

ON THE HABITS AND ADAPTATIONS OF *ALOIDIS (CORBULA) GIBBA*

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(Text-figs. 1-14)

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INTRODUCTION

Aloidis (Corbula) gibba (Olivi) is a small marine eulamellibranch belonging to the Myacea. It is an inhabitant of muddy gravel substrata from below the Laminaria zone to depths of some 80 fathoms, and ranges from Norway to the Mediterranean (Jeffreys, 1865). It is so typical a member of the bottom fauna that Forbes and Hanley (1853) remark that 'its extreme prevalence is a subject of almost petulant complaint from the habitual dredger'. The genus *Aloidis* has many species widely distributed on suitable substrata throughout the world, especially in the tropics, but there are a still greater number of fossil species ranging from the lower Oolite. Despite the abundance of *A. gibba* in British waters, little is known of its habits and nothing of the adaptations which have been responsible for its outstanding success over so wide a period of space and of time as a member of the mud fauna.

Specimens were obtained in adequate numbers by dredging in depths of between 9 and 12 fathoms in Balloch Bay, Isle of Cumbrae, and these were later examined in the Millport Laboratory. Acknowledgements are gladly made for assistance from the Director of the Station, Mr R. Elmhirst, and from members of the staff. The author is also indebted to his colleague, Dr H. F. Steedman, for histological assistance.

SHELL FORM

The specimens collected ranged in size from 0.5 cm. in length up to a maximum of 1.2 cm. long by 0.9 cm. deep. The shell is strikingly asymmetrical, the right valve being, in the words of Jeffreys (1865), 'much larger and more gibbous than the left which it overhangs to a considerable extent'. A variety of Lamellibranchia are inequivalve, e.g. the Anomiidae, many Pectinidae, *Spondylus*, *Ostrea* and the Chamidae. But these are all attached,

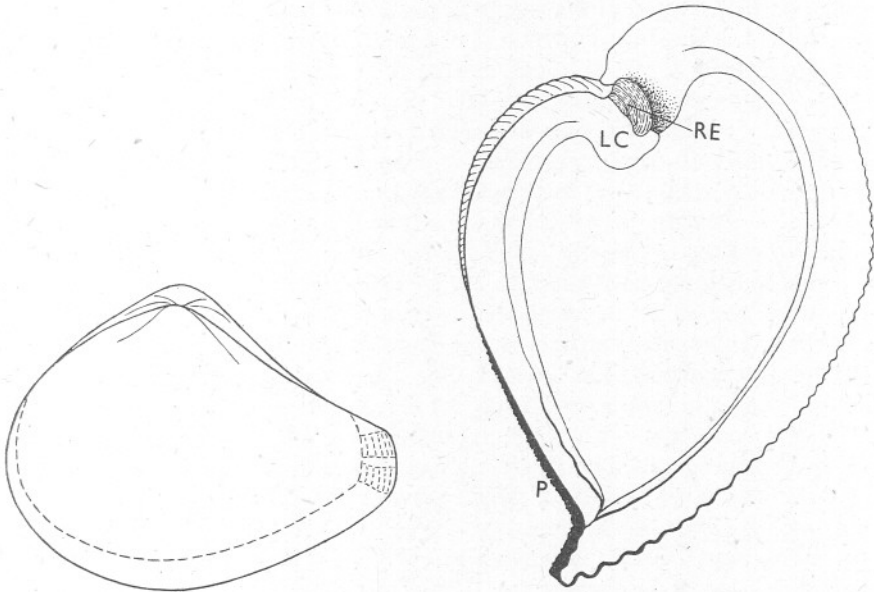


Fig. 1.

Fig. 2.

Fig. 1. *Aloidis gibba*, shell viewed from left side. $\times 4$. Broken line indicates the extent of calcification in the left valve with the calcified marginal plates protecting the siphons shown.

Fig. 2. *A. gibba*, radial section through shell viewed from posterior showing resilium and hinge dorsally and intucking of uncalcified margin of the left valve ventrally. $\times 12$. LC, left cardinal tooth; P, thick periostracum on left valve; RE, resilium.

by byssus or by cementation, with one valve underneath except for the free-living Pectinidae, such as *Pecten maximus*, which retain the horizontal disposition of the shell valves as a legacy from former byssal attachment (Yonge, 1936). Apparently *Pandora*, of the habits of which nothing is known, is the only lamellibranch apart from *Aloidis* in which an inequivalve shell is *not* associated with its horizontal disposition.

The relative size of the shell valves is shown in lateral view in Fig. 1 and in section in Fig. 2. It will be observed that, although the left valve fits into the right one, this is due not only to the smaller size of the former but also to a lack of calcification in the marginal zone. Approximately the outer ninth

of the valve consists exclusively of periostracum which, as shown in Fig. 2, fits tightly against the marginal region of the right valve when the shell is closed. This interesting point appears to have been overlooked by previous workers, none of whom, however, has undertaken a special study of this genus. Both Forbes & Hanley and later Jeffreys note the especially dense and somewhat fibrous periostracum ("epidermis") around the marginal area of the smaller valve (Figs. 2, 3, *P*) and to a less extent of the larger one. It is relatively soft and so rapidly worn away on the exposed, convex surfaces of both valves. In the posterior region of the marginal periostracum of the left valve there are two calcified areas (Fig. 1) which give added protection to the siphons when these are extruded. These areas consist of overlapping scales of calcareous matter. No previous reference to their presence in *A. gibba* has been found. They are not visible externally although easily seen from within, but they will be rubbed off with the periostracum in a dead shell. A very similar accessory area in the left shell valve, but apparently of a more solid character, has been described by Martin (1879-80) and Vincent (1890, 1909) in fossil species of *Corbula* and later by Martin (1918) in the recent *C. tunicata*. These authors also regarded this area of calcification as affording protection to the siphons.

