THE FLUID DYNAMICS OF THE BIVALVE MOLLUSCS, MYA AND MARGARITIFERA

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Despite the importance of hydrostatic mechanisms to bivalve molluscs, little was known of their fluid-muscle systems until the possibility was suggested that water pressure in the mantle cavity was related to siphonal movement (Trueman, 1954). Chapman & Newell (1956) demonstrated that the siphons of *Mya* are extended by the actions of the adductor muscles forcing water from the mantle cavity into their canals. Recent investigations, using more modern recording techniques, of bivalves digging in sand, e.g. *Tellina, Donax, Ensis* (Trueman, 1966; Trueman, Brand & Davis, 1966), have further elucidated their fluid-muscle systems. The object of this research was to investigate the hydraulic system of *Mya arenaria*, using continuous recording techniques for pressure, valve and siphonal movements, and to compare it with that of *Margaritifera margaritifera*, a fresh-water clam of similar size. In contrast to the sessile mode of life of *Mya*, *Margaritifera* moves over or burrows actively into sand.

Study of the fluid muscle system of bivalves involves some understanding of the pallial musculature and of the anatomy of the siphon and foot (Fig. 1). The pallial muscles of *Mya* are particularly well developed in the extensive area of fusion between the inner and middle folds of the mantle margins (Fig. 1*a*) (Yonge, 1957). The mantle cavity is thus completely enclosed apart from the siphonal openings and the pedal aperture. When the terminal sphincter muscles (Fig 1*b*) contract and the muscular mantle edges and valvular flaps of the pedal opening are closely applied, the mantle cavity is virtually watertight (Chapman & Newell, 1956; Chapman, 1958). The siphons of *Mya* are joined together to form a large muscular double tube, the inhalant siphon opening at its base into the mantle cavity while the exhalant siphon leads from the epibranchial chamber. The siphons incorporate the inner surface of the outer fold of the mantle margin, being accordingly encased in periostracum (Yonge, 1957), possess haemocoelic blood vessels and contain circular, longitudinal and less conspicuous radial muscles. The longitudinal muscles are effectively the siphonal retractor muscles (Fig 1*b*) and together with the circular muscles control the extension and retraction of the siphons, while the radials may play some part in controlling the volume of the contained blood (Chapman & Newell, 1956).

Margaritifera is a more generalized bivalve with short siphons and free mantle lobes ventrally and anteriorly. In the absence of ventral mantle fusion its mantle cavity, in contrast to that of *Mya*, cannot be made watertight but, when the valves gape, the mantle folds are distended by blood forming a temporary screen around the mantle margins. In most bivalve molluscs the anatomy of the foot follows a common plan (Trueman *et al.* 1966), being divided into dorsal viscero-pedal and ventral musculo-

pedal regions (Fig. 1a). The latter is relatively large and powerful in *Margaritifera*, being used in locomotion, whereas that of *Mya* is reduced and is rarely to be seen protruding from the mantle cavity. The pedal haemocoele passes down to near the tip of the sac-like musculo-pedal region, frequently being crossed by bands of transverse muscle which together with the protractor muscles cause extension of the foot. Retraction is carried out by the paired anterior and posterior pedal retractor muscles.
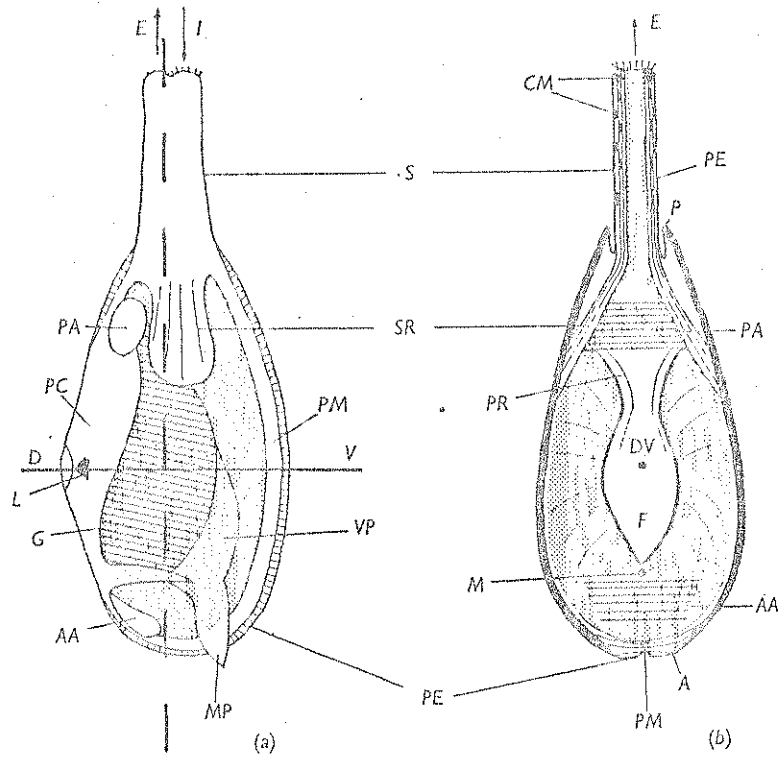

