BURROWING IN *MERCENARIA MERCENARIA* (L.) (BIVALVIA, VENERIDAE)

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INTRODUCTION

The process of burrowing in some members of the Veneridae has been described in broad outline by Quayle (1949) and by Ansell (1962) from general observations and from kymograph recordings. Recently Trueman (1966a) and Hoggarth & Trueman (1966) have developed new techniques of recording activity in benthic invertebrates based on measurements of impedance, hydrostatic pressure and displacement, involving a minimum of disturbance to normal activities, and these techniques have been applied to a study of the dynamics of burrowing in the common littoral bivalves *Tellina tenius, Macoma balthica, Donax vittatus* and *Cardium edule* (Trueman, Brand & Davis, 1966) and *Ensis arcuatus* (Trueman, 1966b). While the basic events occurring during burrowing in these bivalves and in members of the Veneridae are essentially similar, the movements involved differ in details, and a further study of the process of burrowing in the venerid clam, *Mercenaria mercenaria*, using modern techniques, was therefore undertaken with particular reference to those points of difference.

EXPERIMENTAL RESULTS

(a) Materials and methods

The animals were collected from the shore in Southampton Water, from a naturalized population of this American species, and were maintained in tanks containing sand at the Marine Station, Millport, until used in the experiments. Burrowing activity was studied using a multichannel pen recorder (E. and M. Instrument Company, Physiograph) to record (a) changes of pressure in the sand into which the animals were burrowing by means of a Statham P 23 BB pressure transducer; (b) adduction of the shell valves by means of an impedance pneumograph; and (c) vertical displacement or the downward pull exerted during the burrowing cycle by means of light and heavy myographs. These techniques have been described in detail by Trueman *et al.* (1966) and by Hoggarth & Trueman (1966). Cine films of the process of burrowing taken from above and from the side through glass have been used in the initial analysis of the burrowing process.

(b) Description of the burrowing process

In common with that of other bivalves, burrowing in *Mercenaria* takes place by a step-like series of integrated movements involving all body systems which are repeated until a stable position in the substratum is reached. The activity from the start of burrowing until the final position is attained has been termed the 'digging period' (or burrowing period) and the terms 'digging sequence' (Ansell, 1962) or 'digging cycle' (Trueman *et al.* 1966) have been used to refer collectively to those events occurring in association with each downward step. The latter term is now preferred since the events are repeated cyclically.

When *Mercenaria* is exposed on the surface of the sand and burrowing commences the foot is extended sideways and downwards, probing into the sand to obtain a firm anchorage. The first digging cycles serve to erect the shell into a depression formed by the foot, the time per cycle in this stage being relatively long and variable. Following successful penetration of the foot and erection of the shell, further digging cycles follow at more or less equal time intervals until the hinge line is level with the surface of the substratum. Thereafter further digging cycles follow, but with decreasing frequency, until the digging period is completed.

Each digging cycle in *Mercenaria* is similar in essentials to that of *Tellina* and of other bivalves which have been examined in detail. Results from analysis of films and of physiograph records have been combined in Figs. 1 and 2 to summarize the significant events. Fig. 2A is based on filmed records of an animal approximately half buried in sand, while Fig. 2B is based mainly on physiograph records of animals completely buried in sand, and shows the secondary phase of siphonal movements first described by Ansell (1962). Description may be conveniently started at stage ii and comprises the following events:

Stage ii. The siphons close, preventing water from passing through them at the next stage.

Stage iii. Adduction of the shell valves takes place in approximately 0·2 sec. The distal end of the foot is dilated, and water is ejected from the mantle cavity through the ventral mantle margins.

Stage iv. Contraction of the anterior pedal retractor muscles, followed immediately by contraction of the posterior pedal retractors, causing a rocking motion of the shell. During the early part of retraction a downward movement of the shell takes place into the fluid cavity formed in stage iii by the ejection of water through the sand around the proximal regions of the foot.

Stage v. The adductor muscles relax and the gape of the valves increases slowly. The siphon tips re-open and water is taken into the mantle cavity.