Owing to the extent to which the margins of the shell valves are in contact when the adductors are contracted, the mantle edge is withdrawn some distance from the edge of the shell as shown in Fig. 3 A. The mantle edge has the typical tri-lobed character (see Yonge (1936) for details and references), the outer lobe (*OL*) being concerned with the secretion of the outer, calcareous layers of the shell and the periostracum (*P*) arising from the pit between it and the middle lobe (*ML*) the outer surface of which serves to guide the periostracum. This is thrown into folds on the outer surface of the shell and its secretion appears to be continuous because, as shown in Fig. 3 A, it lines the inner side of the marginal regions of the shell valves. This internal layer of periostracum is most developed at the two ends of the shell. Apart from the fact that the left mantle edge does not (after fixation) extend quite so far as the right one the two edges are essentially similar. But the absence of marginal calcification in the left shell valve indicates that the mantle edges must function somewhat differently when the valves are being enlarged. The right mantle edge will then secrete the outer calcareous layers of the shell (the nature of which has not been investigated; see Trueman (1942) for details and literature) and the periostracum at the margin together as in lamellibranchs generally. The probable positions of the outer and middle lobes of the mantle edge during this process are shown in Fig. 3 B, *r*. But the left mantle edge must be capable of laying down periostracum beyond the zone of calcified shell. A possible method whereby this could be brought about is indicated in Fig. 3 B, *l*. The outer lobe of the mantle edge is shown adding to the outer calcareous layers of the shell while the middle lobe, greatly extended (easily possible in lamellibranchs by distension with blood) guides the thick periostracal thread further out to extend the effective margin of the shell valve. The great variation in form and

function found in the marginal mantle lobes of the lamellibranchs makes this suggestion not improbable.

The shell is very thick as shown in Fig. 2, and the inner calcareous layer is especially dense. Jeffreys records numerous instances of shells bored by *Natica* in which the gastropod seems unable to penetrate beyond the somewhat chalky outer layers. These observations have been abundantly confirmed.

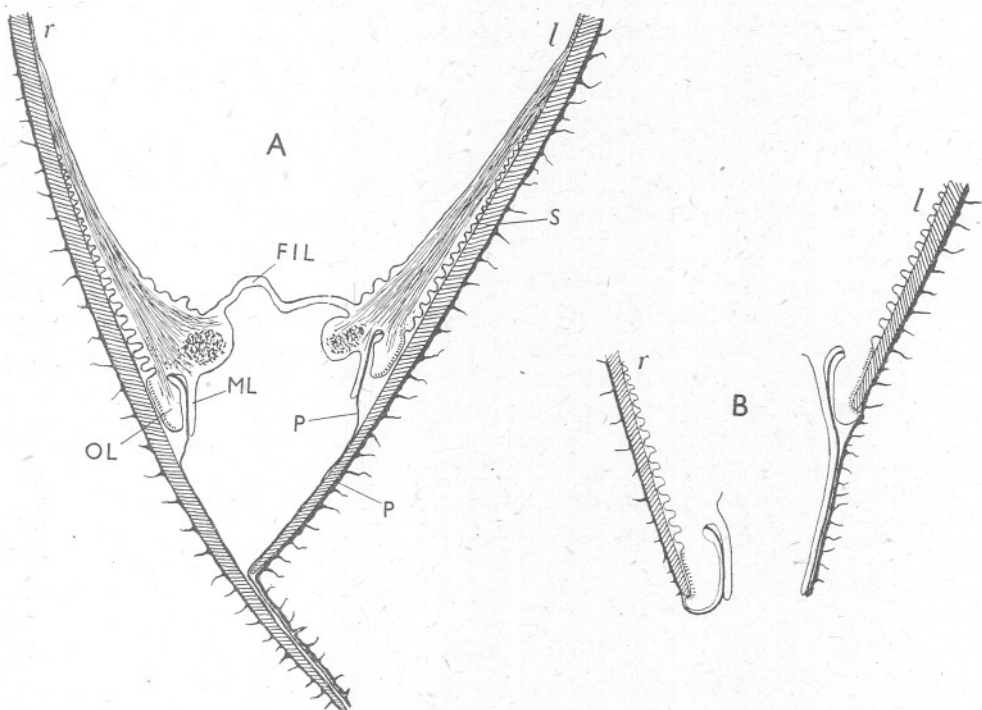


Fig. 3. *A. gibba*, transverse sections through margins of shell valves and mantle, viewed from anterior. A, semi-diagrammatical representation of conditions when shell closed and mantle edges withdrawn; B, indication of possible manner in which asymmetry of valves produced. $\times 100$. FIL, fused inner lobe of mantle edge; ML, middle lobe, outer surface of which guides periostracum; OL, outer lobe which secretes outer calcareous layers of shell; P, periostracum; S, shell. r, l, right and left valves.

The hinge mechanism consists of a prominent recurved cardinal tooth in the right valve (Fig. 7, RC) and a more posterior, spoon-shaped cardinal in the left valve (Fig. 2, LC) with elongated lateral teeth on either side of each (Fig. 7). Into the cavity of the left cardinal tooth there fits the internal elastic ligament or resilium (Fig. 2, RE). This is roughly triangular in section (Fig. 7, RE) and is attached on the other valve within a cavity posterior to the right cardinal tooth as shown in Fig. 2. The partly external fibrous ligament (Fig. 7, EL) is a distinct structure lying dorsal to the resilium but is poorly

developed and hard to distinguish. If the ventral region of the shell valves are broken away, the tissues removed and the resilium then cut through from below, the valves drop apart because the external ligament unaided is too weak to hold them together. *Aloidis gibba* thus approaches the condition found in *Pholas* and other Adesmacea in which the external ligament has been lost and the shell valves are consequently enabled to rock in the antero-posterior axis, on the fulcrum of the condensed resilium (Anthony, 1905). This is an essential feature in the boring mechanism of these animals. In *Aloidis gibba* the reduction of the external ligament, although it also occurs to a less extent in allied members of the Myacea, is possibly associated with the asymmetry of the shell valves. A slight antero-posterior rocking action may be needed to enable the left valve to fit within the right one. The resilium is relatively long from one valve to the other and so permits the extensive hinge movements needed to enable the margins of the left shell valve to tuck into those of the right valve.

HABITAT AND HABITS

A. gibba is a typical inhabitant of thick muddy sand with admixed gravel and small stones. In Balloch Bay it inhabits this type of substratum in company with such other burrowing mollusca as *Nucula nucleus* and *Nuculana (Leda) minuta* (herbivorous deposit feeders; Yonge, 1939); *Aporrhais pes-pelecani* (herbivorous deposit feeder; Yonge, 1937); *Turritella communis* (ciliary suspension feeder; Graham, 1938; Yonge, 1946); *Venus* spp. (ciliary suspension feeders); *Cuspidaria cuspidata* (carnivorous deposit feeder; Yonge, 1928) and species of *Natica* (boring carnivores).



