THE MECHANISM OF LOCOMOTION IN GASTROPOD MOLLUSCS

I. KINEMATICS

By H. W. LISSMANN

Zoological Department, Cambridge

(Received 7 September 1944)

(With Plate 1 and Eleven Text-figures)

Whereas the broad outline of the mechanical events of locomotion can in most animals be readily visualized, the mechanism of propulsion in gastropods is less easily observed. Since the seventeenth century (Lister, 1694) a great deal of attention has been paid to this problem and a wealth of suggestions has been forthcoming; there is, however, a significant absence of convincing experimental data. To some extent the problem is confusing on account of the diversity of locomotory mechanisms existing within the group (Vies, 1907; Parker, 1911; Olmsted, 1917; Weber, 1925). Nevertheless, there can be no room for doubt that one characteristic type of movement depends upon the propagation of waves of muscular activity over the surface of the animal's foot. So far as is known, no adequate account has yet been given of the method whereby this type of activity propels the animal over the surface of the ground. The present paper deals with these problems in respect to three representative genera, Helix, Haliotis and Pomatias.

HELIX

Typically, when a snail (Helix aspersa or H. pomatia) begins to move, a dark transverse band appears near the anterior end of the under-surface of the foot; this band then starts to move forward, but at the same time other bands appear posteriorly to the first until the whole surface of the foot (apart from a narrow lateral margin) is characterized by a pattern of forwardly moving bands. It is important to notice that the formation of the banded pattern begins at the anterior and proceeds to the posterior end of the foot at a speed considerably greater than the velocity with which the bands themselves move anteriorly over the foot; when these bands disappear the animal ceases to move. It seems generally agreed that the forward movement of alternating light and dark bands is due to the passage of co-ordinated waves of muscular contraction and relaxation. Each section of the foot in turn contracts and relaxes and in so doing changes its position forwards or backwards relatively to the rest of the body of the animal. Beyond this there seems no general agreement concerning the nature of these muscular waves or concerning the displacement of the pedal surface relative to the ground. Similarly, it has been suspected for some years that the passage of a muscular wave over a particular region of the foot involves vertical as well as horizontal displacement of the pedal surface. Experimental approach to this problem has, however, yielded two opposing views. Van Rijnberk (1919) and ten Cate (1922), using a manometer, convinced themselves that the visual moving dark waves represent ridges or projections from the surface of the foot; Olmsted (1917), working on various marine gastropods with similar technique, concluded that the areas in question represented furrows or concavities on the pedal surface; the latter conclusion was supported by Bonse (1935) whose technique was based on the displacement of the end of a small metal rod in contact with the surface of the foot. Whilst it is not claimed that the following observations resolve all questions dealing with the kinematics of the snail's movement, they nevertheless clarify the position to some extent.

Horizontal displacement of the pedal surface

Close observation of a snail moving over a glass plate shows clearly the forward movement relative to the ground of any point on the foot over which a dark band is passing, whilst the same point is at rest when lying within the wider and lighter areas. Biedermann (1905), however, claimed that a point on the surface of the foot is continuously in motion, moving at a slower speed when lying within a light area, and at a higher speed when within one of the darker bands. Bonse (1935), on the other hand, states that although movement only occurs during the passage of a dark band, nevertheless, this movement is itself discontinuous.

In order to obtain accurate information concerning horizontal movements, a number of points were defined on the surface of the foot by injection of small quantities of Indian ink or by means of an indelible pencil; the snail was then allowed to move over the surface of a vertical glass plate and cinematograph pictures (8–20 per sec.) were taken of the ventral surface. For more detailed observation of a localized area of the foot identification of fixed points is possible by noting the position of one or more of the relatively conspicuous mucous glands of the foot; these are readily identifiable
For the higher magnification employed and, therefore, form admirable landmarks.