Stage vi. Static period until the next cycle begins.

During the static period probing movements of the foot occur at intervals of approximately 3 sec., the last of these probes in each cycle occurring immediately prior to adduction of the shell valves in stage iii. This final probe corresponds to stage i of Trueman *et al.* (1966). The stages in the cycle of *Mercenaria* therefore differ from those of *Tellina* in that a siphonal closure (stage ii) may precede the final probe with the foot (stage i).

Anchorage of the foot (pedal anchor, Trueman, 1966c) is obtained at adduction

partly by dilation of the entire distal region of the foot to form a wide area pressed firmly against the sand and partly by extension of a heel posteriorly. During contraction of the anterior retractor muscles the anchorage is maintained so that the shell is drawn downwards into the cavity formed below the shell by the ejection of water in stage iii. The ventral limits of this cavity correspond roughly with the extent of the
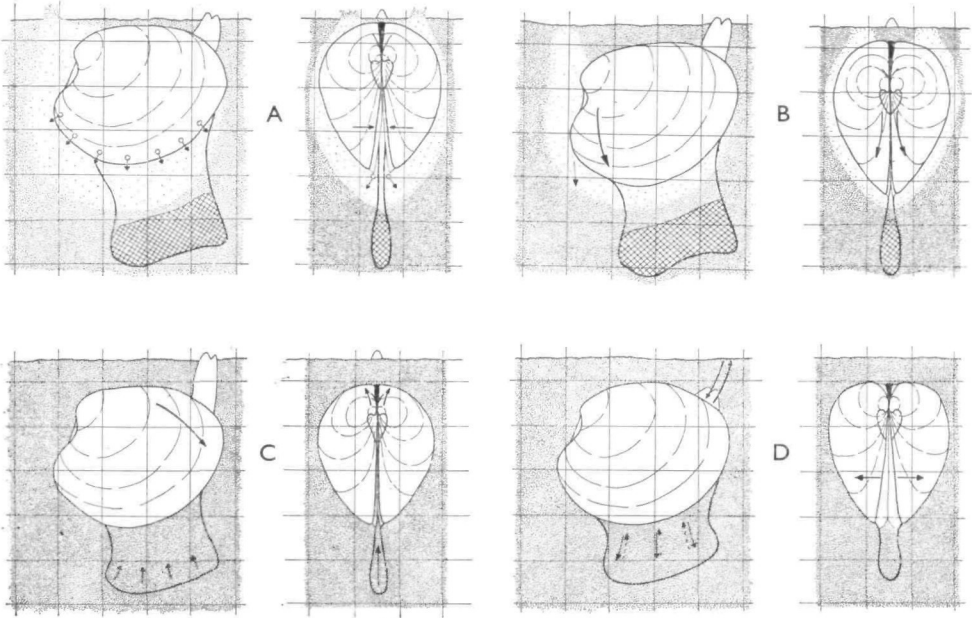

Fig. 1. Stages in the digging cycle of *Mercenaria*. A, Contraction of the adductor muscles (stage iii, fig. 2); B, contraction of the anterior pedal retractor muscles (stage iv); C, contraction of the posterior pedal retractor muscles (stage iv); D, secondary siphonal movements (fig. 2B, 2). The extent of loosening of the sand caused by ejection of water from the mantle cavity (o→) at adduction (→ ←) is indicated by lighter stippling. Movements of the shell, foot, and siphons are indicated by arrows, the area of anchorage of the foot by cross hatching and a centimeter grid is superimposed. Further explanation in the text.

compressed proximal region of the foot near the shell margins (Fig. 1) so that the anchorage of the foot is not affected by the loosening of the sand. During posterior retraction resistance to penetration of the shell becomes greater as the fluid cavity fills by settlement of the sand, and anchorage of the foot is lost. The later stages of contraction of the posterior retractor muscles thus result in some withdrawal of the foot (Fig. 2a). Heel formation in *Mercenaria* is small compared with that in *Venerupis* (Quayle, 1949) and compares with that of *Cardium* (Trueman *et al.* 1966).

