

## THE MECHANISM OF BURROWING OF THE MOLE CRAB, *EMERITA*

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### INTRODUCTION

Advances in electronic techniques have led to a fuller understanding of the mechanisms of burrowing into soft substrata (Trueman & Ansell, 1969). Observations have recently been made on a variety of soft-bodied animals, but no animal with a hard exoskeleton appears to have been investigated with modern techniques. The rapid burrowing behaviour of the mole crab, *Emerita portoricensis* Schmidt, was noted during a visit to Jamaica, the mechanism of its burrowing was investigated and is here compared with that of soft-bodied animals.

Mole crabs characteristically live in open surf-washed beaches where their survival depends on the ability to maintain position in a constantly shifting substrate. *Emerita* buries itself head uppermost, facing the ocean, in the wet sand of sloping beaches where they are covered by the wash of the waves. They extend their long plumose antennae so as to collect suspended food material from the water descending the beach after each wave (Snodgrass, 1952). Most species exhibit tidal migrations (MacGinitie, 1938; Efford, 1966; Cubit, 1969) and the ability both to burrow quickly and repeatedly and to emerge from the sand is an essential requisite of this behaviour. Pearse, Humm & Wharton (1942) described the movements used by *E. talpoides* to burrow in wet sand, observing that dry or moist sand is too hard. These authors pointed out that burrowing takes place backwards, that the uropods throw the sand dorsally while forcing the abdomen posteriorly into the sand and that sand is removed from the burrow by the first three pairs of thoracic legs.

The form of *Emerita*, its posture during burrowing and the movements of the limbs, are shown in Fig. 1. A full description of the anatomy of *E. talpoides* is given by Snodgrass (1952) who emphasized the smooth rounded shape of the carapace, and the long-pointed telson at the base of which project the relatively large uropods and the ways in which the first four thoracic legs are modified for their functions in burrowing.

### MATERIALS AND METHODS

*E. portoricensis* were collected from saturated littoral sand at Port Henderson in Kingston Harbour, Jamaica, and rapidly transported to the marine laboratory of the University of the West Indies at Port Royal where they could be kept for 3 or 4 weeks in small bowls of sand beneath a jet of sea water. On removal from the sand they would immediately burrow. For convenience in handling, a fine thread was attached to the carapace mid-dorsally by a small amount of wax. This did not appear to effect its

behaviour in any way. Observations and cine film of the digging period (overall duration of burrowing activity, Trueman & Ansell, 1969) were made in a glass tank. Isotonic and isometric myographs allowed movement into the sand and force respectively to be recorded while recordings of the pressure fluctuations in sand adjacent to a crab during locomotion facilitated the interpretation of myograph traces. Detail of these techniques is given by Hoggarth & Trueman, 1967.

Recordings and photography were in general limited to animals of length 1.5 cm from head to the base of the reflected telson which were conveniently abundant.

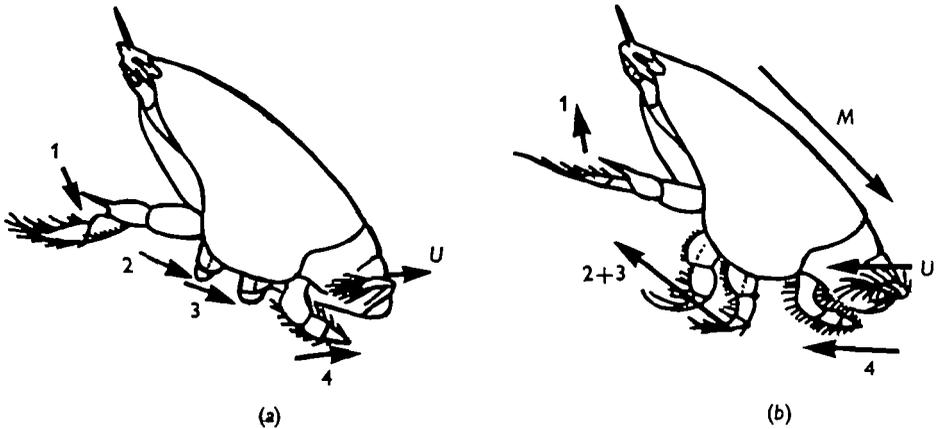


Fig. 1. Diagram of *Emerita* from the lateral aspect showing the position during burrowing with the limbs in (a), the recovery stroke and (b) the power stroke. The arrows indicate movement. 1-4, Thoracic legs; M, motion of animal; U, uropod.

