
On the Structure and Adaptations of the Tellinacea, Deposit-Feeding Eulamellibranchia

C. M. Yonge

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ON THE STRUCTURE AND ADAPTATIONS OF THE TELLINACEA, DEPOSIT-FEEDING EULAMELLIBRANCHIA

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The Tellinacea comprise four families of eulamellibranchs possessing common structural features all associated with the habit of feeding on bottom deposits.

The habits and general structure of all available British species of the Tellinacea have been studied; in particular, *Tellina tenuis* (in greatest detail) and *Macoma balthica* (Tellinidae); *Abra alba* and *Scrobicularia plana* (Semelidae); *Donax vittatus* (Donacidae); *Gari tellinella*, *G. fervensis*, *Solecurtus chamasolen* and *S. scopula* (Asaphidae).

The most significant structures are the very mobile *separate* siphons formed by fusion of the inner (muscular) lobes of the mantle edge, while the middle (sensory) lobe and the periostracal groove continue around the posterior margin of the shell bordering a deep siphonal space from the base of which the siphons arise.

The siphonal apertures are fringed only by six blunt lobes (pinnate and with intermediate lobes in *Donax*). They are also very insensitive.

In the Tellinidae and Semelidae the siphons are very long and the inhalant siphon gropes widely over the surface, actively drawing in bottom deposits. The siphons are shorter and wider in the Donacidae and Asaphidae, but the inhalant siphon opens widely for the passive intake of much material lying on or just above the bottom.

The siphonal retractors are highly developed, while the siphons possess a characteristic arrangement of concentric layers of circular and longitudinal muscles with radiating fibres dividing the major layers of longitudinal muscles into a series of bundles. Six nerves, evenly spaced, run down each siphon, always in the same relative position, terminating in the lobes bounding the aperture.

In association with the mode of life, the foot is very large and active. It is very much compressed laterally in the Tellinidae and Semelidae, more rotund and pointed anteriorly in *Donax*, where there is an additional elevator pedis muscle possibly correlated with the habit of burrowing in firm sand, and rounded in *Solecurtus* (and the Novaculininae), where alone the pedal gape is reduced. Ventral attachment of the siphons in all but the last is reduced to the minimum and takes the characteristic form of the cruciform muscle.

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This muscle consists of crossed bundles of fibres providing, it is here suggested, an ideal tie for the siphons. The anterior attachments will take the strain when the siphons are extended and the posterior ones when they are withdrawn.

There is a sense organ near each of the two posterior attachments consisting of an intramuscular slit opening into a ciliated pit with an associated ganglion and usually communicating with the exterior. Theories concerning the function of the sense organ are discussed and the new view expressed that it is a proprioceptor giving indication of the degree to which the siphons are extended or withdrawn.

Need for such information may reside in the presence both of large siphons and of a large foot in the Tellinacea; escape from danger involving first withdrawal of the siphons and then extension of the foot, i.e. unlike the Solenidae or deep burrowers such as *Mya* in which, respectively, only the foot and the siphons react to danger.

In *Solecurtus* the inner mantle lobes are extensively fused both anteriorly and posteriorly. The cruciform muscle is displaced anteriorly and the pedal gape reduced (hence the superficial resemblance to the Solenidae) and the mantle cavity extended posterior to the shell when the animal is expanded. Broad marginal areas covered with periostracum protect the foot and siphons when these are withdrawn.

Conditions in the subfamily Novaculininae are discussed and evidence produced for its inclusion in the Tellinacea in association with the family Asaphidae. The relationships are discussed between *Tagelus* (with cruciform muscle and no ventral mantle fusion), *Solecurtus* (with cruciform muscle and extensive ventral mantle fusion) and the Novaculininae (with no cruciform muscle but great anterior ventral mantle fusion).

The observations of Atkins (here confirmed) on the ctenidia are discussed. The greatest modifications are in the Tellinidae and Semelidae where the outer demibranch is upturned, consisting of a single surface, and the margin of the inner demibranch has no food groove. These features are associated with the great intake of material. Need to convey this material rapidly forward explains the presence of powerful cirrus-like cilia on the frontal surface of the posterior region of the outer face of the inner demibranchs. These cilia are absent where forward currents exist on the gill axis.

In the Donacidae and Asaphidae the gill is less modified, the outer demibranch being reflected although with a supra-axial extension, while there is a food groove on the margin of the inner demibranch; also on the outer demibranch in *Tagelus*.

In general the palps tend to be large when the gills are small, typically in mud dwellers.

Pseudofaeces are removed in the normal manner through the inhalant siphons; they are extremely abundant in the Tellinidae and Semelidae in which mantle folds (in all species examined) protect them from being swept forward by the inhalant current, concentrated in the narrow inhalant siphon, while there is an additional ventral channel in *Abra* and *Scrobicularia*.

In general the gut is longest in species that take much mud into the mantle cavity; faecal pellets of characteristic form are moulded. The initial region of the mid-gut is associated with the style-sac in all but *Donax*.

The stomach is highly characteristic of the group; it can be readily dissected free from surrounding tissues. It is most highly modified in the Tellinidae and the Semelidae.

The proximal stomach is elongated vertically so that the style is not bent within it as in suspension-feeding eulamellibranchs. The gastric shield is exceptionally large and strong and carries two massive teeth which bear against the side of the style near its head. The style has been observed to rotate in *Tellina tenuis*.

There is evidence of trituration of large particles presumably between the style and the teeth of the gastric shield. In association with this, a new structure, here termed the postero-dorsal caecum, has been developed to act as a safety valve within which the excess accumulations of large particles are temporarily stored before trituration.

The ciliary currents within the stomach are essentially similar to those in other eulamellibranchs, and there is the usual dorsal pouch and food-sorting caecum (this associated with the openings of the ducts into the digestive diverticula). But in general these are less highly developed than in the suspension-feeding eulamellibranchs, but more so in the Donacidae and the Asaphidae than in the two more specialized families.

The appearance and probable mode of action of the *intact* stomach are described and comparisons made with conditions in suspension feeders such as *Mya*.

The only other eulamellibranchs with similarly formed siphons are equally specialized, so that it is necessary to derive the Tellinacea direct from the Filibranchia. The possible course of evolution within the group is discussed. The conditions in *Gari* are least specialized, those in the Tellinidae and Semelidae, on the one hand, and in *Tagelus-Solecurtus*-Novaculininae on the other, are the most specialized.

Different families, genera and species are adapted for life in all types of bottom material, and are there able to exploit as nutriment the contained organic detritus. The nature of this is briefly discussed, but its importance is best indicated by the variety and number of bottom-living invertebrates that would appear to depend upon it.

The Tellinacea are a highly successful group of lamellibranchs which have evolved along characteristic lines with a success revealed by their vast abundance in suitable substrata within both the littoral and sublittoral zones.

I. INTRODUCTION

The general similarity in external appearance throughout the Lamellibranchia was shown by the pioneer morphological studies of Pelseneer (1891, 1911) to conceal wide differences in internal structure, notably as between the Protobranchia on the one hand and the Septibranchia on the other, and these differences have been emphasized by studies on living representatives (Yonge 1929, 1939). But also within the Eulamellibranchia there is much diversity in form and habit, most obviously in the Tridacnidae (Yonge 1936) and the Teredinidae. The Tellinacea, comprising the families listed by Thiele (1935), constitute another well-defined group possessing many highly characteristic features, notably the very long, narrow and separated siphons formed by fusion of the inner mantle lobes exclusively (Yonge 1948*a*), the cruciform muscle with its associated sense organ, and a large and very active foot. Most of these, with other structural features, are associated with the mode of feeding, on the deposits on the surface of the bottom rather than on plankton and other suspended particles as in the majority of other lamellibranchs. Indeed, in their feeding habits and in certain other correlated features of structure and habit, they bear resemblances to the two families of the Protobranchia which are also deposit feeders, although by means of the palp proboscides, namely, the Nuculidae and the Nuculanidae (Yonge 1939).

While investigations have been made by a number of workers into various aspects of structure and habit in various species of the Tellinacea, there exists no comprehensive account of this group. And it is one of great importance. Thiele (1935) lists thirty-eight genera, the numerous species of which inhabit every type of soft substrata in all seas. This paper is based on descriptions of the structure and habits of representatives of all genera available around Great Britain, but the opportunity has been taken to bring together the scattered observations of previous workers on different species and different aspects of their structure and physiology. As will become apparent, the Tellinacea have evolved along lines of their own, and this paper represents an attempt to describe these.

II. GENERAL STRUCTURE AND HABITS

(1) *Tellinidae*

This is the largest and most characteristic family of the Tellinacea, comprising fifteen genera (Thiele 1935), of which two, *Tellina* and *Macoma*, have common British representatives. For a variety of reasons it is most convenient to consider the members of this

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family first and to describe in particular detail the structure of *Tellina tenuis*, the commonest bivalve at Millport and already the subject of considerable work at the marine station. The other species dealt with will be described primarily in terms of the differences between them and *T. tenuis*.

Tellina is the most numerous represented genus of the British Tellinacea. Seven species occur (Winckworth 1932). These inhabit different grades of sandy substrata at varying depths. *T. tenuis* is intertidal, extending only to depths of a few fathoms, the remainder are sublittoral. Broadly speaking they may be divided into inhabitants of fine or of coarse sand, especially where this contains some organic debris. The former include *T. tenuis*, which may occur in densities of over 4000 per metre square (Stephen 1928), and the closely allied *T. fabula*, which overlaps with it in the region immediately below low-water level and extends to depths of up to 30 fathoms (Stephen 1932, 1933), and the rare *T. balaustina*, which is stated by Jeffreys (1863) to live in fine sand at depths of from 18 to 50 fathoms. *T. crassa* and *T. pygmaea (pusilla)*, respectively the largest and the smallest of British species of *Tellina*, live in coarse sand and shell gravel (Ford 1923). They extend to depths of from 50 to 85 fathoms. *T. pygmaea* replaces *T. fabula* as the chief representative of the genus in the northern North Sea (Stephen 1933). *T. donacina*, of about the same size as *T. tenuis* but somewhat more stoutly built and more elongated, is a typical inhabitant of coarse sand and gravel from shallow depths down to about 25 fathoms. *T. squalida* is a larger species, second only to *T. crassa*; it is not common, and no certain information about its habitat has been found. It probably lives in coarse sand.

(a) *Tellina tenuis*. Description is confined to this species; examination of *T. fabula* and *T. donacina* revealed no significant differences. The animal is much compressed laterally, an average specimen, 16 mm. long and 11 mm. deep, being only 3 mm. wide. The general appearance after removal of the right shell valve and mantle lobe is shown in figure 1. The foot is very large and the pedal gape correspondingly long, extending from the anterior adductor (AA) to the base of the inhalant siphon (IS), where the inner lobes of the mantle edges unite in the region of the cruciform muscle (CM). When an intact animal is placed on sand the foot is soon protruded to extend forward and downward and hook repeatedly under the sand until a grip on this is obtained. The animal is then erected and the compressed shell slides diagonally down into the substratum as a result of a series of contractions of the pedal and adductor muscles. When completely buried the animal assumes a vertical position and the siphons are extruded. The entire process of burrowing, from the first extrusion of the foot to final disappearance under the sand, may be completed within 30 sec.

The siphons, as in all Tellinacea, are separate. The inhalant siphon is the more extensile, reaching a length of up to at least four times that of the shell; the exhalant siphon was not observed to exceed the length of the shell. Under normal conditions the former extends along the surface of the sand, a little arched as shown in figure 16*a*, with the tip lying on or a little above the surface. In this position it draws in material lying upon or just above the surface of the sand, but it does not actively pull in bottom material as do the inhalant siphons of *Abra* and *Scrobicularia*. There is no selection, or rejection, of material which can be seen through the transparent walls passing rapidly down the very passive siphonal tube. From time to time, but only after much material has previously entered, there is extrusion

of 'pseudofaeces' through this siphon. Often material can be observed passing back along the siphon for half or two-thirds of its exposed length, only to be withdrawn into the mantle cavity again when the adductors relax. These limited contractions—and they can be no more because the siphon remains fully extended—can only partially reduce the size of the mantle cavity.

The tip of the inhalant siphon is bordered by six blunt lobes, but there are no true tentacles like those possessed by suspension-feeding lamellibranchs where they act as strainers, as in *Spisula* or *Aloidis* (Yonge 1947). In sharp contrast to the great sensitivity of the siphons in the latter, the tip of this siphon in *Tellina* is most *insensitive*, seldom closing even when touched with a needle. It acts as a purely passive agent for the intake of fragments lying on or just above the bottom. When this siphon is withdrawn a round hole is left in the sand, but no evidence was found of any mucous lining to this such as made by species of *Thracia* (Yonge 1937).

The exhalant siphon was never observed to project above the sand although it must be continually open to allow the through passage of the large quantities of water which enter the other siphon. But the sand is sufficiently porous to permit the upward passage of water. When observed extruded in a dish, the exhalant siphon was seen to dilate greatly from time to time and then contract to a mere thread. It also constricted in places, producing a series of bulbous regions. These reactions may be concerned with keeping a passage open through the sand. The tip of this siphon is normally somewhat constricted, as shown in figure 1, the better presumably to concentrate the exhalant current. The orifice is bounded by six very blunt lobes; there are no tentacles or marginal membrane as in suspension feeders.

The mantle edge bears the usual three marginal lobes. The outer one (OL) secretes all but the innermost layer of the shell (Trueman 1942). The middle lobe (ML) bears a single row of short tentacles and is bounded on its outer side by the periostracal groove, the area between this and the outer lobe being thus covered with periostracum (P), as shown clearly in figures 19 and 23. The inner lobe (IL) consists of a low muscular ridge (velum or pallial curtain) which increases in size posteriorly. It is these inner lobes which alone unite to form the siphons, the other two being continued round the posterior margin of the shell bounding an embayment known as the siphonal space. The cruciform muscle (CM), which is situated at the base of the inhalant siphon, represents an enlargement and specialization of the pallial musculature at the point of union of the inner mantle lobes. The significance of this muscle is discussed later in connexion with conditions in all the species studied.

The ctenidia are the most conspicuous organs in the mantle cavity. Each consists of a very large inner and a much smaller, upturned outer demibranch (ID, OD). Atkins (1937*a*) has described their ciliation, and her conclusions will be discussed later. Material is carried very rapidly over the surface of the ctenidia and then forward along the ventral margin of the inner demibranch as shown in figure 1. The labial palps (LP) are of medium size (relatively smaller than in the mud-dwelling genera to be described later), with few and relatively large ridges on the opposed faces. They function in the normal manner, smaller particles and masses entering the mouth, larger ones being rejected by way of their tips. On the mantle surface material is conveyed ventralward and then posteriorly to the base of the inhalant siphon. Its final path lies within a waste canal (WC) arched over dorsally by a pair of mantle folds (MF) which extend for some distance forward from the

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middle of each side of the opening of the inhalant siphon. They project inward along a line somewhat below the ventral margin of the large siphonal retractors (see figure 23). These structures were originally described by Pelseneer (1911), but he regarded them as sense organs, and their correct function was shown by Kellogg (1915) in *Macoma secta*. They allow the accumulated waste material or pseudofaeces (*z*) to collect at the base of the inhalant siphon despite the continual and powerful inflow of water through this. They have thus the same function, although not quite the same position, as mantle folds present in certain of the Mactridae, e.g. *Spisula* and *Lutraria* (Yonge 1948*c*). Contraction of the adductor muscles, by reducing the volume of the ventral areas of the mantle cavity (the mantle edges being closely applied as they invariably are except when the foot is extruded), will force the pseudofaeces up between the membranes and so out through the inhalant siphon.

(*b*) *Macoma balthica*. This is the solitary British species of the genus, although there are several varieties (Winckworth 1932). It is a characteristic member of the intertidal and shallow-water fauna where clean sand is replaced by muddy, often black and foul-smelling, sand (Stephen 1929) where it takes the place of *Tellina tenuis*. It has been found in densities of up to 3071 per metre square (Fraser 1932). In a discussion of her own and previous work, Beanland (1940) suggests that 'the abundance of *Macoma* in estuaries possibly depends on two factors: (*a*) quality and quantity of available food supply, correlated with type of soil; and (*b*) available feeding time, correlated with distance below high-tide mark'. A more northern species, *M. calcarea*, lives at greater depths but also on a mud bottom in association with *Abra alba* (Petersen 1915). The habits of *Macoma calcarea* have been described by Blegvad (1915). The genus may be said to consist of species adapted for life on muddy substrata but is closely allied to *Tellina*, in which its species were formerly included.

Observations were made on specimens collected from areas of thick muddy sand in Ballock Bay, Isle of Cumbrae. The animals were large, about 2 cm. long. The shell is more rotund than that of *T. tenuis*. Burrowing takes place in the same manner but is slower, the process usually taking about 2½ min., due to the shape of the shell and the denser medium. It is probable that this species is relatively static, burrowing deeply and seldom moving unless disturbed. *T. tenuis*, on the other hand, burrows to depths of up to 12 cm. when the tide is out but rises near the surface when the sea returns. In aquaria, *Macoma balthica* burrowed to a depth of about 2 cm. and then extended the siphons. The inhalant siphon behaved much as in *Tellina tenuis*, reaching an exposed length of more than 5 cm. and then moving about while actively drawing in material lying on the surface of the mud. Blegvad (1915) likens this siphon in *Macoma calcarea*, where it may reach a length of 10 cm., to an elephant's trunk in its active, groping movements. The exhalant siphon in *M. balthica* projects vertically above the surface for distances of some 1.5 cm. This is probably due to the nature of the substratum. In structure the siphons, though larger, resemble those of *Tellina tenuis*.

As shown in figure 2, the general disposition of the organs in the mantle cavity is very similar to that in the preceding species. The foot and siphons call for no comment, but the gills are relatively much smaller and the palps very much larger with more numerous and smaller ridges on their opposed faces. The inner palps are attached for some distance to the edge of the inner demibranchs. These differences are probably correlated with the greater ease with which the finer particles from a mud substratum are drawn in (hence the smaller gills) and the greater difficulty of sorting the mass of material (hence the larger palps).

The ciliary currents in the main resemble those of *T. tenuis* and also of *Macoma secta*, as described and figured by Kellogg (1915). The only important difference is the greater extent of forward-directed tracts on the outer frontal surface of the inner demibranchs (see figure 2), the possible significance of which will be discussed later. There is a well-developed waste canal confined beneath a frilled mantle membrane. The mantle edge and cruciform muscle are essentially similar to those in *Tellina tenuis*.

(2) *Semelidae*

The British genera belonging to this family, *Abra* (*Syndosmya*) and *Scrobicularia*, are very closely allied and are adapted exclusively for life on bottoms of soft mud. They have many points of resemblance to the Tellinidae, with an even more compressed shell. The major difference between the two families lies in the structure of the ligament, which, as shown by Trueman (1942), forms an external ridge in the Tellinacea (see figures 1, 2) but is largely internal, posterior to the cardinal tooth, in the Semelidae (figures 3, 4).

(a) *Abra alba*. This is one of the three common British species, the others being *A. nitida* and *A. prismatica*. All are sublittoral, Stephen (1933) referring to *A. alba* as 'very markedly an inshore species, only occurring in the fringe round the North Sea shores in suitable localities such as the muddy grounds of estuaries, etc.', adding that its maximum depth in Scottish waters is some 36 fathoms and in English waters 27 fathoms. *A. nitida* he also states to be common in similar areas but extending in smaller numbers into deep water. *A. prismatica*, on the other hand, he reports as being more widely distributed over the whole of the North Sea. *A. alba*, in particular, may be regarded as the dominant deposit-feeding bivalve on muddy bottoms below the region occupied by *Macoma balthica*, where Petersen's *Macoma* community gives place to his somewhat deeper *Abra* community.

