

THE MECHANISM OF BURROWING OF SOME NATICID GASTROPODS IN COMPARISON WITH THAT OF OTHER MOLLUSCS

By E. R. TRUEMAN

Zoology Department, The University, Hull

(Received 22 January 1968)

INTRODUCTION

Gastropoda are primitively adapted for locomotion over hard substrates, most genera having a foot with a wide sole which may act both as a holdfast and as a locomotor surface. Although relatively few are adapted for burrowing, previous descriptions, e.g. Morton (1964), suggest that movement into soft substrates is a continuation of normal surface locomotion, the anterior part of the foot progressing freely into the sand with the passage of each locomotor wave along the sole of the foot. The locomotor wave has been thoroughly analysed by Lissman (1945, 1946) in respect of surface locomotion, but relatively little attention has been given to the burrowing process of gastropods. Previous accounts, e.g. Yonge on *Aporrhais* (1936) and *Turritella* (1946), Morris (1950) on *Uber (Polinices)* and Brown (1961) on *Bullia*, were largely based on visual observations. Until recently a somewhat similar situation obtained in respect of burrowing by the Bivalvia but the introduction of electronic techniques of recording burrowing activity (Hoggarth & Trueman, 1967), together with the analysis of ciné film has greatly extended our knowledge (Trueman, 1968*b*).

The purpose of this work is to investigate the burrowing process of members of the Naticidae, applying similar techniques to those used on bivalves, and to compare burrowing in the Gastropoda with that of other members of the Mollusca. Naticids characteristically haunt sandy beaches and sublittoral zones, ploughing over and through the sand in search of bivalves on which they feed, frequently burrowing deeply (Fretter & Graham, 1962; Hunter & Grant, 1966).

As far as possible the same terms will be used in this account as have been introduced to describe burrowing in the Bivalvia. Thus 'digging period', which was originally used by Ansell (1962) in respect of members of the Veneridae, describes the duration of the burrowing activity, from commencement until a stable position is attained in the substrate, in all molluscs. During this period the gastropod, e.g. *Turritella* (Yonge, 1946) or *Natica*, makes a series of step-like movements into the substrate, the events associated with each step being referred to as a digging cycle (Trueman, Brand & Davis, 1966).

MATERIAL AND METHODS

The opportunity to study the burrowing habits of members of the Naticidae arose during a visit to the Zoological Station, Naples. *Polinices josephinus* Risso was principally used in this investigation, although experiments were also made with *Natica*

millepunctata Lam. and *N. hebraea* Martyn. All three species burrowed actively in the laboratory in aquaria containing sand, and when removed to experimental tanks the digging period invariably began immediately. Hunter & Grant (1966) reported that the normal active burrowing of *P. duplicatus* is temporarily disturbed by handling and that, when replaced on sand after being marked with paint, they soon burrow deeply but then remain immobile for a period of more than 24 hr. No observations of this duration were made during this investigation, but repeated removal from the substrate led to the commencement of further digging periods. The handling of the snails appeared to have no adverse effect on their ability to burrow.

The techniques employed (Hoggarth & Trueman, 1967) allowed movement and muscle tensions to be recorded by means of threads attached from the shell to isotonic or isometric myographs, and volume changes in the foot to be detected by means of an impedance pneumograph. Free burrowing without any attachments was studied by recordings of the small pressure changes produced in sand during locomotion. Different types of recordings were made repeatedly (up to 20 times) for each species and the examples illustrated (Figs. 2, 4, 5) are extracts from typical traces.

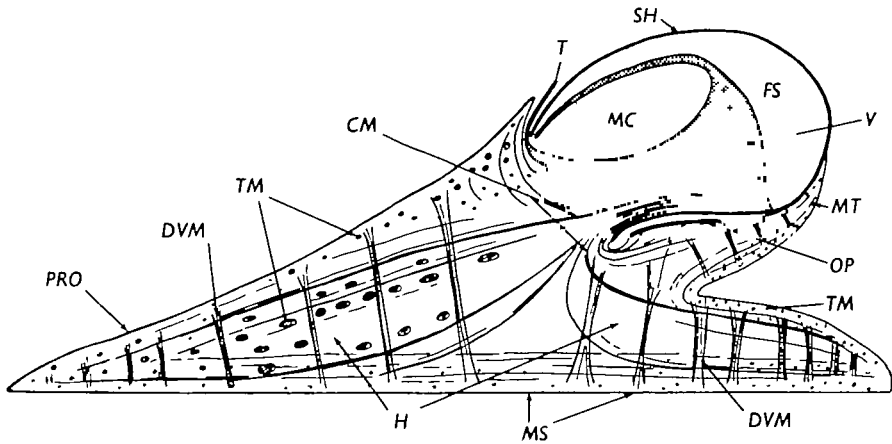


Fig. 1. Diagrammatic parasagittal section of *P. josephinus* showing the principal muscles of the extended foot and the shell with mantle cavity and water-filled space. *CM*, Columellar muscle, inserted into the shell; *DVM*, dorsoventral muscle of pro and mesopodium; *FS*, free space of the shell; *H*, pedal haemocoelae; *MC*, mantle cavity; *MS*, mesopodium; *MT*, metapodium; *OP*, operculum; *PRO*, propodium; *SH*, shell; *T*, tentacle; *TM*, transverse muscle; *V*, viscera (stipple), including the buccal mass.

THE FOOT OF *POLINICES JOSEPHINUS*

(a) Anatomy

It is convenient to outline the morphology of the foot before considering the results of experimental work. When *Polinices* is removed from a sandy burrow, the shell is surrounded and partially enveloped by an extensive fleshy foot (Fig. 1), which has been described by Fretter & Graham (1962) in respect of other members of the Naticidae. The propodium (*PRO*), which forms the anterior part of the sole of the foot, is exceptionally large and is shaped like a ploughshare. It is reflected over the shell anteriorly, covering the entrance to the mantle cavity, while the metapodium (*MT*) conceals the operculum (*OP*) and invests the posterior part of the shell. The mesopodium (*MS*)

forms the larger part of the sole of the foot. The cephalic tentacles (*T*) are widely separated and are pressed against the shell by the propodium when the animal moves forward. The mantle cavity is thus effectively isolated from the environment and delicate movements of the upper region of the propodium regulate the pallial water currents.