#### EXPERIMENTAL OBSERVATIONS

##### (1) *Movements during burrowing*

When suspended over sand and slowly lowered, *Emerita* commences to burrow immediately the posterior part of the body comes into contact with the substrate. The digging period, of rather less than 1.5 sec duration, continues until the crab is completely buried so that the long second antennae may extend to collect suspended food material above the surface of the sand. During burrowing, however, these appendages are folded beneath the large meropod plates of the third maxillipeds (Snodgrass, 1952). The brevity of the digging period is the result of movement into the sand at about 1 cm/sec which may be compared with a rate of 0.25 cm/sec in the most rapid bivalve mollusc, *Ensis arcuatus*, so far reported (Trueman, 1968). In common with many infaunal animals *Emerita* makes a step-like series of movements into the ground during the digging period, the events associated with each step being referred to as a digging cycle.

With an *Emerita* suspended by a thread, contact with the substrate in the posterior region near the base of the telson gave rise to a rapid movement of the uropods and fourth thoracic legs, apparently in unison, and observations were made by means of slow motion cine film. The frequency of movement of these limbs varied between 14 and 21/sec, and when placed on sand the ensuing cloud of grains completely obscured the animal. This made it impracticable to follow the further movements of the legs except at the conclusion of the digging period when the posterior end was

completely buried. However, it was possible to simulate burrowing by gentle tactile stimulation on the base of the telson. This gave rise to a short burst of locomotor activity and it is assumed here that these movements are similar to those occurring beneath the sand. Generally the first three pairs of thoracic limbs moved back and forth in unison at a frequency of about 8/sec. Their function is to push the body backwards into the burrow but they additionally move the sand anteriorly, the first pair of legs principally antero-laterally. To accomplish this their forestroke is the power stroke and their backstroke is recovery. Manton (1952) has likened the various forestroke:backstroke ratios used in forward locomotion by a crustacean to a series of gears using the term middle gear when the ratio is 1:1 and 'low or high gear' when the

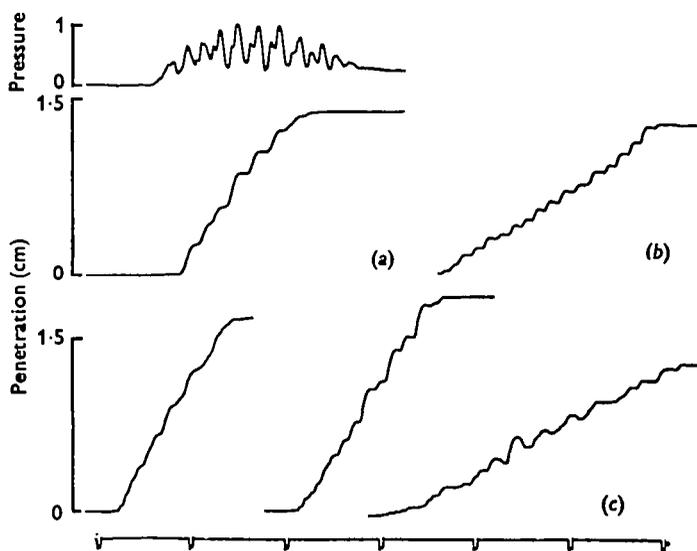


Fig. 2. Recordings of the digging period of *Emerita* showing pressure fluctuations in the adjacent sand (pressure) and movement into the substrate (penetration) in normal crabs and after removal of appendages. (a) Simultaneous record of pressure and penetration, normal crab; (b) recording of the digging period of a crab with fourth pair of legs removed; (c) recordings of normal crab, crab with first pair of legs and first and second pairs removed, from left to right. Time mark 1 sec.

relative duration of the backstroke is longer or shorter respectively. For consideration of the backward locomotion of *Emerita* it is more appropriate to express this ratio as recovery/power stroke for the function of the forestroke and backstroke are effectively reversed. From analysis of film of limb movements a ratio of 1:0.8 has been determined, indicating a moderately high gear. Lochhead (1961) considers that the extent to which higher gears can be utilized by an arthropod depends on the amount of resistance encountered and presumes that species which push through mud employ low gear ratios. In respect of the Diplopoda, which push their legs during burrowing, the power is achieved by the use of bottom gear in which the power stroke is of very much longer duration than the recovery (Manton, 1953). That this is not so in *Emerita* may reflect upon the speed with which it burrows and the soft, rather fluid, condition of the substrate. *Emerita* is unable to burrow in dry or wet unsaturated sand. On the beach

its digging period is restricted to the time between waves when the sand is saturated with water but when the swash is insufficient to dislodge the crab.

