LOCOMOTION OF THE LIMPET, *PATELLA VULGATA* L.

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INTRODUCTION

The foot of *Patella*, in common with that of many gastropods, is adapted for loco-motion over, and adhesion to, hard substrates. In some snails propulsion is effected by cilia on the ventral surface of the foot, but in the majority a wave-like phenomenon of muscular contraction and relaxation passes along the sole and propels the animal.

The pedal waves may pass along the foot in the same direction as the animal is moving, in which case they are termed 'direct' waves, or may pass in the opposite direction to the movement of the snail, these being termed 'retrograde' waves. These definitions are those of Vlès (1907), who defined them in relation to the *direction of movement* rather than to the anterior and posterior of the animal. Where one set of locomotory waves covers the whole width of the foot the wave pattern is termed 'monotaxic' and when one set occurs on each side of the mid-line of the sole they are termed 'ditaxic'. Ditaxic waves are usually alternate. The reviews of Morton (1964) and Gray (1968) both give valuable summaries of previous work and details and examples of further patterns of locomotory activity.

There have been few attempts, e.g. Trappmann (1916), Rotarides (1936) (Un-traceable, source: Rotarides, 1945), Elves (1961), to relate the type of locomotion with the structure of the foot, many of the earlier papers being simply records of visual observations. Limited experiments were first performed on *Helix* by Ten Cate (1922) and Bonse (1935) and their techniques were subsequently considerably modi-fied and improved by Lissmann (1945, 1946). The latter remain the only published detailed investigations of gastropod locomotion. Lissmann studied three species, *Helix pomatia*, *Haliotis tuberculata* and *Pomatias elegans*, all of which exhibit direct waves, *Helix* being monotaxic and the others ditaxic. Unfortunately Lissmann did not study retrograde locomotion, nor did he attempt to relate his results to the disposition of the muscle fibres in the foot.

Previous observations on *Patella vulgata* by Fretter & Graham (1962) indicated that *Patella* is of the direct ditaxic type of forward locomotion, whereas the present in-vestigation has shown it to have retrograde ditaxic forward locomotion but direct ditaxic backward locomotion. Neither Vlès (1907) nor Weber (1925) could distinguish any waves on the sole of *Patella* during locomotion.

The purpose of this work is to investigate the process of locomotion in *P. vulgata* by the use of modern recording techniques, to relate these observations to the anatomy of the foot and to attempt to explain the locomotory mechanism.

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METHODS

(1) *Anatomical*

Longitudinal and transverse serial sections, 12 μ thick, were cut of juvenile and adult specimens of *Patella*. The animals were narcotized with propylene phenoxytol (Runham, Isarankura & Smith, 1965), fixed in Bouin's fixative in sea water, double embedded in celloidin/ester wax, and stained in Mallory's triple stain. Narcotization was considered to be essential prior to fixing in order to minimize distortion. A limited number of histochemical tests were carried out on freshly frozen sections.

(2) *Visual and photographic*

16 mm. black and white films were taken and analysed using conventional techniques. The lighting requirements were critical, strong lateral light sources being necessary to film the movement of the locomotory waves. The animals were allowed to settle and crawl on Perspex plates on which a 1 cm.^{2} grid was scratched. The plate was then clamped vertically in a small tank containing running cooled sea water.

(3) *Surgical*

The sole of the foot of *Patella* has a very uniform coloration which makes detailed film analysis of the locomotion difficult. In an attempt to overcome this various vital dyes were used in an attempt to mark the foot. This was unsuccessful, so sub-parallel cuts were made on the sole of the foot. By cutting in different directions different groups of muscle fibres could be eliminated, or at least their effect during locomotion could be considerably reduced. The depth of cut could not be ascertained accurately though in all cases it exceeded the depth of the highly vascular area adjacent to the sole. One such cut animal was subsequently narcotized, fixed and sectioned.

(4) *Physical*

These involved a method essentially similar to one of Lissmann's (1945) and pressure recordings from beneath the foot. It proved impossible to record the pressure from within the pedal haemocoel of *Patella*.

Lissmann (1945) used two thin glass rods, the ends of which were arranged to be side by side in contact with the sole of the foot. One rod was pivoted so that the end moved vertically and the other so as to move antero-posteriorly in the horizontal plane. The animals were made to crawl over a glass plate with two small perforations, one for each rod. The other ends of each rod were made to write on a smoked drum, enabling movements of the sole of the foot to be recorded during locomotion. Essentially the same apparatus was used in this investigation except that the rods were of aluminium and the recording end of each lever moved an isotonic myograph which was connected to a pen-recorder. Such recordings will be referred to as lever records.

This apparatus was calibrated by the use of dial calipers. These were rigidly clamped so that the free arm moved the sensitive end of each rod a known distance in the appropriate direction.

Pressure records from beneath the foot of *Patella* involved the use of a small Perspex plate through which one or two small (1 mm. diameter) holes were drilled.

The holes were connected by short lengths of rigid plastic tubing to Statham P23BB pressure gauges. Recordings obtained in this manner are referred to as sub-pedal pressure records.

Correlation of physical changes taking place in the foot was carried out by visual observations associated with manual marking of the record.