A. alba, together with *A. nitida*, is abundant on bottoms of soft muddy gravel, especially off the east shores of the Isle of Cumbrae. As shown in figure 3, the shell is somewhat more oval but equally as compressed as that of *Tellina tenuis*. The animal burrows with even greater speed. The siphons are extremely long, the inhalant one extending for lengths of over five times that of the shell. The exhalant siphon, as in *Macoma balthica*, projects vertically upward, sometimes 2 mm. above the surface, although it often lies below this but always within a cavity it has previously made. It is impassive and does not contract even when pushed aside, as frequently happens, by the groping inhalant siphon of an adjacent animal. Oval faecal pellets, as described by Moore (1930, 1931), are frequently expelled and accumulate in piles around the cavity occupied by the exhalant siphon. The siphonal aperture is normally widely open but occasionally constricts, the siphon then elongating after which it reopens.

The inhalant siphon ranges round the point where it emerges from the substratum, sometimes close to this, sometimes greatly extended. It displays quite extraordinary activity by bending and twisting in all directions, while the tip independently makes smaller encircling movements. It never lies passive as that of *Tellina tenuis* often does. The siphon often arches over with the aperture searching the surface of the mud (figure 16*b*) from which it actively *pulls in material* as already described by Petersen & Boysen Jensen (1911). The fragments so pulled in often completely fill the lumen of the siphon. This process of continual rapid intake is interrupted about every 2½ min. by a sudden extrusion of pseudo-

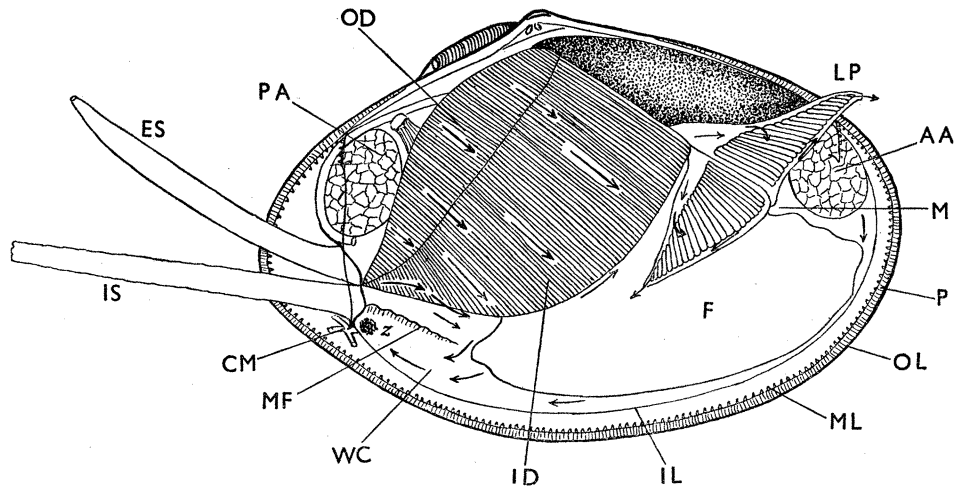


FIGURE 1. *Tellina tenuis*, viewed from right side after removal of right shell valve and mantle lobe (magn. $\times 5$). AA, anterior adductor; CM, cruciform muscle; ES, exhalant siphon; F, foot; ID, inner demibranch; IL, inner lobe of mantle edge; IS, inhalant siphon; LP, labial palp; M, position of mouth (in mid-line); MF, mantle fold; ML, middle lobe of mantle edge; OD, outer demibranch; OL, outer lobe of mantle edge; P, periostracum covering region between outer mantle lobe and periostracal groove; PA, posterior adductor; WC, waste canal; z, accumulation of pseudofaeces. Arrows indicate direction of ciliary currents.

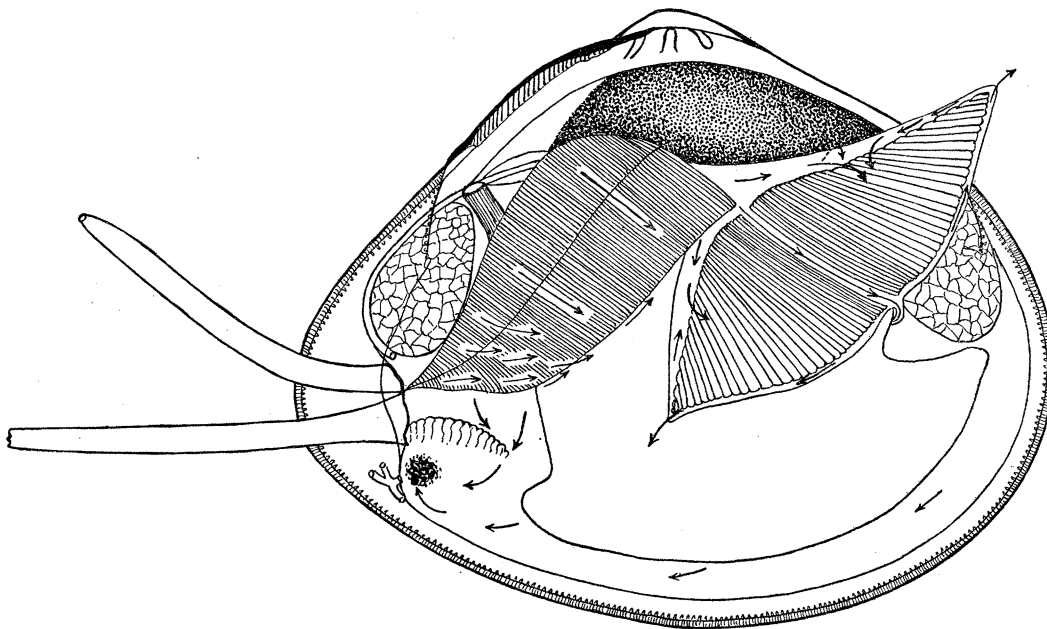


FIGURE 2. *Macoma balthica*, from right side (magn. $\times 5$). Parts as indicated in figure 1.

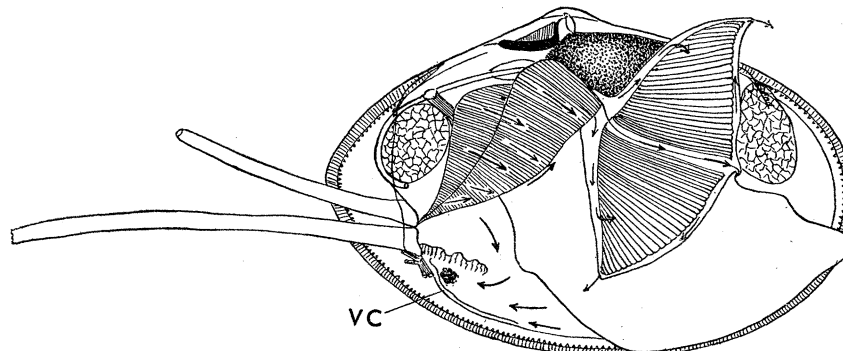


FIGURE 3. *Abra alba*, from right side (magn. $\times 5$). VC, ventral channel. Other parts as indicated in figure 1.

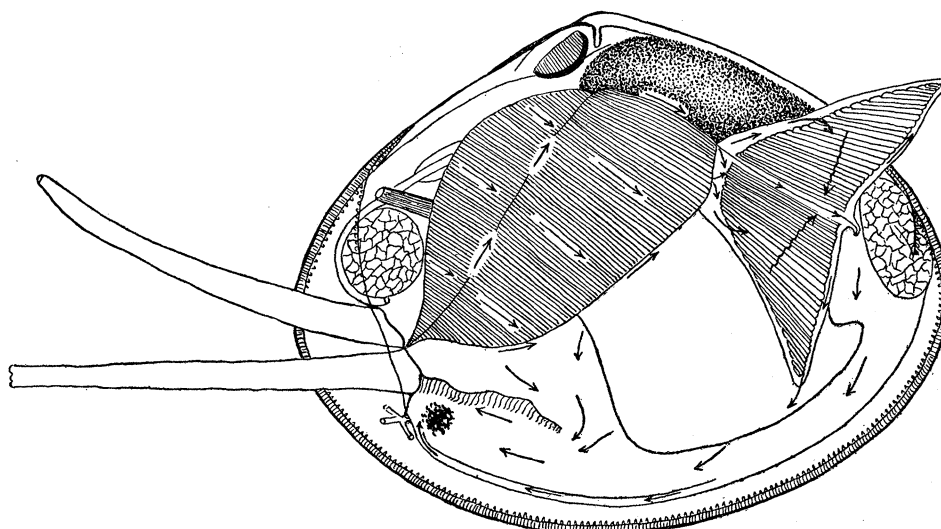


FIGURE 4. *Scrobicularia plana*, from right side (magn. $\times 2\frac{1}{2}$). Parts as indicated in figure 1.

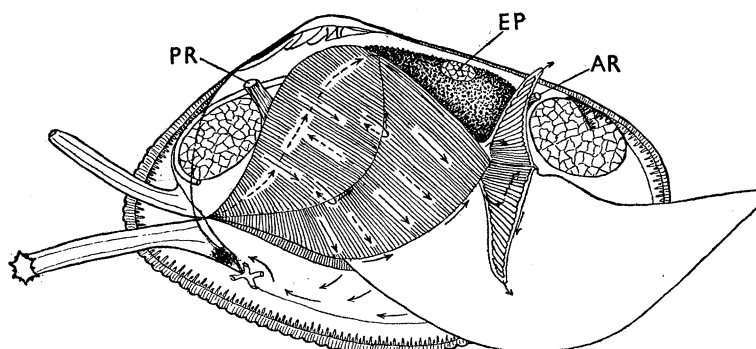


FIGURE 5. *Donax vittatus*, from right side (magn. $\times 7$). AR, anterior retractor pedis; EP, elevator pedis muscle; PR, posterior retractor pedis. Other parts as indicated in figure 1.

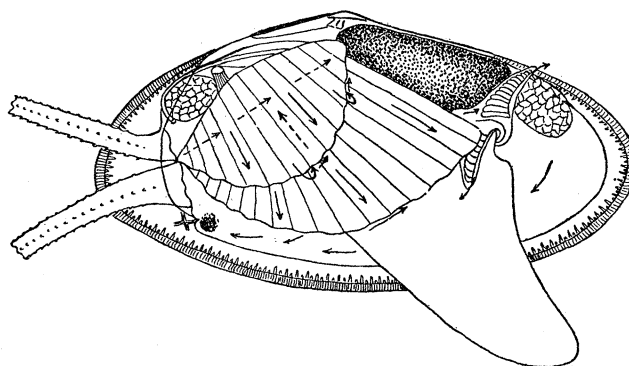


FIGURE 6. *Gari tellinella*, from right side (magn. $\times 3$). Parts as indicated in figure 1.

faeces. The siphon then extends upward, well clear of the bottom, and elongates, while a great flow of material is extruded in a rapid stream for some 3 sec. So much material is taken in and so much periodically expelled that the mantle cavity must be alternately almost completely filled and then emptied. The inhalant siphon is most insensitive to any form of mechanical stimulus and is entirely indiscriminate in its feeding activities, often taking in faecal pellets expelled through the exhalant siphon.

The disposition of the organs in the mantle cavity is shown in figure 3. The palps are relatively still larger and the ctenidia smaller than in *Macoma balthica*. There is the same waste canal bounded above by pallial membranes, but in addition a well-developed ventral channel (VC) is formed by an additional fold (see figure 23) within the pallial curtain which extends along the posterior third of the mantle. Ciliary currents are similar to those already described.

(b) *Scrobicularia plana*. This is the solitary British species of the genus. It is rounded, the depth being some three-quarters of the length, and very compressed. It is a relatively large bivalve attaining lengths of over 4 cm. It occurs exclusively in the soft substratum, rich in organic debris, of mud flats within estuaries or where there is some admixture with fresh water and lives higher up and in less saline waters than *Macoma balthica*, which it may there replace (Stephen 1930). *Scrobicularia plana* is essentially an intertidal species, Spooner & Moore (1940) stating that 'it appears more or less intolerant of permanent immersion'. It occurs in vast numbers in suitable localities such as St John's Lake in the Tamar Estuary, where Spooner & Moore reported densities of up to 1000 per metre square. The mode of life and manner of feeding of this species were originally described by Meyer & Möbius (1872).

Specimens examined at Millport were obtained from mud banks in the upper reaches of Loch Sween, where some fresh water flows over at low tide. A large specimen took some $2\frac{1}{2}$ min. to burrow into mud. In nature the animals live at depths of from 5 to 20 cm., and the siphons have corresponding powers of extension. An animal 3.5 cm. long was observed to extend the inhalant siphon for 15 cm., and this was probably not the limit of possible extension. Buried animals often extended this siphon for lengths of up to 12 cm. along the surface of the mud. This species behaved in essentially the same manner as *Abra alba*, although the inhalant siphon never displayed quite the same violent activity. But it also pulls in the deposits on the surface of the mud and so draws in large masses, up to 2 mm. in diameter. Similar sudden periodic extrusions of great masses of pseudofaeces were observed.

The appearance of the organs in the mantle cavity is shown in figure 4. They are essentially similar to those of *A. alba* with the foot and palps relatively somewhat smaller and the gills larger. As in that species and in *Macoma balthica*, the ridges on the opposed faces of the palps are numerous and small. The mantle membrane is very large, approximately 2 mm. wide in an animal of shell length 3.5 mm., while a ventral channel (see figure 18) is present as in *Abra alba*. On the gills, particles are carried forward along the axis as well as along the margin of the inner demibranch.

(3) *Donacidae*

In this family the shell is much stouter than in members of the two preceding families, while the hinge is situated about one-third of the length from the posterior end. This may

be connected with the great size and power of the foot. As shown below, in the disposition of the organs and in behaviour generally, this family resembles the Asaphidae more closely than it does the two families already considered. It is represented in British seas only by the genus *Donax*.

(a) *Donax vittatus*. This is the only common British species, although *D. variegatus* (*politus*) occurs around the Channel Isles and along parts of the south coast of England. The wedge-shaped shell of *D. vittatus* is characteristically solid and highly polished with knotted margins. It is an inhabitant of clean and usually very firm sand replacing *Tellina tenuis* locally (Stephen 1929) where conditions suit it. It extends into the sublittoral zone down to depths of about 10 fathoms where the bottom sand is suitable.

Small specimens were obtained by dredging in shallow water in Kames Bay at Millport, and these proved adequate for initial examination which was completed on large specimens kindly collected at Aberlady, Firth of Forth, by Dr A. C. Stephen. The foot is broader than in the preceding species and is pointed anteriorly (figure 5). It is adapted for digging in very firm sand and not for almost sliding into soft sand or mud as in the species already described. The initial stages of burrowing take somewhat longer, but once the foot has obtained an adequate grip on the sand the animal soon disappears below the surface. As described originally by Graham (1934*b*), it possesses a pair of elevator pedis muscles (EP) as well as the pairs of protractor with anterior and posterior retractor muscles (AR, PR) possessed by the preceding species. This additional pair of muscles probably aids the animal in the difficult business of burrowing in the firm sand of exposed beaches, for life in which its stout and smooth shell are also advantages. The rarity and small size of this species in Kames Bay indicates that it cannot compete with *T. tenuis* and *T. fabula* in softer sand with a higher content of organic matter. This may be due in part to its rather different mode of feeding which is described below.

Once buried, the siphons, which are stouter than those of the preceding species, are extruded vertically side by side (figure 16*d*), the inhalant to about twice the height above the surface of the exhalant siphon. The former appears capable of extension up to about the length of the shell, about half its length being exposed. The aperture is bordered by the usual six major lobes, but these are larger than in the preceding species with lateral and outward projections, while there are a series of smaller, also compound, tentacular lobes between them. The exhalant siphon bears only the usual six terminal lobes. On both siphons there are six opaque lines each terminating in one of the six terminal lobes. There are notable differences between the behaviour of the inhalant siphon here compared with those in the Tellinidae and Semelidae. There is no exploration of the bottom, the siphon never bends down on to or along its surface; the only movements observed were occasional slight quiverings. On the other hand, it differs from the siphons of suspension-feeding lamellibranchs in the freedom with which material enters because the lips of the aperture with the ring of pinnate tentacular lobes are curled back exposing a trumpet-shaped opening. The tentacles have no sieving action and the siphon shows little sensitivity. The general impression gained confirmed the view that *Donax vittatus* is specialized for life in firm sand where organic debris is largely absent, so that it must feed primarily on suspended matter; the relatively small amounts which enter are reflected by the much less frequent, although when they occur very sudden, extrusions of pseudofaeces. The inability of this

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species to live in regions suitable for *Tellina tenuis* and *T. fabula* may be due to the large amounts of organic debris which will there enter and possibly block the mantle cavity.

While the general arrangement of the organs in the mantle cavity remains the same, as shown in figure 5, the palps are very small and the gills relatively large with the small outer demibranch complete although with a supra-axial extension of the outer lamella (Ridewood 1903). There are forwardly directed ciliary tracts along both the axis and the food groove on the margin of the inner demibranch. There are neither mantle folds nor a ventral channel leading into a waste canal, and pseudofaeces collect, as shown in figure 5, actually *within* the dilated base of the inhalant siphon. This indicates both a more gentle inflow of water and a much slower accumulation of pseudofaeces than in the previous species. The middle mantle lobe is fringed with a double inner row of large and a double outer row of smaller tentacles. The base of the siphons and so the position of the cruciform muscle is slightly more anterior than in the Tellinidae and Semelidae.

(4) *Asaphidae*

The genera grouped by Thiele (1935) within the family Psammobiidae (here, following Winckworth (1932), termed the Asaphidae) exhibit a much greater range in form than do those contained in the other three families. While *Gari* (*Psammobia*) does not differ greatly from the typical form of the Tellinacea generally, genera such as *Tagelus* and *Solecurtus* have assumed an elongate form and a manner of life not unlike those of members of the Solenacea with which they were formerly included. But both on the basis of morphology (Graham 1934*b*) and of shell (Thiele 1935) they are unquestionably members of the Tellinacea, as the following account will confirm. The Asaphidae are separated from the remainder of the Tellinacea primarily on the basis of the disposition of the ligament, here external, and the presence of two principal hinge teeth in each valve without lateral teeth.

(a) *Gari tellinella* and *G. fervensis*. These species, together with *G. depressa* and *G. costulata*, constitute the representatives of the genus in British seas. All have relatively stoutly built and somewhat elongate shells and usually inhabit substrata of coarse sand or shell gravel for which media they appear to be especially adapted. *G. depressa* occurs intertidally, but the remainder are sublittoral although *G. fervensis* is occasionally taken at low water of spring tides, extending, however, to depths of up to 90 fathoms (Jeffreys 1863). Stephen (1933) refers to this species as being widely distributed in the North Sea, whereas he regards *G. tellinella* as 'very markedly an "Atlantic" species, spreading into the North Sea only in the area influenced by "Atlantic" water'. *G. depressa* also occurs in the North Sea, but is confined to southern and western waters.

Both *G. tellinella* and *G. fervensis* were taken at moderate depths in the Clyde sea area, the former in shell gravel and the latter in fine substrata of sandy or muddy gravel, but neither are common, and some additional living specimens of the former were obtained from Plymouth. The burrowing habits of both species were studied, but only the organs in the mantle cavity of the larger *G. tellinella* are figured (figure 6). The foot is powerful and somewhat pointed like that of *Donax vittatus*. The musculature has been described by Graham (1934*b*); there is no elevator pedis muscle. Burrowing is rapid, but the animals appear often to assume a final position oblique to, and not at right angles to, the surface.