The movement of the first thoracic limbs is reminiscent of rowing with the flat surface of the wide dactylopodite, broadly fringed with setae, pushing forwards into the sand with maximal drag during the power stroke (Fig. 1*b*). The two distal segments are effectively feathered during the recovery stroke so that the drag is now minimal (Fig. 1*a*). The second and third limbs are similar to each other, are designed

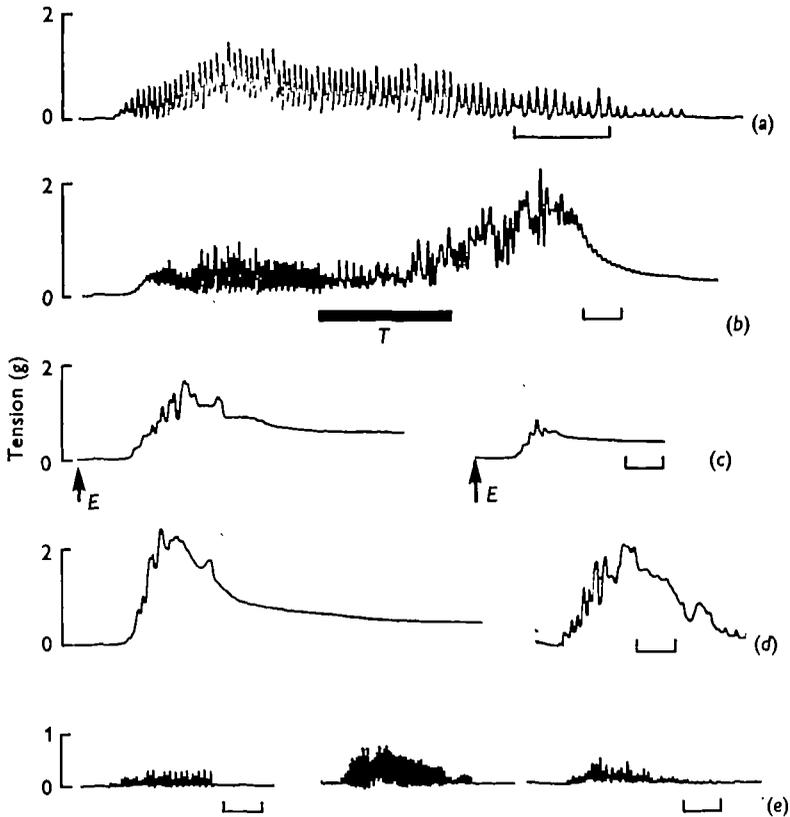


Fig. 3. Recordings of the tension produced during burrowing by *Emerita* attached to an isometric myograph by a thread from the dorsal region of the carapace. (a) suspended so that only the fourth leg and uropod were in contact with the substrate; (b) similar recording in which tension on the thread was slackened (*T*) so that the anterior three legs obtained anchorage in the sand, producing less frequent deflexions but greater force; (c) on left, normal animal allowed to dig (at *E*) with a slack thread so that the record shows no deflexions during the first part of the digging period; on right, recording of the same animal after removal of the first legs; (d) as (c) with removal of fourth legs (on right); (e) recorded from animals suspended as in (a), centre shows normal activity; left, same crab with fourth legs removed; and right, second crab with uropods removed. Time marks 1 sec.

to move forward with an effective push during the power stroke and to recover in a more flexed ventral position partially concealed beneath the branchiostegite folds of the carapace (Fig. 1). Thus the first three thoracic legs operate rather in the manner of oars, the forward stroke being the power stroke with maximal drag which is reduced by the feathering (1) or infolding (2 and 3) of the legs during the backward recovery

stroke. On the basis of their anatomy Snodgrass (1952) suggests that the second and third legs are constructed both for burrowing into and emerging from the sand. The latter function was not observed during this study of *Emerita*, but all successful sand-dwelling animals must be able readily to emerge from the sand either if they are buried too deeply by sand drift or, as in the case of the mole crab, they are migratory in habit.

