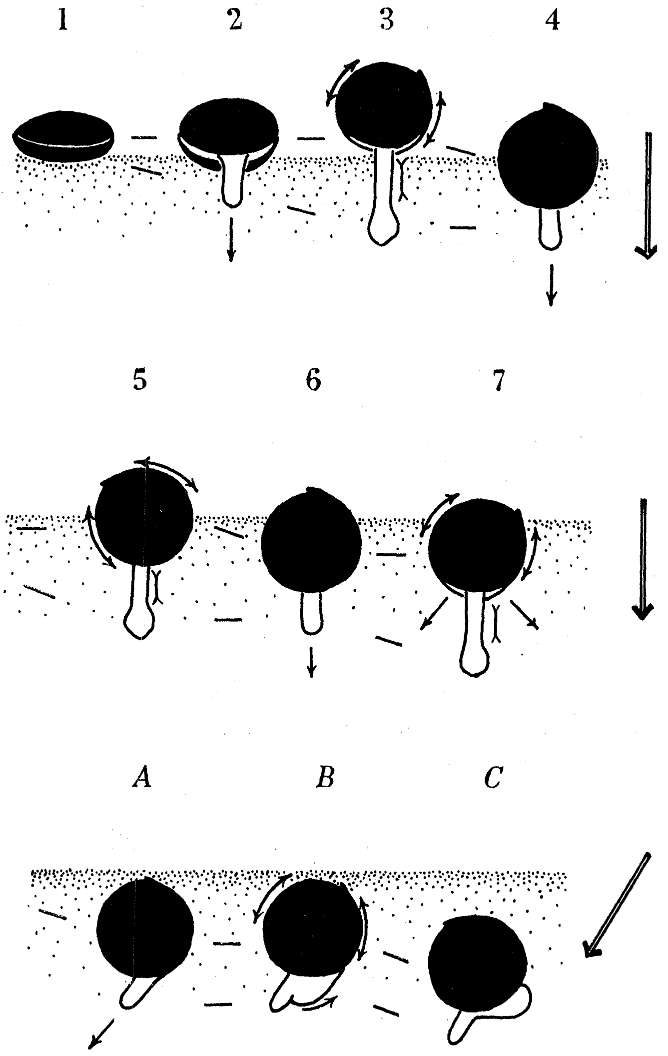


Figure 25. Methods of burrowing in the Lucinacea.

Without the aid of the heel of the foot: (1) Animal lying with its right valve on the substratum. (2) Foot protruded mid-ventrally and pushed vertically down through the substratum. (3) The tip of the extended foot is swollen and bulbous and the foot contracting. Contraction commences proximally and the shell see-saws with the result that the shell is pulled to the vertical position and into the substratum. (4) The foot is again extended vertically downwards. The tip is no longer expanded. (5) The tip of the foot becomes bulbous, contraction of the foot and rotation of the shell is repeated carrying the animal further into the substratum. (6) As for 4. (7) As for 5, but with the addition of the contraction of the shell valves causing the expulsion of water from the mantle which, in its turn, loosens the substratum facilitating the downward passage of the animal.

With the aid of the heel of the foot: (*A*) Submerged shell with the foot partially extended downwards and slightly forwards. (*B*) Foot partially extended. Heel greatly expanded in the anterior region. The shell is see-sawed and the valves may contract with the expulsion of water from the mantle. (*C*) The expansion of the heel moves posteriorly and the shell is moved forwards and downwards by the retractor muscles to the foot.

the substratum. When a length of foot approximately equal to the length of the shell has been extended, the tip of the foot expands. This acts as an anchor. Immediately following this, the pedal retractors contract and the shell is lifted to the vertical or near vertical position. By further, but alternate, contraction of the anterior and posterior retractors the shell is see-sawed backwards and forwards facilitating downward movement. The whole process is repeated until the shell is buried, usually to a depth of 6 to 8 cm, but never more than the maximum extended length of the foot. In addition to the see-saw movement there is often a sharp contraction of the valves followed by a rapid expulsion of water from the mantle cavity which washes away the substratum ventral to the shell.

In the Lucinidae the well-developed heel acts as an additional aid to burrowing. It acts as a plough share during the rocking movement of the shell. The heel alone may be expanded and burrowing is then carried out in the normal lamellibranch fashion. This was observed in those species with a particularly well-developed heel. The animals burrow at an angle to the substratum in a similar manner to that described by Quayle (1949) for *Venerupis pallustra*. *Loripes lucinalis* took approximately 20 min to burrow below the surface but other species took longer. All were in a permanent position and had formed a tube within 10 h of commencing to burrow.

Formation of the anterior inhalent tube

The presence of an anterior inhalent tube was discovered when specimens of *L. lucinalis* were allowed to burrow in their normal substratum contained in a specimen tube. Occasionally animals came to lie by the side of the glass wall and the inhalent tube was attached to it. It was possible to see how the tube was formed. In their permanent position below the surface the shells lie vertically. The contracted foot lies with its tip close to the posterior edge of the anterior adductor muscle. The foot is extended from between the valves at the anterior end of the pedal opening and gradually forces its way upwards by a series of extensions and contractions until the surface is reached. The tip is fully expanded

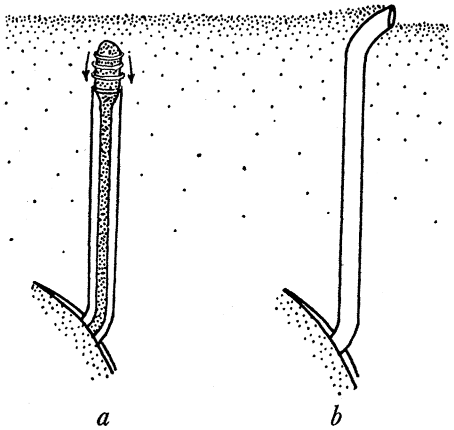


FIGURE 26. Formation of the anterior inhalent tube. *a*, the tube being laid down. The foot is extended and the tip expanded. The latter secretes mucus and the arrows indicate the direction of ciliary beat on the tip compacting the mucus-entangled material. *b*, the tube is fully formed with the last few millimetres lying parallel to the surface of the substratum.

and is responsible for the formation of the wall of the tube. The glands of the tip secrete the mucous lining. Particles are entangled in the mucus while the cilia of the tip beat towards the proximal part of the foot. This action is clear when small quantities of sand are scattered on to the tip. These soon become entangled in a ring of mucus around the tip, while the cilia move the ring towards the non-ciliated part of the foot. The tube can be considered as a series of such rings placed on top of each other. There is no selection of particles, the tube having the character of the substratum. The mucus hardens and it is possible to obtain the larger species with the tube intact (figure 67, plate 18).

The tube does not open vertically to the surface but turns along the surface of the substratum for 2 or 3 mm (figure 26). After it has been formed the foot is periodically protruded so keeping the tube free from debris. The fragile end is frequently broken and new lengths added so that specimens are taken which show several repairs and frequently the remains of previous tips attached to the functional one (figure 67, plate 18). Once the tube is formed the animal remains in the same position for a considerable time and the tube becomes discoloured from the constant passage of particles down it. The shell itself becomes discoloured where the tube enters between the valves. This discoloration is a constant feature in many species, particularly those, such as *Thyasira flexuosa*, that inhabit mud.

Mucous tubes of this kind are not commonly found in the Lamellibranchia. Yonge (1937*a*) showed that in *Thracia pubescens* and also other species of this genus (personal communication) separate mucous tubes are formed by the siphons. In some Gastropoda essentially the same type of tube is formed by the proboscis as shown by Yonge (1937*b*) in *Apporhais* and by Morton (1951) in the Struthiolariidae. This third method of forming a mucus-lined tube appears to be restricted to the Lucinacea.

Ciliary currents of the body

There is variation in the form of the body and the extent of the ciliation, although the direction of the ciliary currents is fairly constant throughout the Lucinacea. All three families tend to develop lateral outpouching of the body which contains much of the digestive gland and gonad. This tendency is greatest in the Thyasiridae (p. 477) where the lateral pouches are lobulated and connect with the central part of the body by a narrow neck (*N*) (figures 21 and 27). The Ungulinidae and the Lucinidae never develop outpouching to this extent. At the most, e.g. *Diplodonta semiaspera*, there is a marked lateral distension. Some species show no sign of lateral pouches. There appears to be no correlation between globosity and the type of substratum inhabited by the species.

The most extensive ciliation of the body is shown by the Ungulinidae. The ciliation can be divided into three main areas (1, 2 and 3; figure 20). The most extensive of these areas (1) extends over the anterior two-thirds of the body, but not including the ventral region from the mouth to where the foot joins the body. Particles on this area are carried to a point *XA* at the edge of the visceral pouch (figure 20). The most anterior particles are carried past the palps and occasional particles are accepted on to the palps. Except close to the lips and palps the cilia are concerned with the rejection of particles.

In the second area (2) extending over the anterior retractor muscles, the cilia beat posteriorly and laterally away from the muscles to a well-defined tract (*TA*) at the junction of the musculature of the foot with the body (figure 20). This tract leads to the heel where most of the particles from this second area accumulate. Particles close to the palps and below the outpouching of the body may get carried to the point *XA*. In *D. semiaspera* the ciliated tract to the heel is absent and all the particles from this ventral area are carried to the point *XA*.

The remaining posterior part of the body constitutes the third area (3). Particles are carried to the heel where they join those from the ventral area in species possessing the ciliated tract (*TA*).

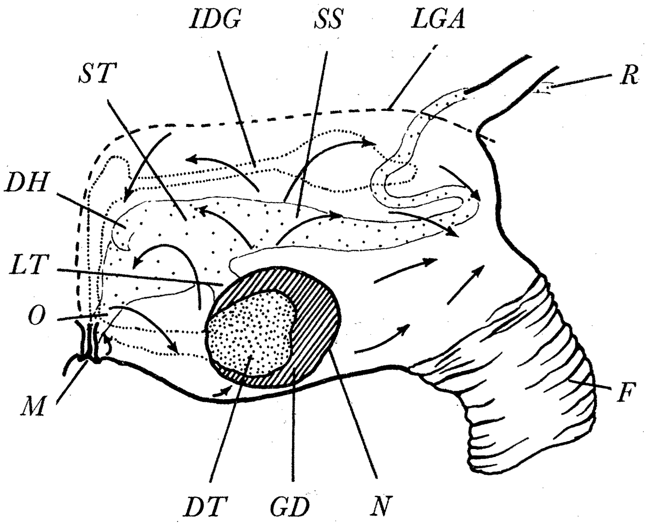


FIGURE 27. Lateral view of the body of *Thyasira flexuosa* with the visceral pouches removed to show the course of the alimentary canal and the direction of the ciliary currents on the body (magn. × 40). *DT*, digestive tubule; *DH*, dorsal hood; *IDG*, inner digestive diverticula; *LT*, left tubule; *M*, mouth; *N*, neck connecting the visceral pouches with the body; *O*, oesophagus; *SS*, style sac. Other lettering as before.

The ciliation close to the lips and palps is better considered in relation to the ciliary mechanisms of the palps (p. 457). Thus, in the Ungulinidae, the main ciliary action on the body leads to the collection of rejected particles at the heel and point *XA* where, enmeshed in mucus, they will eventually drop into the mantle cavity and be conveyed to the posterior inhalent aperture.

In the Thyasiridae there is some variation in the ciliary beat from that described above. This is due to the separation of the lateral pouches from the remainder of the body. The cilia on the pouches carry particles downwards and posteriorly to a point above the main rejection tract of the mantle close to the inhalent aperture. On the body itself, anterior to a line extending vertically from the neck of the pouch to the junction of the gill with body, particles are carried on a circular course from the neck past the palps to the ventral side of the neck and from there to the posterior end of the body (figures 21 and 27). There is no point on the anterior part of the body where rejected material accumulates. Posterior to the line described above, particles are carried on a circular course from the neck to the heel where they join those from the anterior part of the body. Although there is no anterior point of accumulation the basic pattern of the ciliary currents is similar to that of the Ungulinidae.

This basic pattern is shown also by the Lucinidae where three areas corresponding to those in the Ungulinidae can be distinguished. However, there is considerable variation among the species and the ciliation may be much reduced. A series can be traced from *Codakia costata* (figure 22), in which the ciliation is similar to that of *Diplodonta punctata*, to *Phacoides borealis* (figure 39) where the ciliation is reduced to a small area close to the palps. *Codakia costata* differs from *Diplodonta punctata* in possessing an additional, narrow, weakly ciliated tract along the line of fusion of body and gill.

As in the Ungulinidae the first reduction involves the loss of the ciliated tract that runs along the junction of the body and foot to the heel. In addition, cilia are lost ventrolaterally above the foot, resulting in the partial separation of the anterior and posterior ciliated areas. This form of ciliation is found in *Myrtea spinifera* (figure 28).

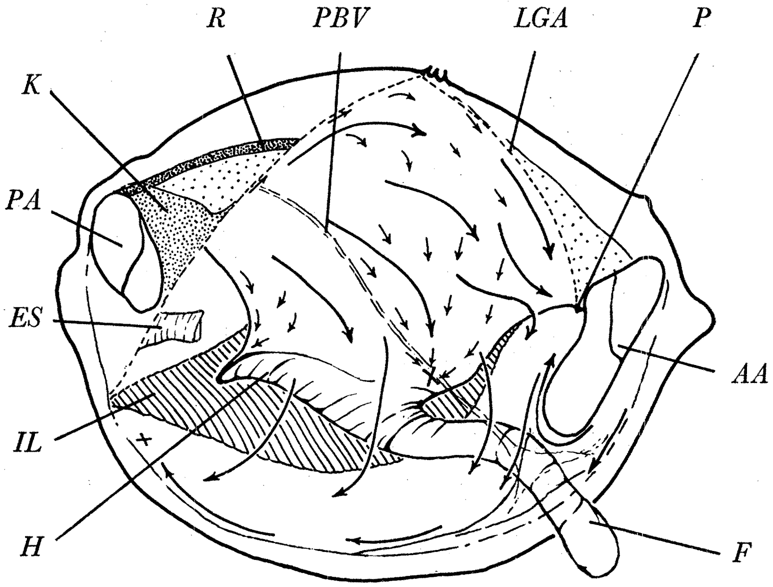


FIGURE 28. Lateral view of *Myrtea spinifera* with the right demibranch removed to show the direction of the ciliary currents on the body (small arrows) and on the mantle (large arrows) (magn. × 8). The symbols *X* indicate accumulation of rejected material on the body and mantle. Lettering as before.

In *Codakia orbicularis* and *C. orbiculata* (figures 29 and 30) the non-ciliated region above the foot is more extensive, resulting in the complete separation of the anterior and posterior areas. There is considerable reduction in the extent of the posterior area and there is modification of the ciliation of the anterior area. Where in the Ungulinidae and the Thyasiridae the most anterior particles are conveyed *past* the palps, in the latter two species there is a ciliated tract leading *to* the palps. Ventral to this tract the cilia continue to beat to the point *XA*.

In *Loripes lucinalis* (figure 24) the ciliation around point *XA* is separate from that of the remainder of the anterior area. The tract leading to the palps is not so circumscribed as that in *Codakia orbicularis* and particles not transferred to the palps accumulate on the antero-ventral part of the body (*XB*). The posterior area in *Loripes lucinalis* is limited to a small area immediately above the heel.

In *Divaricella quadrisulcata* and *Lucina pennsylvanica* (figures 17 and 19) cilia are confined to a small area above the posterior part of the heel and a poorly defined anterior tract to the palps. Finally, in *Phacoides borealis* (figure 39) the ciliation is reduced to a small area close to the palps. The weak current following the junction of gill and body is present in all species.

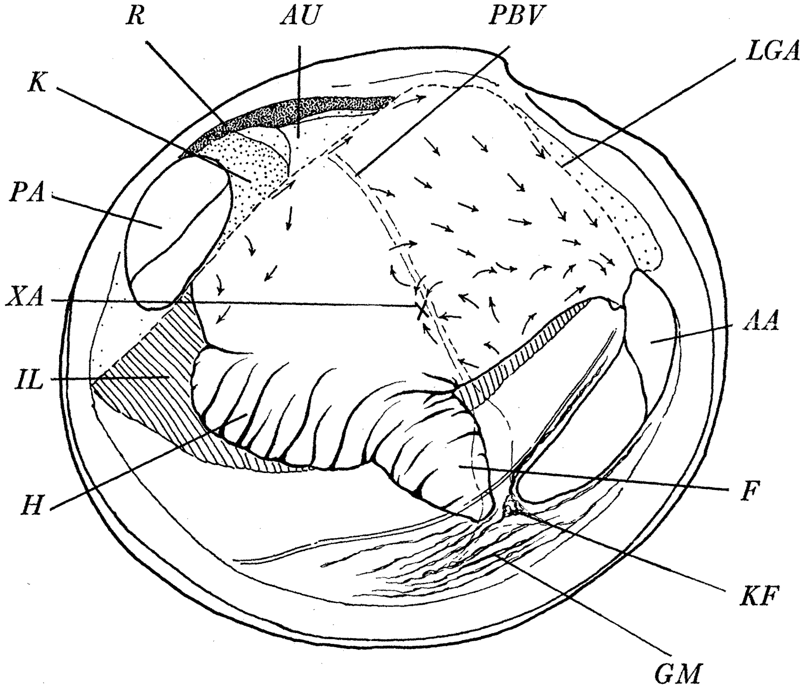


FIGURE 29. Lateral view of *Codakia orbicularis* with the right demibranch removed to show the direction of the ciliary currents on the body (magn. × 1½). Lettering as before.

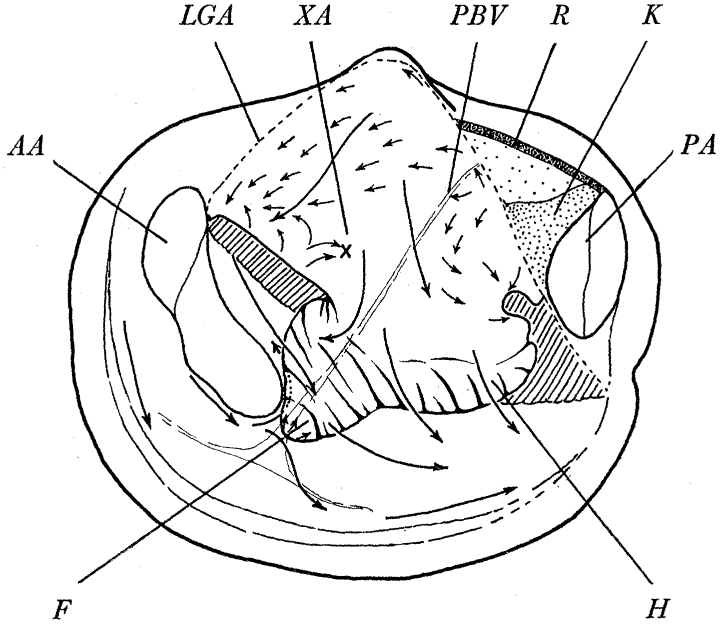


FIGURE 30. Lateral view of *Codakia orbiculata* with the left demibranch removed to show the direction of the ciliary currents on the body (small arrows) and on the mantle (large arrows) (magn. × 6). Lettering as before.