The most important component of the musculature of the foot (Fig. 1) is the columellar muscle which not only effects the withdrawal of the foot into the shell but also pulls the shell down into the substrate in a similar manner to the pedal retractor muscles of the Bivalvia. The columellar muscle together with the other muscles of the foot operate in an antagonistic system about the fluid skeleton formed by the blood contained within the pedal haemocoel. Around the pedal margins this is a diffuse fluid skeleton of the same form as that occurring throughout the foot of gastropods living on hard substrata, e.g. *Patella*. In naticids this fluid system allows monotaxic, direct, locomotor waves to pass along the foot from the posterior (Morton, 1964), while more centrally there are clearly defined fluid-filled cavities (*H*). Similar haemocoelic cavities occur within the foot of other actively burrowing molluscs, e.g. *Ensis* (Trueman, 1967), allowing rapid movement of the blood and the transference of hydrostatic pressure associated with pedal dilation. The foot of *Polinices* is expanded in the same way as in all Mollusca, by the introduction of blood into the pedal sinus and, although the turgor of the foot must be maintained by the pressure of the blood, there may be a continuous circulation through the sinus while the foot is expanded, as Brown (1964) has described in *Bullia* (Nassaridae).

Contraction of the muscles of the mesopodium, particularly the dorso-ventral muscles (*DVM*), forces blood forwards causing dilation of the propodium, where the dorsoventral and transverse muscles (*TM*) are relaxed. Conversely, contractions of the latter muscles bring about elongation of the propodium with displacement of blood posteriorly. The dorsoventral and transverse muscles function in antagonism to the columellar muscle and the operation of this fluid-muscle system will be discussed further in relation to burrowing.

(b) *The role of water in pedal expansion*

The mechanism of expansion and retraction of the foot of *P. josephinus* has attracted the attention of previous workers owing to its swollen oedematous appearance, and the suggestion was made by Schiemenz (1884, 1887) that both blood in the haemocoel and water in aquiferous spaces or canals are involved in its expansion and turgor. His findings obtained general acceptance, although they have never been corroborated; Brown (1964) has shown that in the nassarid, *Bullia*, the great expansion of the foot is carried out entirely by the blood, which is not exceptionally high in volume in comparison with other gastropods.

Observations on *P. josephinus* showed that the foot required considerable tactile stimulation before being folded back into the mantle cavity, when small fountains of water are ejected from several pores around the edge of the propodium (Ziegelmeier, 1958; personal observation). Preliminary examination of sections of relaxed specimens of *P. josephinus* disclosed structures on the anterior margin of the propodium similar to the pores figured by Schiemenz (1884), but it was not possible to confirm his observations on the extent of the aquiferous vessels.

Schiemenz (1884) determined the volume of water given off on contraction of a fully expanded specimen of *P. josephinus* into the shell and showed that it was invariably 2 or 3 times greater than the shell volume. This was confirmed during this investigation, when it was found that an animal with a shell of height 1.8 cm. and 4 ml. external volume gave off 7 ml. of water on withdrawal of the foot into the shell and conversely absorbed 8.5 ml. when allowed to expand fully. The latter was determined over a period of 30 min. by placing a retracted animal in a known volume of water and by measuring the reduction in volume when the expanded animal was removed. The comparable figures for *N. millepunctata*, of shell height 3 cm., volume 8 ml. were 6 ml. of water expelled and absorbed. In a study of the foot of *Uber (Polinices) strangei* Morris (1950) found that the volume given off at retraction was only slightly greater than the volume of the shell and, as she was unable to demonstrate water pores in sections of the foot, her results must be considered as inconclusive evidence of water being absorbed into the foot.

Recently, Brown (1964) has thoroughly investigated the process of expansion and retraction of the foot of *Bullia* (Nassaridae) which shows adaptations convergent to those of *Polinices* for life in marine sand. He observed that the water lost on pedal retraction is almost exclusively derived from the mantle cavity ($1/3$) and free space in the shell ($2/3$), the latter being space between the shell and the living tissues which is only present when the foot is extended (Fig. 1). Brown has conclusively shown that in *Bullia* the contribution of aquiferous spaces to the expansion of the foot is negligible, although water on the surface of the foot and within the proboscis sheath may make some contribution. The presence of free space within the shell of *Polinices* may be demonstrated by holes drilled into the shell (Morris, 1950) and it is probable that in general the role of water in pedal expansion is similar to that of *Bullia*. The foot is expanded by the introduction of blood into the pedal sinus and the principal role of water is in the mantle cavity and free space to replace tissues withdrawn from the shell. In *Bullia*, however, the total volume of water released on retraction of the foot is never greater than the volume of the shell (Brown, 1964). Only when the volume expelled is excess of the shell volume is there need for consideration of mechanisms of water storage other than within the shell. This is unnecessary in *Bullia*, *Uber (Polinices) strangei* (Morris, 1950) and in species of *Natica*. Although the feet of *N. millepunctata* and *N. hebraea* are similar to that of *Polinices*, they are smaller, particularly in respect of the propodium, require less stimulation to withdraw and do not produce water jets from the margin. It appears unlikely that water makes any direct contribution to their expansion. However, since the volume of water absorbed during pedal expansion in *P. josephinus* is at least twice that of the shell, the absorption of water through pores into the foot is a possible explanation in this species. This does not imply that blood flow into the pedal sinus is not the means by which the foot is expanded but rather that water may supplement the blood in its hydrodynamic role during locomotion. Further investigation of the role of water in *P. josephinus* and the mechanism by means of which it is drawn into the foot would be of great interest.