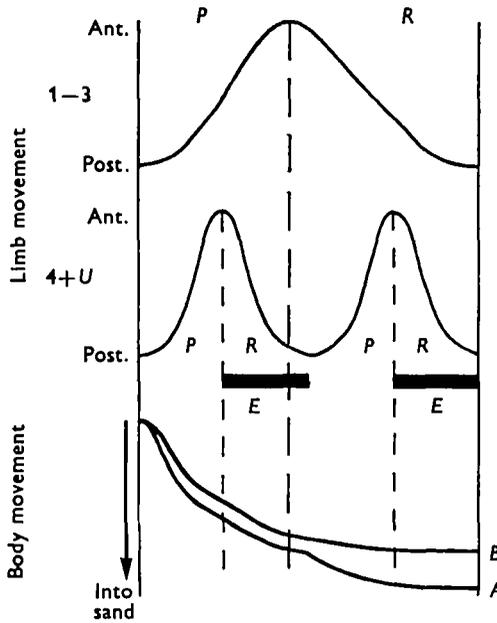


Fig. 4. Diagram summarising the events of a single digging cycle of approximately  $\frac{1}{4}$  sec duration. *A*, Movement of body produced by all limbs; *B*, movement without fourth legs on uropods; *E*, extension of burrow during recovery of fourth legs and uropods occurring twice in each cycle; *P*, power stroke; *R*, recovery stroke; 1-3, first three pairs of legs; 4+U, fourth pair of legs and uropods.

The movements of the fourth thoracic legs and uropods are somewhat different from the foregoing. Their function is to excavate the burrow, to force the sand anteriorly and in so doing to move the crab further into the sand. For these limbs it is difficult to determine which is the power stroke and which is recovery. Since a downward force equivalent to as much as 1 g could be recorded from these limbs using an isometric transducer (Fig. 3*a, e*), the fore-stroke is considered to be the power stroke, the back-stroke, when they are thrusting into the substrate, the recovery (Fig. 1). Snodgrass (1952) described the flexible articulation and musculature of the uropods, pointing out that the principal muscles of the uropods arise in the telson but give a strong forward stroke since the abdomen is flexed ventrally and the telson turned anteriorly. The recovery of these two pairs of limbs is not, however, a passive movement but an important and most effective stage in burrowing, for they thrust back into the substrate so as to extend the burrow (Fig. 4*E*). During the power stroke the fourth legs move forwards and inwards with the setae spread, and during recovery they move posteriorly and laterally. The uropods generally move in unison with the fourth legs, always at the

same frequency; during the power stroke they move forwards with setae and paired distal lobes spread so as to move the sand anteriorly while in recovery they move back in a more folded condition to cut into the sand.

### (2) *The digging period and digging cycle*

In some animals, e.g. bivalve molluscs, the digging period may be divided into two parts: the first, which follows initial penetration, is of very variable duration, while the second is represented by a series of digging cycles in which the time per cycle increases and the depth of penetration per cycle decreases towards the conclusion of burrowing. *Emerita* burrows in one continuous process during which penetration is achieved at a nearly constant rate, for there appears to be no separate phase of initial entry to the substrate (Fig. 2). Similarly there is very little lengthening of the digging cycles as the crab penetrates more deeply. This suggests that the saturated, rather loosely packed, coral sand used in these experiments does not increase in resistance to penetration with depth in the manner of the fine sand commonly used in experiments with bivalves (Trueman & Ansell, 1969). In its normal habitat *E. portoricensis* is only able to burrow in saturated surf-washed sand as Cubitt (1969) has similarly observed in *E. analoga*.

In each digging period the number of digging cycles, shown as steps on recordings using an isotonic myograph, is generally not less than 9. Each cycle consists of penetration of the substrate followed by a more or less static phase. Simultaneous recordings of pressure in the sand and depth of penetration (Fig. 2*a*) shows that during each step the greatest negative deflexion of the pressure trace corresponds with the commencement of movement into the sand. This would be exactly when the greatest force would be required for motion into the burrow and by analogy with similar pressure recordings from other animals, e.g. *Arenicola* (Trueman & Ansell, 1969), suggests that maximal force is then being applied to the substrate.

