

THE DYNAMICS OF BURROWING OF SOME COMMON LITTORAL BIVALVES

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The process of burrowing in the Bivalvia has been studied in a restricted range of species only, notably in members of the Solenacea (Fraenkel, 1927), the Lucinacea (Allen, 1958), and the Veneracea (Quayle, 1949; Ansell, 1962). This previous work, summarized by Morton (1964), makes little reference to burrowing in the common British littoral species and, with the exception of Ansell's paper, lacks the precision which more modern techniques of recording may give. The object of this research was to study the process of burrowing in detail in *Tellina tenuis*, *Macoma balthica*, *Donax vittatus* and *Cardium edule*, common littoral bivalves with very different shell shapes and habits.

Burrowing by a bivalve consists of successive cycles of activity during the penetration of the animal into the substrate. It appears that the general picture for *Ensis* holds good for other 'normal' bivalves, e.g. the Veneridae, and may be summarized as consisting of the following main stages which occur successively (Fraenkel, 1927):

- (a) Protrusion of foot into substrate until fully extended (*Hakenform*).
- (b) Dilation of the distal end to form an anchor (*Schwellform*).
- (c) Pull downwards by contraction of pedal retractor muscles (*Grabstufe*).

Fraenkel groups stages (a) and (b) together as the *Grabschritt*. This summary may be used as a basis for the comparison of the four species investigated. The events which occur in association with each downward movement will be referred to as the digging cycle equivalent to the term digging sequence of Ansell (1962), the term digging cycle, being preferred since the events comprising it are of a cyclical nature. The term digging period (or burrowing period) is used here to describe activity from the start of burrowing until the final position is reached, and generally consists of a large number of digging cycles.

THE ANATOMY OF THE FOOT

Before discussing the results of experimental work on digging it is important to establish, in outline at least, the anatomy of the musculature of the foot, the principal organ used in digging. The description given here applies to the foot of *Macoma balthica* but the foot of the other species is essentially similar.

The foot is relatively large in size and may be regarded as having two parts, a visceropedal region dorsally and a musculo-pedal region ventrally. The latter resembles the blade of an axe when retracted within the shell and, although not so sharply pointed as that of *Tellina*, it is obviously adapted for slicing through mud or sand.

Some previous workers (e.g. Bloomer, 1911; Ghosh, 1920) have differentiated the pedal musculature into two separate parts: extrinsic, which is inserted onto the valves, and intrinsic. For convenience this will be retained here, although the distinction, as noted by Graham (1934), is largely arbitrary, the bulk of these authors' intrinsic muscles merely being the extension into the foot of the extrinsic. The extrinsic musculature consists of three pairs of muscles, anterior and posterior retractors and the protractors located as shown in Fig. 1. The retractor muscles are well developed and obvious but the protractor muscles are weakly developed, as noted by Graham (1934), and not always obvious in dissection or in section. The fibres of this muscle

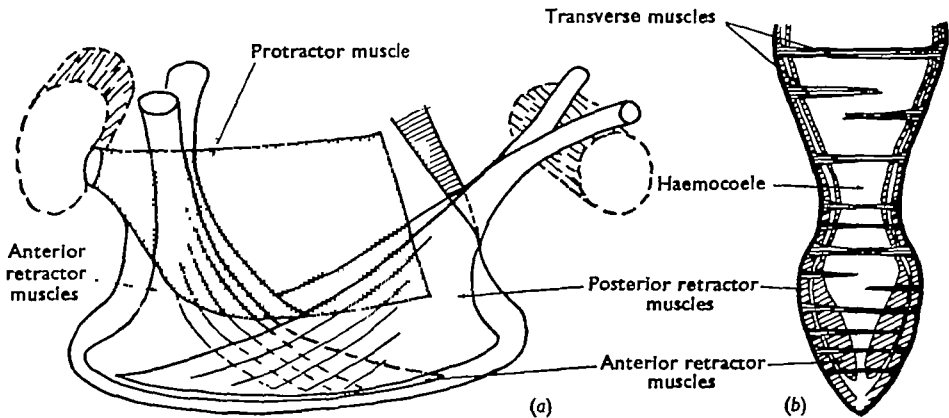


Fig. 1. Generalized diagram of the foot of *Macoma balthica* to show the principal pedal musculature. (a) Stereogram of foot, superficial protractor muscle stippled, geodetic arrangement of anterior and posterior retractor muscle fibres and position of adductor muscles indicated. (b) Vertical section through the centre of the foot. The solid black line around the foot represents both epithelium and connective tissue of basement membrane to which transverse muscles are inserted.

are inserted near the anterior adductor and spread superficially over the visceral region of the foot as a fairly thin layer. The fibres of the posterior retractors run externally to the anterior and the two sets form over much of the surface of the foot a network of muscle fibres, a small portion of which is indicated in Fig. 1a. In *Donax* there is also a pair of elevator muscles (Graham, 1934), which are not present in the other species.

The intrinsic musculature consists of transverse fibres running from wall to wall in *Macoma* (Fig. 1a, b) and some circular muscle fibres in *Cardium*. Although there does not appear to be any linkage between the fibres of anterior and posterior retractors the arrangement of these fibres is in a geodetic pattern. Geodetic muscle fibres alone are not mutually antagonistic (Chapman, 1958); they may allow change of shape by differences in the angle between the sets of fibres or by the shortening of one or other set. Lengthening can only be brought about by additional antagonistic muscles operating through the blood in the haemocoel which is effectively the fluid of the fluid-muscle system. The antagonistic muscles are the fibres passing transversely from wall to wall. In *Macoma* there are no circumferential muscles such as occur in the Annelida; in this phylum circular muscle antagonizes longitudinal muscle by means of the fluid-muscle system. In the feet of the bivalves examined the circular fibres are little in evidence and the transverse muscles are equivalent to the circular fibres.

Accordingly, contraction of the transverse muscles can cause extension of the foot and stretching of the retractors just as in *Arenicola* contraction of the circular muscle elongates the worm. In addition, differential tension in the anterior and posterior retractor muscles allows postural control by virtue of the geodetic system. The exact function of the weak protractor muscle is not very clear. It may partially function as a circular muscle in the visceral part of the foot and therefore aid the transverse musculature in causing protraction. On the other hand, its function may be to pull the visceral region of the foot forward. As will be demonstrated in this paper the transverse muscles are considerably supplemented by the contraction of the adductor muscles in the production of the high hydrostatic pressures used in digging.

Pressures of up to 50 cm. of water have been recorded in the foot of *Ensis* (Morton, 1964), 40 cm. in *Anodonta* (Brand, unpublished) and, as described in this paper, probably 20–30 cm. in *Donax*. Against such pressures some means of limitation of girth of the foot clearly must be provided. In *Arenicola* (Trueman, 1966) this stress is placed directly on the circular muscles, but in the bivalve foot there is little circular musculature and the pressure must be withstood by the transverse fibres. These are inserted into a thin layer of connective tissue immediately beneath the superficial epithelium. It should, however, be pointed out that when the foot is beneath the surface of the substrate the function of the high pressure is to press the foot firmly against the sand and an intrinsic mechanism for the limitation of girth is unnecessary.

EXPERIMENTAL OBSERVATIONS ON BURROWING

(a) *Material and methods*

The specimens used in this investigation were all obtained from beaches near Hull and although most observations were made within 1 or 2 days of collection, when they were generally most active, these bivalves would burrow satisfactorily after some weeks in an aquarium tank.

Burrowing activity was studied both by kymograph and by multichannel pen recorder using a thread, attached to a valve posteriorly (Fig. 2), to operate a lever or mechano-electric transducer. The use of a pen recorder allowed us to record several events simultaneously as in Fig. 6. The traces figured are typical recordings for each species in the same substrate. The largest available specimens of *Tellina*, *Donax* and *Macoma* were used but the *Cardium* used were of only medium size.

Burrowing was also studied by means of cine film taken both from above and from the side through glass. The analysis of films enabled us to make a precise comparison as regards the timing of the events in the digging cycle of each species.

(b) *The digging cycle of Tellina tenuis*

When a specimen of *Tellina* is laid horizontally on sand and commences burrowing the digging period shows two phases. First, the foot is protruded into the sand (Figs. 2a, 3b, X), for no movement of the shell into the sand can take place until the foot penetrates and is anchored in the substrate; and, secondly, a long sequence of digging cycles follow, taking the shell beneath the surface (Z).