THE ANATOMY OF THE FOOT

The muscle fibres of the foot originate on the shell and insert laterally or ventrally on the dermal epithelium of the foot. A few of the fibres insert on the snout and act as retractor muscles for that structure. The pedal muscle fibres may be divided into four
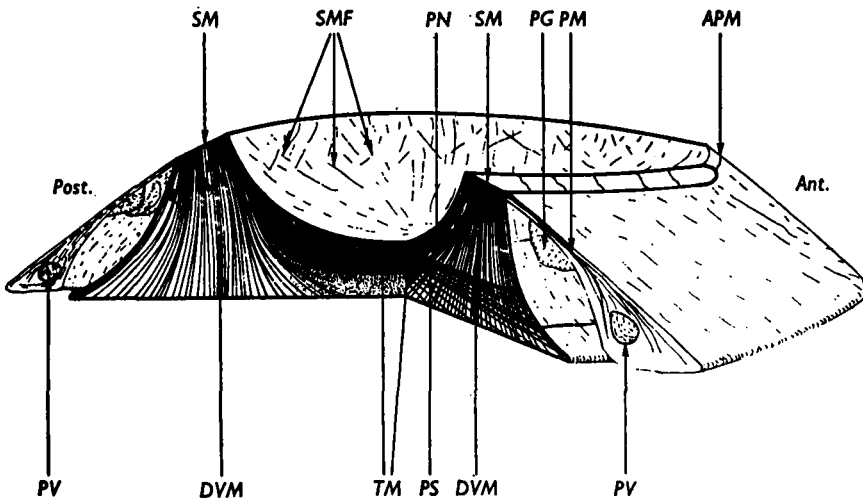

Fig. 1. Stereogram of the foot and mantle of *Patella* to show the orientation of the main muscle fibres of the foot. *Ant.*, anterior; *APM*, attachment of pallial muscle to the shell where the shell muscle is interrupted by the nuchal cavity; *DVM*, dorso-ventral muscle; *PG*, pallial gill; *PM*, pallial muscle; *PN*, pedal nerve; *Post.*, posterior; *PS*, pedal sinus; *PV*, pallial vein; *SM*, shell muscle; *SMF*, fibres of the shell muscle visible through the floor and side of the visceral cavity; *TM*, transverse muscle.

groups: (*a*) those which run from the shell directly to the sole of the foot on the same side of the animal as their origin. These will be called dorso-ventral muscles (Fig. 1, *DVM*); (*b*) those which run from the shell to the sole and lateral margin of the foot on the opposite side to their origin. These will be called transverse muscles (Fig. 1, *TM*); (*c*) those which run longitudinally from their origin and insert on the snout or on the pedal epithelium. These will be called longitudinal muscles; (*d*) those which run spirally in both directions from their origin to their insertion on the sole. These will be called spiral muscles.

The dorso-ventral muscles form the bulk of the foot, comprising about 70% of the musculature. The fibres spread out from their origin and insert on the pedal epithelium more or less at right angles to the sole. No striation can be seen of this or any other pedal muscle.

The transverse muscles are a very distinct group of fibres and form about 25% of

the pedal musculature. They run as a band immediately below the visceral sinus, forming the ventral boundary of the sinus. They remain as a compact group until they cross the mid line of the foot, from where they spread out to their insertions. The mid line of the foot consists entirely of crossing transverse muscle fibres. The transverse fibres pass dorsally to the pedal nerve cord on the same side as their origin and the thickness between the nerve cord and the visceral sinus is made up entirely of transverse fibres (Fig. 1).

The spiral and longitudinal muscles together form the other 5 % of the foot. The spiral muscles retain their identity as bundles for some two-thirds of their length, becoming diffuse as they near the sole. Ansell (personal communication and 1969) has noted that *Patella* has a defence reaction to predators which has been studied using *Nucella lapillus* as a stimulus. The animal raises its shell on the side of contact with the predator and repeatedly brings the shell down on to the substrate with some force. After two or three of these violent contractions the animal will sometimes spin its shell through as much as 90°. As Weber (1925) suggested, it would seem that the spiral muscles rotate the shell.

In the foot of *Patella* there are very few muscle fibres which run longitudinally. Some of these fibres run from the posterior end of the shell muscle, through the transverse muscle and insert on the snout or on the anterior margin of the foot. Some fibres run from the anterior end of the shell muscle and insert on the posterior margin of the foot. Morton (1964) shows a diagram of the foot of a 'generalized prosobranch gastropod' which includes a very thin layer of longitudinal muscle immediately above the sole. No such layer is visible in *Patella* (Plate 1).

The haemocoel spaces of the foot receive blood from the cephalic sinus (Fretter & Graham, 1962). Blood flows into two pedal sinuses, each adjacent to the two pedal nervecords (Fig. 1), whence it diffuses into the remaining pedal haemocoel. There is a region extending for approximately 0·5 mm. above the sole which contains many distinct, more or less spherical, spaces each about 10 μ in diameter. The rest of the foot has very few blood spaces except for several channels running up the side of the foot which may be for the venous return of the blood.

The importance of the blood in the foot should not be underestimated, for, as Clark (1964) points out, the blood forms virtually the only skeletal support for the foot.

Tests for elastic tissue using the orcinol/new fuchsin technique (Pearse, 1960) were carried out on the foot of *Patella* but with negative results.

EXPERIMENTAL OBSERVATIONS

(1) *Visual and photographic*

When *Patella* is crawling forwards the pedal waves pass from anterior to posterior, and there are two alternating sets, one on each half of the foot. Thus *Patella* has retrograde alternate ditaxic forward locomotion. The movement of such waves is represented in Fig. 2. The dark triangular areas (stippled) passing down the foot are areas of fixation to the substrate, and conversely the pale, roughly rectangular regions (unshaded) are areas where the sole of the foot is released from the substrate and moving forwards.