The inhalant siphon usually projects obliquely but with the opening well clear of the bottom as shown in figure 16*c*. It is widely open and, like that of *D. vittatus*, trumpet-shaped with the six terminal lobes bent outward. These are not pinnate and there are no additional tentacles as in *D. vittatus*, but each is pointed like a tentacle and represents the termination of a line of small tentacles that run along the entire length of the siphon as shown in figure 6. Similar rows of tentacles are present on the exhalant siphon. This siphon projects vertically (figure 16*c*) with the opening normally somewhat constricted. The animals collect food in much the same manner as in *D. vittatus*, although the inhalant siphon is held nearer to the bottom so that greater quantities of sediment will be taken in. This is borne out by reports of examinations of the stomach contents (Hunt 1925).

The structure of *Gari tellinella* (and that of *G. fervensis* is not significantly different) is shown in figure 6. The main points of difference from *Donax vittatus*, which it resembles more clearly than members of the first two families, are the still smaller palps, the plications of the gills (which otherwise have the same structure and ciliary currents as those of *D. vittatus*) and the accumulation of pseudofaeces at the posterior end of the mantle cavity. But there are no mantle folds or ventral channel.

(*b*) *Solecurtus chamasolen* (*antiquatus*). This is the first of two species of this most interesting genus to be examined, the other being reported on separately. Both were obtained from Plymouth and examined alive at Millport. *S. chamasolen* is elongated, a typical shell being 5 cm. long and 2·3 cm. deep. The shell is covered with thick and dark brown periostracum. The animal is confined to substrata of stiff homogenous black mud and is sublittoral, extending from 4 to 50 fathoms (Jeffreys 1863).

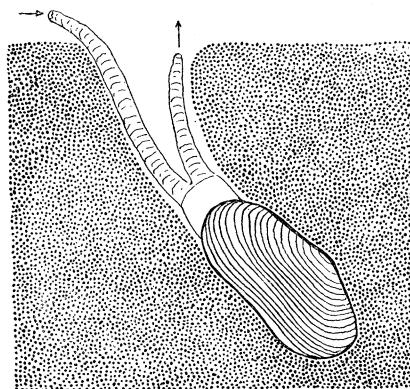


FIGURE 7. *Solecurtus chamasolen*, animal *in situ* in mud (magn. $\times \frac{1}{2}$).

The animal burrows almost vertically by means of the very massive foot which, when fully expanded, is more than equal in size to the shell. Owing to the restriction of the pedal aperture to the anterior half of the body, as shown in figure 8, the foot is extruded anteriorly. In the aquarium, animals burrowed to depths somewhat greater than the length of their shells, so forming a pit in the mud and through this common passage, and not separately, the two siphons, which are conspicuously wider than in any of the previous species, extend to the surface. The condition shown in figure 7 appeared to be the usual one, although from time to time the inhalant siphon was observed to extend for some distance along the surface of the mud. Both siphons are about 0·5 cm. in diameter at their tips and appreciably

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wider near their point of fusion which, when the animal was fully expanded, as shown in figures 7 and 8, was about 1 cm. beyond the posterior margin of the shell. The maximum observed lengths of the siphons were 10 and 7 cm. for the inhalant and exhalant ones respectively. The apertures of both are bounded by six very blunt lobes representing the termination of a corresponding number of opaque lines which run along the siphons as in *Donax*. The surface (although not the aperture) is also covered with many minute tentacles as described and figured by Morse (1919) in *Solecurtus gibbus*. The inhalant siphon lies widely open; no active groping movements were observed, the siphon behaving as do those of *Donax* and *Gari* but lying upon and never projecting above the substratum. An animal removed from its burrow and immediately opened had much mud in the mantle cavity, indicating indiscriminate intake from the surface of the substratum.

The greatly modified structure of *Solecurtus chamasolen* can be seen from the ventral view of an expanded animal (anaesthetized with urethane) shown in figure 8. As in all Tellinacea, the periostracal grooves and the middle mantle lobes (ML) remain free throughout, but the inner lobe (IL) is fused over a wide area instead of merely at the base of siphons. Fusion extends from about the middle of the ventral surface anteriorly to a point 1 cm. posterior to the shell when the animal is expanded (figure 7, also shown diagrammatically in figure 20*b*). The cruciform muscle (CM) moves forward so that it comes to lie in the middle of the ventral surface where there is a characteristic inward curvature of the shell valves, probably due to the constraining influence of these muscles (see figure 8). The pedal aperture is thus confined to the anterior half of the mantle cavity, while this is extended posterior to the shell; the gills, as shown in figure 9, continuing posteriorly to the point where the siphons separate. The siphons are thus *not* united at their bases; it is the posterior extension of the fused inner mantle lobes (PM) (shown also in figure 20*b*) which increases the capacity of the mantle cavity so that it extends, when the animal is expanded, beyond the posterior limits of the shell.

The fused inner mantle lobes (figures 8 and 19) are extremely wide with a corresponding elongation of the cruciform muscles. The shell valves separate widely when the adductors relax, and even when they are contracted the shell gapes at both ends. The adductors may contract independently, the shell rocking on the hinge, the teeth of which are small enough to permit of some lateral movement. Owing to the wide separation of the periostracal groove from the outer lobe of the mantle edge (figure 19, PG, OL), the marginal area around the shell which is covered only by periostracum is here exceptionally wide, as shown in figures 8 and 19 (P). This area forms a horizontal platform ventrally and a narrower vertical one anteriorly and posteriorly when the shell is open. When this closes these marginal areas, then intucked, everywhere meet and so protect the retracted siphons and foot. The arrangement is reminiscent of that in the protobranch, *Solenomya togata*. But in that animal the intucking of the uncalcified mantle margins when the shell closes, by reducing the internal volume of the mantle cavity, appears to be concerned with the expulsion of the great amounts of sand which there accumulate (Yonge 1939). The middle mantle lobes are small and lie just within the periostracal groove (figure 19, ML); they carry a double row of very short tentacles.

Within the mantle cavity the organs, though elongated, are in all fundamental respects similar to those of *Gari* (cf. figures 6, 9). The plicate gills have the same essential form and

the same system of ciliary currents apart from a posteriorly directed current along the base of the outer demibranch. The palps are of moderate size. The inner mantle lobe extends as a well-pronounced ledge around the pedal gape. Pseudofaeces are carried back to the base of the siphons, i.e. some distance beyond the shell.

(c) *Solecurtus scopula (candidus)*. Specimens of this species were also received alive from Plymouth, but, unfortunately, failed to burrow, so that observations are confined to their general structure and ciliary currents. Graham (1934*b*) has given a general account of this species to which only certain points need to be added. It differs from *S. chamasolen* in the white colour of the shell, in the habitat of clean shell gravel, and in the still greater fusion of the inner mantle lobes. The latter has resulted in the further reduction of the pedal aperture anteriorly (figure 10), the margins of which were observed to be very mobile in life, and in the much greater posterior extension of the mantle cavity behind the shell when the animal is expanded as shown in figure 10 (PM). As noted above, it is more satisfactory to regard this region, almost as long as the shell, as an extension of the mantle cavity rather than as the fused base of the siphons as Deshayes* (1848) and Graham (1934*b*) describe it. The gills extend along it up to where the siphonal tubes originate (figure 11). These are relatively short (although it is possible that they extend further when the animal is normally buried). As stated by Graham, they are marked with annular grooves (shown in the figures), and their surfaces are covered with many minute irregularly arranged tentacles (not figured). The apertures are fringed with the usual six blunt lobes.

The fused tissues are even wider ventrally than in the other species, the shell valves open correspondingly further and the cruciform muscle is still longer. The problem of the withdrawal of the great mass of posteriorly extended tissues (as in *S. chamasolen* but to a greater extent) is solved by an intucking along the posterior line of attachment of the inner mantle lobes which is indicated by the broken line in figure 10. After this the adductors contract, and the marginal areas of the mantle covered with periostracum, although narrower than those in *S. chamasolen*, fold over the tissues in the same manner as in that species. The middle mantle lobe bears several rows of small tentacles.

Apparently the ligament is very powerful because the shell valves readily gape, while after fixation they flatten out owing to stretching of the adductors by the elasticity of the ligament. From observations in life it appears that the pressure of the substratum, in which the animal will normally be buried, is needed to maintain the shell valves in their normal position, the powerful ligament normally acting against this pressure. Atkins (1937*c*) has postulated such a need in *Ensis*, the fused ventral mantle margins of which eventually split when animals are removed from the substratum. In very deep burrowers, such as *Mya* and *Lutraria*, the ventral mantle margins are greatly enlarged and probably, when filled with blood, assist the ligament in pushing the shell valves apart against the still greater pressure of the substratum.

Within the mantle cavity the organs are essentially similar to those of *Solecurtus chamasolen* only somewhat more extended longitudinally as shown in figure 11. The ciliary currents have already been described and figured by Graham (1937), and they resemble those of the other species. The gills are plicate with a supra-axial extension of the outer and smaller

* The magnificently illustrated work of Deshayes contains much anatomical information about a variety of species of the Tellinacea.

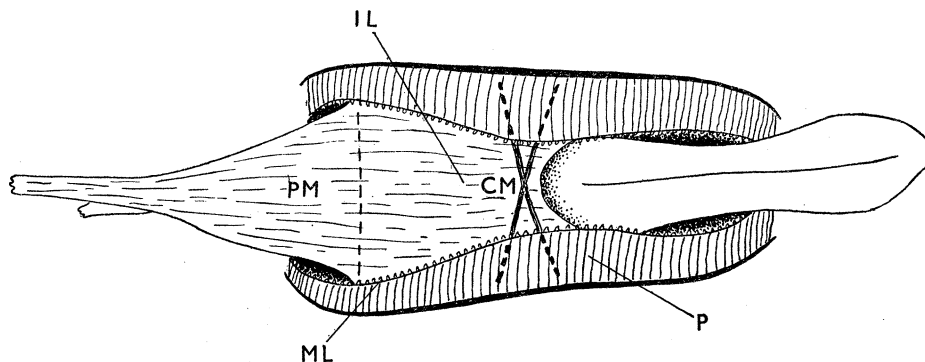


FIGURE 8. *Solecortus chamasolen*, viewed from ventral side with foot and siphons partially extruded (magn. $\times 2$). CM, cruciform muscle; IL, fused inner lobes of mantle edges; ML, middle lobe of mantle edge bearing short tentacles; P, periostracum covering wide area within margin of shell; PM, posterior extension of fused inner mantle lobes. Broken line across base of siphonal space indicates line of intucking when siphons withdrawn.

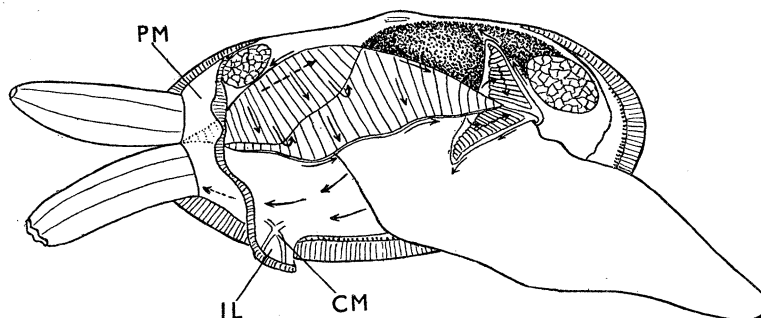


FIGURE 9. *Solecortus chamasolen*, from right side (magn. $\times 1\frac{1}{2}$). Lettering as in figure 8; other parts as indicated in figure 1.

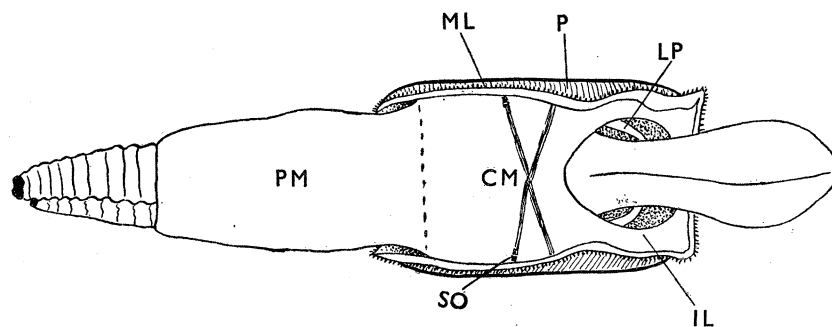


FIGURE 10. *Solecortus scopula*, from ventral side with foot and siphons extruded (magn. $\times 1$). IL, inner lobe of mantle edge bordering pedal gape (fused posterior to this); LP, labial palp; SO, sense organ in cruciform muscle. Other lettering as in figure 8.

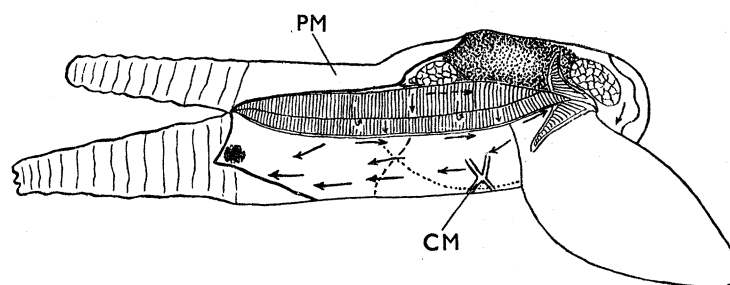


FIGURE 11. *Solecortus scopula*, from right side (magn. $\times 1$). Dotted line indicates ventral and posterior borders of shell, broken line region of intucking when siphons withdrawn. Lettering as in figure 8; other parts as indicated in figure 1.

demibranch. Pseudofaeces pass back to the base of the inhalant siphon, i.e. along the full length of the posterior extension of the mantle cavity, and there collect for periodic extrusion. Kellogg (1915) has given a brief account of the currents in the mantle cavity of the allied *Tagelus californianus*, where they appear to be essentially similar apart from an oralward current along the ventral edge of the outer as well as the inner demibranch.

III. SPECIAL ADAPTATIONS

It has already emerged that the Tellinacea possess a variety of characteristic features, and the more important of these will now be discussed and comparisons made between conditions in the various families and genera. All represent adaptations of the typical eulamellibranch structure which enable members of the Tellinacea in varying degree to collect bottom deposits and utilize these as food. Quantities of material which, if allowed to enter, would completely clog the mantle cavity and ctenidia of the typical suspension-feeding lamellibranchs, are quickly and effectively dealt with in the Tellinacea. The prime structures involved are the siphons. These need to be free from one another, or the inhalant siphon could not effectively grope for and draw in large quantities of material without interference from (and interference with) the exhalant siphon. Their formation exclusively from the muscular inner lobe of the mantle edge may well explain their great mobility, while there is a striking absence of the straining tentacles present in many suspension feeders.

With this characteristic form of the siphons are associated the cruciform muscle with its sense organ, the great development of the foot, special features in the structure or size of the ctenidia and palps, modifications concerned with the collection before ejection of the pseudofaeces, and finally various features of the gut, notably in the form and action of the stomach. These organs will now be considered in the necessary detail.

(1) *Siphons*

The characteristic mode of formation of the siphons by fusion of the inner lobes of the mantle edges only can best be indicated by reference to figures 12 and 14. Posterior to the cruciform muscle (the nature of which is considered in the next section), the outer and middle lobes continue uninterrupted around the posterior margin of the shell. Thus the siphons arise at the base of a deep embayment known as the siphonal space (Ghosh 1920; Graham 1934*a*). As noted briefly elsewhere (Yonge 1948*a*), in other lamellibranchs the siphons may also incorporate the middle or sensory lobe, possibly as in genera such as

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Pholadidea.* In other genera, e.g. *Mya*, *Spisula* and *Lutraria* (Yonge 1948c), the periostracal groove is also incorporated and a flexible protective covering provided while the openings of the siphons are fringed with an outer ring of sensitive tentacles with an inner ring of straining tentacles or a marginal membrane (figure 16e) around the inhalant and exhalant openings respectively. Finally, in the extreme case of the septibranch genus, *Cuspidaria*, all lobes of the mantle edge are concerned so that the fused siphons are protected within a posterior tubular extension of the shell.

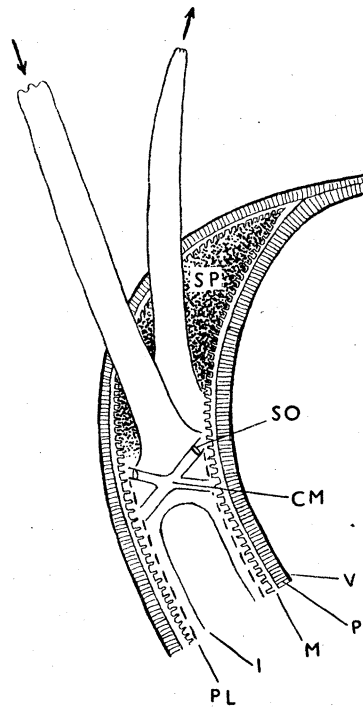


FIGURE 12. Semi-diagrammatical representation of mode of formation of siphons in the Tellinacea.

CM, cruciform muscle; I, inner lobe of mantle edge; M, middle lobe; P, periostracum; PL, pallial line; SO, sense organ associated with cruciform muscle; SP, siphonal space; V, margin of shell valve.

In the Tellinacea, maximum mobility is achieved, and there are no straining tentacles as in the siphonate suspension feeders with a resultant capacity for indiscriminate intake of bottom deposits with suspended material. Great extension is produced by forcing blood into the sinuses, withdrawal by contraction of the highly developed siphonal retractors which spread out, fan-wise, over wide areas of the shell as shown in figures 14 and 15. The great activity of the siphons, involving, especially in the Tellinidae and Semelidae, continuous changes both in length and diameter, may be attributed to the arrangement of their intrinsic muscles.

Throughout the Tellinacea the siphons have a characteristic appearance in cross-section. Rawitz (1892), in an account of those of *Psammobia vespertina* (*Gari depressa*), describes them

* But *not* in the Veneracea or the Cardicea as previously suggested (Yonge 1948a). There the short fused siphons are composed of the inner mantle lobes only, although, correlated with suspension feeding, tentacles are well developed and the intrinsic muscles are not separated into such distinct layers as they are in the Tellinacea.

as consisting, in order from the inner epithelium to the outer, of the following muscle layers: thin circular (constrictor), inner longitudinal (retractor), second circular about twice the thickness of the first, outer and very massive longitudinal, third circular, sparse longitudinal, small circular. Graham (1934*b*) describes all but the last of these in *Gari tellinella*, but it is certainly present, though very narrow, in *G. fervensis*. Thin connective tissue may separate these muscle layers. There are also radially arranged muscle strands (termed compressors by Rawitz) which run from one epithelium to the other and which separate the two middle, and much the largest, longitudinal muscle layers into a series of sharply defined bundles (see figure 13). Examination of transverse sections of the siphons of species of all genera studied in this research has revealed that, with variations in the

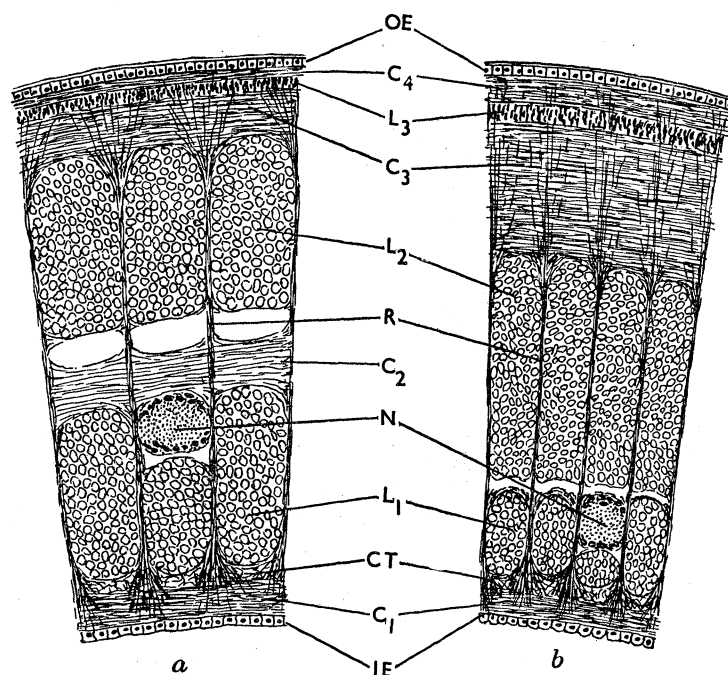


FIGURE 13. Transverse sections through portions of the inhalant siphons of *a*, *Donax vittatus* (magn. $\times 14$); *b*, *Scrobicularia plana* (magn. $\times 22$). C_1 to C_4 , layers of circular muscle; CT, connective tissue; IE, OE, inner and outer epithelium; L_1 to L_3 , layers of longitudinal muscle; N, one of six nerves; R, radial muscle.

thickness of the various layers, the conditions described by Rawitz prevail in *Donax vittatus*, *Gari fervensis*, *Solecortus chamasolen* and *S. scopula*, and differ in the Tellinidae and Semelidae only in the absence of the middle layer of circular muscles (figure 13, C_2) between the two major longitudinal layers (L_1 , L_2). Conditions in *Donax* and *Scrobicularia*, representative of the two groups, are shown in figure 13*a, b*. This separation of the muscle layers in the Tellinacea is in sharp contrast to their intermingling in the siphons of suspension-feeding eulamellibranchs. It may not unreasonably be correlated with the need for continuous movements of the entire siphons and also localized activity within these.