The later cycles of the digging period differ from the earlier cycles in timing and in the occurrence of a secondary phase of siphonal movements. A typical cycle including these movements is summarized in Fig. 2B. During the period following stage v the siphons close, withdraw slowly into the sand for approximately 5 sec., extend slowly again during approximately 5 sec. until extended slightly above the sand surface, and then reopen. At the same time the foot also withdraws slowly and then re-extends, the time sequence of withdrawal and extension corresponding exactly to that of the siphons. The significance of these movements will be discussed later.

(c) The burrowing period

Characteristics of the digging period of *M. mercenaria* were described by Ansell (1962). Variations in the time taken to complete individual cycles delimit three stages in the digging period. In the early cycles the time per cycle is long in comparison with later cycles reflecting the greater time taken for the foot to obtain anchorage during
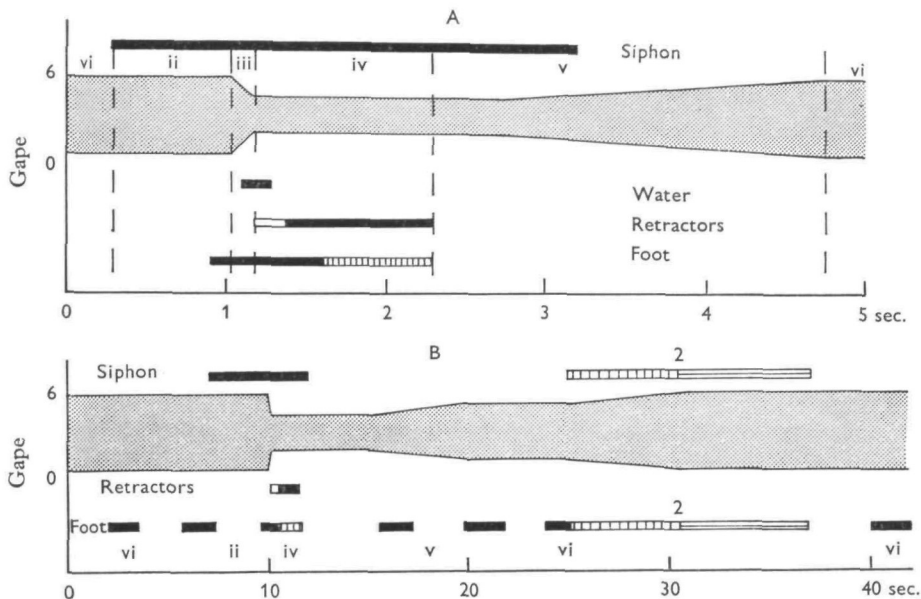
Fig. 2. Analyses of the digging cycles of *Mercenaria* taken from film and recordings. A, Complete digging cycle when partially buried; B, digging cycle with the shell beneath the surface of the sand as in Fig. 1. The period of closure of the siphons (siphon, ■), their secondary withdrawal (2, ▥) and extension (▤), the closing and opening of the valves (gape; angle of gape in degrees by width of stipple), the ejection of water from the mantle cavity, contraction of the pedal rectractor muscles (retractors, □, anterior; ■, posterior) and pedal movements (foot; ■, probing; ▥, withdrawal; ▤, extension) are placed in their correct time sequence.

this initial stabilizing stage. This is followed by a series of cycles of more or less constant time per cycle, during which the shell becomes buried to a position where the hinge margin is approximately level with the surface of the substratum. Finally a series of further cycles occupying progressively longer intervals follows, ending when the final position in the sand is reached.

