

Locomotion, pedal retraction and extension, and the hydraulic systems of *Bullia* (Gastropoda: Nassaridae)

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(With 2 plates and 7 figures in the text)

Surface locomotion and burrowing by *Bullia digitalis* have been analysed by use of ciné film and electronic recording. Both movements are shown to be carried out by a series of steps in which the propodium is first extended whilst the snail is anchored by the posterior of the foot (penetration anchor) and, when buried, also by the shell; secondly the shell is drawn forwards and downwards towards the anchored propodium (terminal anchor). The extremely flattened foot of this snail contains a greatly enlarged pedal sinus containing blood and functions as a hydraulic organ. This contrasts with the foot of most gastropods, e.g. *Patella*, which crawl over hard surfaces and have no large fluid filled pedal cavity.

During each step, or digging cycle, there are two pressure pulses, one effecting propodial extension, the second occurring as the shell is drawn forwards. The pedal haemocoel is isolated from the remainder of the circulation for at least part of the locomotory cycle so enabling the foot to function as a fluid-muscle system at constant volume. *Bullia* exhibits convergence with burrowing bivalve molluscs having a similar pattern of alternating anchorages in sand and in both water is ejected from the mantle cavity to liquefy the sand in front of the shell.

The energy cost of burrowing by *B. digitalis* is estimated to be 6.6×10^{-6} J/mg dry tissue weight, a figure comparable to that of the clam *Donax* provided that burial occurs at a similar rate. By contrast the energy requirement for *Bullia* to move over the surface of sand is about one tenth of that for burial.

Pedal extension involves both blood flow, so that the foot may function as a hydraulic system, and direct muscular antagonism between the fibres of a three dimensional muscle network in the opercular muscle. When the snail is extended the shell contains some sea-water which plays a dynamic role in pedal expansion and retraction independently of the pedal blood sinus. The possible role of this cavity in other prosobranchs is discussed.

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Introduction

Bullia digitalis Meuschen is a prosobranch gastropod which burrows in the sand of South African beaches, reaching particularly high numbers on the west coast. Its ecology

and the factors influencing distribution have been discussed by Brown (1961, 1971) who has also used this species to investigate the role of blood in the expansion and retraction of the gastropod foot (Brown, 1964). Members of this genus are excellent experimental animals, being active in the laboratory and, unlike most gastropods invariably not withdrawing into the shell when needles or cannulae are inserted into the foot. Accordingly, *Bullia* proved to be a very suitable gastropod for this investigation of the mechanism of burrowing and the role of the pedal haemocoel as a hydraulic system in locomotion and in expansion and retraction of the foot. Apart from Brown's (1964) previous study and Dale's (1974) observations of *Helix*, there has been little experimental work on this latter topic even although movement in and out of the shell is of fundamental importance to all snails.

Recent observations on the burrowing of gastropods, for example in *Natica* and *Polinices* (Trueman, 1968*a*), have shown how this differs from the pattern of pedal waves, frequently repeated over the ventral surface of the foot, employed by snails in movement over firm substrata (Jones & Trueman, 1970; Jones, 1973). *Polinices* moves through the sand by first extending the propodium then drawing up the mesopodium in a stepwise manner. Its foot is distended by an extensive system of aquiferous tubules (Bernard, 1968; Russell-Hunter & Russell-Hunter, 1968) distinct from the pedal blood system, which in comparison is somewhat restricted in size. *Bullia* differs from this in at least one major respect, for the foot is almost totally expanded by the introduction of blood into the pedal sinus, sea water absorbed from the exterior playing only a very minor role (Brown & Turner, 1962). The present investigation of the fluid dynamics of the foot of *Bullia* thus affords us an opportunity to compare the adaptations of gastropods for burrowing with those of bivalve molluscs, for example *Ensis* (Trueman, 1968*b*) and to observe how the pedal haemocoel functions as a hydraulic system.

Materials and methods

Bullia digitalis was studied in the laboratories of the Department of Zoology, University of Cape Town, immediately after collection from nearby sandy beaches. The snails were all about 3 cm in shell length and remained very active in the laboratory when kept in tanks of aerated sea water containing a shallow layer of sand. The techniques used for recording details of movements were the same as have been used previously in studies of benthic invertebrates (Trueman & Ansell, 1969). Observations of burrowing were made visually, by means of cinematography and by electronic recording techniques. The latter entailed the attachment of force or movement transducers to the shell by means of a fine thread or the insertion of cannulae into the animal which in turn were connected to Statham pressure transducers by fine nylon tubing. Additional observations were made on *B. laevissima* and *B. rhodostoma* for comparative purposes.

B. digitalis could be suspended in air or water, by a thread attached to the shell, and its foot would remain fully extended either whilst a cannula was inserted into the pedal haemocoel or when the animal was rapidly plunged into liquid nitrogen. The latter technique (Jones, 1973), followed by fixation in chilled alcoholic Bouin, ensured that the foot and tissues could be examined histologically in as naturally relaxed a condition as possible, with the foot completely extended. Serial sections of complete *B. digitalis*, obtained by decalcification prior to embedding, were stained in Mallory's triple stain or in Alcian Blue for mucus (Steedman, 1950). This afforded a means of examining the pedal musculature, blood sinuses and the extent to which the upper whorls of the shell are occupied by the snail when the foot is extended.

Anatomy of the foot and blood circulation

Pedal anatomy

Previous authors (Brown, 1964) have drawn attention to the large size of the oval shaped foot of *Bullia* (Fig. 2). It has an area of some 13 cm² in *Bullia digitalis* of retracted volume 2 ml and is accordingly very thin. Brown calculated it to be on average 1 mm thick,