GILLS

The gills of several British species of the Lucinacea have been described by Atkins (1937*a*, *b* and 1938*a*, *b*) and her observations have been extended. The present study indicates an evolutionary sequence involving secondary reduction in size and ciliation comparable to that shown by the palps and stomach (pp. 457 and 466). It also shows that Purchon (1939) was incorrect in asserting that it is the inner demibranch that is lost in the Lucinidae.

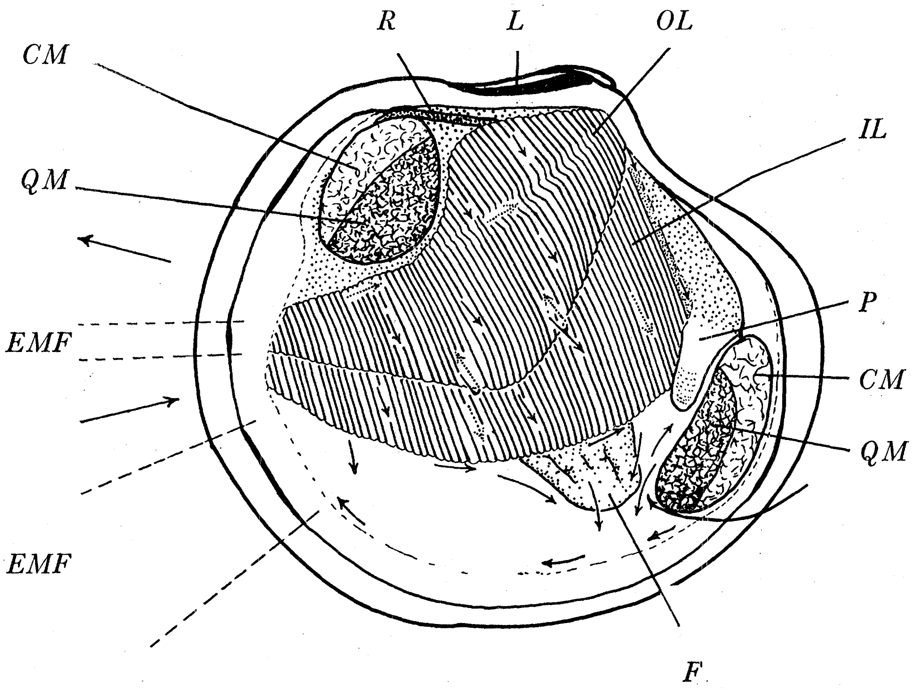


FIGURE 31. Lateral view of *Diplodonta rotundata* to show the direction of the ciliary currents on the gills (magn. × 6). Dotted arrows indicate the direction of the currents on the inner faces of the lamellae. Lettering as before.

In the Ungulinidae both demibranchs are present (figure 31). The inner demibranch (*IL*) is large and extends beyond the ventral margin of the visceral mass, while the outer demibranch (*OL*) is about half this size and has a characteristic angular margin. In *Diplodonta rotundata* and *D. punctata* there is a supra-axial extension anterior to the posterior adductor (figure 31). Unlike the Thyasiridae and Lucinidae, there is very little subfilamentar tissue. The gills are thin (figure 32) and may have an undulating appearance. Sections show that they are homorhabdic and not plicate. This differs somewhat from *D. oblonga* described by Ridewood (1903) in which the gills are plicate (15 filaments/plica), although still homorhabdic. Ridewood considers that such incongruities have little significance and quotes a number of cases where one species is plicate and another closely related, is not. Except posteriorly, where the ascending lamellae of the inner demibranchs are joined at their edges by interlocking cilia, the ascending lamellae of the demibranchs are fused with the body or the mantle.

In the Ungulinidae the ciliary mechanisms of the gills are type C_1 as described by Atkins (1937*b*). There is no oralward current at the edge of the outer demibranch.

Particles on the ascending lamella are carried to the edge, where the smallest particles are carried up the descending lamella and the larger particles fall off on to the inner demibranch. The particles on the descending lamella are carried to the axis and thence to the palps. Particles on the lamellae of the inner demibranch are carried to the grooved edge where the heaviest particles fall off on to the mantle and the finer particles are carried to the palps. In addition to the two main oral currents at the axis and the free edge of the inner demibranch, there are weak oral currents at the dorsal edges of the ascending lamellae. The frontal cilia of the upper 0·5 mm (approx.) of the ascending lamellae beat dorsally to the latter currents.

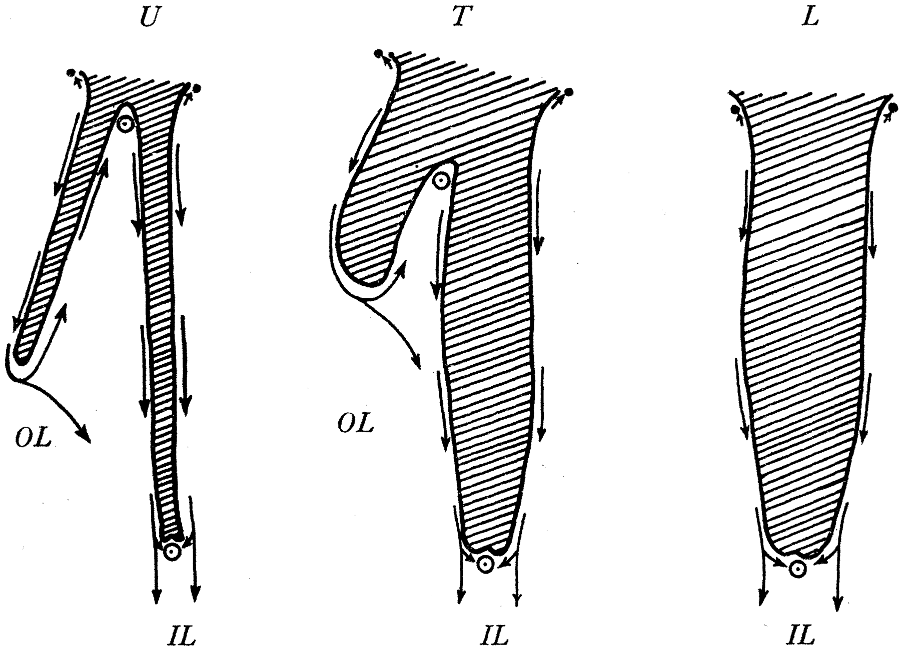


FIGURE 32. Diagrammatic transverse sections to show the variation in the thickness of the gills in members of the Ungulinidae (*U*), Thyasiridae (*T*) and the Lucinidae (*L*). The direction of the frontal ciliary currents is shown and the major currents to the mouth are shown by a ring and dot while the minor currents are shown by a solid circle.

The ciliation of the filaments (figure 33) is typical of the type described by Atkins (1937*a*, p. 368) with eulaterofrontal cilia (*EFC*) (figure 34). The only modification at the free edge of the outer demibranch is an increase in the length of the frontal cilia (*FC*). These beat slightly forward so that there is some movement of the particles anteriorly. The free edge of the inner demibranch is more specialized with a sorting mechanism similar to that described by Yonge (1946) for *Aloidis* and Allen (1954) for *Pandora.* Very long frontal cilia on the posterior half of the tip of the filament carry large particles anteriorly, while those on the anterior half are normal in size and carry smaller particles in to the marginal groove. No coarse cirrus-like cilia are present.

The Thyasiridae, also, possess both demibranchs. The outer is approximately one-third the area of the inner, i.e. relatively smaller than in the Ungulinidae. The demibranchs are flat and homorhabdic with a slight supra-axial extension of the outer lamella, They are much thicker than those of the Ungulinidae due to a considerable amount of subfilamentar

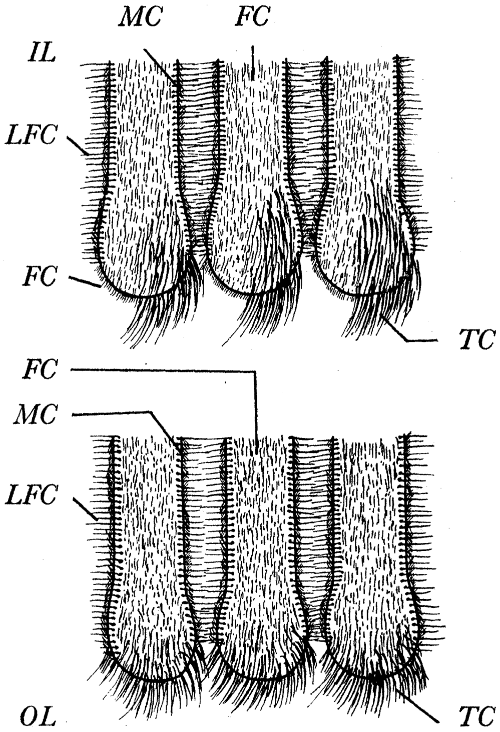


Figure 33. The ciliation at the free edge of the inner (*IL*) and outer (*OL*) demibranchs of a member of the Ungulinidae (magn. × 90). *FC*, frontal cilia; *LFC*, laterofrontal cilia; *MC*, lateral cilia; *TC*, terminal cilia.

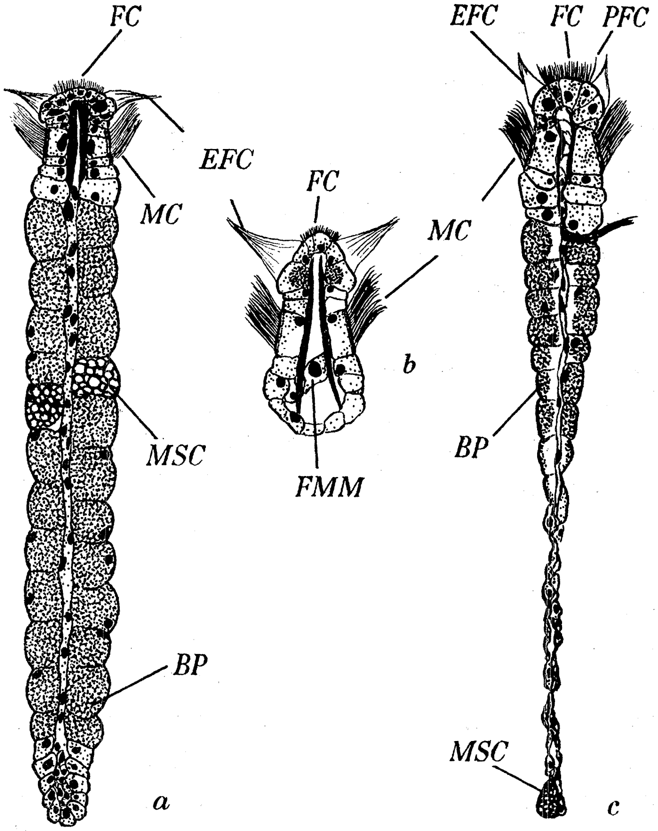


Figure 34. Transverse sections (magn. × 60) through the gill filaments of : *a*, *Divaricella quadrisulcata*; *b*, *Diplodonta punctata*; *c*, *Thyasira flexuosa*. *BP*, cells containing brown pigment granules; *EFC*, eulaterofrontal cilia; *FMM*, muscle fibre; *MSC*, mucus-secreting cell; *PFC*, prolaterofrontal cilia. Other lettering as before.

tissue (figure 34). Dark pigment granules in this tissue give a characteristic brown colour to the gills. The cells (*BP*) containing the brown pigment are large and extend from just below the lateral cilia in a continuous sequence to a depth of up to eight cells. Occasional loose spherules of brown pigment are present within the interfilamentar spaces and it seems possible that the granular material is of an excretory nature. Beyond the pigment cells there is a considerable depth of filament with a terminal mucus-secreting cell (*MSC*).

The ciliation and the ciliary mechanisms of the demibranchs are similar to those of *Diplodonta*. The ascending lamella of the outer demibranch is fused with the body. The ascending lamella of the inner demibranch is attached by ciliary junctions anteriorly to the body and posteriorly to the lamella of the opposite side.

The Lucinidae possess one demibranch and the reduced outer demibranchs of the Ungulinidae and Thyasiridae suggest that it is this lamella that has been lost. Purchon (1939) points out that there is very little evidence to support this assumption although most authorities have done so. Without examining any member of the group himself, Purchon accepts the account of Menégaux (1890). The latter author before discussing the blood supply to the gills states that the 'feuillet reflechi est interne...', but then states that it is this reflected lamella that carries the *afferent* vessel along its edge while the *efferent* vessel runs along the insertion of the gill, i.e. the axis. Purchon states that this description leaves no doubt that the demibranch is the outer one. As the efferent vessel always runs in the reflected (ascending lamella) it is highly probable that one of the statements of Menégaux is incorrect; he merely assumes that it is the external demibranch that is missing.

Sections through the gills of the species examined in this study show that the axis of the gill is to the outside, i.e. the inner demibranch persists as stated by Menégaux. These sections also show that the efferent vessel is carried in the ascending lamella. The afferent vessel connects with the kidney and the efferent vessel with the anterior longitudinal vein. Posteriorly the two vessels connect with each other. The ascending lamella is attached to the body by ciliary junctions but, posterior to the heel of the foot the lamellae of each side are united by tissue junctions.

The demibranchs in the Lucinidae are flat and homorhabdic. They are large, extending below the limit of the visceral mass. The filaments are closely packed and the gill is very thick with even more subfilamentar tissue than is present in the Thyasiridae. There are also similar large cells containing brown pigment granules. These extend almost to the inner limit of the filament (figure 34). Many of the interlamellar extensions fuse with those of the opposite side, especially in the ventral region. Mucus-secreting cells, unlike those in *Thyasira*, usually occur half-way along the filamentar extension.

The ciliation of the gill is simple. The frontal cilia carry particles to the free edge where fine material is transported along the marginal groove to the palps, while large particles and particles entangled in masses of mucus are thrown off on to the mantle. Apart from occasional, cirrus-like, stiff cilia at the free edge and a slight increase in the length of the terminal cilia there is no specialization. As in the other families of the Lucinacea the marginal groove is covered with small uniform cilia. In *Loripes lucinalis* particles travel tangentially across the posterior part of the gill. Careful examination failed to show any specialized frontal cilia of the type described by Atkins (1937*a*) for *Abra alba*. Typically, the frontal cilia adjacent to the laterofrontal cilia beat both towards the free margin and towards the centre of the frontal surface so that particles are carried down the centre (figure 35*a*). In *Loripes lucinalis* the main flow to the free margin is close to the anterior laterofrontal cilia and large particles in particular, tend to be carried on to the next filament (figure 35*b*). In no other species was this observed.

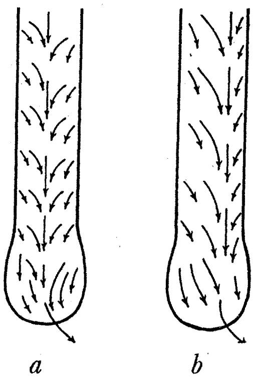


FIGURE 35. Comparison of the beat of the frontal cilia of a typical member of the Lucinacea (*a*) and those of *Loripes lucinalis* (*b*).

PALPS

There is a progressive reduction in the size of the palps in the Lucinacea. The Ungulinidae have a typical triangular palp of moderate size, and at the other extreme, the Lucinidae have palps little wider than the lips and with vestiges of only one or two ridges.

In the Ungulinidae (figure 37), small particles in the depths of the dorsal and marginal grooves of the gills are carried into the distal oral groove (*DOG*) at the base of the palps and from there, via the proximal oral groove, to the mouth. They do not come into contact with the sorting surface of the palp. Particles other than those confined to the narrow oral grooves, are rigorously sorted. Unlike *Ensis* (Graham 1931) where the cilia on the sides of the proximal oral groove, i.e. the lips, beat upwards and backwards to the rejection tract (*VT*) on the ventral side of the lip, those in *Diplodonta* beat downwards and towards the mouth. In *Diplodonta* the rejection tract (*VT*) is very narrow and it continues at the edge of the palps as the ventral marginal tract (*VMT*). Rejected particles reaching the tip of the palp fall off on to the main rejection tract of the mantle. Particles reaching the back of the palps either via the anterior inhalent current or the mantle and body are carried to the dorsal edge and from there on to the folds where they are sorted.

Detailed accounts of the lamellibranch palp are few. Wallengren (1905) gave excellent descriptions of the palps and their ciliary mechanisms in *Mytilus* and *Mya* and later workers suggested several theories as to the manner in which the selection of particles occurs. Yonge (1923, 1926*a*) and Graham (1931) both reviewed these theories and also gave detailed accounts of the ciliation of *Mya, Ostrea* and *Ensis*. Comparison of the ciliation of these species shows a number of differences. Recently Purchon (1955*a*) described in detail the palps of the British Pholadidae and shows that the species of this group not only differ from the accounts of Yonge and Graham for other species but members of this group differ from each other. The sorting mechanisms of the palps of the Lucinacea were studied not only to show the basic form within the group but also to determine features common to all Lamellibranchia.

In *Diplodonta* the number of folds (*PPF*) on the inner surface of the palps varies with the species and the size of the animal. Particles reaching the folds are sorted by a series of ciliated tracts that run the length of the fold. There are eight tracts (figure 36 and table 1).

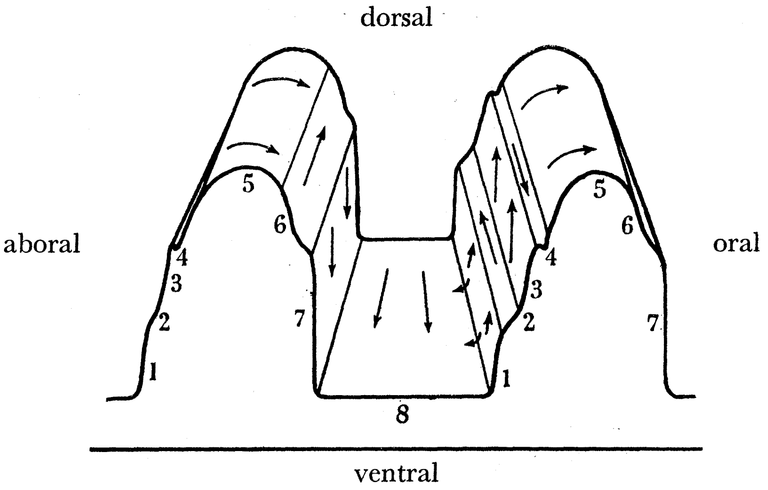


FIGURE 36. Diagrammatic representation of two folds on the inner face of the palps of a member of the Ungulinidae or Thyasiridae showing the direction of beat of the cilia of the eight tracts. For further details see text.