EXPERIMENTAL RESULTS

(a) *The digging period*

When placed on sand with the foot expanded naticids commence to burrow almost immediately and continue, moving obliquely to the surface, until buried. The initial stages of penetration by the propodium occur quite rapidly and are difficult to see. A more convenient method was to suspend the animal about 1 or 2 cm. above the sand by a thread attached to the shell and connected to a myograph. The foot penetrates the sand rapidly, to an extent of several centimetres in *P. josephinus*, and digging cycles commence. Sand is drawn up over the dorsal surface of the propodium by

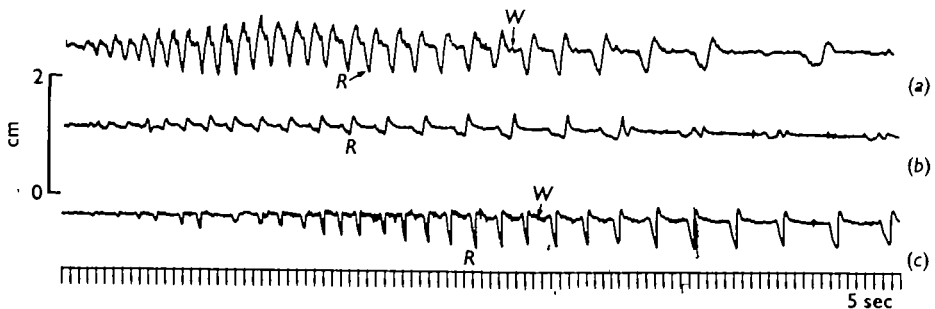


Fig. 2. Recordings of the pressure (cm of water) generated in fine sand during the free burrowing of: (a) *P. josephinus* (shell height, 1.8 cm.); (b) *N. millepunctata* (3 cm.); (c) *N. hebraea* (3.6 cm.). a, c, Each show a digging period which was completed by two further weak retractions; b, represents a complete digging period. R, Retraction of foot causing shell to be pulled into the sand; W, locomotor waves in the propodium during its extension.

ciliary action in conjunction with the secretion of mucus in all three species. This has previously been observed by Copeland (1922) in a study of ciliary and muscular locomotion in *P. duplicata*. The ventral side of the foot is also ciliated but no sand was drawn up on this surface nor were any effects of ciliary action or mucus secretion observed during the later stages of burrowing. It thus appears likely that ciliary action is only of importance during the initial stages of burrowing. This author also described how *P. duplicata* was unable to burrow with the propodium cut off but progressed over the surface of the sand. The converse observation is made here on *P. josephinus* for on one occasion burrowing proceeded with only the propodium expanded. These observations indicate the important adaptive value of the wedge-shaped propodium for ploughing into the sand.

Recordings (Fig. 2) of the pressure changes produced in the sand when naticids are burrowing freely show a series of negative deflexions, each corresponding to pedal retraction (R) when the shell is pulled down into the sand. Between these deflexions the trace shows fluctuations (W) which were observed to correspond to small locomotor waves reaching the anterior margin of the propodium. The negative deflexion on retraction is due to pressure being applied to a sand-water mixture with dilatant properties. Applied pressure disturbs the packing of the system and tends to cause water to be drawn in (Hoggarth & Trueman, 1967). Very similar recordings have been made while the polychaete *Arenicola* was burrowing (Trueman, 1966).

Each retraction and subsequent pedal extension represents a single digging cycle. These may be of variable duration at the commencement of burrowing, as in Fig. 2*b* but as soon as the foot is fully extended they follow each other at regular intervals which gradually increase in duration. This increase in time per cycle allows a longer period of probing or pedal extension in each cycle in the same manner as has been previously observed in *Bivalvia* (Trueman *et al.* 1966; Trueman, 1968*b*) and may be related to the increase in the resistance of the substrate at greater depth. The final cycles of the digging period tend to be of lower amplitude than those preceding (Figs. 2*b*, 5*a*), but naticids burrow obliquely and this may be related to an increase in distance from the transducer attachment.

The digging periods of each of the three species here investigated are similar in duration and in pattern of activity. The deflexion of the trace caused by a relatively small specimen of *P. josephinus* (Fig. 2*a*) is comparable in amplitude with the much larger specimen of *N. hebraea* (Fig. 2*c*) and is some measure of the relative power with which *Polinices* burrows. In a comparison of the burrowing of bivalves of different size, but of similar form (Trueman, 1968*c*) it was observed that small animals take a greater number of shallow steps in their digging periods than do larger specimens. The similarity of the duration of the digging periods and of their number of cycles between *P. josephinus* and *N. hebraea*, the shell and retracted tissues of the former being one half the weight of the latter (Fig. 2*a*, *c*), suggests that their anatomical differences, particularly in respect of the size of the propodium, may be important factors in relation to their ability to burrow (Table 1).

(b) *The digging cycle*

Each digging cycle consists of a number of coordinated activities, involving much of the musculature of the animal, which are repeated in the same sequence for each cycle. The cycle of *P. josephinus* is very similar to those of *N. millepunctata* and *N. hebraea* and is best understood by reference to Fig. 3 which was derived from analysis of ciné film, photographed when burrowing took place against the side of an aquarium tank, and from recordings. The digging cycle consists of four stages, designated 1-4 to avoid confusion with the somewhat similar stages described in respect of the *Bivalvia*.

(1) Extension of the propodium ceases and it becomes dilated.

(2) Maximum dilation of the propodium accompanied by pedal retraction. The contraction of the columellar muscle draws the shell and the posterior part of the foot down into the sand towards the anchored propodium (Fig. 6*b*).

(3) Recovery stage during which the propodium becomes less dilated with the relaxation of the columellar muscle.

