Observations on the Solenacea with Reasons for Excluding the Family Glaucomyidae

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OBSERVATIONS ON THE SOLENACEA WITH REASONS FOR EXCLUDING THE FAMILY GLAUCOMYIDAE

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CONTENTS

The Glaucomyidae and the Solenidae are generally included in the suborder Solenacea, but the systematic position of the Glaucomyidae has always been doubtful. The habit and structure of *Glauconome rugosa* are here described and compared with those of the Solenidae as exhibited in the first place by the species *Pharella acuminata*. The systematic position of the genera comprising the family Glaucomyidae is discussed.

The structure and mode of growth of the external, opisthodetic ligament is described and it is shown that the form and growth of the shell (which includes the ligament) in the Bivalvia can be represented satisfactorily only when the two valves together with the ligament are considered as a unit.

Fusion of the mantle margins ventrally and the formation of the long, united siphons involves the inner marginal folds together with the inner surfaces of the middle folds. In association with the mode of life, the foot is poorly developed and the pedal gape restricted to the anterior end. The ctenidia are capable of dealing rapidly with water containing large amounts of sediment, while the ciliation of the frontal surfaces of the filaments and the currents on them are similar to those of *Petricola pholadiformis*. The style sac and mid-gut are combined.

Also included in the family Glaucomyidae is the genus *Tanysiphon* and shells of *Tanysiphon rivalis* were examined. The ligament of this species is short and, unlike that of *Glauconome rugosa*, extends obliquely across the hinge-plate posterior to the poorly developed cardinal teeth. The relationships between *Glauconome* and *Tanysiphon* are discussed and it is concluded that the latter genus is closely allied to *Lutraria* and should be transferred to the Mactridae. Features, which unfortunately could not be verified, but which probably characterize the animal of *Tanysiphon* and would indicate it to be a member of the Mactridae, are listed.

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Of the three subfamilies previously considered as comprising the Solenidae only the Soleninae remain. The habits and general structure of the available genera now included in the Solenidae are described: in particular *Pharella acuminata* (in greatest detail); *Siliqua patula* (preserved specimens); *Cultellus lacteus* and *C. subellipticus* (shells only); *Phaxus pellucidus*; *Solen marginatus*; *Ensis siliqua*, *E. arcuatus* and *E. ensis*.

In all members of the Solenidae the mantle/shell is elongated posterior to the demarcation line and in the more specialized genera this is accompanied by a marked reduction in depth. The external, opisthodetic ligament is composed of anteriorly and posteriorly secreted fusion layer and outer and inner layers of the primary ligament. A fourth pallial aperture is present in *Siliqua*, *Cultellus* (probably), *Phaxus* and *Ensis* and in these genera the inner marginal folds anterior to the fourth pallial aperture are joined by cuticular fusion. Posterior to the fourth pallial aperture there is complete tissue fusion of the mantle margins. This involves the inner folds only in *Siliqua* and the inner folds together with the inner surfaces of the middle folds in *Phaxus* and *Ensis*. In *Pharella* and *Solen*, tissue fusion is of this latter type along the entire ventral margin. In all genera the inner surface of the middle fold is involved in the formation of the siphons. The ctenidia range from flat and homorhabdic (*Phaxus*) to plicate and heterorhabdic and adjacent tracts of long and short cilia are present on the frontal surfaces of some (*Phaxus*) or all of the lamellae. The style sac and mid-gut are always separate.

The most significant feature of the Solenidae is the posterior elongation of the mantle/shell, and the effect of this on pallial attachment and the position of the adductor muscles is discussed. In *Phaxus*, *Solen* and *Ensis* the primitive ventro-dorsal axis of the anterior adductor muscle is orientated antero-posteriorly. As a result, pallial attachment extends from the posterior end of the elongated adductor anteriorly to the anterior end of the functional ligament.

The systematic position of the family Glaucomyidae (now represented by the single genus, *Glauconome*) is discussed. It is concluded that the Glaucomyidae are venerid bivalves specialized for life deep below the surface of the substrate. The mobility which characterizes the Veneridae has been lost, the animal living permanently embedded in the substrate and maintaining contact with the surface by way of the long siphons. The Glaucomyidae should be included with the Veneridae and Petricolidae in the Veneracea and not with the Solenidae in the Solenacea.

I. INTRODUCTION

During a visit to Singapore in September 1956, living specimens of two genera of bivalves were obtained, a study of which has proved of considerable interest. These two genera, *Glauconome* Gray (*Glaucomya* Bronn) and *Pharella* Gray are members of the Glaucomyidae and Solenidae, respectively, the two families which Thiele (1934) lists as comprising the suborder Solenacea. The systematic position of the Glaucomyidae has always been doubtful. The genus *Glauconome* was originally placed by Gray (1828) in the Veneridae, but Reeve (1844) claimed that it should be included in the Solenacea, while Deshayes (1853), from a study of the anatomy, suggested that the genus was related to *Lutraria*. In recent times, Thiele (1926) in Kükenthal's *Handbuch der Zoologie* includes the Glaucomyidae with the Veneridae and Petricolidae in the Veneracea, but later (1934) he lists the family with the Solenidae in the Solenacea. In this paper the opportunity is taken to compare *Glauconome* and *Pharella* with other members of the Glaucomyidae and Solenidae, respectively, and by so doing to provide an account of the features which characterize these two families of bivalves. The families are compared and the systematic position of the genera which comprise the Glaucomyidae is discussed. The specimens obtained from Singapore were identified by Professor R. Tucker Abbott of the Academy of Natural Sciences, Philadelphia, as *Glauconome rugosa* Reeve (1844) and *Pharella acuminata* (Hanley 1842). Living specimens of *Ensis siliqua* (L.), *E. arcuatus* (Jeffreys) and *Phaxus pellucidus* (Pennant)

were obtained from Millport and specimens of *Ensis ensis* (L.) and *Solen marginatus* Pulteney from Dale Fort, Pembrokeshire. Preserved specimens of *Siliqua patula* Dixon from California were provided by Professor C. M. Yonge, while shells of *Tanysiphon rivalis* Benson, *Cultellus lacteus* (Spengler) and *C. subellipticus* Dunker were kindly lent by the British Museum.

II. Glaucomyidae

This family has been considered to include the two genera *Glauconome* Gray and *Tanysiphon* Benson, while recently Iredale (1936) has added a third genus, *Glauconometta*. Iredale does not explain, however, his reasons for erecting a new genus nor are these reasons apparent from his description. The nomenclature of *Glauconome* is confusing. The genus was originally proposed by Gray (1828) but the name was subsequently rejected as having been anticipated by Goldfuss (1826) and replaced by *Glaucomya* Bronn (1838). It is this name which is used by Thiele (1934). It is now known that Goldfuss's use of the name *Glauconome* for a fossil bryozoan was in 1829 and thus *Glauconome* Gray (1828) must come back into use. The family name, Glaucomyidae, remains valid.

(1) Glauconome rugosa

The shell of *G. rugosa* is equivalve, inequilateral and possesses a greenish, wrinkled periostracum which together with the outer calcareous layer of the valves is invariably worn away in the region of the umbones (figure 1 *a*). Posteriorly, the valve margins do not meet,
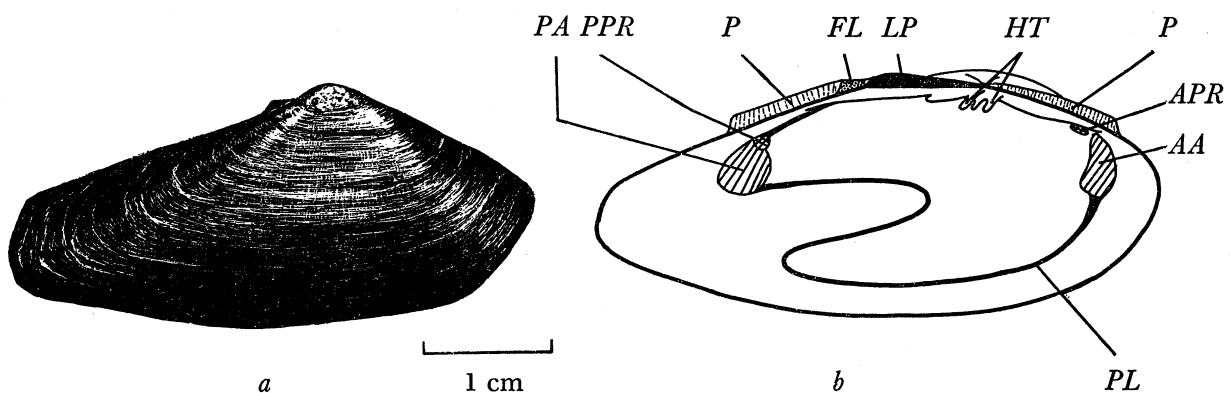

FIGURE 1. *Glauconome rugosa*. *a*, shell viewed from right side; *b*, inner surface of left valve showing the muscle scars and the structures joining the two valves dorsally. For key to the lettering on all figures see p. 97.

leaving a small, permanent gape to the shell, and in preserved specimens there is a similar gape at the anterior end, but in this case the valve margins can be made to meet when pressed together. Thus, despite the external ligament it is possible for the valves to rock slightly about a vertical axis but whether they do so in life is not known. The hinge mechanism consists of an external, opisthodetic ligament and three well-developed cardinal teeth in each valve (figure 1 *b*, *HT*). The two anterior teeth in each valve (figure 3) are slender, lamellate structures projecting more or less at right angles to the hinge plate and they are easily broken when the valves are separated. The posterior tooth of the right valve and the middle tooth of the left valve are strongly bifid.

(a) *Ligament*

The ligament has proved of considerable interest since a study of its structure in *G. rugosa* shows more clearly than in the majority of bivalves the relationship of the various layers comprising the lamellibranch ligament. The mode of origin of the various layers composing the bivalve ligament has been outlined by Owen, Trueman & Yonge (1953). The mantle in the Bivalvia consists of two lobes connected dorsally by the mantle isthmus, the shell in this region being largely uncalcified and constituting the ligament. The inner
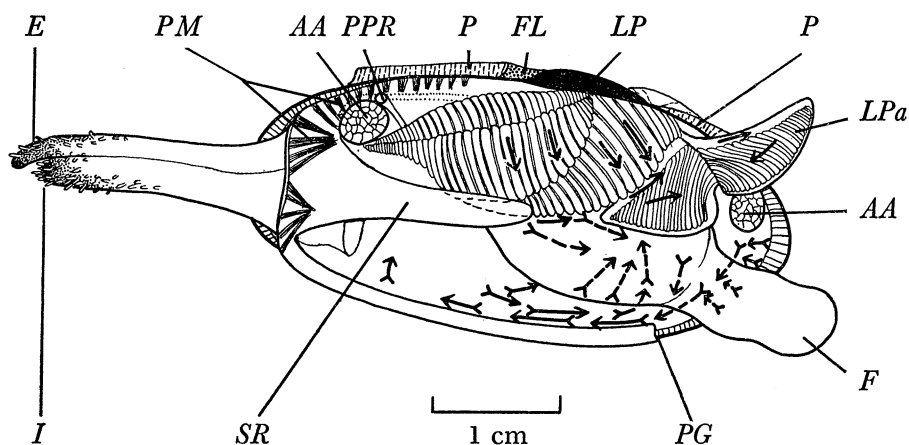

FIGURE 2. *Glauconome rugosa*. Organs and ciliary currents of the mantle cavity viewed from the right side after the removal of the right shell valve and mantle lobe. Feathered arrows represent cleansing and rejection currents.
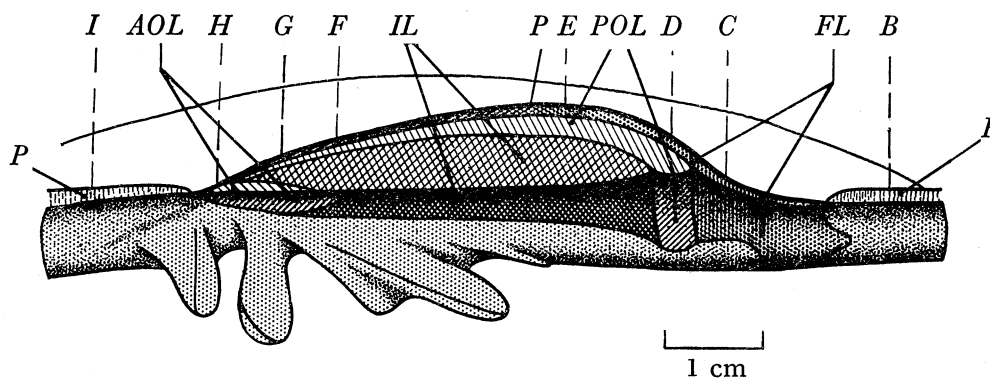

FIGURE 3. *Glauconome rugosa*. Semi-diagrammatic figure of the ligament cut longitudinally and viewed from the left side. The letters *B* to *I* refer to the positions of transverse sections drawn in figures 4 and 5.

layer of the ligament is secreted by the epithelium of the mantle isthmus, while the outer layer is secreted by the outer surface of the outer fold at each end of the mantle isthmus; periostracum is secreted at each end of the ligament by the inner surface of this fold (i.e. all precisely as for the shell valves). These three layers—periostracum, outer layer and inner layer—constitute the primary ligament and form the basis of the ligament throughout the Bivalvia. Secondary extension of this primary ligament results from the fusion of the outer secretory folds of the mantle margins at one or both ends of the mantle isthmus and Yonge (1957) divides this secondary ligament into two types depending on the degree of fusion of the outer folds: (a) periostracum, secreted by the fused inner surfaces of the

outer folds; (*b*) fusion layer, secreted by the fused outer surfaces of these folds. But it is doubtful whether in any bivalve the secretion of periostracum by the fused inner surfaces of the outer folds extends the *functional* ligament (Owen 1958). In *Cuspidaria* and also in
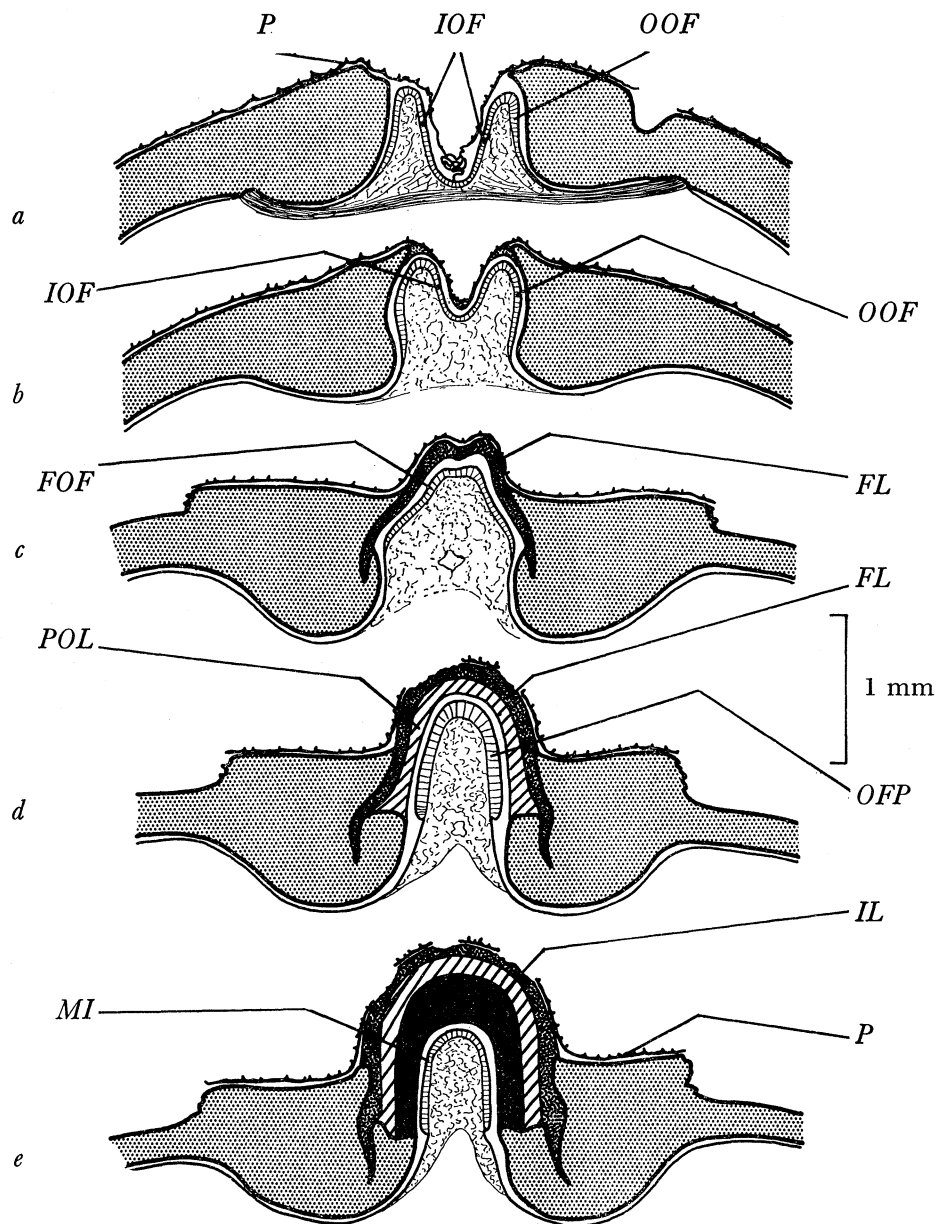

FIGURE 4. *Glauconome rugosa*. Sections through the dorsal margins of the shell and mantle in the regions indicated in figure 3. *a*, is taken from near the region of the posterior adductor muscle.

the Lyonsiidae extension of the primary ligament is probably by way of fusion layer only. In the Mytilacea, on the other hand, the periostracum at the posterior end of the primary ligament is secreted by the extended inner surface of the outer fold, where this bends round from one pallial lobe to the other in the depth of the posterior embayment and it is, therefore, part of the primary ligament (Owen 1958).