The events occurring during a digging cycle may be conveniently considered with reference to Fig. 4. During each digging cycle of approximately  $\frac{1}{4}$ th sec duration, limbs 1-3 make forward (power stroke) and backward (recovery stroke) movements, the major movement of the body corresponding with their power stroke. Operating at about twice the frequency of the latter, the fourth legs and uropods continue to excavate and burrow throughout the digging cycle (*E*), not being suppressed during the power stroke. In many burrowing animals (e.g. bivalve molluscs, *Arenicola*) extension of the burrow is inhibited while the animal moves down into the substrate. Removal (Fig. 2*c*) of the fourth legs or uropods leads to a much more pronounced step-like progression than is normally apparent. Indeed the action of the latter appendages may even serve to force the crab further into the burrow during the recovery of limbs 1-3 as indicated in Fig. 4 at A. Without the action of the fourth limbs or uropods the crab must either remain stationary as at B or slip upwards during the recovery of the anterior limbs. The frequency of the steps is between 6 and 8/sec which corresponds to the frequency of movement of the first three legs when observed in simulated swimming. Thus the main motive force in burrowing appears to be produced by the action of these limbs. It was not possible to record the activity of the fourth thoracic legs and uropods with an isotonic myograph since the crabs moved immediately into a position in which the anterior legs were utilised so masking the effect of the posterior limbs.

There is little doubt, however, that the latter function throughout the digging period. Recordings using isometric myographs in which the crab was suspended so that only the fourth thoracic legs and uropods came into contact with the substrate show bursts of activity (Fig. 3*a, e*) which may persist for longer than the normal duration of the digging period. These recordings gave maximal frequencies of 16–17/sec, comparable to observations from cine film, but showed a reduction to 10/sec after several seconds of activity. The tension exerted by these limbs rarely exceeded 1 g for a duration of less than 0.04 sec. Together with the frequency, the force applied to the myograph decreased towards the conclusion of each burst. One of the highest frequencies recorded for Crustacea is in respect of the legs of *Ligia oceanica* in which each leg executes more than 16 steps per second (Lochhead, 1961). This is closely comparable to the maxima of the fourth legs and uropods of the mole crab, and a decrease in frequency after several seconds (i.e. about fifty locomotory cycles) suggests that fatigue may be the cause. When the thread to the myograph is slackened during a burst of uropod activity the crab moves immediately further into the burrow and the anterior legs become involved (Fig. 3*b*) and a less frequent (7–8/sec) series of peaks of greater amplitude (2 g) is produced. The latter frequency corresponds to that observed for the first three legs and to the frequency of the digging cycles. But whereas on the isotonic myograph these appeared as a series of steps between which there was no movement out of the sand, on an isometric myograph the tension of the spring pulls the crab out of the sand during each recovery stroke. If the crab is allowed to burrow with a thread adjusted so that tension is only applied during the latter part of the digging period then the first rapid movements are not recorded (Fig. 3*c*). Although the fourth legs and uropods normally operate during the entire digging period, they would appear to be most important at the commencement of digging, acting as a particularly well specialized tool for initial penetration of the substrate. In common with all burrowing animals the thrust that *Emerita* can develop for movement into the sand is limited to the anchorage that it can obtain. During the initial stages the only anchorage which may be obtained is derived from a frictional component of the weight of the animal or the first three pairs of legs on the surface of the sand. Forces in excess of the anchorage strength simply move the crab in the opposite direction. The weight in water of the *Emerita* used in these experiments was 0.06 g so that only small forces can be applied to the substrate but the high frequency of their application ensures penetration.

### (3) *The effects of removal of limbs*

Further evidence regarding the function of different limbs during burrowing was obtained by observing the effect of their removal at the level of the basi-ischiopodite. Removal of either first (Fig. 2*c*) or second or third pairs of thoracic legs made little difference to the rate of penetration although rather more digging cycles occurred. However, the amount of thrust into the sand as recorded on an isometric myograph was reduced by 50% with the amputation of the first pair of legs (Fig. 3*c*). Removal of both the first and second legs gave rise to a protracted digging period and an increase in the number of digging cycles as represented by the steps shown in Fig. 2*c*. These steps further showed *Emerita* to emerge from the sand during the recovery stroke, indeed with these limbs missing the crab tended to rotate in the burrow and lacked directional stability. With all three anterior pairs of legs removed attempts at burial were

unsuccessful although some initial penetration was achieved using the fourth legs and uropods.