TABLE 1. A TABULATED COMPARISON OF THE CILIARY BEAT ON THE PALP FOLDS OF SIXTEEN SPECIES OF THE LAMELLIBRANCHIA

The authorities are: *A*, J. A. Allen; *G*, A. Graham; *P*, R. D. Purchon; *Y*, C. M. Yonge.

					dorsal				
		1	2	3	4	5	6	7	8
A	*Diplodonta* and *Thyasira*	← ⟶	↑	↗	↓	⟶	↑	⟶	↓
G	*Ensis siliqua*	⟶	↑	↗	↓	⟶	↑	⟶	↓
Y	*Mya arenaria*	•	↑	↗	↓	⟶	↑	← ↓	↓
Y	*Ostrea edulis*	⟵	↑	↗	↓	⟶	?	?	↓
P	*Pholas dactylus*	→	↑	⟶	↓	⟶	•	⟶	↓
P	*Pholadidea loscombiana*	→	↑	⟶	↓	⟶	•	⟶	↓
P	*Barnea candida*	aboral ↓ →	↑	⟶	↓	⟶	•	⟶	↓ oral
P	*Barnea parva*	→	↑	⟶	↓	⟶	•	⟶↓	↓
P	*Zirphaea crispata*	→	↑	•	↓	⟶	•	⟶↓	↓
P	*Petricola pholadiformis*	•	↑	⟶	↓	⟶	•	⟶	↓
P	*Martesia striata*	•	↑	⟶	↓	⟶	•	⟶	↓
P	*Tridacna crocea*	⟵	•	⟶	↓	⟶	↑	↓	↓
P	*Rocellaria cuneformis*	⟶	•	⟶	↓	⟶	•	⟶	↓
					ventral				

(1) Extends from the base of the fold on the aboral side to a poorly marked shelf situated a third of the distance up the fold. The ciliary beat is weak and directed upwards.

(2) On the shelf, a narrow tract of strongly beating cilia carries particles towards the dorsal edge of the palp.

(3) Above tract 2 a relatively broad band of cilia beat diagonally upwards and towards the dorsal edge.

(4) Above tract 3 there is a second shelf with a narrow groove along its length. Large cilia in the groove beat towards the ventral marginal tract.

(5) The summit of the fold. The cilia beat towards the mouth.

(6) On the oral side, below the summit of the fold, a tract of cilia beats weakly towards the dorsal edge.

(7) The cilia covering the remainder of the oral side beat into the groove between the folds.

(8) The cilia of the floor of the groove beat towards the ventral marginal tract, while the cilia close to the oral side of the fold beat into the centre of the groove.

Comparison with the accounts of Yonge (1923 and 1926*a*), Graham (1931) and Purchon (1954, 1955*a*, *b* and *c*, 1956) shows that the palps of *Diplodonta* most closely resemble those of *Ensis siliqua* (Graham 1931). Minor variations include, (1) inward beating cilia of tract 8 at its junction with tract 1 and, (2) in *Diplodonta* tract 6 is very weak. It is not stated whether tract 4, in *Ensis*, is in a groove.

From the studies of the workers listed above a number of basic features emerge (table 1). Tract 1 shows considerable variation. In *Ostrea* and *Tridacna* the cilia beat towards tract 8. In *Barnea candida* the cilia below the shelf beat in the same direction as those of tract 8. In the remainder of the Pholadidae and in *Martesia*, *Mya* and *Petricola* there are no cilia below the first shelf, but in the Pholadidae a narrow tract of cilia at the edge of the shelf beat orally. In *Ensis*, *Rocellaria* (= *Gastrochaena*), *Diplodonta* and *Thyasira* the cilia of tract 1 extend from the base of the fold to the first shelf and beat upwards. The condition in *Ostrea* and *Tridacna* may be derived from an extension of the inwardly beating cilia at the edge of tract 8 as seen in *Diplodonta* and *Thyasira*.

The cilia of tract 2 beat dorsally. The tract is absent in *Rocellaria* and *Tridacna*.

Tract 3 is present in all genera except *Zirphaea*. The directon of ciliary beat is towards the summit of the fold, although in *Ostrea*, *Ensis*, *Diplodonta* and *Thyasira* the beat is tangential with some movement of the particles towards the dorsal edge.

There are no differences in the direction of ciliary beat in tracts 4 and 5 of those species listed, but tract 4 is not necessarily in a groove.

When tract 6 is present, the cilia beat towards the dorsal edge.

With the exception of *Tridacna* and *Mya*, the ciliary beat of tract 7 is towards tract 8. In these two genera the beat is parallel to tract 8. In *Barnea parva* and *Zirphaea* the cilia of the lower part of tract 7 beat parallel to tract 8 and may represent an intermediate stage between *Tridacna* and *Mya* and the other species listed. In *Mya* there is an additional tract between tracts 6 and 7 and the cilia beat towards tract 6.

Tract 8 is common to all genera.

Past theories on the functioning of the palps have required, in addition to cilia, that the sorting of particles involves one or more of the following: muscular activity, mucus, gravity and reversal of ciliary beat. Ciliary reversal reported by Grave (1916) has not been reported by any worker since. Yonge (1926*a*) is of the opinion that gravity has little effect on the efficiency of the ciliary mechanisms, but the present work shows that a heavier particle is more readily rejected than a lighter one of the same size. Gross muscular activity was seen, but in the Lucinacea such movements do not aid in the sorting of particles. The movements are probably a result of the opening of the mantle cavity, and after a short time the palps lie still and untwisted. Muscular movements, which may expose the ciliary tracts in the lower part of the folds, sometimes occur when large quantities of particles are placed on the palps. It is doubtful whether such quantities are normally dealt with by the palps. However, all experiments show that mucus is important in the functioning of the palps. This agrees with the work of Yonge, Graham and Purchon.

The ciliary mechanisms in *Diplodonta* and *Thyasira* are similar to those described by Purchon (1955*a*) for the Pholadidae. Tract 5 creates a current that carries particles towards the mouth. These particles are influenced by tracts 4 and 6, particularly the former, and thus move across the palp in a characteristic zig-zag fashion. Large and heavy particles are moved to the ventral marginal groove by the strong cilia of tract 4. Tracts 7, 2 and 3 appear to sort the fine particles. Those that slip to the bottom of the groove are rejected by way of tract 8, while the remainder become entangled in skeins of mucus. These skeins, if not too bulky, are carried over tract 4 by the current produced by the cilia of tract 5. Larger, dense masses are rejected along tract 4. It appears that weight, size and quantity of particles are dominant factors in the functioning of the palps. Kellogg (1915) noted that some ciliary action (e.g. tract 4) could only be demonstrated when particles of sufficient size and weight were directed on to them. Yonge (1923, 1926*a*) clearly demonstrates the importance of size and weight. Stenta (1901) and Graham (1931) point out that a distinction must be drawn between water currents produced by ciliary action and the actual movement of particles by cilia, a view that is supported by the present work. Many of the above workers have emphasized the importance of mucus. Present experiments show that large quantities of particles falling on the palps stimulate the production of mucus, so much that *all* particles on the sorting area may be rejected. Some little time elapses before any particles are accepted, even though they are of the type and in the quantity

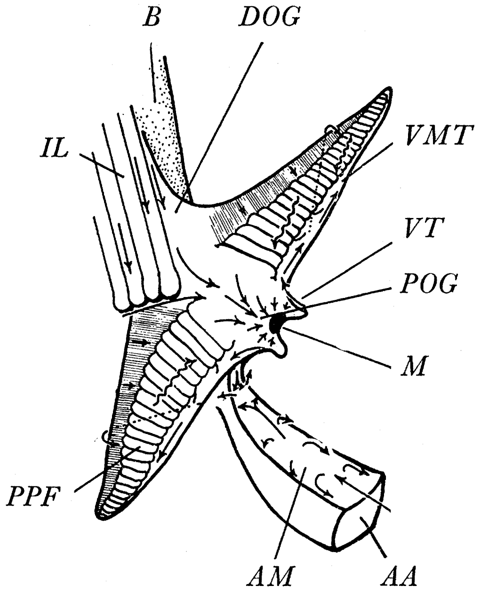


FIGURE 37. To show the general direction of the ciliary currents on the palps of *Diplodonta punctata* (magn. ×10). *B*, body; *DOG*, distal oral groove; *PPF*, folds on the inner face of the palp; *POG*, proximal oral groove; *VMT*, ventral rejection tract of palp; *VT*, ventral rejection tract of lip. Other lettering as before.

normally accepted, i.e. production of large quantities of mucus continues for some time after stimulus ceases. This presumably acts as a safety mechanism when during turbulent conditions there is much suspended material in the sea water.

The palps of *Thyasira flexuosa* are much reduced, the maximum number of folds recorded being seven (figure 38). The folds are similar to those of *Diplodonta* and function in the same fashion. The ventral marginal tract differs slightly in that particles, instead of being rejected at the posterior tip, are rejected opposite the proximal oral fold of the inner palp and the third fold from the proximal end of the outer palp. These are the closest points on the palp to the main rejection tract of the mantle. In the long proximal oral groove ciliation is similar to that in *Diplodonta*. The palps of *Thyasira* resemble those of *Arca tetragona* described by Atkins (1936), in which there is similar reduction and a very long proximal oral groove. There seems little doubt, as will be discussed later (p. 480), that the reduction in the size if the palps in the Lucinacea is related to the increased efficiency of the anterior inhalent mechanisms and the ability to take in food particles of a relatively large size.

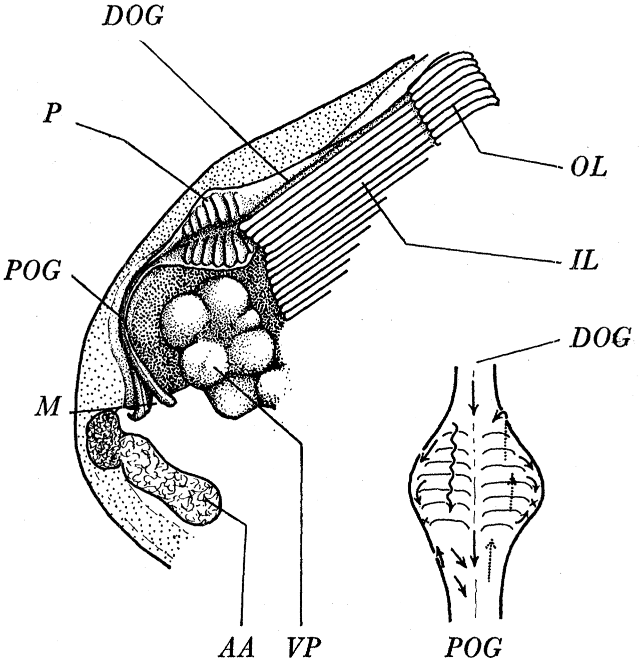


FIGURE 38. To show the form of the palps in *Thyasira flexuosa* and the general direction of the ciliary currents (magn. × 16). Lettering as before.

The palps of the Lucinidae represent no more than slight enlargements of the lips just anterior to the free edge of the anterior gill filament. Their size and their permanently folded state, makes it very difficult to determine their ciliation. Slight indentations indicate the vestiges of three folds on the inner palp (*IP*) and one on the outer palp(*OP*). There are few differences within the species studied (figures 39, 40 and 41).

Small particles travelling in the marginal groove (*GG*) and its continuation between the palps are carried directly to the mouth. Except for the narrow rejection tract at the edge of the lips, particles on the sides of the proximal oral groove are directed downwards and oralwards. The ciliary movements on the palps themselves are not well defined. There is one groove (*OG*) on the outer palp forming a rejection tract from the proximal oral groove to the edge of the lips and this probably corresponds to tract 8 in *Diplodonta* and *Thyasira*. Apart from the ventral marginal tract, no further homology can be made. The rejection groove (*OG*) is situated at the oral end of the palp. Between this groove and the aboral end, the cilia on the lower part of the palp close to the proximal oral groove beat downwards and to the mouth, while those on the upper half beat towards the ventral marginal tract. The point at which material is rejected, is immediately aboral to the rejection groove.

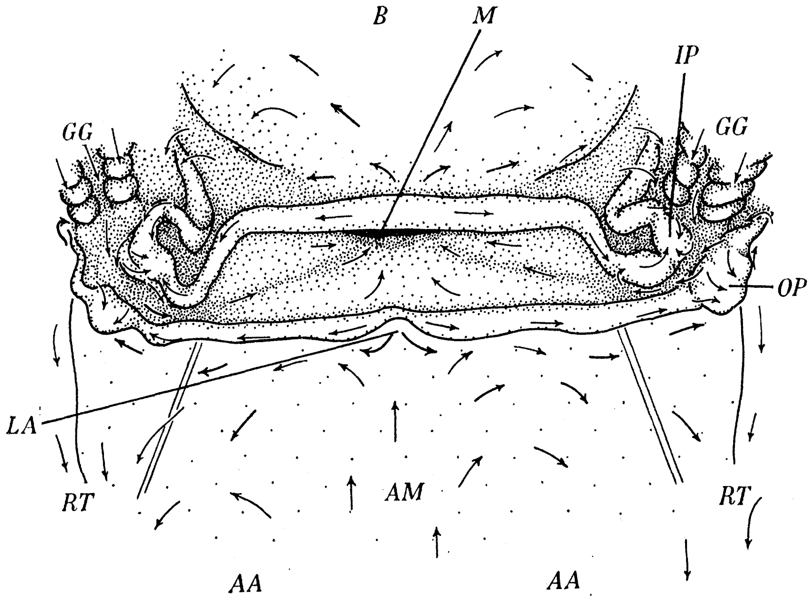


FIGURE 39. The direction of the ciliary currents in the region of the mouth and palps of *Phacoides borealis* (magn. × 25). *GG*, groove at the free edge of the gill; *IP*, inner palp; *OP*, outer palp. Other lettering as before.

In some specimens of *Loripes lucinalis* one or two additional grooves (*AG*) were present on the aboral side of the rejection groove (*OG*). Occasional specimens of other species had an additional groove also on the aboral side of the rejection groove. However, these were not constant features and did not appear to influence the overall ciliary mechanisms of the palp (figure 40).

The inner palp has three poorly defined folds. The centre fold (*IT*) is triangular in shape, the edges of the triangle being slightly raised (figure 40). There is a ventral marginal groove at the free edge of the palp and the point of rejection of material on to the mantle is opposite the distal fold (figures 39, 40 and 41). As in the outer palp, the ciliary beat on the lower part is towards the proximal oral groove and mouth, while that on the upper part is towards the ventral marginal tract. While there is some tendency for the grooves between the folds to reject particles and the folds to accept particles, there is no complex system of ciliated tracts as described for other lamellibranchs. Particles in contact with the upper part of the palp are immediately rejected to the ventral marginal tract. Material travelling along the oral groove, yet large enough to be in contact with the strongly beating cilia of the upper part of the palp is rejected. If the latter avoids rejection distally it is rejected along the groove (*OG*) at the proximal end of the outer palp. All other particles on the palps close to the proximal oral groove are accepted. When abnormally large numbers of particles are present quantities of mucus are secreted and all are rejected.

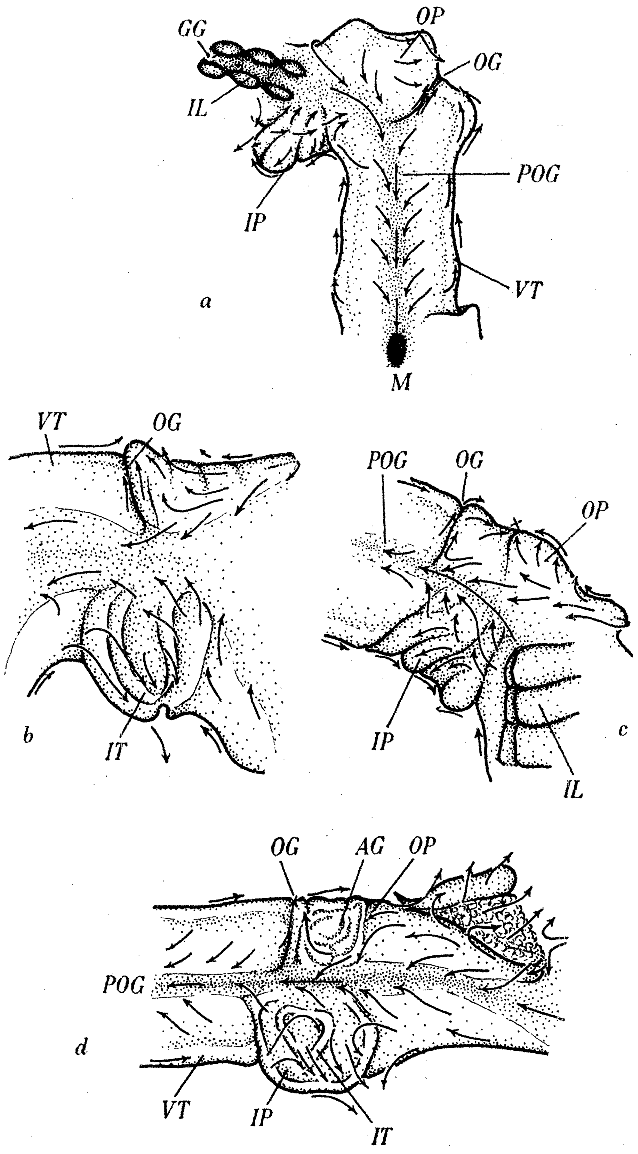


FIGURE 40. The direction of the ciliary currents on the inner surface of the palps and lips (magn. × 25) of *a*, *Codakia orbicularis*; *b*, *Phacoides borealis*; *c*, *Divaricella quadrisulcata*; *d*, *Loripes lucinalis*. *AG*, additional grooves on the lips; *IT*, triangular fold of the inner palp; *OG*, groove on the outer palp. Other lettering as before.

The above accounts concern material arriving at the palps via the gills, and do not include the great bulk of material arriving via the anterior inhalent current. The acceptance tract on the anterior adductor muscle is narrow. In the Lucinidae, accepted particles fan out just before reaching the lips. As they do so, particles may join them from a ciliary tract (*LA*) at the junction of the adductor muscle and outer lip (figures 39 and 41). These additional particles are carried from the oral end of the palp to a position opposite the mouth and from there on to the muscle. Accepted particles on the muscle arriving opposite the oral end of the palps are directed either on to the back of the outer palp or on to the main rejection tract of the mantle. A few may get carried to the ciliary tract (*LA*) and eventually return to the stream of accepted particles on the adductor muscle (see above). Particles that reach the back of the outer palps, together with any that may be present on the upper part of the back of the lip, are directed to the aboral end of the palp close to the proximal oral groove. They then join the particles arriving from the gills.