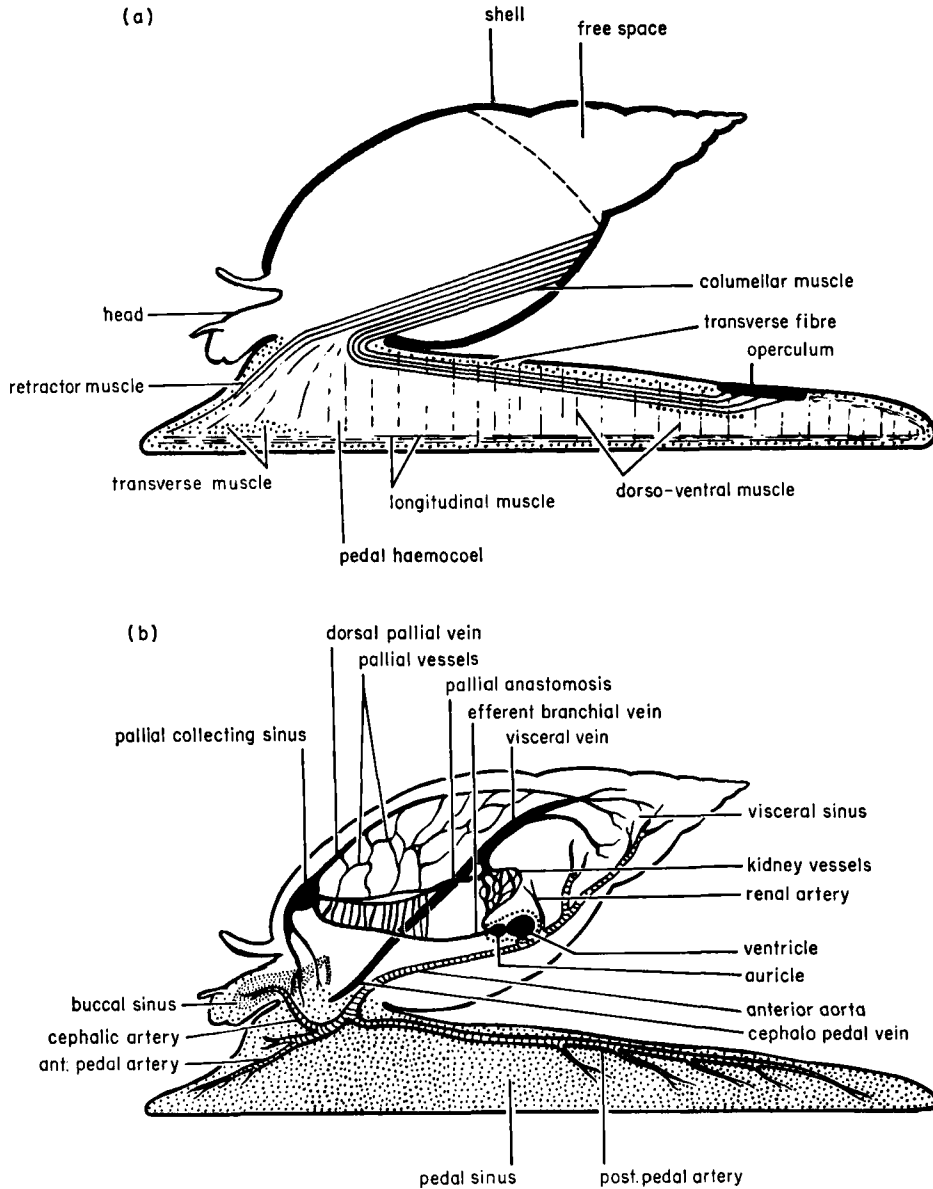


FIG. 1. Diagrammatic sagittal sections of *Bullia digitalis* with the foot extended as during locomotion showing (a) pedal musculature, extent of pedal haemocoel, location of mantle cavity and "free-space" within the shell; (b) blood circulation (after Brown, 1964).

which corresponds well with the thickness observed in sections (Fig. 1(a)). The surface of the foot is covered by columnar epithelial cells and mucus is secreted by epithelial and subepithelial glands which are located principally in the anterior (propodium) and lateral regions of the foot. There is no evidence, in our sections, of any collagenous trellis near the surface of the foot comparable to that described in some worms (Clark & Cowey, 1958).

The most significant feature of the foot is the large blood-filled sinus of the pedal haemocoel and the great extent of its cavity in comparison with the muscle fibres in the foot (Fig. 1(a)). Brown (1964) has shown that the foot is expanded when blood is introduced into the pedal sinus and that the expansion of the foot does not depend on an exceptionally high blood volume compared with other gastropods. However, the foot of *Bullia* with a large haemocoel cavity, evolved as a hydraulic system for burrowing, contrasts with the foot of gastropods which crawl over hard surfaces. In the limpet, *Patella*, the foot is much more muscular and the haemocoel is largely in the form of a large number of small spherical vesicles, each of about 10 μm in diameter (Jones & Trueman, 1970). In *Bullia* similar structures have been observed close to the dorsal and ventral surfaces of the foot (Plate I(c)) and some have their lumina in continuity with the pedal sinus, suggesting its formation from a number of expanded vesicles.

The principal muscle of the foot is the columellar muscle (Fig. 1(a)). It originates from the columella in the lower part of the second whorl of the shell and its muscle fibres radiate to all parts of the foot, but particularly to the propodium and the dorsal surface of the metapodium where many fibres are inserted onto the operculum. There are four other important groups of muscle fibres (Fig. 1(a), Plate I(b) and (c)):—i, dorso-ventral; ii, transverse; iii, longitudinal and iv, oblique fibres which lie immediately above the pedal sole obliquely to the longitudinal axis of the foot. Within the expanded foot the columellar muscle, located near the dorsal surface, probably functions similarly to the ventrally situated longitudinal fibres but the principal function of this muscle is to effect pedal retraction. Although muscle fibres, particularly transverse, are somewhat more concentrated in the propodium, all muscles are widely spaced when compared to those in the foot of *Patella*. Indeed the volume of the foot of *Bullia* occupied by muscle is little more than 10% whereas in the limpet about 80–90% of the foot is composed of muscle as estimated by viewing sections of the foot. Within the foot the muscle fibres are arranged essentially in each of three directional planes, antero-posterior, transverse and dorso-ventral, and those muscles in any one plane antagonize the others by means of the fluid in the pedal haemocoel in the manner of a classical fluid skeleton (Chapman, 1958). Maintenance of a steady tension in one set of muscles allows direct antagonism between those fibres in the two remaining planes and in this manner changes may be effected in the shape of the foot the nature of which are considered in relation to locomotory stepping. The absence of longitudinal muscles from the sole of the foot of *Patella* should also be contrasted with those occurring in the foot of *Bullia*.

The columellar muscle draws the foot into the shell and a large number of its fibres pass to the operculum for this is the last part to enter the shell (Fig. 1(a)). Within this opercular muscle, fibres also occur with their contractile axes in the dorso-ventral plane at right angles to the main fibre axis and there are other adjacent fibres in the transverse plane of this muscle (Plate II). These fibres form a three dimensional muscle network similar to that observed in the squid mantle. In this latter tissue, longitudinal muscle maintains constant mantle length and radial and circular fibres, whose contractile axes are perpendicular to

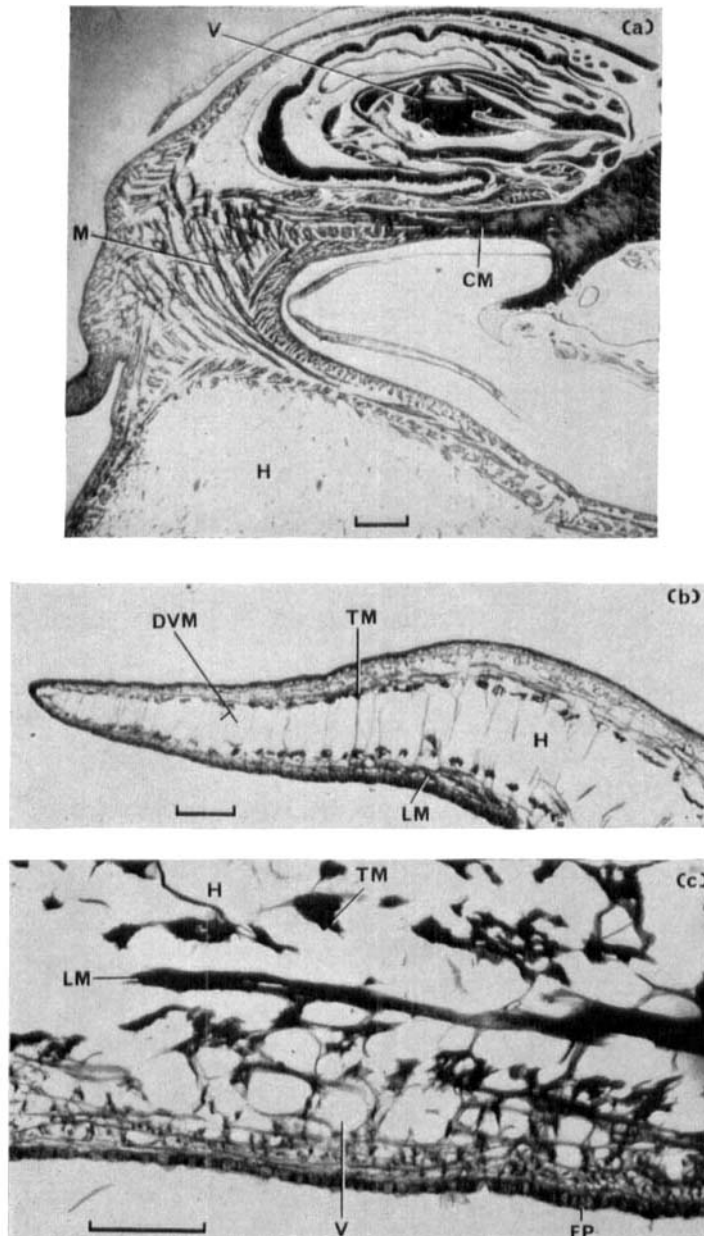


PLATE I. Longitudinal sections of *Bullia digitalis*. (a) Snail with foot extended, CM, columellar muscle; H, haemocoel cavity within foot; M, network of muscle fibres between foot and viscera; V, viscera. Scale line 1 mm. (b) Anterior extremity of foot, DVM, dorso-ventral muscle fibres; LM, longitudinal muscle fibres; TM, transverse muscle. (c) Ventral pedal sole, EP, epithelium; V, vesicle. Scale line on (b) and (c) 100 μ m.