When cinematograph records of this type are projected—or indeed when individual landmarks are observed by the naked eye—it can be noted that each landmark remains more or less stationary on the ground until one of the dark moving bands approaches it from a posterior direction; at this moment, the landmark begins to move forward with increasing velocity, but at a rate which is always less than that at which the wave itself is passing over the foot. As the centre of the wave passes the landmark, the velocity of movement of the latter falls until it finally comes to rest until the approach of the next

Fig. 1. Three types of forward motion of the mucous glands on the sole of *Helix pomatia*, as recorded by cinematography. The animal was moving vertically upwards. (a) represents the normal type of forward motion; (b) shows a certain amount of slip; (c) shows a passive forward drag in the relaxed state.
wave. The detailed analysis of the cinematograph records obtained from animals moving vertically upwards confirms this visual picture, but indicates a certain degree of variability in minor respects. The most common type of movement exhibited by a point on the surface of the foot is shown in Fig. 1a in which each period of forward movement is followed and preceded by a period of rest; the records show, however, that the periods of rest are definitely shorter than the time which elapses between the passage of two successive dark bands. In other words, the period during which a point is in motion has also been observed at or near regions which been subjected to strong stimuli and in consequence show tonic contraction. It is therefore necessary to allow some time to elapse before records are made from landmarks made by the injection of Indian ink.

In order to correlate the movement of individual points with the functional state of their underlying muscles it is necessary to observe the movements of two adjacent points relative to each other and to the ground. An analysis of this type, derived from cinematograph records, is shown in Fig. 2a. In this figure the positions of three points A, B, and C

is not restricted to the period of passage of the visual dark wave (see below). Other records (Fig. 1b) show, however, that there is often a definite backward movement at the completion of each phase of forward movement—in other words backward slip occurs: this phenomenon is particularly noticeable in the case of points lying near the anterior part of the foot or when the snail is made to creep a number of times over a track which is covered with the mucus deposited by previous movements, or when it was loaded. In the case of regions lying near the posterior end of the foot, landmarks often show continuous forward motion (Fig. 1c) indicating that they are kept in motion by energy derived from regions lying more anteriorly: this type of motion relative to the ground are shown on the ordinate, whilst time is plotted along the abscissa. The figure also shows the form, position and velocity of the waves (also plotted to scale from the photographs). It will be noticed that the distances between the two points A and B alternately increase and decrease; they are nearest together when they lie within the dark bands and farthest away when they lie at rest between two successive bands. This fact is shown very clearly in Fig. 2b. These results show conclusively that the dark bands seen on the pedal surface are essentially regions of longitudinal muscle contraction, whereas the lighter bands are regions of longitudinal relaxation.

So long as there is no slip between the ground and
The mechanism of locomotion in gastropod molluscs

The cycle of contraction and relaxation of each muscle fibre, shown diagrammatically in Fig. 3, is such that the duration of relaxation is twice that of contraction, and consequently for every fibre which is contracted there are two which are relaxed, and during the passage of one complete wave each of three fibres contracts once and each point on the pedal surface moves forward a distance which represents the difference between the length of full relaxation and contraction, provided that during contraction no significant vertical displacements accompany longitudinal movement.

Vertical displacements of the pedal surface

In the case of Helix, vertical displacements of the pedal surface are undoubtedly relatively small, but an attempt to define their nature was made as follows. A hole 2 mm. in diameter was cut in a glass or celluloid plate and through this hole passed the rounded end of a small glass recording lever; any vertical displacement of the pedal surface above or below the surface of the plate could thus be recorded (Fig. 4c). By observing and marking the passage of the muscular waves by means of a tapping key it was found that an upward movement of the lever coincided with the passage of the dark phases of the muscular waves. It has been claimed, however (ten Cate, Bonse), that marking with a tapping key introduces an error due to the reaction time of the observer. An attempt was made to avoid this complication by combining the record of the vertical displacement (Fig. 4c) with a simultaneous record of the horizontal displacement (Fig. 4b). Since the end of the lever in contact with the surface of the foot is dragged in the direction of the animal’s movement, it may be assumed that any displacement thus recorded will have a value varying directly with the speed of an area gliding over it, i.e. it would correspond to the lowest point of a tracing as indicated in Fig. 4b. As the speed of this particular section of the sole decreases and finally comes to rest, the lever tends to swing back under its own
weight to its normal position, corresponding to the highest position in the tracing. A record thus obtained is given in Fig. 5.

From the above data it is possible to reconstruct the path of movement of any section of the pedal surface throughout one complete cycle of its muscular activities. Such a reconstruction can be followed graphically from Fig. 6. It will be noted that as a wave of contraction and relaxation passes over any section on the pedal surface, the section in question is first moved upwards and forward, but later, whilst still travelling forward, begins to descend again to the surface of the substratum, where it comes to rest and exerts a downward pressure against the ground.