Changes in shell gape during the initial cycles of the stabilizing stage are indicated by the impedance pneumograph record given in Fig. 3, which shows initial probing movements and the first four digging cycles in sand of an animal 6·3 cm. length. With the shell on the surface, probing (P) occurs with frequency of 1 probe/3 sec and causes clear rhythmical opening and closing of the valves although such movements are small in amplitude as compared with adduction (A). As the shell penetrates the soil the probing movements (P) are damped by the resistance of the sand and progressively decrease in amplitude until with the shell completely buried the probing movements cause no changes in shell gape (Fig. 5, lower record). Trueman *et al.* (1966, fig. 10)

illustrated similar initial probing movements in *Donax* causing sinusoidal pressure waves in the sand. In contrast, pressures in the sand caused by *Mercenaria* probing are very small; a *Tellina* less than 1 cm. in length caused greater pressures than did a *Mercenaria* of 6 times this length (Fig. 4).

Selected parts of a complete record of one digging period for *M. mercenaria*, 6·3 cm. ength in Kames Bay sand (Fig. 4), shows the gradual extension of the time per cycle as the digging period progresses, and the intermittent establishment of the secondary phase of siphonal movements when the animal reaches a position with the distal valve margins level with the sand surface. In the early cycles, before the shell is completely buried in the sand, the interval between siphonal closure and adduction is less than 1 sec. In later cycles the interval lengthens and it may extend to 5 sec. when the shell is below the surface of the substratum. Extension of the time per cycle for the later stages of the digging period is thus the result of extension of the time taken to complete both stages 11 and vi. The lower records in Fig. 4 made simultaneously with
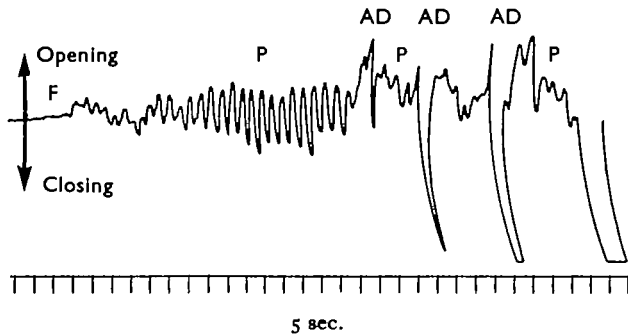

Fig. 3. Impedance record (a.c. coupled) of valve movements during the commencement of burrowing. The foot is extended on to the sand at F and makes a series of rapid probes (P) resulting in very small movements of the valves. The first four adductions (AD) of the digging period show increasing magnitude and duration as pedal anchorage is obtained. During the last two adductions the recorder pen reached the limit of its travel.

the external pressure recordings, show both the rhythm of the heart and changes of gape of the shell (A) and downward movement at retraction (stage iv) (B). Before the shell valves are buried adduction causes a decrease in pressure in the surrounding sand, but as the shell progressively enters the substrate so water is forced into the sand from the mantle cavity, producing positive external pressures (Fig. 4A, AR). A slight positive pressure associated with retraction (R) is clearly seen, at first increasing in amplitude as the shell becomes buried and then having more or less the same value at each cycle. In some cycles a negative pressure in the sand during the later part of the contraction of the retractor muscles may be seen. This is caused by withdrawal of the foot as pedal anchorage is lost.

Phenomena associated with the secondary siphonal movements are shown in greater detail in Fig. 5 which includes simultaneous recordings of pressure changes in the substratum and of gape of the shell during three cycles with the shell completely buried, movements of the siphon and foot in the secondary phase of siphon movements being marked by visual observation along the time-marker trace. During

withdrawal, pressure in the sand falls and the gape of the shell increases, while on pedal and siphonal extension the pressure returns to its former level.