each other, have been shown to antagonize each other directly without the participation of any discrete skeleton (Packard & Trueman, 1974). Muscle antagonism can take place without a separate skeleton, either fluid or hard skeleton, provided the fibres are arranged

in a three dimensional network. When any one dimension is held constant then the muscles in the other two planes may antagonize each other directly. While there is no experimental proof that the opercular muscle system functions in the same way as the cephalopod mantle, there is no reason why a similar situation should not obtain. The longitudinal retractor and dorso-ventral groups of fibres would be mutually antagonistic provided the transverse fibres maintain the opercular muscle at a constant width. Thus shortening of the



PLATE II. Transverse (a) and longitudinal sections of the opercular muscle of *B. digitalis*. DV, Dorso-ventral fibres; H, haemocoel cavity; L, longitudinal fibres; T, transverse fibres. Scale lines 100 μ m.

muscle would result in its thickening with extension of the dorso-ventral fibres and conversely tension in the latter must cause elongation of the longitudinal fibres. The roles of the transverse and dorso-ventral fibres may be reversed allowing the width of the muscle to increase rather than its thickness but the mechanism of antagonism remains the same and may be contrasted with that of the longitudinal muscles in the sole of the foot (Plate

I(b) and (c)). These have no similar intimate association with any fibres whose axes lie in different planes and must be antagonized by the force developed in other pedal muscles being transferred by the agency of the blood in the pedal haemocoel, that is, in the normal manner of a fluid skeletal system. Extension of the opercular muscle, by means of direct muscular antagonism may assist in pedal expansion. This has been previously generally envisaged as being carried out by blood flow in *Bullia* (Brown, 1964) or by pumping movements of the mantle cavity in pulmonates (Dale, 1974).

The blood and other fluid systems

Brown (1964) has described the circulatory system of *Bullia laevissima* in some detail and his findings are summarized in Fig. 1(b). The pedal sinus is supplied with blood from the anterior aorta, and occupies the whole of the foot and part of the head. Blood may leave the sinus either by the large cephalopedal vein or by two pallial collecting vessels which carry the blood to a large pallial sinus. The dorsal pallial vein, largest of the pallial vessels, connects with the visceral sinus system so providing direct vascular communication between anterior and posterior regions of the body. Blood passing from the foot by the cephalopedal vein will meet blood from the visceral sinuses and may drain into the kidney vessels. The cephalopedal and visceral veins are in reality sinuses, having no valves or projections to impede blood flow so that an increase in pressure in the pedal sinus may cause blood to flow into these veins and even into the visceral sinus system. This occurs when the snail retracts into the shell and the reverse was assumed during pedal protraction. The pallial sinus does not apparently constitute an important pathway. Brown (1964) considered that a rise or fall of blood would occur in the cephalopedal and visceral veins during activity by the contraction and relaxation of the pedal muscles on the one hand and the tone of the visceral musculature, on the other. Examination of our serial sections of *Bullia digitalis* shows little visceral musculature, this certainly being inadequate to oppose the muscles of the foot directly. For the foot to function as a fluid skeleton the fluid contained within the pedal haemocoel must remain at constant volume. No valvular mechanism has been observed in sections which would restrict blood flow from the foot. However, the neck of tissue between the visceral mass and the head-foot is crossed by numerous muscle fibres which may function to restrain blood flow effectively (Plate I(a)).

When *Bullia* retracts rapidly into its shell it produces triple jets of water from the margin of the foot, possibly as a defence mechanism. About two thirds of this water comes from a cavity, termed the free-space cavity, between the viscera and the shell when the snail is expanded (Fig. 1(a)) and nearly one third from the mantle cavity although the water of each jet is of mixed origin (Brown, 1964). The presence of a free-space cavity in the upper part of the shell was confirmed by examination of serial sections of relaxed *B. digitalis*. There are only very small water spaces in the foot and their contribution to the jets is negligible. A little water also drips off the foot but this is thought to come from the proboscis sheath (Brown, 1964).

Retraction of the snail takes place in air or water but emergence only occurs in water for in no circumstances will the animal draw air into its free-space cavity. This retention of water in the free-space of the shell may be a common, though unrecognized, feature of many marine gastropods. In *Bullia* it is exploited both as a possible defence mechanism and as a reservoir of water which it brings ashore where it leaves the sea. The pressures

developed in the mantle and free-space cavities during locomotion and pedal retraction and protraction have been determined during this work and will be discussed in relation to these earlier findings.

Experimental observations

Movement over sand

B. digitalis frequently crawls over the surface of damp sand and leaves a distinctive track in which the outline of the foot may be readily recognized at intervals of about 0.5 cm, this distance representing the step length. This method of crawling was investigated further in the laboratory using the bottom of a glass aquarium tank, sometimes lightly covered by

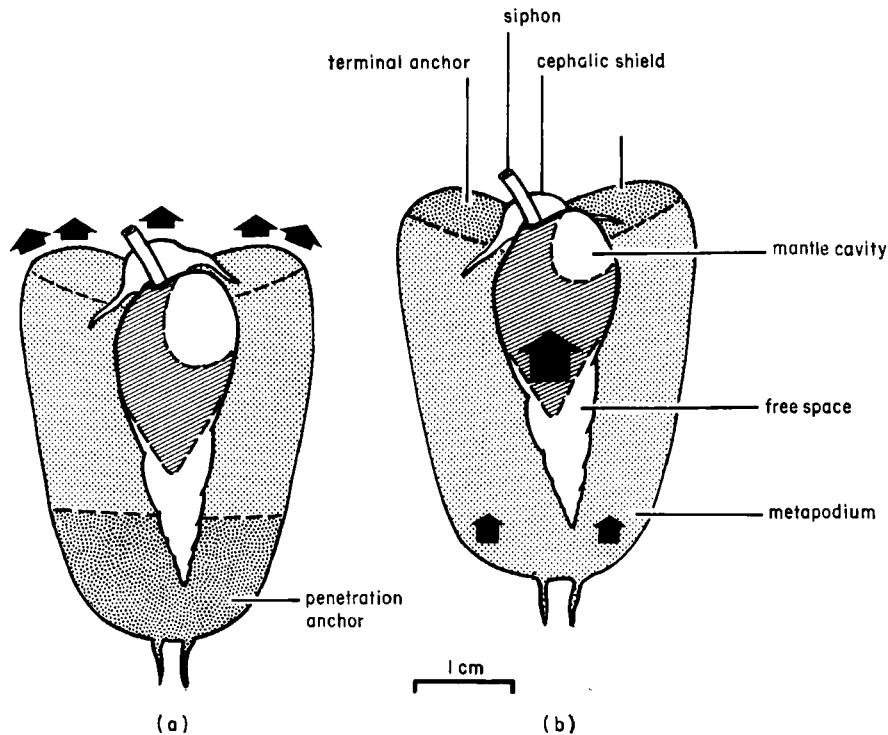


FIG. 2. Diagrams of *B. digitalis* taken from ciné film showing movement of foot during locomotion on glass. (a) Extension of propodium in "breast stroke" (arrows) with the cephalic shield being forced forwards and upwards, the posterior of the foot being anchored; (b) the shell and metapodium being drawn forward (arrows) and the head downwards. The positions of the mantle cavity and free-space of shell are indicated.

sand, as a substratum. *Bullia* does not appear to use cilia in locomotion as has been observed in *Polinices* (Trueman, 1968a). Locomotion was achieved by alternate movement and anchorage of the propodium and metapodium (Fig. 2). With the posterior region of the foot anchored the propodium is slightly raised and thrust forwards and at the same time the cephalic shield advances and is raised. In the second phase the propodium becomes anchored anteriorly allowing the shell and metapodium to be drawn forwards while the cephalic shield moves down and backwards. When viewed from above this motion resembles the breast stroke used in swimming. The manner of attachment of the

propodium to the substratum was not apparent but the impression of the outline of the foot made when crawling on sand suggests that it presses downwards as the shell is drawn forward.