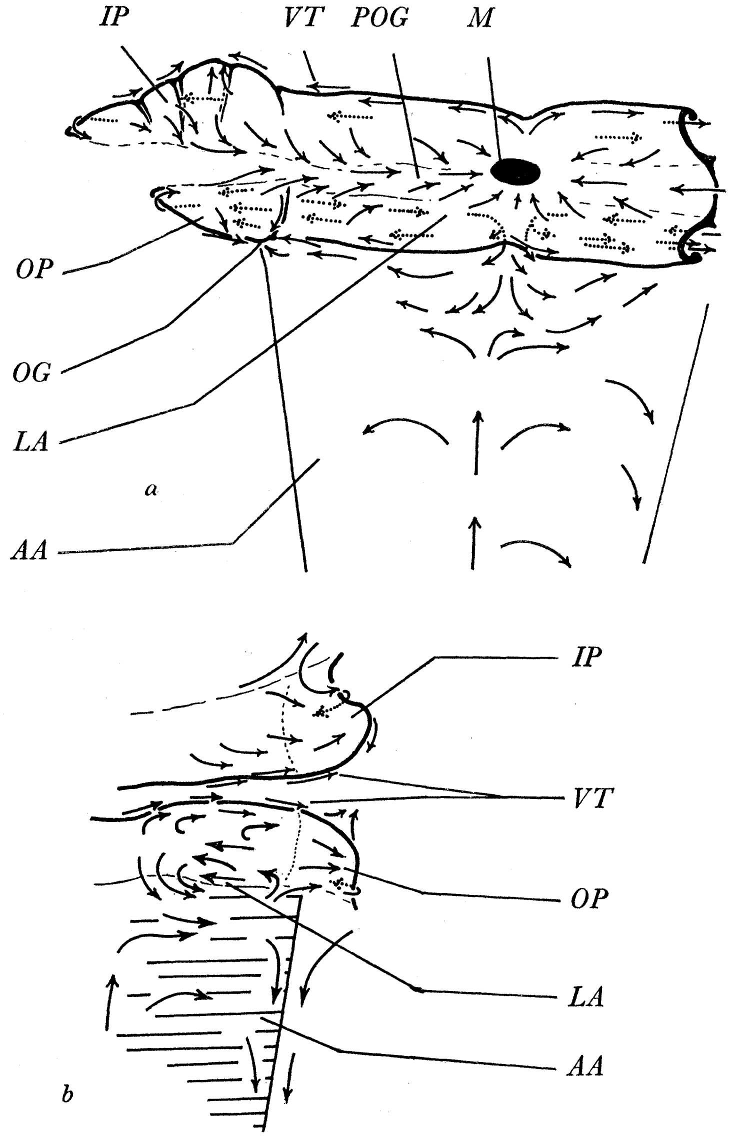


FIGURE 41. The direction of the ciliary currents on and close to the palps of *Codakia orbiculata* (magn. × 25). *a*, a comparison of the currents on the inner surface of the palps and lips (lined arrows) with those on the outer surface of the palps and lips (dotted arrows). *b*, The currents on the outer surface of the lips and palps and on the anterior adductor muscle, the palps have been turned inwards. Lettering as before.

Occasionally strings of mucus with enmeshed particles were seen to be carried from the acceptance tract on the anterior adductor, over the outer lip with its rejection groove, directly into the mouth. The string of mucus entrapped particles was pulled into the mouth mainly by the action of the style (p. 468). This was not observed very often and only when large quantities of mucus were present following experiments with large numbers of particles. The arrangement of ciliary tracts is such as to preclude this being the normal method of acceptance of particles arriving via the anterior inhalent tube.

The ciliary mechanisms of the Ungulinidae and the Thyasiridae are similar to those described above. The ciliary tract at the junction of the outer lip and the adductor muscle is not well marked, but in front of the mouth on the anterior adductor muscle there is a strong ciliary beat away from the lips (figure 37). This current prevents direct egress to the mouth and ensures that incoming particles are directed towards the back of the palps. Particles passed on to the back of the palps are carried aborally to the dorsal edge, where they are transferred to the sorting ridges of the palp. As in the Lucinidae, particles entangled in mucus were occasionally carried from the acceptance tract of the anterior adductor over the ventral tract at the edge of the lip close to the palp and from there to the mouth. This usually occurred after experiments with large quantities of particles when large amounts of mucus were produced. Probably it does not normally occur.

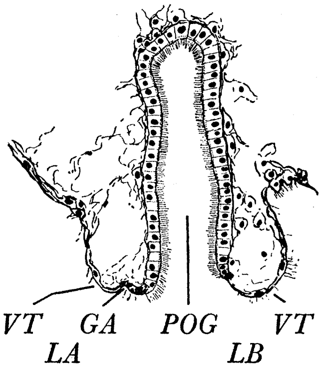


FIGURE 42. High-power transverse section of the proximal oral groove and lips of *Divaricella quadrisulcata* (magn. × 100). *GA*, groove at the edge of the outer palp; *LA*, outer lip; *LB*, inner lip. Other lettering as before.

The sorting of particles entering the mantle cavity anteriorly is never so thorough as of those few that enter posteriorly. Some fine particles may be drawn on to the gills by the respiratory current. Large, heavy particles are quickly eliminated and there is also considerable rejection of material due to the narrowness of the acceptance tract and the close proximity to it of the strong rejection currents. Correlated with the poor development of the sorting mechanisms within the mantle cavity, particularly in the Thyasiridae and Lucinidae, the alimentary canal is able to take in large particles.

The back of the inner palp is never so strongly ciliated as the back of the outer lip. Particles are carried from the back of the inner lip (figure 41) towards the dorsal edge of the palps and so on to the sorting area. Most of these particles have been carried close to the palps by the cilia on the anterior part of the body (p. 449). On the body opposite the mouth there is an outwardly directed current similar to that on the adductor muscle. This current soon fans out and carries particles parallel to the lip to the back of the palps or, failing that, to point *X* on the posterior part of the body.

Sections show that the proximal oral groove is lined with thickly ciliated cuboid epithelial cells. This is in contrast to the pavement type epithelium at the back of the lips and palps which is not thickly ciliated. The outer lip has a distinct groove (*GA*) separating the ventral marginal tract from the proximal oral groove. This was not observed in sections of the inner lip (figure 42).

ALIMENTARY CANAL

The course of the alimentary canal in the Lucinacea is not complex. A short oesophagus (*O*) opens in to a relatively large stomach (*ST*). The dorsal hood (*DH*) is poorly developed in most of the species examined. The combined style sac (*SS*) and mid-gut (*MG*) leave the stomach posteriorly. The remainder of the gut forms a simple loop within the visceral mass before passing dorsally to open at the anus near the posterior adductor muscle (figures 20, 24 and 27). In small specimens the gut can be seen through the body wall. It lies closer to the left side of the body in many species and the body wall can be stripped off and the digestive diverticula displaced to show the entire length of the gut. In these smaller specimens the gut wall is sufficiently transparent to enable the course of material in the alimentary canal to be followed.

The stomach was opened from as many different points as possible and fine carborundum and carmine were used to determine the ciliary currents. In addition, serial sections were cut for histological detail and confirmation of the observations on the dissected stomach. As most workers on the lamellibranch stomach have pointed out, it is impossible to open and draw the inside of a globular structure such as the stomach without distortion. By drawing different views and confining distortion to the gastric shield it is believed that a true picture of the ciliated surfaces has been obtained.

Stomach

The stomach is least modified in the Ungulinidae where its morphology and functioning resembles that of other Eulamellibranchia described by Graham (1949), Owen (1953) and Purchon (1955*a*). However, a detailed description of this stomach is necessary for the understanding of the much modified stomachs of the Thyasiridae and the Lucinidae. The nomenclature adopted is that proposed by Owen (1953).

In the Ungulinidae the short oesophagus is lined with longitudinal ridges which terminate close to the entrance of the stomach. The oesophagus (*O*) opens antero-ventrally. Forming the rim of the opening is a narrow groove (*CG*) from which the deep dorsal groove (*DG*) originates on the right dorsal side (figure 43*a*). Anteriorly and on the left side there is the opening to the left pouch (*LP*) into which fits the recurved portion of the gastric shield (*GS*). Posteriorly the aperture to the left caecum (*LC*) lies close to the posterior border of the gastric shield. On the right side postero-ventrally there is the opening to the right caecum (*RC*) into which a loop of the major typhlosole (*GT*) penetrates before terminating in the left caecum. A number of ducts to the digestive diverticula, the number varying according to the species, open independently on the right wall of the stomach anterior to the opening of the right caecum. In *Diplodonta punctata* there are four; two open anteriorly near the dorsal groove (RD_{I} and RD_{II}), one posterior to the oesophagus (*RD*) and one in front of the aperture to the mid-gut (RD_{III}). In *D. rotundata* there are two apertures posterior to the oesophagus and five close to the dorsal groove, but in *D. semiaspera* there is a single aperture posterior to the oesophagus. The number of apertures appears to be correlated with the size of the species, the larger species the more apertures.

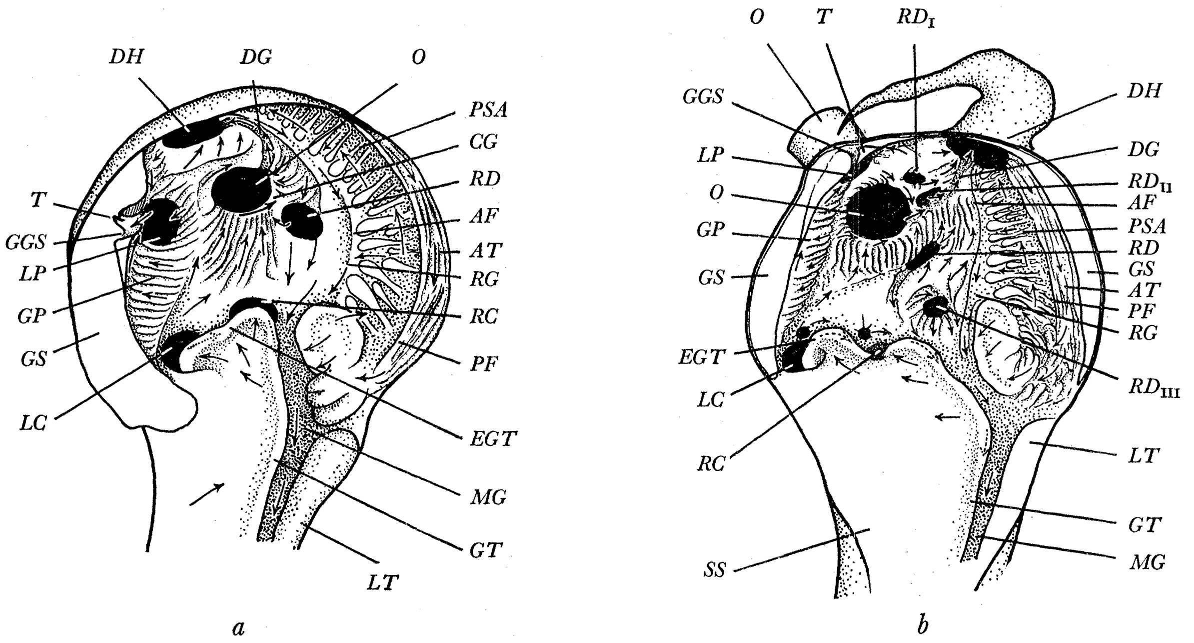


FIGURE 43. The stomachs (magn. × 15) of *a*, *Diplodonta semiaspera* (opened along the junction of the gastric shield with the acceptance tract) and *b*, *D. punctata* (opened longitudinally along the centre of the gastric shield) to show morphological details and the direction of the ciliary currents. *AF*, anterior fold; *AT*, acceptance tract; *CG*, circular groove; *DG*, dorsal groove; *EGT*, extension of major typhlosole; *GP*, grooves in area of left pouch; *GS*, gastric shield; *GT*, major typhlosole; *GGS*, groove in the gastric shield; *LP*, left pouch; *LT*, minor typhlosole; *MG*, mid-gut; *PF*, posterior fold; *PSA*, posterior sorting area; *RC*, right caecum; $RD_{\text{I–III}}$, right ducts; *RG*, rejection groove; *T*, tooth. Other lettering as before.

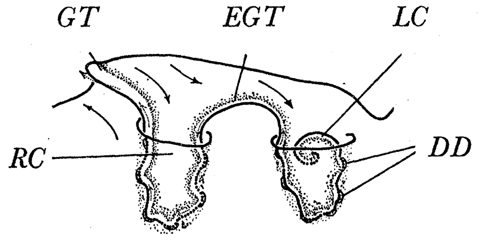


FIGURE 44. The left and right caeca and major typhlosole of *Diplodonta rotundata* (magn. × 40). Lettering as before.

The style sac and mid-gut communicate but their cavities are separated by the major and minor typhlosoles (*GT*, *LT*). The major typhlosole terminates within the left caecum (figure 44) in the manner described by Owen (1953, 1955) for *Glossus*. The minor typhlosole ends at the base of the acceptance tract (*AT*) as a pad of tissue distinct from the remainder of the typhlosole (figure 43). The acceptance tract extends over the dorsal wall of the stomach from the dorsal hood to a position posterior to the opening of the mid-gut. The gastric shield is well developed in the Ungulinidae and lies on the left and dorsal sides of the stomach (figure 43). It extends from the dorsal hood to the style sac and is held in position by two flanges, one penetrating the dorsal hood (*FDH*) and the other the left pouch. The tooth (*T*) on the shield close to the left pouch prevents the crystalline style (*S*) (figure 47) from entering the dorsal hood. Extending from the mid-gut to the tip of the dorsal hood is the posterior sorting area (*PSA*) which is bounded on the dorsal side by the posterior fold (*PF*) and the longitudinal ridges of the acceptance tract, and ventrally by the anterior fold (*AF*) which separates it from the region of the right ducts. The posterior sorting area is similar to that found in other eulamellibranchs, with numerous transverse sorting ridges and a rejection groove lying alongside the anterior fold. Two minor ridged areas are present. One (*GP*) is on the left side of the gastric shield with ridges lying at right angles to the length of the shield and the other is on the posterior side of the oesophageal aperture.

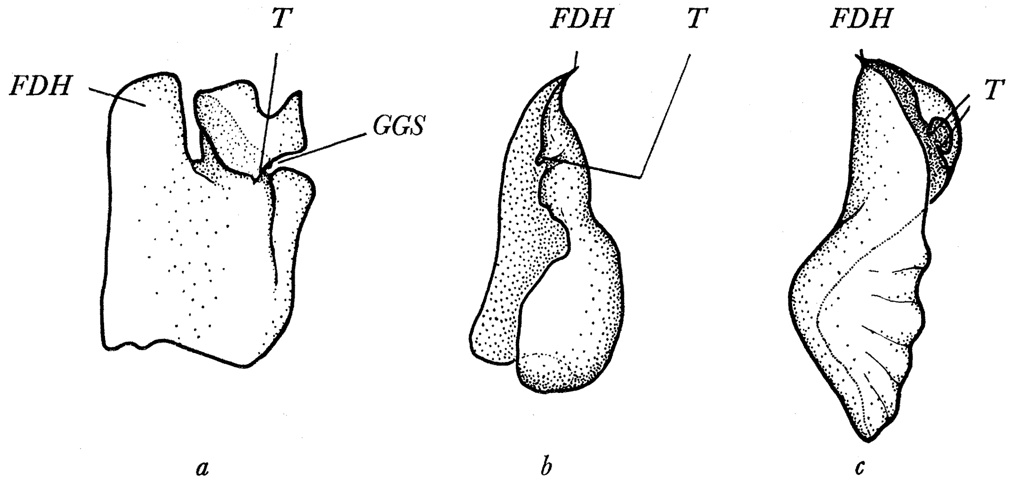


FIGURE 45. The gastric shields of *a*, *Diplodonta punctata* (frontal view) (magn. × 20); *b*, *Thyasira flexuosa* (left lateral view) (magn. × 45); *c*, *Loripes lucinalis* (right lateral view) (magn. × 20). *FDH*, flange of the gastric shield. Other lettering as before.

The dorsal hood is similar to that in *Glossus* (Owen 1953) and figure 46 represents the interior viewed from the stomach. The following ciliated areas penetrate the hood; (1) the acceptance tract, (2) the posterior fold, (3) the posterior sorting area, (4) the anterior fold, and (5) the dorsal groove together with the flange of the gastric shield. The acceptance tract, beyond the end of the flange of the gastric shield, is reduced to a deep groove (AT_1). The folds of the posterior sorting area extend to the tip of the hood as does the posterior fold. The anterior fold recurves before the head of the hood and terminates in a slightly bulbous tip in front of the flange of the gastric shield. The dorsal groove terminates shortly after it enters the hood. Extending inwards from the gastric shield are a series of ill-defined ridges.

Most of the accepted material enters the oesophagus within a string of mucus that becomes wrapped around the tip of the style. The style probably acts in the manner of a capstan (Orton 1923; Yonge 1949; Morton 1952). It rotates in a clockwise direction when viewed from the stomach (figure 47). The head of the style is grooved in the manner described by Yonge for the Tellinacea, the tooth of the gastric shield forming the groove and preventing the head of the style from blocking the openings of the oesophagus and dorsal hood. It is difficult to state with certainty what happens to particles released from the head of the style, since the style quickly dissolves and stops rotating when the stomach is opened. However, the movement of particles seen through the wall of the stomach while the style is still rotating supports the suggestion of Owen (1953, 1955) that the released particles are brushed on to the posterior sorting area. Here they undergo rigorous sorting, fine and light particles being carried from crest to crest over the ciliated ridges to the head of the dorsal hood, while heavy particles are carried to the rejection groove by the cilia of the grooves. These rejected particles are carried posteriorly to the mid-gut. Particles reaching the dorsal hood are either carried in to the groove of the acceptance tract or are directed towards the flange of the gastric shield and so on to the head of the crystalline style. These particles may undergo some trituration before they join the particles on the acceptance

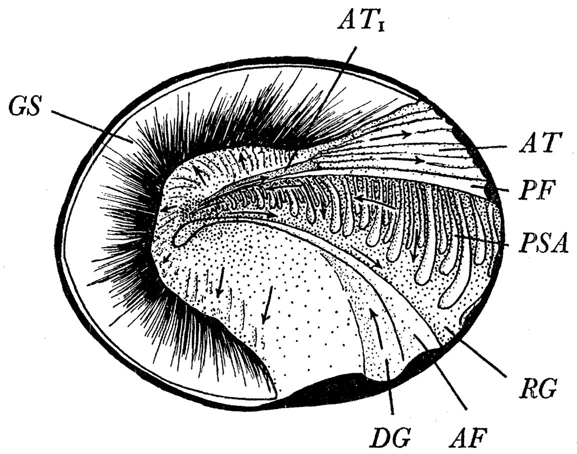


FIGURE 46. The dorsal hood of *Diplodonta punctata* viewed from the stomach (magn. × 50). Lettering as before.