In backwards locomotion, which happens rarely, the waves start at the anterior end

of the foot as in forward locomotion and are alternate ditaxic. However, as they are now travelling in the same direction as the animal is moving then they are direct waves. The darker waves now represent moving areas of the foot and numerous creases can be seen in these dark regions, indicating that the foot is here compressed longitudinally. The paler areas thus represent fixed and stationary regions of the foot.
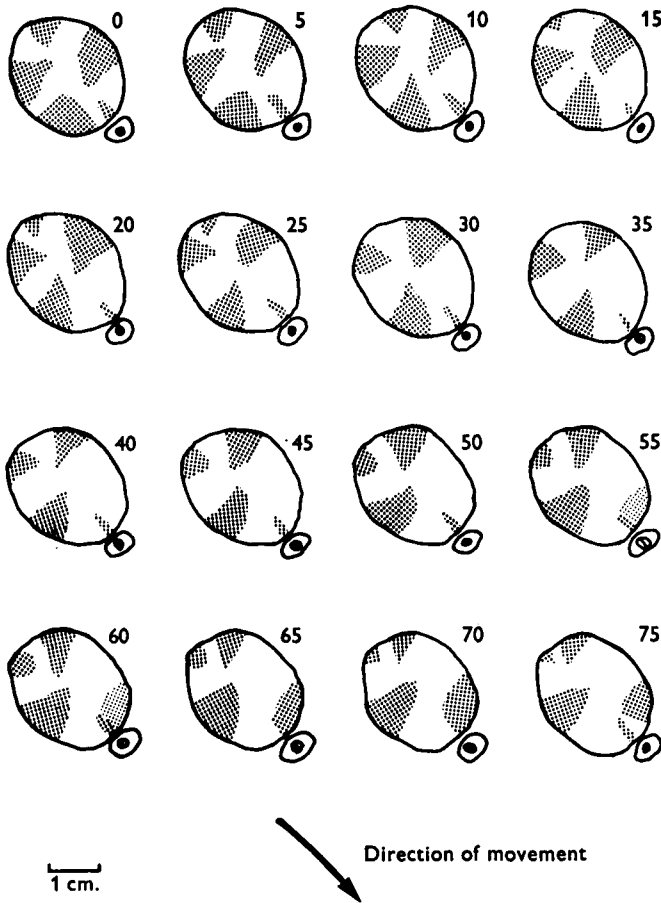

Fig. 2. Diagrams drawn from cine film of the normal forward locomotion of a limpet when turning slightly to its left. The stippled areas are regions in which the foot is attached to the substrate; the unshaded areas indicate where the foot is released from the substrate and moving forwards. The numbers give time in sixteenths of a second.

More frequently observed than rearward locomotion are very tight turning movements when the animal turns in virtually its own length (Fig. 3). To accomplish this the animal uses forwards locomotion on the outer half of the foot and backwards locomotion on the inner half of the foot. At first sight this is quite remarkable, as the animal appears to be using normal forwards locomotion, there being alternate light and dark waves on both sides of the foot. Close inspection, however, shows that the foot of *Patella* exhibits three 'shades' of lightness and darkness. The resting and stationary areas of the foot are of a neutral shade (the stippled areas of Figs. 2 and 3); the forward moving regions during retrograde waves are lighter (the unshaded areas of

Figs. 2 and 3); and the backward moving regions during direct waves are darker (the hatched areas of Fig 3).

The shades observed on the foot reflect the degree of expansion or compression of the epithelium of the sole; the darker the shade, the more compressed is that region. Thus in retrograde locomotion the forward-moving epithelium of the sole, being lighter in colour, is more stretched than the stationary parts (Fig. 4B; and Parker, 1911). In direct locomotion the sole is darkest and maximally compressed when raised from the
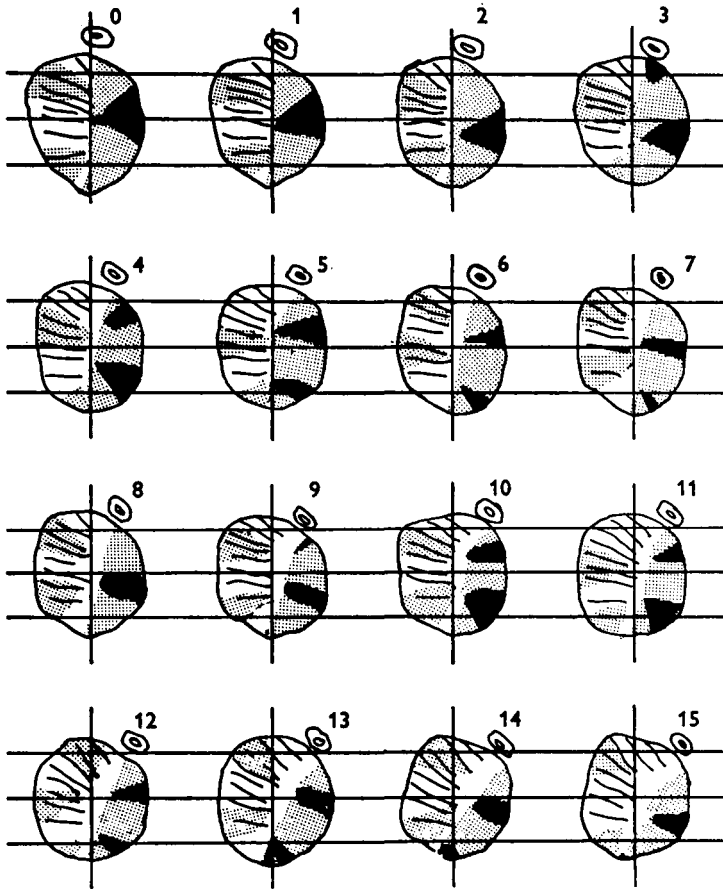

Fig. 3. Diagrams drawn from film of a limpet turning tightly to its left. The right half of the foot was cut transversely eight times. The stippled and unshaded areas are as Fig. 2, but the cross-hatched areas are regions where the foot is released from the substrate and moving backwards. The parallel lines are 1 cm. apart and the numbers give the time interval in seconds.

substrate, similar to the condition described by Lissmann (1945) in respect of direct locomotion in *Helix* (Fig. 4A). In *Patella* the dark waves may be observed to be associated with numerous small angular creases formed by the infolding of the epithelial surface.