The interpretation of the structure of the ligament of *G. rugosa* will be more readily understood by comparing the sections shown in figures 4 and 5 *a* to *i*, with the diagrammatic

representation of the ligament shown in figure 3. The posterior end of the primary ligament is secondarily extended by fusion layer (*FL*) and as a consequence, the functional ligament is composed of a superficial periostracum (*P*), fusion layer (*FL*) and outer (*POL*) and inner (*IL*) layers of the ligament. It extends posteriorly from the umbones approxi-
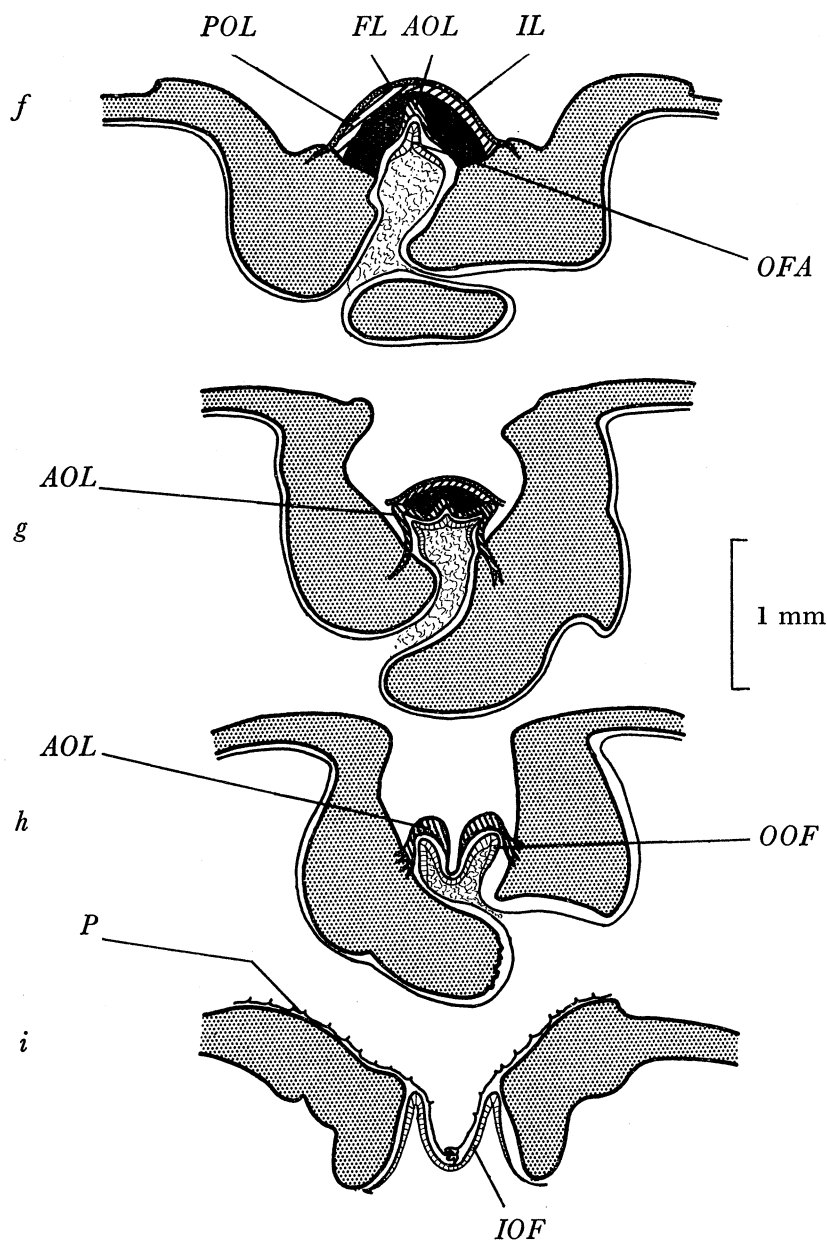
FIGURE 5. *Glauconome rugosa*. Sections through the dorsal regions of the shell and mantle in the regions indicated in figure 3.

mately one-third the distance to the posterior end of the shell. Posterior to the primary ligament (figure 4*c*), the two valves are joined by an inverted U-shaped structure which is the fusion layer (*FL*) secreted by the fused outer surfaces of the outer folds (*FOF*) of the mantle margins posterior to the mantle isthmus. In the mid-line between the two valves this fusion layer is secreted beneath the periostracum while laterally it extends beneath

the calcareous layers of the valves. As growth proceeds the lateral regions of the fusion layer are progressively embedded in the calcareous layers of the shell and it undoubtedly serves to attach the ligament firmly to the valves (figures 4*d*, *e*). Outer layer of the ligament (*POL*) is secreted beneath the fusion layer by the outer marginal fold (*OFP*) at the posterior end of the mantle isthmus where this bends round from one pallial lobe to the other, while the inner layer of the ligament (*IL*) is secreted by the epithelium of the mantle isthmus (*MI*). Underlying the inner layer at the anterior end of the ligament and extending a short distance anterior to the umbones is the anterior outer layer (*AOL*) secreted by the outer marginal fold at the anterior end of the mantle isthmus. Thus, all the possible constituents of the lamellibranch ligament (Yonge 1957), with the exception of anterior fusion layer, are present and their relationship to one another, particularly at the anterior end, are almost diagrammatically obvious.

Throughout the Bivalvia the structure of the ligament is dependent on the degree of pallial fusion or separation at each end of the mantle isthmus while the form of the ligament, on the other hand, is dependent on the growth pattern of the entire shell. Growth of the shell results from marginal increment and its form in different species can be related by the use of radial co-ordinates arranged about a 'node' or point where growth is absent or at a minimum (Yonge 1952). The umbo of the lamellibranch shell valve is generally regarded as representing such a 'node' or point, but this suggests the existence of two points where growth is at a minimum and results in the misleading impression that the bivalve shell consists of two separate portions represented by the two shell valves. A consequence of this is that the growth lines of a single valve are usually represented as a series of closed coaxial circles. The two pallial lobes, however, remain connected dorsally by the mantle isthmus and growth of the shell can be represented satisfactorily only when the two valves together with the ligament are considered as a single unit. It will then be seen that the lines of growth of each valve are laid down, not as a series of closed coaxial circles, but as open coaxial figures which are continuous with one another by way of the non-calcified ligament (figure 6*a*). In those bivalves possessing an opisthodetic ligament there is a single region of minimum growth situated near the anterior end of the ligament and, as can be seen from figure 6*a*, growth of the ligament results from marginal increment as does that of the shell valves.

Figure 6*b* is an attempt to represent diagrammatically the growth of the ligament in *G. rugosa*. The functional ligament is bounded by the lines *OA* and *OZ*, while the broken line *OM* intersects each growth stage at the point of minimum growth. Posterior to *OM* marginal increase is directed posteriorly, while anterior to *OM* it is directed anteriorly. The outer layer (*POL*) secreted by the outer fold (i.e. the mantle margin) at the posterior end of the mantle isthmus, extends posteriorly beneath the fusion layer (*FL*) and is in turn underlaid by the inner layer (*IL*) secreted by the epithelium of the mantle isthmus. The outer fold at the anterior end of the ligament lies astride the region of minimum growth (between lines *OA* and *OB*) and as growth proceeds it extends both posteriorly beneath the anterior region of the inner layer and anteriorly beyond the anterior end of the inner layer. It is the posteriorly directed growth of part of the outer fold at the anterior end of the mantle isthmus which results in the anterior outer layer (*AOL*) forming the innermost layer of this region of the ligament (see figures 5*f*, *g*).
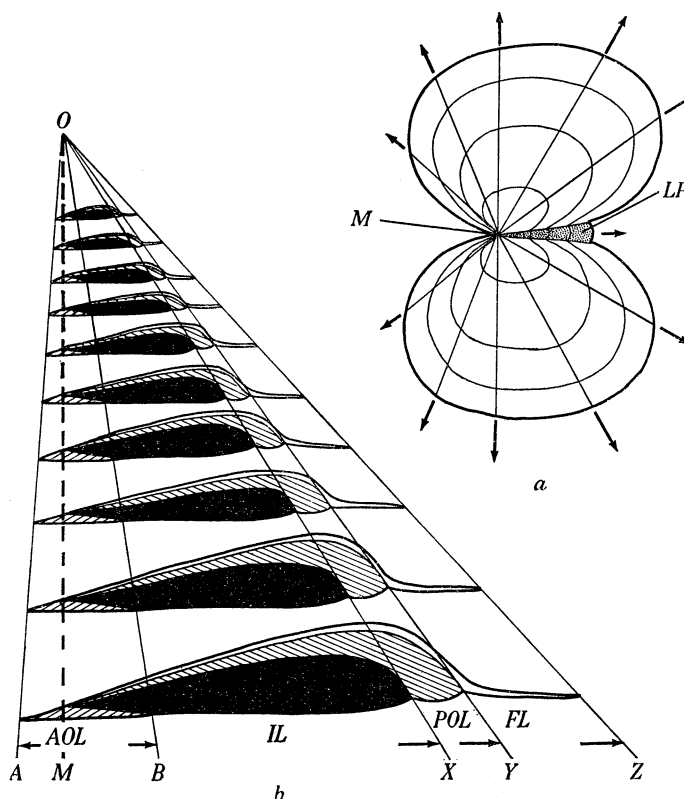
FIGURE 6. *a*, diagrammatic representation of a bivalve shell spread out flat and viewed from above to demonstrate the unity of the valves and ligament, i.e. parts of one structure. The arrows indicate the direction of growth at the mantle/shell margin. *b*, diagrammatic representation of the structure and growth of the ligament of *Glauconome rugosa*. The broken line *OM* indicates the region of minimum growth which occurs at *M* in figure *a*; the lines *OA* and *OB* indicate the anterior and posterior ends of the outer layer (*AOL*) secreted by the outer marginal fold at the anterior end of the mantle isthmus; the line *OX* indicates the posterior end of the inner layer (*IL*) secreted by the epithelium of the mantle isthmus; the line *OY* indicates the posterior end of the outer layer (*POL*) secreted by the outer marginal fold between *OX* and *OY* at the posterior end of the mantle isthmus; the line *OZ* indicates the posterior limit of the fusion layer, i.e. secondary ligament (*FL*), secreted by the fused outer surfaces of the outer marginal folds between *OY* and *OZ* posterior to the primary ligament. The arrows indicate the direction of growth. Thus the posterior outer layer extends beneath the fusion layer while the inner layer extends beneath both. The anterior outer layer extends both anteriorly beyond the inner layer and posteriorly beneath the anterior region of the inner layer.

(*b*) *Mantle fusion*

The mantle margins are fused except in the regions of the siphons and of the relatively small pedal gape (figure 2). The extensive fusion of the mantle margins ventrally is complete (figure 7*b*) and involves the inner folds together with the inner surfaces of the middle folds (Type B; Yonge 1957). The extent of the outer surface of the middle fold (*OMF*) separating the periostracum (*P*) on each side is very small. Dorsal to the anterior and posterior adductor muscles, fusion involves the inner marginal folds together with both surfaces of the middle folds (Type C; Yonge 1957). As a result the inner periostracal-secreting surfaces of the outer folds are continuous and the periostracum diverges on each

side to cover the shell valves (figure 4 *a*). Where fusion of the mantle margins in the anterior and posterior embayments is of this type, pallial attachment is retained (Owen 1958) and so in *G. rugosa* the line of pallial attachment extends beyond both adductors to near the anterior and posterior limits of the functional ligament (figure 2, *PM*). But in the depth of the posterior embayment there is a short region posterior to the fusion layer of the ligament where the two valves are still joined by periostracum but where, nevertheless, pallial attachment is absent (figure 4*b*). This is the region where the inner surface of the outer fold bends round from one pallial lobe to the other in the depth of the posterior embayment; there is a similar region at the anterior end of the ligament (figure 5*f*). Thus although anterior and posterior to the functional ligament, the two valves are joined by a continuous sheet of periostracum, there is no *fusion* of the inner surfaces of the outer folds in these regions.
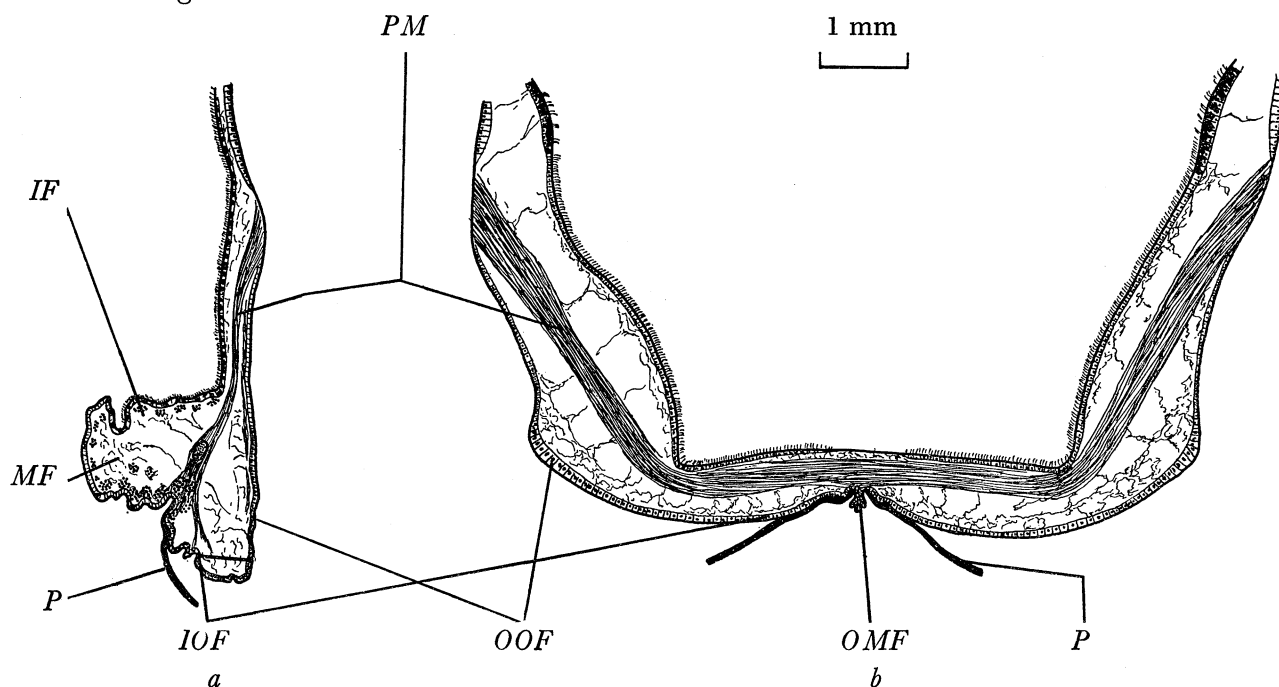

FIGURE 7. *Glauconome rugosa*. Transverse sections through mantle margins. *a*, region of pedal gape; *b*, region of fusion of the ventral margins posterior to the pedal gape.