These movements involve extension of the siphons following each downward movement below the surface, and Ansell (1962) considered that such movements might play an important part in co-ordination of the digging period by giving information through
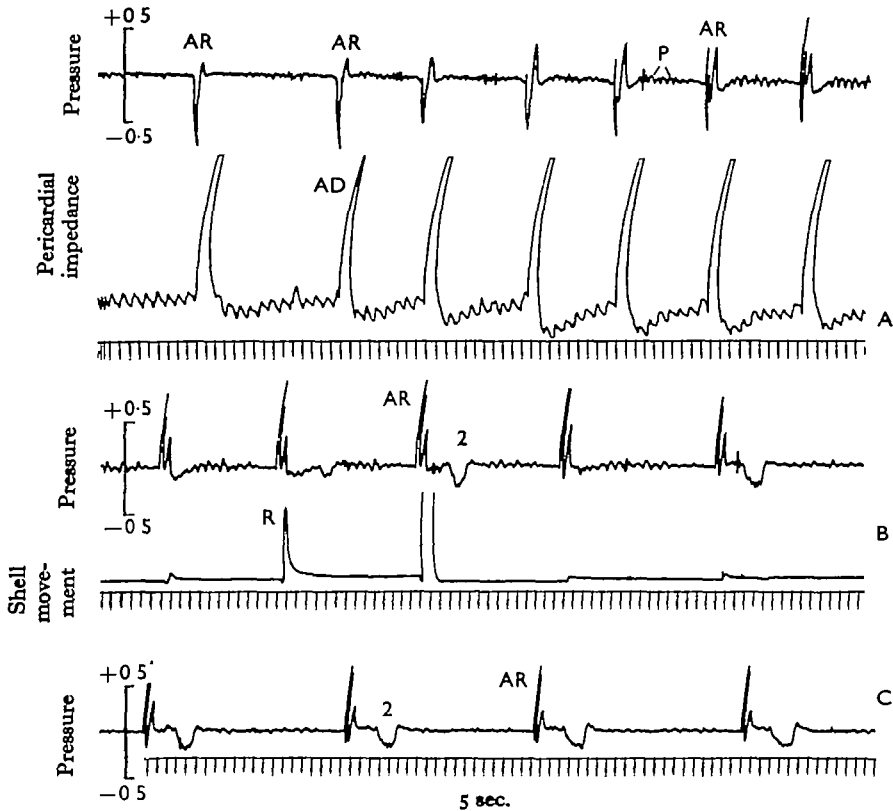

Fig. 4. Extracts from a recording of a complete digging period of *Mercenaria*. A, Commencement of burrowing showing external pressure as recorded from the adjacent sand (pressure in cm. of water) and an impedance recording (pericardial impedance) of the heart beat and adduction (AD) recorded by insertion of electrodes through the valves into the pericardium. Pressure exhibits first negative and subsequently complex positive wave-forms at successive adduction-retractions (AR) as the shell penetrates the substrate more deeply. Pedal probing (P) occurs between these peaks. B, 70 sec. after A, the lower record is of a light myograph attached by a thread to a valve to show retraction (R). Secondary siphonal and pedal retraction (2) commences intermittently as depth of burial increases. C, 290 sec. after B, succession of digging cycles with secondary cycle (2). These continued in a similar manner for another 75 min.

proprioceptors in the siphons of their degree of extension and hence of the relative depth of burial, such stimuli eventually causing cessation of burrowing. The new observation that movements of the foot occur simultaneously with those of the siphons suggests an alternative or additional function for these movements, namely, in aiding the opening of the valves thus increasing their gape. In *Mercenaria* pressures exerted by *withdrawal* of the foot and siphons appear to be transmitted through the agency of the double fluid skeleton of haemocoele and mantle cavity to act in opening the

valves. Other observations show that movements of the foot similar to those described here occur in other venerids, in *Glycymeris*, in the tellinid *Arcopagia crassa*, and in the freshwater unionid *Margaritifera* (Trueman, 1966c).