Fig. 4. *A. gibba*, with foot extruded. $\times 4$.

When placed on softer mud without gravel, *Aloidis gibba* appears to find difficulty in maintaining its siphons flush with the surface. The same difficulty has been noted in the case of *Aporrhais pes-pelecani* (Yonge, 1937) and *Turritella communis* (Yonge, 1946). On the other hand *Aporrhais serresiana*, specialized for life in soft mud, experiences difficulty in burrowing in a stiffer substratum (Yonge, 1937).

Placed on its normal substratum, *Aloidis gibba* extrudes the thin foot, rounded in cross-section, to a distance which may exceed the length of the shell (Fig. 4). A thin byssus groove extends along the under (posterior) surface (see Fig. 8). Cilia line the sides of this groove and beat towards the body. Their function is not obvious. In burrowing, the foot pushes almost vertically down and the

animal is drawn after it as a result of a series of intermittent but powerful contractions of the pedal muscles. At each of these the shell is erected almost vertically to fall back to an angle with the horizontal which gradually increases as burrowing progresses. When finally buried the long axis of the body is usually more or less vertical. The posterior end of the shell is then flush with, or slightly below, the surface of the mud. The last act of the foot is to plant a single byssus thread on a suitable piece of gravel or stone. Anchored in this way, the animal appears seldom to change position unless forcibly disturbed.

The process of burrowing is slow. For instance, an animal 1 cm. long took about 30 min. and, owing to the long intervals between successive contractions of the pedal muscles, the process is often slower. On the other hand specimens of *Abra abra* of about the same shell length disappeared below the surface in less than a minute. It is interesting to compare the two species, *A. gibba* a sedentary suspension feeder and *Abra abra* a deposit feeder which has frequently to change its feeding area (the inhalant siphon actively draws in the surface deposits). The former has a stout rounded shell and makes slow and difficult progress into the stiff substratum whereas the latter has a much flattened shell and foot and slides quickly into the softer mud it inhabits. The same contrast in habits is found in the gastropods *Turritella communis* and *Aporrhais pes-pelecani* which feed respectively in the same two ways (Yonge, 1946).

SIPHONS

As shown in Figs. 5 and 7, the siphons of *Aloidis gibba* are very short. The common sheath is fringed with some forty or more short tentacles which, when the animal is buried, extend outwards over the surface of the mud (Fig. 5) much as in the septibranch *Poromya* (Yonge, 1928). The inhalant siphon has a relatively large, rounded opening surrounded by a further ring of up to twenty tentacles which point upwards and inwards. The exhalant siphon is tubular, as noted by Forbes and Hanley and by Jeffreys, with a terminal opening smaller than that of the inhalant siphon. In an animal 1 cm. long this siphon was 1.75 mm. in length. The tentacles are colourless, but the siphons generally are flecked with reddish orange and opaque white areas, the edge of the mantle below being fringed with a dark brown band.

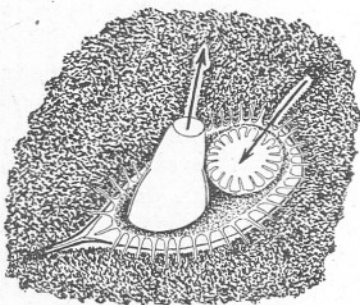


Fig. 5. *A. gibba*, siphons fully open after the animal has burrowed in the substratum. $\times 20$. Arrows indicate the direction of the inhalant and exhalant currents.

The activities of the siphons are interesting and highly characteristic. When the shell valves separate and the siphons are extruded, the inhalant siphon opens first and water is drawn in owing to the increase in the volume of the

mantle cavity. The water passes through the ctenidia into the exhalant chamber and, apparently when a certain pressure of water is reached, the exhalant siphon, hitherto withdrawn, is extruded and opens. At the same time the inhalant siphon opens to its fullest extent (Fig. 5). An exceptionally powerful inhalant current is set up owing to the relatively large size of the ctenidia (see later section). Much sand and mud are frequently drawn in with this; the tentacles surrounding the inhalant opening are very insensitive, although they do appear to have some function as strainers by preventing the entrance of relatively very large particles. But a continuous stream of sediment may be introduced into the opening, by pushing it in from the surrounding substratum with a needle, without causing the siphon to close.

Eventually this continual inward passage of sediment does result in the contraction of the adductor muscles and the closure of both siphons. The exhalant siphon is very sensitive to contact stimuli closing immediately when

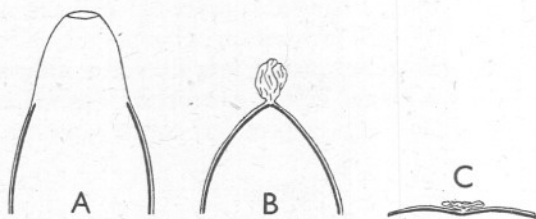


Fig. 6. *A. gibba*, diagrams to illustrate mode of closure of the exhalant siphon. A, open; B, partial contraction of the closing muscles; C, complete contraction.

touched with particles of mud or by the tip of a needle. By stopping the free passage of water through the mantle cavity, such closures cause a temporary stoppage of the inhalant current although the siphon remains open.

Closure of the exhalant siphon is produced by the contraction of two paired bands of muscles, one on the dorsal and the other on the ventral side. These muscles extend from the base along rather more than half the length of the siphon (Figs. 5, 6), a shallow encircling concavity marking their termination. The process of siphonal closure is indicated, semi-diagrammatically, in Fig. 6 A-C. In partial closure, which frequently follows mechanical stimulation, the muscles arch inwards until they meet while the distal regions of the siphon are gathered into a folded mass (B). This is usually followed, after a few seconds, by re-opening (as in A). More powerful external stimulation, and also stimulation from within the mantle cavity, causes the complete contraction indicated in C. The muscles then become horizontal, the proximal region of the siphon collapsing while the distal portion is gathered into a compact folded mass. Subsequent contraction of the siphonal retractors brings about a folding of the common siphonal sheath over both siphons and their complete withdrawal within the protection of the shell. On relaxation

of the muscles the siphons are again protruded, opening of the inhalant again preceding that of the exhalant siphon.