Fig. 1. Diagrams of *Mya arenaria* showing the extent of the mantle cavity (stippled) and the location of the pallial musculature. (a) Specimen with left mantle lobe and valve removed, with the foot protruding through the pedal aperture and with the position of the dorso-ventral axis (*DV*), about which the valves divaricate, indicated. (b) Represents the dorsal part of *Mya* cut in horizontal longitudinal section along the plane indicated by the broken line in (a). Gills and labial palps are omitted to show the extent of the mantle cavity clearly. This section illustrates the antagonistic arrangement of the adductor and siphonal retractor muscles. *A*, anterior margin of valves; *AA*, anterior adductor; *CM*, circular muscles of siphon which form a terminal sphincter; *E*, exhalant ciliary current (arrow); *F*, foot; *G*, gill; *I*, inhalant ciliary current (arrow); *L*, hinge ligament; *M*, mouth; *MP*, musculopedal region of the foot; *P*, posterior margin of valves; *PA*, posterior adductor; *PC*, pericardium; *PE*, periostracum; *PM*, pallial muscles, cross-fused between the lateral mantle lobes ventrally and anteriorly; *PR*, posterior pedal retractor muscles; *S*, siphon; *SR*, siphonal retractor muscle; *VP*, viscero-pedal region of the foot.

MATERIAL AND METHODS

Specimens of *Mya* were sent from the Marine Station at Millport to Hull and, although these were always used shortly after arrival, they survived in aquaria for at least several months even with holes drilled in the shell and cannulae inserted. *Margaritifera* was collected from the river Lune (Lancashire) and recordings were made im-

mediately on returning to Hull. It was used in this investigation on account of its size, activity in the laboratory and its relatively thick shell which allowed cannulae to be easily fixed into the body so that the animal could carry out normal burrowing activity without their dislodgement. The digging activity and the pressure recordings obtained should be regarded as being typical of the majority of bivalves that burrow
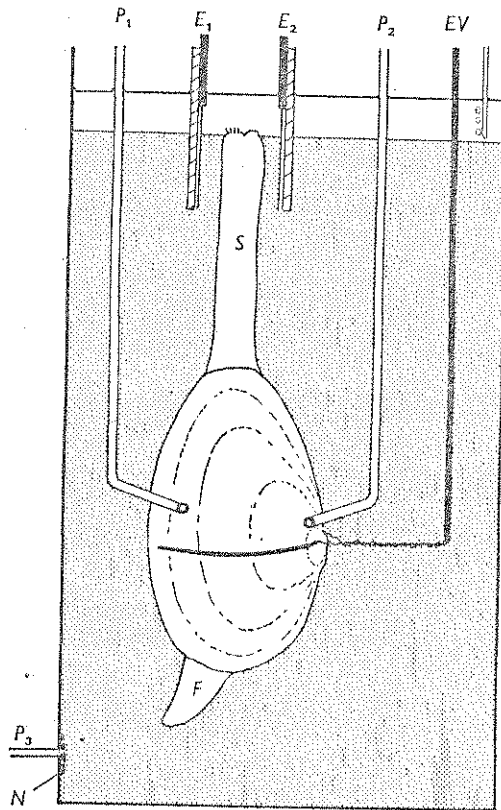

Fig. 2. Diagram of a section of a tank containing a *Mya* in sand (stipple) in its normal buried position showing the arrangement of electrodes used to record impedance changes and the connexions to pressure transducers. E_1 and E_2 electrodes attached to Perspex bridge to record siphon movements; *EV*, pair of electrodes attached to record valve movements; P_1 and P_2 tubing connecting a cannula inserted in the mantle cavity or pericardium to a pressure transducer; P_3, a similar tube covered by a coarse nylon mesh (*N*) used to record pressures developed externally in the sand by burrowing activity; other letters as in the previous figure.

actively. In both genera the cannulae were placed so as to open into the mantle cavity (Fig. 2, P_1) and into the pericardium (P_2). A wide bore hypodermic needle (1 mm., the end cut obliquely) was used for cannulation, being fixed into the shell by wax and allowed to protrude only a few mm. into the tissues. The exact location of each was checked after completion of recordings.

This investigation involved the use of a multichannel pen recorder (E. and M. Instrument Co. Inc., Physiograph), Bourdon and Statham (Model P23BB) pressure transducers and myographs to record shell movement (Trueman, 1966). Pressure changes occurring in the sand during burrowing were recorded by means of the

Statham transducer connected to a tube opening near the foot of a burrowing bivalve (Fig. 2, P_3). Interpretation of such recordings was related to direct observations of the animal's activity. Valve movements have also been recorded from beneath the sand by means of light wire electrodes attached to the valves (Fig. 2, EV) and by a long length of wire to an impedance pneumograph. Movement of the valves affected the impedance between them and a voltage proportional to this change was fed to a pen recorder by a.c. or d.c. coupling. The former allowed opening or closing movements to be recorded about a preset level (Fig. 3a) while d.c. coupling indicated sustained
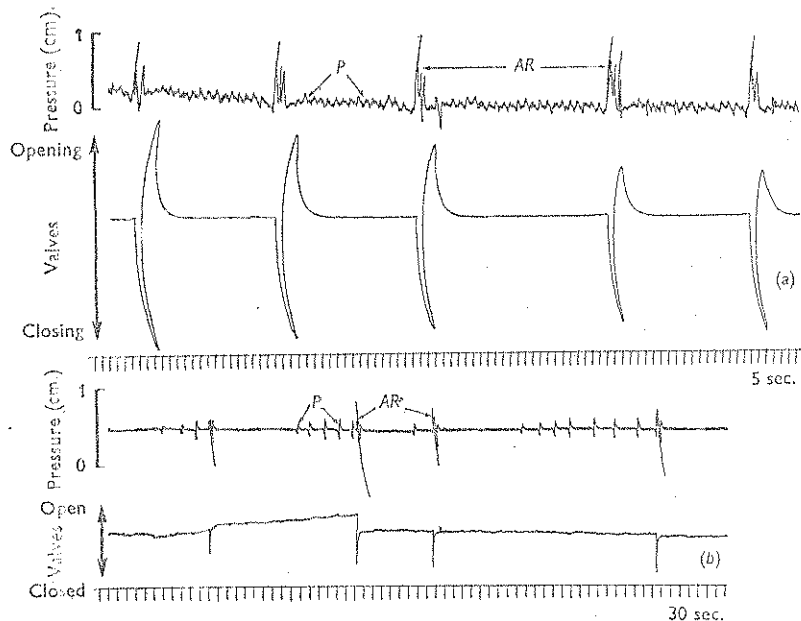