During the passage of a lighter wave down the foot in retrograde locomotion the adjacent margin of the foot is slightly pulled inwards, but during the passage of the darker direct waves down the foot the margin is slightly pushed out. At no time does

the margin of the foot actually leave the substrate, there being a sealing flap of turgid tissue round the entire margin of the foot.

Apparently the only other gastropod which has been observed to turn in a similar fashion to that described above is *Gibbula cinerarius* (Gersch, 1934). This uses normal forward locomotion (in this case direct waves) on the outer half of the foot and reverse locomotion on the inner half of the foot. However, as they pass backwards while the foot moves backwards these waves are still direct waves, not retrograde as stated by Fretter & Graham (1962).
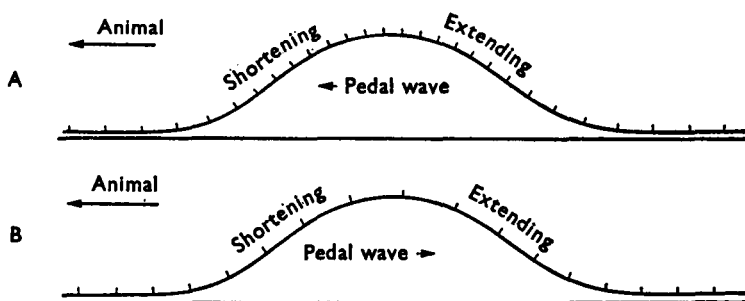

Fig. 4. Diagram summarizing the differences between (A) a direct wave and (B) a retrograde wave (after Lissmann, 1945).

Patella can turn less sharply than the forward/reverse turns already described. To achieve this the animal produces a longer step-length than normal on the outer half of the foot, and possibly a shorter step-length on the inner half of the foot. Such a turn is shown in Fig. 2, the animal turning slightly to its left.

(2) *Surgical*

Figure 3 is drawn from a film of an animal with eight transverse cuts on the right half of the foot. If a layer of longitudinal muscle were present immediately above the sole as Morton (1964) and others have suggested, then its effect during locomotion would be considerably reduced. However, cuts such as these have no appreciable effect either on the forward or the backward locomotion of *Patella*.

The cuts enable film sequences to be analysed in respect of movement of the sole (Fig. 5). The curves A–E represent the movement of five points on the nearly parallel cuts, the positions being plotted at intervals of one twelfth of a second. The diagonal hatching of Fig. 5 represents the passage of a neutrally shaded area down the foot (stipple in Fig. 2), the unshaded regions indicating the passage of a lighter region and periods of movement of the sole. This is readily apparent as the five curves successively move forward only in the unshaded parts of the diagram, although some forward and backward slip is recorded.

The rate of forward locomotion of *Patella* exceptionally has a value of about 1 cm. in 23 sec., though even this speed is usually maintained only for short distances. Each locomotor (lighter) wave is about 0·8 cm. long and advances the animal by about 0·25 cm.

Figure 6 shows the positions of the first three points of Fig. 5 plotted in relation to point D. This clearly shows that points on the foot are stretched apart when the

sole is lifted off the substrate during the passage of a retrograde locomotory wave (Parker, 1911). This is in contrast to *Helix* and *Haliotis*, where, during direct loco-motory waves, the foot is compressed when lifted off the substrate (Lissmann, 1945) (Fig. 4). Gray (1968) explains how forward locomotion is achieved with retrograde waves in an earthworm, attachment to the substrate occurring when each segment is at its shortest length. The shortening of regions of the limpet when applied to the substrate is directly comparable.
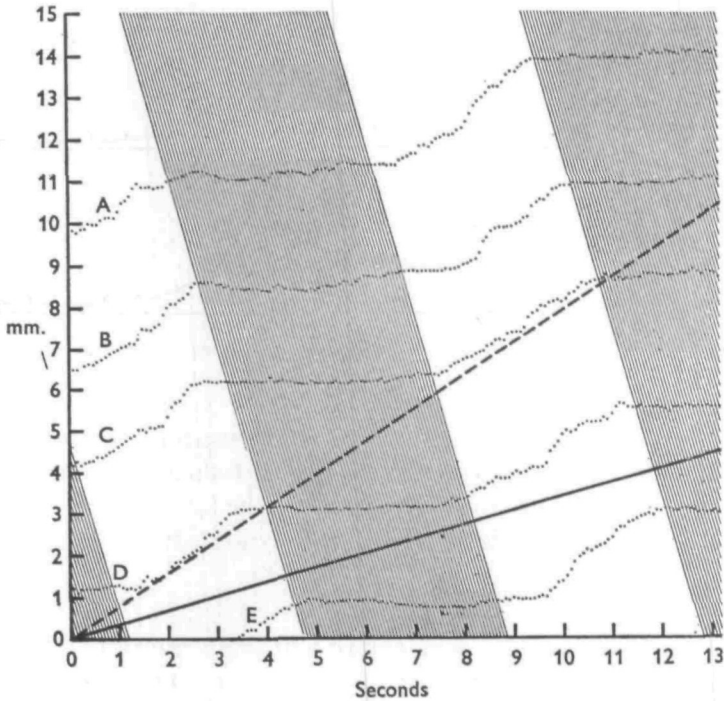

Fig. 5. Graph obtained from cine film of the forward locomotion of *Patella*. The five points A–E are five points on the foot arranged from anterior to posterior. The heavy line represents the average speed of the animal and the broken line the average speed forwards of a point in movement. The diagonal shading represents the attachment of the sole to the substrate which accompanies the passage of a darker locomotory wave down the foot.