Taking the segment $F$ in Fig. 6a it will be noted that its posterior edge lifts first and is the first to be placed on the ground in its new position of rest. In other words, the whole segment acts somewhat as the foot of a plantigrade vertebrate—the heel lifted before the toes, and is also placed on the ground before the toes. It should be borne in mind that in Fig. 6 the vertical displacement of the segment is relatively very much greater than is actually the case in Helix. It is, however, convenient to emphasize this vertical movement in view of the phenomena to be described below for Pomatias.

**HALIOTIS TUBERCULATA**

Like Helix, Haliotis moves by means of a system of direct muscular waves. It is a very active creeper, with agile turning movements, and in some ways presents a clearer mechanical picture than the snail.

In Haliotis the locomotory waves are ditaxic in the sense that they alternate on the two sides of the foot; the form and frequency of these waves are highly characteristic. At any one time one complete and two partial, anteriorly moving, areas of somewhat darker appearance are visible on the sole of the foot (Fig. 7). Whenever one of these dark waves has reached the middle of the left half of the foot, the right side of the foot exhibits, at its anterior end, the posterior border of a dark area just fading out, whilst simultaneously another one is beginning to form at the hind end of the right half of the foot. As in Helix, the dark areas represent regions of maximum longitudinal contraction. These are most conspicuous along the outer lateral margin of the foot and seem to increase in length somewhat as they approach the anterior end; the zone of contraction, however, extends both in front and behind the dark areas.

The general co-ordination of movement relative to the body of a number of points along both halves of the foot is represented in Fig. 8, which is the analysis of a cinematograph record of Haliotis moving at a speed of 1 cm./sec. This shows: (i) the rhythm of contraction and relaxation of each section of the foot; (ii) the strict alternation of waves on the right and left half of the foot; (iii) two points on the sole, which are about 3.5 cm. apart when the intermediate zone is fully relaxed, approach each other to about 2 cm. when the intermediate zone is fully contracted (length of foot 5.5 cm.). In Haliotis the degree of contraction, in this case 1.5 cm., makes up the total distance of one 'step' relative to the ground, and obviously the length of a step $\times$ frequency of steps (waves) equals the speed of the animal relative to the ground.

Each of the marked points on the sole of Haliotis moves forward relative to the ground in essentially the same manner as they do in Helix, though in Helix every wave of contraction carries the point forward by 0.3-1.2 mm., while in Haliotis the corresponding distance amounts to between 1.5 and 2.3 cm. (Fig. 9). This condition is true for any point along the lateral part of the foot, where there
For descriptions of Figs. 6a and 6b see p. 64.

Fig. 6a. Lateral view.

Fig. 6b. Ventral view.

The mechanism of locomotion in gastropod molluscs 63
is a regular alternation of forward motion and rest. Fig. 9 suggests that, as in Helix, three different types of forward motion can occur: Towards the anterior region of the animal a minute backward slip can be observed after the phase of forward motion; this is normally absent towards the middle of each lateral area of the foot, whereas at the posterior end the sole occasionally fails to engage the ground and is passively drawn forward in a relaxed state.

This picture, however, applies only to the outer lateral margin of the foot, for in Haliotis there is no alternation of relaxation and contraction along the median line. Any two points on this line always keep the same distance apart, and move forward at a more or less uniform speed while the animal is in motion (Figs. 9, 10). The underlying muscular tissue cannot be regarded as active in any locomotory sense.

As can be seen from Fig. 7, in Haliotis the contraction of longitudinal muscles does not only become apparent from a shortening of a distance between two points in the contracted region, or from a change of its optical properties, but also from a lateral deformation of the foot. At the outer lateral margin an outwardly directed bulge accompanies the passage of each longitudinal contraction, and any point at the same level on the median line is pushed in the opposite direction. As a result of the functional alternation on the two halves of the foot any point on the median line, though moving forward at a constant speed, performs at the same time lateral movements of the same frequency as the locomotory waves (Fig. 10). At the present state of our knowledge, it appears uncertain whether this lateral displacement may be taken as being indicative of an antagonism between longitudinal and transverse fibres in the sole of the foot, as assumed by Vlés (1908), or merely as resulting from a thickening of the contracted longitudinal fibres.