On a glass surface without any sand there is often some loss of adhesion by the propodium so as to cause slipping and the step length in consequence is shorter than on sand. Extension of the foot must involve relaxation of the longitudinal muscles anteriorly, tension in the transverse fibres to maintain a constant pedal width and the application of the force of contraction of other muscles by means of the hydraulic system. This results in stretching of the pedal sole anteriorly in precisely the same way as occurs at the commencement of any retrograde wave, as for example in the anterior segments of an earthworm (Trueman, 1975). However, instead of travelling progressively down the foot as a locomotory wave in *Patella* (Jones & Trueman, 1970) extension of the propodium is followed by its anchorage and the contraction of longitudinal pedal muscles and anterior fibres of

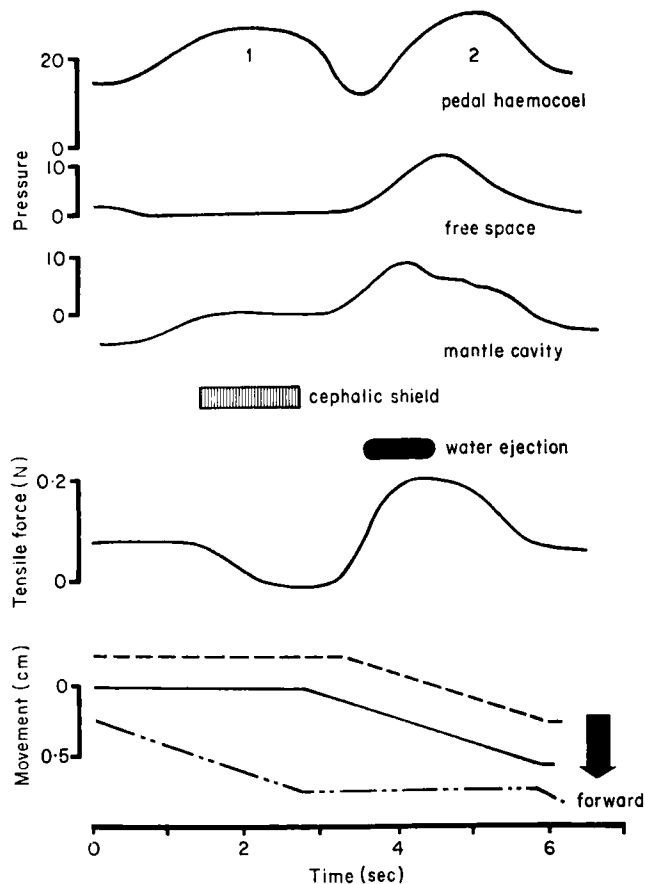


FIG. 3. Analysis of the activity of *B. digitalis* during a single digging cycle reconstructed from ciné film and recordings when the snail was just beneath the sand, showing the relationship between pressure ($\times 10^{-2}$ N cm $^{-2}$), tensile force and movement. Force was measured by a thread from the shell to a transducer, maximal values being obtained when the shell was drawn forwards, minimal when the propodium was being extended as indicated by the movement curves (---, shell; —, metapodium; - · - · -, propodium), water ejection from the mantle cavity and the raising of the cephalic shield are also indicated.

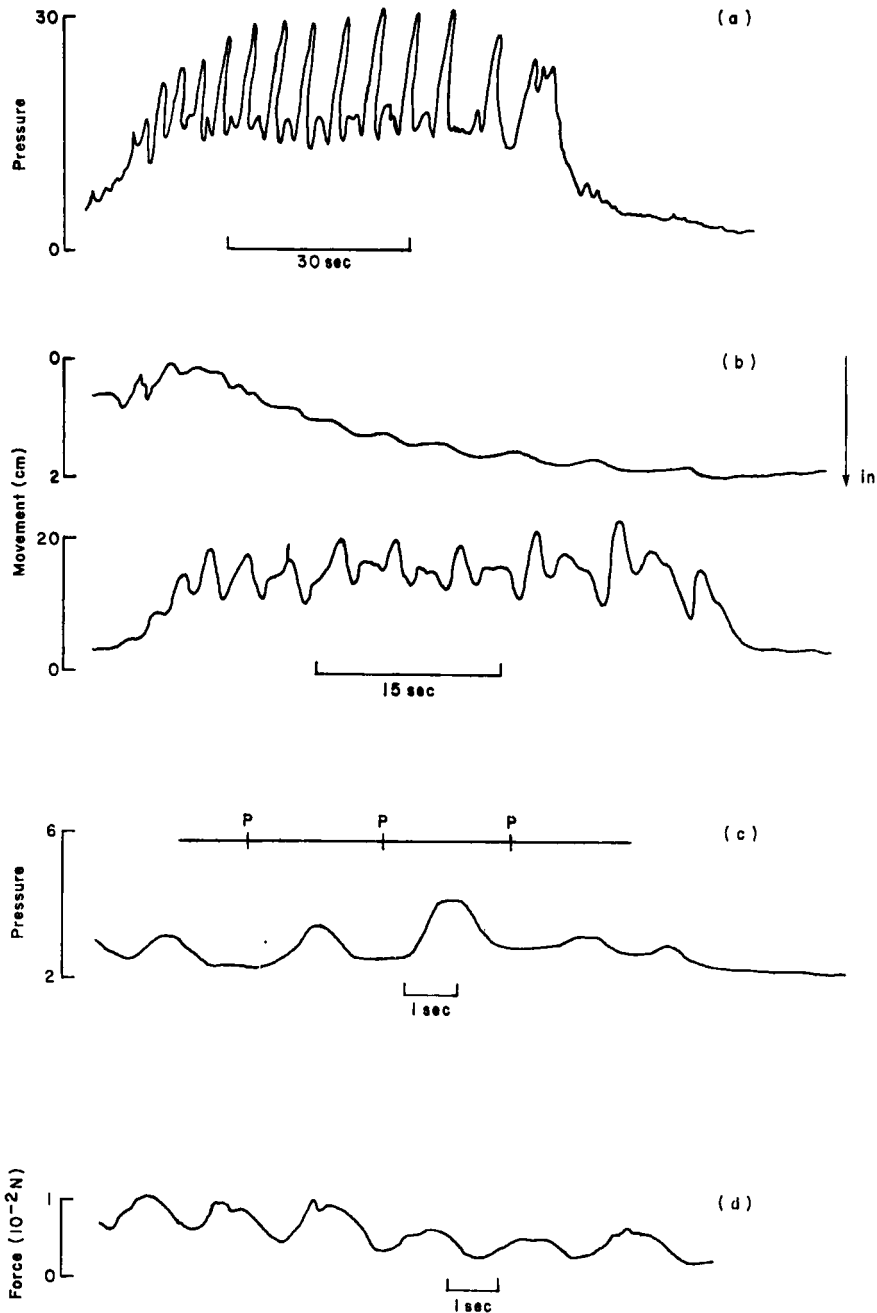


FIG. 4. Recordings of movement, tensile force and pedal haemocoel pressure ($\times 10^{-2}$ N cm $^{-2}$) exerted by *B. digitalis* when burrowing into sand (a) and (b) and over a glass surface (c) and (d). (a) Complete digging period, burrowing terminates when edge of tank is reached; (b) synchronous recording of movement and pressure showing relation of pressure pulses to movement of shell into sand (arrow); (c) pressure pulses generated during surface locomotion, at the end of the trace *Bullia* remained stationary; P, indicates commencement of movement of posterior margin of foot (marked by visual observation); (d) as (c) but showing force exerted by the snail on a thread attached to the shell during successive locomotory cycles.

the columellar muscle to pull the metapodium and shell, respectively, forwards in a step-like movement.