(*c*) *Siphons*

When fully extended the siphons may exceed the length of the shell (figure 2). But for a short region near the pigmented extremities the inhalant (*I*) and exhalant (*E*) portions are united, with the exhalant siphon somewhat the longer. They can be withdrawn completely within the shell valves and the proximal portions then project far into the mantle cavity; withdrawal is effected by a combination of introversion and muscular contraction. The inhalant aperture is fringed with alternating long and short tentacles, while the opening of the exhalant siphon is bounded by a valvular membrane. Slender pale tentacles are scattered over the external surface of both the inhalant and exhalant siphons being most numerous over the dorsal and ventral regions of the extremities and decreasing both in size and number basally. The inner folds together with the inner surfaces of the middle folds are involved in the formation of the siphons (Type B; Yonge 1957)

and the periostracum is secreted by the inner surfaces of the outer folds at the base of the siphonal process. As recently described by Yonge (1957), the tentacles and membrane surrounding the inhalant and exhalant apertures represent the margin of the inner fold of the mantle margin, while the external surface of the siphons is formed from the now greatly extended outer surface of the middle fold.

(d) Mantle cavity

The appearance of the animal after the removal of the right valve is shown in figure 2. Anterior (AA) and posterior (PA) adductor muscles and siphonal retractor muscles (SR) are well developed. The foot (F), which is whitish in colour, is poorly developed although it is capable of a reasonable extension (5 to 6 cm) beyond the anterior margin of the shell. When extended it is strap-like and laterally compressed, but when contracted within the mantle cavity its appearance is similar to the foot of *Mya arenaria*. The posterior pedal retractor muscle (PPR) is slender and inserted on the shell on each side at the antero-dorsal margin of the posterior adductor, while the anterior retractor is inserted on each side near the margins of the valves between the anterior adductor and the anterior end of the ligament (figure 1*b*, APR). The longitudinal fibres of both pedal retractors extend into the foot where they intermingle. They also spread over the surface of the globular visceral mass; there is no protractor muscle. The ciliary currents over the internal surface of the mantle are shown in figure 2. The ctenidia, details of which are given in the next section, are heterorhabdic and plicate with the plicae arranged in pairs and extending on to the supra-axial extension of the outer demibranch. The inner demibranch does not extend between the well-developed labial palps, while the outer demibranch is approximately two-thirds the length of the inner. Cuticular fusion of the type described by Atkins (1937*c*) connects the ascending lamellae of the outer demibranchs and the mantle, the ascending lamellae of the inner demibranchs and the visceral mass and the ascending lamellae of the inner demibranchs of both ctenidia posterior to the visceral mass.

(e) Ctenidia, labial palps and feeding

The direction of the frontal ciliary currents of the ctenidia are indicated in the diagrammatic transverse section shown in figure 8*a*. They are similar to Atkins's category C (1*c*) (Atkins, 1937*b*). The ciliation of the frontal surfaces of the filaments and the currents on them are similar to those of *Barnea candida* and *Petricola pholadiformis*, but unlike the lamellae of *Barnea candida*, those of *Glauconome rugosa* are plicate and heterorhabdic. The coarse cirri characteristic of this category of lamellibranch gills are restricted to the posterior margins of the frontal surfaces of a small number of apical filaments on each plica. Near the free margins of the lamellae the cirri are more numerous and are also present on the filaments forming the sides of the plicae; they are never present on the principal filaments. The cirri are $25\,\mu$ in length and, despite their uniform appearance in living animals, sections of preserved material reveal that each cirrus consists of a fused tuft of numerous long cilia arising from a single cell situated between the normal frontal cilia and the pro-lateral cilia (figure 9). The cilia comprising the cirrus fray out under the chemical effects of the fixative. As in other members of Atkins's category C (1*c*) there are anteriorly directed currents in the ctenidial axis and along the free edges of the inner and outer demibranchs (figure 8*a*). A peculiar feature of the gills of *G. rugosa* is that, although

no dorsally directed currents were detected over the frontal surfaces of the ascending lamellae of the inner and outer demibranchs, weak anteriorly directed currents are present along the dorsal edges of these lamellae. There is no groove at the free margin of the outer demibranch, the oralward current being due to the presence of coarse terminal cilia (Atkins 1937 *b*). The deep and narrow groove at the free margin of the inner demibranch is protected by fan-shaped groups of guarding cilia.
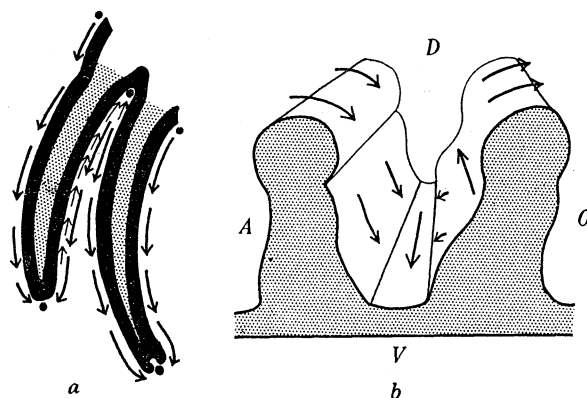

FIGURE 8. *Glauconome rugosa.* *a*, diagrammatic transverse section showing the form of the gill and the direction of the currents on the frontal surface of an apical filament. Black circles indicate oralward current; *b*, diagram showing the direction of the ciliary currents on the folds of the labial palps.

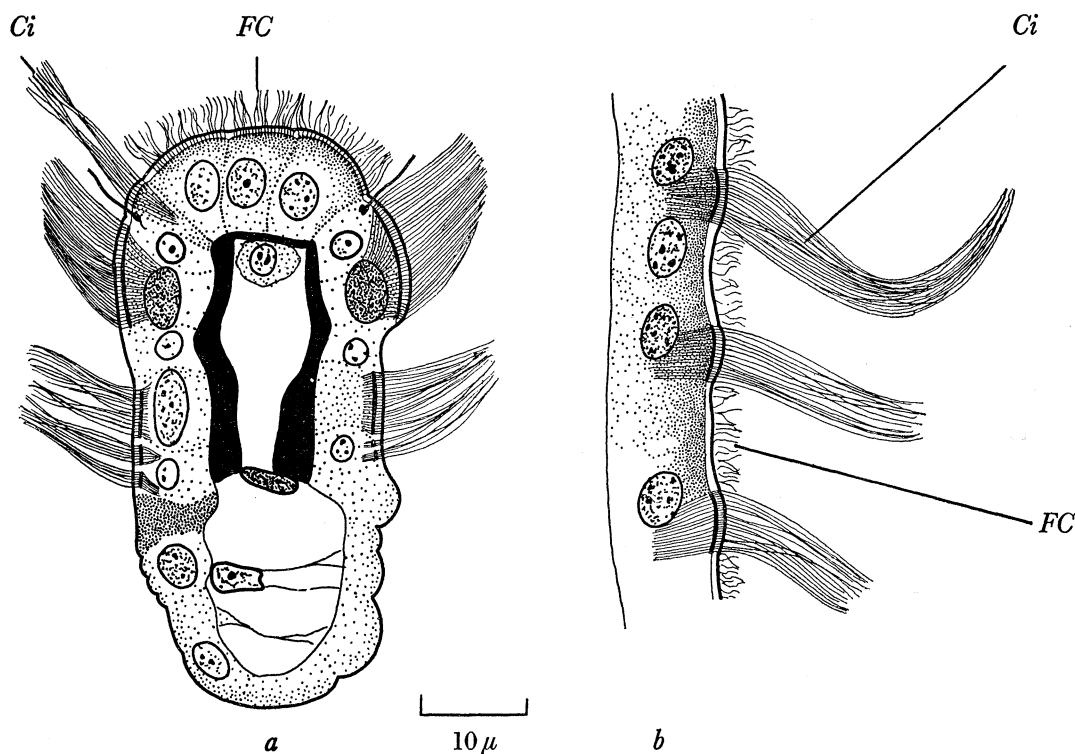FIGURE 9. *Glauconome rugosa.* Sections of the gill filaments to show the arrangement of the cirri (*Ci*) and frontal cilia (*FC*). *a*, transverse section of an apical filament showing the cirrus consisting of a tuft of long cilia arising from a single cell on the posterior side of the frontal surface; *b*, longitudinal section of the frontal surface of an apical filament showing the ventrally beating cirri.

The gills of *G. rugosa* are beautifully adapted for dealing rapidly with water containing large amounts of sediment. Over both lamellae of the inner demibranchs, coarse particles are transported rapidly to the free edge by the long cirri present along the posterior margin of the frontal surfaces of the filaments. Due to the presence of guarding cilia and the muscular properties of the marginal groove, they are unable to enter the groove. Fine particles are conveyed ventrally by the short frontal cilia and enter the marginal groove between adjacent groups of guarding cilia. Over the outer surface of the outer demibranchs, coarse and fine particles are similarly conveyed ventrally by both the cirri and the short frontal cilia. The cirri do not continue to the free edge but cease a short distance from it where the plicae flatten out. Their place is taken by the long coarse cilia which extend over the posterior half of the frontal surface of each filament. They beat towards the free edge and forward and are responsible for the incipient oralward current present at the free margins of the outer demibranchs. Their main function appears to be that of sending coarse particles off the edge of the demibranch and on to the mantle or the descending lamella of the inner demibranch. Over the anterior region of the frontal surface of each filament the short frontal cilia are continuous round the bend at the free edge and convey particles from the ascending to the descending lamella. Over the descending lamella of the outer demibranch, fine particles are conveyed dorsally by the short frontal cilia and anteriorly along the ctenidial axis. Coarse particles, on the other hand, are conveyed ventrally by the cirri and fall off the free edge of the demibranch.

The plicae also contribute to the sorting effect exercised by the gills. As already described, the cirri are largely restricted to the filaments forming the apices of the plicae. When the lamellae are flooded with carborundum the gills contract, drawing the plicae together. Over both lamellae of the inner demibranchs and the ascending lamella of the outer demibranch the cirri rapidly transport all material ventrally to the free margins. With the gill in a contracted state it is prevented from entering the marginal groove of the inner demibranch by the guarding cilia, or falls off the free edge of the outer demibranch due to the presence of the coarse terminal cilia. Over the descending lamella of the outer demibranch, approximation of the plicae results in most of the material present on the surface of the lamella being conveyed ventrally by the cirri; only very fine particles pass between adjacent plicae and travel safely, dorsally to the ctenidial axis. This sorting mechanism is similar to that described by Atkins (1937*a*) for the plicate gills of *Pecten* and *Ostrea*, where the frontal surfaces of the filaments possess tracts of coarse and fine cilia beating in opposite directions; cirri are not present in these genera. Under certain conditions, such as the presence of much sediment in the water, the increased gill surface resulting from plication may be a distinct disadvantage. Although the plicae and frontal cirri of *G. rugosa* may be utilized as sorting mechanisms in the manner described, the cirri must be considered primarily as a specialization for preventing the gills becoming clogged in water containing large quantities of silty material.

The labial palps are relatively large with the usual ridges on their inner surfaces (figure 2). The ciliary currents on these ridges are shown in figure 8*b*. In dissected animals, in addition to the usual muscular activity of the palps, these ridges frequently underwent violent muscular contractions, a feature probably associated with life in a substratum containing mud or silt and the need to prevent clogging of the palp surfaces.

(f) Alimentary canal

The tubular oesophagus enters the antero-dorsal region of the stomach (figure 10, *Oes*), while the combined style sac (*SS*) and mid-gut (*MG*) leaves the stomach posteriorly and ventrally. The style sac extends ventrally to the ventral margin of the foot before curving anteriorly and dorsally. Within the visceral mass the mid-gut is thrown into two loops while the hind-gut ascends dorsally posterior to the style sac to pass through the ventricle of the heart and the posterior aortic bulb where it is attached to the mid-dorsal wall. The anus opens on the posterior surface of the posterior adductor muscle. Only the external form of the stomach is represented in figure 10 since, apart from the relative
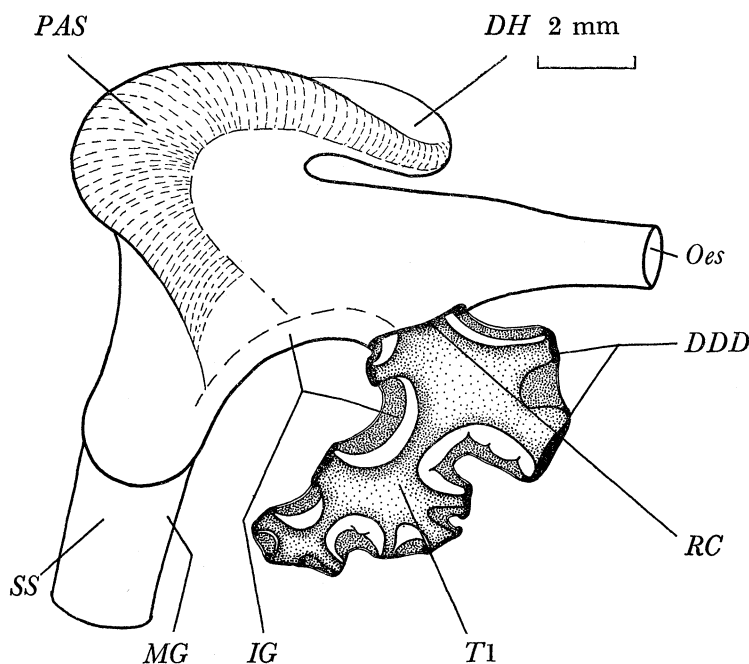

FIGURE 10. *Glauconome rugosa*. The stomach viewed from the right side and showing the right caecum. The broken lines indicate features of the internal anatomy visible through the wall of the stomach.

proportions of the various regions, the internal anatomy is very similar to that of *Glossus humanus* (Owen 1953 b) and many other suspension-feeding eulamellibranchs. Compared with *G. humanus* the anterior region of the stomach is elongated, and is only slightly greater in diameter than the oesophagus, while the dorsal hood (*DH*) extends forward over the receiving region before curving to the left to end blindly on the left wall of the stomach. The posterior region of the stomach is compressed antero-posteriorly so that the ventral region of the well-developed posterior sorting area (*PAS*) has the form of a V-shaped pouch projecting from the right side of the stomach.

(2) Tanysiphon rivalis

The animal was not examined but shells of *Tanysiphon rivalis* from Benson's original collection were kindly lent by the British Museum. The shell is small, 14 mm long by 7 mm deep, and very fragile (figure 11 b). There is a permanent gape to the shell both

anteriorly and posteriorly, the valve margins merely touching each other in the region of the ligament and of the ventral margins. The hinge dentition (*HT*) consists of two small, diverging cardinal teeth on each valve while the inner layer (*IL*) of the short, opisthodetic ligament extends obliquely across the hinge plate immediately posterior to the cardinal teeth. The extent of the pallial line (*PL*) on the inner surface of the shell (Owen 1958) suggests that the ligament is secondarily extended by way of fusion layer for a short distance anterior and posterior to the primary ligament. The pallial sinus is very large, occupying some 50% of the internal surface of the valve.
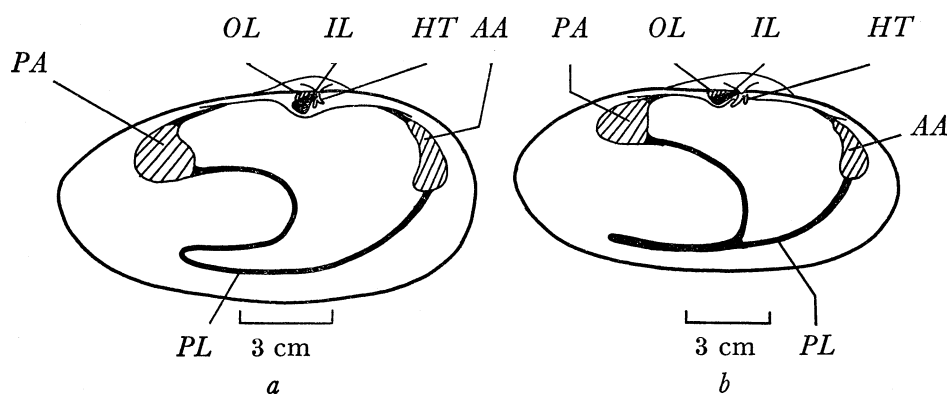

FIGURE 11. The internal surface of the left valves of *a*, *Lutraria lutraria*; *b*, *Tanysiphon rivalis* showing the muscle scars and the structure of the ligament and hinge.