During the first phase the valves open, the foot is gradually protruded onto the surface of the sand, and a series of rapid pulsations of the foot occur at a frequency of

about 2/sec. These are recorded on the kymograph as small movements of the valve when the recording lever is delicately adjusted (Fig. 3*b* at *X*). For each pulsation there is an increase of turgidity of the foot, successive pulsations giving the appearance of pressure being built up and applied to the substrate rhythmically. This is confirmed

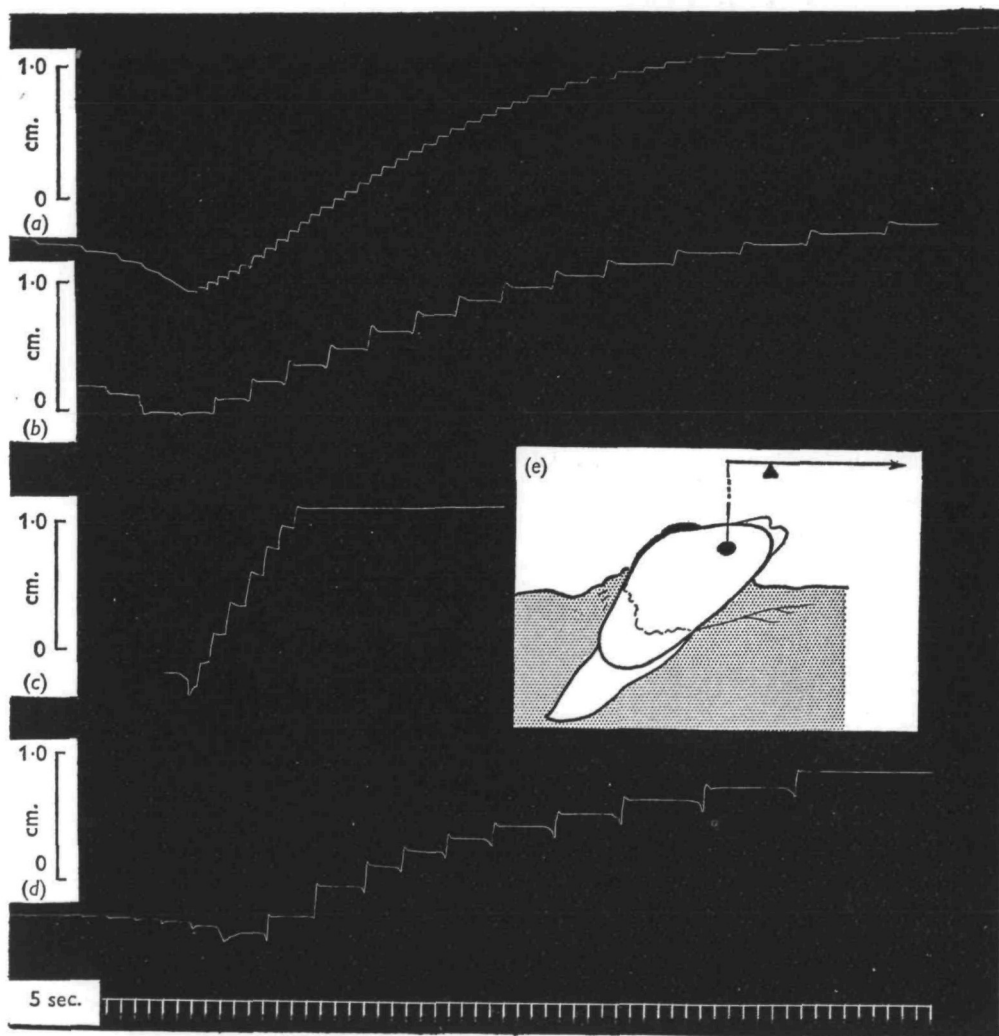


Fig. 2. Kymograph records of the digging period of: (a) *Tellina tenuis*, (b) *Cardium edule*, (c) *Donax vittatus*, (d) *Macoma balthica*, (e) represents *Donax* digging, showing angle of digging in line with long axis of shell and method of recording by the attachment of a thread to the valve.

All traces read from left and upward movement of trace represents movement of valves into sand. The same sand was used for all recordings, and the magnification of the lever was constant (1:5). Further information given in text.

by recording the pressure applied by the foot to the sand during this phase of activity (Fig. 10). Each of these pulsations probably does not involve any great hydrostatic pressure, as the application of a force to the substrate by a bivalve lying on sand in a horizontal position without other means of attachment is limited by the

weight of the animal or the frictional component of this between the valves and the sand. Application of high pressure would simply cause the shell of the *Tellina* to move. This is indeed what is being recorded, but to a very minor extent, as the foot extends into the sand (X).

When the foot has entered the sand sufficiently to obtain some anchorage then, and only then, does the contraction of the retractor muscles erect the valves into a near vertical position. Fig. 3b at Y shows two attempts to do this, the second of these being successful (the downward deflexion of the trace representing the lifting of

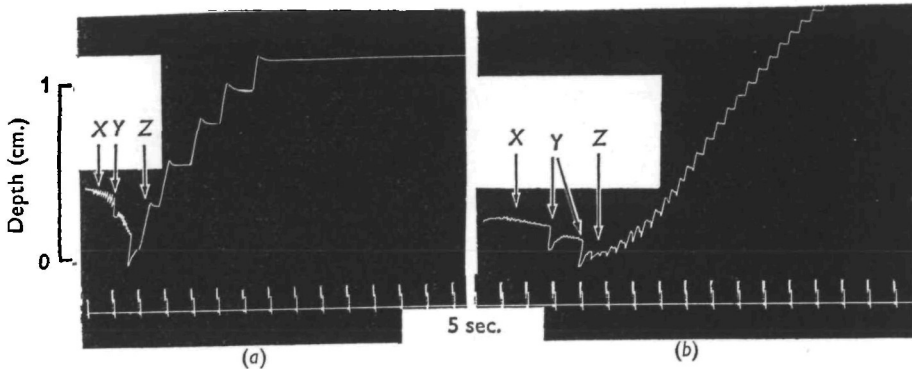


Fig. 3. Kymograph records of burrowing in (a) *Donax vittatus*, (b) *Tellina tenuis*, demonstrating probing by the foot (X), followed by unsuccessful attempts to erect the shell (Y) prior to the normal sequence of digging cycles (Z). Further information given in text.

the shell into the vertical position) and the second phase of burrowing commences (Z). It should also be noted here that only animals placed on the sand left side uppermost erect the shell; those placed right side uppermost slide under the sand at an angle to the horizontal, as observed by Holme (1961) and correlated with the animals habit of lying below the surface with the right side uppermost. The pedal retractions in this first phase of the digging period are obviously much less frequent than in the second phase. The transition from the first to the second phase of the burrowing period occurs when the valves are erected, the foot then having sufficient grip in the substrate for this purpose. The firmness of anchor of the foot may thus be an important factor in determining the recurrence frequency of pedal retraction, perhaps the single most important event of the digging cycle.

Once a firm anchor is obtained the digging cycles of the second phase follow (Figs. 2a, 3b at Z) in a similar manner in all specimens of *Tellina*. Downward movement of the shell into the sand (upward deflexion of trace) is due to contraction of the retractor muscles. The slight dip preceding it is due to the raising of the shell, clearly observed in film, when the foot probes into the sand at the beginning of each digging cycle. After each movement into the sand there is a short period, between 2 and 10 sec., during which no activity is shown on the trace prior to the next downward movement. Each digging cycle may be considered to extend from one movement into the substrate to the next, and Fig. 2a clearly demonstrates that the length of the cycle increases during burrowing. This is remarked on by Ansell (1962) in the Veneridae, who observed that time/cycle (sequence) increases and the depth/cycle

decreases as burrowing proceeds. This is confirmed for *Tellina*, but it is even more apparent in the traces of burrowing in *Macoma* and *Cardium* (Fig. 2*b, d*). The reasons for this slowing down of burrowing are discussed below.

It is quite common for a *Tellina* to exhibit a series of about 40 digging cycles in the process of burrowing before activity ceases for a longer period. This can involve burial to a depth of 2 cm. so that the valves are completely beneath the surface, but the siphons can, of course, be extended as burrowing proceeds. Penetration into the substrate in each digging cycle is not more than 1 mm., but this is compensated for by the high recurrence frequency of the cycle, the rate of which falls from about 3 to 10 sec. per cycle during a burrowing period of about 4 min. Burrowing by means of a long series of shallow digging cycles occurring in rapid succession is characteristic of *Tellina tenuis*.

The details of the movements of *Tellina* during the digging cycle have been elucidated largely by means of film taken over complete digging periods both from lateral and frontal aspects. The results of these films are summarized in Fig. 4*a*. The graphs of changes in gape of the valves and of the movement in and out of the sand are measurements taken during a typical digging cycle of a specimen 1.7 cm. long with approximately half of the shell beneath the sand, while the other information is displayed in the correct time sequence by means of examination and measurement of digging cycles in this and other specimens. The figure shows the principal changes occurring during each digging cycle; each vertical sweep of the trace in Fig. 2 corresponds with the movement into the substrate shown at 0.75-1 sec. (Fig. 4*a*), and in the period between these movements the shell shows little change in position.

The digging cycle consists of a series of closely integrated movements of different regions of the body. This series is the same in all digging cycles. The cycle, which is best understood by reference to Fig. 4*a*, comprises the following stages reading from left to right:

(i) The foot makes a major probe downwards tending to raise the shell if pedal penetration is not easily achieved, followed by dilation of the foot.

(ii) Siphons close, preventing water passing out through them during the next stage.

(iii) Adduction of the valves, which occurs rapidly in 0.1 sec. and corresponds with (a) maximum pedal dilation, and (b) ejection of water from the ventral mantle margins.

(iv) Contraction of retractor muscles, the anterior being immediately followed by posterior, resulting in movement downward into the substrate.

Siphons reopen during retraction and pedal dilation is reduced at the end of retraction.