Fig. 3. Recordings of the digging activity of (a) *Margaritifera margaritifera*, and (b) *Mya arenaria*. Both show the pressures produced in the sand (above) and the movements of the valves (below, recorded by detection of impedance changes). *Margaritifera* was approximately a quarter buried and gave a fairly regular rhythm of digging cycles as indicated by adduction and retraction (*AR*) and the probing or protraction of the foot (*P*). *Mya* placed in sand as in Fig. 2 gave only spasmodic and irregular digging cycles chiefly during the first day after burial. a.c. coupling was used for the impedance pneumograph in (a), d.c. coupling in (b).

angles of gape of the valves (Fig. 3b). A similar impedance technique was used to record siphonal movements (Fig. 2, E_1 and E_2) without any direct contact or hindrance to the siphons. A full account of these techniques, which afford means of continuously monitoring activity of a buried bivalve, is given by Hoggarth & Trueman (1966).

EXPERIMENTAL RESULTS

(a) Locomotory activity

Burrowing by bivalves consists essentially of a series of step-like movements into the substrate, each termed a 'digging cycle' (Trueman *et al.* 1966). Locomotion over the surface of sand has recently been shown in *Margaritifera* to involve the same actions, apart from the orientation of the foot, as in deeper burrowing (Trueman, 1967). Each

cycle involves the integration of adduction and the reopening of the valves with retraction and protraction of the foot. Adduction causes high pressure in the haemocoele and as a consequence the foot becomes swollen to form a pedal anchor. Immediately after adduction the retractor muscles contract, pulling the shell down and sustaining the pedal pressure and anchorage. Subsequently the opening thrust of the ligament reopens the shell and presses the valves against the substrate, so forming a shell or secondary anchor which holds the animal firmly while the foot extends and probes downwards. This activity appears to be common to all actively burrowing bivalves (Trueman *et al.* 1966). It is shown for *Margaritifera* (Fig. 3*a*) as a series of digging cycles, each adduction-retraction (*AR*) forming a major peak in the external pressure record coincident with the closing and opening of the valves. Pedal probing (*P*) occurred continuously between the '*AR*' peaks. Using this means of locomotion over the surface of the sand, *Margaritifera* can attain speeds of 1 cm./digging cycle or about 20 cm./hr.

By contrast the digging activity of *Mya* is sporadic although it appeared to conform to the usual bivalve pattern (Fig. 3*b*). Digging cycles can usually be recorded within a day or so of establishing a specimen in the experimental tank (Fig. 2) but subsequently little digging was observed. Digging cycles occur at irregular intervals, each showing very different amounts of pedal probing. With the extensive fusion of the ventral mantle margins and the reduced musculo-pedal region of the foot, *Mya* is poorly adapted for active burrowing.

Chapman & Newell (1956) comment that the foot is only rarely protruded and it would seem from these recordings that this is indeed so. *Mya* penetrates the substrate in early post-larval life, perhaps before mantle fusion is complete, and becomes more deeply embedded in the substrate as it grows, possibly by sinking gradually rather than by digging.

(*b*) *Internal pressure recordings*, Margaritifera

Recordings of the hydrostatic pressures developed in *Margaritifera* during normal burrowing showed synchronous peaks of pressure of approximately equal amplitude in the pericardium and in the mantle cavity (Fig. 4*a*). The principal difference between the pressures is in respect of duration, that of the pericardium lasting for longer both because it is sustained by pedal retraction and because the mantle cavity does not constitute a water-tight system. The free mantle lobes border the mantle cavity ventrally and when distended by blood may by their apposition control the pressure to a limited extent, for in some recordings with the animal on the surface of the sand the mantle cavity pressure at successive adductions ranged from near zero to that of the pericardium. When *Margaritifera* was more deeply buried the pressures were invariably equal in both mantle cavity and pericardium which suggests that the adjacent sand has some effect on the pressures recorded. The muscular tension developed by the adductors affects the magnitude of the pressure peaks, but the variations in mantle cavity pressure were recorded while peak pressures of constant amplitude were obtained in the pericardial cavity. Similar pressures have been previously recorded in the mantle cavity of *Cardium* when completely free of the substrate (Trueman *et al.* 1966), so that the ability to produce and possibly to control mantle cavity pressures is of general occurrence in bivalves with free ventral mantle margins.

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The pressure may be utilised for cleansing of the mantle cavity or during digging to produce a jet of water to loosen the sand adjacent to the valves.