(d) Opening thrust of the ligament

In view of the observation that pressure exerted by withdrawal of the foot and siphons supplements the action of the ligament in opening the valves it is of interest to consider the opening thrust generated by the ligament in relation to that necessary to open the shell when completely buried in the sand. For specimens of the same size as those used for recording, the thrust of the ligament, determined as a moment (opening moment) per unit area of the valves (Trueman, 1954) was found to be 12 g. mm./mm.^{2} with the valves closed and not more than 7·5 g. mm./mm.^{2} at 5
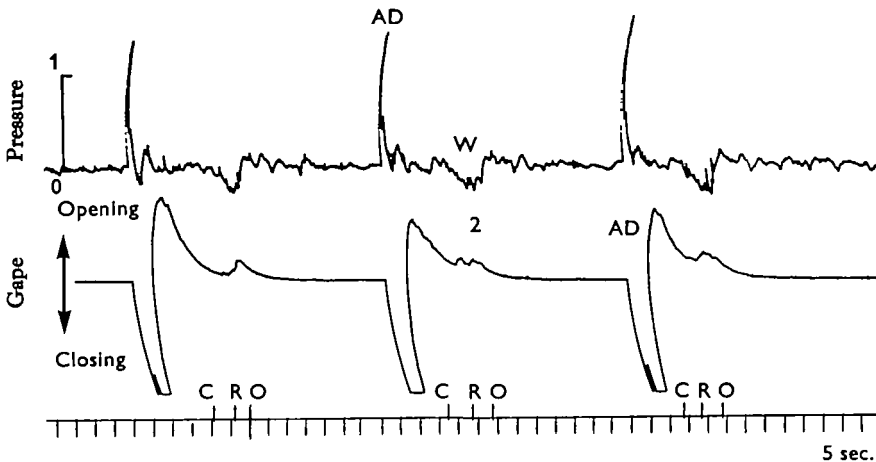

Fig. 5. Recording of the pressure changes in the sand (cm. of water) and valve movements (below, gape) during the latter part of the digging period of *Mercenaria*. Adductions (AD) correspond with the adduction peaks of successive digging cycles and the secondary opening of the valves (2) with the negative pressure recorded at pedal withdrawal (W). Movements of the siphon during the secondary cycle are marked above the time trace by direct observation; C, Siphons close; O, siphons open; C–R, siphonal retraction; R–O, siphonal extension.

degrees of gape. Trueman (1954) found that a steady thrust of 6 g. mm./mm.^{2}/degree of gape was required to open the valves of *Mya arenaria* in sand from Kames Bay, Millport, and on this basis the opening moment of *Mercenaria* is equivalent to only a 2-degree gape, In the absence of other factors the ligament would seem to be of use to open the valves fully (6 degrees, Fig. 2) only when less than one-third of their surface area is in the sand. When completely buried the action of the ligament must be supplemented by some other means of applying an opening thrust, unless the valves open at a time in the digging cycle when the sand is still loosened. When deeply buried, partial opening during stage v of the digging cycle is possible, but complete opening by means of the ligament alone is prevented. Pressures exerted internally by the slow contraction of the pedal and siphonal musculature then appear to supplement the action of the ligament.

(e) Retraction strength

Downward movement takes place at stage iv in the digging cycle and involves two processes: (a) passive settlement of the shell into the cavity formed by the ejection of water ventrally from the mantle cavity at stage iii, and (b) active downward sliding movement of the shell over the proximal regions of the extended and anchored foot caused by contraction of the proximal parts of first the anterior and then the posterior retractor muscles. The force involved in downward movement was measured by suspending a burrowing *Mercenaria* from a mechano-electrical transducer arranged as a myograph so as to prevent downward movement. A *Mercenaria* of 6·3 cm. length
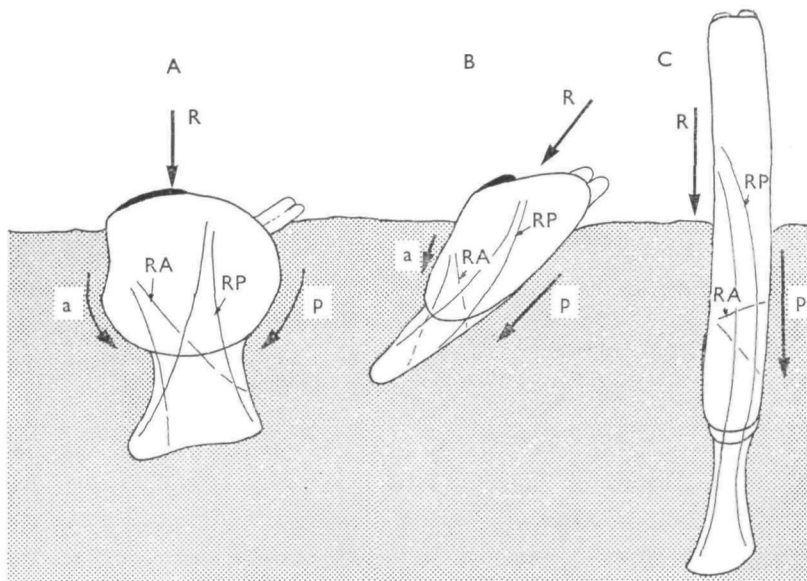