(v) Adductor muscles relax, gape of valves increases.

(vi) Static period until the next cycle commences at (i). During this period protrusion of the foot and slight lifting of the shell occur, repetitively.

A generalized diagrammatic representation of these stages is presented in Fig. 5.

Probing movements of the foot occur at intervals of between 0.5 and 1 sec. during the static period so that the number per digging cycle depends on the length of the static period. These protrusions are most marked when the shell is lying horizontally and initial penetration of the foot into the sand takes place, as shown in Fig. 3*b, X*.

The number of probes increases as the digging period goes on, for the frequency of digging cycles is reduced and the static period, shown as the successive plateau in Fig. 2a, lasts longer. It would not be unreasonable to suggest that the reduced frequency of digging cycles may be due to the increasing difficulty that the foot has in

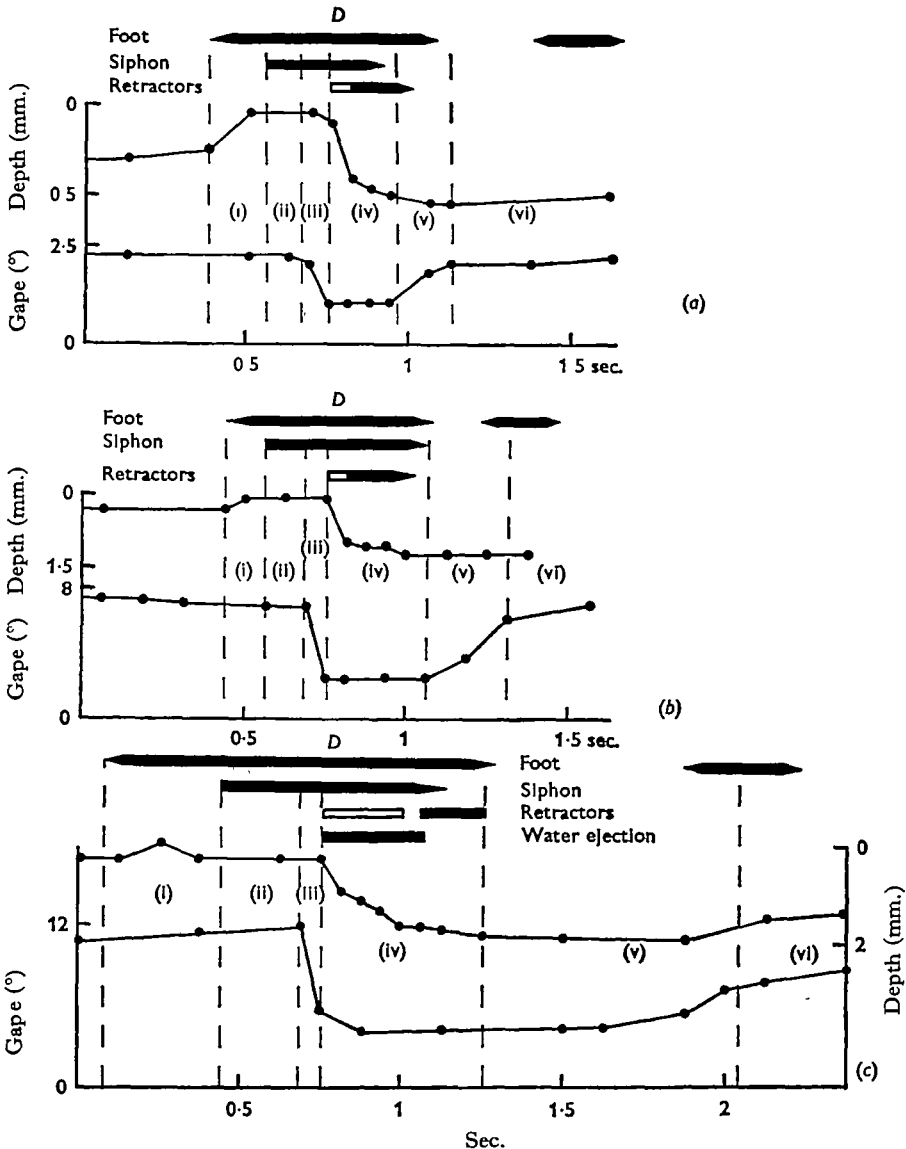


Fig. 4. Detailed analysis of the digging cycles in: (a) *Tellina tenuis*, (b) *Donax vittatus*, and (c) *Cardium edule*, taken from films. In each of the valves and depth of penetration are actual measurements taken from a single typical digging cycle when the bivalve was approximately half buried. The probing action of the foot (Foot), the time of its maximum dilation (D), the period of closure of the siphons (Siphon), contraction of the retractor muscles (Retractors; □, anterior; ■, posterior), and the period of water ejection (in c) are placed in the correct time sequence by observation of many digging cycles. Stages of digging cycle are indicated by i-vi, see text for further information.

penetrating the substrate. Further details, which have been observed in filmed sequences of *Tellina*, will be discussed after consideration of the digging period and cycle in other species.

(c) *The digging cycle of Donax, Macoma and Cardium*

Although many observations have been made on the burrowing of these other bivalves they will be dealt with in detail only where they differ from *Tellina*. *Tellina* was chosen for more detailed consideration because its thin shell allowed it to burrow close to glass and observations could accordingly be most easily made.

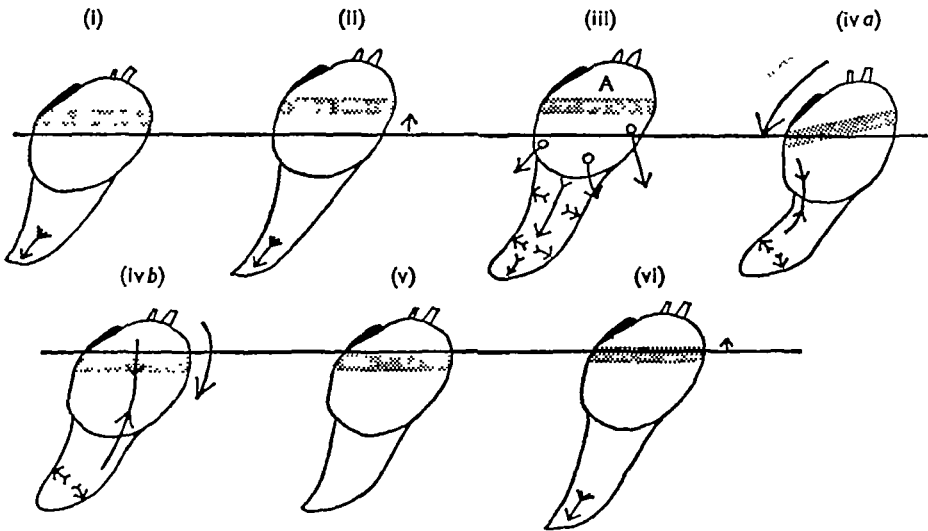


Fig. 5. Series of diagrams of a generalized bivalve at the different stages of the digging cycle (i-vi as Fig. 4.), to show the changes involved at each stage. The reference line on the shell (stippled) indicates movements of the animal with regard to the surface of the sand (horizontal line). (i) Foot probing downward, pressure exerted by the intrinsic muscles. (ii) Siphons close, foot still probing downward, shell moves upwards slightly. (iii) Adduction (A), water ejected from mantle cavity, foot maximally dilated. (iv a) Anterior retractor contracts, foot anchored by pressure, shell moves as arrow, siphons open. (iv b) Posterior retractors contract, foot still anchored, shell moves as arrow. (v) Relaxation of adductors, valves gape, pedal pressure down, anchorage not required. (vi) Valves held firm in sand as foot probes by intrinsic musculature, shell pushed upwards slightly. ← movement of shell. ←○ movement of water from mantle cavity, ←◀ probing of foot by pressure changes due to intrinsic muscles, ←◀ hydrostatic pressure derived primarily from adductor muscles and secondarily from retractor muscles, →← contraction of retractor muscles.

The general pattern of the digging period exhibited by *Tellina* is common to the other species examined. *Macoma balthica*, *Donax vittatus*, and *Cardium edule* each show the two phases of digging when laid horizontally on sand. At first the foot probes into the substrate (Fig. 3 a, X), the pedal retractor muscles contract in attempts to pull the shell vertical (Figs. 2, 3 a, Y) and not until an anchor is obtained do the normal digging cycles commence (Z). *Donax* is the most rapid in this respect, both on account of its very active foot and the more oblique angle at which the shell may enter the sand (Fig. 2). The digging cycles trace a series of steps comparable with those recorded for *Tellina*, but each step shows greater penetration and a lower recurrence frequency.

All the traces shown in Fig. 2 were made in the same sand and under the same conditions of recording, so that they are directly comparable. The short duration of the digging cycle (5 sec./cycle) and the great penetration for each cycle in *Donax* results in very rapid burrowing. This initial bout of burrowing enables the animal quickly to gain an anchorage in the sand, and activity ceases often with little more than half the shell buried. The final position in the sand, with only the siphons exposed, is achieved by two or three extra cycles (not shown in Fig. 2), which characteristically follow after a short inactive period. This activity, with rapid initial fixation, is obviously in keeping with the surf-zone habitat in which this genus lives (Jacobson, 1955).