The epithelia bounding the inner and outer surfaces (IE, OE) are never ciliated, that of the outer surface bears a cuticular margin which is particularly well developed in *Gari* and *Solecortus*. Rawitz described numerous mucous glands beneath the outer epithelium in *Gari depressa* and under both epithelia in *Solecortus strigillatus*. The same is true respectively

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of *Gari fervensis* (though the glands are sparse) and of *Solecurtus chamasolen* and *S. scopula*. They are especially numerous under the outer surface in *S. chamasolen* and under the inner surface in *S. scopula*. No mucous glands have been found under either epithelium in any of the other species.

The arrangement of the nerves is also characteristic. In every species examined there are six nerves (though Rawitz reports the occasional presence of eight in *Gari depressa* and Hoffmann found eight in *Tagelus dombeyi*). They terminate in the six siphonal lobes. Their position is constant, namely, at evenly spaced intervals within the inner zone of the area occupied by the inner of the two major layers of longitudinal muscle (figure 13, N). The general disposition of the nervous system in *Gari tellinella* has been described and figured by Graham (1934*b*). As shown by Rawitz, the siphons of *Gari* and *Solecurtus* bear six longitudinal rows of sense organs corresponding in position with the lines of the six nerves.

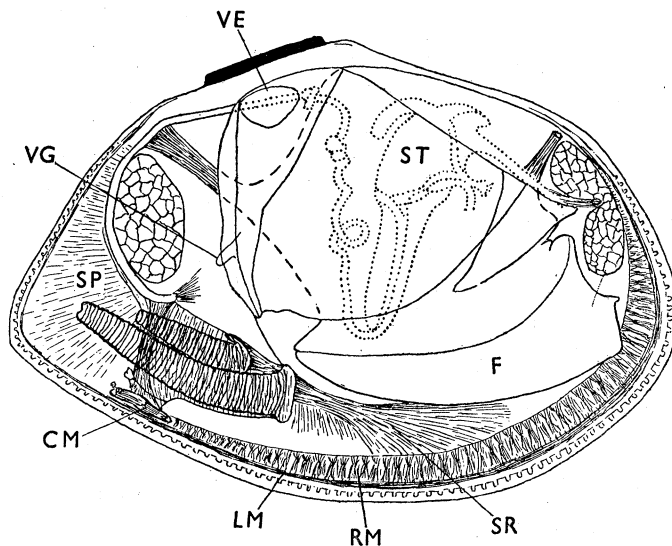


FIGURE 14. *Tellina tenuis*, drawing of cleared and stained specimen, with siphons fully withdrawn, from right side (magn. $\times 5$). LM, RM, longitudinal and radial muscles of mantle edge; SR, siphonal retractor; ST, stomach; VE, ventricle; VG, visceral ganglion. Other lettering as before. Alimentary canal indicated by dotted lines.

Each sense organ consists of a rounded bud lying within a slight depression and carrying a series of sensory cells with associated ganglion cells and nerve fibres. These organs are absent in *Donax* and in the Tellinidae and Semelidae. Rawitz further described the presence in *Gari depressa* of small sensory structures, each consisting of two supporting cells and one sensory cell, on the surface of the lobes around the siphonal openings. Simple unicellular sense organs are also scattered thinly over the outer surface of the siphons. In other Tellinacea examined he found only these unicellular sense organs, particularly on the marginal lobes. These observations have been confirmed. Rawitz suggested that the simpler sense organs are concerned with tactile stimuli and those of the longitudinal rows in *Gari* and *Solecurtus* with the detection of more delicate water movements. Compared with those of typical suspension feeders, the siphons of the Tellinacea in general are very insensitive, but they do react to tactile stimuli above a certain intensity, those of the Asaphidae (and to a less extent those of *Donax*) being more sensitive than those of the other

families. There seems no reason for ascribing other than tactile functions to any of these sensory structures.

There is a further difference between the siphons of the Tellinidae and Semelidae and those of the other two families. In the first group, for instance in *Tellina tenuis* (figure 14), the very extensile siphons are connected with the mantle surface by way of a very thin, non-muscular but elastic membrane. This forms a sheath around their bases when the siphons are extended, as in figure 1, but allows these to be withdrawn for a considerable distance anterior to the cruciform muscle which represents morphologically their point of origin. This condition is shown in figure 14 and also diagrammatically in figure 17. It may be correlated both with the great length of the siphons in species of these families and also with the very limited space available between the greatly compressed shell valves. With it is associated a narrowing of the retractor muscles before they enter, as separate bundles, the two siphons. The contrast between conditions in *Donax vittatus* and *Scrobicularia plana* is shown in figure 15, and the appearance in cross-section of the posterior region of the siphonal retractor in *Abra nitida* in figure 23.

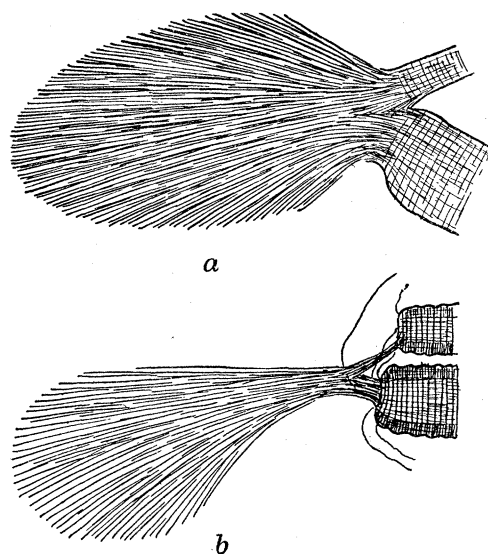


FIGURE 15. Surface views of left siphonal retractors of *a*, *Donax vittatus*; *b*, *Scrobicularia plana*, showing insertion into base of siphons (magn. $\times 6$).

In the other two families the siphons are much wider but relatively much shorter, and at their bases they blend, without intervention of such membranous tissues, with the mantle lobes. The shell valves are also less compressed so that the siphonal space is adequate, at any rate in *Donax* and *Gari*, for housing the contracted siphons. In *Solecurtus scopula* and to a somewhat less extent in *S. chamasolen*, the massive nature of the siphons and the extensive fusion of the very wide inner mantle lobes raises a problem of accommodating the retracted tissues which is met by the intucking of the fused inner mantle tissues as indicated in figures 8 and 10. But the mass of the retracted siphons and intucked mantle tissues is such that they are only with difficulty accommodated within the shell by the aid of the mantle margins covered with periostracum.

This difference between the siphons in the two groups is associated with differences, discussed later, between their ctenidia and in the mode of accumulation of pseudofaeces.

But these are the consequences of the differences in the lumina of the siphons and so of the strength of the resultant inhalant current. In the Tellinidae and Semelidae, where the inhalant siphons are very narrow, the inhalant current caused by the beating of the lateral cilia on the ctenidia is concentrated to such an extent that, especially in *Abra* and *Scrobicularia*, it enables the bottom material to be literally torn off and sucked in. In the Donacidae and Asaphidae, where the siphons are relatively much shorter and wider, the current is less concentrated and correspondingly less powerful. Hence only the loose surface deposits with suspended material are taken in although much more freely and in far greater quantity than in the true suspension feeders. Comparisons between the siphons in all genera except *Solecortus* (see figure 7) together with those of a suspension feeder are shown in figure 16.

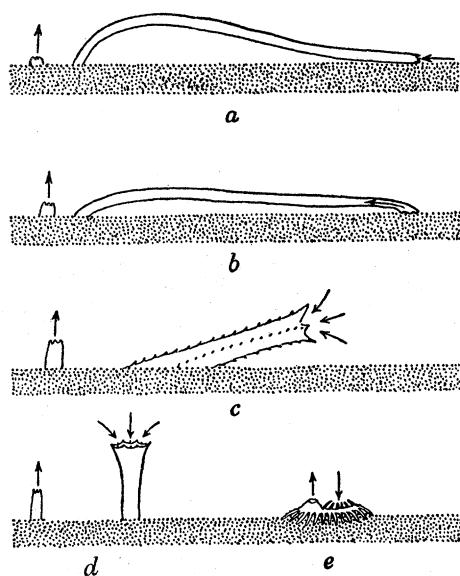


FIGURE 16. Appearance of siphons above substratum in *a*, *Tellina* and *Macoma*; *b*, *Abra* and *Scrobicularia*; *c*, *Gari*; *d*, *Donax*; *e*, suspension feeder such as *Mya*. Varying magnifications.

(2) *Cruciform muscle and associated sense organ*

The cruciform muscle (figures 17 to 19) consists of two compact bundles of transversely running fibres which stretch diagonally between the shell valves running through one another in the middle of their lengths. These fibres probably represent specialized areas of the radial muscle (figure 14, RM) attached along the pallial line and extending into the inner mantle lobe or pallial curtain as shown in figures 19 and 23. The cruciform muscle lies at the anterior extremity of the posterior fusion of the inner mantle lobes and so immediately ventral to the base of the siphons. Only in *Solecortus* and related genera are conditions somewhat different owing to the extensive fusion of these lobes of the mantle. Dorsal to the cruciform muscle, further modification of the pallial muscles gives rise to the massive siphonal retractors previously discussed.

The cruciform muscle occurs only in the Tellinacea, and it seems reasonable to associate its presence with the formation of long, free siphons together with a pedal gape of maximum size. This involves a very localized area of attachment to the mantle (except in the special case of *Solecortus*). Although other Eulamellibranchia, e.g. the Veneracea, have an equally

extensive pedal gape, the fused siphons are not so long, while the animals are much less active burrowers.

Various theories have been advanced about the function of the cruciform muscle. They have been reviewed by Graham (1934*a*) who has added his own. Von Ihring (1901) considered that it acted as an additional adductor of the shell valves; both Hoffmann (1914) and Graham (1934*a*) consider it as essentially only a part of the sense organ present near the posterior attachment of each muscle. Graham rightly dismisses the theory of Von Ihring, pointing out that a simple transverse band of muscle would be as efficient, or more efficient, for this purpose. It might be added that the existing adductors are large and powerful (again less so in *Solecurtus*). The views of Hoffmann and of Graham will be discussed later when considering the sense organ. But it does not seem reasonable to subordinate the cruciform muscle to the associated sense organ. The muscle must have preceded the sense organ, and its presence can reasonably be explained without immediate reference to the sense organ.

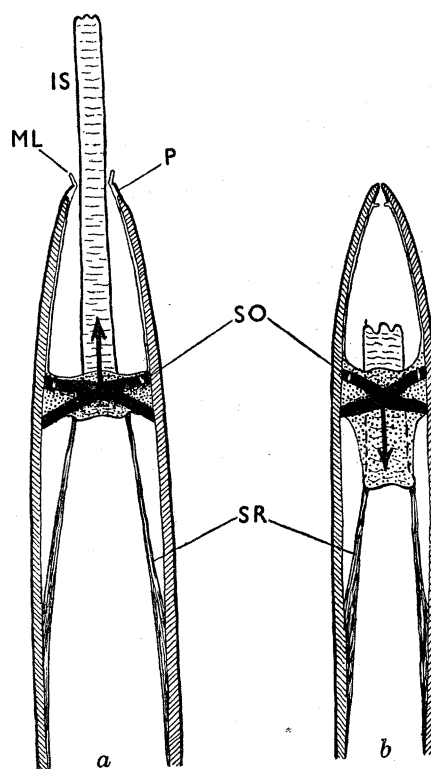


FIGURE 17. Ventral view (semi-diagrammatical) of the attachments of the inhalant siphon in the Tellinidae and Semelidae, showing how the cruciform muscle acts as a tie taking both the backward strain when the siphon is extruded (*a*) and the forward strain when it is withdrawn (*b*). Lettering as before.

As indicated in figure 17, the cruciform muscle can best be regarded as a tie which takes the strain both of the backward pull due to blood pressure when the siphons are extruded (figure 17*a*) and the forward pull due to the contraction of the siphonal retractors when the siphons are withdrawn (figure 17*b*). The disposition of the crossed muscles when fixed in contraction is shown in figure 18. The anterior ends are pulled forward. The cruciform arrangement now becomes explicable, the anterior attachments take the strain when the

siphons are extruded and the posterior attachments when they are withdrawn. The crossed muscles are certainly more effective for this purpose than would be a single transverse band. The extent to which the siphons can be extended, especially in the Tellinidae and Semelidae, and the force with which they must be pulled back by the siphonal retractors (see figure 14) both demand a secure zone of attachment. The great size of the foot (see next section) involves a pedal gape of maximum size. Hence the area of attachment of the siphons ventrally is reduced to the minimum. Within this area crossed strands of muscle represent the most efficient means of attachment to the ventral margins of the shell. Their presence influences the form of the shell in the area of attachment where there is a characteristic kink in many species of the Tellinacea.* The special case of *Solecortus* will be considered after discussing the possible function of the sense organ.

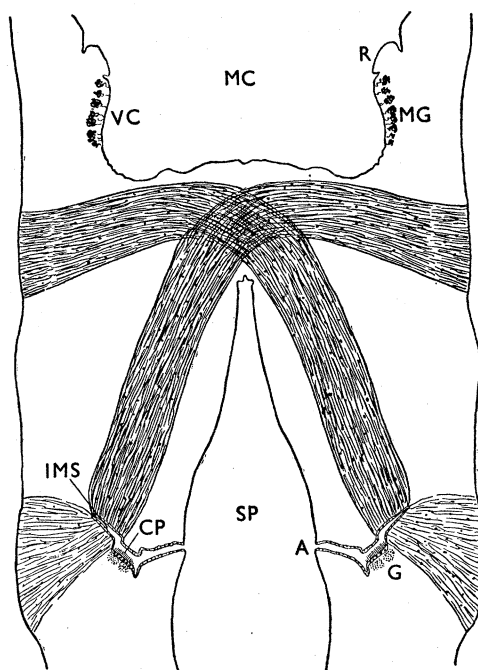


FIGURE 18. *Scrobicularia plana*, cruciform muscle in horizontal section (reconstructed from a series of sections) showing details of sense organ; fixed when siphons withdrawn hence the anterior pull on the muscle (see figure 17*b*) (magn. $\times 30$). A, external opening of sense organ; CP, ciliated pit; G, ganglion below sensory epithelium of sensory pit; IMS, intramuscular slit; MC, mantle cavity; MG, mucous glands; R, ridge bounding ventral channel (VC); SP, siphonal space.

Graham (1934*a*) has described the structure of this sense organ in *Tellina crassa*, *Macoma balthica*, *Scrobicularia plana*, *Donax vittatus*, *Gari tellinella* and *Solecortus scopula*. As shown in figures 18 and 19*c*, it consists of a slit (IMS) near the posterior attachment of the muscles, thus partially separating these into two portions. This slit is in free communication with a ciliated pit (CP) which is lined in part with a sensory epithelium. Beneath this is a ganglion (G) which is connected with the visceral ganglion by way of a branch of the posterior pallial nerve. Graham has also shown that in *Tellina*, *Gari* and *Solecortus* (figure 19*c*, A) this pit opens directly to the exterior, in *Macoma* by way of a short duct and in *Scrobicularia*

* There is an asymmetry in the attachment of the cruciform muscle in *Tellina assimilis* in which the right siphonal retractor is also only half the size of that on the left (Pelseneer 1911).

(figure 18, A) by way of a longer one. In *Donax*, however, there is no external opening and this appears also true of *Tagelus dombeyi*.

In the last species, Hoffmann (1914) thought that the ciliated pit opens into a blood sinus and that the function of the sense organ is to detect and regulate the blood pressure in the region of the siphons. But, as Graham points out, his conclusions were probably based on

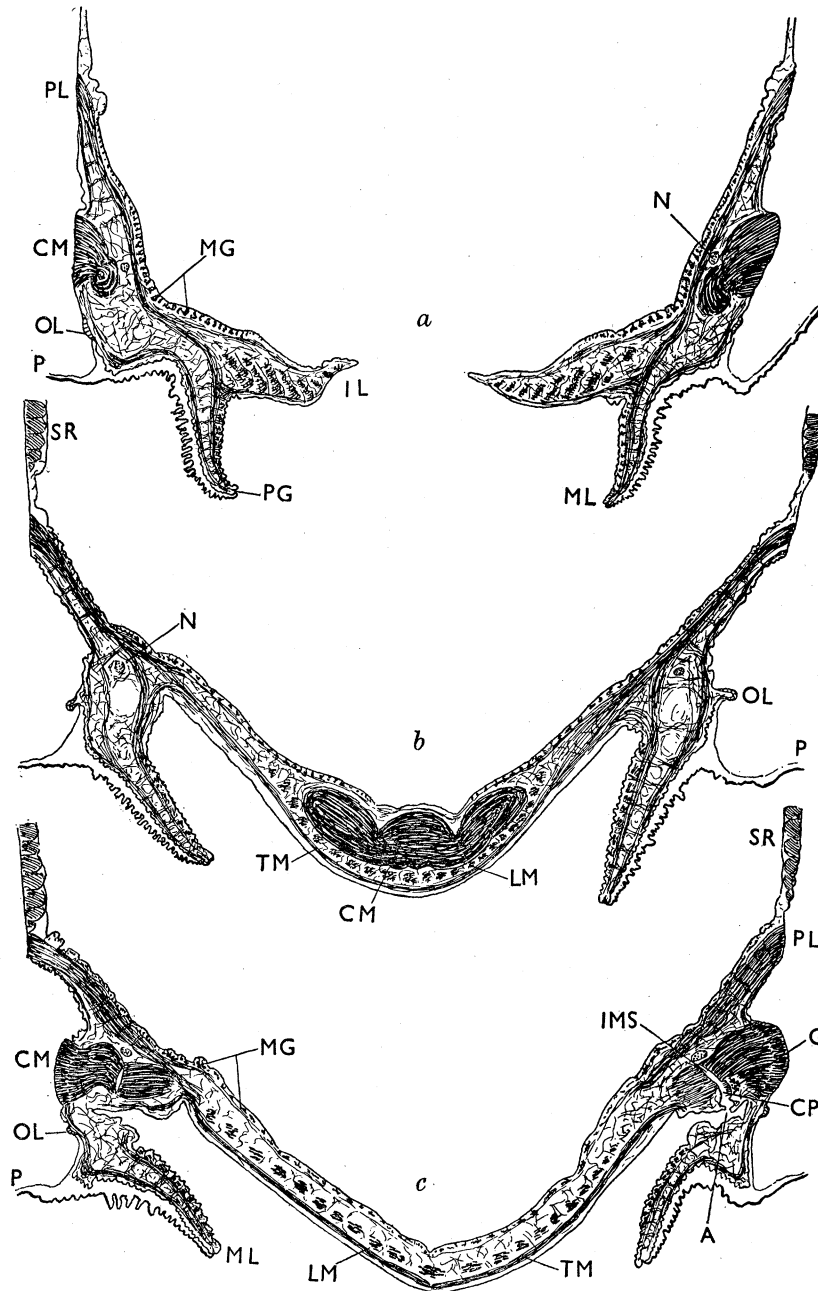


FIGURE 19. *Solecurtus chamasolen*, transverse sections through mantle margins, *a*, anterior to fusion of inner lobes and showing anterior insertions of cruciform muscle; *b*, more posterior where inner lobes fused and cruciform muscle crossing; *c*, farther posterior showing posterior insertions of cruciform muscle and sense organ (magn. $\times 15$). LM, longitudinal muscle; N, pallial nerve; OL, outer lobe of mantle edge (represents position of ventral margin of shell); PG, periostracal groove adjacent to middle mantle lobe (ML); PL, pallial line; TM, transverse muscle. Other lettering as before.

faulty sections. There is certainly no such communication with the blood sinuses in any other species examined. Graham himself considers that the sense organ is concerned with testing water and that the cruciform muscle is purely the agent whereby the organ is opened and closed. This theory is very unconvincing; Graham admits the difficulty of reconciling this function with the absence of an external opening in *Donax* and probably in *Tagelus*. Moreover, even where it does open to the exterior, the sense organ merely communicates with the water in the siphonal space (in *Solecurtus* (figure 19c) with that on the ventral side of the body). The nature of the water there may be very different from that brought in through the inhalant siphon. In the cases, for instance, of *Macoma balthica* and *Scrobicularia plana*, the animals are buried, often from 10 to 20 cm. deep, in black mud or muddy sand where the presence of sulphur bacteria indicates absence of oxygen and where the water must usually be very foul. But the siphons are drawing in well-oxygenated and clear water from above the surface of the mud. The animal cannot gain anything by testing the water deep in the substratum where the body lies.