The form of the exhalant siphon and the restricted opening which concentrates the exhalant current combine to direct the powerful stream of water well clear of the inhalant opening, as indicated in Fig. 5, and also prevent stirring up of the soft surface deposits.

The relatively very large quantities of bottom material which must normally be carried in with the inhalant current lead to great accumulations of this within the inhalant chamber where, as in lamellibranchs generally, it is consolidated with mucus into pseudo-faeces and carried by ciliary currents along the ventral side of the mantle cavity to the posterior end where it collects (Fig. 7, *PS*). From time to time these masses are removed in the usual manner, namely by sudden contractions of the 'quick' portions of the two adductors which are well developed (Fig. 7, *AQ*, *PQ*). If the accumulations are small, partial contractions occur but on occasions the inhalant chamber must be almost filled with pseudo-faeces and then more powerful contractions are needed. Here the asymmetry of the shell probably plays its part by permitting a much greater reduction in the size of the cavity with a correspondingly greater outflow through the inhalant siphon than is possible in a bivalve with symmetrical shell valves. It may be that this process is assisted by a certain rocking action, the contraction of the anterior slightly preceding that of the posterior adductor, a process made possible, as already indicated, by the reduction of the external ligament and concentration of the resilium. The same need for extrusion of large masses of sediment carried into the mantle cavity appears to be the reason for the lack of marginal calcification in both valves of the protobranch, *Solenomya*, where both margins tuck in when the adductors contract (Yonge, 1939).

On one occasion, after much sediment had been taken into the mantle cavity of *Aloidis gibba*, the unique spectacle was seen of the tip of the foot being pushed out through the inhalant siphon. After groping round the surface of the surrounding substratum for about a minute or less the foot was withdrawn. To perform this operation the foot must have twisted round within the mantle cavity so that its tip pointed posteriorly. This extrusion was only observed once, but it may represent an extreme method of clearing the mantle cavity comparable to the action of the swab-like mantle gland of the Pinnidae (Grave, 1911) although this lies in the exhalant chamber. The habits of the animals are not dissimilar; both the Pinnidae and *A. gibba* live vertically embedded in the substratum with the exhalant opening in the one case and the inhalant opening in the other flush with the surface and liable to take in much bottom material. Both are sedentary and attached by byssus, although to a much greater extent and more permanently in the Pinnidae.

PALLIAL ORGANS

The appearance of the animal after the left shell valve and mantle fold have been removed is shown in Fig. 7. The mantle margins are fused except in the region of the siphons and of the long pedal gape, the margins of which are lined with tentacles (*T*) arising from the middle lobe of the mantle margin. The adductors are well developed and each approximately equally divided

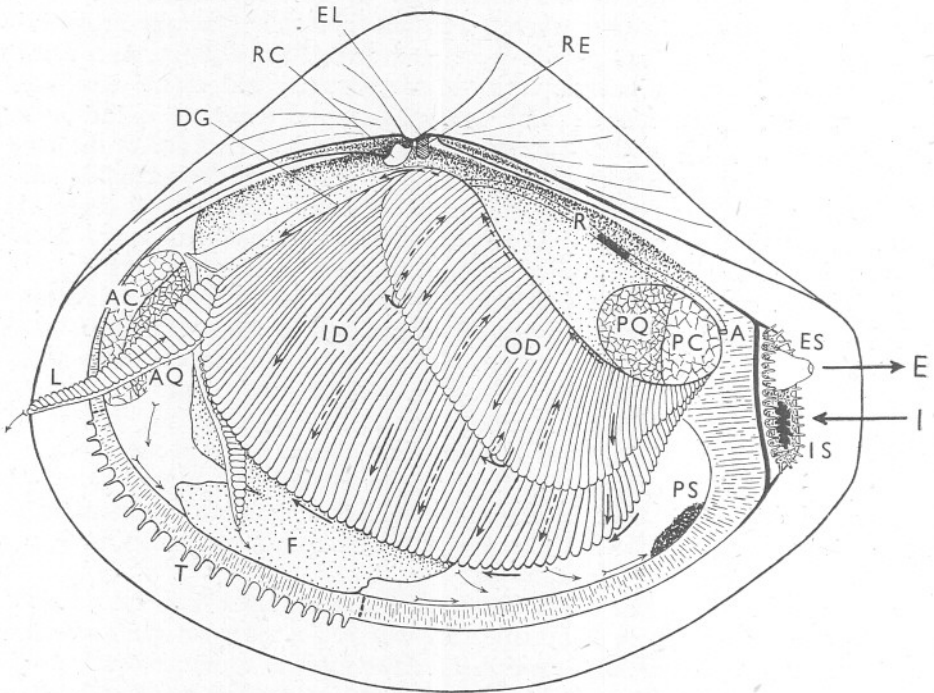


Fig. 7. *A. gibba*, body exposed after removal of the left shell valve and mantle lobe. $\times 10$. A, anus; AC, AQ, 'catch' and 'quick' muscles of anterior adductor; DG, distal oral groove; EL, external ligament; ES, exhalant siphon; F, foot; ID, inner demibranch of left ctenidium; IS, inhalant siphon; L, labial palp; OD, outer demibranch; PC, PQ, 'catch' and 'quick' muscles of posterior adductor; PS, pseudo-faeces; R, rectum; RC, right cardinal tooth; T, tentacles on right mantle lobe lining pedal gape. Other lettering as before. Large arrows indicate inhalant (I) and exhalant (E) currents; small arrows ciliary currents on exposed surfaces, broken arrows currents on inner surfaces of demibranchs; feathered arrows rejection currents.

between outer 'catch' (AC, PC) and inner 'quick' muscle (AQ, PQ). The reason for the considerable development of the latter has already been noted. The ctenidia, details of which are given in the next section, consist of moderate sized outer (OD), and very larger inner (ID), demibranchs. The labial palps (L) are long with the usual ridges on their inner faces. They function in the customary manner, selecting smaller particles and masses and rejecting larger ones from their tips whence they pass on to the surface of the mantle. Here,

together with material rejected from the ctenidia (see next section), they are carried ventrally, as indicated by the feathered arrows in Fig. 7, and then posteriorly (i.e. upward) to accumulate as mucus-laden pseudo-faeces (*PS*) at the base of the inhalant siphon for later ejection. Paired masses of mucous glands, one on either side of the pedal gape, the other near the base of the siphon, provide the necessary mucus.