(4) Extension of the propodium accompanied by the swelling of the mesopodium (Fig. 6*a*). Small locomotor waves pass along the foot from behind forwards, causing movements of the tip of the foot corresponding to the rhythm recorded during free burrowing (Fig. 2, *W*). The dilated mesopodium and the shell act as an anchor (mesopodial and shell, or penetration anchor) so that the animal remains still as the propodium ploughs forward. By analogy with the *Bivalvia* this stage may be termed the 'static period' and is represented in Fig. 2. by the intervals between the retractions (*R*).

The first stage of the digging cycle commences as the wave of elongation, which passes along the propodium, reaches the tip and extension of the foot is maximal.

While the dilation of the propodium was visually observed only as retraction began, it was recorded electronically during stage 1. This was accomplished by recording the impedance changes across the upper part of the propodium by means of a pair of electrodes attached to the shell so as to extend on each side of the foot. Increase in impedance between the electrodes represents the swelling of the propodium (Fig. 4). This is brought about during stages 1 and 2 by blood being forced forwards from the

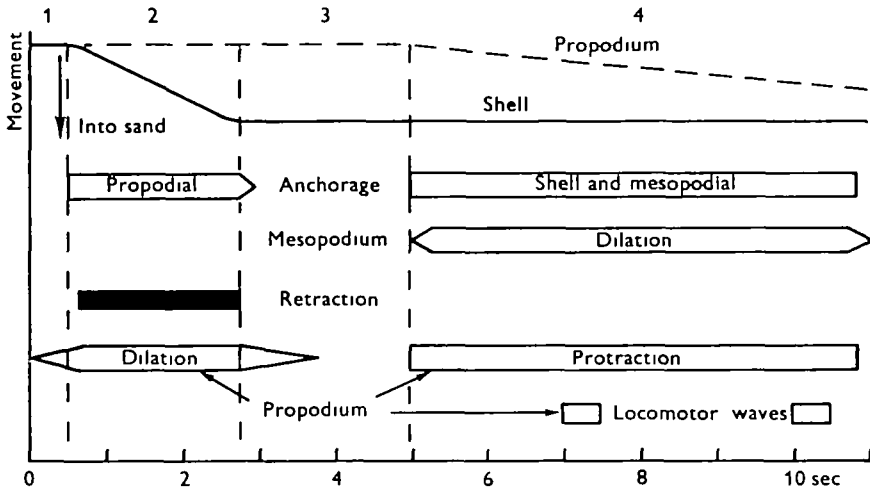


Fig. 3. Analysis of the activity of *P. josephinus* during a single digging cycle (stages 1-4 indicated). Movement of the shell into the sand (above, continuous line) occurs while the propodium is dilated (propodium anchor), whereas extension of the propodium (broken line) takes place when the shell remains static and the mesopodium is dilated (shell and mesopodial anchor).

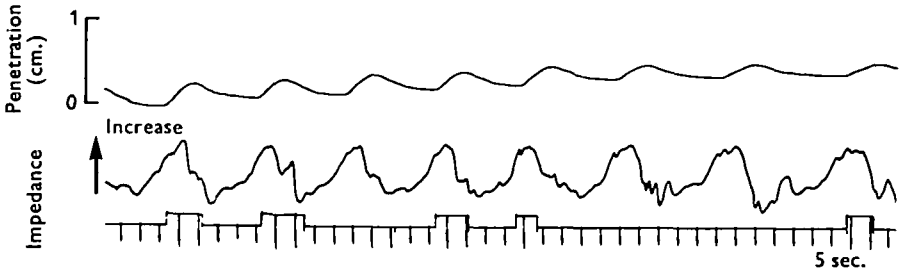


Fig. 4. Extract of a recording of the digging activity of *P. josephinus* showing penetration of substrate by use of an isotonic myograph and dilation of the propodium by visual observation (marks over time trace) and by increase of impedance (impedance pneumograph, a.c. coupled). Further information in the text.

mesopodium due to the contraction of the dorsoventral muscles and by tension being exerted in the collumellar muscle (Fig. 1). With greater retractile tension the swollen propodium presses outwards more strongly on to the substrate so increasing the strength of the propodial or terminal anchorage. During retraction the dorsal surface of the propodium rises, pushing the sand upwards and the anterior tip of the foot is not displaced or withdrawn from the substrate. The latter suggests that the shortening of the columellar muscle principally occurs in its proximal region so that the propodium only becomes shorter at retraction because of the downward movement of