Burrowing movements

Essentially the same movements were observed during burrowing as described for locomotion on the surface of sand. Similar movements have been previously outlined for *Bullia melanoides* (Ansell & Trevallion, 1969). However, the forces used in burrowing are much greater, by a factor of about $\times 20$ in respect of tensile force exerted on the shell (Figs 4(d) and 5(b)) and $\times 7$ in respect of pressure pulses in the pedal haemocoel (Fig. 4(a))

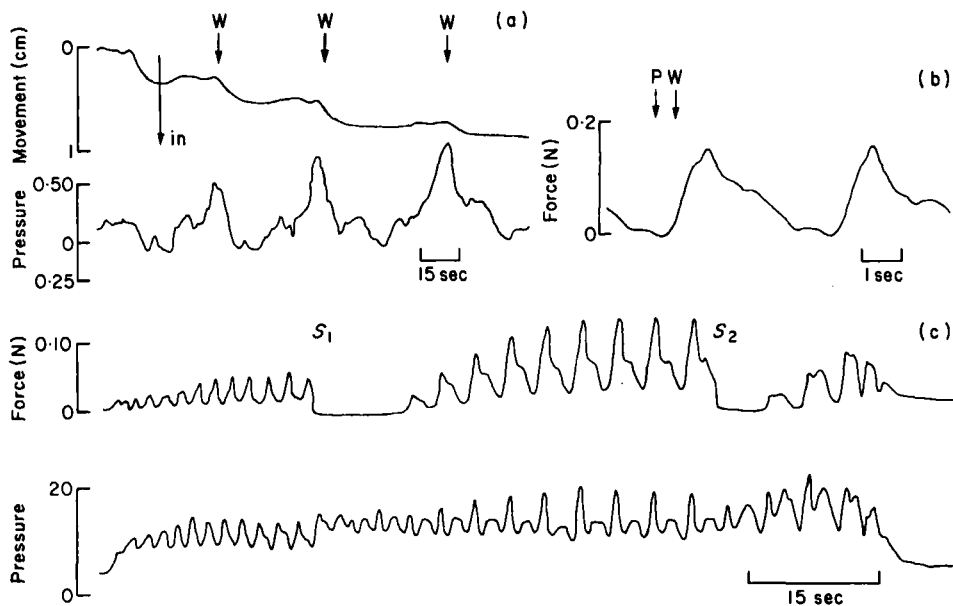


FIG. 5. Recordings of *Bullia digitalis* burrowing into sand. (a) Pressure ($\times 10^{-2}$ N cm $^{-2}$) recorded externally in sand and movement, with ejection of water (W) from mantle cavity marked by visual observation; (b) force exerted by burrowing snail when tethered by a thread attached to a transducer during two digging cycles with water ejection (W) and forward movement of metapodium (P) marked by visual observation; (c) force and pressure within the pedal haemocoel recorded during burrowing into sand whilst tethered. The thread was twice slackened (S, 1 & 2) to allow the snail to become completely buried.

and (c)). The greater force exerted by the fibres of the columellar muscle inserted into the propodium is a measure of the increased anchorage of the foot when buried, which allows the shell to be pulled forward more powerfully.

In conformity with previous usage the term 'digging period' is used to refer to the duration of digging activity from commencement until a stable position is attained in the sand and "digging cycle" to indicate the series of events associated with each locomotory step (Trueman & Ansell, 1969). In a snail such as *Bullia*, which may plough along just beneath the surface of the sand, it is often difficult to mark the termination of the digging period. However, under experimental conditions burrowing is generally complete within some 10–16 cycles. The period illustrated in Fig. 4(a) terminates when the snail reaches the edge of the tank, making a prolonged thrust before ceasing activity.

Each digging cycle consists essentially of the events described in surface locomotion. Further analyses have been made of ciné film and recordings and a composite diagram of all events during the digging cycle is presented (Fig. 3). Points of detail are referred to below in relation to particular aspects of burrowing but the curves for movement of shell, posterior foot and propodium should be noted. When the propodium advances, the shell and remainder of the foot are stationary, acting as a penetration anchor and *vice versa* when the propodium acts as a terminal anchor towards which the shell is drawn by the columellar muscle (Fig. 2). Penetration by the propodium is probably aided by the simultaneous lifting of the cephalic shield and would result in water being drawn into the space beneath the shield. This pattern of locomotory stepping is very similar to that of other burrowing animals, e.g. *Bivalvia* (Trueman, 1968*b*).

Blood pressure recordings during locomotion

In order to record pressure within the pedal haemocoel a cannula was carefully introduced through the dorsal surface of the foot and apparently caused very little hindrance, for the digging period was completed quite normally on numerous occasions with the cannula inserted. Indeed, removal of the cannula resulted in very little bleeding and the ability of the snail to burrow immediately was unimpaired. This suggests that *Bullia* is able to seal small wounds very readily. In typical recordings (Fig. 4(a)) the pressure is built up rapidly at the commencement of the digging period to a plateau level equivalent to about half the amplitude of maximal pressure pulses. At the cessation of burrowing the pressure drops quite swiftly to a resting level of $2-4 \times 10^{-2} \text{N. cm}^{-2}$. A similar feature occurs during movement over a surface (Fig. 4(c)) when the haemocoel pressure is only raised above the resting pressure during locomotion. During the early cycles of the digging period the pattern of pressure pulses is a little confused but as penetration of the substratum proceeds two pressure pulses occur (Fig. 4(a)). The first, or primary pulse is associated with the extension of the propodium and the second pulse with the shell being drawn forwards (Figs 3 and 4(b)). Similar recordings were obtained from all regions of the foot except the propodium where insertion of a cannula effectively prevented locomotion. During normal burrowing the secondary pulse is of greater amplitude than the primary. When *Bullia* was tethered to a force transducer, by means of a thread attached to the apex of the shell, the secondary pulses were of greater amplitude, as in normal burrowing, and coincided with the shell being drawn forwards (Fig. 5(c) centre of recording); but when the thread was slackened at S_2 , allowing further progress into the sand, the primary pulse increased in amplitude. More force was then used in extension of the propodium than in drawing the shell and metapodium forward. Significantly lower pressures are generated during surface locomotion (Fig. 4(c)), a single pulse commonly occurring during each locomotory cycle coincident with pedal extension.

The shell is drawn forwards by tension in fibres of the columellar muscle and the force recorded by means of a transducer attached by a thread to the shell is a measure of this. There is a general relationship between this force and the amplitude of the secondary pressure pulse, weak forces being associated with lower pressures (Fig. 5(c)). It may thus be suggested that the secondary pulses are largely generated by tension in the columellar muscle. The absence of peaks of tensile forces corresponding to the primary pulses (Fig. 5(c)) indicates that these are generated by the intrinsic pedal musculature with little if any participation of the columellar muscle.