Limpets which have been cut in the above manner have been observed to turn sharply so that the cut side is that which travels backwards involving maximal com-pression of the sole. Their ability to do this suggests that if any longitudinal muscle is present immediately above the sole then it plays little part in the locomotory pro-cesses. The problem then arises as to how the anterior edge of the foot is pulled backwards at the commencement of a direct wave travelling from anterior to posterior. Longitudinal muscle fibres are inserted on the anterior edge of the foot but are located away from the sole and would not be severed by the cuts made. Contraction of such fibres could initiate a direct locomotory wave.

The effect of longitudinal cuts varies according to their position. If the cuts are away from the mid line of the foot the animal is slightly slowed in its movement, but

otherwise animals were little affected by this operation, except for a lateral bulge on the cut side, indicating that the numerous transverse muscles had been cut.

The centre of the foot consists almost entirely of crossing transverse muscle fibres, and a longitudinal cut in this region has rather drastic consequences. The viscera protrude through the opening and as a result of shell-muscle contraction are further squeezed out. However, it is possible to attach such a wounded animal to a transparent substrate and for it to live in apparently fair health for a few days. The foot becomes more circular in outline, and the incision opens so that the viscera are adjacent to the substrate. Animals in this condition do move forwards, albeit somewhat slowly, and very little blood is lost.
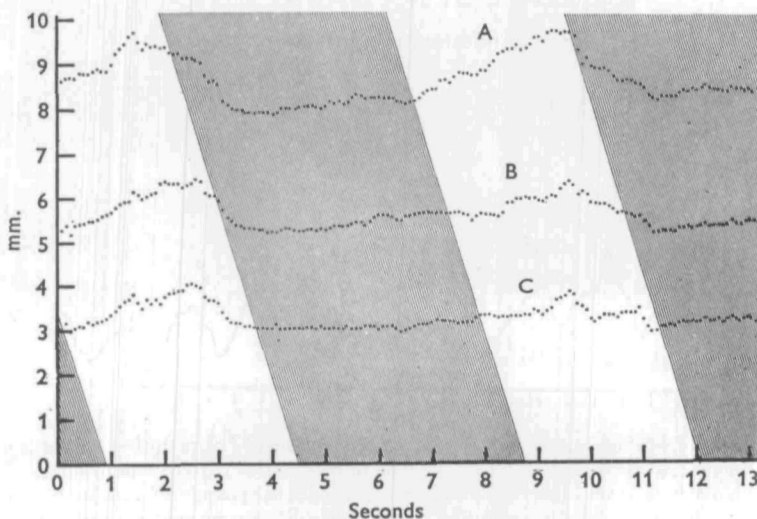

Fig. 6. Graph obtained from the data of Fig. 5 to show the stretching of the foot as a locomotory wave passes and the foot is raised off the substrate. 0 mm. is the position of Point D of Fig. 5.

Simultaneous transverse and longitudinal cuts have no more effect than the sum of the two individual cuts. The foot is rather more rounded than usual and the rate of locomotion is slower than normal.

Very little loss of blood occurs as a result of these cuts but exactly how this is achieved is not clear. Examination of sections of a partially healed specimen shows connective tissue fibres bridging the cut and no distinct wall of tissue between the outside medium and the haemocoel spaces of the foot. However, as the pedal haemocoel consists of a large number of small spherical cavities, the contraction of adjacent muscle fibres is possibly enough to effectively seal the cut.

(3) *Physical*

Figure 7a is a recording obtained from *Patella* while one half of the foot passed over the ends of the levers. The upper trace (i) is from the antero-posterior lever and the lower trace (ii) is from the dorso-ventral lever. A downward deflexion indicates forward movement and dorsally directed movement respectively, thus it can be seen that the forward movement of the foot coincides with its lifting off from the substrate.

Figure 7b shows the relative positions of the neutrally shaded waves of the foot, the trace deflexions (o) being visually co-ordinated with the passage of such waves over the recording end of the dorso-ventrally moving lever. They occur when this lever is ventrally positioned which, from Fig. 7a, is when that part of the foot is stationary.

Using this apparatus it was possible to measure the amount of deflexion of the levers during the passage of a locomotory wave. The horizontally displaced lever moves distances in some way proportional to the forward sliding friction of the foot, thus
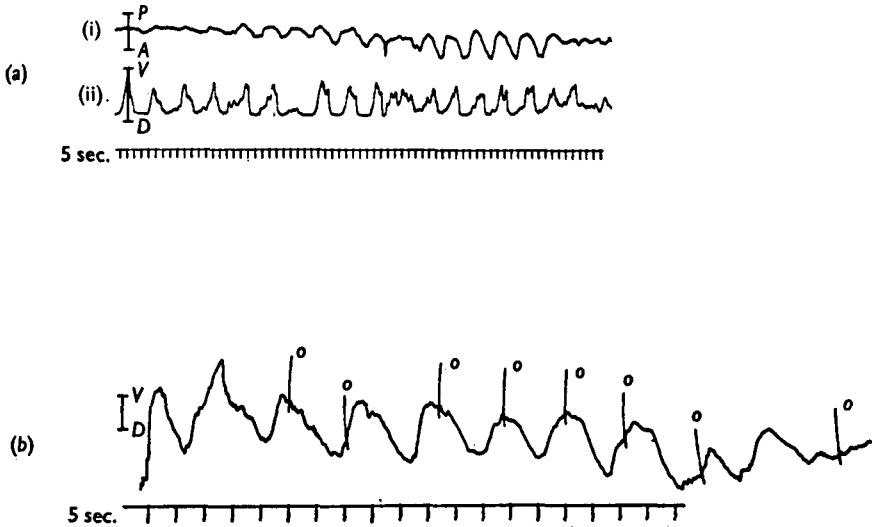