CTENIDIA AND FEEDING

The arrangement of the ctenidia in semi-diagrammatic transverse section is shown in Fig. 8. There is a certain asymmetry between the two due to that of the shell valves and mantle, but this in no way affects their function. The inner lamellae of the inner demibranchs are not fused to the side of the visceral mass for some distance about the middle of their length as shown in Fig. 8¹. Instead there is a ciliary connexion which separates on fixation and very readily in life so that direct connexion can here be temporarily established between the inhalant chamber below, and the exhalant chamber above, the ctenidia, and this may well be associated with the almost complete obliteration of the inhalant chamber when the shell is closed and the margin of the left valve tucks into that of the right valve. This will force water upward against the ctenidia and might impose an undue strain upon them were it not for this region of possible free passage into the exhalant chamber. It was noted in the intact animal that carmine added to the inhalant current was occasionally ejected by way of the exhalant siphon and so was other material, apart from the faecal pellets. This material may have passed into the exhalant chamber by way of these openings from the inhalant chamber.

As shown in Figs. 7 and 8, material is carried by the frontal cilia to the free margin on the outer side of the outer demibranchs and on both sides of the inner demibranchs, but to the axis on the inner side of the outer demibranchs. There is no food groove along the free margin of the outer demibranchs and material passes to the labial palps by way of the axis or by way of the food groove along the free margin of inner demibranchs. This agrees with the condition found in many other eulamellibranchs (Atkins, 1937*b*) although, as described below, there are a variety of interesting modifications in *A. gibba*. Material from the food grooves passes directly between the palps (see Fig. 7); material from the axis reaches the palps by way of the long distal oral groove (*DG*).

The detailed structure of the ctenidia is interesting and worthy of full description because *Aloidis* is one of the few British genera of Lamellibranchia the ctenidia of which have not been described by Atkins (1936, 1937*a*, 1937*b*, 1938, 1943) in her very beautifully detailed series of papers. The gill lamellae are flat and homorhabdic, i.e. all filaments are similar without enlarged principal filaments on which the frontal ciliation may differ from that of the ordinary filaments as in *Ostrea* (Yonge, 1926) and many other species (Atkins, 1936, 1937*b*). Interlamellar junctions (not indicated in Fig. 8) are numerous

¹ This limited freedom of the inner demibranch is found in other eulamellibranchia e.g. *Anodonta*.

although it is possible to separate the two lamellae of a demibranch by means of needles. The filaments are some 35μ broad and are relatively widely separated by distances of 20μ or more, this space being well guarded by the long latero-frontal cilia (*LFC*) as shown in Figs. 10 and 12. Adjacent filaments are united by interfilamentary junctions arranged in rows some 180μ apart. These run along the inner (suprabranchial) surface of the filaments and the skeletal supporting rods within the filaments are continued through them. Thus when

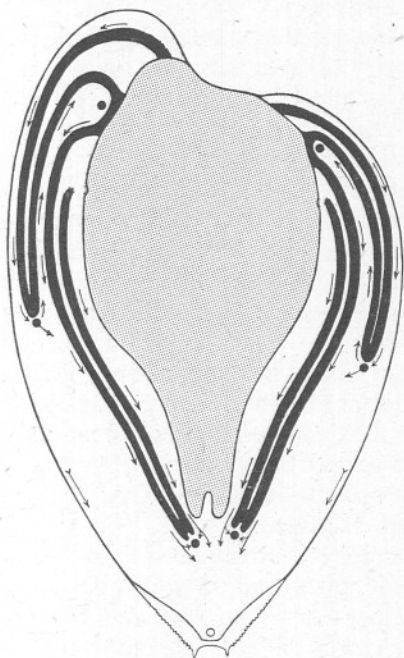


Fig. 8.

Fig. 8. *A. gibba*, semi-diagrammatical transverse section through middle of visceral mass, viewed from anterior. $\times 30$. Arrows indicate direction of ciliary currents, filled circles position of currents directed towards mouth, hollow circle position of main rejection current for pseudo-faeces. The ciliary junctions between the inner lamellae of the inner demibranchs and the visceral mass are indicated.

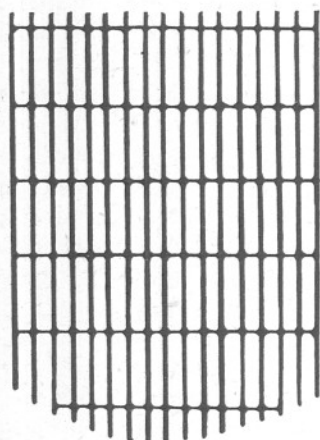


Fig. 9.

Fig. 9. *A. gibba*, portion of edge of ctenidial lamella macerated to show the lattice-like skeletal framework. $\times 50$.

the lamellae are macerated a lattice-like skeletal framework remains as shown in Fig. 9. These skeletal cross connexions, noted by Ridewood (1903) and described by Elsey (1935) in *Ostrea*, are very well developed in *Aloidis gibba* where the added support they supply permits the presence of the wide ostia (*O*) needed for the through passage of the powerful water currents.

Throughout the ctenidia lateral cilia (*LC*) are well developed and most active, producing the powerful respiratory and feeding current. Latero-frontal cilia (*LFC*) are large, some 30μ long, and agree with the description given by Atkins (1938) of eu-latero-frontal cilia having smaller subsidiary

pro-latero-frontal cilia (detectable only in sections) between them and the frontal cilia (*FC*) which are, as usual, small.

In the inner demibranch (Figs. 10, 11) the frontals give place, some 100μ from the free margin, to increasingly long terminal cilia (*TC*), which attain a length of 25μ . Near the margin these cilia deflect particles anteriorly. The food groove (*FG*) is protected on either side by a rampart of fine guarding

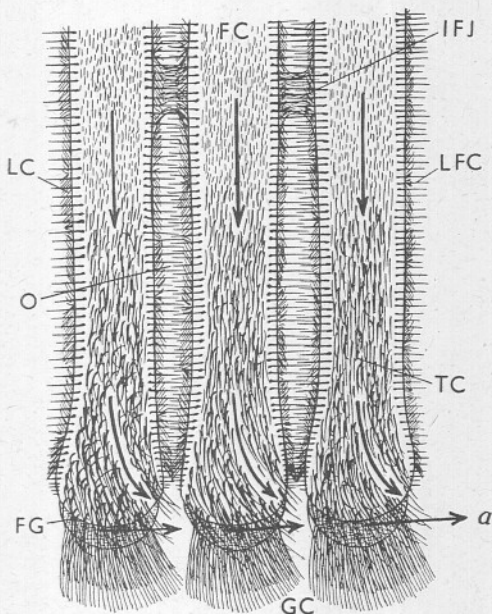


Fig. 10.