The sequence of events, such as siphonal closure (S) and adduction (A), occurring during a single digging cycle are marked on Fig. 4b, c. The first peak (i) corresponds with adduction and the second (ii) with anterior retraction (AR). Contraction of the posterior retractors maintains only a low pressure in the pericardium although high pressure appears to persist in the haemocoele of the foot, so prolonging the duration of the pedal anchorage until retraction is completed (Trueman, 1966).
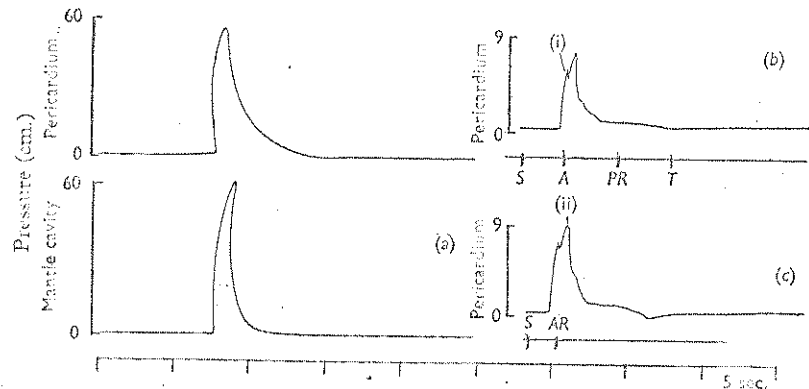

Fig. 4. Recordings of the pericardial and mantle cavity pressures in *Margaritifera* when (a), half buried, (b) and (c) when moving over the surface of the sand. (a) Synchronous pressure peaks of nearly equal amplitude in the mantle cavity and pericardium, those in the latter showing longer duration. (b) and (c) Separate recordings of pericardial pressure during a digging cycle with the following events marked by visual observation: A, adduction; AR, anterior retraction; PR, posterior retraction; S, siphonal closure; T, termination of retraction; (i) and (ii) different parts of the pressure peak discussed in the text.

(c) *Internal pressure recordings*, Mya

The burrowing activity of *Mya* occurs too occasionally to record internal pressures during digging cycles. However, when *Mya* was set up in the normal buried position (Fig. 2) repeated adductions of the valves took place and produced pressure changes in the body of *Mya* similar to those described for *Margaritifera*.

For ease of recording it was convenient to mount the *Mya* horizontally in a dish of sea water, to record pressures from cannulae inserted as in Fig. 2, valve movement by a light myograph attached to the upper valve mid-ventrally and siphonal movement by detecting changes in impedance (Fig. 5). When *Mya* is buried the ligament causes the valves to open and to press against the adjacent sand, but lying horizontally in a dish the ligament is only opposed by the adductors. A weight just less than the opening moment of the ligament (Trueman, 1954) was placed on the centre of the upper valve to avoid putting too great a continual strain on the adductors. 200 g. was a convenient weight to apply to the specimen (10 cm. shell length) used for the recordings shown in Fig. 5a, b, and under these conditions *Mya* remained active during experiments lasting up to 14 days.

Adduction of the valves causes simultaneous pressure peaks, on some occasions of over 100 cm. of water, in both mantle and pericardial cavities. The recordings (Fig. 5a) show that these peaks are of approximately equal amplitude and duration

and that the pressures produced are superimposed on the rhythm of ventricular contraction (Fig. 5 b). While previous work has shown that high pressures in the mantle cavity are related to valve movement (Trueman, 1954; Chapman & Newell, 1956) this investigation indicates that the whole of the animal contained within the shell is subjected to pressure at adduction. Between adductions the pressure in the mantle cavity fell to zero but in the pericardium a small positive resting pressure was maintained (Fig. 5 a, b).

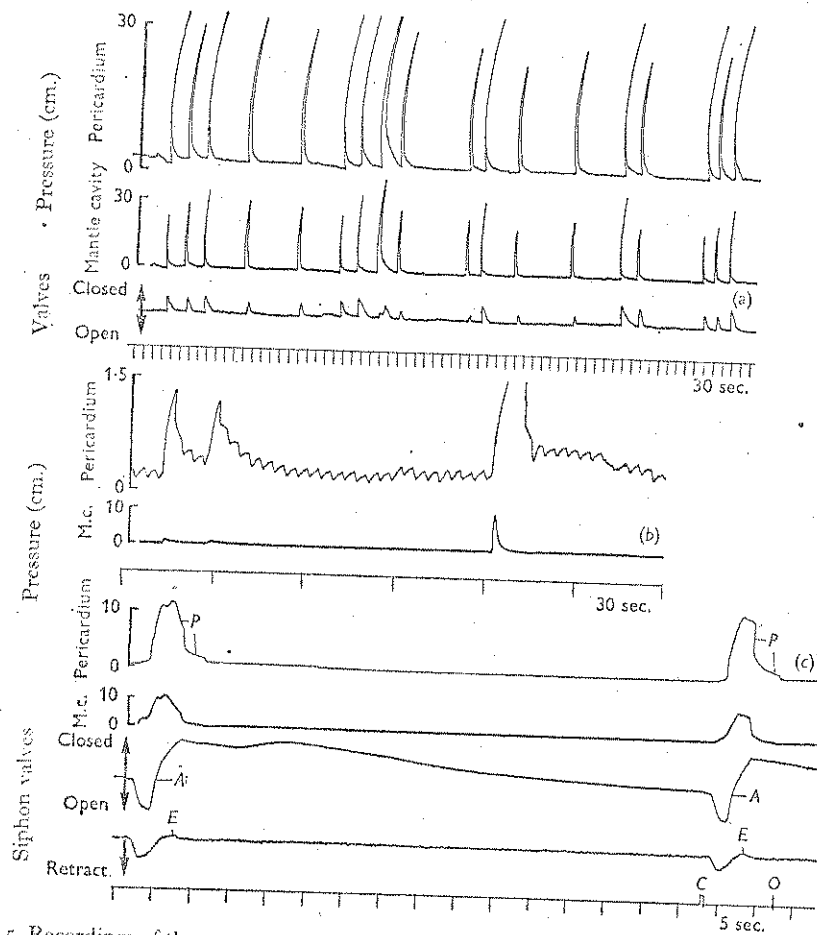In *Margaritifera* it has been shown that, during digging, adduction causes part of