(3) *The systematic position of* Tanysiphon rivalis

The genus *Tanysiphon* was originally proposed by Benson (1858) for the species *T. rivalis* which he obtained from near low water, embedded at some depth in the mud of the banks of the Jumna River near Calcutta. Benson described the genus as allied to the Myacidae but Gray (1858), from an examination of the ligament and hinge teeth, claimed that '*Tanysiphon* is evidently very nearly allied to *Glauconome*'. In an appendix to the *Genera of recent Mollusca* by Adams and Adams, published in November, 1858, *Tanysiphon* is included with *Glauconome* in the family Glaucomyidae and this classification has been followed in all subsequent publications. Although it has not been possible to compare the animal of *Tanysiphon* with that of *Glauconome*, sufficient differences exist between the shells of the two genera to justify removing *Tanysiphon* from the family Glaucomyidae. The most significant of these differences are those shown by the ligament and hinge teeth. The ligament of *Tanysiphon* is short and extends obliquely across the hinge plate to the inner margin, while in *Glauconome* the ligament is a relatively long hemicylindrical structure inserted along the outer margin of the hinge plate. Much of the confusion over the systematic position of *Tanysiphon* has arisen from Benson's inaccurate description of the hinge dentition. He described the genus as possessing three cardinal teeth on the right valve and two on the left, the posterior tooth on each valve being the largest. The structure which Benson interpreted as representing the posterior tooth on each valve is, however, the anterior margin of the spoon-shaped structure supporting the inner layer of the ligament. The hinge dentition of *Tanysiphon* consists of two small diverging cardinal teeth on each valve, although Thiele (1934) describes the left valve as possessing a single bifid tooth.

The characters of the shell of *Tanysiphon* leave little doubt that the genus is closely allied to *Lutraria* and is a member of the Mactridae (compare figures 11*a*, *b*). The ligament of *Lutraria*, although usually described as internal, is essentially an opisthodetic structure, the inner layer of which extends obliquely across the hinge plate (figure 11*a*, *IL*). The outer layer (*OL*), secreted at the *posterior* end of the ligament, extends between the valve margins dorsal to the inner layer. The structure of the ligament of *Tanysiphon* is similar (figure 11*b*) although in this genus the outer layer (*OL*) is relatively longer. In Benson's original account the siphons of *Tanysiphon* are described as resembling those of *Mya truncata* and as being 'united in a finely annulated compressed scabbard nearly equalling the length of the shell. A raphe or seam appears along the inferior margin of the scabbard.' This description suggests that the siphons are encased in periostracum and are of Type C (Yonge 1957), which is a feature of the Mactracea. Other features in which the animal of *Tanysiphon*, as a member of the Mactridae, may differ from that of *Glauconome* are: (*a*) the presence of mantle folds enclosing a ventral waste canal; (*b*) a fourth pallial aperture at the base of the inhalant siphon (Yonge 1948); (*c*) fusion of the mantle margins ventrally may involve cuticular attachment of the inner folds together with the inner surfaces of the middle folds as in *Lutraria lutraria* or there may be complete tissue fusion of these folds as in *Schizothaerus nuttalli* (Yonge 1957); (*d*) mid-gut and style sac separate.

III. Solenidae

The characters of the Solenidae have been previously described by Bloomer (1903) and Ghosh (1920), but subsequent to the appearance of these papers many genera have been removed from the family. *Solecurtus* (Graham 1934), *Tagelus* (Thiele 1934) and *Novaculina* (Yonge 1949) have been transferred to the Tellinacea and of the three subfamilies considered by Ghosh as comprising the Solenidae only the Soleninae remain. Six of the nine genera included by Ghosh in the subfamily Soleninae are considered in this paper, the genus *Pharella* being described in detail. The three remaining genera are *Solena* Browne, *Neosolen* Forbes and *Ceratisolen* (*Pharus* Leach, see Yonge 1958*b*).

(1) *Mantle/shell*

Living specimens of *Pharella acuminata*, as with *Glauconome rugosa*, were obtained from the market place in Singapore and no observations were made on the habitat of the animal, but in common with other members of the Solenidae *Pharella acuminata* is highly adapted for rapid vertical burrowing. The shell is elongated, about four times as long as it is broad, with the umbo situated one-third to one-quarter the distance from the anterior end (figure 12). The shell valves are thin and covered externally by a well-developed periostracum which, together with the outer calcareous layers of the valves, is worn away in the region of the umbones. When the adductor muscles are fully contracted the valves meet along the ventral margins only. Dorsally, anterior and posterior to the ligament, they diverge to produce a permanent gape at the anterior and posterior ends of the shell (figure 12*a*); the gape is wider anteriorly presumably to accommodate the greatly developed foot. The hinge dentition is typical of the Solenidae with slender blade-like cardinal teeth, three on the left valve and two on the right (figure 14, *HT*). The external, opisthodetic ligament is short and powerful.

(a) *Ligament*

In the primitive bivalve pallial attachment extended round the periphery of each pallial lobe from the anterior and posterior ends of the primary ligament (Yonge 1953). Throughout the Bivalvia, there is usually some degree of secondary extension of the primary ligament resulting from the fusion of the outer secretory folds of the mantle margins anterior and posterior to the mantle isthmus (Yonge 1957). This secondary ligament is of
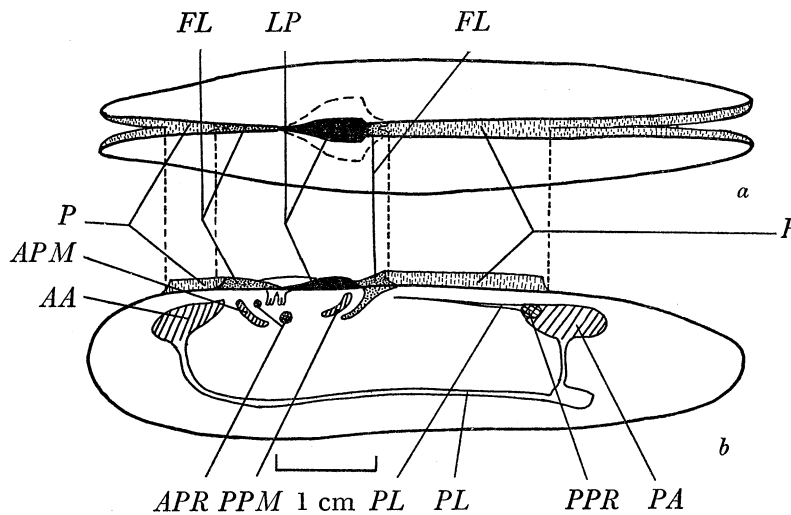

FIGURE 12. *Pharella acuminata.* *a*, the shell viewed from above and showing the structures joining the two valves dorsally; *b*, the internal surface of the left valve showing the muscle scars. The broken lines indicate the anterior and posterior ends of fusion layer and periostracum joining the two valves.
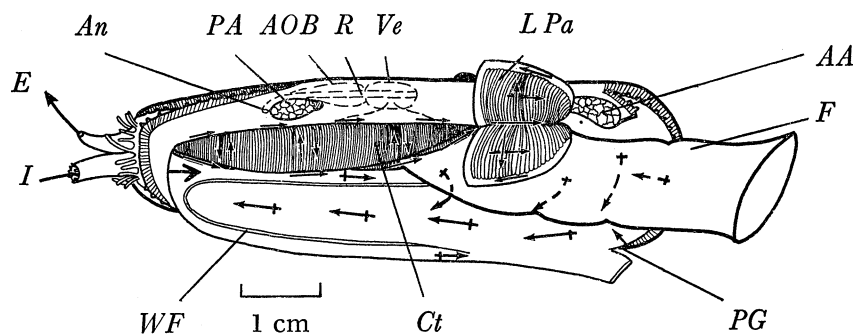

FIGURE 13. *Pharella acuminata.* Organs and ciliary currents viewed from the right side after the removal of the right shell valve and mantle lobe. Large arrows indicate the inhalant (*I*) and exhalant (*E*) currents; small arrows, ciliary currents on the exposed surfaces of the gills (*Ct*) and labial palps (*LPa*); crossed arrows, cleansing and rejection currents over the mantle surface.

two types. Fusion of the inner periostracal secreting surfaces of the outer folds results in extension by way of periostracum, while where the outer surfaces of these folds are fused, extension is by way of fusion layer. Where extension of the primary ligament is of the first type, i.e. by way of periostracum, pallial attachment to the shell valves is retained, but where the two valves are secondarily united by fusion layer there is also an accompanying loss of pallial attachment (Owen 1958). In consequence, in many bivalves the anterior and posterior ends of the pallial line on the internal surface of the valves indicate the anterior
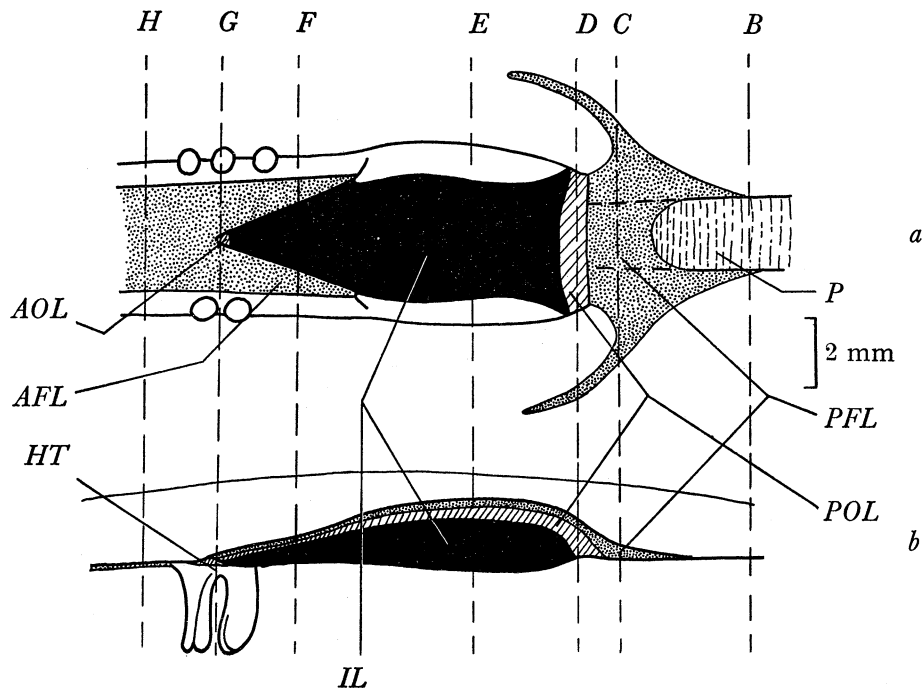
FIGURE 14. *Pharella acuminata*. Structure of the ligament. *a*, ligament viewed from the inner, i.e. ventral surface; *b*, longitudinal section of the ligament. The letters *B* to *H* refer to the positions of transverse sections drawn in figures 15, 16 and 17.
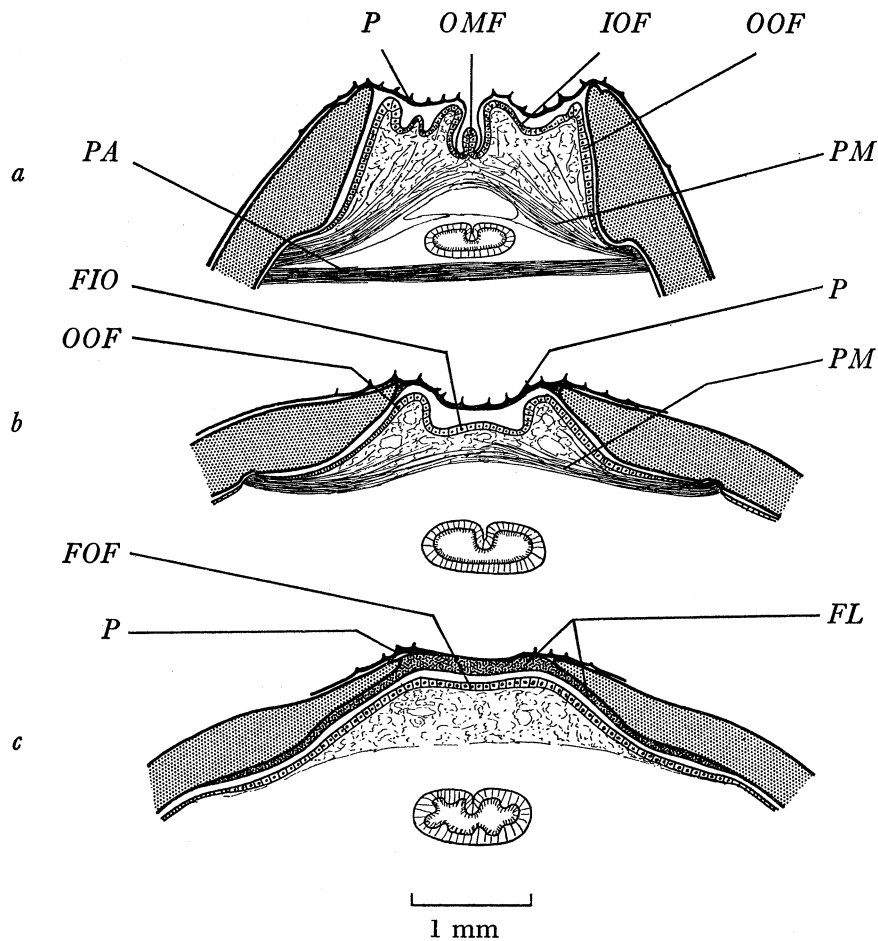
FIGURE 15. *Pharella acuminata*. Structure of the ligament. Transverse sections through the dorsal margins of the shell and mantle posterior to the primary ligament in the regions indicated in figure 14. Section *a* is from the region dorsal to the posterior adductor.

and posterior limits of the fusion layer at each end of the ligament. The functional ligament of *P. acuminata* comprises a superficial fusion layer, which probably includes periostracum although this cannot be identified as a discrete layer, and outer and inner layers of the ligament (figures 14, 16*e*). Posterior to the ligament the outer folds of the mantle margins fuse dorsal to the posterior adductor muscle. The pallial line, however, as shown in figure 12*b* (*PL*), extends from near the posterior end of the primary ligament, round the periphery of the valves, to the anterior adductor (*AA*). Thus posteriorly (figure 15*b*), fusion involves for the most part only the inner surfaces of the outer folds (*FIO*) and the two valves are joined by periostracum (formed by this inner surface) which protects the
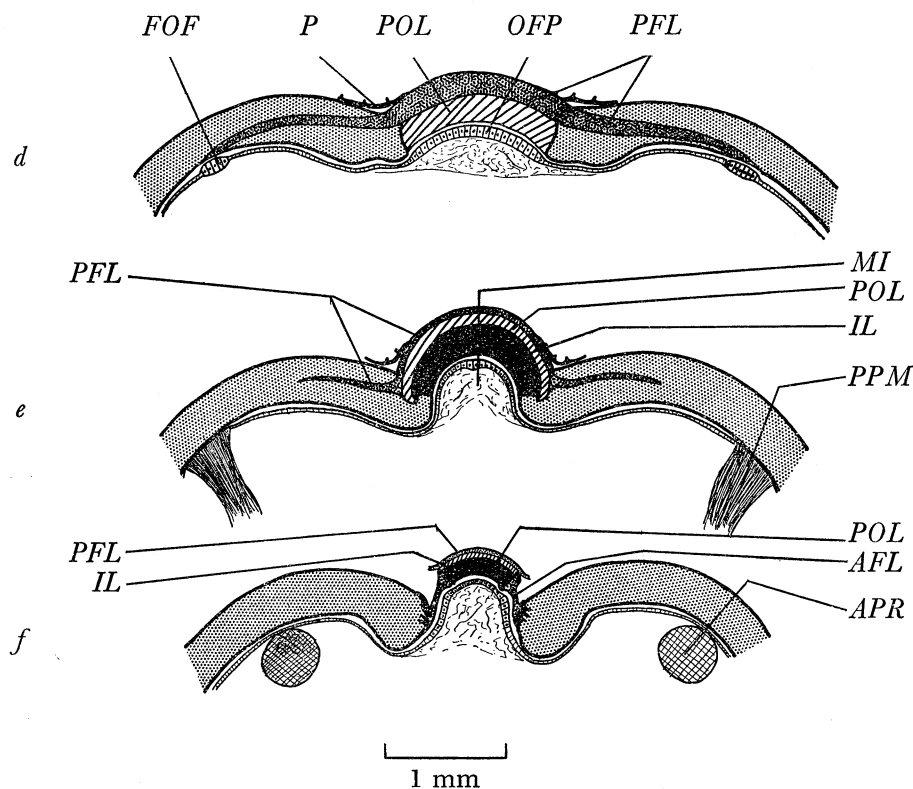