Fig. 6. Diagram comparing the burrowing of: A, *Mercenaria mercenaria*; B, *Donax vittatus*; C, *Ensis arcuatus*. showing in each the left valve, ligament, siphons and anterior (RA) and posterior (RP) retractor muscles. Movement brought about by these (→ a, and p, respectively) and the resultant direction (←, R) of the shell into the sand (stipple) is indicated. Not to scale.

attached to the myograph when almost completely buried in sand gave a downward pull at retraction equivalent to 26–27 g. The weight of the same animal in water was found to be approximately 21 g. so that the retraction strength exerted by the contraction of the retractor muscles was equivalent to only 5–6 g., only one-quarter of the weight of the animal in water. This contrasts with values of 50 g. for *Donax vittatus* of 2 cm. length, and 800 g. for *Ensis arcuatus* of 13 cm. length. The force pulling the shell downwards is controlled by both the strength of the retractor muscles and the effectiveness of the pedal anchor. The latter is especially strong in *Ensis* because of the bulbous form of the foot during digging (Fig. 6C).

DISCUSSION

The observations made here, using modern recording techniques, enable further interpretation of the functional significance of movements in the digging process of *Mercenaria*, noted by Ansell (1962), to be made. It is also of interest to compare the digging process of *Mercenaria* with that of other littoral bivalves which have been studied in detail by these techniques.

The most significant difference between the movements described for *Mercenaria* and those of *Tellina, Donax, Macoma* and *Cardium* (Trueman *et al.* 1966) lies in the appearance in the former of the secondary phase of siphonal and foot movements when the animal is below the surface of the substratum. In *Cardium* and *Donax*, burrowing activity normally ceases when the posterior dorsal margin of the shell is at a level with the surface of the substratum. Similar movements to those described here would not therefore be expected to occur in these species. Both *Tellina tenuis* and *Macoma* on the other hand burrow deeply below the surface and similar movements might have been expected to occur. Their absence may be explained by (*a*) the more rapid rate at which the movements of the digging cycle are performed, and (*b*) the greater opening moment of the ligament per unit area of shell surface. Thus, in *Tellina tenuis* the movements of siphonal closure, adduction, and contraction of the pedal retractor muscles, stages ii to iv of the digging cycle, together extend for less than 0·5 sec. Downward movement is completed and shell gape increases rapidly approximately 0·2 sec. following adduction. The increase in shell gape takes place while the sand around the shell is still disturbed by the ejection of water from the mantle cavity at adduction, and when the resistance of the sand to shell movement is consequently lowered. The relatively strong ligament of *Tellina* (Trueman, 1964) is able to open the shell to full gape against this reduced resistance and additional aid from the foot is not required. In *Mercenaria*, the ejection of water from the mantle cavity at adduction causes a disturbance of the sand ventrally and laterally to the shell which lasts for no more than 0·5 sec. Increase in gape does not occur until some 2–5 sec. following adduction and opening of the shell in *Mercenaria* must take place against the full resistance of the packed substratum. The opening moment produced by the ligament is unable to overcome this resistance when the whole of the shell is buried and the withdrawal of the foot and siphons produces a force which supplements that available from the ligament. Trueman *et al.* (1966) observed that the foot, shell, and muscles in bivalves act as an hydraulic system in which forces produced by the adductors can be transferred to a region of application in the foot, the increased pressure in the haemocoele causing the flattened foot to press against the substratum to obtain a firm anchorage. Similarly, forces produced by adduction can be transferred to act on the siphons, as during the extension of the siphons by hydrostatic pressures in the mantle cavity in *Mya* (Chapman & Newell, 1956). The present observations show that under certain conditions these processes are reversed in *Mercenaria*, which in contrast to *Mya* has free ventral mantle margins, pressures generated in the haemocoele and mantle cavity by the withdrawal of the foot and siphons being used to bring about extension of the adductor muscles.