Fig. 5. Recordings of the pressure in the mantle cavity and pericardium together with the valve and siphonal movements of *Mya* fixed horizontally in a dish of sea water. In (a) and (b), a load of 200 g. was applied to the centre of the upper valve, in (c), 500 g. Valve movement recorded by a thread from the mid-ventral point of the shell to a myograph, siphonal movements by impedance changes detected in electrodes similar to Fig. 2, (E_1 and E_2) suspended over the end of the siphon. (a) Similar pressure peaks in the mantle cavity and pericardium occurring at adduction. (b) As in (a) but with pericardial pressures more highly amplified to show rhythm of the heart beat. (c) Demonstrates the antagonistic nature of the relationship between adductor and siphonal retractor muscles. Recorded with a load on the valves in excess of the opening thrust of the ligament. Retraction of the siphons causes increase in pressure first in the mantle cavity, subsequently in the pericardium and maximum opening of the valves. Adduction (*A*) prolongs the pressure peak (*P*) and allows the siphons to re-extend (*E*). *C* and *O* on the time trace indicate closure and opening of the siphons.

the foot protruding from the shell to become swollen by means of an increase in the blood pressure. In *Mya* the foot is usually within the mantle cavity but the long siphons protrude and are similarly affected by adduction, although the fluid utilized is the water in the mantle cavity. The pallial water system functions at constant volume by the closure of the siphonal and pedal apertures so that the contraction of the adductors, and possibly also of the other pallial muscles (Fig. 1, *PM*), tends to cause
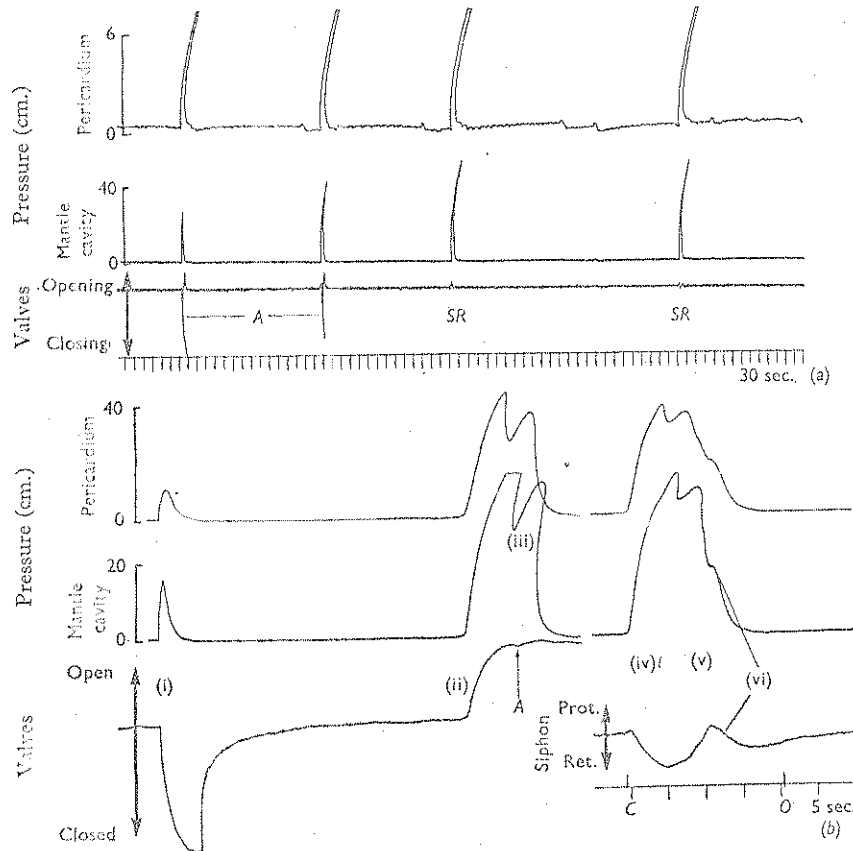

Fig. 6. Recordings of pressure changes, valve and siphonal movement in *Mya* buried in sand in the experimental conditions shown in Fig. 2. (*a*) Pressure peaks caused by adduction (*A*) or by siphonal retraction (*SR*) with only slight movement of the valves. The heart rhythm is just visible in the pericardial trace. Valve movement recorded with a.c. coupling. (*b*) At (i), pressures caused by adduction; at (ii), valves open further by siphonal retraction; slight adduction at *A* causes second pressure peak (iii) as siphons are re-extended. At the break in the trace 30 sec. elapsed while the impedance pneumograph was connected to the electrodes used to detect siphonal movement. Retraction caused the first pressure peak (iv), protraction (prot.) at (v) is associated with a second peak, probably caused by adduction, and a final peak (vi) corresponds to slight siphonal retraction (ret.). *C* and *O* on the time trace indicate the closing and opening of the siphonal apertures. Valve and siphonal movement recorded with d.c. coupling.

elongation and swelling of the siphons. The latter is generally restricted by the circular muscle fibres (Chapman & Newell, 1956) and elongation of the siphons results (Fig. 7*a*).