FIGURE 16. *Pharella acuminata*. Structure of the ligament. Sections through the primary ligament in the regions indicated in figure 14.

mantle tissues exposed as a result of the posterior gape of the shell (figure 12*a*). At the posterior end of the primary ligament (figure 15*c*) the outer surfaces of the outer folds (*FOF*) are also fused and the two valves are joined by fusion layer (*FL*). Periostracum (*P*) joins the outer surface of the fusion layer on each side and cannot subsequently be distinguished as a discrete layer above the fusion layer. The epithelium of the fused outer surfaces of the outer folds extends laterally on each side beneath the calcareous layers of the valves as a narrow sickle-shaped band (figures 14*a*, 15*c*). As growth proceeds, outer and later inner layers of the ligament are secreted on to the inner surface of the fusion layer in the mid-line, while inner calcareous layer of the valves is secreted on to the inner surface of the lateral regions. As shown by a transverse section through the posterior end of the ligament (figure 16*d*), the fusion layer (*PFL*) joining the two valves in the mid-line is underlain by outer layer of the ligament (*POL*), while laterally two small, and apparently

isolated, regions of outer fold epithelium (*FOF*) continue to secrete fusion layer; the intervening regions of the fusion layer are embedded in the calcareous layers of the valves. Thus, the fusion layer forms the outermost layer of the functional ligament and extends laterally on each side as a wing-like expansion, which for the most part is embedded in the calcareous layers of the valves (figures 12*a*, 16). As in *Glauconome*, these lateral extensions of the fusion layer, i.e. secondary ligament, undoubtedly serve to attach the ligament firmly to the shell valves. The ligament of *P. acuminata* is opisthodetic and growth takes
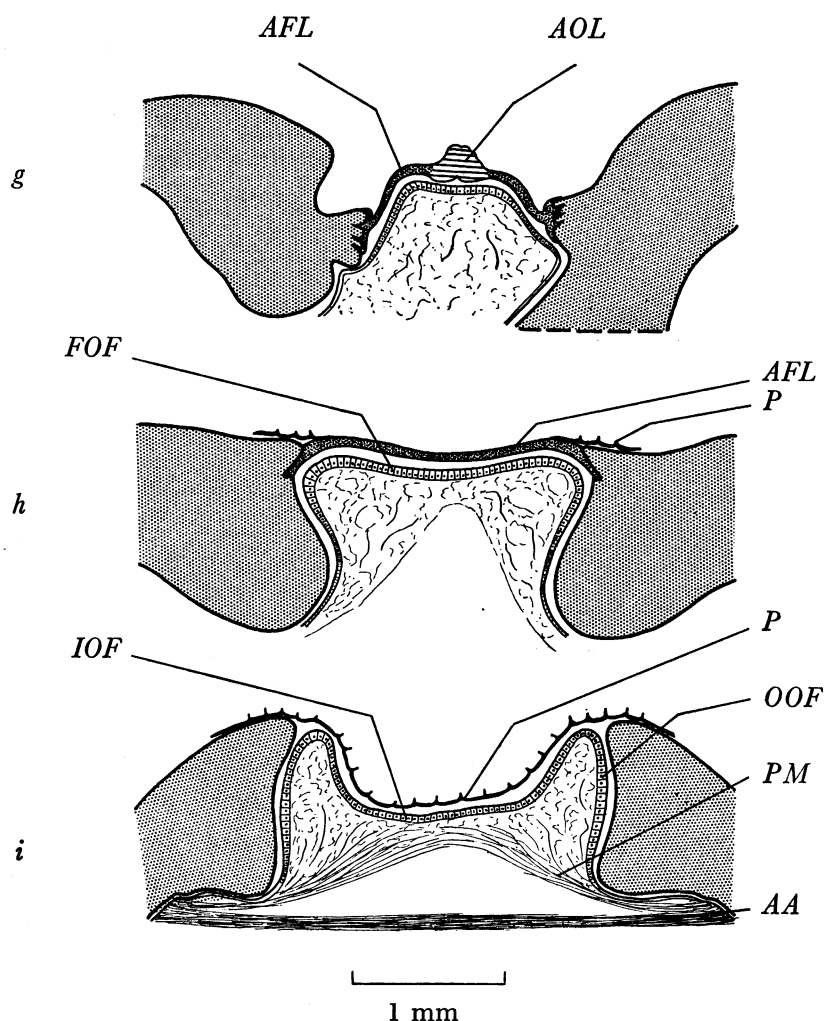
FIGURE 17. *Pharella acuminata.* Structure of the ligament. Sections through the dorsal margins of the shell and mantle anterior to the ligament in the regions indicated in figure 14. Section *i* is from the region dorsal to the anterior adductor muscle.

place in a posterior direction. Thus, the outer layer of the functional ligament is secreted by the outer marginal fold at the posterior end of the mantle isthmus and as growth proceeds it is progressively underlain by the inner layer of the ligament secreted by the mantle isthmus (see figure 6*b* for the growth of the ligament of *Glauconome rugosa*).

Anterior to the ligament the outer marginal folds fuse dorsal to the anterior adductor muscle and there is a short region where the two valves are joined by periostracum (figure 12). Between the anterior adductor and the anterior end of the ligament, fusion

of the mantle margins involves the outer surfaces of the outer folds and the two valves are joined by fusion layer (figures 12, 17*h*). An interesting feature of the ligament of *Pharella acuminata* is that while the posterior region of the ligament is attached directly to the valves on each side, the anterior third is not. This anterior region is secondarily connected to the valve margins by fusion layer which is continuous with the fusion layer anterior to the ligament (figures 14, 16*f*). Presumably, the anterior region of the ligament becomes progressively detached from the valve margins as growth proceeds. As a consequence of this, it is only the posterior two-thirds which can contribute to the opening of the valves. This progressive detachment of the anterior region of the ligament is probably a result of the anterior gape of the shell.

In all other members of the Solenidae studied, there is no fusion of the inner surfaces of the outer folds (i.e. no joining of the valves by periostracum) anterior and posterior to the functional ligament, but apart from this, the structure of the ligament is essentially similar
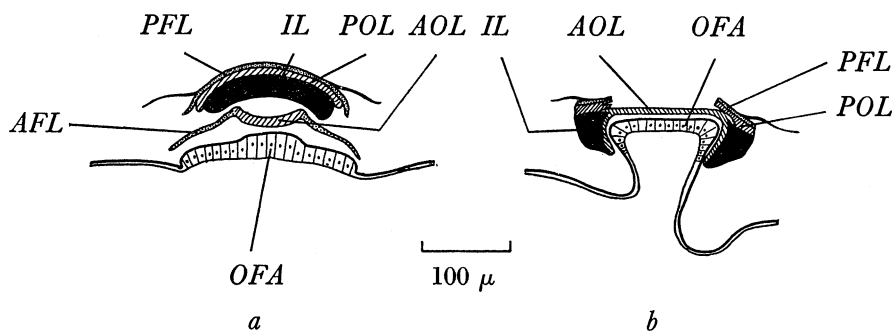

FIGURE 18. Sections through the anterior region of the ligaments of decalcified specimens of *a, Ensis ensis*; *b, Solen marginatus*.

to that of *P. acuminata*. Anterior and posterior to the mantle isthmus there is a short region where the outer surfaces of the outer folds are fused, resulting in a secondary extension of the ligament by way of fusion layer. The anterior region of the ligament shows minor differences in the different genera. In *Phaxus* and *Siliqua*, as in *Pharella*, the anterior region of the ligament is secondarily attached to the valve margins by fusion layer, but the region over which this secondary attachment occurs is very short. In *Ensis* the outer marginal fold at the anterior end of the mantle isthmus is posterior to the umbones. As growth proceeds this anterior fold extends posteriorly beneath the functional ligament and, as shown in figure 18*a*, a section through the anterior end of the ligament of *E. ensis* shows: (*a*) an outermost fusion layer (*PFL*), (*b*) outer layer of the ligament (*POL*), both secreted at the posterior end of the ligament, (*c*) inner layer of the ligament (*IL*), (*d*) anterior outer layer (*AOL*) secreted beneath the anterior end of the ligament with laterally fusion layer (*AFL*). In *Solen* (figure 18*b*), the functional ligament above the anterior outer fold (*OFA*) splits in the mid-line in a manner similar to the anterior end of the ligaments of *Mytilus* (Trueman 1950) and *Glossus* (Owen 1953*b*). In both *Mytilus* and *Glossus*, splitting of the anterior end of the ligament results from the effect of a tangential component on the growth of the shell (Owen 1953*a*; Yonge 1955), but in *Solen* it is due to the posteriorly directed growth of the outer marginal fold at the anterior end of the mantle isthmus. None of the Solenidae possesses the bulky anterior 'cardinal ligament' (probably anterior

outer layer) characteristic of those members of the Tellinacea which possess an external opisthodetic ligament, e.g. *Tellina tenuis* (Trueman 1949), *Gari ferevensis* and *Solenotellina* sp. (personal observations).

(b) Mantle fusion

In *Pharella acuminata* the mantle margins are fused except in the regions of the siphons and of the anteriorly situated pedal gape, which is fringed on each side by a row of small, darkly pigmented tentacles borne on the middle fold of the mantle margin; there is no fourth pallial aperture. The extensive ventral fusion of the mantle margins is complete (figure 19 a) and involves the inner folds, together with the inner surfaces of the middle
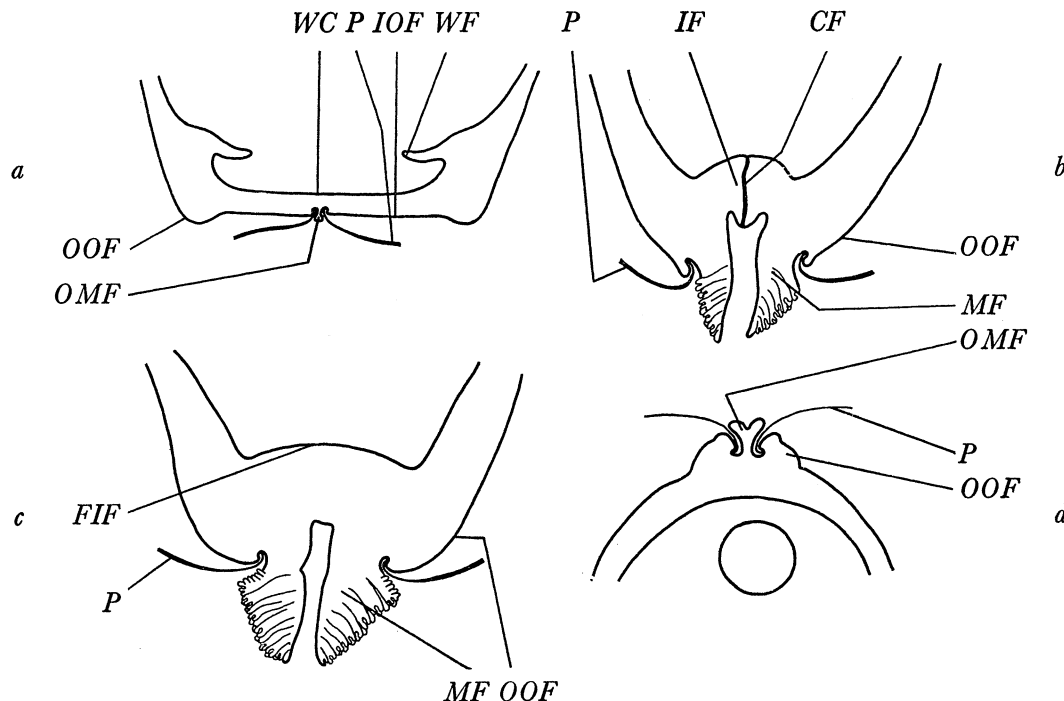

FIGURE 19. Mantle fusion in the Solenidae. *a*, *Pharella acuminata*. Fusion of the mantle margins ventrally involving the inner marginal folds together with the inner surfaces of the middle folds; *b*, *c* and *d*, *Siliqua patula*; *b*, cuticular fusion of the inner folds ventrally anterior to the fourth pallial aperture; *c*, tissue fusion of the inner folds posterior to the fourth pallial aperture; *d*, tissue fusion of the mantle margins dorsally posterior to the functional ligament involving the inner folds together with the inner surfaces of the middle folds.

folds (Type B, Yonge 1957). The extent of the outer surface of the middle fold (OMF) separating the periostracum (P) on each side is very small and is represented by a single series of pigmented tentacles, while the inner surfaces of the outer folds (IOF) secreting periostracum are correspondingly extended. Dorsally (figure 15a), fusion of the inner folds together with the inner surfaces of the middle folds extends between the siphons and the region of the posterior adductor muscle where, as already described, fusion also involves the outer surfaces of the middle folds.

In *Solen*, as in *Pharella*, tissue fusion involving the inner folds and the inner surfaces of the middle folds extends along the entire ventral margin and there is no fourth pallial aperture. Fusion of a similar type also occurs along the dorsal margin from the siphons to

the posterior end of the functional ligament. In *Phaxus* and *Ensis* the mantle edges along the ventral margin are also united for most of their length but there are interesting differences from *Pharella* and *Solen*. In the first named two, the anterior region of the mantle margins ventrally are united by cuticular fusion of the inner folds as described by Atkins (1937c) (the anterior third in *Phaxus* (figure 24f) and the anterior two-thirds in *Ensis* (figure 24h)), while along the posterior region there is complete tissue fusion of the inner folds together with the inner surfaces of the middle folds as in *Pharella* and *Solen*. Between these two regions of fusion there is a small fourth pallial aperture (*A*4). In both *Phaxus* and *Ensis*, fusion of the mantle edges along the dorsal margin is similar to *Solen* (i.e. Type B). In *Siliqua patula*, as in *Ensis* and *Phaxus*, the anterior region of the mantle margins ventrally are united by cuticular fusion of the inner folds (figure 19b), while along the posterior region fusion is complete (figure 19c). Between these two regions is a small fourth pallial aperture, a feature not previously noted in this genus (figure 24c). From preserved specimens it is difficult to be certain of the extent of cuticular fusion, but the appearance of the inner folds in this region suggests that it extends to the anterior end of the ventral margin. Thus, in *Siliqua* also the pedal gape is functionally restricted to the anterior region, but unlike other members of the Solenidae tissue fusion along the posterior region of the ventral margin involves the inner folds only, the middle folds being represented on each side by a row of dentritic tentacles (figure 19c, *MF*). These tentacles diminish in size, until finally at the base of the inhalant siphon the inner surfaces of the middle folds are also fused and take part in the formation of the siphons. Dorsally, between the posterior end of the functional ligament and the siphons (figure 19d), fusion involves the inner folds and the inner surfaces of the middle folds, the periostracal groove being separated by a single row of tentacles (*OMF*) in contrast to the double row present ventrally.

(c) Siphons

The short and apparently separate siphons of *Pharella acuminata* resemble superficially those of the Tellinacea (figure 13). A careful examination shows, however, that unlike those of the Tellinacea (Yonge 1949) the inhalant (*I*) and exhalant (*E*) portions are joined basally and the distal margin of this basal region is produced into a common ring of long, slender tentacles which surrounds the separate inhalant and exhalant regions. The ctenidia do not extend into the fused basal region as is the case in *Solecurtus* and where the basal portion of the siphons is really a posterior extension of the mantle cavity (Yonge 1957). The aperture of the inhalant siphon is surrounded by a series of small tentacles or lobes, while the margin of the exhalant siphon is entire. When fully extended the inhalant siphon extends some 2 to 3 cm beyond the valve margins with the exhalant siphon somewhat shorter.