Of the bivalves whose digging behaviour has been studied in most detail *Mercenaria* contrasts most markedly with *Ensis*. These types may be seen as two extremes in

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adaptation in the burrowing process. The normal habitat of both is in soft substrata, in shallow water or in the littoral zone where wave and current disturbance of bottom materials may be expected; both are subject to predation mainly by epifaunal inverte-brates and demersal fish. In *Mercenaria* protection from predators is afforded by the heavy shell, and its response to disturbance, involving stimulation of the siphons, is withdrawal of the siphons and closure of the shell; burrowing occurs normally only after gross disturbance when the animal has been exposed on the surface of the substratum, or in response to continued unfavourable conditions of the overlying water. In *Ensis* response to disturbance consists in rapid burrowing, stimulation of the siphons playing a major role in initiating this reaction (Fraenkel, 1927). The rapid withdrawal of the whole animal into the sand forms an effective protection from pre-dators. In *Mercenaria* the foot is extended ventrally, penetration involves antero-posterior rocking caused by the successive contraction of the almost equally sized anterior and posterior pedal retractor muscles. Passive sinking of the heavy shell into the cavity formed by ejection of water at adduction combined with a retraction force equivalent to only one quarter of the animal's weight in water leads to downward movement by a large number of small steps. In *Ensis* (Fig. 6), the foot is extended anteriorly; there is no rocking for the anterior retractors function only as protractor muscles; penetration is straight into the sand and occurs in few steps each involving considerable movement caused by the rapid contraction of the posterior pedal re-tractor muscles which form a straight line between the anchored foot and their inser-tion; the retraction force is equivalent to about 200 times the weight of the animal in water. *Donax* may be considered an intermediate condition between these two ex-tremes (Fig. 6). The shell extends into the substratum obliquely, with the foot ex-tended anteriorly; the retractor muscles are subequal with the greater force being produced by the posterior retractor so that rocking movements rarely occur. In temperate seas *Donax* sp. occur in a zone near low water on clean exposed sandy beaches, subject to considerable disturbance by wave action. Their burrowing move-ments seem well adapted to maintaining this position, An extreme example of adaptive burrowing behaviour evolved from this habit is seen in the migratory behaviour of *Donax* species on surf beaches in all parts of the world (Mori, 1938, 1950; Turner & Belding, 1957)

SUMMARY

1. Burrowing of the bivalve *Mercenaria mercenaria* has been re-examined using modern recording techniques. Burrowing activity consists of a series of movements, repeated cyclically termed the 'digging cycle', involving extension of the foot, closure of the siphons, adduction of the shell valves and retraction of the foot, Final position in the sand is only reached after many digging cycles, constituting a digging period.

2. Closure of the siphons and apposition of the mantle margins temporarily seals the mantle cavity to form a pressure chamber through which forces produced by adduction can be transmitted to act elsewhere. Adduction causes dilation of the distal regions of the foot, aiding pedal anchorage, and ejection of water from the mantle cavity loosens the sand ventrally and laterally.

3. Downward movement is by the passive dropping of the heavy shell into the fluid cavity formed at adduction, and by active movement caused by contraction of the

retractor muscles pulling the shell downwards on to the anchored foot. The strength of pedal retraction is 5–6 g. in an animal of 21 g. wt. in water.

4. With the shell completely covered by sand the opening moment of the ligament is shown to be too small to effect complete opening of the valves, and under these circumstances pressures generated by withdrawal of the foot and siphons in a secondary phase of siphonal movements supplement the action of the ligament.

5. Burrowing movements in *Mercenaria* are compared with those of *Tellina, Donax, Macoma, Cardium* and *Ensis*.

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