The sense organ has certain resemblances to the otocyst which also consists of a pit lined with sensory epithelium and which is open to the exterior in many protobranchs and certain filibranchs and closed in the remainder of the Lamellibranchia. It would seem best regarded as a proprioceptor. When the siphons are extended the backward pull on the cruciform muscle will tend to stretch the anterior and shorten the posterior halves of the two muscles (figure 17c). This will have the effect of closing the intramuscular slit with consequent passage of water into the ciliated pit, to be passed on to the exterior or else to dilate the pit where there is no external opening. When the siphons are withdrawn the anterior halves of the muscles will be shortened and the posterior halves pulled out with resultant opening of the intramuscular slit as shown in figure 18. Water will then enter from the ciliated pit. These water movements over the surface of the sensory epithelium in the pit will take place no matter whether this opens to the exterior or not.

It remains to consider what function this possible proprioceptor may serve. On the above explanation of its mode of operation it should provide evidence about the extent to which the siphons are at any time extended or withdrawn. This may be of value in one of two ways. The length of the siphons, particularly in the Tellinidae and Semelidae, and their bulk in *Solecurtus*, is such that an appreciable time must be allowed for their withdrawal before the adductors can contract without nipping them between the posterior margins of the shell. This danger, however, may be overcome by some co-ordination between the contractions of the siphonal retractors and those of the adductors. The other and more probable alternative has to do with the presence in the Tellinacea of *both* very large siphons and a very large foot. Both of these demand much blood for their extrusion, and only when blood has been withdrawn from the one is it available for the other. The contrast, to be discussed at greater length in the next section, between *Ensis*, in which the foot alone is large, *Mya* or *Lutraria*, in which the siphons alone are large, and the Tellinacea, in which both are large, is shown in figure 21. These animals react to danger by immediate movements of the foot in the first case and by those of the siphons in the second. But the Tellinacea first withdraw the siphons and then descend deeper into the substratum by means of the foot. A not unreasonable view is that the sense organ in the cruciform muscle is a proprioceptor which, by providing information about the state of contraction of the siphons, enables the animal

to transfer blood into the foot at the precise moment when adequate quantities are available.

The special conditions in *Solecurtus* (here, on the authority of Mr R. Winckworth, considered to include the two genera *Zozia* and *Solenocurtus* listed by Thiele (1935)), may best be considered in relation to those in allied genera. In *Tagelus*, where the shell is similarly elongated with the dorsal and ventral surfaces parallel and the animal is large, the siphons arise direct from the point of fusion of the inner mantle lobes essentially as in *Gari*. The pedal gape is similarly of maximum size (figure 20 *a*) and the cruciform muscle lies below the base of the siphons (see Bloomer (1907) on *Tagelus gibbus* and *T. divisus*, Hoffmann (1914) on *T. dombeyi* and Kellogg (1915) on *T. californianus*). The major differences from *Gari* reside in the cylindrical form of the shell and foot, the latter apparently acting in much the same manner as that of *Ensis*. *Tagelus californianus*, which is up to 10 cm. long, lives in vertical burrows as deep as 40 cm. with separate openings up to 5 cm. apart, for the protrusion of the two siphons (Weymouth 1920). The foot is too large to be completely withdrawn, the animal apparently relying on deep withdrawal for safety.

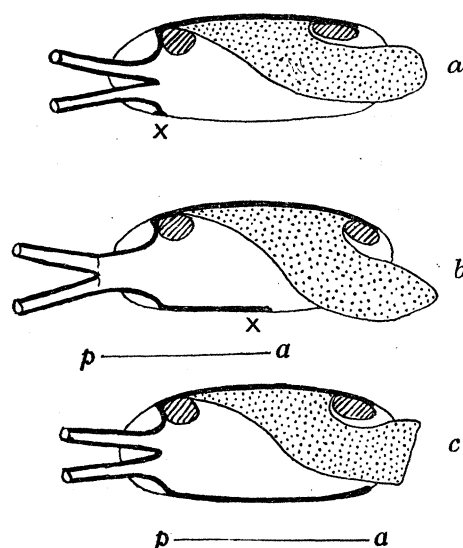


FIGURE 20. Longitudinal outlines of *a*, *Tagelus*; *b*, *Solecurtus*; *c*, *Novaculina* (after Ghosh 1920), showing extent of ventral mantle fusion (*a* to *p*) and position of cruciform muscle (X).

In *Solecurtus* the shell has the same elongate form but is rather less cylindrical. The foot is equally large, and this, together with the extensive posterior fusion of the inner mantle lobes, has tended to displace the adductors dorsally. The difficulty of withdrawing the siphons and especially the foot is considerable and is only partially met by the marginal extension of the periostracum, though to a greater extent in *S. chamasolen* (figure 8), where all the tissues can be withdrawn, than in *S. scopula* (figure 10) where they probably cannot. The habits of these animals are none too clear; *S. scopula* failed to burrow in the aquarium* and *S. chamasolen* may not have behaved entirely normally. It is possible that both may inhabit vertical burrows for which the form and anterior extrusion of the foot and the shape of the body would seem to fit them. The mucous glands in the outer walls of the siphons

* Atkins (1937*b*) observed a burrowing specimen 2.8 cm. long in which the inhalant and exhalant siphons were respectively 11.5 and 9 cm. in length.

might be concerned with the consolidation of the walls of a burrow. The broad fusion of the inner lobes of the mantle edge along much of the ventral surface (figures 8, 10, 19, 20*b*) is probably correlated with the feeble powers of the reduced and dorsally displaced adductors by preventing the shells from gaping too widely under pressure from the foot and siphons and by acting as additional adductors. As shown in figure 19, the fused tissues contain bands of transverse muscle fibres (TM) with more superficial ones running longitudinally (LM). The pressure of the substratum may also assist, especially if the animals inhabit burrows. The cruciform muscle is displaced anteriorly, as shown in figures 8, 10 and 20*b*. It certainly can no longer act as a tie for the siphons which now originate a considerable distance to the posterior. But it will probably still be affected by the outward or inward movement of the siphons so that the sense organ (figure 19*c*) can function in the same manner as suggested for the other Tellinacea. The only function left to the muscle, which is very massive, as shown in figure 19, is to prevent the shell valves from gaping too widely and to pull their ventral margins together when the shell closes. The cruciform muscle may here have some of the function originally suggested by Von Ihring (1901) but only in association with the other transverse fibres.

The subfamily Novaculininae was erected by Ghosh (1920) to include the one species, *Novaculina gangetica*, to which a second, *Sinonovacula constricta*, was added by Annandale & Prashad (1924). These authors, and also Thiele (1935), regarded these animals as primitive members of the family Solenidae. But study of the descriptions and examination of the figures given of them makes it clear that they should be included in the Tellinacea, probably as a subfamily of the Asaphidae. The siphons are separate (as in *Tagelus*), arise from the base of a deep siphonal space, are fringed only with tentacular lobes, and are covered with minute tentacles exactly as in *Solecurtus*. They are not capable of complete withdrawal. In the shell characters also and in the size and disposition of the adductors they further resemble the Asaphidae. The mantle margins are extensively fused along the ventral surface (figure 20*c*), leaving only a rounded anterior gape for the protrusion of the cylindrical foot which ends in a convex disk. In *Novaculina* these fused tissues are much broader laterally than in *Sinonovacula*, but in both they are much broader than in any of the Solenidae. There ventral fusion, although including only the inner lobe of the mantle edge, is exclusively cuticular, *not* involving the tissues, so that even the outward pull of the ligament when the animals are removed from the substratum will cause the fused areas to separate (Atkins 1937*c*). In the Novaculininae, although the point is nowhere stated in the descriptions because its significance was not realized by the authors concerned, there can be little doubt, when comparison is made with conditions in *Solecurtus*, that the broad band of ventral fusion is the result of complete fusion of the tissues.

A striking feature is the *absence* in both species of a cruciform muscle. With the extension of fusion along the entire ventral surface all reasons for its persistence must disappear. No longer necessary as a tie for the siphons in *Solecurtus*, in the Novaculininae the ventral fusion has extended so far forward that it is also no longer needed to reinforce the ventral attachment between the shell valves. Finally, anterior migration beyond a certain point will place it beyond the zone where it can be affected by the movements of the siphons so that the sense organ will become useless. Significant also in this connexion is the fact that the siphons cannot completely be withdrawn. Starting from conditions generally similar to

those now existing in *Tagelus*, the evolution both of *Solecurtus* and of the Novaculininae may be postulated on somewhat divergent lines, as indicated in figure 20. In *Solecurtus* (figure 20*b*), ventral fusion of the inner lobes of the mantle edges extends both posteriorly and anteriorly, so that the siphons appear to be fused at their bases while anteriorly the pedal opening is reduced, the cruciform muscle being retained. In the Novaculininae (figure 20*c*) there is no posterior fusion, but anteriorly this extends along the entire ventral surface and the cruciform muscle is lost. Conditions in this subfamily appear to provide additional evidence in support of the views here expressed about the nature and function of the cruciform muscle and its associated sense organ.

(3) *Foot and pedal gape*

The Tellinacea are characterized by the possession of a large and very active foot and with a correspondingly extensive pedal gape. This is particularly true of the Tellinidae and Semelidae where the great demands of the foot, here very compressed laterally and correspondingly elongated, may be regarded as a factor in reducing to a minimum the area of fusion of the two mantle lobes and so, perhaps, in the origin of the cruciform muscle. The animals have to reconcile the need for long, yet adequately attached, siphons and for a foot suitable for rapid and deep burrowing. In *Donax* and *Gari*, where the shell is somewhat more rotund, the foot is wider and the base of the siphons extends a little farther anterior with a slight reduction in the extent of the pedal gape. In both, although particularly in *Donax*, the foot is protruded more anteriorly than in the Tellinidae and Semelidae. Finally, in *Solecurtus*, where the shell is much wider, there is extensive fusion of the inner lobe of the mantle edges and the pedal gape is much restricted. Hence the more rounded foot is protruded anteriorly not unlike that of the Solenidae, to which members of this genus have the superficial resemblance which explains their former incorporation in this fundamentally very different family. Graham (1934*b*) has made a comparative study of the pedal musculature in the Tellinacea and shown that, apart from the additional elevator pedis muscle in *Donax vittatus*, it has a constant pattern. The anterior retractor pedis muscle has a single insertion in each valve and lies, in the foot, internal to the posterior retractor while the protractor pedis is well developed. In *Cultellus pellucidus*, taken as an example of the Solenidae, the anterior retractor has two insertions in each valve and, in the foot, lies external to the posterior retractor while the protractor is poorly developed and is indeed absent in some members of this family.

The Tellinacea are exceptional in the possession both of a large and active foot and often of very long siphons. Members of the Tellinidae and Semelidae are capable of burrowing as deeply as any bivalve relative to their size. It is illuminating to compare these animals with the Solenidae on the one hand and with such deep burrowers as *Mya*, *Lutraria* and *Panope* (all belonging to different families but having a common mode of life) on the other. In the Solenidae (figure 21*a*) the siphons are very short, but, by the aid of the highly specialized foot, the animals can retreat rapidly downward for protection against enemies or the effect of exposure at low tide. In the other genera (figure 21*b*) the adult is embedded permanently at a considerable depth (up to 90 cm. in the extreme case of *Panope generosa*) maintaining contact with the surface by way of the very long fused siphons which are encased in periostracum. The foot is much reduced, least in *Lutraria*, but atrophies in *Panope generosa*.

The animal itself is in no danger from enemies or from exposure, only the siphons need to be withdrawn. It is significant that all of these animals, the Solenidae included, are suspension feeders whose food is constantly being renewed by water movements so that the animals never need to change position.

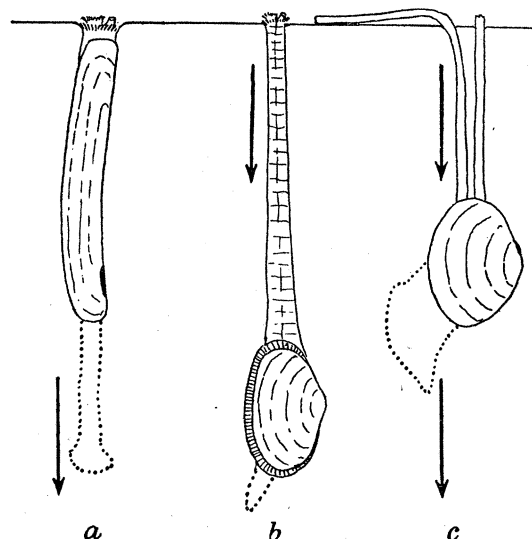


FIGURE 21. Positions *in situ* of *a*, Solenidae; *b*, *Mya* (as example of deep burrower); *c*, *Scrobicularia* (as example of Tellinacea). Extent of foot when protruded shown by dotted outline, arrows indicating movements in response to danger, in *c* withdrawal of siphons followed by movements of foot.

In the Tellinacea both siphons and foot are large and active. As indicated in figure 21 *c*, the former can be initially withdrawn and then the latter extended (though probably not simultaneously as already discussed), a problem which does not arise in the other cases (cf. figure 21 *a*, *b*). The Tellinidae and Semelidae, in particular, move above actively, most of the time vertically but in some also on occasion horizontally. The former movements enable them to escape enemies and, in the case of intertidal species such as *Tellina tenuis*, which may descend to depths of 12 cm., and *Scrobicularia plana*, which may be found 20 cm. below the surface, to counter the effects of wave action and of desiccation. The softness of the deposit-laden substrata in which the Tellinacea normally live is also a factor demanding mobility. Horizontal movements may permit the animals to exploit the local supplies of edible bottom deposits more thoroughly. The long and very vulnerable siphons of these deposit feeders combined with their mode of feeding demand accompanying powers of mobility conferred by a foot of maximum size and activity.

(4) *Ctenidia and palps*

The form of the ctenidia and the general course of the currents upon them has already been described and figured. Observations made here amount essentially to no more than a confirmation of the beautifully detailed work of Atkins (1937 *a*, *b*), on a selection of whose figures those given in figure 22 are based. It should be emphasized that the form of the gill and the course of the food-collecting currents upon it are *no* evidence of relationship. Thus Atkins (1937 *b*) has shown differences between the closely related *Barnea parva* and *Pholadidea loscombiana*, and between *Cultellus pellucidus* on the one hand and species of *Solen* and *Ensis* on the other. Similarly, in the Myacea, the gills of *Aloidis gibba* (Yonge 1947) differ from

those of *Mya arenaria*, the former resembling those, for instance, of *Pholadidea loscombiana* (Pholadidae) and the latter those of *Lutraria lutraria* (Mactridae). Clearly it is not relationship but habitat and the nature of the material carried in with the inhalant current that controls the form of the gill and the nature of its currents. Thus the views of Ridewood (1903) and of Pelseneer (1911) on the origin of the upturned outer demibranch in the Tellinidae and Semelidae, which are further discussed by Graham (1937), need not be further considered.

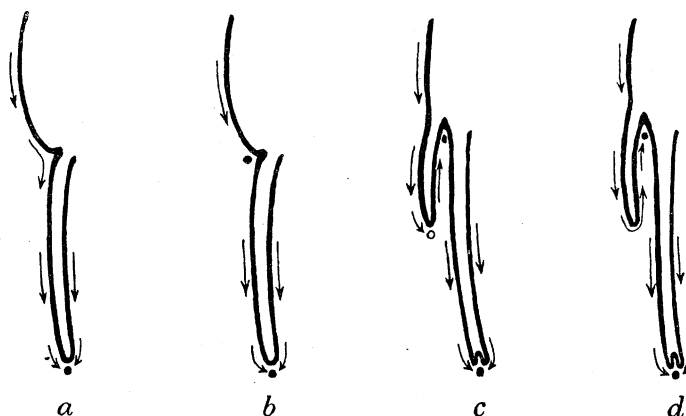


FIGURE 22. Diagrams showing the form in transverse section of, and the major ciliary currents on, one demibranch of *a*, *Tellina tenuis*, *T. fabula*, *T. donacina*, *Macoma balthica*, *M. secta* (Kellogg), *Abra alba*, *A. nitida*; *b*, *Tellina crassa*, *Scrobicularia plana*; *c*, *Donax vittatus*, *Gari tellinella*, *G. fervensis*; *d*, *Solecurtus chamasolen*, *S. scopula*. Arrows indicate direction of major currents, solid circles oralward currents, hollow circle incipient oralward current.

Throughout the Tellinacea the inner demibranch is well developed with currents on both faces carrying material to the margin where it is conveyed forward, but in respect of the outer demibranch the species here considered are divisible into the four groups shown in figure 22. Taking them in the same order as before, in the first group (figure 22*a*) the outer demibranch is upturned and consists of a single flat supra-axial surface, although in the Tellinidae the posterior region is somewhat recurved as originally described by Ridewood (1903). Particles are carried direct from the surface of the outer demibranch, over the axis, on to the outer face of the inner demibranch and so to the margin of this. This condition exists in all Tellinidae so far examined except *Tellina crassa*, namely, in *T. tenuis*, *T. fabula*, *T. donacina* and *Macoma balthica* (Atkins 1937*b* and here confirmed) and also in *M. secta* (Kellogg 1915). It similarly exists in all Semelidae examined except in *Scrobicularia plana*, i.e. in *Abra alba*, *A. nitida* (Atkins 1937*b* and here confirmed) and *Semele decisa* (Kellogg 1915). The same type of gill with similar currents is present in the Anatinacea (Ridewood 1903; Atkins 1937*b*). The second group (figure 22*b*) contains the two species *Tellina crassa* (Atkins 1937*b*; Graham 1937) and *Scrobicularia plana* (Atkins 1937*b* and here confirmed), which differ from the group of figure 22*a* only in the presence of a forward-running current along the gill axis.