The siphons of *Ensis* (figure 20b) and *Phaxus* (figure 20a) are short and similar to those of *Pharella*. The exhalant (*E*) and inhalant (*I*) portions are joined basally and surrounded by a common ring of long slender tentacles. The aperture of the inhalant siphon is surrounded by a series of small tentacles among which are four or five larger spatulate tentacles. In *Solen* and *Siliqua*, and unlike other members of the Solenidae, the siphons are relatively long and joined for most of their length. In *Siliqua* (figure 20c) the valvular membrane of the exhalant siphon is surrounded by numerous slender tentacles while the

inhalant aperture is guarded by a series of pinnate tentacles which arch over the opening and form an efficient straining system (Yonge 1952). Scattered over the dorsal and ventral surfaces of the siphons are a number of small, simple tentacles. In *Solen* (figure 20 *d*), as in *Siliqua*, the base of the valvular membrane surrounding the exhalant aperture bears a ring of large conical tentacles and a similar circlet of tentacles surrounds the inhalant siphon a short distance from the terminal margin. The margin of the inhalant siphon is divided into a series of small lobes similar to those of *Ensis* and *Pharella*. In the contracted state the siphons of *Solen* show annular constrictions and in contrast to other members of the Solenidae they are capable of autotomy (Ghosh 1920; Atkins 1937 *a*) as are the siphons of some members of the Tellinacea (e.g. the Asaphidae).
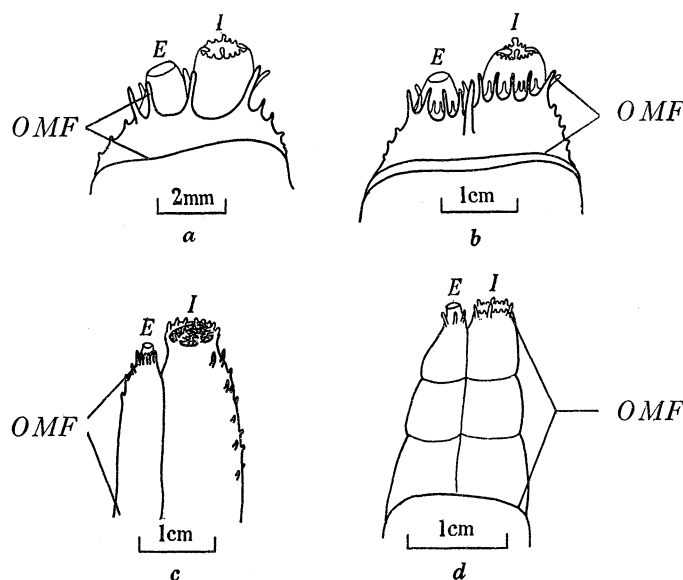

FIGURE 20. Semi-diagrammatic figures of the siphons of *a*, *Phaxus pellucidus*; *b*, *Ensis siliqua*; *c*, *Siliqua patula*; *d*, *Solen marginatus*. Note the extent of the outer surface of the middle fold (*OMF*).

Structurally, the siphons of the Bivalvia represent hypertrophy of the posterior regions of the mantle margins and may be formed by the fusion of one or more of the marginal folds (Yonge 1957). In the Solenidae the siphons are of Type B, both the inner and middle folds being involved in their formation. In siphons of this type the opening of the exhalant siphon is usually bounded by a valvular membrane, while the inhalant aperture bears one or more series of tentacles. Both membrane and tentacles represent the margin of the inner fold, while tentacles borne on the middle fold usually form a common ring round both siphons (Yonge 1957). In the siphons of *Pharella*, *Phaxus* and *Ensis* (figures 20 *a*, *b*) the external surface of the fused basal region represents the outer surface of the middle fold (*OMF*), while the margin of this fold bears the common ring of tentacles round the separate inhalant and exhalant regions. These separate regions of the siphons are formed from the inner folds only and represent an extension of this fold beyond the middle fold. The distal region of the exhalant siphon may be regarded as a greatly extended valvular membrane and as such it is withdrawn by inversion and not by contraction, while the distal region of the inhalant siphon represents a corresponding extension of the inner fold at the inhalant aperture. The siphons of *Siliqua* and *Solen* (figures 20 *c*, *d*) are more obviously those of

Type B, because the external surface of the entire region between the distal extremities and the base represents the greatly extended outer surface of the middle folds (*OMF*). In *Solen*, the ring of simple tentacles round both the inhalant and exhalant apertures represents the margin of this fold, while the valvular membrane and the lobed margin of the inhalant aperture represent the margin of the inner fold. Similarly, in *Siliqua* the simple tentacles are borne on the middle folds, while the pinnate tentacles of the inhalant aperture, despite their similarity to those borne on the middle folds along the ventral margins, are here probably borne on the inner folds (cf. Myacea, etc., Yonge 1957).

(2) *Musculature*

The muscle impressions visible on the internal surface of the shell valves in *Pharella acuminata* are shown in figure 12.

(a) *Pallial musculature*

Both the anterior (*AA*) and posterior adductor (*PA*) muscles are elongated, with the posterior somewhat smaller than the anterior. The pallial line (*PL*) is well marked and, as already described, extends from the posterior end of the functional ligament round to the anterior adductor muscle scar. The pallial sinus is poorly developed, but ventrally there is a marked thickening of the pallial line representing the insertion of the siphonal retractor muscles.

(b) *Pedal musculature*

As in other members of the Solenidae the foot is long, oval in cross-section, and of nearly uniform depth with a flattened terminal sole. A crescent-shaped scar (*APM*) posterior to the anterior adductor marks the insertion of the anterior protractor pedis muscle. The fibres fan out from their insertion on the shell over the surface of the visceral mass and proximal region of the foot forming a sheet beneath the pedal epithelium. A similar crescent-shaped scar (*PPM*) beneath the posterior end of the ligament marks the insertion of what is here described as a posterior protractor pedis muscle. It occupies a position similar to that of the elevator pedis muscle in other lamellibranchs but in *P. acuminata* the fibres from this muscle insertion radiate over the surface of the visceral mass and proximal region of the foot in a fashion similar to, and beneath those of, the anterior protractor. Unlike *P. orientalis* (Bloomer 1903 *b*) the free portions of the anterior pedis retractor (*APR*) are bifurcated and there is a double insertion on each valve between the two protractors. The more anterior and dorsal of the two insertions is small and comprises a small number of fibres only. The insertion of the anterior retractor is some distance from the anterior adductor and as a result of this posterior insertion, the fibres of the anterior retractor proceed anteriorly directly into the foot and are the most internal of the pedal muscles. On each side, external to those of the anterior retractor are the longitudinal fibres of the posterior retractor. These proceed posteriorly and are inserted on the shell on each side at the anterior margin of the posterior adductor muscle.

The pallial musculature of the various genera will be discussed later in relation to the form of the shell. The musculature of the foot of the Solenidae has been described by Bloomer (1901), Ghosh (1920) and Graham (1931, 1934) and has been used as a character of systematic value. In *Siliqua*, *Phaxus* and *Ensis* (figure 24) the protractor muscle (*PM*)

is inserted on the shell on each side near the posterior margin of the anterior adductor. It is weakly developed, the fibres extending superficially over the proximal region of the foot. In *Solen* (figure 24*g*) the protractor is inserted some distance from the posterior margin of the anterior adductor, but the disposition of the fibres is essentially the same as in the other genera. There is no trace in these four genera of a posterior protractor muscle. In *Ensis* (figure 24*h*) the anterior pedis retractor has two insertions on each valve and, as in *Pharella*, the fibres pass into the foot internal to the longitudinal fibres of the posterior retractor. The anterior retractor in *Phaxus* (figure 24*f*) also has a double insertion on each valve, but in this genus the fibres spread superficially over the surface of the foot *external* to the longitudinal fibres of the posterior protractor. In *Solen* (figure 24*g*) the anterior retractor has only a *single* insertion on each valve inserted posterior to that of the protractor, and as in *Phaxus* the fibres are external to those of the posterior retractor. Bloomer (1901) describes the anterior retractor in this genus as having a double insertion on each valve. From his figure it would appear that he regarded the adjacent protractor muscle as a bifurcation of the anterior retractor. In *Siliqua* (figure 24*c*) the anterior retractor has a single insertion on each valve and within the foot the fibres mingle with those of the posterior retractor. In all genera of the Solenidae the posterior retractor (*PPR*), as already described for *Pharella*, is inserted at the anterior margin of the posterior adductor.

It was possible to examine only the shells of two species of *Cultellus* (figure 24*e*), but some information can be obtained from the muscle impressions on the internal surface of the valves. The anterior adductor (*AA*), unlike that of *Phaxus* which was originally included in this genus, is circular in cross-section. The pallial line (*PL*) extends anteriorly, beyond the slightly elongated posterior adductor scar (*PA*), to near the posterior end of the primary ligament. Beneath the umbones there is a bilobed muscle scar, and from examination of the shell alone it is impossible to tell whether or not this represents a partial double insertion on each side of the anterior pedis retractor. The most likely interpretation is that the more dorsal and posterior region of the scar represents a single insertion on each valve of the anterior retractor, while the anterior and ventral region represents the insertion of the protractor muscle. According to Ghosh (1920) the fibres of the anterior retractor spread irregularly both inside and outside those of the posterior retractor.

(3) *Mantle cavity*

The disposition of the organs in the mantle cavity of *Pharella acuminata* is shown in figure 13. Ventrally, in the region of mantle fusion, are a pair of poorly developed folds (*WF*) which enclose a ventral waste canal leading to the base of the inhalant siphon. The mantle surface is generally ciliated anteriorly but posteriorly, with the exception of the region between the mantle folds, cilia are apparently absent. Material which falls on to the surface of the mantle is directed to the anterior end of the waste canal and then carried posteriorly to the base of the inhalant siphon. Among members of the Solenidae, mantle folds enclosing a ventral waste canal have previously been described only in *Siliqua patula* (Yonge 1952).

The gills (*Ct*) are long and narrow and are plicate and heterorhabdic, while the inner demibranchs do not extend between the bases of the large labial palps. Cuticular fusion (Atkins 1937*c*) joins the dorsal edges of the ascending lamellae of the outer demibranchs

to the mantle, and a similar junction joins the dorsal edge of the ascending lamellae of the inner demibranchs to one another and to the foot. The direction of the frontal currents of the ctenidia are indicated in the diagrammatic transverse section shown in figure 22 *a*. Oralward currents are present not only in the marginal grooves at the free edges of the demibranchs, but also along the dorsal edges of all the ascending lamellae. A characteristic feature of the frontal ciliation of the filaments in the Solenidae is the presence of adjoining tracts of short and long cilia beating in opposite directions (Type C (2*a*), Atkins 1937*b*; Yonge 1952). In *Ensis* the long and short cilia are arranged in two tracts, and in *Solen* in three tracts (Atkins 1936). *Pharella acuminata* is similar to *Ensis* in this respect, the frontal
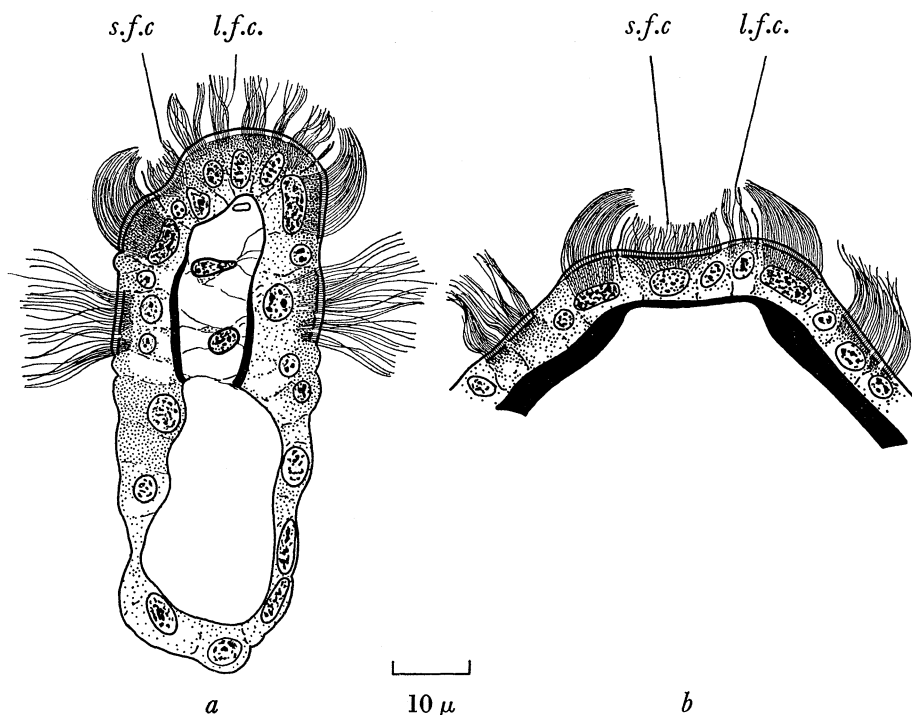

FIGURE 21. *Pharella acuminata*. Transverse sections of the gill filaments to show the arrangement of the tracts of long (*l.f.c.*) and short (*s.f.c.*) frontal cilia. *a*, apical filament showing the narrow tract of short cilia beating dorsally on the anterior side and the broad tract of long cilia beating ventrally on the posterior side; *b*, principal filament showing the broad tract of short cilia on the anterior side and the narrow tract of long cilia on the posterior side.

cilia being arranged in two tracts (figure 21). While observation on living specimens of *P. acuminata* showed only dorsally directed currents on the frontal surfaces of the principal filaments, sections of the gills indicate that they also possess narrow tracts of long cilia in addition to the broad adjoining tracts of short cilia (figure 21 *b*). Thus in *P. acuminata*, unlike *Solen* and *Ensis*, both the ordinary and principal filaments possess tracts of long and short cilia, their disposition ranging from the broad tracts of long cilia (*l.f.c.*) on the apical filaments (figure 21 *a*) to the broad tracts of short cilia (*s.f.c.*) on the principal filaments in the depths of the grooves (figure 21 *b*). Two tracts of cilia are present on the frontal surfaces of all the filaments of both lamellae of the inner demibranch and of the ascending lamella of the outer demibranch of *Phaxus pellucidus*, but in this species the gills are flat and homorhabdic (Atkins 1936).

The sorting mechanisms of plicate gills possessing adjoining tracts of long and short cilia have been fully discussed by Atkins (1937*a*). Fine particles are carried dorsally by the short cilia and reach the mouth by way of the safe oralward currents at the dorsal edges of the lamellae. Particles carried ventrally by the long cilia are likely to be transferred from the margins of the demibranchs to the surface of the mantle. This is the case where the particles are large or numerous. Atkins (1937*a*) has suggested that probably all plicate gills, by means of horizontal muscles, are capable of approximating the plicae. This certainly occurs in *Pharella acuminata* and results in most of the particles falling on the apical filaments with their broad tracts of long, ventrally beating cilia. Moreover, on a number of occasions the plicae in localized regions of the lamellae were seen to close rapidly and so shoot particles out of the grooves clear of the surface of the gill. Similar movements have been described in *Pecten* by Kellogg (1915), in *Ostrea* by Yonge (1926), in *Ensis siliqua* by Atkins (1936) and in *Solenotellina* (personal observation).
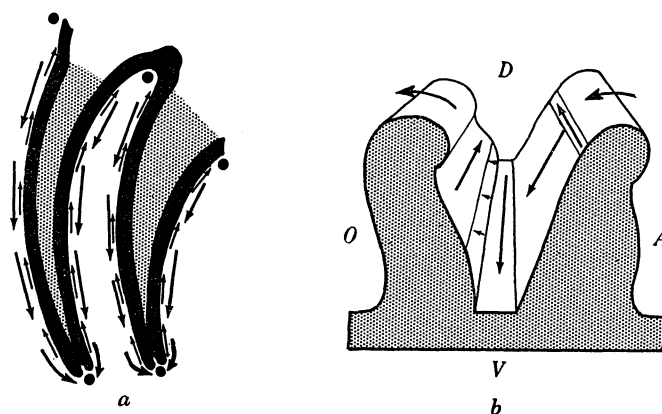

FIGURE 22. *Pharella acuminata.* *a*, diagrammatic transverse section showing the form of the gill and the direction of the frontal currents. Black circles indicate oralward currents; *b*, diagram showing the direction of the currents on the folds of the labial palps.

The labial palps are large with numerous fine ridges and grooves on their inner surfaces. The ciliary currents over the ridged surfaces are shown in figure 22*b* and are similar to those described in *Ensis siliqua* by Graham (1930).