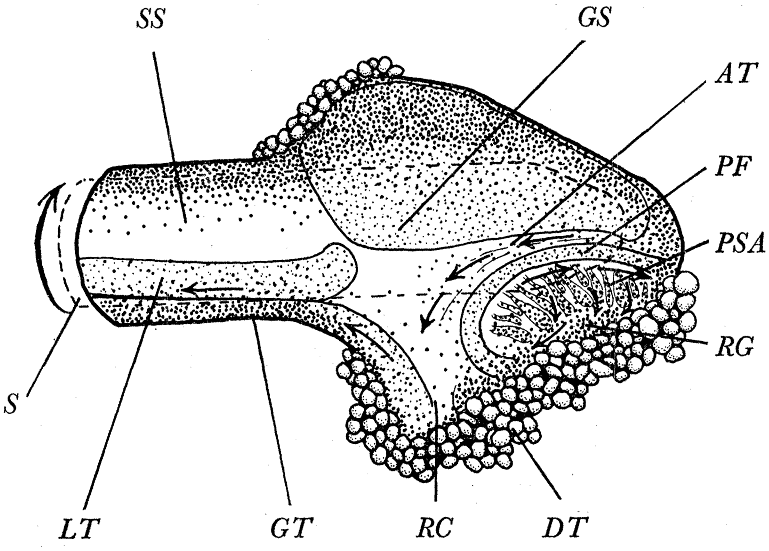


FIGURE 47. External view of the stomach of *Diplodonta semiaspera* as seen from the postero-dorsal side (magn. × 18). *DT*, digestive tubule; *S*, style. Other lettering as before.

tract. The style is a solid structure that may well be capable of triturating organic particles, but there is no postero-dorsal caecum containing sand grains such as is described by Yonge (1949) for the Tellinacea and Purchon (1955*a*) for the Pholadidae.

Particles on the acceptance tract are conveyed posteriorly to the head of the minor typhlosole and then across on to the major typhlosole, where they are directed anteriorly to the openings of the right and left caeca. The typhlosoles bridge over the opening to the mid-gut so that no particles are lost. This accumulation of particles at the entrance of the caeca agrees with the findings of Owen (1953, 1955) and Allen (1954) and in no way confirms the view of Purchon (1955*a*) that the 'ciliated surfaces lining the stomach are designed to hinder the passage of particles into the cavities of the right and left caeca and any of the ducts of the digestive diverticula which open independently'. While agreeing with the latter author that muscular activity of the stomach wall and visceral mass may play a part in the movement of food particles in to the digestive ducts, from this and other work on various eulamellibranch species (Graham 1949; Owen 1955; Allen unpublished work) it is clear that the ciliation of the stomach is such that it not only sorts the particles, but also presents suitable material at the entrance of the ducts leading to the diverticula. This view will be further discussed (p. 480) when the ciliary mechanisms of the whole group have been described. Accepted particles that are carried past the mouths of the caeca and on to the ciliated ridges along the ventral side of the gastric shield are directed to a groove running along the side of the gastric shield and so to the left pouch. Others are carried to the isolated right ducts posterior to the oesophagus, or on to the ridges around the oesophageal aperture and so into the circular groove (*CG*). The particles are conveyed along the circular groove to the dorsal groove and so to the head of the style and again circulate in the stomach. In *Diplodonta punctata* and *D. rotundata* the right ducts close to the dorsal groove are supplied by particles direct from the edges of the dorsal groove.

Rejected material from the right and left caeca travels to the mid-gut beneath the flap-like major typhlosole. Most of the rejected material from the isolated right ducts posterior to the oesophageal aperture is passed posteriorly to the mid-gut, definite rejection grooves being present in both *D. punctata* and *D. rotundata*. Some of the material may be carried to the mouth of the oesophagus and so to the dorsal groove and thus recirculate in the acceptance currents. The most anterior of the isolated right ducts and the left pouch have no rejection paths to the mid-gut and material passing from these ducts is recirculated. In this the Ungulinidae resemble both *Glossus* (Owen 1953) and *Pandora* (Allen 1954). In the case of the isolated anterior right ducts the rejected material is probably directed to the dorsal hood via the dorsal groove, while material from the left pouch is probably pulled over the groove (*GGS*) (figures 43 and 45) in the gastric shield below the tooth and so on to the crystalline style.

The action of the style must be considered in any description of the working of the lamellibranch stomach. Not only does it act as a capstan, enzyme carrier and (sometimes) triturating organ, but its revolutions may have an effect on the ciliary currents. The style in many of the Lucinacea can be seen through the stomach wall as also can the grooves and ridges of the wall itself (figure 47). Observations on the intact stomach clearly show that particles close to and in contact with the wall of the stomach are transported in the manner described above. Particles close to the style are clearly influenced by its rotation. This supports the view of Nelson (1918, 1925) and Yonge (1949) that the style has the additional function of mixing and stirring the stomach contents, and it also illustrates the importance of the space between the style and the stomach wall. Purchon (1955*a*) postulates a centrifugal action of the style which throws heavier particles on to the wall of the stomach where they are rejected, but at the same time suggests that large particles are isolated and used in trituration. It is difficult to reconcile the two views, for if the first supposition is correct then the particles used in trituration will immediately be thrown against the wall and rejected. The present observations give no support to this theory of centrifugal action.

Although for reasons to be discussed later (p. 479) the Thyasiridae are considered to be more closely related to the Ungulinidae than the Lucinidae, it is more convenient to consider the stomach of the latter group first. The stomach of the Lucinidae is much simplified. Of nine species examined only minor differences in the morphology of the stomach were noticed (figure 48). The stomach is relatively shorter than that of the Ungulinidae. This is correlated with the reduction in the number of apertures to the digestive diverticula and the reduction in the sorting areas (see below). The dorsal hood is also reduced. The oesophagus opens antero-ventrally and the combined mid-gut and style sac posteriorly. The combined mid-gut and style sac is relatively broad and long. The apertures to the digestive diverticula are large. In *Codakia orbicularis*, the largest species examined, there are three apertures, but in the remaining species only two. In the latter cases the two apertures can be identified as a very much reduced left caecum and an isolated right duct. In *C. orbicularis* the third aperture is a much reduced right caecum. The apertures are identified by the fact that the major typhlosole normally originates in the left and traverses the right caecum, e.g. Ungulinidae. The left pouch is absent and the lateral flange of the gastric shield is lost (figures 45 and 48). The curved portion bearing two teeth is still present but the groove (*GGS*) is lost. The loss of the latter gives some support to the theory that in the Ungulinidae rejected material from the left pouch passes over the groove on to the style. The gastric shield remains extensive and the flange into the dorsal hood, although reduced in size, persists. The remaining major variation from the stomach of the Ungulinidae is the lack of a posterior sorting area.

Accepted particles enter the mouth and the majority are entangled in a string of mucus that is wound on to the style. Because of the presence of dark particles embedded in the periphery of the style, which could be seen through the style sac, it was possible to count its speed of rotation in *Loripes lucinalis*. The following three speeds were recorded, each from different specimens; 20, 23 and 44 rev/min. This compares with 11 to 13 rev/min recorded by Nelson (1918) for *Modiolus* and *Anodonta* and 36 to 90 rev/min by Yonge (1926*a*) for the spat of *Ostrea*. The presence of particles within the style also agrees with the observations of Nelson (1918, 1925), Allen (1921) and Orton (1923) that particles become embedded in to the style despite the action of the cilia of the typhlosoles which beat forward into the lumen of the mid-gut.

Apart from those on the acceptance tract, all the cilia in the region of the dorsal hood beat towards the hood. Thus particles can only be carried posteriorly from the head of the style by way of the acceptance tract. In the Lucinidae the acceptance tract is a single groove which is bordered on one side by a ridge which separates it from the edge of the gastric shield and on the other by the posterior fold. On reaching the posterior limit of the tract the material is passed on to the head of the minor typhlosole and from there across to the major typhlosole and so to the left caecum (and right caecum when this is present). Material not entering the caecum is carried to the isolated right duct, while particles anterior to the right duct are conveyed to the circular groove surrounding the oesophageal aperture and so to the dorsal hood via the dorsal groove. There is great reduction in the number of ciliated grooves and ridges and in smaller species, such as *Codakia costata*, they

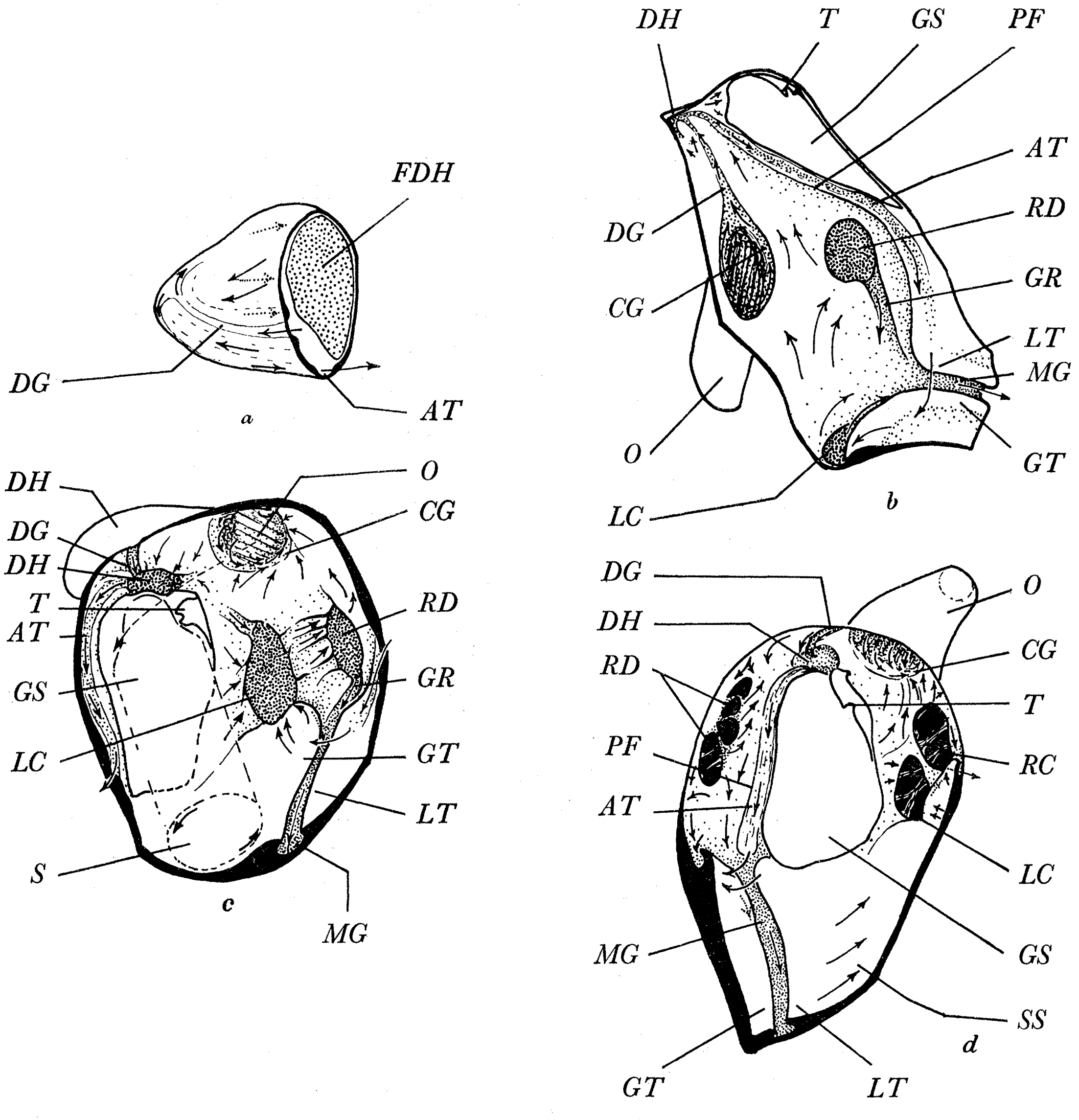


FIGURE 48. Morphological details and the direction of the ciliary currents in the stomachs of various species of the Lucinidae. *a*, generalized diagram of the dorsal hood showing details of the ciliary currents by transparency. Dotted arrows on the far wall, lined arrows on the near wall; *b*, stomach of *Lucina pennsylvanica* opened to show the ciliary currents leading to and from the dorsal hood (magn. × 25). Part of the gastric shield and style sac have been cut away and the remainder of the stomach flattened out; *c*, the stomach of *Loripes lucinalis* cut along the line of the posterior fold (magn. × 25); *d*, the stomach of *Codakia orbicularis* opened longitudinally between the right caecum and the right duct (magn. × 7). *GR*, rejection groove from the right duct. Other lettering as before.

are confined to the acceptance tract, dorsal groove and the two rejection tracts mentioned below.

Rejected particles from the caecum are passed to the mid-gut beneath the flap of the major typhlosole in the normal manner. Much of the material from the isolated right duct is carried to the mid-gut by a groove (*GR*) that runs parallel to the acceptance tract but terminates under the flap of the minor typhlosole. A small amount of the material from this duct may be carried anteriorly to the dorsal groove and thus will be recirculated. Loss of the posterior sorting area results in simplification of the dorsal hood. Material is passed to the head of the hood via the dorsal groove and the cilia between it and the acceptance tract and those on the face opposite the flange of the gastric shield (figure 48).

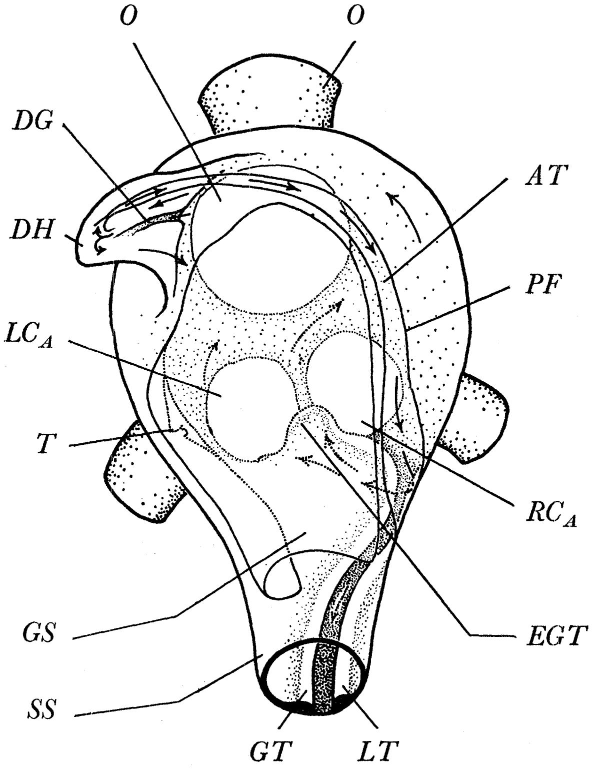


FIGURE 49. Diagrammatic drawing of the stomach of *Thyasira flexuosa*. Details of the ciliary currents seen by transparency through the dorsal side (magn. × 30). LC_A, RC_A, apertures to digestive tubules. Other lettering as before.

Particles reaching the head of the hood via the dorsal groove either enter the acceptance tract or are directed to the head of the style, where they will possibly undergo some trituration before passing on to the acceptance tract. Although experiments are inconclusive, it seems probable that it is the smallest particles that pass directly to the acceptance tract. This, if it occurs, is the only sorting that takes place in the stomach. The apertures to the digestive ducts are large, as are the digestive ducts and tubules, and it is clear that the ciliary mechanisms of the Lucinidae have been modified for the acceptance of large particles.

The stomach of *Thyasira* is similar to that of the Lucinidae (figures 49 and 50). The left pouch and the posterior sorting area have disappeared as have the isolated right ducts.

Of the apertures to the digestive tubules only two remain (RC_A, LC_A) and these are relatively huge openings on the ventral floor of the stomach. These can be correlated with the remarkable development of the body pouches which contain most of the digestive tubules. No digestive ducts are present and the apertures lead directly into the digestive tubules (see p. 477). However, as the major typhlosole terminates at the left aperture and traverses the posterior edge of the right, it is probable that they are homologous with the apertures to the left and right caeca of other Eulamellibranchia.

The ciliary mechanisms are similar to those described for the Lucinidae. As the isolated right duct and its rejection groove are absent, the groove below the major typhlosole is the sole rejection tract. Apart from the acceptance tract and the dorsal groove there are no ridges and grooves to the wall of the stomach.

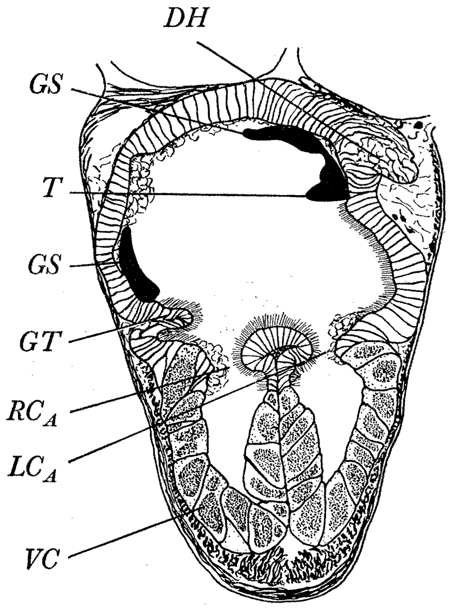


FIGURE 50. Transverse section through the stomach of *Thyasira flexuosa* in the region of the openings to the digestive tubules (magn. × 35). Parts of the dorsal hood and gastric shield are seen. The section is viewed from the anterior end of the stomach so that the morphological right is to the left side of the figure. *VC*, vacuolated cell. Other lettering as before.

Digestive diverticula

Examination of living and sectioned material shows a number of differences between the digestive diverticula of the three families. Those of the Ungulinidae are similar to the diverticula described for other Eulamellibranchia (Owen 1955). They form a greenish-brown mass surrounding the stomach. The digestive ducts branch repeatedly immediately after their junction with the stomach, and it is difficult to determine any arrangement of the ducts other than that they serve those regions adjacent to the main opening in to the stomach. The tubules (*DT*) are small and measure approximately 100 μ in their external diameter. Sections show that the tubules resemble those described by Yonge (1926*b*) and Owen (1955). Main ciliated ducts and secondary ducts, similar to those described by Owen (1955) were identified. The ciliated tract (*TT*) of the main ducts is poorly defined in the Ungulinidae and is not bounded on each side by a marked ridge or typhlosole.