Siphonal retraction causes a similar increase in pressure and leads to the valves

gaping more widely. The antagonistic action of retractor and adductor muscles in a fluid-muscle system in which all body fluids are involved is shown in Fig. 5c, where a load of 500 g., i.e. in excess of the opening moment of the ligament, was placed on the upper valve of a *Mya* horizontally mounted. Such a specimen could only open the valves beyond the limit of the opening moment of the ligament by siphonal retraction causing a temporary increase in pressure, first in the mantle cavity and about $\frac{1}{2}$ sec.
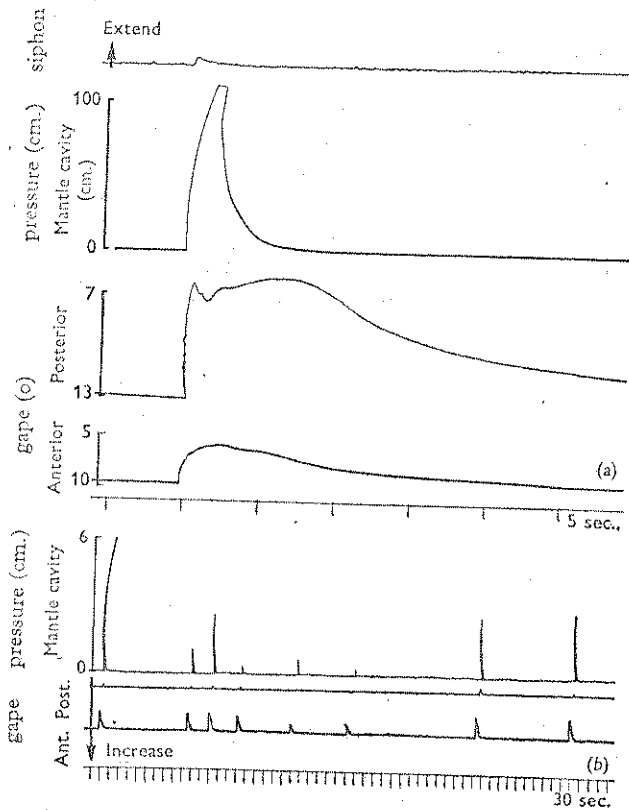

Fig. 7. Recordings showing the effect of divarication of the shell by the anterior and posterior adductors about the dorso-ventral axis (Fig. 1, *DV*). *Mya* was laid horizontally in a dish, gape was recorded by threads attached from the antero- and postero-ventral extremities of the upper valve to myographs, siphonal movements by impedance pneumograph, d.c. coupled to the pen recorder. (a) Angular changes at anterior and posterior valve margins at high-pressure peak and extension of the siphon. (b) Record of posterior divarication, caused by contraction of the anterior adductor with little closure of the valves posteriorly during some successive siphonal retractions. Posterior divarication is not shown as an increase in gape posteriorly because of the setting of the myograph.

later in the pericardium. Adduction produces simultaneous increases in pressure, since movement of the valves influences both the pallial water and the blood system directly. A brief opening of the valves takes place with the siphons closed (*C*) by means of siphonal retraction and is terminated by a sharp adduction of the valves (*A*). This produces a prolongation of the pressure peak (*P*) which in turn appears to cause some re-extension of the siphons (*E*). The gradual reopening of the valves with the siphons open (*O*) is due to the thrust of the ligament and allows the return of the fluid-muscle system to its initial condition.

Although the loading of the valves of a *Mya*, fixed in a horizontal position, demonstrates the antagonism of the two muscle systems, it may be argued that it is no test of what may actually happen in life. Accordingly recordings were made of the activity of *Mya* buried in sand with the siphons protruding slightly (Fig. 2) and similar results were obtained (Fig. 6). Pressure peaks were, however, produced both with and without adduction (Fig. 6a). Those without adduction (*A*) always gave slight opening of the valves and were probably associated with siphonal retraction (*SR*). It was not possible to record valve and siphonal movements simultaneously as only one impedance pneumograph was available, but a rapid change from one to the other was made in some recordings (Fig. 6b). Adduction (i) caused simultaneous pressure increases, and after the reopening of the valves a further increase in gape is associated with another pressure peak (ii). The latter, which is probably due to siphonal retraction, is followed by a slight adduction (*A*), indicating some increase in tension in the adductors and corresponding to an additional pressure peak (iii). This is supported by evidence from the second part of Fig. 6b where siphonal closure (*C*), retraction (iv) and protraction (v) are followed by a minor retraction of the siphon accompanied by a small pressure peak (vi). Siphonal retraction, generally of about 0·5 cm., appears to be invariably followed by adduction in order to restore the siphons to their former length. It is apparent from such recordings (Figs. 5, 6) that the antagonistic relationship between siphonal and adductor muscles must involve their close integration. It is hoped to investigate this further in the near future.