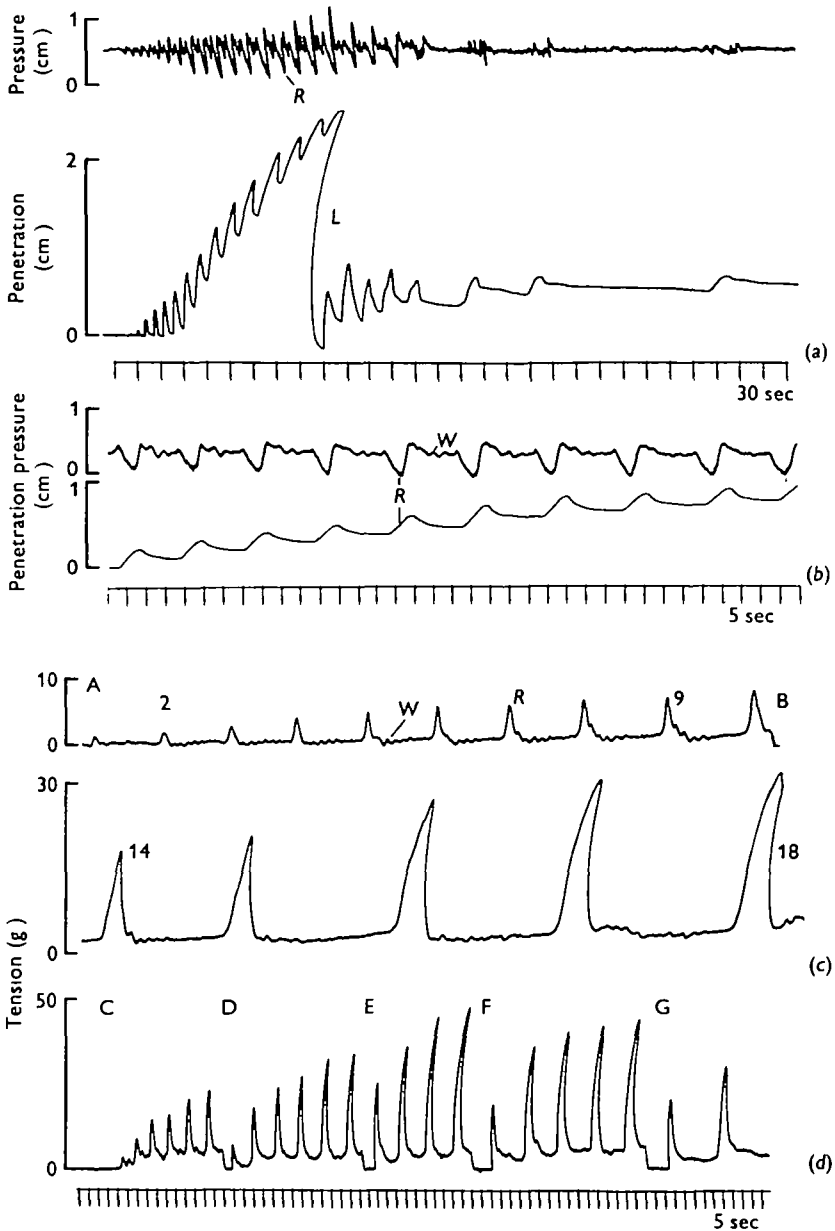


Fig. 5. Recordings of *P. josephinus* (shell height, 2.2 cm.) (a-c) and *N. hebraea* (3.6 cm.) (d) burrowing in fine sand. (a) Simultaneous recording of the external pressure changes (pressure, cm. of water) and movement into the substrate (penetration, recorded by isotonic myograph minimally loaded) for a complete digging period. The myograph was lowered at L to allow continued recording. (b) Extract of a similar recording to (a). (c) Extracts from a recording (isometric myograph) of a digging period showing tension exerted at retraction (numbers refer to successive cycles) and lower tension sustained during extension of the propodium. Zero tension was recorded with shell suspended 1 cm. above the sand (A) and when the myograph was lowered to allow further penetration (B). (d) Similar recording to (c), commencing with the foot just touching the sand (C) and as penetration proceeded the myograph was lowered 0.5 cm. at D-G. Other lettering as in previous figures.

the shell upon it. Thus the shape of the propodium is unaffected and allows the propodial anchor to be operative throughout retraction.

Recordings of penetration of the substrate, made by means of an isotonic myograph attached to the shell by a thread, show that movement is essentially a stepwise progression into the sand (Fig. 5*a, b*). The extent of the static period (stage 4) between retractions is apparent from the horizontal parts of the penetration trace (Fig. 5*b*) which represents the time when the propodium is elongated and ploughs forwards into the sand. This process of protraction occurs as a contractile wave spreads forwards

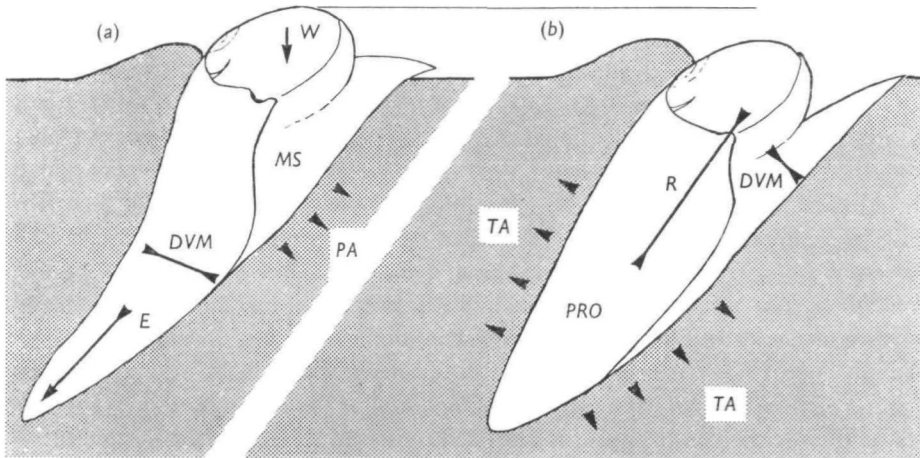


Fig. 6. Diagram of successive stages of the burrowing of *P. josephumus* into sand (stipple). (a) Mesopodium distended, by displacement of blood from the propodium, forming the mesopodial and shell, or penetration anchor (*PA*, arrowheads). *E*, Propodium extending by contraction of dorsoventral (*DVM*, $\blacktriangleleft\blacktriangleright$) and transverse muscles; *W*, weight of the shell. (b) Propodium dilated, by displacement of blood from the mesopodium by the contraction of dorsoventral muscles (*DVM*, $\blacktriangleleft\blacktriangleright$), forming propodial or terminal anchor (*TA*, arrowheads). The shell is then pulled down by the contraction of the columellar muscle (*R*, $\blacktriangleleft\blacktriangleright$). Other lettering as in previous figures.

along the propodium, involving the shortening of the dorsoventral and transverse muscles and causing the anterior part of the foot to become more slender. When this wave reaches the tip and the propodium is fully extended pedal retraction follows immediately. This contractile wave is distinct from and additional to the small locomotor waves observed in the propodium (Figs. 2, *W*, and 3).