Removal of either the fourth legs or uropods resulted in a lengthy digging period comprising a large number of shallow steps, indicating the small amount of penetration made during each digging cycle (Fig. 2*b*). Since the penetration per cycle must partially depend on the rate of excavation of the burrow by the fourth legs and uropods, it is not surprising that amputation of one pair of these has this effect.

When an *Emerita* with the fourth legs removed is allowed to burrow attached to an isometric lever, the maximal tension developed is comparable to what it was before amputation (Fig. 3*d*) in contrast to removal of the first legs. But with the posterior extremity beneath the sand, so that only the forces developed by the fourth legs and uropods are recorded, *Emerita* develops about half the penetration force with either pair of limbs removed but at essentially the same frequency of action (Fig. 3*e*). With both of the fourth legs and uropods removed penetration could not be achieved, it was then difficult to induce burrowing movements by tactile stimuli; and, when elicited, burrowing movements resulted in movement over the surface of the sand by the action of the anterior three pairs of legs.

#### DISCUSSION

In the burrowing of *Emerita* the function of the fourth legs and uropods is to excavate the burrow while that of the first three pairs of legs is to propel the crab into the substrate. These functions were confirmed by the removal of appendages. Amputation of one pair of either group of limbs might protract the digging period, but its essential function was adequately carried out by the other members of the group. However, the inability of the crabs to burrow with all appendages of either group removed indicated that their function was not sufficiently plastic to allow for such a degree of adaptation. The division of the locomotory apparatus into two functional groups, is comparable to what occurs in many soft-bodied animals that burrow. Specialized structures such as the proboscis in *Arenicola* or the physa in the anemone *Peachia* (Trueman & Ansell, 1969) achieve penetration into the substrate, and the fourth legs and uropods are equivalent to these. Progression of the body into the sand is brought about in *Emerita* by a motion of the first three thoracic limbs similar to rowing, or in soft-bodied animals by contraction of the longitudinal body musculature.

In *Emerita*, and in all soft-bodied animals investigated, progression is achieved by a series of steps or digging cycles in which the body is alternately moved into the substrate and anchored (penetration anchor), while the burrow is being further excavated. In soft-bodied animals the body is pulled down by longitudinal muscles towards an anchor formed terminally (terminal anchor) by the dilation of part of the body wall (Trueman & Ansell, 1969). This carries out effectively the same function as the anterior three legs during the power stroke, the points of anchorage being their terminal segments. The more secure the anchorage the further the body will progress. Extension of the burrow takes place not only between power strokes but also simultaneously with them. This is shown schematically in relation to the events of a single digging cycle in Fig. 4. The possibility of different groups of limbs acting independently is one of the principal advantages over soft-bodied animals that a crustacean has in burrowing. The action of the fourth legs and uropods must be reinforced by the power stroke of the

anterior three legs; but during their recovery stroke the crab is not securely anchored and the force applied by the fourth legs and uropods must be limited to the weight of the crab and the friction between the body and the enveloping sand.

The mode of action of the anterior three limbs is remarkably similar to rowing and it seems appropriate to extend the analysis of rowing made by Alexander (1968) to the locomotion of *Emerita*. Alexander shows that the theoretical efficiency of a propellor ( $E_1/E_1 + E_2$ , where  $E_1$  represents the energy used in overcoming drag on the body and  $E_2$  that used in giving backward momentum to the fluid to drive the crab forward) is comparable to the ratio between the speed of the body and that of the limbs ( $U/u$ ). This depends on the relative sizes and drag coefficients of the body and legs, and is maximal when large quantities of fluid are being accelerated to a small velocity. Hence a high value demands limbs of large frontal area moving at low velocity. Mean values of  $U$  (1 cm/sec) and  $u$  (6 cm/sec, determined from cine film of simulated burrowing) give a theoretical velocity of only 0.17. If the movement of the limbs is considered to be restricted to one half when in sand this value is doubled by reduction of their rate of movement; but it is still relatively inefficient compared with 0.7 determined for the swimming of the water beetle, *Acilius* (Nachtigall, 1960). Nachtigall determined the total efficiency ( $E_1$ /total energy used in locomotion) of the locomotory mechanism of *Acilius* to be 0.45 by additionally measuring the drag on a leg in a water tunnel in the positions of both the power and recovery strokes, and by calculating the amount of energy used in pushing the water sideways. These values for *Acilius* can only be very approximate for *Emerita*, but on this basis the total efficiency of the locomotory mechanism is about 0.23. This relatively low value emphasises the mechanical difficulties encountered in burrowing rapidly into a soft substrate. Rapid movement even when the sand is in a relatively fluid condition is an inefficient process.