It is well known that in *Mya* as in certain other bivalves, such as *Platyodon* (Yonge, 1951b), the shell valves may move about a dorso-ventral axis (Fig. 1, *DV*). When the siphons are withdrawn, the anterior adductor contracts, and the posterior margins (Fig. 1b, *P*) of the valves separate, so widening the gape for the reception of the siphons. Similarly, the posterior adductor may cause divarication anteriorly (Fig. 1b, *A*). The localized internal ligament acts as a pivot for such rocking motions of the valves (Trueman, 1964) whereas that of *Margaritifera* extending along the dorsal valve margin only allows the simple opening and closing movement. The relationship of divarication to mantle cavity pressures is indicated in Fig. 7. Similar valve movements are made by *Mya* in the course of burrowing into stiff mud; rock boring in *Platyodon* and in the pholads represents further modification of the deep burrowing habit (Yonge, 1951b, 1955). This suggests the use of fluid pressures by pholads in boring through rock.

(d) The haemodynamics of Mya

The general anatomy of the heart, pericardium and open circulatory system is shown in lateral aspect in Fig. 8d. When considering the haemodynamics of *Tresus* (Mactridae) Smith & Davis (1965) have described valves which control blood flow at the auriculo-ventricular openings and in the aortae, while noting the absence of a valvular mechanism between the veins and the auricles. These observations are confirmed in *Mya*.

Chapman (1958) remarks on the common belief that 'blood pressure' suffices to supply the motive force for many movements in molluscs but justifiably considered that the forces generated by the muscles of the body-wall were far greater than those derived from the heart. This is substantiated by recordings (Fig. 5b) of pericardial

pressures when those caused by adduction greatly exceeded those of ventricular contraction. Direct recordings (Fig. 8) of the blood pressure in the posterior and anterior aortas give values at systole of only 0·3 cm. while maximum ventricular pressures of 2·5 cm. were recorded. No positive pressures were obtained in the auricles in this investigation, possibly because the insertion of a cannula was difficult and involved cutting open the pericardium, so destroying the normal hydrodynamic conditions.

Johansen & Martin (1962) in a study of the heart and circulation of the octopus observed an increase in diastolic pressure coincident with the greater muscular tone
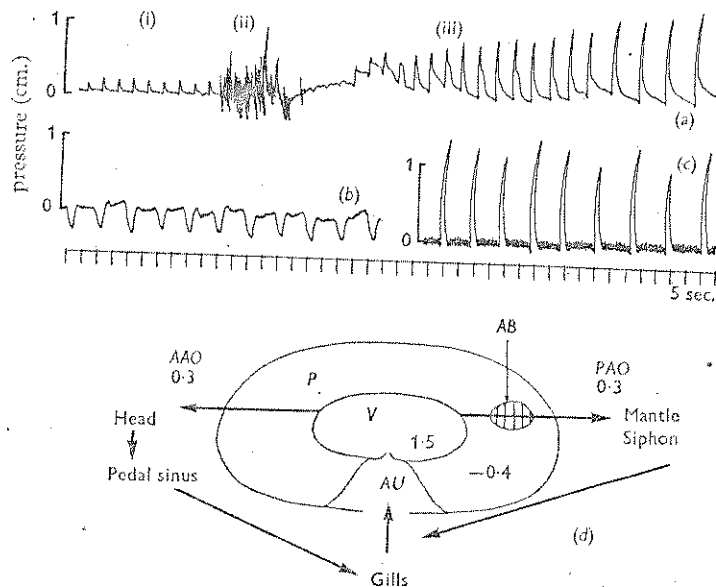

Fig. 8. Pressure recordings of the heart of *Mya*. (*a*) With cannula inserted into the posterior aorta (i), pushed forward (ii) into the ventricle (iii). (*b*) Cannula inserted into the pericardium through a small window cut in the valve. The negative pressure corresponds to ventricular contraction. (*c*) Similar recording but with the cannula inserted into the ventricle, the disturbance at diastole being due to very slight vibration of the bench. (*d*) Diagram of the heart and pericardium of *Mya* showing some typical pressures recorded at systole. *AAO*, anterior aorta; *AB*, aortic bulb; *AU*, auricle; *P*, pericardium; *PAO*, posterior aorta; *V*, ventricle.

which occurred during activity. The diastolic pressures recorded in the ventricle of *Mya* and *Tresus* (Smith & Davis, 1965) were generally zero. However, recordings from the pericardium of *Mya*, when the minimal possible disturbance of normal conditions was made (Fig. 5*b*), showed a changing level of diastolic pressure at adduction and a continuous low positive pressure (0·2 cm.) when the valves were steady. Although the pressures recorded in this work were similar to those of Smith & Davis (1965), rather higher diastolic pressures, derived from the tone of the body musculature, may occur during normal life.

Ramsay (1952) and Krijgsman & Divaris (1955) suggest that the mechanism of diastole is related to the hydrodynamic conditions in the pericardium and that blood being pumped from the ventricle causes a reduction in pericardial volume, so tending

to develop a negative pressure which will favour the filling of the thin walled auricle. Smith & Davis (1965), however, observed that the pumping of an isolated heart resembled that of the intact heart and considered that the auricles and pericardium were unnecessary for ventricular filling. Recordings of the pericardial pressures through a small window in the shell of *Mya* gave a series of negative spikes (Fig. 8*b*) of approximately the same frequency but of rather longer duration than the systolic ventricular pressures (Fig. 8*c*). These negative pressures correspond to the rhythm recorded from the pericardium during studies of siphonal movement (Fig. 5*b*) but here they represent a drop in pressure rather than a negative pressure owing to the small positive resting pressure maintained in the pericardium. A negative pressure in the pericardium must exert a suction-like effect, drawing more blood into the auricles from the veins outside the pericardium, and would appear to be a mechanism for the filling of the auricles at low venous pressures. The conditions of operation of the heart are summarized in Fig. 8*d*.