The effect of water currents on pedal pressures

B. digitalis has often been observed to raise its foot like a sail and allow the waves to bring it ashore (Brown, 1961) and it was also apparent in the laboratory that this species was very sensitive to water currents. Accordingly the pressure in the pedal haemocoel was monitored whilst the water in the experimental tank was stirred by blowing across its surface. When pulled out of the sand the pedal pressure rose sharply (Fig. 6(a) at P) and whilst on the sand surface gentle water movement (M) led to an immediate increase in pressure and the foot being raised. Successive water movements eventually elicited a burrowing response and a complete digging period followed. In a second experiment (Fig. 6(b)) *Bullia* had been quiescent beneath the sand for about 30 min and made no response to gentle tapping of the tank, vibration of the bench or scratching movements with a needle

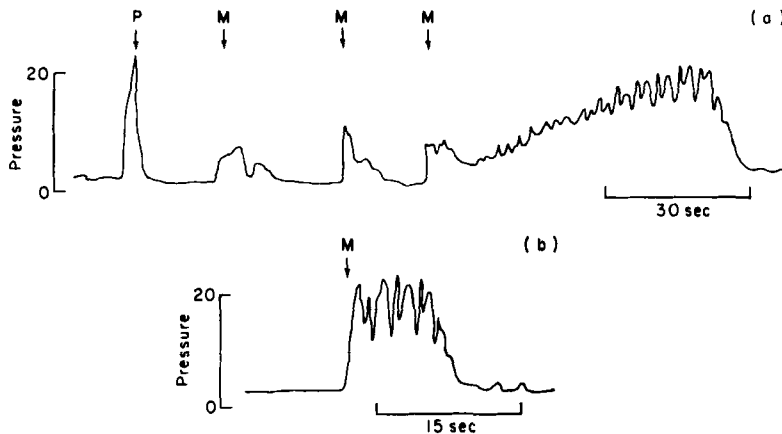


FIG. 6. Recordings of pressure ($\times 10^{-2}$ N cm $^{-2}$) within the pedal haemocoel illustrating the reaction of *B. digitalis* to water movements (M) produced by very gentle stirring. (a) succession of water movements, after being pulled out of sand (P), each resulting in the foot becoming turgid followed by burial; (b) sequence of three digging cycles recorded from buried *Bullia* when water movement occurred after long inactive period.

in the sand adjacent to the foot, all stimuli to which the tropical sandy beach bivalve, *Donax denticulatus* has been shown to respond readily (Trueman, 1971). By contrast, *Bullia* responded immediately to a single gentle stirring motion of the water, resulting in an increase in pedal turgidity and several digging cycles. It is apparent from such traces that the resting pressure in the pedal haemocoel can be increased instantaneously to 20×10^{-2} N cm $^{-2}$ in response to water movement. This cannot be due to additional blood passing into the foot or to increase in circulatory pressure in the absence of any signs of heart pulse pressures in the pedal sinus. It is more likely that the pressure pulses are due to tension being developed in the pedal muscles and since slight pedal protraction also occurs the role of the columellar muscle is probably minimal.

Pressure in the mantle cavity and free-space

Recordings of pressure have been made from the two large water filled cavities present in *Bullia*, the mantle cavity and the free-space of the shell (Figs 1(a) and 2). Our attention was drawn to the possible importance of these cavities by the observation of a small quantity of water being ejected through the sand during burrowing, to the right and just

in front of the shell as it is being drawn forwards (Fig. 3). Introduction of methylene blue solution into the siphon, normally held just above the sand surface, whilst a snail was burrowing, led to the water ejected during the next digging cycle being coloured blue, so indicating that the source of the water was the mantle cavity.

This ejection of water corresponds to movement of the shell or development of tension in the columellar muscle and recordings of pressure in the sand adjacent to the snail

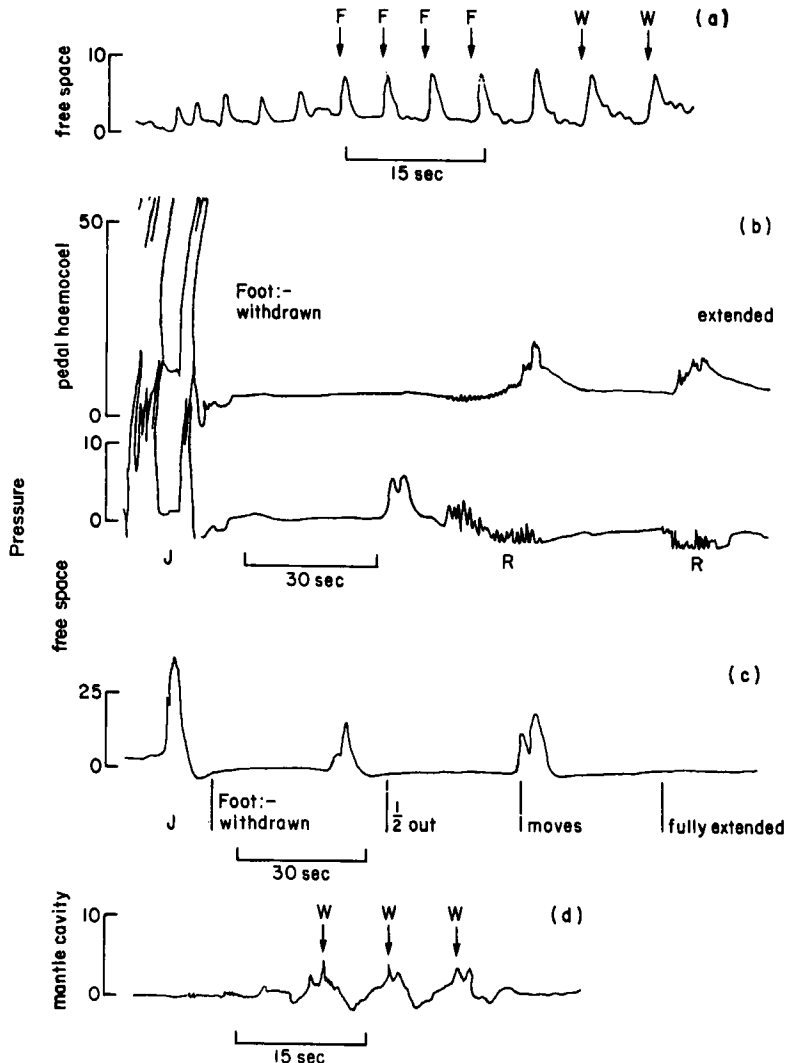


FIG. 7. Recordings of pressure within the foot, free-space of the shell and mantle cavity of *B. digitalis*. (a) Succession of pressure pulses in free-space from commencement of burrowing, each pulse corresponding to a digging cycle; (b) pressure in pedal haemocoel and free-space during tactile stimulation of foot causing its withdrawal into the shell and subsequent protraction, the snail being suspended in water by a thread attached to the shell allowing some free rotation (R); (c) similar record to (b) showing only free-space pressures; (d) pressure within mantle cavity during burrowing, the peak pressure corresponding to water being ejected. F, Commencement of pull forward of the snail into the sand; J, visual observation of jets of water from pedal margin; W, visual observation of water ejected from mantle cavity.

exhibited a positive pulse, of low amplitude, when water was observed to be ejected from the mantle cavity (Fig. 5(a) and b). There can be little doubt that the function of the water is to liquefy the sand so as to facilitate movement of the shell.