A further consequence of the contraction of the transverse and dorsoventral muscles of the propodium is for blood to be displaced posteriorly into the mesopodium, which with the relaxation of its dorsoventral muscles then becomes swollen. The swelling, together with the resistance of the shell to being pushed upwards, tends to hold the animal still while the propodium extends and represents the mesopodial and shell anchorage (Figs. 3, 6*a*). Recordings on an isotonic myograph (Fig. 5*a, b*) all show retraction followed by a fall in the trace during propodial elongation. This is due to the shell being raised by the down-thrust of the foot into the sand. The amount that it is lifted is principally dependent upon the strength of the mesopodial and shell anchorage, the force used in propodial extension and the resistance of the substrate to penetration

by the foot. The recordings shown in Fig. 5 were made in fine sand, whereas in gravel the shell was hardly raised since penetration was more readily achieved. When at the surface of the sand, as in Fig. 6*a*, the probing of the foot is limited by the weight of the shell rather than by the friction between foot and substrate, and forces in excess of the weight would tend to push the animal backwards. The use of cilia during the initial stages of burial is an adaptation which facilitates penetration by the foot when the pressure applied may thus be limited.

(*c*) *The fluid dynamics of burrowing*

It has already been pointed out that water in the mantle cavity, the free space of the shell and in the aquiferous system of the foot plays a role in pedal expansion in *Polinices*. Jets of water are produced from all these sources when the animal withdraws rapidly into its shell. In view of the role of water ejected from the mantle cavity during the digging cycle of bivalves (Trueman, 1967) particular attention was paid to observing whether water jets play any part in the burrowing process of naticids. No water was observed to be ejected during the burrowing of any of the three species here investigated. Recordings of the pressures produced by bivalves externally in the sand commonly show a negative deflexion during each cycle only at the beginning of the digging period, for as soon as the valves are beneath the surface of the sand, the water ejected superimposes a positive peak on the negative deflexions, e.g. in *Ensis* (Hoggarth & Trueman, 1967; Fig. 2). In naticids, as in *Arenicola* (Trueman, 1966), the negative deflexions of the external pressure persist throughout the digging period (Fig. 2), and this is further evidence that water is not used to loosen the sand during the burrowing of these animals.

Attempts made to record pressure changes during burrowing, by the insertion of cannulae into the foot, met with no success. Previous authors, e.g. Morris (1950), have observed water emerging at retraction from holes cut into the shell of naticids, and the insertion of a cannula through the shell about $\frac{1}{2}$ whorl from the margin produced a recording of peaks of hydrostatic pressure of 5 cm of water which corresponded to the retraction of the foot in each digging cycle. The propodium forms a cephalic shield which covers the opening of the mantle cavity and effectively seals the opening of the shell particularly at retraction when the propodium and shell are drawn closely together. This prevents the loss of water from the mantle cavity and free space of the shell while ensuring that the rise in fluid pressure within the shell is the same as in the pedal haemocoel at retraction. This is very similar to the manner in which pedal retraction has been shown to sustain high pressure in the foot of bivalves (Trueman, 1967). In the naticids, as in the bivalves, this pressure is utilized to produce dilation of parts of the body so that the animal may be drawn into the substrate.

For the foot to function in the manner described above it is necessary for the blood to remain at nearly constant volume. During retraction the tension developed by the columellar muscle increases the fluid pressure throughout the body and it is not necessary to envisage a mechanism to retain the blood within the foot. However, for propodial dilation it is essential for the blood to remain in the anterior part of the foot. This requires the contraction of the dorsoventral muscles in the mesopodium (Fig. 1) and it is only when these muscles relax at stage 4 of the cycle that blood flows back into the mesopodium. It is not clear how blood is retained within the foot during

extension of the propodium. No valve-like structures have been observed which might prevent its return to the visceral or pallial sinuses and one can only fall back on Brown's (1964) suggestion that in *Bullia* pedal turgor is maintained by the visceral musculature.

(d) *The strength of retraction and pedal extension*

The strength of retraction has been determined from recordings made by suspending the shell from an isometric myograph. The shell of a specimen of *P. josephinus* was first placed 1 cm. above the sand, and as the foot extends a series of peaks are obtained (Fig. 5c), each representing pedal retraction. The amplitude of these peaks increases with the greater penetration of the substrate (2-9) and corresponds with the increasing amplitude of the negative deflexions occurring in the recordings of external pressure

Table 1. *Comparative data of the digging period of some molluscs in fine sand*

	<i>P. josephinus</i> (shell height, 2.2 cm.)	<i>N. mille-</i> <i>punctata</i> (shell height, 3 cm.)	<i>N. hebraea</i> (shell height, 3.6 cm.)	<i>Glycymeris</i> <i>glycymeris</i> (shell length, 5.2 cm.)	<i>Maetra</i> <i>corallina</i> (shell length, 4 cm.)	<i>Dentalium</i> <i>inaequico-</i> <i>statum</i> (shell length, 3.5 cm.)
Duration of digging period (min.)	10	8	10	48	0.58	9
No. of digging cycles	34	19	31	39	6	14
Ratio of retraction strength/weight in water (g.)	35/3 = 12	22/5.5 = 4	48/6 = 8	48/12 = 4	47.7/3 = 16	1.7/0.3 = 6
Rate of penetration (cm./min.) (immediately after initial pedal extension)	0.6*	—	—	0.125	8.5	0.1*

* Represents oblique burrowing. Data derived from original observations and Ansell & Trueman (1967), Trueman (1968a, c).