In contrast with *Donax* and *Tellina*, *Macoma* and *Cardium*, whose shells have a greater degree of lateral bulging, show a lower frequency of digging cycles, although penetration for each cycle is quite considerable. When *Macoma* commences to burrow the duration of the digging cycle is about 7.5 sec. per cycle, and this time is doubled after 10 cycles. In *Tellina* the duration is doubled only after 30 cycles, but these take about the same total time as those of *Macoma* and lead to only slightly greater depth of burial. *Macoma*, like *Tellina*, continues to burrow until well below the surface, whereas *Cardium*, like *Donax*, stops when only the siphons are exposed. The deeper burrowing of the former two species is clearly related to the length of their siphons.

The second phase of the digging period of *Tellina* gives a trace of essentially simple steps, but in *Cardium* and *Macoma* the digging cycle shows a slightly more complex pattern. It is difficult to interpret the traces precisely in terms of the stages of the digging cycle, for they are records in two dimensions only of movements occurring, often simultaneously, in three dimensions. Their exact form is thus also affected by lateral movements of the valves and movement of the animal across the sand, as well as by the exact position of the attachment of the thread to the valves. The more complex pattern in *Cardium* and *Macoma* is caused by the separate contractions of the anterior and posterior retractor muscles imparting a rocking motion on the valves. The dip before the upstroke on the trace (Fig. 2*b*, *d*) is thus caused both by the slight raising of the shell during the final stages of pedal protrusion (Fig. 4), and by the initial contraction of the anterior retractors causing the anterior of the valves to dip, and the posterior to rise. The upstroke on the trace, or movement into the sand, is then caused by the continued contraction of the anterior retractors, particularly evident in *Macoma*, and the posterior retractors pulling the posterior end down. This is then followed by a slight rise of the animal in the sand, with consequent drop on the trace, caused by the pedal protrusion of the next cycle.

The rocking motion that these separate contractions cause are particularly evident in *Cardium* and *Macoma*, and must greatly assist penetration of a bulging shell by providing movements oblique to the plane of greatest resistance. Rocking is less marked in *Tellina*, and hardly ever seen in *Donax*, both of which enter the sand more directly. The relationship between the amount of rocking, the angle at which the bivalve burrows and the orientation of the pedal musculature, will be discussed below.

Donax most closely matches the pattern of *Tellina* but the magnitude of the movements is greater. The angle and duration of closure of the valves and the amount of penetration per cycle are all larger in *Donax* (Fig. 4), but the rate of both closure

and opening of the valves is similar in both genera. Penetration of *Donax* and *Cardium* into the sand shows a distinct step corresponding to the change from anterior to posterior retraction of the foot. Stages (i)–(v) of the digging cycle of *Cardium* occur much more slowly, taking almost twice as long as in *Donax* or *Tellina*. Most of this increase is taken up in stages (iv) and (v), namely, in contraction of retractors and relaxation of the adductors. The maximum gape of the valves is only reached when the next cycle commences. Although adduction is sudden, just as in *Tellina*, the reopening of the valves is very much slower and is probably aided by the foot during its protrusion as in (vi), Fig. 4c. This probing of the foot lifts the shell slightly, gives some impetus to the gaping of the valves and may recur several times during the static period before the cycle recommences.

In the digging cycles of all four bivalves examined in detail the principal operative part of the cycle (i.e. closure of siphons, adduction closely followed by anterior and then posterior pedal retraction—stages (ii), (iii) and (iv)) is very similar. The static period (vi) which forms a plateau in the traces (Fig. 2) shows most variability in respect of different species and of the part of the digging period under examination. The length of the static period is related to the ability of the foot to penetrate further into the sand to obtain a new anchorage. Additional probing by the foot requires a longer static period. The holding power of the anchorage of the foot is in turn related to the resistance of the substrate to the penetration of the shell and hence to shell shape. This is borne out by recordings we have made on the effect of shell shape and substrate on penetration and will be discussed in a separate paper.

(d) *Ejection of water from the mantle cavity*

An important aspect of the digging cycle, to which attention has not so far been directed in this paper, is the ejection of water from the mantle cavity during burrowing. The use of a jet of water by bivalves to aid their progress into the sand has been appreciated for some time, e.g. Drew (1907). Its function is to loosen the sand so that resistance to movement of the shell is greatly reduced. In all the species investigated here the use of water in burrowing is quite apparent by the disturbance it makes to the surface of the sand. This occurs maximally, and often quite spectacularly, in the most bulging shell, that of *Cardium edule*.

Closely related to the ejection of water from the mantle cavity is the closing of the siphonal apertures (Fig. 4ii) prior to adduction. This prevents or limits the escape of water upwards from the mantle cavity when the valves are adducted. The siphons reopen quite soon after adduction, generally during period (iv), for easy access of water from above the sand is essential to prevent the entry of sand grains into the mantle cavity which might otherwise occur during the reopening of the valves. Loosening of the adjacent sand accordingly occurs at the commencement of contraction of the retractor muscles when it is important that the valves shall be as free as possible to move. It is important, of course, that the jet of water produced is not directed at the foot. Loosening of the anchorage would prevent the foot from pulling the shell into the sand. Accordingly, the folds of the mantle margin must be involved in directing the escape of water from the mantle cavity. The direction of the jet is particularly evident in *Donax*, where the margins of the mantle open just in front of the cruciform muscle to produce quite a strong jet, directed posteriorly (or upwards)

In at least the earlier stages of burrowing. The ejection of water is similar in the other bivalves examined, but these also employ an anterior jet, as evidenced by the disturbance of the sand surface. The occurrence of free, unfused ventral mantle margins would accordingly appear to be important in actively burrowing bivalves here examined, so that the direction of water ejection may be controlled. The possible function of the cruciform muscle in respect of control of water ejection or in relation to digging should not be overlooked. The cutting of the cruciform muscle by means of a longitudinal incision in *Macoma* did not, however, have any noticeable effect on its ability to burrow.

It is of interest to make some estimate of the volume of water (V) expelled from the mantle cavity during the digging cycle.

$$V = \frac{1}{2}AH(G_1 - G_2),$$

where A = projected surface area of the valve (cm.²),

H = height of the shell (cm.),

G_1 and G_2 = ventral gape, in degrees, before and after adduction, respectively, measured from film.

For a specimen of *Cardium edule*, 1.6 cm. in height, $V = 0.35$ ml. while for *Tellina tenuis*, 1.15 cm. in height, $V = 0.021$ ml. These figures are not strictly comparable because of the size discrepancy but, on the basis of these figures, a *Tellina* of the same size as *Cardium* would only eject approximately one-fifth the volume of water. This difference is largely determined by the angular change at adduction. In *Cardium* the valves gape during burrowing to a maximum of 12° and close through 8°, while in *Tellina* the corresponding figures are 2.25° and 1.25°.

These are the extreme values for the species under investigation, the greatest angular change being for the most bulging shell and conversely. The rapid burrowing of *Donax* is undoubtedly aided by the large volume of water discharged, as indicated by an angular change at adduction of about 5° (Fig. 4*b*), as compared with *Tellina*. It would be of interest to investigate this aspect of burrowing more extensively.

(e) *The hydrostatics of burrowing*

In order to understand more completely how bivalves burrow an attempt has been made to determine the hydrostatic pressures in the haemocoel and mantle cavity during the digging cycle. For this purpose a multichannel pen recorder was coupled to different transducers to record digging movements, adduction and pressure changes simultaneously. Movement into the sand was recorded by a mechano-electric transducer attached by a thread, as in Fig. 2*e*, and adduction by an impedance pneumograph, one fine wire electrode being attached to each valve. A small alternating current of approximately 2 μ A. is passed through the electrodes and the voltage across them is directly proportioned to the impedance between them. Valve movement changes the impedance and the voltage to the pen-recorder amplifier. This is a very useful device for recording the activity of a bivalve when buried. A recording during digging cycles of *Cardium* (Fig. 6) demonstrates the occurrence of adduction (downward deflexion upper trace) $\frac{1}{4}$ th sec. before retraction of the foot (upward deflexion lower trace). Siphon closure (1), contraction of anterior retractor (2) and posterior

retractor (3) are marked by visual observation. Such recordings confirm the observations presented above.

A point not demonstrated previously in this paper is the raising of the upper trace indicating an increase in gape of approximately 1.5° immediately before adduction. This was possibly not seen on the films used for making the measurements of Fig. 4 because the specimens were then more deeply buried. The resistance of the sand to the opening of the valves could effectively eliminate the increase in gape. This feature has been observed previously by Quayle (1949) in *Venerupis*, using a kymograph, but with the use of transducers to record valve movement it appears to be fairly widespread. It is possibly due to relaxation of the slow adductor muscles just before rapid adduction.