At adduction the blood in the haemocoele is affected in the same manner as the water in the mantle cavity. This particularly applies in respect of the haemocoelic vessels of the siphons where the blood pressure may reinforce that of the mantle cavity during siphonal extension. Between adductions it is somewhat doubtful if the heart can effectively maintain a circulation of blood through the siphons, for they may extend to more than 10 cm. above the shell. The presence of blood in the siphons must, however, contribute to their turgidity, for this is maintained between adductions when the siphons and the pallial system remain open to the exterior.

The role of the heart is thus limited to producing a sluggish circulation at rest and to functioning during activity as a valve preventing the back-flow of the blood. In bivalves, such as *Mya* and *Margaritifera*, where at adduction the pressure is raised simultaneously in the mantle cavity and the tissues of the body, there is no strain from a differential pressure effect except in the siphons or extended foot. Both are particularly muscular and withstand the pressure by extension or dilation respectively. Retraction, however, tends to force fluid from these organs into other regions of the body. In *Margaritifera* the flap-like Keber's valve restrains the blood from surging from the foot, possibly into the gills for there is low pressure in the mantle cavity at pedal retraction and a marked pressure differential must exist between foot and gill. By contrast, in *Mya*, because of almost complete mantle fusion, siphonal retraction is accompanied by high pressures in both mantle cavity and the tissues of the body. In the absence of an internal pressure gradient there is little chance of damage to tissues.

DISCUSSION

Margaritifera is a representative of bivalves which dig actively and has a double fluid-muscle system consisting of the blood and mantle cavities. Adduction of the valves affects both systems causing pedal dilation and the production of strong jets of water which serve to loosen the sand adjacent to the valves immediately prior to retraction, thus facilitating penetration of the substrate (Trueman, 1966, 1967; Trueman *et al.* 1966). By contrast, *Mya*, with reduced foot and extensive mantle fusion, is well adapted for sessile life in which the two fluid systems effectively operate together in respect of siphonal movement. Prolonged tactile stimulation of the siphons

causes their fairly rapid retraction, frequently with some adduction of the valves. Some water is then ejected from the mantle cavity, commonly through the inhalant siphon or the pedal aperture, at apparently quite high pressures. This resembles the ejection of water during the digging cycle, but whereas this may be put to a useful purpose during digging, the hydraulic system of *Mya* normally operates at constant volume and loss of water can only represent a mechanism for the control of exceptionally high pressures. The pressures recorded during normal activity, of up to 100 cm. of water, suggest that the mantle cavity is watertight over this range although the observations of Chapman & Newell (1956) suggest that the pedal opening is only watertight at pressures of up to 40 cm.

The siphons of *Mya* are hollow muscular organs and the principles applicable to the fluid-muscle systems of worms may be applied to them (Chapman, 1950). There are two important differences, however, for the siphons have haemocoelic vessels in their walls which may play some part in elongation, and they are open at each end so that their contained volume may be varied (Chapman & Newell, 1956). But if the whole hydraulic system of a *Mya* is considered then a parallel may be drawn with an asteroid tube foot. The body enclosed in the shell resembles the ampulla, the adductor and other pallial muscles being equivalent to the ampullary muscles in causing protraction, while the tube foot and siphons are retracted by similar longitudinal muscles.

The deep-burrowing and sessile Myacea are characterized by the long siphons and the reduced foot. In active burrowers, e.g. *Cryptomya* (Myacea, Yonge, 1951*a*), *Ensis* (Trueman, 1966), the siphons are generally short but the foot is always large and powerful. The hydraulic system of bivalves appears to be able to function in respect of either the foot and associated digging activity or the movement of long siphons, but not in respect of both in the same animal. An exception to this might appear to occur in the Tellinacea, e.g. *Tellina*, *Scrobicularia*, where active burrowing is associated with long siphons, formed exclusively from the inner mantle folds (Yonge, 1949, 1957). Changes in length and shape of the siphons of *Scrobicularia* are, however, effected solely by the muscles of their walls being antagonized through the constant volume of blood contained therein (Chapman & Newell, 1956). The hydraulic system of the mantle cavity is utilized either to extend the siphons or to produce water jets and it appears that these are alternatives which rarely occur together.

SUMMARY

1. A comparison is made of the fluid dynamics of a shallow, yet actively, burrowing bivalve, *Margaritifera*, with the sessile, deeply buried *Mya arenaria*.

2. In both adduction produces high pressures (up to 100 cm.) in the mantle and the pericardial cavities which are utilized in *Margaritifera* for locomotory purposes, in *Mya* principally for siphonal extension.

3. With siphonal and pedal apertures closed the mantle cavity of *Mya* is virtually watertight and acts, together with the blood, as the fluid of an antagonistic muscle system, whereby adduction causes siphonal extension and siphonal retraction produces an increase in gape of the valves. The close interaction between these two muscle systems is illustrated by pressure recordings of *Mya* in the normal buried position.

4. Siphonal movements are shown to be associated with divarication of the valves and accompanying pressure changes.

5. Consideration is given to the haemodynamics of *Mya* and by contrast with the high pressures involved in locomotion or siphonal movement, maximum pressures of only 2·5 cm. were recorded from the heart, producing a sluggish circulation. The higher pressures derived from the body musculature make an important contribution to movements of the blood.

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