(Figs. 2, 5a) at the beginning of a digging period. Greater penetration of the substrate leads to a more secure propodial anchorage and more powerful retraction is effected. This phenomenon continues after the shell has been lowered (at B) just on to the surface of the sand and finally (cycle 18) maximal strength was recorded with the foot extended at least 4 cm. beneath the surface. Similar recordings of both *N. hebraea* (Fig. 5d) and *N. millepunctata* were made, the strength of the former being larger than *Polinices* because of the larger size of the animal. A more valid comparison between species may be obtained from the ratio between the retraction strength and the weight of the animal in water (Table 1). This ratio shows the powerful retraction of *P. josephinus* which may be attributed to the relatively larger propodium and that *N. hebraea* burrows more powerfully than *N. millepunctata*. This ratio has previously been utilized in respect of *Bivalvia* to compare the role of the retractor muscles with the weight of the animal which allows the shell to fall into a cavity formed in the sand by the jets of water from the mantle cavity (Trueman, 1968b). Since water jets do not occur in the Naticidae the ratio is here only a means of comparing the strength of animals of

different size. It is of interest, however, to note that the ratio for *P. josephinus* is greater than that of some bivalves, e.g. *Glycymeris* (Table 1), *Mercenaria* (Trueman, 1968*b*) and only a little less than *Maetra corallina*, a particularly active and rapidly burrowing bivalve. It may also be inferred from these ratios that the effectiveness of the propodial anchorage of naticids is comparable to that of the pedal anchor of most bivalves.

Recordings obtained by the isometric myograph also show the effect of the rhythmical locomotory waves (Fig. 5*c*, W) which occur during the protraction of the foot. Each of these waves has an amplitude of approximately 1 g., although the tension sustained on the myograph between retractions gradually increases. Zero tension is only achieved when the myograph is lowered as at *B* (Fig. 5*c*) and at *D-G* (Fig. 5*d*), while the maximum tension sustained in each recording is respectively 3.5 and 6 g. This is slightly in excess of (*P. josephinus*) and the same as (*N. hebraea*), the weight of the animals used in these recordings, and suggests that the snail is held firm in the sand by a force at least equivalent to its own weight. A less secure mespodial and shell anchor would result in more marked downward deflexions of the trace between each retraction.

DISCUSSION

The burrowing process of naticid gastropods consists essentially of the repeated extension and retraction of the propodium integrated with the application of two anchors. The timing of these processes in relation to a single digging cycle (Fig. 3) shows that movement of the shell occurs while the propodium is static and vice versa.

The method of burrowing used by all soft-bodied animals is essentially the same (Clark, 1964; Trueman, 1966). Part of the body is dilated to form an anchor while the head or terminal region is forced further into the substrate. From a functional aspect this may be conveniently termed the 'penetration anchor', which is represented by the mespodial and shell anchor in naticids, the shell anchor in bivalves (Trueman, 1968*b*) and Scaphopoda (Trueman, 1968*a*), the flange anchor in *Arenicola* (Trueman, 1966) and the column anchor in the anemone, *Peachia* (Ansell & Trueman, 1968), for in each the same function is served. Subsequent to penetration of the substrate the terminal region becomes swollen to form a new anchor which enables the remainder of the animal to be drawn down into the sand. This terminal anchor, the propodial anchor of naticids, is functionally similar in all the animals mentioned above; in molluscs it allows retraction to pull the shell into the sand (Fig. 7), and in worms and anemones the hindermost region into the burrow.

Gastropoda are adapted for locomotion over hard surfaces, the pedal muscles contracting rhythmically to produce locomotory waves which in the Naticidae are monotaxic and direct (Morton, 1964). In this group burrowing is a continuation of normal surface movement with the propodium inserted into the substrate as a mobile wedge. Previous authors, e.g. Weber (1925), Zeigelmeier (1958), have described surface locomotion in naticids and the locomotor gallop of *P. josephinus*. This method of locomotion involves the extension of the propodium, while the posterior part of the foot is in contact with the substrate, followed by the shell being pulled forward on to the attached propodium. These two regions of the foot play very similar roles in burrowing. Locomotor gallops have also been described in *Aplysia* and in *Helix* (Morton, 1964) and the movements of *Aporrhais* (Yonge, 1936) are somewhat similar, but the shell is

used in addition to the posterior part of the foot during the extension of the propodium in a manner comparable to burrowing in *Polinices*. Many gastropods, e.g. *Bullia*, *Philine*, *Scaphander*, *Actaeon*, have a specialized foot with broad sole and wedge-shaped anterior contour and burrow in the manner of *Polinices*. A notable exception is *Terebra* (Morton, 1964) with a narrow unspecialized foot in which the anchorage is produced by the distension of the entire distal region rather as in the Bivalvia.

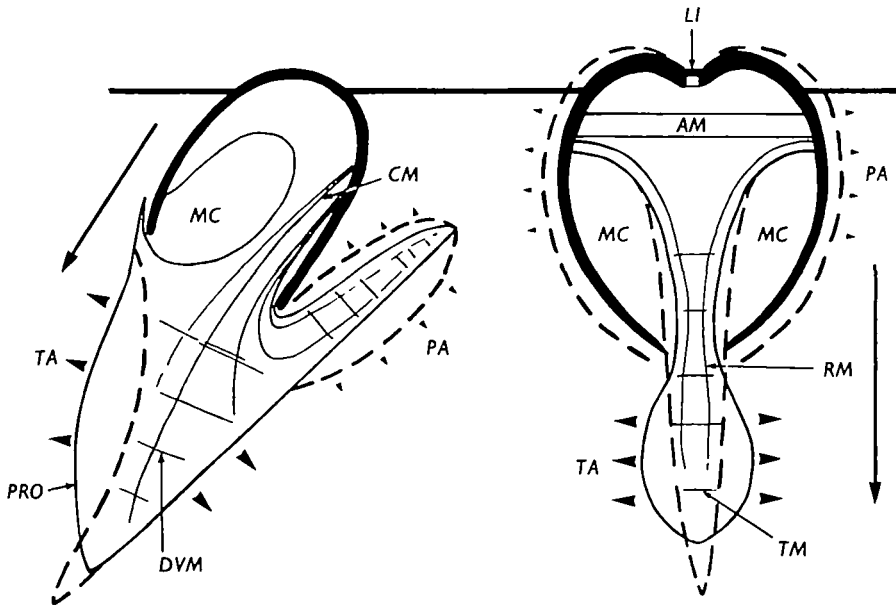


Fig. 7. Diagram comparing the burrowing of a naticid (longitudinal section) with a bivalve (transverse section). Both are shown passing beneath the surface of the substrate (horizontal line) at the end of pedal retraction, the large arrow indicating shell movement. The terminal anchor (*TA*, large arrowheads) is formed in the naticid by dilation of the propodium, in the bivalve by distension of the entire distal region of the foot. Subsequently the penetration anchor (*PA*, small arrowheads) is applied by the opening of the valves or by the swelling of the mesopodium (naticid) prior to pedal extension. This stage of burrowing is indicated by broken lines. *LI*, hinge ligament; other letters as in previous figures.