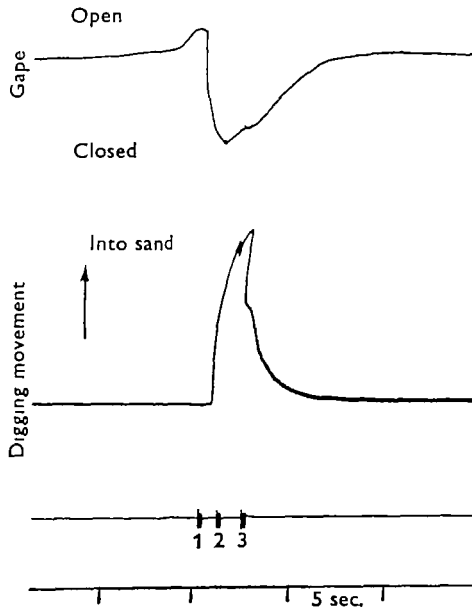


Fig. 6. Simultaneous recordings of valve movement (gape, above) and of penetration into sand (digging movement, centre) during burrowing of *Cardium edule*. Siphonal closure (1), anterior retraction (2), and posterior retraction (3) are marked by observation. Anterior retraction causing the initial pull downwards into the sand follows adduction (upper record) by 0.2 sec. Note increase of gape before adduction, presumably due to relaxation of slow muscle prior to contraction of quick muscle fibres. Further information in text.

Adduction of the valves serves not only to produce a jet of water from the mantle cavity, but also to raise sharply the hydrostatic pressure in the whole animal. An attempt was made to record this pressure, during the digging cycle, in the mantle cavity, foot, and pericardium. A small hole was drilled through the postero-ventral region of the valve of *Cardium* and *Macoma* and a very short hypodermic needle (bore 0.75 mm.) was inserted into the mantle cavity. This was connected to the pen recorder by means of a Bourdon gauge and transducer (for detail of technique see Trueman, 1966). Unfortunately, specimens treated in this way did not burrow, but normal opening and closing of the valves occurred. Fig. 7a shows a typical recording for *Cardium*. Each adduction resulted in a hydrostatic pressure in the mantle cavity of 10–15 cm. of water, although some adductions (Fig. 7b, I) resulted in pressures

as high as 30 cm. when the animal was stimulated to adduct by being touched. A natural adduction (Fig. 7*b*, II) causes a peak in pressure which lasts for about 1 sec. before tailing off. The complete adduction (Fig. 7*b*, I) caused by tactile stimulation is clearly in three phases corresponding to three stimuli. Natural pressure peaks were also recorded in *Macoma*.

It should be emphasized that these pressures were recorded with the specimens completely free of the substrate, so that the outflow of water is only limited by the

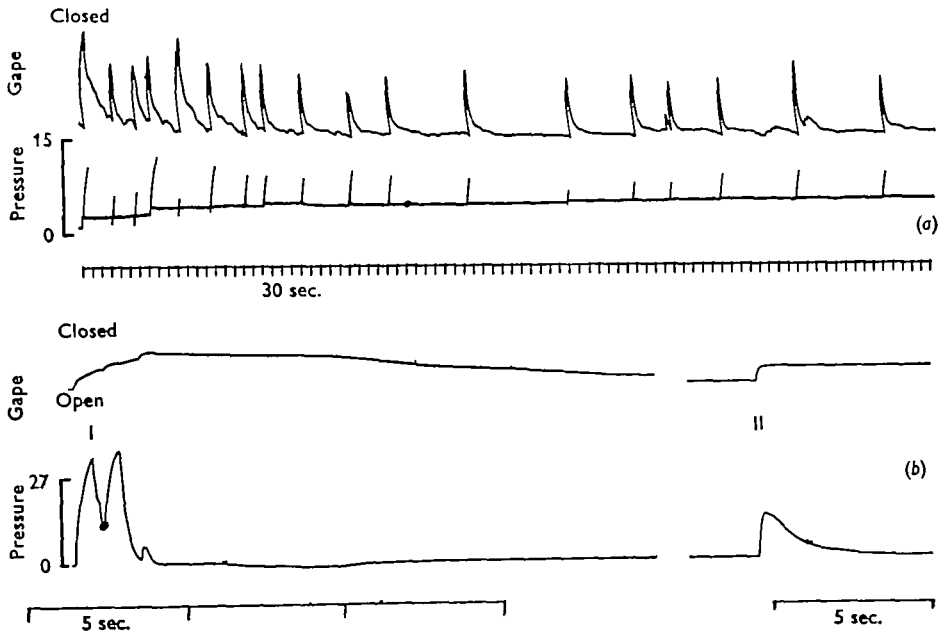


Fig. 7. Simultaneous recordings of mantle cavity hydrostatic pressure (pressure) and adduction (gape) in *Cardium edule*. (a) Naturally occurring series of adduction of about 8° amplitude with corresponding pressure peaks. (b) Adduction caused by tactile stimulation (I) followed 30 sec. later by natural adduction (II) with corresponding pressure changes. The complete adduction is clearly in three steps corresponding with three stimuli given in quick succession. In this paper all pressure recordings illustrated are given as cm. of water. Further information in text.

marginal folds of the mantle. In sand the pressures would certainly be as high and clearly adequate water pressure can be generated in the mantle cavity to loosen adjacent sand at adduction. Wells (1945, 1961) demonstrated that for an *Arenicola* to blast a vertical channel to the surface of the sand from its burrow the pressure head required is that of a column of water rather higher than the depth of the sand. On this basis *Cardium* should have more than enough hydrostatic pressure available to move the sand when digging. The pressure available in the mantle cavity on adduction in these bivalves, where there is no ventral mantle fusion, is comparable to that recorded in *Mya* (Trueman, 1954) with extensive ventral mantle fusion. Chapman & Newell (1956) have shown that whereas the extension of the siphon in *Mya* is due to hydrostatic pressure in the mantle cavity, in *Scrobicularia*, in which ventral mantle fusion does not occur, the intrinsic siphonal musculature and contained blood are involved. From these recordings ventral mantle fusion does not appear to be an essential factor

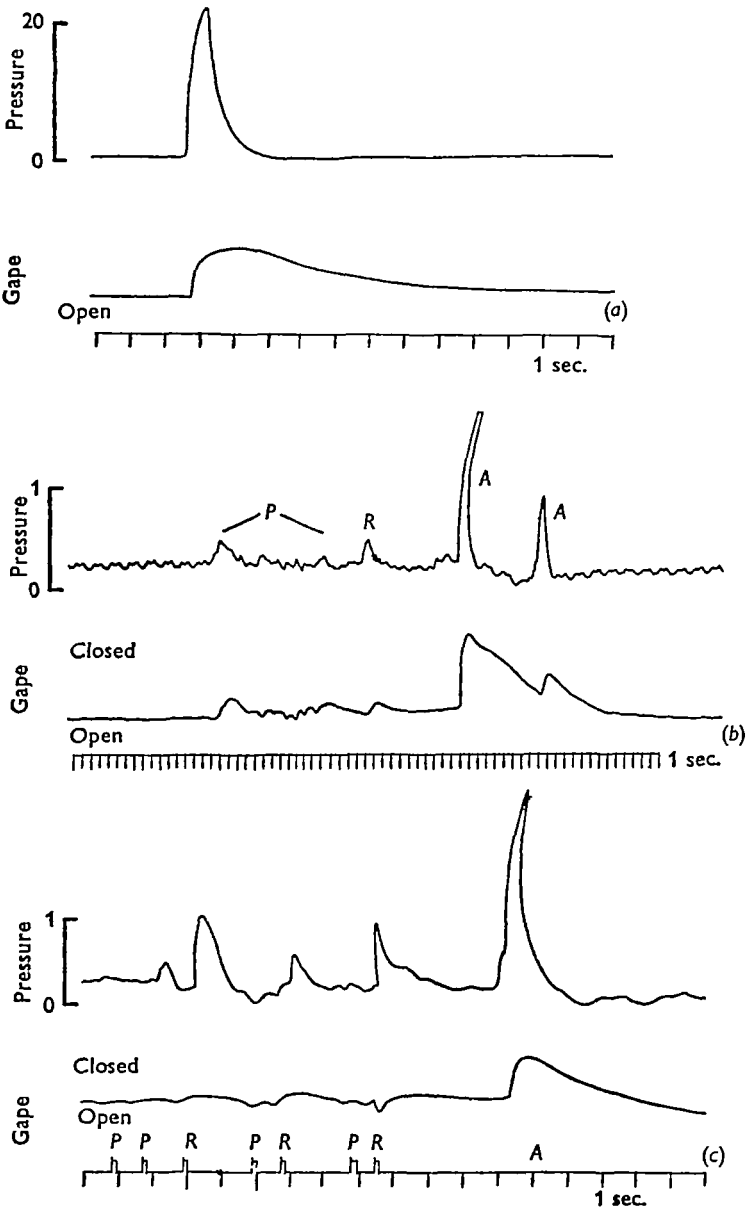


Fig. 8. Simultaneous recordings of pericardial pressures (pressure, above) with adduction of the valves (gape) in *Donax vittatus*. The specimen was fixed horizontally on wax and actively protruded its foot. (a) Single natural adduction showing maximum amplitude of pressure peak. (b) Recordings during probing of foot and adduction. Rhythmical pressure of heartbeat alone at start and finish of record, probing of foot giving small peaks of pressure (*P*) and some movement of valves, followed by pressure increase at retraction of foot (*R*) and adductions (*A*). (c) Similar to *b* but with probing of foot (*P*) and retractions (*R*) marked above time trace. Little pressure change during probing by intrinsic musculature activity, small peaks at retraction, and maximum peak at adduction. For further information see text.

for mantle cavity pressures adequate to extend the siphons. *Macoma*, when buried, has been observed to use mantle cavity pressure to clear a passage through the sand with a jet of water from the tip of the siphon, which then extends into the space cleared, using its own intrinsic hydrostatic system.