The power required in burrowing is  $DU$ , where  $D$  represents the drag on the body and  $U$  is the velocity of movement. The maximal tension developed in burrowing while restrained by an isometric myograph was about 2g. This has been shown to be produced by the action of the first three pairs of legs and must normally be more than sufficient for the crab to become buried. Thus the drag on the body cannot exceed this figure. Estimating, from recordings, a mean velocity of 1 cm/sec, the power required is  $2 \times 10^3$  ergs/sec. Allowing for the low efficiency of propulsion the power required to be developed would be about  $1 \times 10^4$  ergs/sec. It is difficult to estimate the weight of muscle used in backward locomotion by the three anterior limbs but assuming it is not more than a fifth of the crab's weight of 0.5 g. then the power output of the muscle would be  $1 \times 10^5$  ergs/sec/g muscle. Although rarely sustained for more than 1 sec, this is comparable to the power outputs quoted for various muscles by Bainbridge (1961). It would be of greater interest however, to compare the power requirement of *Emerita* with that of other burrowing animals, particularly in relation to their speed and efficiency, but unfortunately sufficient data is not yet available.

#### SUMMARY

1. The mechanism used by the mole crab *Emerita* for burial in sand has been studied by the analysis of cine film and electronic recordings.
2. Digging is initiated by tactile stimulation of the base of the telson and is carried

out by the fourth thoracic legs and uropods continuously excavating a cavity in the substrate.

3. The crab moves into this in a series of steps by the action of the first three pairs of legs. These limbs function in the manner of oars, being feathered during the recovery stroke.

4. The efficiency of locomotion and the power required for burial are determined.

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#### REFERENCES

- ALEXANDER, R. MCN. (1968). *Animal Mechanics*. London: Sidgwick and Jackson.
- BAINBRIDGE, R. (1961). Problems of fish locomotion. *Symp. zool. Soc. Lond.* **5**, 13-32.
- CUBIT, J. (1969). Behaviour and physical factors causing migration and aggregation of the sand crab *Emerita analoga* (Stimpson). *Ecology* **50**, 118-23.
- EFFORD, I. E. (1966). Feeding in the sand crab, *Emerita analoga* (Stimpson) (Decapoda, Anomura). *Crustaceana* **10**, 166-82.
- HOGGARTH, K. R. & TRUEMAN, E. R. (1967). Techniques for recording the activity of aquatic invertebrates. *Nature, Lond.* **213**, 1050-1.
- LOCHHEAD, J. H. (1961). Locomotion. In *Physiology of Crustacea*, Vol. 2, pp. 313-56. Ed. T. H. Waterman, New York: Academic Press.
- MACGINITIE, G. E. (1938). Movements and mating habits of the sand crab (*Emerita analoga*). *Am. Midland Natur.* **19**, 471-81.
- MANTON, S. M. (1952). The evolution of arthropodan locomotory mechanisms. Part 2. General introduction to the locomotory mechanisms of the Arthropoda. *J. Linn. Soc. (Zool.)* **42**, 93-117.
- MANTON, S. M. (1953). The evolution of arthropodan locomotory mechanisms. Part 4. The structure, habits and evolution of the Diplopoda. *J. Linn. Soc. (Zool.)* **42**, 299-368.
- NACHTIGALL, W. (1960). Über Kinematik, Dynamik und Energetik des Schwimmens einheimischer Dytisciden. *Z. vergl. Physiol.* **43**, 48-118.
- PEARSE, A. S., HUMM, H. J. & WHARTON, G. W. (1942). Ecology of sand beaches at Beaufort, N.C. *Ecol. Monogr.* **12**, 137-90.
- SNODGRASS, R. E. (1952). The sand crab *Emerita talpoida* (Say) and some of its relatives. *Smithsonian Misc. Collections* **117**, no. 8.
- TRUEMAN, E. R. (1968). A comparative account of the burrowing process of species of *Mactra* and of other bivalves. *Proc. malac. Soc. Lond.* **38**, 139-50.
- TRUEMAN, E. R. & ANSELL, A. D. (1969). The mechanisms of burrowing into soft substrata by marine animals. *Oceanogr. Mar. Biol. Ann. Rev.* **7**, 315-66.