Fig. 7. Records from the sole of *Patella* obtained by means of levers during forwards locomotion. (a) Simultaneous antero-posterior (i) and dorso-ventral (ii) records. (b) Dorso-ventral record with deflexions (o) visually marked to coincide with the passage of a darker wave (regions of pedal attachment) over the recording lever. Scale lines represent 0·1 mm. *A*, anterior; *D*, dorsal; *P*, posterior; *V*, ventral.

actual distances are meaningless. The vertically displaced lever moves in direct proportion to any vertical movements of the foot, so that the distance moved by this lever is the distance the sole of the foot is raised and lowered during the passage of a locomotory wave. As can be seen from a comparison of Fig. 7a (ii) with Fig. 7b, there is considerable variation in the value of different recordings, but from these and other such recordings an estimate of mean upward deflexion of the lever can be obtained. This is 0·2 mm., some deflexions being as small as 0·05 mm. and some as large as 0·35 mm. (all these being from adults of about 4 cm. shell length).

These results and those of the photographic analyses enable an estimate to be made of the volume contained under the foot by the pedal waves, thus the total displacement of the foot as a result of locomotion. At any one time during locomotion about 58 % of the foot surface is raised off the substrate and moving forwards (in Fig. 2 the total area of the foot is 4·0 cm.^{2}, with 1·7 cm.^{2} stationary, and 2·3 cm.^{2} raised and moving). If the area of movement is multiplied by the depth of wave, 0·2 mm., then the result, 0·046 ml. is approximately the volume of fluid under the pedal waves. Therefore during locomotion there is an upward displacement equivalent to about 0·046 ml., and it is probable that this volume of blood is displaced from the foot. The

total blood volume of *Patella* is high, about 65·73 % ± 7·26 S.D. of the wet weight (minus the shell). This was determined by the injection of inulin into the blood, the analysis method was that of Roe, Epstein & Goldstein, 1949. In limpets of the size used in these experiments this means that the blood volume is 3 ml. So out of a total volume of 3 ml. only about 0·046 ml. is being displaced as a result of locomotion. This is a very small proportion of the total (1·57 %) and it is unlikely to cause large variations in pressure over the standing pressure in the pedal haemocoel.
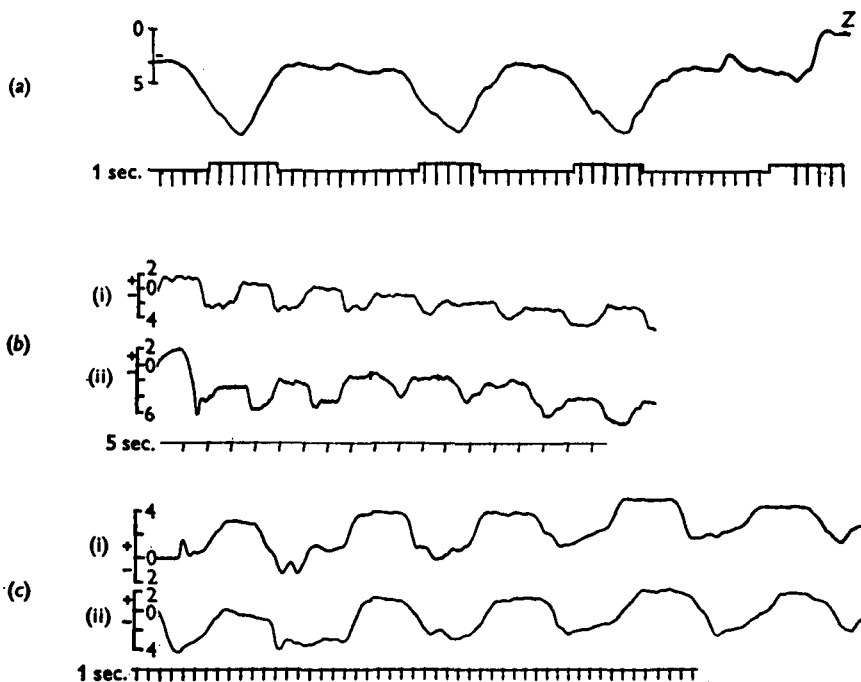

Fig. 8. Pressure records from beneath the foot of *Patella* during forwards locomotion. (*a*) From one half of the foot. The elevations of the time trace were marked visually to coincide with the passage of a pale wave (elevation of the sole) over the pressure gauge; *Z*, the zero level of this record caused by the animal passing off the pressure gauge. (*b*) Simultaneous records from (i) the right and (ii) the left halves of the foot. (*c*) Records from two gauges 1 mm. apart in the longitudinal plane. The upper trace (i) is from the gauge 1 mm. anterior to that from which the lower trace (ii) was obtained.

As a limpet crawls over a plate through which a cannula is connected to a pressure gauge a reduction of pressure of about 6 cm. of water is recorded when the foot is raised off the substrate (Fig. 8). The elevations of the time trace of Fig. 8*a* were visually marked to coincide with the passage of a lighter wave, i.e. raising of the foot, over the pressure cannula.

Figure 8*b* is a recording obtained from two pressure cannulae arranged sub-pedally so that one was recording from each lateral half of the foot as the animal passed over. The downward deflexions are alternate, showing that the pedal waves are alternate.

Figure 8*c* is obtained from two sub-pedal cannulae about 1 mm. apart in the antero-posterior plane, the upper trace (i) being anterior to the lower (ii). Clearly, as the

animal crawls forward over the cannulae the posterior one will be reached first and Fig. 8c (ii) shows a deflexion before (i). Thereafter both traces have a very similar shape, the anterior one (i) showing negative pressure slightly sooner than the posterior trace (ii) due to the rearward direction of the locomotory wave.