In the remaining genera of the Tellinacea the outer demibranch is reflected but with a considerable supra-axial extension. Frontal cilia carry particles round the margin of this and up the inner face to the axis where there is a forward-directed current. In the third group (figure 22*c*) the ventral margin of the outer demibranch, although without a groove,

has what Atkins (1937*b*) describes as 'an incipient oralward current' owing to the presence here 'of coarse cilia on the posterior half of the frontal surface of each filament'. These terminal cilia create a slight longitudinal current although frequently forcing particles off the filament. This condition is found in *Gari tellinella* and *G. fervensis* and in *Donax vittatus* (Atkins 1937*b* and here confirmed), as well as in species of two other families, *Pholadidea loscombiana* (Atkins 1937*b*) and *Aloidis gibba* (Yonge 1947). In the fourth group (figure 22*d*), which includes *Solecurtus chamasolen* and *S. scopula* (Atkins 1937*b* and here confirmed), there is no such incipient forward current. This last condition occurs in a very large number of eulamellibranchs from a variety of families. *Tagelus californianus*, according to Kellogg (1915), has a forward-directed current along the margin of the outer demibranch* and so should be included in yet a fifth group.

It remains to consider the extent to which the gills are specialized in connexion with the mode of life in the different species and also the relationship between the size of the gills and that of the palps. The latter do not vary significantly, apart from size, in different species. In the Tellinidae and Semelidae, the gills are large and palps small in *Tellina tenuis* (figure 1), *T. crassa* (Graham 1937), *Semele decisa* (Kellogg 1915) and, with the palps relatively larger, in *Scrobicularia plana* (figure 4). The gills are little, if any, larger than the palps in *Tellina donacina*, *T. fabula* (Atkins 1937*a*), *Macoma balthica* (figure 2) and *M. secta* (Kellogg 1915), while in *Abra alba* and *A. nitida* (Atkins 1937*a* and figure 3) the palps are relatively even larger.

Atkins (1937*a*) has drawn attention to the presence in certain Tellinacea of powerful cirrus-like cilia on the frontal surface on the posterior region of the outer face of the inner demibranch. As shown in figures 1 to 3, they carry material diagonally forward across this surface of the gill. They occur in *Tellina donacina*, *T. fabula* and *T. tenuis* (Atkins 1937*a* and here confirmed), to the greatest extent in the first and to a progressively less extent in the other two, but *not* in *T. crassa* (Atkins 1937*a*; Graham 1937). They are very well developed in *Macoma balthica*, extending over the posterior quarter of the gill (figure 2), and to a less extent in *Abra alba* (figure 3) and *A. nitida* (Atkins 1937*a*), but are absent in *Scrobicularia plana* (figure 4), although, as pointed out by Atkins (1937*a*), there is here a broad band of these cirri along the posterior part of the ventral margin of the inner demibranch. Finally, in none of these species is there a true food groove along the margin of the inner demibranch which is merely flattened.

The characteristic form of the ctenidia in the Tellinidae and Semelidae (figure 22*a, b*) may reasonably be correlated with the mode of feeding which involves the continuous intake of relatively immense quantities of bottom material. By the upturning of the outer demibranch, three surfaces become one with corresponding lessened risk of choking the gill and with much greater efficiency of transport and sorting of material upon it. Atkins (1937*a*) has suggested that the function of the cirrus-like frontal cilia is to increase the power of the inhalant current and that they are correlated with the presence of very long inhalant siphons. While the second statement is in a measure probably true, it seems more probable that these cilia are concerned with the rapid forward passage of the great quantities of material that enter through these siphons. The gill is narrow posteriorly, and there would be much delay and clogging in this region if the material carried in had all to be conveyed

* This has now been confirmed. There is a food groove along the edge of the outer demibranch.

first to the margin of the demibranch before moving forward. It is significant that these frontal cirri are absent in *Tellina crassa* and *Scrobicularia plana*, in which there is a forward current on the gill axis which will have the same effect of clearing the posterior region of the gill. The force of the inhalant current can be accounted for, as already suggested, by concentration in the narrow lumen of the siphon. There appears, indeed, to be a tendency to keep the gill as small as possible consonant with the production of an adequate inhalant current in view of the problems presented by the volume of material drawn in. The absence of the food groove is certainly associated with the need to reduce as much as possible the volume of material carried forward. The greater part will pass from the margin of the gill on to the mantle to be accumulated by way of waste canals within the protection of the mantle folds before ejection as pseudofaeces. Finally, the inverse relationship that exists between the size of the palps and that of the gills indicates that where the gills are large they are capable of considerable selection before material is passed to the palps, but where they are small greater quantities of material pass to the palps which have a correspondingly heavier task of selection before material finally enters the mouth. There is a general tendency, supported by conditions in the other two families, for the palps to be larger in the mud-living species where much very fine material is taken into the mantle cavity.

In *Donax vittatus* there extend for varying distances from the ventral margin of the demibranchs a single row of long stout cilia along the posterior side of the frontal surface of each filament (Atkins 1937*a*). On both surfaces of both demibranchs these beat towards the ventral margin, even where the frontal cilia beat in the opposite direction. They are correlated, like similar ones in *Spisula subtruncata* (Atkins 1937*a*; Yonge 1948*c*), with life in sand and they help to sift particles of this from the surface of the gills. The small palps in this species (figure 5) may be correlated with the absence of much finely divided material, and the larger gills with reflected outer demibranchs with the shorter and wider siphons in this species. That the inflow is more gentle is shown by the absence of mantle folds to prevent washing forward of the pseudofaeces.

In *Gari tellinella* and *G. fervensis* the deep food grooves on the inner demibranchs possess guarding cilia in common with a wide variety of other lamellibranchs listed by Atkins (1937*a*) which all inhabit substrata with much silt or mud. There is a beautiful distinction, as she points out, between *Solecurtus chamasolen*, which inhabits mud and has guarding cilia, and *S. scopula*, which lives in clean shell gravel and is without them. The latter species possesses a very deep food groove which Atkins observed to open and close. Although the palps in neither species are large, those of *S. chamasolen* which lives in mud are relatively the larger (cf. figures 9, 11). In general, it may be said that in *Gari* and *Solecurtus* as well as in *Donax* there are no special features on the gills which may be correlated with deposit feeding, all those referred to being found also in suspension feeders.

(5) *Disposal of pseudofaeces*

Throughout the Tellinacea, pseudofaeces are expelled by the most usual route, through the inhalant siphon. Despite the very great quantities of material that enter the mantle cavity in the Tellinidae and Semelidae, there is no fourth pallial aperture for its removal as there is in certain Mactridae, e.g. *Spisula subtruncata* and *Lutraria lutraria* (Yonge 1948*c*). On the other hand, members of both groups have in common a pair of mantle folds

(figures 1 to 4, MF). In the Tellinidae and Semelidae these prevent the accumulation of pseudofaeces below the base of the siphons from being washed forward by the very concentrated inhalant current, while in the Mactridae they are primitively associated with the presence of a siphonal membrane which directs the inhalant current towards the ventral surface of the mantle cavity (Kellogg 1915; Yonge 1948*c*). In *Abra* and *Scrobicularia*, though not in *Tellina* and *Macoma*, there are additional low ridges (figures 18, 23, R) near the

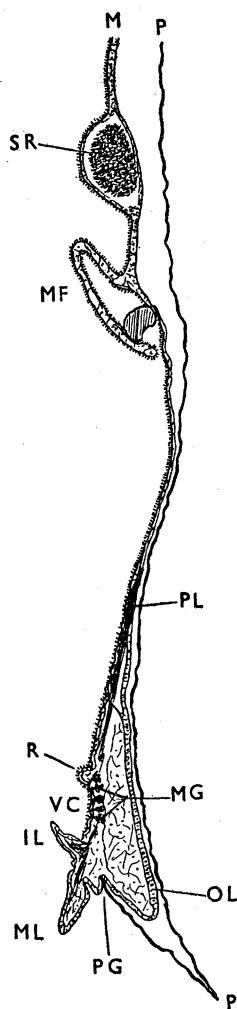


FIGURE 23. *Abra nitida*, transverse section through ventral region of mantle edge a little anterior to base of siphons (magn. $\times 58$). M, mantle; MF, mantle fold curled down and enclosing sand grain; R, ridge forming dorsal boundary of ventral channel (VC) into which open mucous glands (MG). Other lettering as before.

ventral margin between which and the middle mantle lobe (ML) runs the ventral channel (figures 3, 4, VC), into which open numerous mucous glands (figures 18, 23, MG). (Similar glands are numerous on the dorsal surface of the inner mantle lobes in *Solecurtus* (figure 19).) Judging from Kellogg's figure of *Semele decisa*, where neither mantle folds nor ridges are shown, the condition in *Abra* and *Scrobicularia* is not necessarily characteristic of all Semelidae. The complex series of folds into which the ventral region of the inner mantle surface is thrown in *Abra nitida* is shown in figure 23, and conditions are similar in *A. alba* and *Scrobicularia plana*.

In the species examined of *Donax*, *Gari* and *Solecurtus*, no such folds occur. This may be correlated with the less concentrated current that enters through the relatively much wider inhalant siphons; indeed, in *Donax vittatus* the pseudofaeces actually accumulate within

the base of this (figure 5). In both species of *Solecurtus*, they are carried to the true base of the siphons, i.e. at the posterior end of the long fused area of the inner mantle lobes (figures 9, 11, II).

(6) *Alimentary canal*

The course of the alimentary canal in *Tellina tenuis* is shown in figure 14, while that in a variety of species of the Tellinacea has been described and figured by Graham (1934*b*). The most conspicuous feature is the very capacious stomach which is dealt with in detail below. A relatively straight oesophagus leads into this. The style-sac and mid-gut are united in *Tellina*, *Macoma*, *Scrobicularia*, *Gari* and *Solecurtus* (Graham 1934*b* and here confirmed) and in *Tagelus dombeyi* (Hoffmann 1914) but *not* in *Donax vittatus*, as described by Graham (1934*b*) and shown in figure 28, or in *Novaculina* (Ghosh 1920) and *Sinonovacula* (Annandale & Prashad 1924). This difference has no systematic significance; it is paralleled by conditions in the Myacea where in *Aloidis gibba* the style-sac and mid-gut are united (Yonge 1947), whereas they are not in *Mya arenaria* (Yonge 1923). The fused condition is certainly primitive, being universal in the Protobranchia (Yonge 1939), but no functional significance appears to be attached to the secondary separation where this occurs. It is possibly the result of local pressures or strains set up during development.

There is considerable variation in the degree of coiling, i.e. in total length, of the mid-gut. In *Tellina crassa*, Graham refers to a moderate degree of coiling though, judging from his figure, it is somewhat greater than in *T. tenuis* (figure 14). In *Macoma balthica* coiling is certainly greater, Graham figuring a series of coils behind the stomach and on a level with it. In *Scrobicularia plana* he shows it to be still more extensive and conditions in *Abra* are similar. Both in *Donax vittatus* and *Gari tellinella*, on the other hand, the mid-gut is much shorter. It is a little longer in *Solecurtus scopula* and *S. chamasolen* and apparently very similar in *Tagelus dombeyi* (Hoffmann 1914). It appears to be significantly longer in *Novaculina* (Ghosh 1920), with which *Sinonovacula* is stated to agree closely (Annandale & Prashad 1924). There is little to be gleaned from these differences apart from the greater coiling in those species that take great quantities of mud into the mantle cavity, i.e. *Macoma balthica*, *Scrobicularia plana*, *Abra alba* and *A. nitida*. *Solecurtus chamasolen*, though it lives in mud does not take so much into the mantle cavity as in the other species with their thin elongate siphons and groping habit.

The length of the mid-gut is correlated with the need to consolidate the faecal pellets. The continual extrusion of large numbers of these in *Abra alba* was particularly noticeable. The pellets of *Abra alba*, *A. nitida*, *Tellina crassa* and *T. donacina* have been described by Moore (1930, 1931). In the two first the pellets are oval, being very regular in shape in *Abra alba* with a length-breadth ratio of 1.75, and rather smaller and irregular with frequently constrictions in *A. nitida*. In *Tellina crassa* they are occasionally rod-shaped but are more usually cut up into round-ended pellets with a length-breadth ratio of 1.35. In *T. donacina* they are very similar, but the two ends are less rounded and the pellets are often irregular, the length-breadth ratio being frequently 1.30.

Observations in the course of this research were confined to *Scrobicularia plana* and *Tellina tenuis*. In the former the pellets are relatively large, some 0.65 mm. long and 0.43 mm. broad, the ratio being 1.5. In *T. tenuis* material begins to be massed together about the middle of the ascending region of the mid-gut posterior to the stomach (see

figure 14). The cilia throughout the mid-gut are very active and some 40μ long. The initial mass is divided up, at first irregularly but later into regular cylindrical pellets, the posterior end of each being convex and the anterior end concave so that the front end of one fits into the hind end of the one behind it. This is clearly seen through the transparent walls of the gut, as shown in figure 24. It is in this form that they pass through the hind-gut and are expelled at the anus, each some 0.32 mm. long and 0.30 mm. wide, the ratio being 1.07.

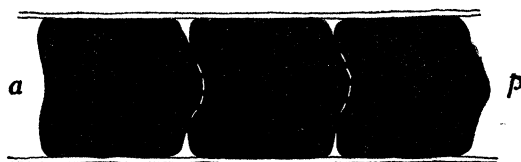


FIGURE 24. *Tellina tenuis*, faecal pellets shown within mid-gut (magn. $\times 60$). *a*, anterior; *p*, posterior.

The stomach demands particular attention; it is considerably modified and highly characteristic throughout the Tellinacea. In the great majority of lamellibranchs the wall of the stomach is so delicate and so intimately attached to the surrounding connective tissue and muscle that it is excessively difficult to dissect free without damage. This is not the case in the Protobranchia, as previously described (Yonge 1939), nor is it so in the Tellinacea. Here careful removal of the enfolding tubules of the digestive diverticula and of the gonads exposes the intact and semi-transparent stomach. Hence it is possible in these animals to describe the intact organ and not to rely, as previous workers (including the author) have done, on cutting it open along one side and describing the contained ridges and grooves with their often complex ciliary currents. Such observations and descriptions can give only a limited indication of how the intact stomach, into which the head of the style projects in life, really functions. Descriptions of the ciliary currents in the stomachs of *Tellina crassa* and *Solecurtus chamasolen* have recently been given by Graham (1949) in an important and comprehensive account of the stomach throughout the Lamellibranchia and Gastropoda which the author has had the privilege of reading in manuscript. There is nothing to add to Graham's detailed account of the ciliary currents, but much to report about the modifications and mode of functioning of the intact stomach.

Initial description will deal with the stomach of *Tellina tenuis* which is shown when viewed, freed from all adjacent tissues, from both left and right sides in figure 25 *a* and *b*, and from the dorsal surface and after progressive degrees of exposure from above in figure 27 *a* to *d*. It consists of the usual two parts noted by Graham (1949), namely, a proximal globular region, into which open the oesophagus and the ducts of the digestive diverticula, and a distal style-sac. But the proximal region (usually regarded as 'the stomach') is unusually small in relation to the wide style-sac. The two lie in the same vertical axis, and the massive style (*S*) is straight and projects directly upward into the proximal region of the stomach, the lumen of which it largely fills (figure 25 *a*).

The greater part of the internal walls of the proximal region of the stomach is covered by the cuticular investment of the gastric shield which is shown, dissected free as it is easily possible to do, in figure 26. Distally it almost enfolds the opening into the style-sac, being interrupted only in the region of the intestinal groove (figures 25 *b*, 27 *d*, IG). As shown in

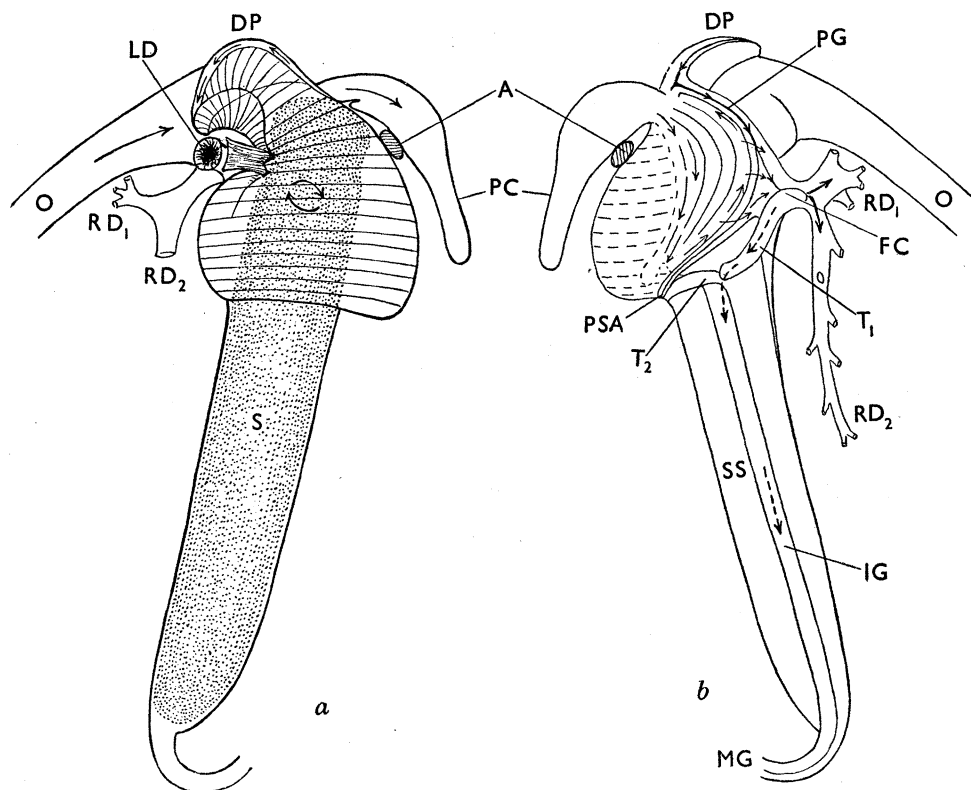


FIGURE 25. *Tellina tenuis*, lateral views of intact stomach (magn. $\times 16$). *a*, from left side showing style *in situ*, entrance of food from oesophagus and passage into dorsal pouch and postero-dorsal caecum; *b*, from right side showing passage out of pouch and caecum and into ducts of digestive diverticula and intestinal groove. A, small adductor muscle; DP, dorsal pouch; FC, food-sorting caecum; IG, intestinal groove; LD, left duct of digestive diverticula; MG, mid-gut; PC, postero-dorsal caecum; PG, proximal groove; PSA, posterior sorting area; RD₁, RD₂, right ducts of digestive diverticula; S, style (shown stippled); SS, style-sac; T₁, T₂, major and minor typhlosoles; O, oesophagus. Gastric shield covering left wall of stomach shown lined in *a* and its limited extent over right side by broken lines in *b*. Arrows denote direction of ciliary currents.

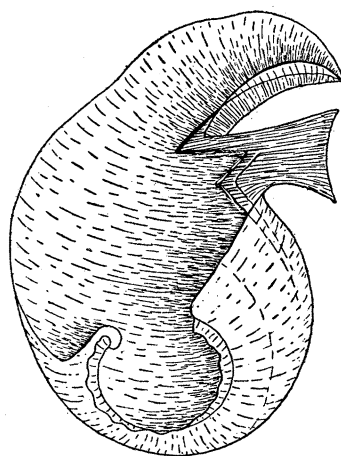


FIGURE 26. *Tellina tenuis*, gastric shield after dissection drawn from right side showing encirclement of opening into style-sac except in region of intestinal groove, also dorsal and ventral teeth and dorsal extension into base of pouch (magn. $\times 25$).

figures 25 *a* and 27 *d*, it entirely covers the left side of the proximal region of the stomach and also extends for some distance around the postero-lateral wall on the right side (figure 25 *b*). Two prominent teeth, one above the other so that they may be designated dorsal and ventral (DT, VT), project inward on the anterior surface. They are shown in lateral view in figures 25 *a* and 26 and from above in figure 27 *c* and *d*. The upper surface of the dorsal tooth is continuous with the right side of a V-shaped wing into which the gastric shield projects antero-dorsally (figures 25 *a*, 26).