The detailed structure and ciliation of the gills of *Phaxus*, *Solen* and *Ensis* have been described by Atkins (1936) and of *Siliqua patula* by Yonge (1952).

(4) *Alimentary canal*

The oesophagus of *Pharella acuminata* is dorso-ventrally flattened and enters the antero-dorsal region of the stomach (figure 23*a*). Compared with the suspension feeding species *Cardium edule* (Graham 1949) and *Glossus humanus* (Owen 1953*b*) the stomach of *Pharella acuminata* is elongated antero-posteriorly. The posterior sorting area (*PAS*) has the form of a prominent well-developed pouch protruding from the right wall of the stomach and extends over the dorsal surface on to the left wall as a well-developed dorsal hood (*DH*). Internally, with one exception, the anatomy and ciliary currents are similar to those described in *Ensis siliqua* by Graham (1949). In this species Graham shows the posterior sorting area extending into a large pouch (*SAPC*) distinct from a smaller structure which he considered comparable with the dorsal hood of other lamellibranchs. Dissections of the

stomach of *E. siliqua* do not support this distinction and the large pouch into which the posterior sorting area extends is undoubtedly the dorsal hood, as in *Pharella acuminata*. All the ducts from the digestive diverticula open either into the right (*Ca*) and left caeca, which are well developed, or into the left pouch. As in other eulamellibranchs, the ducts of the digestive diverticula are of two kinds, ciliated main ducts and non-ciliated secondary ducts, while the darkly staining cells of the tubules bear long flagella (Owen 1955). The descending limb of the intestine which is separate from the large curved style sac (*SS*) leaves the ventral surface of the stomach and passes ventrally anterior to the style sac. It then extends dorsally and anteriorly and forms two or three loops before ascending
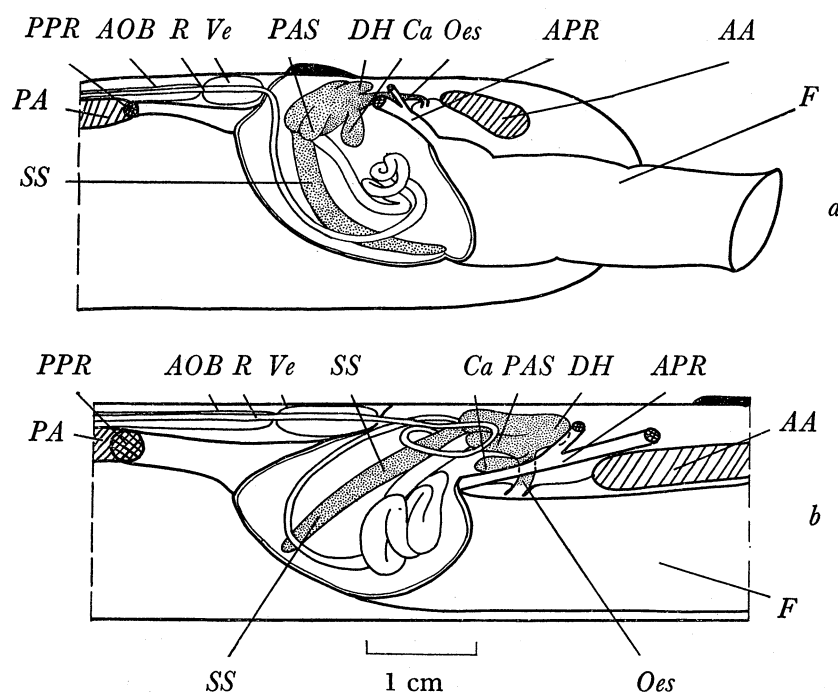

FIGURE 23. Semi-diagrammatic comparison of the course and orientation of the alimentary canal in *a*, *Pharella acuminata* and *b*, *Ensis siliqua*. In the latter genus, the stomach when compared with *Pharella acuminata* and other genera of the Solenidae is rotated through 90°, a consequence of the tremendous posterior elongation and accompanying loss of depth of the mantle/shell.

posterior to the style sac and stomach. The hind-gut passes through the ventricle (*Ve*) of the heart and the dorsal region of the well-developed aortic bulb (*AOB*) which extends from the ventricle to the region of the posterior adductor (*PA*) muscle. Finally, the hind-gut opens at the anus on the posterior side of the adductor.

The form of the stomach in all the species examined is essentially similar to that of *P. acuminata*. The posterior sorting area is well developed and the dorsal hood is a large and prominent feature of the stomach. The style sac and mid-gut are separate, but the course of the intestine shows minor differences in the different genera. In *Solen* and *Siliqua* the style sac is long and curves anteriorly into the foot, as in *Pharella*. The descending limb of the intestine forms a number of loops within the proximal region of the foot before curving round the distal end of the style sac and ascending posterior to the stomach. In *Phaxus* the style sac is relatively short and wide and only slightly curved. It extends vertically downwards to the ventral margin of the foot. The descending limb of the intestine

extends a considerable distance into the pedal cavity beyond the distal end of the style sac. This description of the intestine of *P. pellucidus* differs from those given by Bloomer (1902) and Graham (1934). The former described the style sac as long and curved and extending anteriorly into the pedal cavity the same distance as the intestine. Graham, on the other hand, describes the style sac as short and relatively straight, but figures the descending limb of the intestine thrown into a number of loops near the distal end of the style sac. In three specimens of *P. pellucidus* obtained from Millport, the style sac conformed to the description given by Graham. The course of the intestine varied slightly depending on the degree of extension of the foot, but any folds present were never as pronounced as those figured by Graham. In a specimen with the foot well extended the descending and ascending limbs followed a relatively straight course, and as already described, extended into the pedal cavity some distance beyond the end of the style sac.

The orientation of the stomach of *Ensis* differs from that of the other genera (figure 23 *b*). In this genus the visceral mass extends dorsal *and* anterior to the foot (*F*), a feature associated with the tremendous elongation and accompanying reduction in depth of the mantle/shell. As a consequence of this, the stomach of *Ensis*, when compared with other genera of the Solenidae, is rotated through 90° in a clockwise direction when viewed from the right side. The oesophagus (*Oes*) is short and extends dorsally from the ventrally situated mouth to enter the stomach antero-ventrally. The style sac (*SS*) leaves the stomach posteriorly and curves in a postero-ventral direction across the proximal region of the foot. Anterior to the style sac the descending limb of the intestine forms a number of loops while the ascending limb also forms a loop on each side of the stomach.

(5) *Pallial attachment and shell form in the Solenidae*

As emphasized by Yonge (1953, 1955) the final form assumed by the Lamellibranchia is the result of interaction of the growth of the body on the one hand and of the shell on the other. It is convenient to regard the primitive bivalve as an equilateral dimyarian (figure 24 *a*) in which the demarcation line (Yonge 1955; replaces 'normal axis', Owen 1953 *a*) intersects the ventral margin at the zone of greatest marginal increase. The generating curve, represented by the valve margin, is more or less circular and the demarcation line (*DL*) divides each mantle lobe into equal anterior and posterior territories. This primitive symmetry of the mantle/shell can be altered by changes in the growth gradients around the mantle margins (Owen 1953 *a*) and many of the features of the Solenidae are correlated with the extreme posterior elongation and the accompanying reduction in depth of the mantle/shell characteristic of members of this family (Yonge 1952). The effect of elongation of the mantle/shell on pallial attachment and the position of the adductor muscles in the Lamellibranchia as a whole has already been described (Owen 1958). Figure 24 *b* represents a hypothetical condition where the single ventrally situated region of greatest marginal increase is replaced by two regions of maximum marginal increase symmetrically disposed at each end of the ventral margin. The generating curve, although still symmetrical about the demarcation line, now has the form of an ellipse. As in the primitive bivalve, the pallial line (*PL*) terminates at each end of the primary ligament (Owen 1958), but extension of the mantle/shell on either side of the demarcation line results in a corresponding extension of the regions of cross-fusion of the pallial muscles in the anterior and posterior

embayments of the mantle. The regions of the fused pallial muscles which undergo hypertrophy to form the adductors are, for functional reasons, situated near the anterior and posterior margins of the shell and the line of pallial attachment extends beyond the adductors to the anterior and posterior ends of the primary ligament.
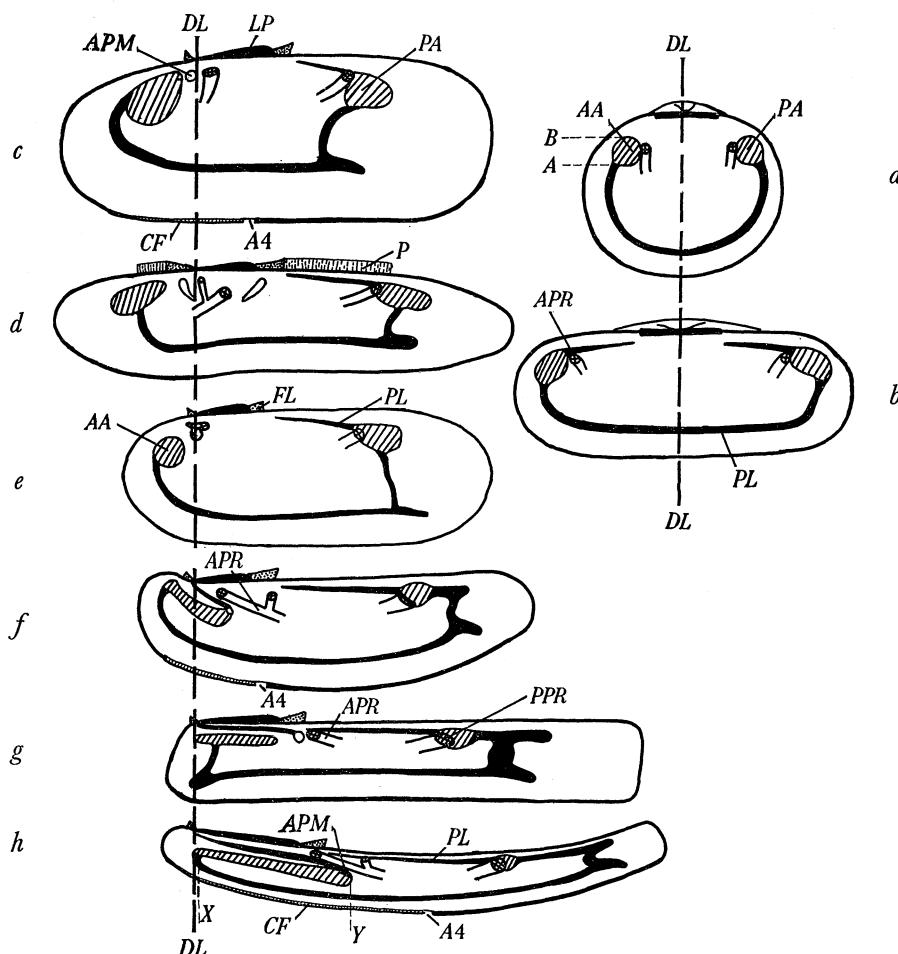

FIGURE 24. A series of diagrams of the internal surface of the right valves of members of the Solenidae showing the elongation of the shell posterior to the demarcation line (*DL*) and the insertion of the muscles. *a* and *b* are hypothetical conditions showing the effect of elongation of the mantle/ shell on either side of the demarcation line on the line of pallial attachment (*PL*). *c*, *Siliqua patula*; *d*, *Pharella acuminata*; *e*, *Cultellus lacteus*; *f*, *Phaxus pellucidus*; *g*, *Solen marginatus*; *h*, *Ensis ensis*. In *Phaxus* (*f*), *Solen* (*g*) and *Ensis* (*h*) elongation of the mantle/shell posterior to the demarcation line (*DL*) is extreme and, as indicated by the continuation of pallial attachment from the posterior end of the anterior adductor to the anterior end of the ligament, there is an embayment of the pallial line extending posterior to the demarcation line. The primitive ventro-dorsal axis of the anterior adductor (*a*, *AB*) is now orientated antero-posteriorly (*h*, *XY*).

In the Solenidae there is a single region of maximum marginal increase situated posteriorly and the mantle/shell is asymmetrical about the demarcation line. The percentage of the mantle/shell posterior to the demarcation line in the various genera is given in table 1. In both *Siliqua* (figure 24*c*) and *Pharella* (figure 24*d*), the anterior adductor is situated near the anterior end of the ligament and, as in the primitive bivalve, represents the hypertrophied pallial muscles in the depth of the anterior embayment. The extension

of the mantle/shell posterior to the demarcation line results in a corresponding extension of the posterior embayment and thus of the region of cross-fusion of the pallial muscles. The posterior adductor (*PA*) is situated near the posterior margin of the shell and the line of pallial attachment (*PL*) extends beyond the adductor along the dorsal margins of each pallial lobe to the posterior end of the functional ligament. In *Phaxus* (figure 24*f*), *Solen* (figure 24*g*) and *Ensis* (figure 24*h*) the asymmetry of the mantle/shell about the demarcation line (*DL*) is extreme and, as in *Siliqua* and *Pharella*, the posterior adductor is far removed from the posterior end of the ligament, but pallial attachment extends anteriorly beyond the adductor to the posterior end of the functional ligament. In *Solen* and *Ensis* the region of fusion of the pallial muscles also extends posterior to the posterior adductor. The marked reduction in the relative size of the posterior adductor at its insertion on the shell in these two genera, when compared with *Siliqua* and *Pharella*, is a result of the tremendous extension of the region of cross-fusion of the pallial muscles in the posterior embayment of the mantle. The anterior adductor (*AA*) of *Phaxus*, *Solen* and *Ensis*, unlike that of *Siliqua* and *Pharella*, extends posterior to the demarcation line. This posterior extension of the anterior adductor is not the result of a simple extension of the posterior margin of the muscle. As indicated by the continuation of the pallial muscle from the posterior end of the anterior adductor to the anterior end of the functional ligament, the effect of the tremendous posterior elongation, coupled with minimum growth anteriorly, is to produce an embayment of the pallial line which extends posterior to the demarcation line. The primitive ventro-dorsal axis of the anterior adductor (figure 24*a*, *AB*) is now orientated antero-posteriorly (figure 24*h*, *XY*). This posterior extension of the anterior adductor is most pronounced in *Ensis*.

TABLE 1. POSTERIOR ELONGATION AND LOSS OF DEPTH OF THE SHELL IN THE SOLENIDAE

	length of shell posterior to the demarcation line (%)	ratio of length to depth
Siliqua patula	60	2·5:1
Pharella acuminata	60	4·7:1
Cultellus lacteus	80	3·0:1
Phaxus pellucidus	85	4·2:1
Solen marginatus	95	6·0:1
Ensis ensis	95	9·0:1

It is in *Ensis* that the effect of changes in the form of the mantle/shell on the body are most marked, although elongation of the mantle/shell posterior to the demarcation line is approximately the same in both *Ensis* and *Solen*. A factor which must be taken into account when considering extension posterior to the demarcation line is the accompanying reduction in depth of the mantle/shell which may also occur. The ratio of length to depth of the mantle/shell of *Ensis ensis* is 9:1, while in *Solen marginatus* it is only 6:1. The ratio of length to depth of the mantle/shell of other genera of the Solenidae is given in table 1. Extension of the mantle/shell posterior to the demarcation line is approximately the same in both *Siliqua* and *Pharella*, but in the latter there is also a marked decrease in depth. In *Pharella*, unlike *Siliqua*, the anterior pedal retractor has on each side a double insertion on the shell, and it is interesting to speculate whether this double insertion of the anterior retractor is primarily a result of loss of depth of the mantle/shell rather than of elongation

posterior to the demarcation line. Thus, *Phaxus* and *Ensis* may be regarded as having evolved from ancestors in which loss of depth preceded posterior elongation, while *Solen* and probably *Cultellus* are derived from ancestors in which posterior elongation preceded any marked loss of depth. Other effects on the body of changes in the form of the mantle/shell have been discussed by Yonge (1952).

(6) *Characters of the Solenidae*

The mantle/shell. In all members of the Solenidae the mantle/shell is elongated posterior to the demarcation line. In the more specialized members there is also a marked reduction in depth, *Ensis ensis* presenting the greatest length to depth ratio of any bivalve. The hinge dentition consists typically of laterally compressed, blade-like cardinal teeth, two on the right valve and three on the left (*Solen* has a single cardinal tooth on each valve). The ligament is external and opisthodetic and comprises an outermost fusion layer and outer and inner ligament layers (the periostracum cannot be identified as a discrete layer over the external surface of the ligament in any members of the Solenidae). Over a short region anterior and posterior to the mantle isthmus, the outer marginal folds are fused and the primary ligament is secondarily extended by way of fusion layer. In *Pharella* the inner (periostracal-secreting) surfaces of the outer folds are fused anterior and posterior to the functional ligament with the result that the two valves are joined by a continuous sheet of periostracum.