Attempts were made to monitor the pressure in the mantle cavity during locomotion by introduction of a fine plastic cannula through the siphon but it proved very difficult, for the snail invariably expels the plastic tubing before moving normally. Introduction of a cannula through a small hole drilled in the shell also proved largely unsuccessful and only on a few occasions were satisfactory recordings obtained (Fig. 7(d)). The mantle cavity pressure is clearly at a maximum when water is expelled, while the shape of these pulses is in general similar to those recorded directly in the sand (Fig. 5(a)). Burrowing bivalves are noted for generating pressure pulses in their mantle cavities during burrowing by rapid adduction of the valves but this mechanism is of course not available to a snail. In sections of *Bullia* there appears to be relatively little mantle musculature and we would suggest that the most probable mechanism for the expulsion of water is the contraction of the columellar muscle drawing the shell towards the foot and compressing the mantle cavity. Another feature of the recordings from within the mantle cavity is the tendency of the pressure to fall below atmospheric pressure after water has been ejected (Fig. 7(d)). This is possibly due to the cavity tending to expand more rapidly than water can re-enter but we have not been able to make any observations of the mechanism of expansion of the mantle cavity.

Pressure recordings from the free-space of the shell proved to be obtained more easily than from the mantle cavity. The terminal two or three whorls of the shell were removed, a short hypodermic needle was introduced into the cavity, fixed in position by wax, and connected to a pressure transducer by fine nylon tubing. Brown (1964) pointed out that the uppermost whorls of the shell are usually partitioned off and do not remain in contact with the free-space. Accordingly particular attention was paid to obtaining true records from the free-space. In each digging cycle a single pressure pulse occurred (Fig. 7(a)) and was simultaneous with the secondary pulse in the pedal haemocoel although of somewhat lower amplitude (Fig. 3). These recordings confirm Brown's earlier observations of water being ejected through holes drilled into the top of the shell during locomotion or withdrawal into the shell. The pulses in the free-space occur after the ejection of water from the mantle cavity (Fig. 7(a)) but are probably caused by the same agency, the contraction of the columellar muscle, and represent a general raising of pressure throughout the viscera.

Protraction and retraction of the foot

Brown (1971) observed that both pedal retraction and expansion occur in two stages and that during retraction the first phase involves folding of the foot, some reduction of blood volume but not of turgor. The second phase is marked by the production of water jets, loss of pedal turgor and the foot shrinking rapidly as it is drawn into the shell. Retraction is brought about by contraction of the columellar muscle while reduction in pedal volume is partially the consequence of retraction forces and in part the contraction of intrinsic pedal muscles. Blood then flows from the foot into the visceral sinus through the cephalopedal vein. Sudden pedal retraction, with little evidence of the first phase, was produced experimentally by tactile stimuli whilst recording pressure both from the pedal haemocoel and the free-space (Fig. 7(b)). High pressures were recorded in both cavities during jetting and during subsequent shrinkage of the foot. After retraction the tendency of the traces to fall

below atmospheric pressure possibly indicates some relaxation of the musculature and a short interval before blood circulates freely in the pedal sinus. It is unusual, however, for a pressure cannula to remain in the foot during retraction and expansion and the recording may be abnormal in this respect. The pressure within both systems then returned to normal and the foot showed signs of emergence when a double pulse occurred in the free-space. This characteristic double pulse was observed in other recordings (Fig. 7(c)) but no specific movement could be related to it. It may be caused by the snail adjusting its position within the shell after some water had been introduced into the free-space by means of either ciliary currents or muscular activity. To produce such a pulse of approximately 10 sec duration, the tissues of the visceral mass must fit tightly against the shell or water would be ejected from the free-space, but it is impossible to say how this is brought about. The second phase of expansion has often to be induced by gentle rotation of the shell in water (Fig. 7(b), *R*), pressure then increases only within the pedal sinus. Blood may flow to refill the foot both from the visceral sinus by way of the cephalopedal vein and from the heart via the anterior artery. However, there was no trace of a heart rhythm in recordings from the pedal sinus, which we might expect to observe either in the recordings illustrated, or at higher levels of amplification, if the heart was the principal source of blood flow to the foot. Pedal protraction continues when no pressure pulses occur in the haemocoel (Fig. 7(b)) which probably indicates the use of some other protractor mechanism, such as the fibres of the opercular muscle, in addition to pedal blood pressure.

In spite of such uncertainties, these and similar recordings (Fig. 7(b) and (c)) do show that the free-space cavity plays a dynamic role in the expansion and retraction of *Bullia* independently of the pedal blood sinus; and that adjustment of the posture of the foot during extension is associated with blood flow into the foot and contraction of the intrinsic pedal muscles. It was unfortunately impossible to record changes of pressure from within the mantle cavity during withdrawal or expansion of the foot.

Discussion

The mechanism of locomotion of *Bullia digitalis* has been described together with observations on pressure changes occurring in the pedal haemocoel, mantle cavity and free-space of the shell. The pattern of locomotory activity is essentially the same for movement over firm substrata as for burrowing. Additional observations made on *B. rhodostoma* and *B. laevissima* showed a similar mechanism.

During each digging cycle a primary pressure pulse is produced by the intrinsic pedal muscles and brings about protraction of the propodium. A secondary pulse associated with the shell being pulled forward is generated largely by contraction of the columellar muscle (Fig. 3). The same muscle appears to be the cause of pressure peaks, recorded simultaneously with the secondary pulse, in the mantle and free-space cavities. The lack of adverse reaction by *Bullia* to the insertion of cannulae enabled us to investigate the role of the free-space cavity but just how far our observations are typical of other prosobranchs is difficult to say. Certainly all snails must have the fundamental ability to move in or out of the shell and we would suggest that during pedal extension all aquatic gastropods must greatly enlarge their mantle cavity or develop free-space near the apex of the shell, or possibly do both. One further alternative is employed by species of *Polinices* which enlarge their foot by taking sea-water into aquiferous tubules rather than by blood flow into the

pedal sinus (Russell-Hunter & Russell-Hunter, 1968). But even so, the function of the free-space appears to be similar to that of *Bullia* (Morris, 1950). It should be recalled that fibres of the columellar muscle of *B. digitalis* passing to the operculum possibly elongate by direct muscular antagonism and may play an important role in the expansion of the foot. It is not yet known how widespread this phenomenon is in other gastropods but a somewhat similar arrangement of muscle fibres has been described in the siphon of the bivalve *Scorbicularia* (Chapman & Newell, 1956). While *Bullia* does not normally extrude its foot in air completely if the free-space is emptied of water (Brown, 1964), terrestrial pulmonates, e.g. *Helix*, increase the air content of their pulmonary cavity to compensate for the displacement of the foot (Dale, 1974).

Locomotion of *Bullia* is essentially a retrograde pattern of stepping with first a posterior and second an anterior anchorage (Fig. 2). A complete locomotory cycle takes about 5 sec to pass across the foot so that at any instant only part of a wave is apparent and results in a stepping motion in contrast to the continual progression characteristic of locomotory waves in many other snails. Retrograde locomotion is best known in *Patella* (Jones & Trueman, 1970) where the front of the foot is raised from the substratum and extended forwards at the commencement of each wave similarly to *Bullia*, although to a much lesser extent. Pedal extension is brought about in the limpet by dorso-ventral muscles while the width of the foot is held constant by tension in transverse fibres. In this respect also, *Bullia* is very similar to *Patella* but in the latter the waves move across the foot by contraction of dorso-ventral muscles without the participation of longitudinal fibres which are absent from the region of the pedal sole. By contrast, in *Bullia* the posterior of the foot is drawn forward by contraction of longitudinal muscles located near the sole.

Stepping slowly with alternate penetration and terminal anchors is essentially an adaptation of gastropod locomotion for infaunal life or movement over sand in a shallow burrow. The loping motion of *Helix*, using a small number of retrograde waves at the same time, is intermediate between the locomotion of *Patella*, by numerous simultaneous waves, and that of *Bullia*. The queen conch *Strombus gigas* shows a further stage in this series for the shell is used as an anchor while the foot thrusts forward, each step being completed by the shell being lifted off the substratum and drawn up to the extended foot (Trueman, 1975).