DISCUSSION

The results described have shown that *Patella* moves forward by means of retrograde pedal waves during which regions of the sole are progressively raised and moved forwards and then lowered, and that there is no longitudinal muscle adjacent to the
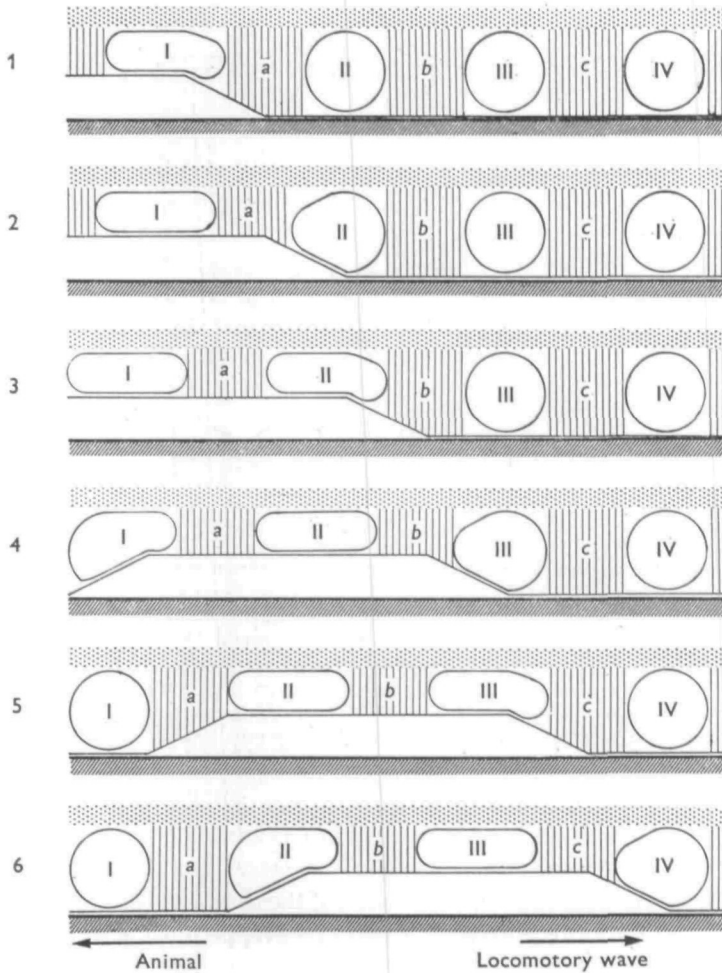

Fig. 9. Sequence of six diagrams of a model to show a possible mechanism of locomotion of *Patella*. See text for explanation.

sole of the foot. With this evidence and that of the other experiments, it is possible to approach the problem of how a limpet moves. This may be best answered by the consideration of two supplementary problems, firstly, what happens as a locomotory

_wave passes to cause forward movement, and secondly, how is the anterior edge of the foot moved forwards at the start of a locomotory wave.

Figure 9 shows six diagrams to represent the sequence of events in a possible model which answers the first of the two problems. This produces forward movement utilizing the dorso-ventral muscles as the main propulsive agents, with the haemocoel spaces of the foot and the transverse muscles as essential factors. The pedal haemocoel consists largely of spherical cavities, I–IV, immediately above the epithelium of the sole, these are assumed to be of constant volume and to have no lateral displacement. The latter is not strictly true as the foot is slightly narrowed as the foot passes, but this complements the following explanation and does not detract from it. That a constant volume of blood is retained in the haemocoel cavities is suggested by the absence of bleeding when incisions are made in the foot.
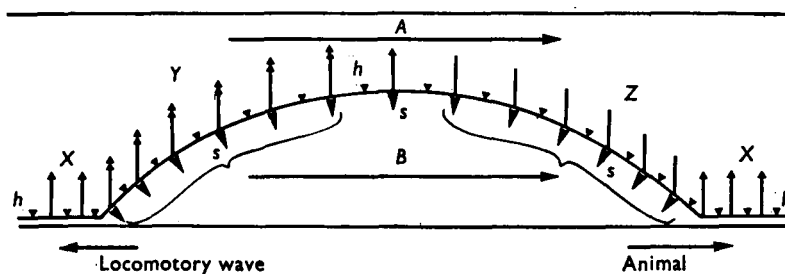

Fig. 10. Diagram showing the antagonism between the relaxing and the contracting dorso-ventral muscle fibres of the foot and the forces acting on the sole during the passage of a locomotory wave. See text for explanation.

Referring to Fig. 9, as the dorso-ventral muscle (a) contracts (diagrams 1 and 2), the fluid space II is squeezed upwards against the roof of transverse muscle fibres. With a haemocoel cavity of constant volume and posterior muscle (b) attached to the substrate, the anterior margin of II must be pushed anteriorly (to the left of the diagram). This will continue until the muscle (a) is fully contracted, provided that the transverse muscle prevents lateral expansion.

As the pedal wave passes posteriorly the next muscle (b) contracts (diagrams 3 and 4) affecting the shape of space III and so causing it to be pushed forward in a similar manner to that already described. As muscle (b) moves forwards it will push space II forwards which, in turn, will advance muscle (a) even further. This process may be repeated any number of times, depending on the length of each pedal wave and the step-length.

As the trailing edge of a locomotory wave approaches, the muscle (a) will start to relax (Fig. 9, 5 and 6). Two forces will tend to draw the sole back on the substrate, so extending this muscle. They are the low but positive pressure in the haemocoel and the negative pressure beneath the pedal wave.