It is worth noting that in Haliotis the lifting of the

Legend to Text-figures 6a and 6b.

Fig. 6. Diagram illustrating in 8 successive positions the movement of a section of the snail's foot. a, lateral aspect; b, ventral aspect. The fully relaxed sections of the foot are fixed to the ground. A complete wave of contraction involves at any one time five adjacent sections, e.g. B—F in position 6, showing a varying degree of shortening. The ratio of full relaxation to full contraction of any one section is taken to be 3:1. The phase of contraction is associated with simultaneous vertical and horizontal displacements of the pedal surface. As represented in the diagram, any one point completes its phase of forward motion after 6 successive positions. The horizontal distance travelled by any one point (XY for the posterior edge of section F) equals the difference in length of all sections involved simultaneously in contraction (YZ for the sections BCDEF in position 6) and the length of all these segments in a state of full relaxation (XZ in position 1). Therefore: the length of one step, for the posterior edge of section F, \(xy = xz - yz\). Obviously the speed of the animal is equal to the length of a step \(\times\) frequency of the waves.
LISSMANN—THE MECHANISM OF LOCOMOTION IN GASTROPOD MOLLUSCS (pp. 59–69)
The mechanism of locomotion in gastropod molluscs

The mechanism of locomotion in gastropod molluscs is clearly observable, and it sometimes gives the appearance as if the surface of the sole is thrown into folds through longitudinal contractions. Furthermore, as the phase of contraction progresses forward the anterior border of the lateral bulge (Fig. 7) becomes irregular in outline; this phenomenon may be due to the detachment by the action of the longitudinal fibres of regions of the sole which are adhering to the ground.

and left halves being separated by a distinct median line. Movement is initiated by a slight swelling of one half of the foot which expresses itself as a lateral and medial expansion (Fig. 11); it is accompanied by a corresponding decrease of the surface area of the adhering surface of the other half. While this process is still in progress, a wave of contraction passes over the smaller half, causing it to be lifted off the ground and to be shortened longitudinally. The wave quite

---

**Fig. 8. Co-ordination of movement relative to the body of 10 points on the sole of *Haliotis tuberculata* moving at a rate of 1 cm./sec.; a and 1 show the position of the anterior margin of the foot, e and 5 the posterior margin. Note the strict alternation of the right and left halves of the foot, and that the sections a-c, c-e, 1-3, 3-5 show the absolute maximum degree of shortening, which in this case amounts to about 1.5 cm.**

**POMATIAS ELEGANS**

In 1882 Simroth gave a general account of the locomotory movements of a specimen of *Pomatias elegans*. Unfortunately his description and interpretation are closely linked up with his theory of active muscular extension, and they cannot be confirmed in a number of essential details; he, and earlier observers, agree on the difficulty of observing this rather shy species.

The following description is based on a film-analysis of animals moving on a vertical glass plate (Pl. 1). When the animal is at rest, the foot is approximately symmetrical about the median line, the right obviously starts from the hind end, first detaching the posterior and outer lateral margin, and running obliquely forward, the region near the median line being detached somewhat later. This phase of contraction involves the entire length of one half of the foot, which for some short period is completely lifted off the ground. No sign of waves passing over the raised half of the foot can be discerned on the photographs, nor have any such waves been noticed on the living animals—contrary to Simpth's description.

The stationary half foot swells up until the other half is lifted, but the lateral extension of its sole begins to decrease as soon as relaxation sets in in the
Fig. 9. Movement relative to the ground of nine points on the sole of *Haliotis tuberculata*. Note that the phases of forward motion and rest, which can be seen on the laterally situated points, are more clearly differentiated in the anterior region. The points along the median line progress at a constant speed. In the outline figure, initial positions of the points are marked.
The mechanism of locomotion in gastropod molluscs

ed half. This relaxation causes the posterior border of the relaxing half foot to be brought down on to the substratum first, thereby obviously establishing a posterior point d’appui against which the anteriorly situated regions spread forward as relaxation proceeds in the same direction. Ultimately this half comes to rest in a more anterior position relative to the foot which remained stationary. When both halves are thus again completely placed on the movement is twice the distance of the initial short step.