One other important feature of *Bullia* is the large pedal haemocoel, particularly when compared with the small vesicles in *Patella*. Large fluid-filled cavities are only necessary as a hydraulic system where force must be transferred over relatively large distances or when major changes in shape take place (Packard & Trueman, 1974). These two features are found in many burrowing animals. Clark (1964) argues very cogently that the coelom originated as a functional hydraulic system for use in burrowing by worms. The same has occurred in the Mollusca where the primary body cavity is used rather than the coelom. This is notably so in the infaunal Bivalvia, with which *Bullia* shows remarkable convergence. Somewhat similar to *Bullia* are species of *Polinices* and *Natica* but here the fluid cavity of the foot consists largely of aquiferous tubules. Species of the Terebridae, a group of infaunal carnivorous gastropods, also exhibit features similar to *Bullia*. Thus on at least three separate occasions adaptation of prosobranchs to life in sand has led to similar modifications of pedal structure and there can be little doubt that the prime function of the pedal haemocoel of *Bullia* is as a hydraulic system. In this role the pedal sinus must conform to the requirements of a fluid-muscle system in a classical sense as discussed by

Chapman (1958), namely that the fluid should be virtually incompressible, of low viscosity and maintained at constant volume. Brown (1964) has shown that blood flows freely up or down the cephalopedal and visceral sinuses so inferring that these function together as a continuous fluid system. It was not possible to monitor pressure in the visceral sinus but pulses are shown to occur simultaneously in mantle cavity, free-space and foot at pedal retraction and it is probable that this secondary pressure pulse also occurs in the visceral sinus. On the other hand the primary pressure pulse, produced by the intrinsic pedal muscles, is restricted to the foot which at the instant of this pulse, at least, must operate as a self-contained fluid-muscle system. This requires that the blood must be retained in the foot to maintain a constant fluid volume. Examination of serial sections of *Bullia* did not disclose a specific valvular mechanism such as Keber's valve in *Bivalvia* (Trueman, 1968*b*). Nevertheless, the narrow neck tissue between the head-foot and the viscera is crossed by many muscle fibres and the opening of the cephalopedal vein may additionally function as a sleeve valve in a similar manner to the stomodaeum of a sea anemone (Trueman, 1975). Either, or perhaps both, of these devices could prevent outflow of blood from the foot, but any valvular mechanisms must be relaxed during pedal retraction when blood flows to the visceral sinus.

The ejection of water from the mantle cavity of *Bullia* is also remarkably convergent with *Bivalvia* which adduct their valves to eject water from the mantle cavity to liquefy the sand immediately before the shell moves forward (Trueman, 1968*b*). The foot of bivalves, e.g. *Ensis*, is not divided into functional regions but changes its entire function at different stages of the digging cycle. It alternatively probes to penetrate the sand and dilates to form a terminal anchor so that pedal retraction allows the shell to be drawn down towards the tip of the foot. During burrowing the foot of *Ensis* shows only a single large amplitude pressure pulse at valve adduction and a short sequence of smaller pulses each corresponding to a probing movement. These probing pulses are functionally equivalent to the primary pulse in *Bullia*, all being concerned with pedal protraction.

When considering the fluid muscle systems of worms such as *Arenicola* or clams such as *Mya*, it has been possible to estimate muscle tensions from the dimensions of the animal and recordings of pressure (Trueman, 1975). In *Bullia* there is no simple relationship between pressure and tension for pressures of the same magnitude occur with a wide range of tension as recorded by a transducer attached to the shell apex (Fig. 5(c)). However when these tensions are considered as being those of the columellar muscle a maximal force of about 14 N cm^{-2} is developed, which is comparable to that of the pedal retractor muscle of *Ensis* (about 20 N cm^{-2}). For this purpose the cross-sectional area of the columellar muscle was measured in sections near its attachment to the shell.

In this article a comparison has been attempted between *Bullia* and other molluscs expressed entirely in qualitative terms. These lack the precision of quantitative comparisons and the only terms in which the latter may be made are in respect of the energy requirement for locomotion expressed in this article as joules per mg dry tissue weight. One difficulty with respect to *Bullia* is the interpretation of what is burial, for locomotion may continue for many cycles before a stable position has been reached in the sand. Accordingly the energy cost has been determined for a digging period of 10 cycles when the shell has normally passed beneath the surface of the sand.

Energy cost may be determined from oxygen consumption during burial, but it is difficult to achieve satisfactory results using a respirometer. An alternative method has

already been utilized in respect of small crabs (*Emerita*) and the clam *Donax* spp. (Ansell & Trueman, 1973). This involves measurement of the rate of movement (U) from recordings or film and the drag (D), DU representing the power required for burial. Drag cannot be measured directly but the maximum force exerted by a burrowing animal whilst restrained by a thread attached to a force transducer may be readily recorded. This force must normally overcome drag and may be taken as an estimate of the maximal drag normally experienced. *B. digitalis*, of shell length 3 cm, develops a tensile force of about 0.17 N during burial, or 0.01 N during movement over glass. On the surface of sand each step was at least 0.5 cm but this diminishes with burial and a movement of 3 cm over 10 digging cycles, lasting 45 sec is probably a realistic estimate. This gives a mean velocity of about 0.067 cm/sec and a power requirement of 1.1×10^{-4} J/sec. Over a digging period of 45 sec this represents a total energy requirement (E_t) of about 5×10^{-3} J and the mean energy per cycle (E_c) is thus 5×10^{-4} J. Expressed in terms of dry body weight (for a 750 mg animal) these are $E_t = 6.6 \times 10^{-6}$ J/mg and $E_c = 6.6 \times 10^{-7}$ J/mg. The comparable values for *Donax incarnatus*, a clam occurring on tropical sandy beaches, are $E_t = 2.2 \times 10^{-5}$ J/mg and $E_c = 4.4 \times 10^{-6}$ J/mg (Ansell & Trueman, 1973). The greater amount of energy used by *Donax* is probably related to its greater speed of burial, the digging period being only 4–5 sec. Unfortunately we have little other data with which to make comparisons. However, the temperate zone species *D. vittatus* is similar in size (2 cm length) and shape to *D. incarnatus*, although much slower moving (digging period, 40 sec). Assuming the same value for drag in both species of *Donax* we arrive at a similar energy requirement to *Bullia*. This suggests that molluscs living in similar sand may use approximately the same energy for burial provided they move at the same speed. By contrast the energy requirement for movement by *B. digitalis* over a sandy surface is about one tenth of that for burial when determined from recordings by the same method. This emphasizes the need of additional forces for burrowing and the importance of the large fluid-filled cavity in the foot of *Bullia* compared with the small vesicles of *Patella*.

Account may be taken of the efficiency of propulsion, i.e. the energy to overcome drag/total energy used in locomotion, which is likely to be of the order of 0.2 by analogy with previous calculations (Ansell & Trueman, 1973). Converted into calories, the total energy requirement for burrowing is thus 6×10^{-3} cal for a snail of 750 mg dry tissue weight over 45 sec. Brown (unpublished) has recorded an oxygen consumption of about 1.25 mg O_2 /g/h for *B. digitalis* of this size when suspended in a respirometer. During these measurements the foot was expanded and performed active movements. Assuming an oxycaloric equivalent of 3.4 cal/mg O_2 , *Bullia* has an energy requirement in these conditions of 4×10^{-2} cal over 45 sec. The energy of burial (10 cycles) is thus only about one seventh of the above requirement which suggests that the energy cost is small compared with the advantage to the snail of the avoidance of prolonged exposure on a sandy beach.

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