The foot becomes most dilated and presses maximally on the substrate just after adduction of the valves. When this is observed through glass, as is most easily done with *Tellina*, the foot becomes translucent at, and immediately after, adduction as it is pressed flat against the glass. It has not been possible to introduce a cannula into the foot of the bivalves here investigated, but consideration of the body pressures

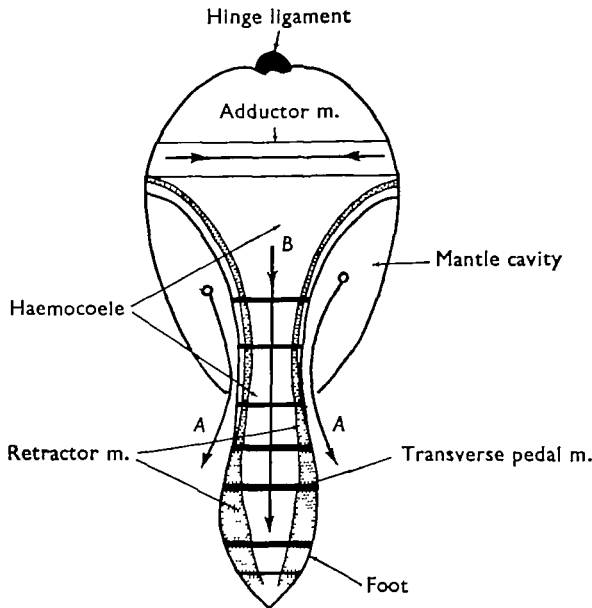


Fig. 9. Representation of a section of a bivalve such as *Cardium* showing the water and blood movements in mantle cavity (A, $\leftarrow\circ$) and haemocoelae (B, $\leftarrow<$) respectively during adduction ($\rightarrow\leftarrow$). The results of adduction are water ejection to loosen the sand and the dilation of the foot under pressure to form an anchor. The transverse pedal and longitudinal retractor muscles operate antagonistically in the fluid-muscle system. The major pressure peaks are however produced by the effect of adduction.

during adduction indicates that when the pressure increases in the mantle cavity so it must also increase in the body contained within the valves. Maximum pressures of 25–50 cm. are reported by Morton (1964) for *Ensis* during the retraction stage of the digging cycle and Brand (unpublished) has recorded 40 cm. in the foot of *Anodonta anatina* immediately following adduction.

The pressure in the pericardium of *Donax* was, however, recorded using a technique similar to that used in the case of the mantle cavity, but employing a more sensitive pressure transducer (Statham gauge). During this recording the *Donax* was fixed by wax in a dish so that the valve movements (lower trace) could be recorded simultaneously with pressure (upper trace). The results (Fig. 8) immediately confirmed that adduction led to increase of pressure in the pericardium. Fig. 8a, obtained when using the pressure transducer at low amplitude, indicated that the pressure in the

pericardium (20 cm.) was comparable to that previously recorded in the mantle cavity at adduction. At higher amplification the pressure in the pericardium could be demonstrated to consist (Fig. 8*b*) of a rhythmical wave-form of not more than 0.1 cm. amplitude, which is due to the beating of the heart. Superimposed on this are major pressure peaks at *A* when the valves are adducted and some minor peaks (*P*) corresponding to the probing actions of the foot which was protruded outside the valves. That this probing also caused some disturbance to the gape of the valves is evident in the lower trace. Retraction (*R*), in Fig. 8*b, c*, always caused a peak in pressure even when it did not follow adduction as it does in the digging cycle. Although the pressure in the pericardium is clearly disturbed by the probing of the foot, major pressure changes occur in the pericardium, and presumably in the whole body, principally on adduction and pedal retraction. Pressure change in the body probably corresponds to a similar change in the protruded foot. Clearly the pressure recorded in the pericardium could force blood into the foot and adduction is the cause of maximum dilation during digging. The conditions obtaining at adduction are summarized in Fig. 9 where the arrows indicate the ejection of water from the mantle cavity (*A*), usually anterior and posterior to the foot, and the movement of blood into the protracted foot (*B*). Any increase in pressure dorsally, caused by adduction, is thus transmitted to the foot where pressure is exerted on the adjacent sand. The pressure derived directly from the heart is clearly small in relation to that from the adductor muscles (Fig. 8*b*). Chapman (1958) observes that the heart in bivalves is hardly powerful enough to operate the hydrostatic system of the foot. This view is fully borne out by the present work. The foot, shell and muscles can be thought of as a hydraulic system in which the force produced by the adductor of the bivalve can be transferred to a region of application in the foot. The shell acts both as a basis for muscular action and as a pressure box hinged in the mid-line. Maximum pressure is therefore exerted by the foot on the substrate immediately after adduction. This may cause some additional penetration but, most importantly, it enables an anchor to be obtained by the wedging of the foot in the sand. An anchorage having been obtained, retraction follows and the shortening of the foot sustains the pressure.

In contrast with the large hydrostatic pressures produced at adduction, normal protrusion of the foot from the shell, its probing into the sand and the initial stage of its terminal dilation (Fig. 4*i, ii*), are brought about without adduction or obvious retraction by the transverse and retractor muscles of the foot in antagonism, via the blood in the haemocoel of the foot. During this activity no great hydrostatic pressure is generated by the animal (Fig. 8*b, c*). As mentioned above, unless the bivalve is firmly attached to the substrate, pressure on the sand in excess of its weight would simply cause backward movement. Initial penetration of the foot into the substrate is carried out not by the exertion of strong direct forces, but by the undulation or pulsation and agitation of the pedal margin so as to scrape rather than to push a way into the sand.

Immediately following adduction (Fig. 4*iv*) the retractors contract, pulling the shell downwards. For this a firm anchorage of the foot is required and is brought about by the following:

(*a*) Dilation of the lower part of the foot, possibly by the contraction of the transverse muscle of the visceropedal region and the protractor muscle.

(b) Adduction, increasing the hydrostatic pressure in the haemcoele so as to cause the flat foot to press against the substrate to obtain a firm anchor (Fig. 5 iii).

(c) Retraction, the pedal hydrostatic pressure being maintained by the shortening of the retractor muscles. Retraction also exerts a negative pressure or suction on the sand adjacent to the foot (see the following section).

(d) Adhesion; sand grains are frequently observed to adhere to the surface of the foot presumably because of mucus secretion.

Observations of the foot during retraction show that the most distal part visible outside the valves hardly changes in shape. Shortening of the retractor muscles must thus occur principally in the proximal regions within the valves, as has previously been described by Quayle (1949) in *Venerupis*.

Not only does adduction of the valves, immediately prior to retraction, ensure an anchor for the foot, but it reduces the profile of the shell to be pulled downwards. When the foot is again probing downwards during the static period (vi) the valves gape to their maximum, so procuring some resistance to any upthrust from the foot. The gaping of the valves to grip the burrow wall while the foot extends has previously been observed by Drew (1907) in *Ensis* and Pohlo (1963) in *Solen sicarius*. The maintenance of pressure on the burrow walls by the valves is an important function of the ligament in these genera, and a relatively powerful ligament (Trueman, 1964) must be an advantage to active burrowing. It is apparent from the recording of the gape of the shell (Fig. 4a) that adduction during the digging cycle never completely closes the valves. Complete closure cannot occur with the foot protruded, but the valves close down apparently fairly tightly on the surface of the foot and may serve to retain blood distally.

(f) Pressure fluctuations in sand during burrowing

Although it was impossible to record directly the pedal pressures in small bivalves, it has proved possible to record the pressures applied by the foot to the sand. The bivalve was allowed to burrow near the side of a Perspex box containing sand. Through the side passed a tube of 3 mm. bore which was cut off flush on the inside of the box, the opening being covered by a coarse mesh. The tube was attached to a sensitive Statham pressure transducer by means of which we were able to record quite easily pressure changes down to 1 mm. The absolute values of pressure recorded by this method had little meaning as they were affected by the depth of sand, but the relative values were accurately displayed. Pressure changes simultaneous with adduction could be detected with the bivalve several inches from the side of the box.