Fig. 10. *A. gibba*, portion of outer surface of inner lamella of right demibranch showing the food groove. $\times 290$. *FC*, frontal cilia; *FG*, food groove; *GC*, guarding cilia; *IFJ*, interfilamentary junction; *LC*, lateral cilia; *LFC*, latero-frontal cilia; *O*, ostium; *TC*, terminal cilia. Arrows indicate direction of ciliary currents, those in food groove being directed anteriorly (*a*).

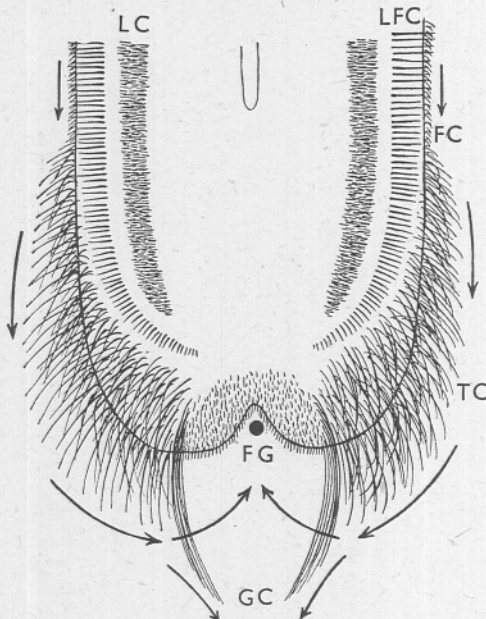


Fig. 11.

Fig. 11. *A. gibba*, lateral view of free margin of a single filament from inner demibranch. $\times 450$. Lettering as before.

cilia (*GC*) up to 45μ in length, which do not beat but act as a sieve preventing any but the finest particles from entering the food groove. Larger particles, as shown in Figs. 8 and 11, are largely deflected on to the mantle surface, whence they join the mass of pseudo-faeces. Atkins (1937*a*) has described guarding cilia in a variety of other lamellibranchs, and associated their presence with life in a substratum containing silt or mud. This correlation exists also in the case of *Aloidis*.

The outer demibranch (Figs. 12, 13) shows interesting differences from the inner one. As already noted there is no food groove, but a group of terminal cilia (*TC*) extending round from the free margin for some little distance along the inner face (see Fig. 13) deflect larger particles anteriorly, so that they

are carried for a short distance along the free margin but are soon transferred to the outer surface of the inner demibranch where they are carried towards the food groove. These terminal cilia on the outer demibranch thus act as a selective mechanism, preventing larger particles from passing along the inner surface of the demibranch and so into the food stream along the axis (see Fig. 8). It is interesting to note that the terminal cilia only extend over the posterior half of the tip of the filaments in the posterior region of the outer

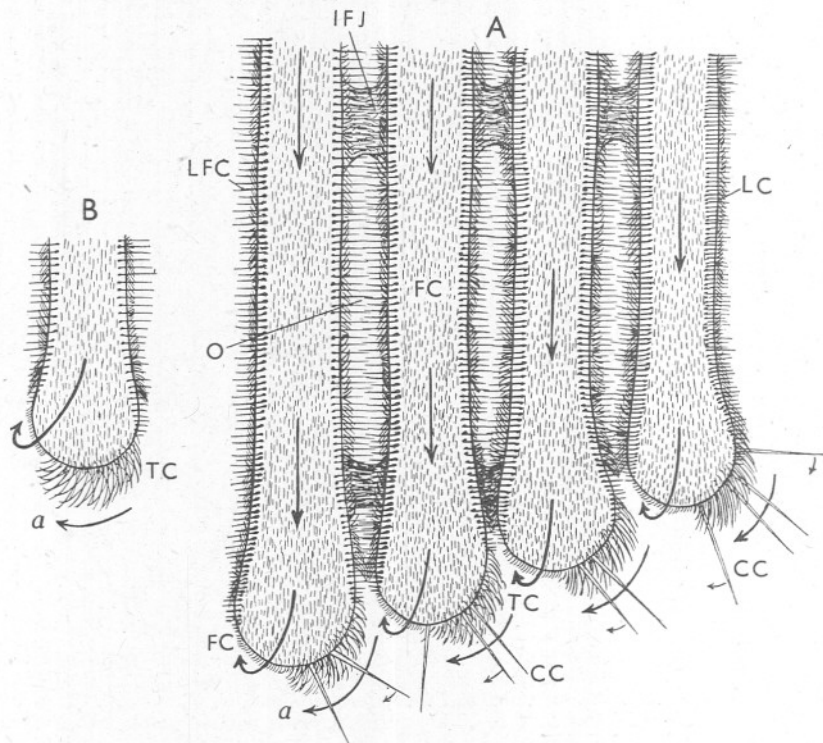


Fig. 12. *A. gibba*, portions of outer surface of outer lamella of left demibranch; A, filaments from posterior end of lamella; B, filament from anterior end. $\times 290$. CC, coarse cirrus-like cilia. Other lettering as before.

demibranch (Fig. 12A) but gradually extend further forward until, in the anterior filaments, they cover the greater part of the free margin (Fig. 12B). The zone of unmodified frontal cilia is gradually displaced from the anterior half of the tip of the filaments round to the anterior surface (compare Fig. 12 A, B).

Coarse, cirrus-like cilia (Fig. 12, CC) some 50μ long, occur along the free margin of the inner demibranch. They are very numerous posteriorly, as many as four or five occurring on the tip of each filament, but they gradually diminish anteriorly and finally disappear (Fig. 12B). Similar cilia have been described in a variety of lamellibranchs (see Atkins, 1937*b*). They apparently

only beat on stimulation when they execute a relatively slow forward movement as indicated in Fig. 12. They are concerned with the movement of large particles and masses which tend to accumulate at the free margin, and they reinforce the action of the terminal cilia. Similar coarse cilia occur scattered at intervals of between 40 and 80μ over the inner surface of the outer demibranch (Fig. 13, CC) and, more sparsely, over the outer surface of the inner demibranch. They arise on the frontal surface near the posterior margin, extending over the breadth of the filament behind. Their beat is directed anteriorly, and so at right angles to the line of the filaments. Presumably in life they tend to move large particles forward between the opposed faces of the two demibranchs, but no appreciable activity was observed when the demibranchs were laid flat for inspection under the microscope.