The oesophagus enters on the anterior side, near the dorsal surface and immediately above the dorsal tooth of the gastric shield as shown in figure 27 *c* and *d*. Above this and to the left lies the caecum named by Graham (1949) the dorsal pouch (figures 25, 27, DP), the ventral surface of which is occupied by the V-shaped wing of the gastric shield. From the right side of the dorsal surface of the stomach there projects backward an extensive, although very contractile, postero-dorsal caecum (figures 25, 27, PC). This extends round the posterior wall of the stomach for some distance ventrally (see figure 25), being separated from this by a thin adductor muscle (A) which here runs between the two shell valves as shown in figure 27 *a*. The digestive diverticula form a dense mass of brown tubules around the stomach into which they open by three ducts, one on the left (figures 25 *a*, 27, LD) and two on the right (figures 25, 27). Of the latter, the first (RD₁) runs to the right, the second (RD₂) extends ventrally as shown in figure 25 *b*. All three ducts open into a food-sorting caecum situated in the middle of the anterior wall of this region of the stomach (figures 25 *b*, 27 *d*, FC) the arrangement of ridges and grooves on which, with their ciliated currents, resemble those described by Graham (1949) for *T. crassa*. This caecum is bounded on the left by the teeth on the gastric shield as shown in figure 27 *d*. The only other features to be noted are the ciliated ridges and grooves which extend over the limited area, on the anterior half of the right wall and the right half of the anterior wall with the dorsal projections of the two pouches, which are not covered by the gastric shield. They will be described in the account which follows of the manner in which the stomach functions.

The mode of action of the style requires initial attention. Unlike many lamellibranchs in which the style-sac is curved, the style in *T. tenuis* (and in most other Tellinacea) is straight. It is also relatively stout, the diameter being about one-sixth of the length. It is assumed, therefore, that it rotates with great efficiency. Although rotation of the style was originally suggested by List (1902), it was first actually observed by Nelson (1918) after careful opening of the stomach in *Modiolus* and *Anodonta*. Rotation was clockwise when viewed from the anterior end, and the maximum observed speed was 13 r.p.m. at 25° C in *Modiolus* and 11 r.p.m. at 11.5° C in *Anodonta*. In the intact larva and spat of *Ostrea edulis* the style has been observed to rotate at rates of between 36 and 90 r.p.m. in the former and between 60 and 70 r.p.m. in the latter (Yonge 1926). On one occasion the style in *Tellina tenuis* continued to rotate, although slowly and certainly not at normal speed, when projecting through an opening in the wall of the proximal region of the stomach. Rotation was clockwise when viewed from the dorsal aspect (i.e. corresponding to the anterior aspect in other eulamellibranchs, see figure 29). Mucous strings were also observed wound around its head, acting like a capstan, as suggested, though never actually seen, by Orton (1923). When removed the intact style is always grooved close to the head end. This, as shown in figure 25 *a* is due to the dorsal and ventral teeth on the gastric shield which project into the

lumen. These teeth serve to keep the style clear of the openings both of the oesophagus and of the food-sorting caecum as shown in figure 27*d*. The teeth will also assist in restraining the forward (here dorsalward) pressure of the style; the head itself bears against the roof

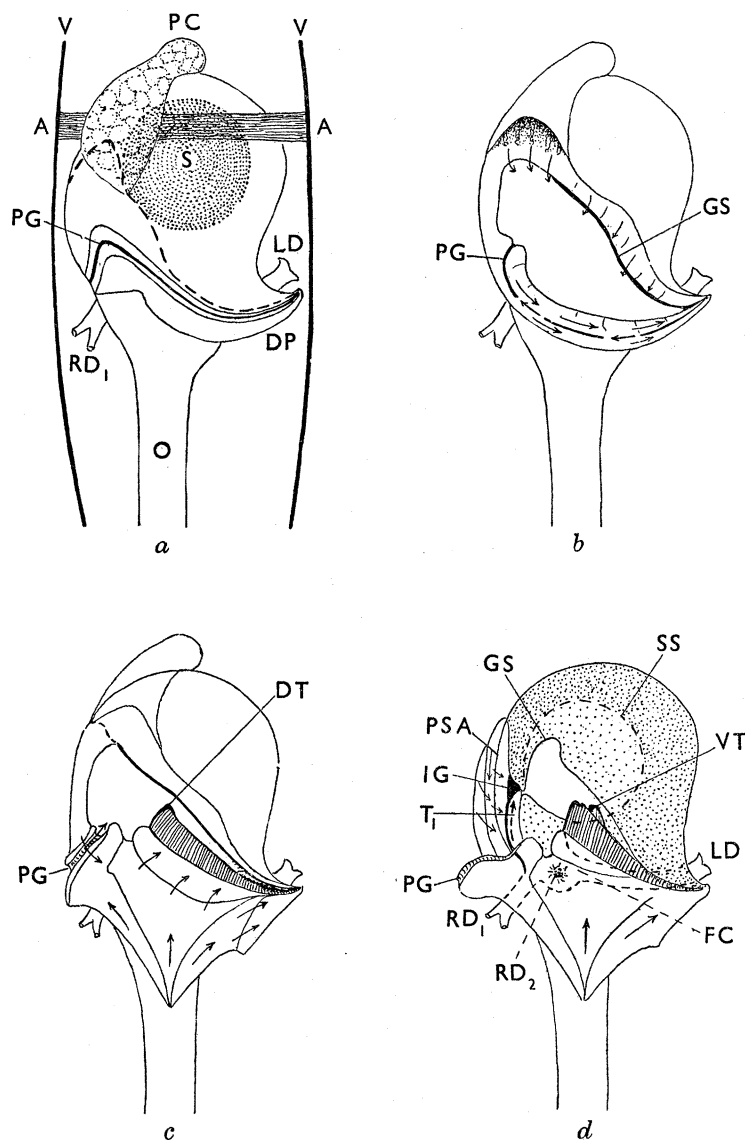


FIGURE 27. *Tellina tenuis*, stomach viewed from dorsal aspect, *a*, intact and *b*, *c*, *d*, after progressive degrees of exposure (magn. $\times 20$). *a*: PC, postero-dorsal caecum shown full of sand grains; limits of gastric shield indicated by broken line; V, shell valves. *b*: GS, margin of gastric shield. *c*: DT, dorsal tooth. *d*: GS, dorsal margin of gastric shield (full extent indicated by stippling; SS, opening into style-sac (indicated by broken line); VT, ventral tooth. Other lettering as in figure 25.

of the stomach where this is covered with the gastric shield (figures 25*a*, 27*a*). It is noteworthy that the head of the style does not here bear against the teeth of the gastric shield as it is usually assumed to do.

Apart from the liberation of the digestive enzyme (or enzymes) which accompanies the slow dissolution of its head in the less acid medium of the stomach (Yonge 1925, 1926), the style has important mechanical functions. As originally postulated by Nelson (1918, 1925) it stirs and mixes food and other particles in the stomach. It also, as already noted, draws

in mucous strings through the oesophagus both faster and more efficiently than can be done by the cilia on the epithelium of this. But, in conjunction with the gastric shield, it would also appear in this case to act as an organ of trituration. The maximum size of sand grains was measured in three regions, first in the accumulations of pseudofaeces in the mantle cavity, second in the stomach (especially from the postero-dorsal caecum), and third in the faecal pellets from the mid-gut. The measurements (maximum diameters of irregular but roughly rounded particles) were (1) 400μ , (2) 320μ , (3) 80μ (particles of this size were rare in the faecal pellets, the great majority not exceeding 40μ). It appears that representatives of only the very largest of the sand grains that enter the mantle cavity fail to be taken into the stomach. There (as shown below) many initially tend to pass into the postero-dorsal pouch. But only particles of at most a quarter of the diameter of the largest particles found in the stomach appear in the faeces. It is at this size that they must pass into the intestinal groove (figures 25*b*, 27*d*, IG), so that trituration must occur in the proximal region of the stomach as a result of their being ground by the head of the style against the gastric shield and possibly in particular the teeth of this. Thus the characteristic form of the stomach, with its straight and massive style and exceptionally well-developed gastric shield, is correlated with the unselective intake by the inhalant siphon of large quantities of coarse bottom material. In the Nuculanidae and Nuculidae among the Protobranchia where there is a similar intake of coarse bottom material by way of the palp proboscides, the stomach wall has similar triturating properties (Yonge 1939).

Before being thus ground down, many of the larger particles, especially sand grains, enter the postero-dorsal caecum (figures 25, 27, PC). This structure, although found in varying degrees of size in all Tellinacea examined (see below), does not appear to have been previously described; Graham (1949) failed to note it for reasons which will become apparent. The caecum opens to the right side of the dorsal extension of the gastric shield (figure 27*b*). The opening constantly closes and then dilates while the caecum itself varies greatly in size. When filled with particles it dilates to the extent indicated in figures 25 and 27, collapsing into a straight, narrow tube when it is empty. If its attachments are cut it contracts still further from a maximum observed length of 2 mm. (in an animal of shell length 1.7 cm.) to a rounded mass no more than 0.1 mm. in diameter. This occurs when the stomach is opened for examination and so explains why the caecum has previously been overlooked. It appears to serve for the temporary accommodation of the larger particles when these enter the stomach in quantity. It was normally found full of sand grains (see figure 27*a*) when animals were examined immediately after feeding, but was usually empty and deflated in starved animals. Presumably particles are forced into it by the action of the style, and against the opposing forces of both the cilia which line the rugose walls of the caecum (figure 27*b*) and the elasticity of these. Too great an influx of large particles would block the proximal region of the stomach and impede normal functioning. The caecum acts as a safety valve preventing this, while as soon as the intake of new particles into the stomach is reduced the combined action of cilia and elasticity will force particles from the caecum into the lumen of the stomach for trituration between style and gastric shield.

Smaller particles, which will include those of food value, entering the stomach will come under the influence of cilia on its anterior and right walls. Many will pass into the dorsal

pouch (figures 25, 27, DP). This is less developed in the Tellinacea than it is in typical suspension-feeding lamellibranchs, where it may consist of a complex series of ridges and grooves as it does in *Modiolus* (Nelson 1918), *Mya* (Yonge 1923), *Ostrea* (Yonge 1926) and in many other cases described in full detail by Graham (1949). There these particles pass into what may be designated the proximal groove (figures 27a to d, PG) which, as shown in figure 27b, extends into the food-sorting caecum (FC) into which its cilia convey particles. This caecum, which is largely cut off from the general cavity of the stomach, also receives material direct from the central lumen of the stomach by way of ciliary currents running transversely across a ridge that extends from the postero-ventral region of the proximal stomach up its right side to the entrance of the dorsal pouch (see figure 25b). After sorting within the caecum (for details see Graham 1949), smaller particles only entering the ducts of the digestive diverticula, the rejected material is conveyed into the intestinal groove (IG) which runs along the right side of the style-sac and finally into the mid-gut (MG). This passage of rejected material (including waste from the digestive diverticula) is indicated by the broken arrows in figures 25b and 27d. The groove in which it is carried is bounded on the right side by the proximal extension of the major typhlosole (T_1) which, with the minor typhlosole (T_2) which only extends for a short distance into the proximal stomach, separates the intestinal groove from the style-sac.

Finally, there is a smaller ciliated sorting region described by Graham (1949) in *Tellina crassa* and *Solecurtus chamasolen* and designated by him the posterior sorting area. This lies in the postero-ventral region of the stomach at the base of the ridge which runs up the right side of the stomach and where the minor typhlosole also originates (see figures 25b, 27d, PSA). Particles are carried here from the area adjoining the margin of the gastric shield, including many that may emerge from the postero-dorsal caecum (see arrows in figure 25b). Sorting activity has the effect of sending smaller particles forward and upward either direct into the food-sorting caecum or by way of the dorsal pouch; larger particles may pass direct into the intestinal groove by way of the inner surface of the minor typhlosole. But this area is poorly developed in *Tellina tenuis* and is probably of minor importance.

The end-result of the combined activities of the rotating style, acting in conjunction with the highly developed gastric shield, and the ciliary currents on the ridges and groove, may thus be summarized. All particles are reduced to a maximum diameter of some 80μ (the majority much less), they are mixed with the enzymes liberated by the dissolving head of the style, they are then subjected to the sorting activities of the posterior sorting area and the much more important food-sorting caecum. Finally, smaller particles enter the ducts of the digestive diverticula for ingestion and intracellular digestion within its tubules, while the larger ones pass into the intestinal groove for elaboration within the mid-gut into the faecal pellets already described.

The stomachs of the other species of Tellinacea were also examined though not all in the same detail as that of *T. tenuis*. Conditions are essentially the same in *Macoma balthica* and also in *Abra alba* and *Scrobicularia plana*. The stomach of the last named was examined with particular care and closely resembles that of *Tellina tenuis*. The postero-dorsal caecum is equally conspicuous and even longer though narrower (figure 29c). The contents consisted invariably of sand grains.

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Conditions are fundamentally similar but differ in certain details in the other two families. The stomach of *Donax vittatus* is shown in figure 28. The major difference from the preceding cases, the separation of the style-sac (SS) and mid-gut (MG), has already been mentioned. But the style-sac is also relatively longer and is curved. The gastric shield (GS) does not extend so far around the posterior half of the right wall of the stomach but is otherwise similar with the same two conspicuous teeth. The postero-dorsal caecum (PC) was very small (as shown) in all specimens examined, but these had previously been starved, so that it may be capable of further dilation although it is certainly very much

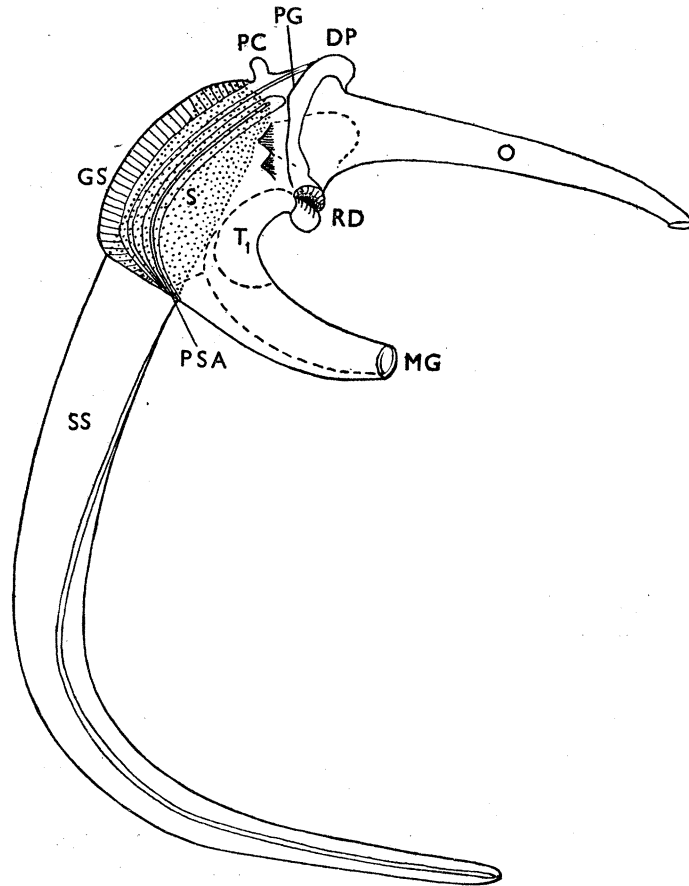


FIGURE 28. *Donax vittatus*, stomach viewed from right side (magn. $\times 10$). Lettering as in figures 25 and 27. Extent of gastric shield (GS) on right wall of stomach only shown lined, style (S) shown stippled in proximal stomach.

smaller than that in all Tellinidae and Semelidae. On the other hand, the dorsal pouch (DP) and the posterior sorting area (PSA) are better developed. In brief the stomach in this species is somewhat less highly adapted for dealing with large particles needing trituration and better developed for sorting smaller particles. This is correlated with the smaller, largely suspended, particles that are drawn in by the inhalant siphon (see figure 16*d*).

The stomachs of *Gari* and *Solecortus* are very similar to one another. They resemble those of the Tellinidae and Semelidae in the straight style-sac, with an associated intestinal groove, and in the presence of a postero-dorsal caecum larger than that of *Donax*, especially

in *Gari* where it is elongated. But in both (as in *Donax*) the stomach is not so easy to dissect free; the walls are less firm and the gastric shield, although almost as extensive, is more delicate and the teeth are less pronounced. The folds and other ciliated areas are better developed and, owing to the anterior extension of the stomach (shown semi-diagrammatically for *Solecurtus* in figure 29 *b*), more free to deal with particles without interference from the style. The stomach in species of both of these genera might be described as an organ capable of dealing with a certain proportion of large particles needing some trituration but being more generally concerned with the sorting of fine particles, even the largest of which can be sent directly into the intestinal groove.

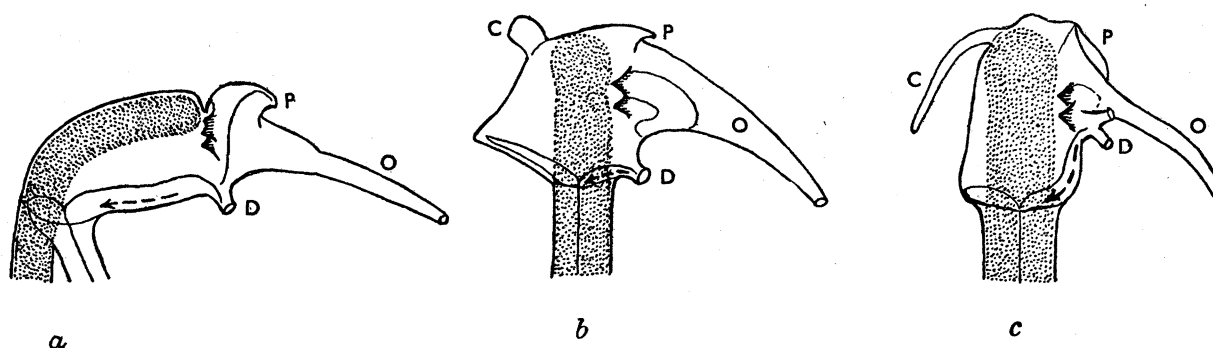


FIGURE 29. Semi-diagrammatical drawings of stomachs, viewed from right side, of *a*, *Mya* (as type of suspension-feeding eulamellibranch); *b*, *Solecurtus chamasolen*; *c*, *Scrobicularia plana*. C, postero-dorsal caecum; D, right duct of digestive diverticula; O, oesophagus; P, dorsal pouch. Dorsal and ventral teeth of gastric shield shown, with style (stippled) and typhlosoles, also ciliary current (broken arrows) alongside major typhlosole leading into intestinal groove.