Representative recordings from *Donax* and *Cardium* during burrowing are given in Figs. 10 and 11 respectively. Fig. 10a shows different stages of free, unrestricted burrowing in *Donax*, the first half of the record being the initial phase of the digging period when the foot is continually probing into the substrate. This occurs rhythmically, but as penetration increases the rhythm slows and the pressure pattern of the digging cycle supercedes it. In Fig. 10b the movement of the shell is recorded (below) simultaneously by means of a very light actograph. Each step into the sand (contraction of retractor muscles) is preceded by a positive pressure of maximum amplitude generated by the adduction of the valves. Between each major peak a lesser peak represents the probing of the foot downwards during the static period of the digging

cycle. In this particular example, burrowing rapidly, a single probe of the foot by means of the intrinsic pedal muscles between each adduction appears adequate. In Fig. 10c, when the *Donax* was attached to the spring of a myograph instead of to a very light lever, seven probings of the foot occurred between adductions (lower recording). When this means of attachment of the shell was used the animal was

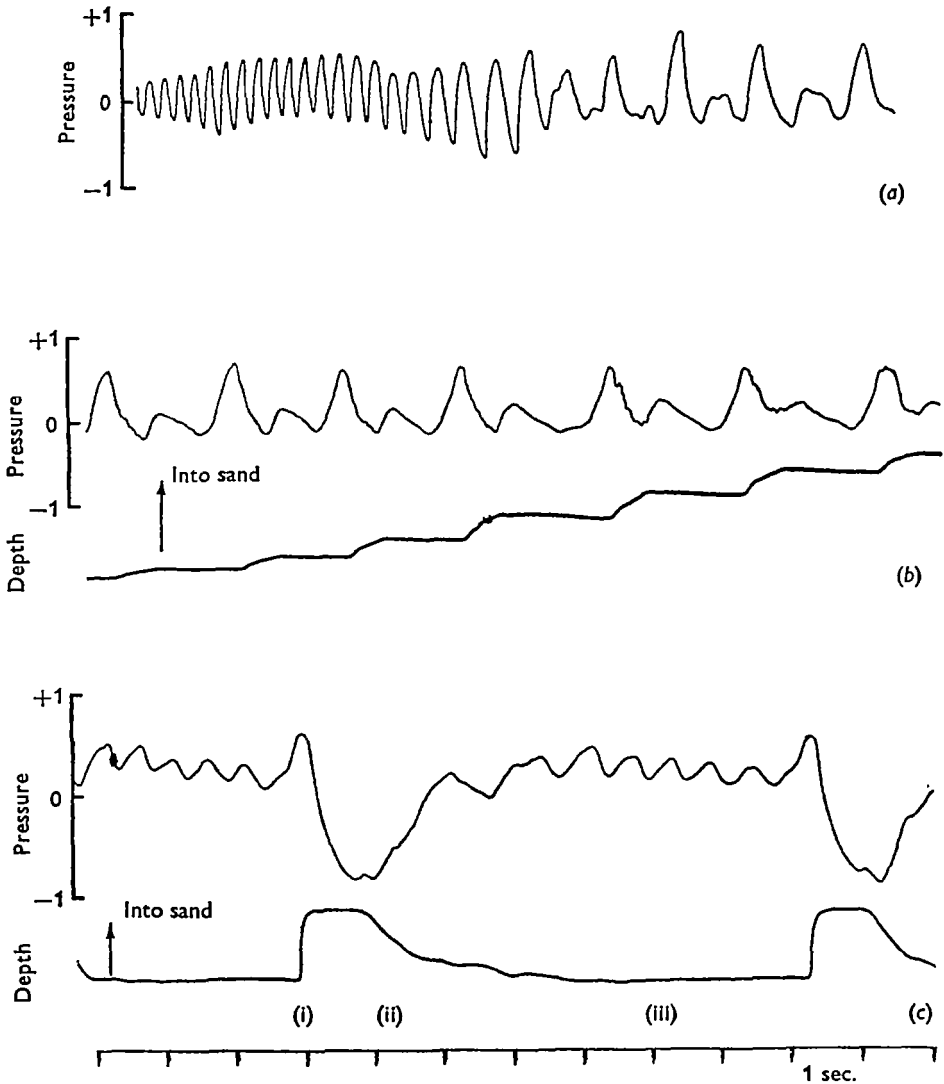


Fig. 10. Recordings of the pressure changes in sand adjacent to the foot of a burrowing *Donax*. (a) Series of sinusoidal pressure waves during the initial probing of the foot of a *Donax* lying horizontally, followed by major peaks of pressure caused by adduction in digging cycle. (b) Pressure (above) and corresponding penetration into sand recorded on a low-tension actograph (below). Adduction corresponds to major peaks while the intermediate peaks of lower amplitude represent probes by the foot. (c) Similar recording to *b* but with penetration into the sand recorded on a spring myograph. This effectively pulls *Donax* out of the sand (ii) after each digging cycle (retraction at (i)). Note maximum pressure at adduction (just before (i)) followed by negative pressure on retraction (ii), and at least seven probes by foot during the longer static period (iii). Compare with *b*. Further information in text.

unable to burrow. Contraction of the retractor muscles tended to pull the foot out of the sand rather than the shell downwards. The upward deflexion (i) represents a pull down into the sand, but as the foot lost its anchorage (ii) so the bivalve returned to its starting level (iii). As the anchorage is lost so a negative pressure is recorded, due to the effect of the foot being withdrawn. The suction which normally helps to anchor the foot is thus demonstrated. This trace does very clearly demonstrate the pulling down of the shell (i) at maximum pedal pressure. Recordings made of *Tellina* are very similar and again demonstrate retraction occurring at maximum pedal

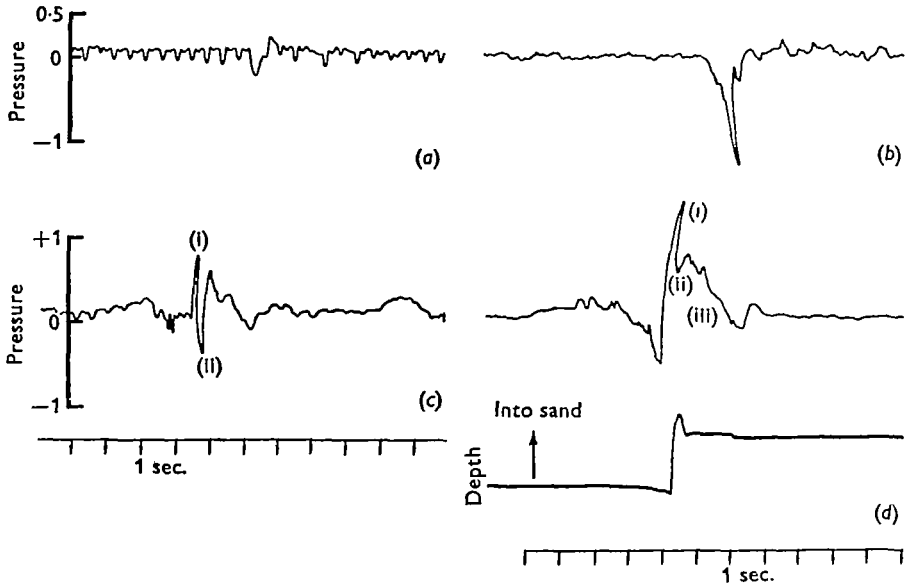


Fig. 11. Recordings of the pressure changes in the sand adjacent to a burrowing *Cardium edule* taken from one continuous digging period lasting about 4 min. (a) Initial probing of foot causes small pressure peaks, the great resistance to penetration of the shell results initially in withdrawal of the foot at the retraction stage of the digging cycle rather than in penetration of the shell, with a corresponding negative pressure in the sand. (b) The negative pressures increase in amplitude as the foot extends down into the sand and the shell is pulled into the vertical position. (c) As normal digging cycles commence, adduction gives rise to a positive peak (i) followed by a negative swing at retraction. (d) As the depth of burrowing increases the pressure at adduction (i) increases due to the increased restriction of the mantle edges. The firmer anchorage of the foot results in a reduction in amplitude of the negative pressure at retraction (ii) and a long-lasting positive pressure (iii). Movement into the sand (lower trace) occurs 0.2 sec. after the pressure swing at adduction. Further information given in text.

pressures, followed immediately by a stronger negative pressure. When negative values occur as markedly as in *Tellina* it suggests that, in this species, the foot may not obtain such a good anchorage, and may explain the shallow steps in burrowing by this genus.

The recordings of pressure generated by *Cardium* are taken from a complete digging period lasting 4 min. Strong positive pressures are not in evidence in early stages of burrowing (Fig. 11 a) but negative swings occur whenever the foot retracts. The great resistance to penetration by the bulging shell results initially in withdrawal of the foot rather than in penetration by the shell, with corresponding negative pressures in the substrate. These are small at first but increase in amplitude as the

foot further penetrates the substrate and the shell is pulled into the vertical position (*b*). As normal digging cycles commence (*c*) adduction gives rise to a positive peak (*ci*) in pressure followed by a negative swing (*cii*) at retraction. In (*d*) the positive swing of the upper trace at adduction (*i*) occurs 0.2 sec. before the movement into the sand recorded below, and is also of greater amplitude. This increase of pressure with depth is probably due to the increase in the restriction of the mantle edges by the substrate. Similarly the reduction, with depth, in amplitude of the negative swings associated with pedal retraction is indicative of the better anchorage achieved as the foot extends down into the sand. The pressure recordings of the digging activity of *Macoma* resemble those of *Cardium* and are accordingly not figured.

These observations on the pressures exerted during burrowing show (*a*) the importance of adduction for the ability of the foot to obtain an anchorage in the sand, (*b*) the negative pressure due to the suction effect on the adjacent sand at retraction, and (*c*) the probing pressure of the relatively powerful foot of *Donax*. The latter pressures are produced by the intrinsic musculature of the foot and do not involve adduction.