Apart from this tract, the main ducts are lined with regular cuboid or columnar cells which have a brush border (*BB*). The cytoplasm is granular and contains refractive bodies (*CI*) (figure 51). Amoebocytes occur, but there are no mucus-secreting cells. The cells of the ciliated tract are smaller than those of the brush border and not so regular in shape. The cytoplasm is granular but does not contain any refractive bodies. The lumen of the ducts is circular in cross-section and it is doubtful, due to the lack of well-defined typhlosoles, whether the ciliated tract can be isolated from the non-ciliated portion of the duct. Non-branching secondary ducts connecting the tubules with the main ducts are lined with a brush border epithelium similar to that lining the main ducts. The junction between the former and the tubules is sharply defined. The lumen of the tubules is oval in cross-section and at each end of the long axis there is a shallow crypt (*C*) (figure 52). The cells of the tubules are similar to those described by Yonge (1926*b*) and Owen (1955). The crypt cells (*DC*) are non-vacuolated with a heavily staining cytoplasm. The surrounding vacuolated cells (*VC*) often encroach the crypts to such an extent that only a very small area is open to the lumen. Long cilia project from the crypt cells in to the lumen of the tubule; they are so fine that it is difficult to determine their exact length and number, but there appear to be several cilia to each crypt cell. Cilia were not observed in any other cell of the tubule. Yonge (1926*b*) considers that the crypt cells are young stages of the vacuolated cells. Sections of *Diplodonta* suggest that new vacuolated cells may also arise from 'interstitial cells' (*IC*) that are wedged between the bases of the vacuolated cells. Except that no cilia are present, the interstitial cells closely resemble the crypt cells. Morton (1956) records similar cells in *Lasaea rubra*. The vacuolated cells are similar to those described by Yonge (1926*b*) and Owen (1955). They are large cells with a granular cytoplasm. The number and size of the vacuoles varies, and they are filled with a greenish-brown material that gives the characteristic colour to the diverticula. Various stages in vacuole formation were seen. Small vacuoles form and coalesce until one or two large vacuoles remain and occupy much of the cell. These larger vacuoles are packed with material and release their contents usually in the form of excretory spheres (Yonge 1926*b*; Owen 1955). Sections indicate that when one large vacuole is present, its contents may be discharged directly into the lumen in the manner described by Oldfield (1955) for *Turtonia minuta* or, possibly, the whole cell may be cast off.

Because of the unique arrangement of the digestive diverticula in the Thyasiridae it is better first to consider those of the Lucinidae. The tubules of the latter are light brown in colour and much larger than those of the Ungulinidae (140 to 220 μ in external diameter) (figure 52). In the smaller species the course of the ducts can be seen easily and they can be separated out and traced to their finest division where they terminate in grape-like clusters of tubules (figure 51). The basic course of the ducts was similar in all species examined. Two main ducts open into the much reduced left caecum. The larger of these ducts passes posteriorly and divides into two main branches, to the right and to the left. This division may be close to the stomach or may occur as far back as the style sac. The smaller duct extends on the left side of the body anteriorly and then dorsally in front of the stomach. In *Codakia orbicularis* both right and left caeca are present into which several ducts open. From each caecum one large duct passes posteriorly and that of the left is probably comparable to the main posterior duct from the left caecum of other species.

The isolated right duct branches close to the stomach and gives off a small posterior branch that terminates at the posterior limit of the style sac and an anterior branch that is far more extensive than the corresponding duct from the left caecum. This anterior branch extends dorsally in front of the stomach and then posteriorly over the stomach (figure 51*a*). The ducts, like the tubules, are larger than those of the Ungulinidae. This increase in size is not confined to the diameter of the lumen but also exhibited by the cells of the ducts and tubules. Thus in animals of similar size, the height of the vacuolated cells of the tubules is approximately 25 μ in *Diplodonta punctata* while those of *Divaricella quadrisulcata* are approximately 35 μ.

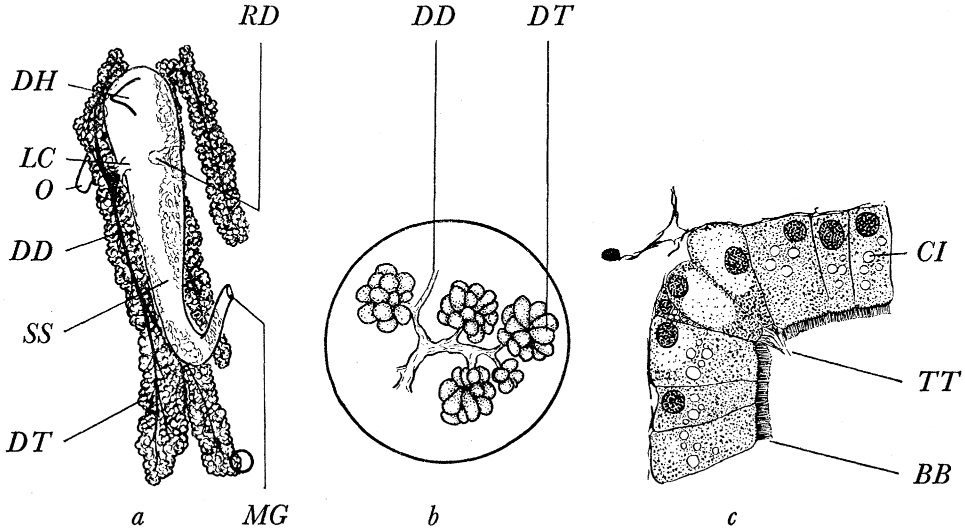


FIGURE 51. Digestive diverticula. *a*, *Loripes lucinalis* (magn. × 10). To show the typical arrangement of the digestive diverticula in the Lucinidae. *b*, an enlarged portion of the digestive diverticula ringed in *A* (magn. × 100). *c*, a high-power transverse section through part of a main duct of *Diplonta punctata* (magn. × 400). *BB*, brush border epithelium; *CI*, cell inclusions; *DD*, digestive duct; *TT*, ciliated cells of the main duct. Other lettering as before.

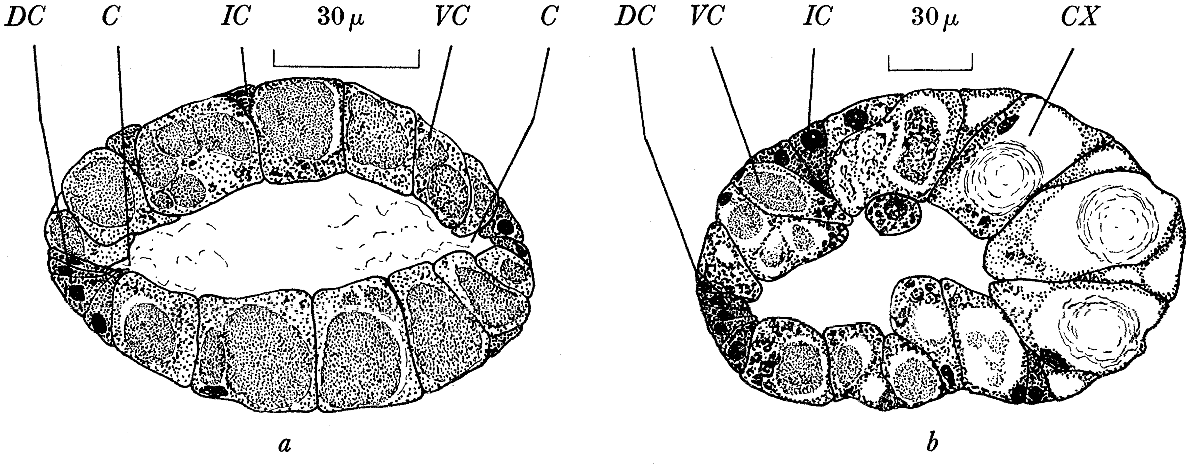


FIGURE 52. Transverse section of a digestive tubule of *a*, *Divaricella quadrisulcata* and *b*, *Diplodonta punctata*. *C*, crypt; *CX*, large vacuolated cell (see text); *DC*, crypt cell; *IC*, interstitial cell. Other lettering as before.

The epithelium of the main ducts differs somewhat from that of the Ungulinidae. A ciliated tract is not present and there is a striated border to all the cells. The contents of the epithelial cells are similar to those described above for the Ungulinidae. The lumen of the tubules is round without definite crypts but with occasional concentrations of what appear to be interstititial cells or non-ciliated crypt cells. These are usually found at the head of the tubule. The tubules resemble those described by Oldfield (1955) and Morton (1956) for *Lasaea rubra*, large cells (*CX*) with a large vacuole containing semi-fluid material being present. Mrs Oldfield was unable to determine the nature of the contents of these vacuoles. Those found in the Lucinidae stained heavily with Alcian blue. In other cells, in addition to vacuoles containing particulate material, small vacuoles occur which give the same reaction with Alcian blue. The cells with large clear vacuoles are not exclusively found at the blind end of the tubules as is the case in *Lasaea*. Particulate matter appears to be excreted in the same manner as in the Ungulinidae.

The Thyasiridae are remarkable in that the digestive diverticula do not possess ducts distinct from tubules. Characteristic tubule cells line the whole ramification of the diverticula. These are dark brown in colour. Apart from a small branch, given off between the aperture to the stomach and the neck to the visceral pouches, which extends dorsally over the stomach (figure 27), all the tubules are contained in the lateral pouches of the body. The branched tubules come together in a single tube at the neck of tissue connecting the body with the pouches. The tubules are always on the outer side of the pouches, while the similarly branched gonads are on the inner side. The lumen of the tubules is circular in cross-section and completely lined with vacuolated cells. The external diameter of the tubules and the height of the vacuolated cells is approximately the same as in the Lucinidae. No crypts were seen although scattered interstitial cells occur. Groups of these cells are present at the blind end of each branch of the tubules. No cilia were seen. The vacuolated cells are similar to those described for the Ungulinidae. No large clear vacuoles of the type seen in the Lucinidae were observed.

CIRCULATORY SYSTEM

Only in connexion with the ctenidia and the functioning of the mantle gills was the circulatory system studied in detail. Apart from these divergences discussed in detail on pp. 432 and 456, the system is not significantly different from that of other Eulamellibranchia. In all species studied the ventricle is elongate in the antero-posterior axis. The rate of heart beat was recorded in *Loripes lucinalis* where it varied from 12 to 22 beats/min at a temperature of 18 °C. The paired auricles are large and triangular and pericardial glands are present. In *Diplodonta punctata* and *D. semiaspera* this tissue is scattered in the mantle at the sides of the pericardium, i.e. 'pericardial' as described by White (1942). In *Thyasira flexuosa* the pericardial gland lies on the inner anterior wall of the auricles, while posterior to the point of fusion of the auricles with the ventricle the gland is continued on the ventral wall, i.e. 'auricular' (White 1942). In all species of the Lucinidae examined glandular tissue occupies the walls of the auricles often to the extent of giving a brown coloration.

Excretory organs

The paired excretory organs are similar in structure in the three families of the Lucinacea. They are elongate and extend immediately anterior to the posterior adductor forward under the posterior end of the pericardium. They are typically U-shaped tubes which, particularly in the Ungulinidae, may show various convolutions. There is a small reno-pericardial aperture in the anterior lobe and laterally, immediately posterior to the more conspicuous gonadial aperture, there is the opening into the mantle cavity. The broadest part of the organ is immediately in front of the posterior adductor and at this point there is a cross-connexion between the organ of each side. Sections show no histological differences from other Eulamellibranchia.

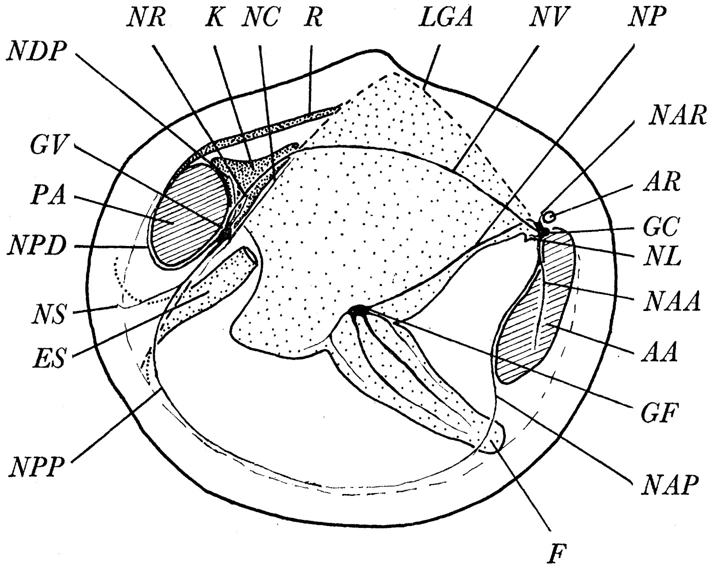


Figure 53. Generalized drawing of the nervous system in the Lucinacea. *GC*, cerebral ganglion; *GF*, pedal ganglion; *GV*, visceral ganglion; *NAA*, nerve to the anterior adductor muscle; *NAP*, anterior pallial nerve; *NAR*, nerve to anterior pedal retractor muscle; *NC*, ctendial nerve; *NDP*, dorsal pallial nerve; *NL*, nerve to palps; *NP*, cerebro-pedal commisure; *NPD*, posterior dorsal pallial nerve; *NPP*, posterior ventral pallial nerve; *NR*, renal nerve; *NS*, siphonal nerve; *NV*, cerebro-visceral connective. Other lettering as before.

Nervous system

The nervous system, like the excretory, shows no major deviation from that of other members of the Eulamellibranchia, and there is little difference between the species studied (figure 53). The three major paired ganglia are present together with the main cerebro-pedal and cerebro-visceral connectives. The cerebral ganglia (*GC*) can be seen through the body wall just anterior to and on either side of the mouth immediately above the dorsal lip. The two ganglia are joined by a short commisure anterior to the oesophagus. Each ganglion gives rise to the following nerves: (1) cerebro-visceral connective (*NV*) and close to the root of this on the dorsal side, (2) a fine nerve to the anterior pedal retractor muscle (*NAR*). To the ventral side of the cerebro-visceral connective there is (3) the cerebro-pedal connective (*NP*). Anteriorly, (4) several small nerves pass to the labial palps (*NL*) and also a large nerve that immediately splits to give (5) a nerve to the anterior adductor muscle (*NAA*), and (6) the anterior pallial nerve (*NAP*) that passes down the inside edge of the adductor muscle and into the mantle edge.

The visceral ganglia (*GV*) are very closely applied to each other and lie close to the ventral side of the posterior adductor muscle. The cerebro-visceral connective joins them anteriorly. The ganglia give rise anteriorly to (1) a renal nerve (*NR*) and (2) a dorsal pallial nerve (*NDP*), both of which are very fine. Ventrally a very stout nerve (3) passes to the ctenidial axis (*NC*) and posteriorly a large nerve is given off which gives rise to (4) the posterior ventral pallial nerve (*NPP*) which connects with the anterior pallial nerve, (5) the siphonal nerve (*NS*) and (6) the posterior dorsal pallial nerve (*NPD*) passing round the back of the posterior adductor muscle. In addition fine nerves supply the posterior adductor and posterior retractor muscles.

The closely joined pedal ganglia (*GF*) are very large in the Lucinacea and are situated above the vermiform portion of the foot at the junction of the digestive gland with the foot musculature. They each give rise to four large nerves supplying the foot. The most anterior of these supplies the superficial musculature of the anterior side of the foot, while the most posterior supplies the musculature of the heel and the superficial musculature of the posterior part of the foot. The two other nerves that are given off from the ganglion supply the inner musculature of the foot and lie anterior and posterior to the central sinus.

PARASITES

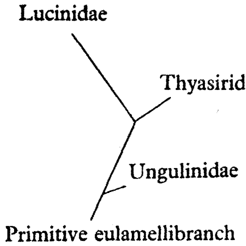
A number of parasites were recorded from members of the Lucinidae, but none from the Thyasiridae and Ungulinidae. The copepod parasite *Trococheres cylindraceus* (Pelseneer 1928), and the protozoan ectoparasite *Probovaria loripedes*, and the endoparasite *Plagiospira crinila* (Chatton & Lwoff 1949) previously reported for *Loripes lucinalis* were recorded again. A similar species of *Bovaria* to that found in *Loripes* was taken from *Codakia orbicularis*. This was found attached to the posterior end of the gills close to the inhalent aperture and also on the palps and lips.

A new species of parasitic copepod *Myocheres inflata* was taken from *Lucina pennsylvanica*, *Divaricella quadrisulcata* and *Codakia orbiculata* (Allen 1956). The female shows adaptation to the feeding mechanisms of its host, for it was always found attached to the anterior adductor muscle immediately over the acceptance tract. It seems probable that the female never leaves the host. The male was found in various positions within the mantle cavity and is probably not restricted to one host.

DISCUSSION

The present study shows that three families of the Lucinacea form an evolutionary sequence in the development of characteristic morphological features and habits. Observations show that they can live, often in large numbers, in habitats ranging from gravel and coarse sand to fine mud. The particular habitats they occupy do not support a very rich fauna and, conversely, members of the Lucinacea are not common in what appear very similar environments but which do possess a rich infauna. Presumably competition is here too great. It is clear that a detailed comparative analysis of the substrata is essential. At Roscoff, excessive quantities of hydrogen sulphide were the cause of the paucity of infauna, but at other localities the reason was not so obvious. Analysis of the functional morphology of the group shows that it is probably the ability to construct an anterior inhalent tube that has enabled these animals successfully to inhabit these environments. The respiratory and feeding current in the primitive lamellibranch enters the mantle cavity anteriorly, e.g. Nuculidae (Protobranchiata), but the Lucinacea possess the posterior inhalent and exhalent apertures of typical Lamellibranchia; the anterior inhalent current represents a secondary specialization.

The possession of the anterior inhalent tube is accompanied by modification of many structures concerned with feeding. A series of evolutionary stages can be traced from the Ungulinidae, which are closest to the primitive eulamellibranch, through the Thyasiridae to the extremely modified Lucinidae. Each of the three families, however, has to some extent specialized along lines of its own.



A major evolutionary trend, leading to the ability to accept large particles, is the reduction of those areas concerned with the sorting of incoming particles. This simplification emphasizes the essential mechanisms concerned with the conveyance of food to the digestive diverticula and leads to the better understanding of such mechanisms in the Eulamellibranchia generally.

A detailed account of the course of evolution within the Lucinacea has been given, but the following points appear significant.

(1) Possession of an anterior inhalent tube can be correlated with the hypertrophy of the anterior adductor muscle and the development of its ciliary sorting mechanisms. As the efficiency of these mechanisms increases there is a corresponding reduction in the size of the gills and palps and of the efficiency of the sorting mechanisms upon them. This modification of the gills and palps is also related to the ability to take in large food particles.

(2) The ciliary mechanisms of the anterior adductor never reach the level of efficiency in sorting found in the gills and palps of other Eulamellibranchia. In fact the Lucinacea live in environments where the food supply is so low that all available particulate food must be accepted and thus sorting mechanisms are necessarily poorly developed.

(3) The posterior inhalent current is very slight and little or no food enters posteriorly. The main respiratory current is also anterior and this is emphasized by the development of 'gills' close to the anterior adductor, and by the fact that at least some of the species live in substrata where the oxygen content is negligible.

(4) The stomach shows progressive modification for dealing with larger food particles. This includes the loss of the sorting areas and the reduction in the number of apertures leading from the stomach to the digestive diverticula with a corresponding increase in the size of those remaining. This secondary simplification of the stomach emphasizes the

importance of the acceptance tract, the typhlosoles, the left caecum, the dorsal groove and the tooth on the gastric shield. The study supports the accounts of Owen (1953, 1955) on the functioning of the eulamellibranch stomach. It clearly shows that particles are directed over the openings of the digestive ducts. Particles may pass into the digestive diverticula by muscular pumping of the stomach, or as a consequence of the absorptive functions of the vacuolated cells (Owen 1955). There is no support for the view of Purchon (1955) that the ciliary currents on the stomach prevent particles from entering the ducts to the digestive diverticula.