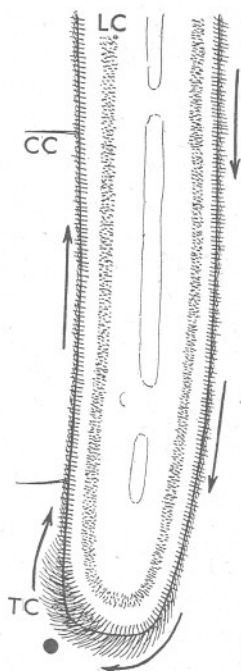


Fig. 13.

Fig. 13. *A. gibba*, lateral view of free margin of a single filament from outer demibranch. $\times 225$. Lettering as before.

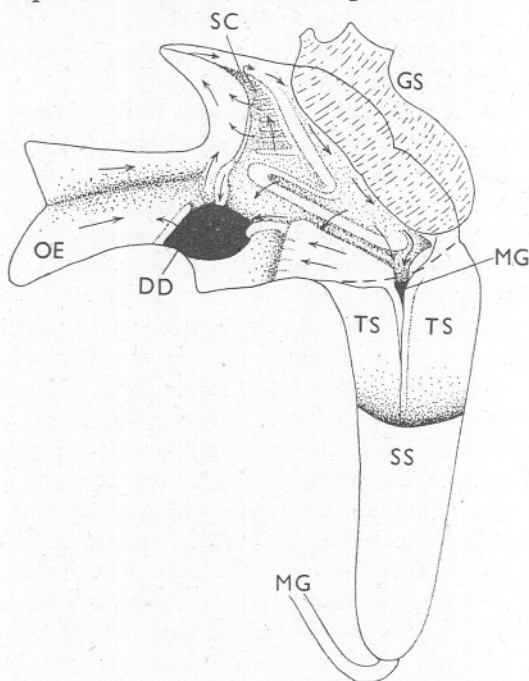


Fig. 14.

Fig. 14. *A. gibba*, stomach opened from right side. $\times 20$. DD, single duct into digestive diverticula; GS, gastric shield; MG, mid-gut, opening from stomach and its separate course after end of style-sac; OE, oesophagus; SC, food-sorting caecum; SS, style-sac (cut away above, limit indicated by broken line); TS, typhlosoles separating cavities of style-sac and mid-gut. Arrows indicate direction of currents in stomach.

ALIMENTARY CANAL

The main feature of the alimentary canal is the relatively very large size of the stomach which lies somewhat to the left side of the visceral mass, the mid-gut coiling below and to the right of it. The appearance of the stomach when

opened from the left side is shown in Fig. 14. Material passed into the mouth from the labial palps is carried along the broad oesophagus (*OE*) into the elongated stomach. Into this opens a very broad style-sac (*SS*) which must normally contain a massive crystalline style. But the style-sac is in communication with the mid-gut, the two cavities being separated only by the two projecting typhlosoles (*TS*), and, as in all lamellibranchs without a separate style-sac, the style is dissolved when the normal activities of the animal are suspended (Yonge, 1926). It is interesting to note that, in the allied genus *Mya*, the style-sac is separated from the intestine (Yonge, 1923). The size of the style is indicated by the extensive gastric shield (*GS*), against which the head of the style bears normally, which covers the entire roof of the stomach. In life the style will rotate against this structure and the contents of the stomach be kept in continual slow circulation, any free starch from the plant constituents in the food being digested by the amylase liberated from the slowly dissolving mass of the style.

As in all lamellibranchs, the walls of the stomach are everywhere ciliated except for the region covered by the gastric shield. The effect of this ciliation, broadly speaking, is to separate the stomach contents into larger particles which are carried into the opening of the mid-gut (*MG*) and smaller ones which pass into the single, large opening into the digestive diverticula (*DD*). In lamellibranchs, generally, this separation is largely carried out by a food-sorting caecum such as that described in *Modiolus* (Nelson, 1918), *Mya* (Yonge, 1923) or *Ostrea* (Yonge, 1926). Such a caecum (*SC*) occurs in the stomach of *Aloidis gibba*, but is not well developed, and the details of its mode of operation (which must, of course, be considered in relation to the closed stomach with the style rotating within it) are difficult to determine with accuracy. Cilia, on the summits of a series of low ridges, carry particles to the tip of the caecum whence they turn and are carried along the side of the gastric shield and into the opening of the mid-gut. Smaller particles that pass into the intervening grooves are carried to the left (in the figure), and so pass either along a ridge into the large duct of the digestive diverticula or else into the zone occupied in life by the revolving head of the style. Cilia on the floor of the stomach beat towards the opening into the digestive diverticula. The single opening of this is unusual, there being, for instance, two openings in *Mya* and three in *Ostrea*. Material enters primarily by way of two ridges, one on the floor of the stomach and the other from the side of the food-sorting caecum; material rejected after intracellular digestion within the cells of the tubules of the diverticula is extruded along the side bordering the oesophagus as shown in Fig. 14.

The large size of the stomach, and possibly the single large opening into the digestive diverticula, is presumably correlated with the nature of the food, which is mixed with much inedible matter in the form of fine particles of mud and sand. In other words, a great deal of material has to enter the gut if the animal is to be able to obtain adequate nutrition from the relatively small proportion of organic matter contained in this. Selection on the gills and

palps is certainly effective in preventing large particles from entering the gut, but occasional sand grains up to 35μ in diameter were found in the mid-gut.

The structure of the digestive diverticula, of the mid-gut and of the rectum (Fig. 7, R) calls for no special comment. The two latter regions are concerned exclusively with the consolidation of the material passed on from the stomach into compact, rounded faecal pellets, in which form they are expelled from the anus (Fig. 7, A) and ejected with force through the exhalant siphon.