DISCUSSION

It is useful to consider briefly the results of this investigation both in respect of previous work and of its application to other bivalves. The digging period and cycle of *Tellina*, which have been described in detail, appear to correspond fairly closely with those previously described. Perhaps the most significant difference is the production of a heel in the posterior part of the foot during the first stage of the digging cycle to assist the anchoring of the foot in members of the Veneridae (Quayle, 1949; Ansell, 1962) and in the Lucinidae (Allen, 1958). Clearly such a heel is an aid to the anchoring of the foot and may be of particular importance in burrowing in bivalves which have rounded shells. However, this method of anchorage only occurs to a slight extent in *Cardium*. The digging cycle appears to be essentially similar in all bivalves including *Ensis* (Fraenkel, 1927) and other members of the Solenacea (Pohlo, 1963), although it would be of interest to make fresh observations in the light of this present work.

The phenomenon of rocking or see-sawing by the successive contraction of anterior and posterior retractors is one aspect of the digging cycle which has been widely observed by previous authors, for example, Allen (1958) in the Lucinacea, Quayle (1949) and Ansell (1962) in the Veneridae, Saleuddin (1964) in *Cyprina* and Pohlo (1963) in *Siliqua patula*. In this work the rocking effect was most apparent in *Cardium edule* which, with its broad ridged shell, had most difficulty in burrowing, and least in *Donax vittatus*. The shell of the latter species enters the sand obliquely (Fig. 2*e*), has a very slender profile and is pulled down directly in the line of the foot. The anterior location of the foot in digging and the relatively large posterior retractor muscles reduce the differential action. In both *Cardium* and *Macoma*, where rocking was evident, the foot more nearly approximates to the mid-ventral position, the axes of the retractors are more divergent (Fig. 1) and these muscles move the shell in somewhat different directions to produce the see-sawing. In *Solen rosaceus* (Pohlo, 1963) there is no rocking and burrowing is straight into the sand. The posterior retractor is much larger than the anterior and forms a straight line between the

anchored foot and its insertion, parallel to the long axis of the shell. If the extreme opposite condition is taken to be that of *Cardium* or *Cyprina*, where rocking takes place and burrowing is shallow, then *Donax* may be considered as an intermediate condition.

It has been observed above that the digging cycle becomes reduced in frequency and penetration as burrowing proceeds. Ansell (1962) has made similar observations on the Veneridae and considers whether the slowing down of the burrowing process is due to some intrinsic nervous mechanism controlling burrowing or to extrinsic environmental factors. He comments that fatigue is unlikely to be the cause of cessation of burrowing, since animals will repeatedly burrow after removal from the substrate immediately on completion of the digging period. Observations on the effect of shell shape on the penetration of sand, shortly to be published, do, however, suggest that resistance to penetration increases considerably with depth of burrow. At the end of the digging period effort per cm. of penetration is accordingly maximal. Reduction in frequency of the digging cycle is due to the extension of the static period (vi) and allows more probing of the foot between cycles (Fig. 10*b, c*). This may be required both to obtain sufficient anchorage and adequate extension of the foot for the maximal effort towards the end of the burrowing period.

The siphons maintain contact with the surface of the sand throughout the digging period and extension of the siphons follows each downward movement. Ansell (1962) considers that burrowing may cease in response to stimuli concerning the state of extension of the siphons. Such sensory structures in the Veneridae are presumably stretch receptors in the siphonal wall, but Ansell pointed out that in more active bivalves they may form recognizable sense organs. Yonge (1949) suggested that the sense organ associated with the cruciform muscle may serve this function. The experiment of cutting the cruciform muscle in *Macoma* by a longitudinal median incision and then allowing burrowing shows no obvious differences from normal burrowing activity. In *Donax* the association of the cruciform muscle with an area of the mantle margin from which a jet of water is produced in burrowing has been observed above. The possibility of the cruciform muscle in some way controlling the direction of the jet should not be overlooked.

In considering the hydrostatic pressures produced in bivalves it should be realised that the heart circulates the blood at relatively low pressures, 6.0 cm. according to Picken's (1937) observations on *Anodonta* and perhaps rather less in *Donax* (Fig. 8*b*). Although this pressure circulates the blood to the foot it is much less than the pressures involved in the fluid-muscle system of the haemocoel and pedal muscles. Probing and dilation of the foot is brought about by the transverse and retractor muscles in antagonism, together with the protractor muscle, and is followed by the adductor muscles contracting, when maximal pressures are produced. The adductor muscles, through closing the valves, act as a major transverse component of the fluid-muscle system. Their contraction is always followed immediately during the digging cycle by the major contraction of the retractors to pull the shell downwards. The integration and co-ordination of the digging cycle is well established in each species investigated, but as yet we know little about the pathways by means of which this is carried out. Contraction of the retractors before the pressure falls ensures anchorage of the foot and the contraction of these muscles does further serve to continue the pressure in

the foot and accordingly its anchorage until retraction is complete. On adduction the pressure in both mantle cavity and body tissues is raised sharply. Since all the animal enclosed in the shell is subjected to approximately the same pressure there is little danger of damage to delicate structures. Any pressures produced by retraction of the foot, however, will tend to force the blood out of the foot. Keber's valve or a similar structure between the haemocoel of the foot and the vessel to the kidney and gills serves to retain the blood in the foot. This is clearly important both to prevent blood at high pressure surges from reaching the gills and to conserve the fluid in the foot during active probing.

The foot in the Tellinacea is in the form of a broad flat triangle; anchorage is obtained by the application of pressure over a wide area. This is in contrast to the marked terminal expansion which has been described in members of the Solenacea (Drew, 1907; Fraenkel, 1927; Pohlo, 1963). According to Morton (1964) this involves pressures of 25–50 cm. of water, which is rather more than have been recorded during this investigation. It would be clearly of interest to reinvestigate digging in *Ensis*, using modern recording techniques, and we hope to do so in the near future.

The function of the adductor muscles in digging also involves the production of water jets to aid burrowing. In a study of the effect of shell shape on burrowing the authors of this paper have been able to demonstrate quantitatively the effect of such water jets. These results, which it is hoped to publish shortly, make it clear that without loosening of the adjacent sand burrowing could hardly be achieved in any bivalve. As a counterpart to the adductor muscles the role of the ligament in opening the valves during burrowing should not be overlooked. The greater the force with which the valves gape the more firmly is the shell held in the burrow during the static period while the foot is probing downwards. For a rapid digging cycle rapid opening of the valves must occur after adduction and retraction. This has been shown to occur in *Tellina* and *Donax* but is absent in *Cardium*. Indeed, the opening of the valves in the latter probably results from their being pushed open by the foot. While this may also occur in *Tellina tenuis*, the powerful ligament of this species is undoubtedly an asset in rapid burrowing in comparison with the weak ligament of *Cardium* (Trueman, 1964). The strength of the ligament and the rate of opening of the valves are clearly relevant to burrowing.

The manner in which anchorage is obtained by a broad flat foot such as that of *Tellina* or *Donax* is of interest. The dilatant properties of the sand-water mixture, of increasing resistance to increased rate of shear, are obviously of importance. When the substrate is compressed by the application of pressure from the foot a closer packing of the sand grains results from the disturbance of the sand-water mixture. When this occurs the substrate on either side of the foot becomes much more firm and forms rigid walls against which the foot presses. The ejection of water from the mantle cavity to loosen the sand for the downward movement of the shell must not, of course, be directed at the pedal anchorage. *Ensis*, where the foot dilates into a bulb, *Pharus* (Yonge, 1959) with a frilled lateral margin of the foot and *Nucula* (Stoll, 1938) with a cleft foot, all appear to represent advances over the flattened foot in *Tellina* in respect of anchoring. But the feet of *Tellina* and *Donax* are both extremely well adapted for rapid penetration of the substrate and this may be the overriding factor in their littoral habitat.

SUMMARY

1. The burrowing activity of *Donax vittatus*, *Tellina tenuis*, *Macoma balthica* and *Cardium edule* consists of a cyclical series of changes, termed the digging cycle, involving protraction of the foot, closure of the siphons, adduction of the valves and retraction of the foot.

2. Detailed comparison shows marked difference in the time involved in pedal protraction and a see-saw motion of entry to the sand by *Cardium* and *Macoma* with bulging shells in contrast to a more direct downward movement of *Donax* and *Tellina* with slim shells.

3. The structure of the foot and the hydrostatic fluid-muscle mechanism is described.

4. Recordings were made of the hydrostatic pressures directly by cannulation of the mantle cavity or pericardium and indirectly from the sand adjacent to the foot.

5. While extension and probing occurs at relatively low pressures dilation of the foot and ejection of water from the mantle cavity occur simultaneously at pressures of 25 cm. of water and are caused by the adduction of the valves.

6. The foot obtains a firm anchorage by means of the dilation while the pedal retractors pull the shell downwards and so sustain the pressure in the haemocoel.

7. Water ejection from the mantle cavity loosens the adjacent sand so that penetration by the shell is facilitated.

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