(5) In the Thyasiridae and the Lucinidae the ducts and tubules of the digestive diverticula are enlarged and simplified, so that the exact course of the ducts from tubule to stomach can be followed by dissection alone. The ducts of the Lucinidae, unlike those of the Ungulinidae, show some histological differences from other eulamellibranchs described by Owen (1955). There are no ducts in the Thyasiridae. The tubules show few differences from descriptions of other Eulamellibranchia. It is likely that the variations in the Lucinidae and Thyasiridae are related to the changes in the feeding mechanisms.

(6) The tendency to develop lateral body pouches appears to be characteristic of all the families of the Lucinacea and it is difficult to relate it to feeding mechanisms or to the type of substratum in which the animals live.

(7) The foot is well adapted both for burrowing and for constructing the anterior inhalent tube. The heel becomes well developed and, in some species of the Lucinidae, quite distinct from the vermiform part of the foot. Thus, in the latter family, the heel is used for movement through the substratum, while the vermiform foot is almost exclusively used in tube building.

It must be concluded that the Lucinacea have successfully adapted themselves to conditions in which food is at a minimum and where the oxygen content of the substratum is very low.

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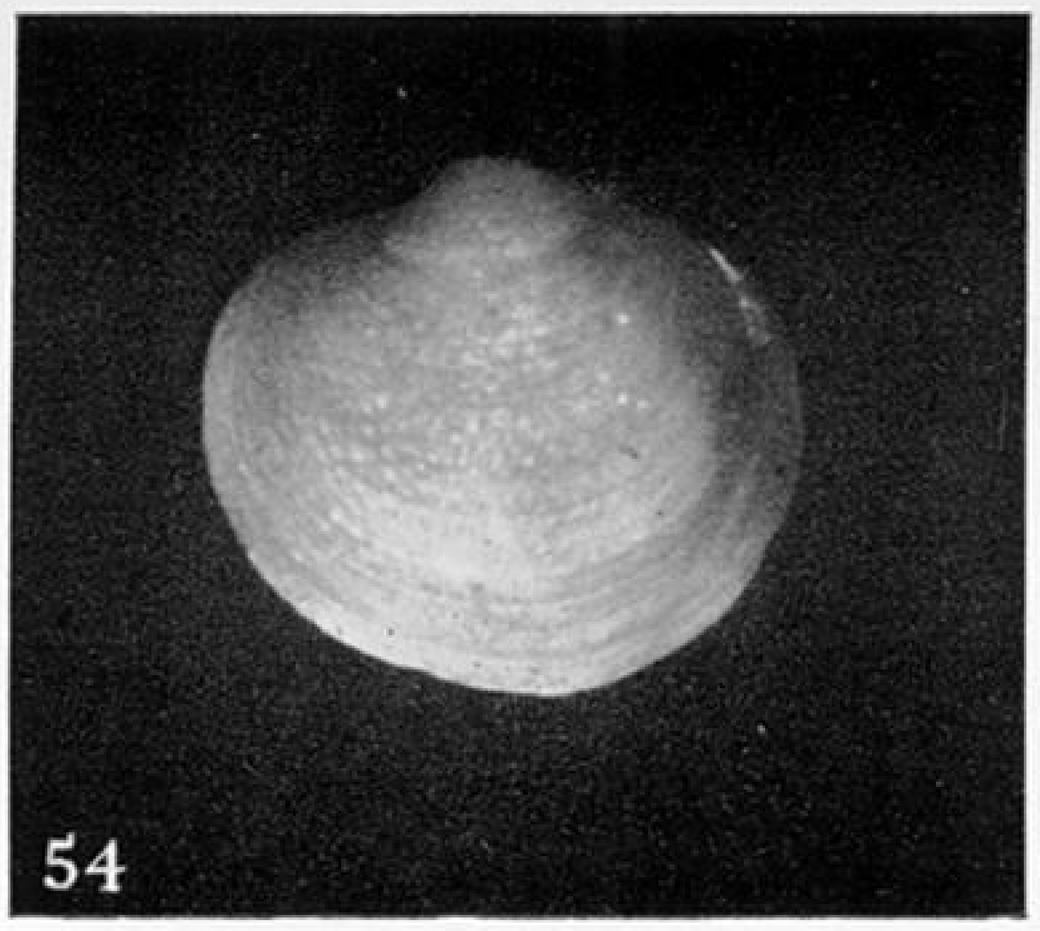
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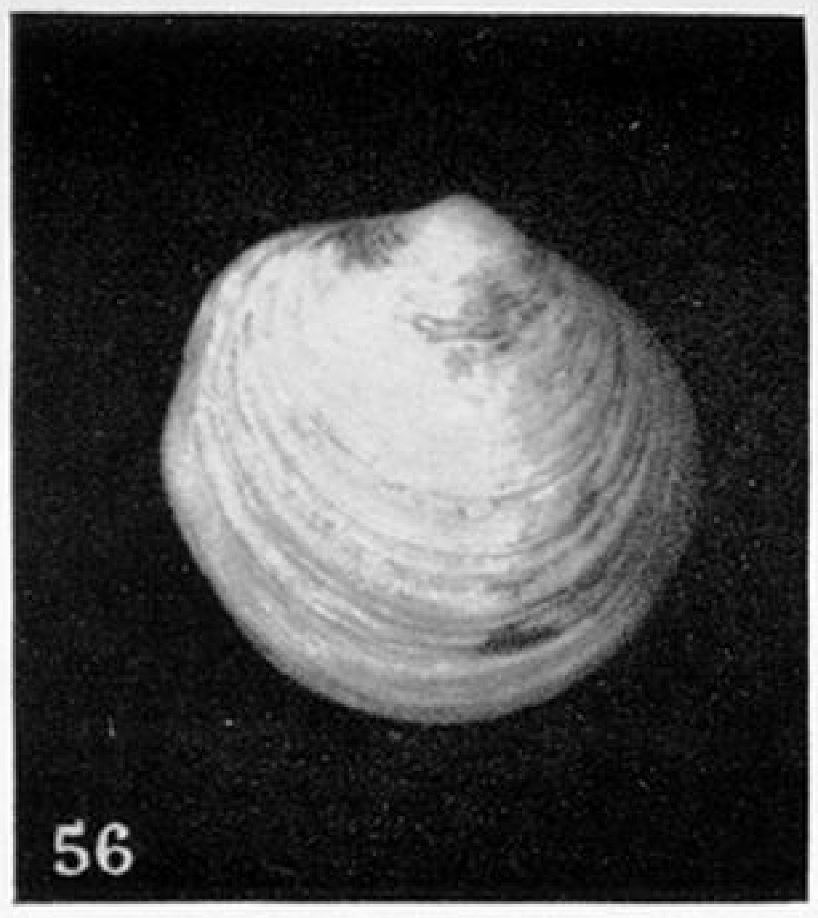