The stomach throughout the Tellinacea has thus certain important features, the nature and significance of which can best be realized after comparison, in broad outline, with the stomach of a typical suspension feeder, such as a member of the Myacea or Veneracea. This comparison is made in figure 29 which shows, semi-diagrammatically, the major features in *a*, *Mya*; *b*, *Solecurtus*; and *c*, *Scrobicularia*. All have certain common features, the anterior oesophagus (O), the dorsal pouch (P), which contains in *Mya* the extensive 'grooved area' (Yonge 1923), the teeth of the gastric shield on the anterior wall of the stomach and the ventral opening of the style-sac (separate from the mid-gut in *Mya*). In all the style rotates, though doubtless with more efficiency in the Tellinacea, and there is initial accumulation and some sorting in the dorsal pouch which is much more highly developed in *Mya*. Both in *Solecurtus* and *Scrobicularia*, what corresponds to the dorsal wall of the proximal stomach in *Mya* (and suspension feeders in general) has become the posterior wall, so permitting the style to become upright with the teeth of the gastric shield impinging against it laterally some distance from the head. Accompanying this, as previously noted, is the great increase in thickness and to some degree in extent of the gastric shield (actually the entire dorsal wall of the stomach in *Mya* along which the style lies is covered with a thin cuticle which is united to the teeth). This change in disposition of the proximal stomach has enabled this to act as an agent of trituration as in the similarly disposed stomach in the primitive Protobranchia (Yonge 1939), although muscle in the stomach

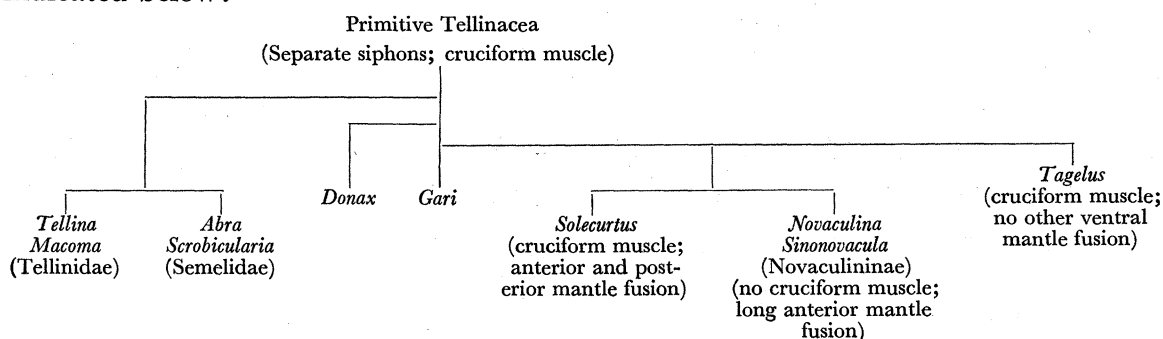
wall is there the active agent. Associated with the power of trituration is the advent of the postero-dorsal caecum (C). In *Mya*, and similar suspension feeders, the floor of the stomach is extensive and a long fold, representing the origin of the major typhlosole, runs along it from the right duct of the digestive diverticula (D) to the opening of the mid-gut. The ciliary current carrying particles into the mid-gut (corresponding to the intestinal groove) runs along its left side (see broken arrows). In *Solecurtus*, although the anterior region of the proximal stomach is much reduced and with it the length of this fold, this still remains ventral. But in the more specialized *Scrobicularia* (and *Tellina*), where the ducts into the digestive diverticula have moved dorsally with the still greater vertical elongation of the stomach, this fold runs down the anterior walls of the stomach. These changes in the orientation of the stomach are directly associated with the changes from the habit of feeding on finely divided suspended matter, introduced in relatively small amounts by the controlling influence of sensitive and straining tentacles around the aperture of the inhalant siphon, to that of feeding on coarser bottom deposits taken in large amounts. It is impossible to agree with Graham (1949) when he says that the stomachs in *Tellina crassa* and *Solecurtus chamasolen* are essentially similar to those in *Paphia pullastra*, *Cardium edule* and *Venus fasciata*—all typical suspension feeders.

IV. DISCUSSION

Two matters remain for final discussion, first what light the foregoing account of the Tellinacea throws upon the origin and evolution of this group, and secondly, the significance of the characteristic features which have been evolved. Much the most important of these features, with which the others, notably the cruciform muscle, the gills and the stomach, have been shown to be correlated, is the presence of characteristically formed and usually narrow and very extensile separate siphons. Relationships must therefore be sought among lamellibranchs in which the siphons (or inhalant and exhalant apertures) are also separate. The other groups of the Eulamellibranchia in which they are so formed, namely, the Erycinacea, Petricolidae, Tridacnidae and Anatinacea, are no less specialized in different ways than are the Tellinacea. It is only possible to derive the latter from Filibranchia where siphons are not developed but where the inhalant and exhalant apertures may be bounded, as, for instance, in *Mytilus*, by folds of the inner lobe of the mantle edge. From animals so constituted eulamellibranchs with siphons of all types must have evolved, and it is not necessary to assume a common origin of all Eulamellibranchia.

The particular forms which evolution has taken within the Tellinacea have already been adequately outlined, and a broad distinction found between conditions in the Asaphidae and Donacidae on the one hand and the Tellinidae and Semelidae on the other. The least specialized condition is found in *Gari* with two major lines of further specialization. One, largely within the Asaphidae, leads to increased size, a generally cylindrical form and life within largely vertical burrows. *Tagelus*, *Solecurtus* and the Novaculininae have probably evolved by somewhat divergent paths from primitive members of the Asaphidae. *Donax* would seem to have evolved on very similar lines to *Gari* but with special features, notably of the shell and of the foot with its elevator muscle, all possibly correlated with life within relatively firm substrata. The other major line of specialization leads to the closely allied Tellinidae and Semelidae which, with their greatly elongated siphons, mantle folds, more

specialized gills and alimentary canal, are most highly and most successfully adapted for feeding on bottom deposits. The possible general course of evolution within the Tellinacea is indicated below:



The Tellinacea have been enabled by means of the adaptations here outlined to exploit as food the organic deposits on the floor of the substratum in which they live. The characteristic nature of their stomach contents has been noted by various workers. Blegvad (1915) examined these in species of *Tellina*, *Macoma*, *Abra* and *Scrobicularia*, and noted that they consisted of 'roughly sorted bottom detritus'. Kellogg (1915) was impressed by the great quantities of sand in the mantle cavity and throughout the gut in *Macoma secta*. Hunt (1925) classified species of *Abra*, *Tellina* and *Gari* as deposit feeders owing to the presence in their stomachs of sand and detritus as well as of living organisms.

The food value of these organic deposits is very difficult to assess. Mare (1943) made a detailed survey of the bottom fauna and flora and deposits in a muddy bottom off Plymouth. Taking a volume of deposit 1 metre square and 10 cm. deep, she found that detritus was responsible for 1 kg. of organic carbon but the total fauna and flora only for between 5 and 10 g. Detritus would therefore appear to represent the major source of food for deposit feeders. Its value as food remains debatable. Boysen Jensen (1915), in analyses of the detritus in the Limfjord, found little digestible protein and only pentosans in appreciable quantity among non-nitrogenous compounds. Detritus does, however, support bacteria and other micro-organisms, and these may form part of the food of deposit feeders. Wernstedt (1942) fed *Cardium edule* and *Macoma balthica* on both diatoms and detritus. His results, while not very conclusive, did show that *Cardium* grew well on a diet of suspended *Nitzschia* and *Macoma* best on deposits, but only when these were rich in diatoms. He concluded that the food value of detritus itself was small although not necessarily negligible. It is significant that in the Tellinacea the feeding organs and the gut are specialized for dealing with very much greater amounts of incoming material than are those of suspension-feeding lamellibranchs. This would indicate that the concentration of food in the deposits is low, and Kellogg (1915) not unreasonably compared the feeding habits of *M. secta* to those of an earthworm.

Much remains to be done on the nature and food value, directly and indirectly, of bottom detritus. But the best indication of its importance lies in the variety and abundance of the often highly adapted members of the invertebrate infauna (see Yonge 1948*b*) which would certainly appear to depend upon it. This fauna includes among Mollusca, in addition to the Tellinacea, the protobranch Nuculidae and Nuculanidae, the gastropods *Aporrhais* and *Turritella*, echinoderms such as the ophiuroid *Amphiura* and the echinoids *Brissopsis* and

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Echinocardium, decapod Crustacea such as *Calocaris* and *Gebia*, with many annelids and other worms. These animals form a significant part of the food of many demersal fishes.

To revert, in conclusion, to the opening remarks in this paper, it is now apparent that under the superficial similarity of structure throughout the Eulamellibranchia there exists a wide range of specialization. A few obvious instances are the Erycinacea which tend towards commensalism and even parasitism, the Adesmacea which are specialized for boring into rock and wood, and the Tridacnidae which have been profoundly modified in structure and habit owing to association with symbiotic algae. The capacity for deep burrowing has been evolved independently in the Solenacea (for temporary protection) and in genera such as *Mya*, *Lutraria* and *Panope* which, from distinct origins, have reached the same endpoint of permanent life deep below the surface. The Tellinacea are similarly specialized as a group for exploiting the food content of bottom deposits and with considerable adaptive radiation within the constituent families, genera and species. While all are essentially non-selective feeders, the Asaphidae and Donacidae feed passively, while the Tellinidae and Semelidae, with their long siphons that scour the bottom, in many instances actively pull in the surface deposits for the reception of which the gills, the rejective mechanisms in the mantle cavity, and the alimentary canal, are all highly specialized. Throughout the Tellinacea, different species are adapted for life in all types of bottom material, from finely graded mud to muddy gravel and from fine sand (firm or silty) to coarse shell gravel, although, as emphasized by Beanland (1940), their abundance will depend on quality and quantity of food as well as on suitable 'soil', i.e. the quantity of organic matter in any 'soil' must determine their abundance. The success of the Tellinacea is shown by the vast abundance of many of their species on suitable substrata either between tide marks or in the sublittoral zone.

The bulk of this research was carried out at the Millport Laboratory largely on specimens collected locally, although some were sent living from Plymouth, while Dr A. C. Stephen kindly collected living specimens of *Donax vittatus* at Aberlady and sent them to Glasgow. Acknowledgements for help are due to the late Mr R. Elmhirst and members of the staff at Millport. Much technical assistance was received from my friend and colleague Dr H. F. Steedman and also from Miss N. M. Davidson and Mr A. McKinnon at the Department of Zoology, University of Glasgow. As on former occasions, Mr R. Winckworth has given invaluable assistance on matters of nomenclature.

REFERENCES

- Annandale, T. N. & Prasad, B. 1924 Report on a small collection of molluscs from the Chekiang Province of China. *Proc. Malacol. Soc. Lond.* **16**, 24–49.
- Atkins, D. 1937*a* On the ciliary mechanisms and interrelationships of lamellibranchs. Part II. *Quart. J. Micr. Sci.* **79**, 339–373.
- Atkins, D. 1937*b* On the ciliary mechanisms and interrelationships of lamellibranchs. Part III. *Quart. J. Micr. Sci.* **79**, 375–421.
- Atkins, D. 1937*c* On the ciliary mechanisms and interrelationships of lamellibranchs. Part IV. *Quart. J. Micr. Sci.* **79**, 423–445.
- Beanland, F. L. 1940 Sand and mud communities in the Dovey Estuary. *J. Mar. Biol. Ass. U.K.* **24**, 589–611.

- Blegvad, H. 1915 Food and conditions of nourishment among the communities of invertebrate animals found on or in the sea bottom in Danish Waters. *Rep. Danish Biol. Sta.* **22**, 41–78.
- Bloomer, H. H. 1907 On the anatomy of *Tagelus gibbus* and *T. divisus*. *Proc. Malacol. Soc. Lond.* **7**, 218–223.
- Boysen Jensen, P. 1915 Studies concerning the organic matter of the sea bottom. *Rep. Danish Biol. Sta.* **22**, 1.
- Deshayes, G. P. 1848 Histoire naturelle des Mollusques. 1. Mollusques acéphalés. *Exploration scientifique de l'Algérie*, 1840–42. Sciences Physiques. Zoologie. Paris.
- Ford, E. 1923 Animal communities of the level sea-bottom in the waters adjacent to Plymouth. *J. Mar. Biol. Ass. U.K. N.S.* **13**, 164–224.
- Fraser, J. H. 1932 Observations on the fauna and constituents of an estuarine mud in a polluted area. *J. Mar. Biol. Ass. U.K. N.S.* **18**, 69–85.
- Ghosh, E. 1920 Taxonomic studies on the soft parts of the Solenidae. *Rec. Indian Mus.* **19**, 47–78.
- Graham, A. 1934*a* The cruciform muscle of lamellibranchs. *Proc. Roy. Soc. Edinb.* **54**, 17–30.
- Graham, A. 1934*b* The structure and relationships of lamellibranchs possessing a cruciform muscle. *Proc. Roy. Soc. Edinb.* **54**, 158–187.
- Graham, A. 1937 On the ciliary currents on the gills of some Tellinacea (Lamellibranchiata). *Proc. Roy. Soc. Edinb.* **57**, 128–134.
- Graham, A. 1949 The molluscan stomach. *Trans. Roy. Soc. Edinb.* (in the Press).
- Hoffmann, F. 1914 Beiträge zur Anatomie und Histologie von *Tagelus dombeyi* (Lamarck). *Jena. Z. Naturw.* **52**, 521–561.
- Hunt, O. D. 1925 The food of the bottom fauna of the Plymouth fishing grounds. *J. Mar. Biol. Ass. U.K. N.S.* **13**, 560–599.
- Jeffreys, G. 1863 *British Conchology*, vol. 2. London: Van Voorst.
- Kellogg, J. L. 1915 Ciliary mechanisms of lamellibranchs with descriptions of anatomy. *J. Morph.* **26**, 625–701.
- List, T. 1902 Die Mytiliden. *Fauna u. Flora Neapel*, **27**.
- Mare, M. F. 1943 A study of a marine benthic community with special reference to the micro-organisms. *J. Mar. Biol. Ass. U.K.* **25**, 517–554.
- Meyer, H. A. & Möbius, K. 1872 *Fauna der Kieler Bucht*. Bd. 2. *Die Prosobranchia und Lamellibranchia*. Leipzig: W. Engelmann.
- Moore, H. B. 1930 The specific identification of faecal pellets. *J. Mar. Biol. Ass. U.K. N.S.* **17**, 359–365.
- Moore, H. B. 1931 The systematic value of a study of molluscan faeces. *Proc. Malacol. Soc. Lond.* **19**, 281–290.
- Morse, E. S. 1919 Observations on living lamellibranchs of New England. *Proc. Boston Soc. Nat. Hist.* **35**, 139–196.
- Nelson, T. C. 1918 On the origin, nature, and function of the crystalline style of lamellibranchs. *J. Morph.* **31**, 53–111.
- Nelson, T. C. 1925 Recent contributions to the knowledge of the crystalline style of lamellibranchs. *Biol. Bull. Woods Hole*, **49**, 86–99.
- Orton, J. H. 1923 An account of investigations into the cause or causes of the unusual mortality among oysters in English oyster beds during 1920 and 1921. *Fish. Invest. Ser. II*, **6**, no. 3.
- Pelseneer, P. 1891 Contribution à l'étude des lamellibranches. *Arch. Biol., Paris*, **11**, 147–312.
- Pelseneer, P. 1911 Les lamellibranches de l'expédition du 'Siboga'. Partie anatomique. 'Siboga' *Exped.* **53a**.
- Petersen, C. J. G. 1915 On the animal communities of the sea bottom in the Skagerak, the Christiania Fjord and the Danish Waters. *Rep. Danish Biol. Sta.* **23**, 3–28.
- Petersen, C. J. G. & Boysen Jensen, P. 1911 Valuation of the sea. 1. Animal life of the sea bottom, its food and quantity. *Rep. Danish Biol. Sta.* **20**, 3–76.
- Rawitz, B. 1892 Der Mantelrand der Acephalen. Dritter Teil. *Jena. Z. Naturw.* **27**, 1–232.

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- Ridewood, W. G. 1903 On the structure of the gills of the Lamellibranchia. *Phil. Trans. B*, **195**, 147–284.
- Spooner, G. M. & Moore, H. B. 1940 The ecology of the Tamar Estuary. VI. An account of the macrofauna of the intertidal muds. *J. Mar. Biol. Ass. U.K.* **24**, 283–330.
- Stephen, A. C. 1928 Notes on the biology of *Tellina tenuis* da Costa. *J. Mar. Biol. Ass. U.K.* N.S. **15**, 683–702.
- Stephen, A. C. 1929 Studies on the Scottish marine fauna: the fauna of the sandy and muddy areas of the tidal zone. *Trans. Roy. Soc. Edinb.* **56**, 291–306.
- Stephen, A. C. 1930 Studies on the Scottish marine fauna: additional observations on the fauna of the sandy and muddy areas of the tidal zone. *Trans. Roy. Soc. Edinb.* **56**, 521–535.
- Stephen, A. C. 1932 Notes on the biology of some lamellibranchs in the Clyde area. *J. Mar. Biol. Ass. U.K.* N.S. **18**, 51–68.
- Stephen, A. C. 1933 Studies on the Scottish marine fauna: the natural faunistic divisions of the North Sea as shown by the quantitative distribution of the molluscs. *Trans. Roy. Soc. Edinb.* **57**, 601–616.
- Thiele, J. 1935 *Handbuch der systematischen Weichtierkunde*. Dritter Teil. Classis Bivalvia. Jena: G. Fischer.
- Trueman, E. R. 1942 The structure and deposition of the shell of *Tellina tenuis*. *J. Roy. Micr. Soc.* **62**, 69–92.
- Von Ihring, H. 1901 The musculus cruciformis of the Order Tellinacea. *Proc. Acad. Nat. Sci. Philad.* 1900, pp. 480–481.
- Wernstedt, C. 1942 Studies on the food of *Macoma baltica* and *Cardium edule*. *Vidensk. Medd. naturh. Foren.* **106**, 241–252.
- Weymouth, F. W. 1920 The edible clams, mussels and scallops of California. *Fish. Bull., Sacramento*, no. 4.
- Winckworth, R. 1932 The British marine Mollusca. *J. Conch.* **19**, 211–252.
- Yonge, C. M. 1923 The mechanism of feeding, digestion, and assimilation in the lamellibranch *Mya*. *Brit. J. Exp. Biol.* **1**, 15–63.
- Yonge, C. M. 1925 The hydrogen-ion concentration in the gut of certain lamellibranchs and gastropods. *J. Mar. Biol. Ass. U.K.* N.S. **13**, 938–952.
- Yonge, C. M. 1926 Structure and physiology of the organs of feeding and digestion in *Ostrea edulis*. *J. Mar. Biol. Ass. U.K.* N.S. **14**, 295–386.
- Yonge, C. M. 1929 Structure and function of the organs of feeding and digestion in the septibranchs, *Cuspidaria* and *Poromya*. *Phil. Trans. B*, **216**, 221–263.
- Yonge, C. M. 1936 Mode of life, feeding, digestion and symbiosis with Zooxanthellae in the Tridacnidae. Great Barrier Reef Exped. 1928–29, *Sci. Rep. Brit. Mus. (Nat. Hist.)*, **1**, 283–321.
- Yonge, C. M. 1937 The formation of siphonal openings by *Thracia pubescens*. *Proc. Malacol. Soc. Lond.* **22**, 337–338.
- Yonge, C. M. 1939 The protobranchiate Mollusca: a functional interpretation of their structure and evolution. *Phil. Trans. B*, **230**, 79–147.
- Yonge, C. M. 1947 On the habits and adaptations of *Aloidis (Corbula) gibba*. *J. Mar. Biol. Ass. U.K.* **26**, 358–376.
- Yonge, C. M. 1948a Formation of siphons in Lamellibranchia. *Nature*, **161**, 198.
- Yonge, C. M. 1948b Bottom fauna of the sea. *Research*, **1**, 589–595.
- Yonge, C. M. 1948c Cleansing mechanisms and the function of the fourth pallial aperture in *Spisula subtruncata* (Da Costa) and *Lutraria lutraria* (L.). *J. Mar. Biol. Ass. U.K.* **27**, 585–596.