In the Naticidae burrowing involves the alternate swelling of two regions of the foot and movement of blood within the pedal sinus. The shell is pulled into the sand with the propodium dilated to form a terminal anchor by the fluid pressure developed from the columellar and intrinsic pedal muscles. By contrast, in the Bivalvia the terminal anchor is formed in the entire distal region of the foot into which the blood flows because of the pressure generated by the adduction of the valves and sustained by pedal retraction (Trueman, 1967). The fundamentals of the burrowing mechanisms of these two groups are summarized in Table 2 and compared diagrammatically in Fig. 7. Whereas the method of pulling the shell down into the substrate by retractor or columellar muscle is essentially similar in all molluscs, the subsequent extension of the foot, by means of locomotor waves in the Gastropoda, by a stabbing action in the Bivalvia and Scaphopoda, is quite different.

The foot of bivalves is laterally compressed and blade-like in form and in most

genera, e.g. *Macoma* (Trueman, *et al.* 1966) has no sole. It penetrates the substrate by a rhythmical probing movement set up by the antagonistic action of the transverse and retractor muscles over the entire distal region of the foot. Those bivalves which have changed from the primitive infaunal to an epifaunal mode of life, progress over a hard substrate by means of the typical bivalve rhythm of extension and retraction of the foot rather than by the locomotor waves characteristic of gastropods. Bivalvia are primitively adapted for movement over or through soft substrates and no group of animals is better fitted to this life, for their hinged shell acts as the basis of a double fluid-muscle system. The pressure produced by the adductor muscles drawing the valves together not only causes dilation of the foot but also generates powerful jets of water which assist movement of the shell by loosening the adjacent sand (Trueman, 1967, 1968*b*). Penetration of the substrate is further assisted by the reduction of the profile of the shell at adduction. These features of burrowing have not been observed in Mollusca other than the Bivalvia.

Table 2. *Comparison of the principal activities of different animals during a single digging cycle*

	Event	
	Terminal anchor, allowing shell (or body) to be pulled into the substrate	Penetration anchor, allowing extension of foot (or head)
Bivalvia (from Trueman, 1968 <i>b</i>)	(ii) Siphons close, pedal dilation and anchorage commences (iii) Adduction of valves, maximal anchorage, water jets loosen sand, reduction of shell profile (iv) Pedal retraction	(v) Pedal anchor lost, valves and siphon open, shell anchor established (vi) Pedal protraction with probing movements
Naticidae	(1) Dilatation of propodium commences (2) Maximal dilation establishing propodial anchor, followed by pedal retraction	(3) Propodial anchor lost (4) Dilatation of mesopodium, establishment of mesopodial and shell anchor and protraction of propodium with rhythmic locomotory waves
Scaphopoda (from Trueman, 1968 <i>a</i>)	(a) Pedal dilation, epipodial lobes raised, establishing pedal anchor (b) Pedal retraction	(c) Pedal anchor lost (d) Weak shell anchor secures animal, pedal protraction with probing movements
<i>Arenicola</i> (from Trueman, 1966)	Dilation of anterior trunk segments, establishing the dilation anchor Contraction of longitudinal trunk muscles pulling worm into burrow	Dilation anchor lost, flange anchor established as worm elongates allowing the head to penetrate further into the substrate with proboscis extrusion

The bivalved shell has a further advantage for the hinge ligament not only opens the valves but also presses them outwards against the substrate to form a secure penetration or shell anchor (Fig. 7). Those with relatively weak ligaments, e.g. *Glycymeris*, have a less secure anchorage, show weak probing, lengthy digging cycles (Ansell & Trueman, 1967) and a low rate of burial (Table 1). Similarly in the Scaphopoda, although the retraction strength is relatively high (Table 1), the burrowing ability is limited by weak probing associated with a poor penetration anchor (Trueman, 1968*a*). In the Gastropoda the same conditions probably occur in *Terebra* (Morton, 1964),

but in the Naticidae, where the penetration anchor includes both shell and the mesopodium, a more rapid rate of burial, comparable to that of many bivalves (Trueman, 1968c), is achieved.

SUMMARY

1. The burrowing activity of naticid gastropods, described by use of ciné film and electronic recordings, shows four stages, together termed the digging cycle, which are repeated cyclically until burial is complete.

2. In each cycle the retraction and extension of the propodium is integrated with the alternate swelling of two regions of the foot by the movement of blood within the pedal sinus. The shell is pulled into the sand with the propodium dilated by the fluid pressure generated by the columellar and intrinsic pedal muscles. The role of water in the expansion of the foot of *Polinices* is discussed.

3. In a comparison of the burrowing process of naticids with that of other molluscs a general similarity is observed throughout the phylum and in other soft-bodied invertebrates. The major differences between the burrowing of gastropods and that of bivalves are discussed and indicate that in former burrowing is an adaption of normal surface locomotion, whereas the bivalves are more primitively adapted to an infaunal mode of life.

Experimental work in connexion with this paper was carried out during a short visit to the Stazione Zoologica, Naples, and it is a pleasure to record my gratitude to the Director and to members of the staff. I am grateful to Professor P. G. 'Espinasse for his continued interest and support during this investigation.

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