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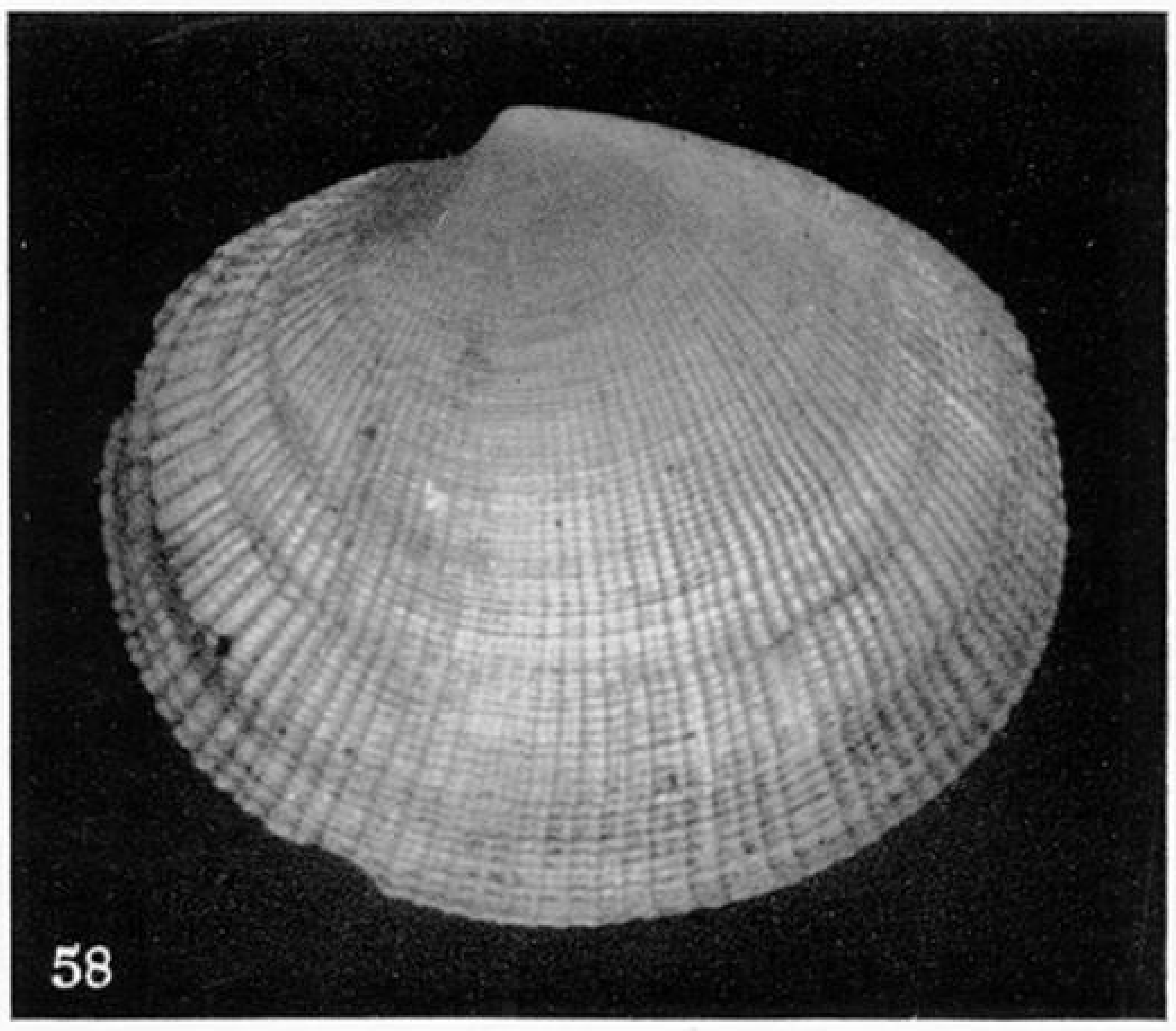
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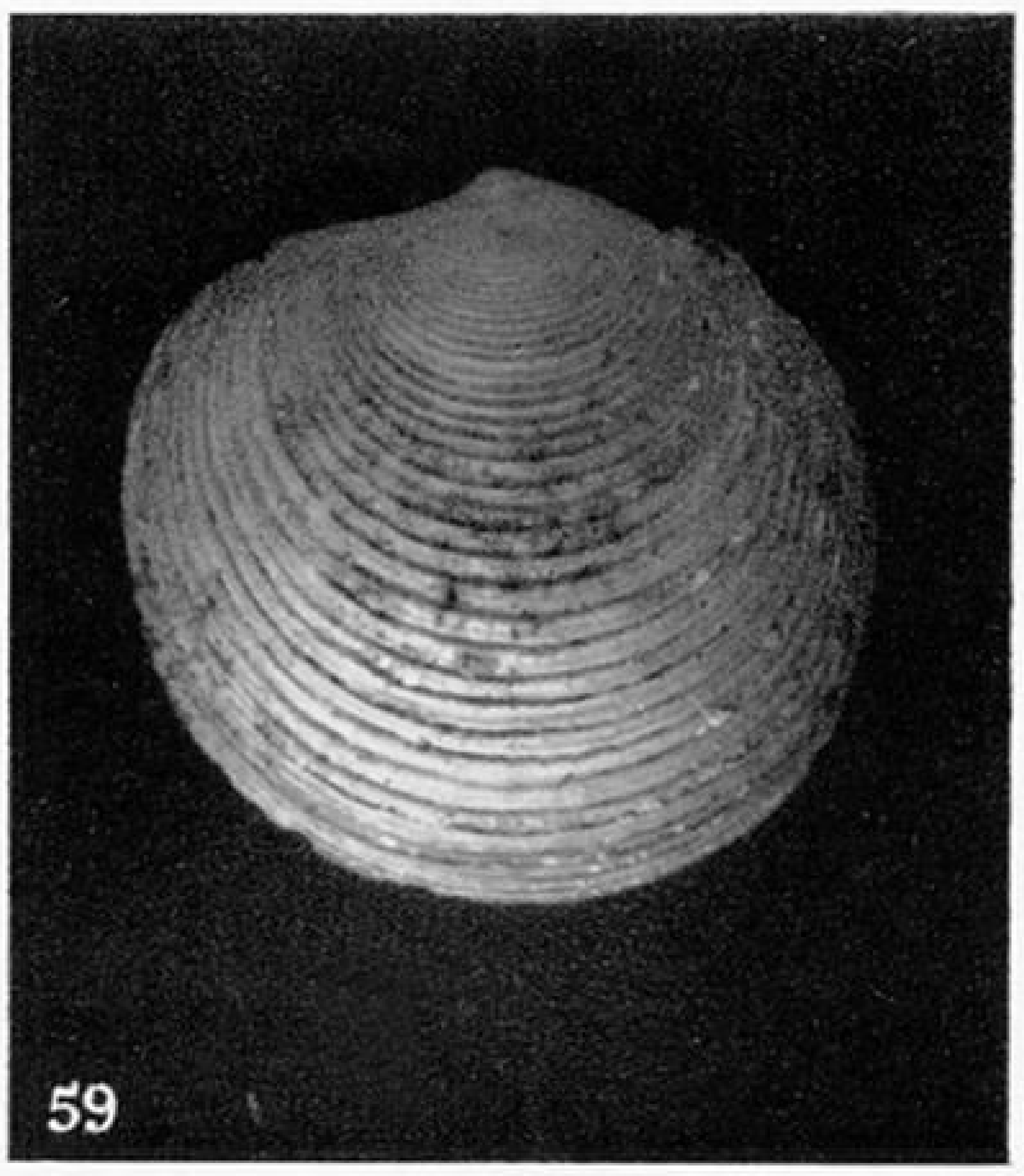
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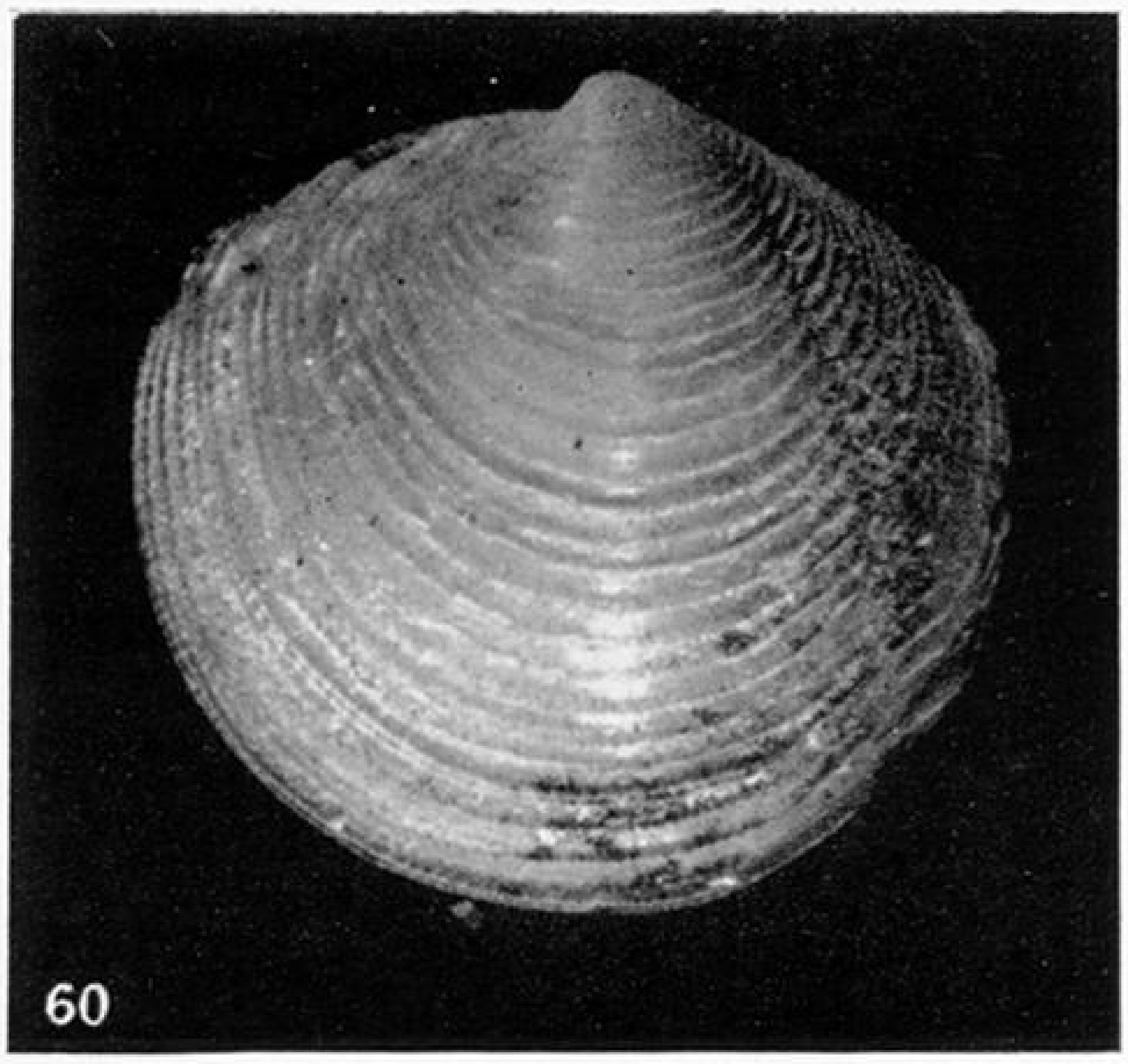
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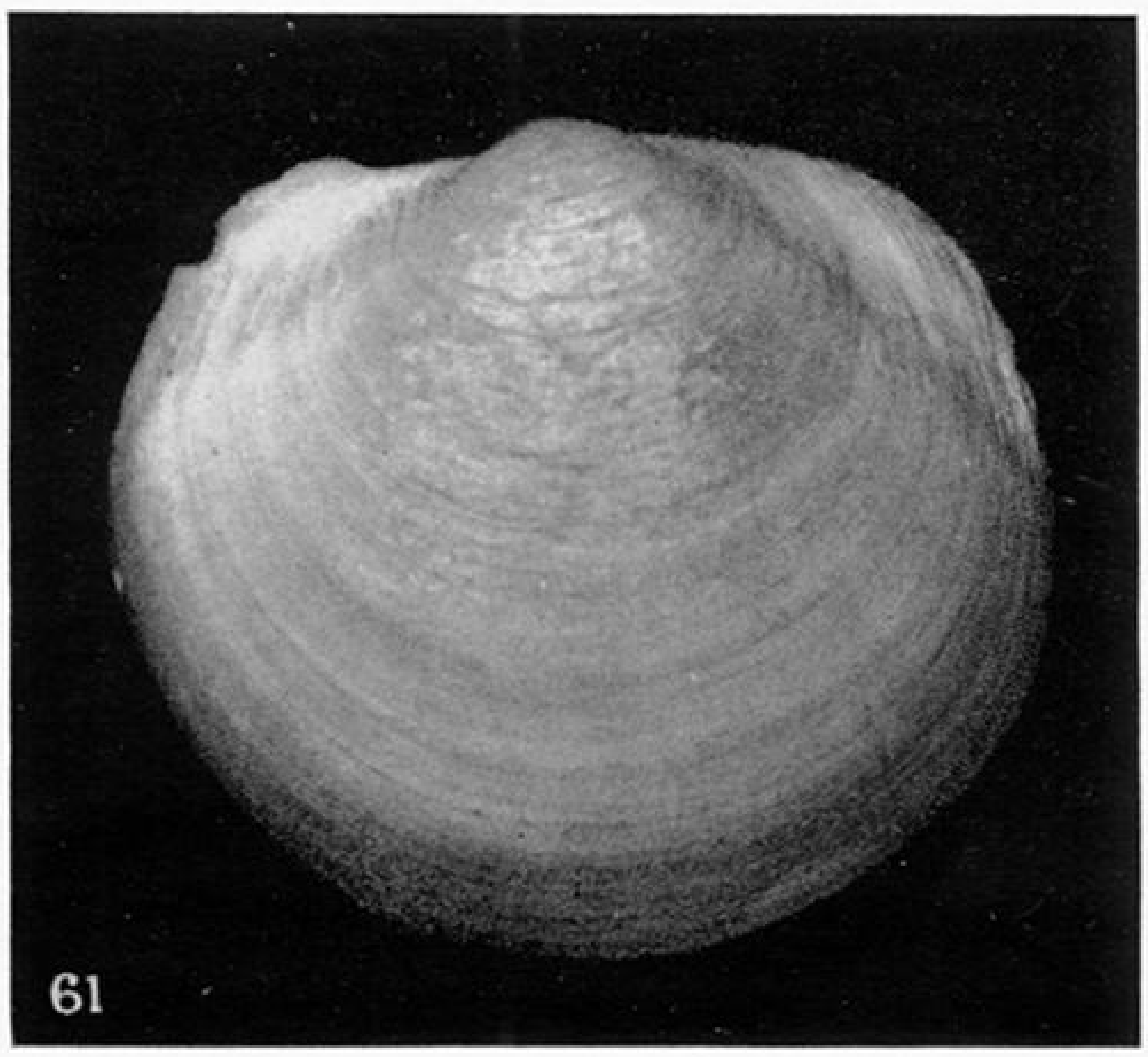
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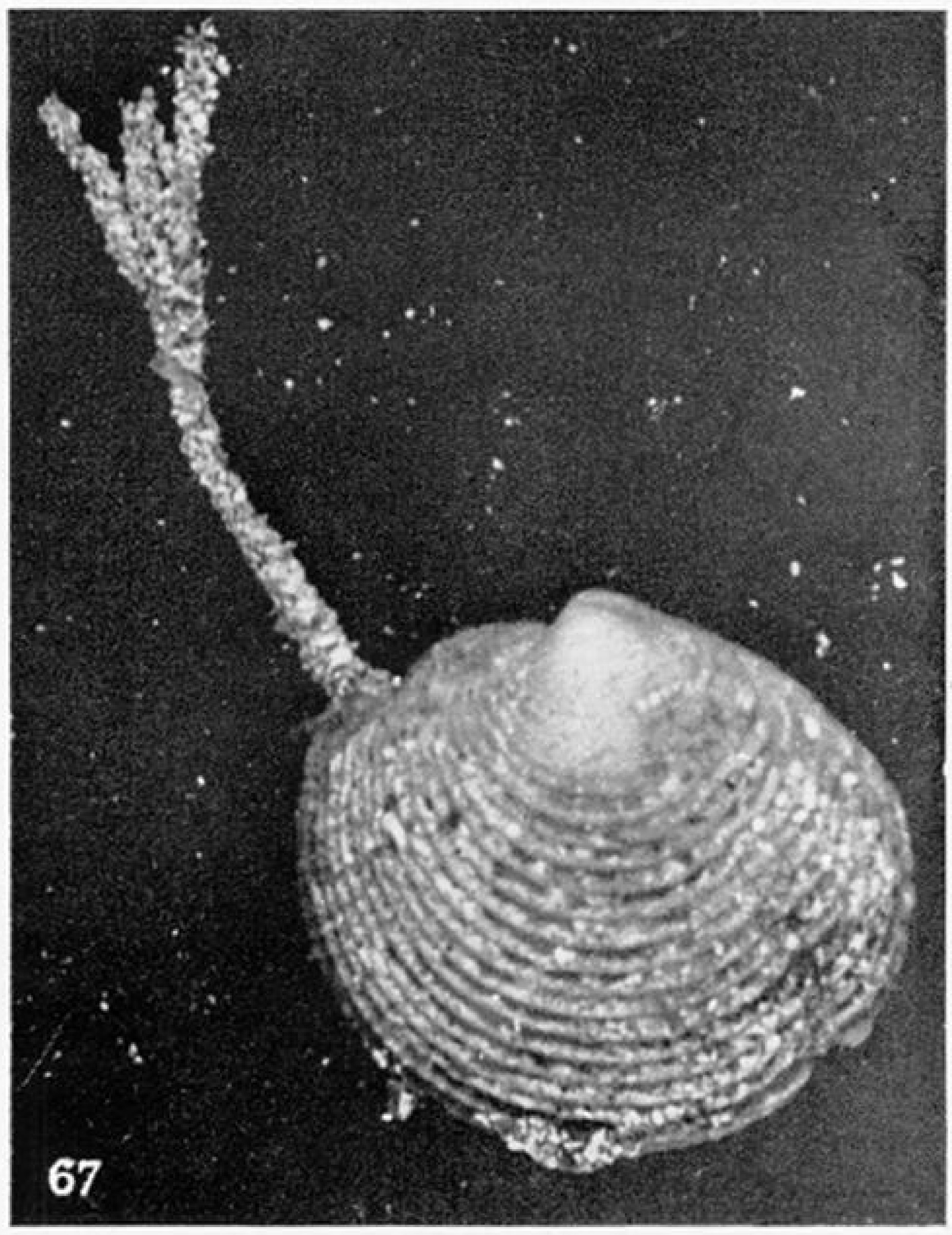
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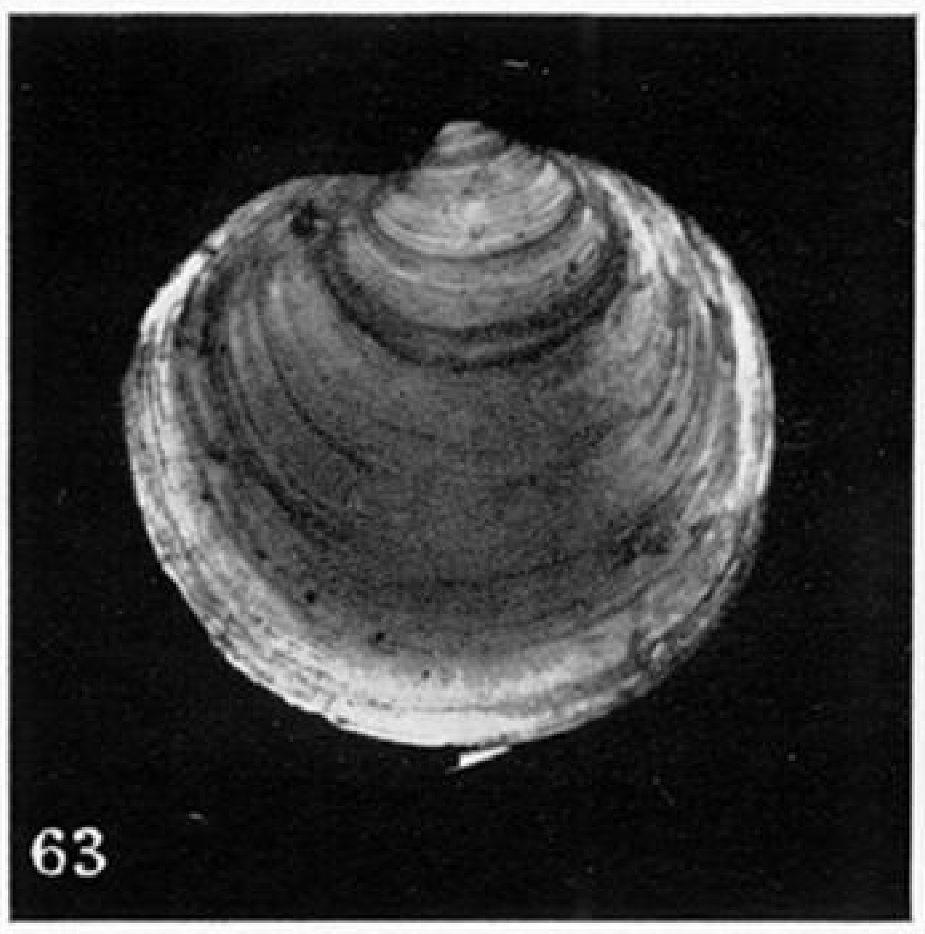
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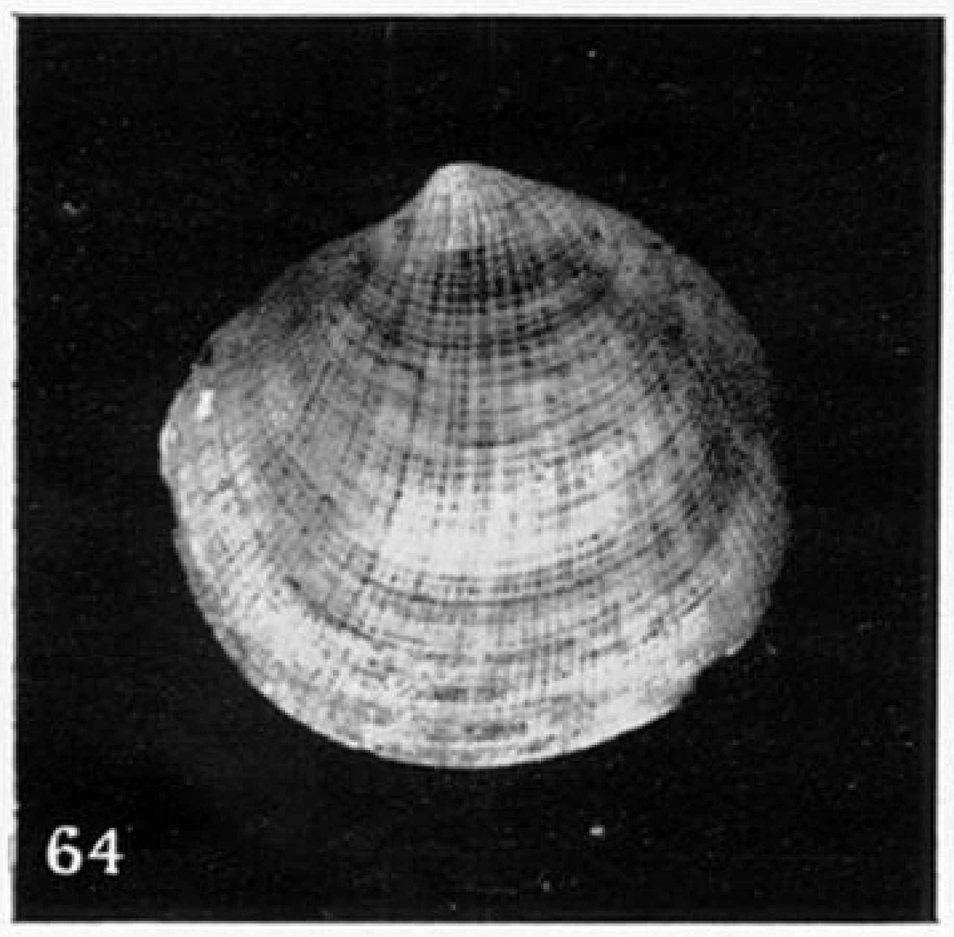
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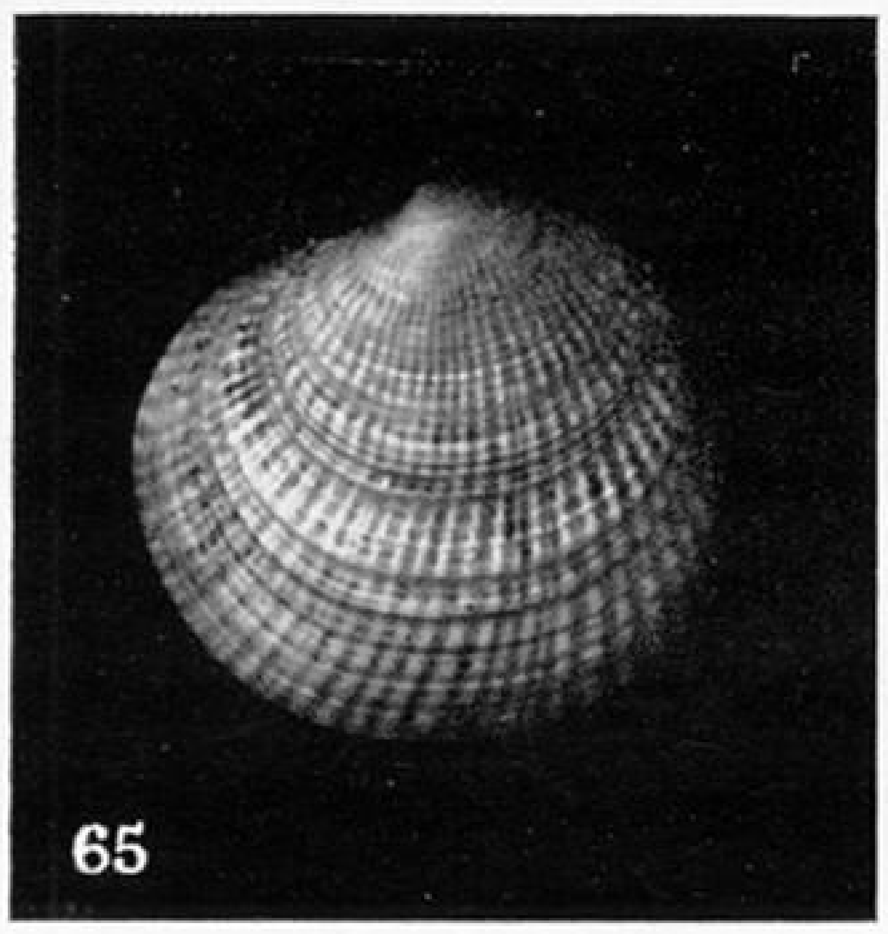
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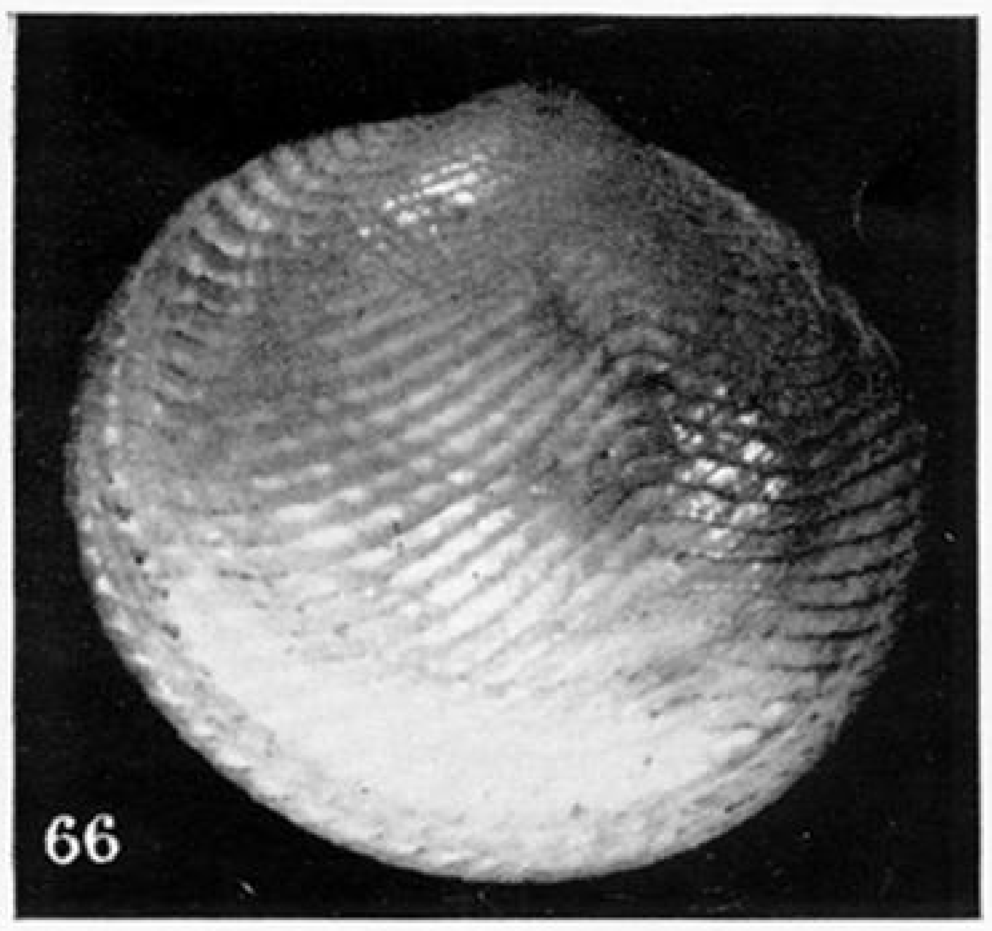
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FIGURES 54 TO 67. Valves of the species of the Lucinacea studied. 54, *Diplodonta semiaspera* (×3); 55, *D. rotundata* (×1); 56, *D. punctata* (×1·5); 57, *Thyasira flexuosa* (×4); 58, *Codakia orbicularis* (×1); 59, *Phacoides borealis* (×1·5); 60, *Lucina pennsylvanica* (×1·5) 61, *L. chrysostoma* (×1·5); 62, *Myrtea spinifera* (×3); 63, *Loripes lucinalis* (×2); 64, *Codakia costata* (×3); 65, *C. orbiculata* (×3); 66, *Divaricella quadrisulcata* (×1·5). 67, *Lucina pennsylvanica* with the anterior inhalent tube intact showing clearly the repaired end that lies at the surface of the substratum.