Figure 10 shows the forces acting on the sole of the foot and the antagonism which occurs between the relaxing and the contracting dorso-ventral muscle fibres inserted on to the sole. At the anterior and posterior margins of the wave (Fig. 10, X) the dorso-ventral muscles may be considered to be at rest (single-headed arrow) and their tension counterbalances the downward thrust derived from blood pressure in the pedal haemocoel (arrow heads, h). As the leading edge of a pedal wave passes down the

foot the dorso-ventral muscles contract (Y), exerting an upward force on the sole of the foot (double-headed arrows). This upward force would cause a slight local increase in the pressure in the pedal haemocoel *and* a decrease in pressure under the foot (arrow heads, s). The relaxing dorso-ventral muscle (at Z) will be drawn down and restored to its resting length both by the positive pressure in the haemocoel (Fig. 10, arrow A) and by the negative pressure under the foot (arrow B).

All that is needed to produce movement of the wave down the foot is for the successive contraction and relaxation of the dorso-ventral muscles to proceed posteriorly, forward movement of the foot could then be produced solely by the hydraulic properties of the foot.

Chapman (1958) points out that the primary function of a skeleton is to provide a means by which opposing muscles may be antagonized or brought to bear on each other for the restitution of their relaxed state. Since the enclosed cavity of the pedal wave of *Patella* would seem to act to restore the fibres at the trailing edge of the pedal wave to their resting length by the contraction of the fibres at the leading edge of the wave, then it is possible to regard the cavity as a rather novel type of external hydrostatic skeleton. In this case the fibres of the leading edge of the wave are antagonistic against fibres at the trailing edge of the wave.

Some of the work done by the contracting dorso-ventral muscle fibres is therefore expended in the restitution of other muscle fibres to their resting length, but most of the remainder may be turned into a propulsive force by the hydraulic properties of the foot. This system, as already stressed, requires that the lateral extension of the foot be strictly controlled, and in *Patella* there exist numerous transverse muscle fibres which may perform this function. This is evidenced by the reduction of speed when the transverse muscles are cut.

The other main problem concerning the limpet's locomotion is how the anterior margin of the foot is advanced at the start of a pedal wave. The solution is a continuation of the preceding paragraphs. If the pedal haemocoel near the front of the foot is vertically narrowed and little or no blood escapes then either a lateral or forward extension of the foot must occur. The lateral extent of the foot is controlled by the transverse muscles so that forward movement must follow and the process described above may then proceed.

The backward locomotion of *Patella* using direct waves may be similarly explained despite the lack of longitudinal muscle next to the sole. The contraction of the longitudinal muscle that inserts on the anterior margin of the foot (but runs for most of its length away from the sole) could cause a compression of the anterior edge of the foot. Such a compression is observed as a series of angular inpushings of the sole of the foot in this region. Once this initial compression has been achieved then all that is necessary is for the dorso-ventral muscles behind the compressed area to contract so as to cause this area to automatically pass backwards, assuming that the epithelium of the foot is not entirely rigid. Relaxation of the dorso-ventral muscles would occur at the trailing edge of the wave in a similar manner to that described for the retrograde locomotory wave, except that slight increase in pressure under the foot may be expected. It would seem that the epithelium of the sole of the foot of *Patella* is not able to be compressed beyond its resting length as it is thrown into angular folds by the initial contraction of the longitudinal muscle. This can be compared to Lissmann's (1945)

examples of direct locomotory waves, where in *Helix* the foot has relatively smooth but apparently deep waves, and in *Haliotis*, where the foot has arched and creased waves. The latter enables a longer step-length (10 mm.) than either *Helix* (1 mm.) or *Patella* (2·5 mm.).

The above explanation requires no longitudinal muscle in the foot except for some fibres inserted on the anterior margin of the foot of *Patella* or the rear margin of the feet of *Helix* and *Haliotis*. *Helix* has longitudinal muscle in the foot which inserts on the posterior margin of the foot (Trappmann, 1916; Weber, 1925; Elves, 1961). Weber (1925) could find no longitudinal muscle in the foot of *Haliotis* but there are muscles running down from the shell to the posterior edge of the foot and which could pull the latter forwards at the commencement of a direct pedal wave.

These remarks concerning the locomotion of *Haliotis* and *Helix* require further experimental elucidation, but in *Patella* the observations discussed show that the dorso-ventral muscles alone are capable of producing forward locomotion, some of the work done being converted into forward locomotion by the hydraulic properties of the foot. Rearward locomotion may also be produced solely by the action of the dorso-ventral muscles but only after some longitudinal muscle has pulled back the anterior edge of the foot.

SUMMARY

1. The locomotion of *Patella* has been studied by histological, photographic and experimental techniques. The foot consists principally of dorso-ventral and transverse muscles and has no longitudinal muscle fibres near to its sole. The pedal haemocoel is limited to a region of small spherical cavities, extending for 0·5 mm. above the sole, two pedal sinuses and several lateral vertical channels.

2. *Patella* moves forward by means of retrograde alternate ditaxic pedal locomotory waves, but during rarely observed backward movement the waves are direct. During tight turns the limpet uses forward locomotion on one half of the foot and backward locomotion on the other.

3. During the passage of a retrograde locomotory wave the foot is lifted off the substrate by about 0·2 mm. and the pressure beneath the sole falls by about 6 cm. of water.

4. A model is proposed to account for locomotion utilizing the dorso-ventral muscles as the sole propulsive agents in the hydraulic system of the foot. This system consists principally of the dorso-ventral and transverse muscles, the spherical cavities of the pedal haemocoel and the fluid enclosed beneath each locomotory wave. Both fluid systems may be utilized during contraction and relaxation of different groups of dorso-ventral muscles.

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EXPLANATION OF PLATE

Micrograph of longitudinal section of *Patella* showing the epithelium of the sole and the region immediately dorsal to it. Note the lack of longitudinal muscle near the sole and the numerous spherical cavities of the pedal haemocoel. Scale line = 0·1 mm.

Plate 1

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