REPRODUCTION

In the course of this work certain general observations were made on reproduction. *Aloidis gibba* is not hermaphrodite and no evidence of change in sex was found. When the gonads are maturing it is easy to distinguish the males with white testes from the females with pink ovaries. When observations began in early August the gonads were filling but not ripe, the testes appearing better developed than the ovaries, but there were no active sperm. By the end of August the ovaries were filling, but ripe sperm were not found until the middle of September. Specimens examined on 25 September had ripe gonads, the relatively large, yolky eggs rounding off when liberated and the sperm being very active. Bad weather prevented further collecting until 10 October when all individuals, of both sexes, were spent.

It appears, therefore, that spawning occurs about the beginning of October. The only other mollusc from the same habitat which spawns at that time appears to be *Cuspidaria cuspidata*, the gonads of which were ripening with those of *Aloidis gibba* in late September, although no specimens were obtained later to prove the actual time of spawning. The other molluscs were all spent in August and had presumably spawned in spring or early summer. This autumnal spawning in *A. gibba* may indicate origin in deep water, already postulated for other reasons in *Cuspidaria* (Yonge, 1928), where the highest temperatures occur late in the season. Whether there is sufficient yolk in the eggs to permit of direct development or with a much shortened larval life, as in the great majority of arctic and arctic-boreal lamellibranchs examined by Thorson (1936) and also characteristic of deep-sea species, remains to be determined. Incubation in the mantle cavity does apparently not occur.

DISCUSSION

- *Aloidis (Corbula) gibba* is specialized for life in a substratum of muddy sand mixed with larger pieces of gravel and stone necessary for the planting of the single byssus thread. This habit of attachment, together with the rounded shell and the tapering foot which make movement cumbersome and slow, indicates a sedentary mode of life which observation has confirmed. The majority of mud- and sand-dwelling lamellibranchs are relatively mobile, apart from the filibranch Pinnidae, in which byssal attachment is highly developed, and *Panope* (the geoduck of the northern Pacific coasts of North America), in which the power of locomotion is lost and the animal relies for protection on

the exceptionally deep burrow made possible by the great length of the very extensive siphons.

In *Aloidis gibba* the inhalant siphon is flush with the surface of the substratum so that the feeding current is drawn in from the lowest water levels, and so contains much bottom material which will include bottom-living diatoms and bacteria as well as much organic debris. The animal is thus in a position to tap a valuable source of food. The necessary force to draw in this suspended material is supplied by the lateral cilia on the very extensive ctenidial surface. The wide ostia on the ctenidia aid in this, general support being given by the well developed lattice-work of skeletal rods. There is little evidence, either from observation of the living ctenidia or from sections, of a muscular control of the size of the ostia such as that demonstrated in life by Elsey (1935) and Nelson & Allison (1940) in species of *Ostrea*. Control of 'pumping' in *Aloidis gibba* appears to be largely, if not entirely, the function of the highly sensitive exhalant siphon with its two paired bands of closing muscles. There is the usual branchial musculature, details of which are given by Elsey (1935) and Atkins (1943), which will enable the ctenidia and the individual demibranchs to shorten when the shell closes, and possibly also the demibranchs of each side to draw together. But there is no such muscular aid to the selective activities of the gill as exist in genera such as *Ostrea* with plicated ctenidia (Yonge, 1926; Elsey, 1935).

An inevitable result of the collection of food from near the surface of the substratum is the accompanying entrance of much inorganic bottom material. It becomes necessary to dispose of the great mass of pseudo-faeces which consequently accumulates. This involves: (a) The asymmetry of the shell which enables the inhalant chamber to be largely obliterated when the adductors contract. In association with this are possibly the reduction in the external ligament and condensation of the resilium, and also probably the free communication between the inhalant and exhalant chambers in the region where the inner lamellae of the inner demibranchs are only attached by ciliary junctions to the visceral mass. (b) The large size of the 'quick' portions of the adductors which provide the force necessary for the periodical expulsions of pseudo-faeces. (c) The occasional action of the foot in clearing the inhalant chamber. (d) The great selective activity of the ctenidia with their highly developed terminal, guarding and cirrus-like cilia. Even after this necessarily quantitative rather than qualitative selection, much material must enter the gut if the animal is to obtain sufficient organic matter for adequate nutrition. The large size of the stomach makes this possible.

The asymmetry of the shell in *A. gibba*, while effectively reducing the inhalant chamber when the shell is closed, is an interesting feature in view of the fact that the same function is apparently performed by the absence of marginal calcification in *both* valves not only in the protobranch *Solenomya*, but also in the allied Pacific genus *Corbula luteola* in which, according to Johnson & Snook (1927), 'the margins turn inward, forming a submarginal ridge'.

SUMMARY

1. *Aloidis* (*Corbula*) *gibba* is a eulamellibranch specialized for life in muddy gravel substrata to depths of up to about 80 fathoms.

2. The shell is asymmetrical, the margin of the smaller, left valve being uncalcified and so fitting within the marginal region of the right valve. A possible manner in which this asymmetry is produced by the differential secretory activities of the two mantle edges is discussed.

3. The marginal periostracum of the left valve has strengthening calcified regions posteriorly, probably to protect the siphons when extruded.

4. The external ligament is reduced and the resilium condensed, possibly permitting some antero-posterior rocking of the shell valves when the adductors contract.

5. The process of burrowing is described; on its completion the animal is anchored by a single byssus thread.

6. The siphons are very short, the tentacles of the siphonal sheath lying on the surface of the substratum. The inhalant siphon is wide and relatively insensitive; it draws in much bottom material. The exhalant siphon is tubular and very sensitive. It is controlled by two paired bands of muscle.

7. The great quantities of pseudo-faeces which accumulate are expelled by periodical contractions of the 'quick' portions of the adductor muscles, the asymmetry of the shell valves causing great reduction in the size of the inhalant chamber. The foot may also assist in clearing the chamber.

8. The large ctenidia create a very powerful current; they are adapted for dealing with large amounts of sediment by means of specialized terminal, guarding and cirrus-like cilia. Control of 'pumping' is primarily by means of the exhalant siphon.

9. The stomach is large in correlation with the great amounts of inorganic material carried in with the food.

10. Spawning occurs in early October.

11. *A. gibba* is regarded as having exploited the rich food supply of diatoms, bacteria and organic debris, on the surface of the substratum. It is specialized for dealing with the large quantities of inorganic matter inevitably taken in with this food.

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