Mantle fusion. The degree of fusion of the mantle margins ranges from cuticular fusion of the inner folds to complete tissue fusion of inner folds together with the inner surfaces of the middle folds (Type B, Yonge 1957), but in all members of the family fusion of at least some part of the mantle margins is of this latter type. Despite various accounts to the contrary, it is probable that the pedal gape is functionally restricted to the anterior end in all members of the family. It has not been possible to check this in *Cultellus* and Ghosh (1920) describes the pedal gape in this genus as extending to nearly half-way along the ventral margin. It is probable, however, that the ventral margins of the mantle over this anterior region are joined by cuticular fusion, and that *Cultellus* also possesses a fourth pallial aperture. A fourth aperture is not present in all members of the Solenidae.

The siphons. These are of Type B (Yonge 1957) in all members of the Solenidae, being formed from the inner and middle marginal folds.

Musculature. Graham (1934), discussing the Tellinacea and Solenidae, described the characters likely to be possessed by 'ideal' members of the two groups. Of the Solenidae he states, 'The posterior adductor is much smaller than the anterior, which is always narrow and elongated. The anterior retractor muscle of the foot has two insertions on each valve, and, in the foot, lies *external* to the posterior retractor.' It will be seen that this account of the musculature of an 'ideal' member of the Solenidae fits the genus *Phaxus* only. The musculature varies considerably in the different genera and there is little which can be regarded as characteristic of the family.

Gills. These vary from flat and homorhabdic (*Siliqua* and *Phaxus*) to plicate and heterorhabdic, but the gills of all members of the family are characterized by the possession on the frontal surfaces of some, or of all, the filaments of adjacent tracts of long and short cilia beating in opposite directions. There are three tracts on the frontal surfaces of the filaments

of *Solen* and two tracts on those of *Pharella*, *Phaxus* and *Ensis*. There is no information on *Siliqua* and *Cultellus*.

The alimentary canal. The style sac and mid-gut are separate in all members of the family and the descending limb of the intestine usually forms a number of loops. The stomach has a well-developed posterior sorting area and a prominent dorsal hood, both features associated with suspension feeding; all the ducts from the digestive diverticula open into either the right and left caeca or the left pouch.

IV. Discussion

From the foregoing account there can be little doubt that the most important feature of the Solenidae, and the one with which all others, as shown in this paper and by Yonge (1952), are connected, is the marked posterior elongation of the mantle/shell. The result is to produce a very elongate animal, highly adapted for rapid vertical burrowing particularly through soft unstable substrata, while the ciliary sorting mechanisms of the gills and the well-developed posterior sorting area and dorsal hood of the stomach are characteristic of highly specialized suspension feeding bivalves. The form which evolution has taken within the Solenidae has already been outlined. There are good reasons for believing that *Siliqua*, *Cultellus* and *Solen*, in which posterior elongation may have preceded loss of depth, form one line of development leading to the specialized condition in *Solen*, while *Pharella*, *Phaxus* and *Ensis* represent the other major line of development culminating in *Ensis*. Regarding the question of the origin of the family, many workers have suggested a close relationship between the Tellinacea and the Solenidae and undoubtedly there are points of similarity between them. The features which distinguish the Tellinacea have been fully discussed by Yonge (1949) but one point is worthy of further consideration. In all members of the Solenidae maximum marginal increase of the shell takes place posterior to the demarcation line, but in the Tellinacea the region of maximum marginal increase is situated *anterior* to the demarcation line (*Tellina*, *Donax*) or, in those genera with elongate shells which most closely resemble the Solenidae (*Solecurtus*, *Tagelus* and *Novaculina*), the demarcation line divides the shell into more or less equal anterior and posterior territories.

Both the Solenidae and Tellinacea comprise active deep-burrowing bivalves possessing a large and well-developed foot, but while the former are suspension feeders, the latter are essentially specialized deposit feeders (Yonge 1949). As suspension-feeding bivalves obtaining their food from the water above the substrate, members of the Solenidae never need to change position horizontally and the result of evolutionary change within the family has been to increase the speed and efficiency of *vertical* burrowing and so provide temporary protection for the animal. This capacity for rapid vertical burrowing is connected with many of the features which characterize the family, in particular, elongation of the shell posterior to the demarcation line, the extensive fusion of the mantle margins ventrally and the restriction of the pedal gape to the anterior end of the animal. In the Tellinacea, on the other hand, while the deep-burrowing habit provides protection, most members move about horizontally enabling them to exploit the bottom deposits on which they feed. This ability to move horizontally within the substrate appears to be connected with elongation of the shell anterior to the demarcation line and the retention of an extensive pedal gape, features which, among others, serve to distinguish the majority of the

Tellinacea from members of the Solenidae. Those members of the Tellinacea which most closely resemble the Solenidae (i.e. *Tagelus californianus*, *Solecurtus chamosolen* and *Novaculina gangetica*) inhabit stable muddy substrata rich in supplies of organic detritus and the ability to move horizontally has been lost. Adoption of this mode of life is associated with an elongate shell and there is also a tendency towards a more extensive fusion of the mantle margins ventrally (i.e. restriction of the pedal gape). These are features exhibited by members of the Solenidae, but their appearance in members of the Tellinacea is undoubtedly the result of convergence. Possibly because of their evolution from bivalves which already possessed the capacity for both deep burrowing and horizontal movement, growth of the shell anterior to the demarcation line is either equal to, or less than, that which takes place posteriorly. Moreover, *Novaculina* (Ghosh 1920), *Solecurtus* (Yonge 1949) and *Tagelus* (Yonge 1953) possess the long separate siphons characteristic of members of the Tellinacea and speed of vertical movement is not of prime importance.

During the visit to Singapore, living specimens of *Glauconome rugosa* were obtained from the market place and no observations were made on the habitat of the animal. The species is listed in Allan's (1950) book *Australian shells*, where the habitat is described as the mud of mangrove creeks and the mouths of rivers, while Iredale (1936) gives the habitat of *Glauconometta plankta* as the Parramatta River, Sydney Harbour. From the details of the anatomy and feeding currents given in the previous sections there can be little doubt that *Glauconome rugosa* is specialized for life in a stable substrate of mud. The phrase 'partially embedded in the mud' used by Reeve (1844) and Allan (1950) to describe the habit of the genus is difficult to understand. The reduction of the foot suggests that the animal lives permanently embedded in the substrate at some depth maintaining contact with the surface by way of the well-developed siphons. Through the kind offices of Professor R. D. Purchon the following information has been received from Mr D. Pathansali of the Department of Fisheries, Malaya. The specimens collected were larger than those obtained in Singapore, but Professor Purchon confirms that they are the same species. 'They occur intertidally on the banks of streams running through mangrove swamps and although there is a good tidal flow the conditions are calm and well protected from wave action. The water is brackish and almost fresh at high water. They are found in stiff mud at a depth of 7 to 10 in. and the maximum density observed was eighteen to twenty-two animals/sq.yd. The locality was Batu Maung on the Island of Penang and the bivalves are known in Malay as "Siput Changkol".' The ciliation of the gills and stomach indicates that *G. rugosa* is a suspension feeder and the presence of cirri on the frontal surfaces of the gills suggests that large quantities of suspended material are liable to be drawn into the mantle cavity with the inhalant current. Atkins (1937*a*) suggested that coarse cirri serve to remove large particles of sand or rock from the frontal surfaces of the gills and that they are probably not efficient in dealing with particles of mud. Whether relatively large particles are likely to enter the mantle cavity of *G. rugosa* is not known; further information is required on the nature of the substrate.

Most workers are agreed that the Glaucomyidae constitute a well-defined family of the Bivalvia, but the relationships of this family have always been doubtful, being sometimes included with the Veneridae and Petricolidae in the suborder Veneracea (Thiele 1926) and sometimes with the Solenidae in the suborder Solenacea (Thiele 1934). The

diagnostic features of these four families are summarized in table 2. Data on the Veneridae were obtained from various sources and on the Petricolidae from the recent papers on *Petricola pholadiformis* and *P. carditoides* by Purchon (1955) and Yonge (1958a), respectively. A comparison of these features and also of the four genera, *Venus, Venerupis, Petricola* and *Glauconome* (figure 25), with those of the genera comprising the Solenidae (figure 24) leaves no doubt that the Glaucomyidae should be included in the suborder Veneracea. The hinge teeth, the absence of fusion layer at the anterior end of the primary ligament, the form of

TABLE 2. A COMPARISON OF THE VENERIDAE, PETRICOLIDAE,
GLAUCOMYIDAE AND SOLENIDAE

|	Veneridae	Petricolidae	Glaucomyidae	Solenidae
hinge teeth	3 L, 3 R	3 L, 3 R	3 L, 3 R	3 L, 2 R
fusion layer	posterior only	posterior only	posterior only	anterior and posterior
mantle fusion and siphons	Type B	Type B	Type B	Type B
pallial sinus	moderate	large	large	small
pedis protractor muscle	absent	absent	absent	present
ctenidia				
(a) supra-axial extension	well developed	well developed	well developed	poorly developed
(b) ciliation	Type C (1b), C (2)	C (1c)	C (1c)	C (1d), C (2a)
style sac and mid-gut	joined	joined	joined	separate
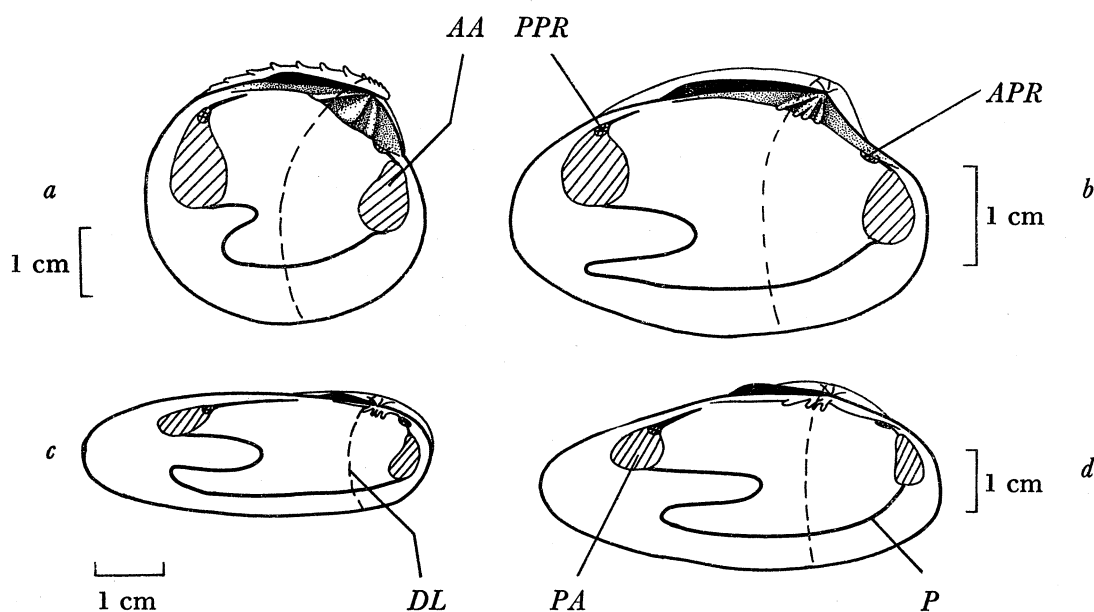
FIGURE 25. Diagrammatic comparison of the left valves of *d, Glauconome rugosa* and members of the Veneracea. *a, Venus casina; b, Venerupis decussata; c, Petricola pholadiformis.*

the pallial line, the ability to introvert the base of the siphonal process, the absence of the protractor muscle and the combined style sac and mid-gut are features common to the Veneridae, Petricolidae and Glaucomyidae and distinguish them from the Solenidae. There remain a number of characters in which the Glaucomyidae differ both from the Veneridae and from the Petricolidae. These are the long, united siphons, the extensive fusion of the mantle margins ventrally and the marked reduction of the foot. It was the existence of these features which led Deshayes (1853) to suggest that *Glauconome* and *Lutraria*

were closely related. While there can be little doubt that *Tanysiphon* and *Lutraria* are closely related, the similarities which exist between *Glauconome* and *Lutraria* are the result of convergence. They represent adaptations to life deep below the surface of the substrate and have been evolved independently in a number of bivalves (e.g. *Mya*, *Panope*) which from distinct origins have reached the same end-point. Members of the Veneridae are essentially adapted for life near the surface of the substrate and the majority do not penetrate this to any considerable depth. Liable to frequent disturbance they are active bivalves, the powerful wedge-like foot protrudes through the extensive pedal gape and enables the animal to regain quickly the protection of the substrate. In the Glaucomyidae this mobility has been lost and the animal is embedded permanently in the substrate at a considerable depth, maintaining contact with the surface by way of the long fused siphons. Specialization within the Bivalvia is frequently associated with increased protection of the adult animal. Typical examples are the deep burrowing bivalves already mentioned (i.e. *Mya*, *Lutraria* and *Panope* and to which must now be added *Glauconome*) and the wood- and rock-boring Adesmacea. In the pholads, boring represents a further specialization of the deep-burrowing habit, but in the Petricolidae as in the Hiatellidae, as recently discussed by Yonge (1958 *a*), the boring habit has evolved from a byssally attached, nestling habit. Within the Veneridae, both the burrowing habit and the byssally attached, nestling habit are exhibited by various species of the genus *Venerupis*. In this genus the shell is somewhat elongated posteriorly and the siphons are relatively well developed, the degree of fusion of the inhalant and exhalant portions varying in the different species. These are features which have undergone further specialization in the Petricolidae and Glaucomyidae and a detailed study may well suggest a close relationship between the genus *Venerupis* and members of these two families. Thus, within the suborder Veneracea boring and deep burrowing have evolved independently from the typical venerid form with its stout globular shell, short siphons, extensive pedal gape and wedge-like foot, the Petricolidae being venerid bivalves specialized for boring, while the Glaucomyidae are venerid bivalves specialized for deep burrowing.

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KEY TO THE LETTERING USED IN THE FIGURES

A	aboral	*MF*	middle fold
*A*4	fourth pallial aperture	*MG*	mid-gut
AA	anterior adductor muscle	*MI*	mantle isthmus
AFL	anterior fusion layer		
An	Anus	*O*	oral
AOB	aortic bulb	*Oes*	oesophagus
AOL	anterior outer layer	*OFA*	outer marginal fold at the anterior end of the mantle isthmus
APM	anterior protractor muscle		
APR	anterior pedis retractor	*OFP*	outer marginal fold at the posterior end of the mantle isthmus
		OL	outer layer of the ligament
Ci	cirri	*OMF*	outer surface of middle fold
Ca	right caecum	*OOF*	outer surface of the outer marginal fold
CF	cuticular fusion of the inner folds		
Ct	ctenidia	*P*	periostracum
		PA	posterior adductor muscle
D	dorsal	*PAS*	ridges of the posterior sorting area visible through the wall of the stomach
DDD	apertures of the ducts leading to the digestive diverticula		
DH	dorsal hood	*PFL*	posterior fusion layer
DL	demarcation line	*PG*	pedal gape
		PL	pallial line
E	exhalant siphon	*PM*	pallial retractor muscle
		POL	posterior outer layer
F	foot	*PPM*	posterior protractor muscle
FC	frontal cilia	*PPR*	posterior pedis retractor
FIF	tissue fusion of the inner folds		
FIO	fused inner surfaces of outer marginal folds	*R*	rectum
		RC	opening of the right caecum into the gastric cavity
FL	fusion layer		
FOF	fused outer marginal folds	*SS*	style sac
		SR	siphonal retractor muscle
HT	hinge teeth		
		*T*1	major typhlosole within the right caecum
I	inhalant siphon		
IF	inner fold		
IG	intestinal groove	*V*	ventral
IL	inner layer	*Ve*	ventricle
IOF	inner surface of outer marginal fold (i.e. periostracal secreting surface)		
		WC	waste canal
LP	primary ligament	*WF*	folds enclosing the waste canal (*WC*)
LPa	labial palp		