A lifting of the contracted half has never been observed to begin from the median line, as stated by Simroth, nor has any instance been recorded when the foot was put down with the anterior edge touching the ground first. Occasionally, in less active animals, the more medially situated regions of the foot are not raised at all, but in every case

Fig. 10. Successive positions relative to the ground and to each other of nine points on the sole of Haliotis tuberculata in locomotion, showing a lateral movement of the median line. In A the points marked lie near the posterior end of the animal, in B the points are situated midway along the foot, and in C they lie further towards the anterior end. The transverse lines connecting the points indicate coincident positions. The lowest of the transverse lines in each of the three diagrams shows the initial position relative to the ground of the three points marked on the sole; the uppermost transverse line shows the points when the animal has reached the position indicated by the outline. Note that the ground is more effectively engaged by the points lying at the anterior end of the animal than by the points lying further behind.

ground, there is a considerable interval during which no forward movement occurs. It can be noticed, however, that during this period the conditions for the next step are being prepared by a reversed swelling and de-swelling of the two half feet (Fig. 11).

After the initial short step, each subsequent longitudinal contraction moves the contracting half foot anteriorly to a position level with the stationary foot, and each succeeding relaxation causes it to move to a position more anterior than that which is occupied by the stationary foot, i.e. the total both the raising and the lowering, which coincide with longitudinal contraction and relaxation, start from the hind end and spread forward.

In Pomatias the proboscis plays a part in locomotion. It can be seen to attach itself after being pushed forward, and naturally it must be detached from time to time as the foot advances. Its activity does not seem to be rigidly correlated with the rhythmic alternation of pedal movements. Pending further investigations it is suggested that its activity is mainly governed by the tone of the columellar muscle.
Fig. 11. Changes in the lateral extensions of the right (A) and left (B) half of the foot of *Pomatias elegans* in locomotion (ventral aspect). + indicates the position when the lateral margin is lifted off the ground. The width of the stationary half of the foot increases medially and laterally until the other half is lifted. The outline of the foot indicates the final position reached.

CONCLUSIONS

The diversity of locomotory types—ranging from undulations of a peristaltic nature to alternate stepping—encountered here within a group of relatively close phyletic coherence such as the gastropods, recalls similar conditions in other groups, viz. arthropods, vertebrates, etc.

The movement of the two halves of the foot of *Pomatias elegans* can best be compared with the ambulation of a bipedal vertebrate. The heel is lifted first, then the toes; the heel is put down first with the toes following. In *Helix*, on the other hand, the conditions are more comparable to a millipede or a caterpillar, although here again the movement of each localized area of the foot is comparable to that of the plantigrade surface of a tetrapod limb. *Haliotis* occupies an intermediate position between *Helix* and *Pomatias*. The diagonal co-ordination of movement of the sole of *Haliotis*, with three simultaneous areas of motion separated by three areas of support, is clearly reminiscent of conditions found in hexapods, and offers some obvious advantages with regard to stability (Gray, 1944) and turning movements. In this connexion it appears significant that, according to Robert (1907), in the similarly moving *Trochoeochlea* the locomotory waves can be reversed on one side when a turning movement is executed. It is clear that the difference between *Helix*, *Haliotis*, and *Pomatias* consists merely in a difference of wave-length relative to the total length of the locomotory surface, in that longer series of muscle fibres are grouped together into one continuous region of contraction. When this process has gone so far as in *Pomatias*, and involves the whole length of the foot, the functional alternation of the two halves of the foot becomes an absolute mechanical necessity.

It must be borne in mind that the three genera discussed here represent but a small selection of modifications in locomotory methods found amongst gastropods. However, while it is impossible at the present state of our knowledge to offer a plausible suggestion as to why such a great functional variety has arisen, the conditions appear suggestive enough to look for an explanation along similar lines as has been advocated for vertebrates, where, in the course of evolutionary changes, land-living tetrapods have emerged from an undulating aquatic type. From a physiological point of view the locomotory waves of *Helix* are usually classed with undulations as seen to pass over the body of a moving fish or annelid worm (peristalsis). It is, however, important to remember that the locomotory waves in *Helix* cannot, for mechanical reasons, represent the primary waves of locomotion of an organism originally swimming through water, because their direction would tend to drive the animal backwards. It seems more profitable to take into account the facts which point to a turbellarian resemblance of gastropods. So far as locomotory types are concerned, a great number of parallels can be found existing in both groups: (i) ciliary locomotion, common in Turbellaria and occurring in some gastropods (Copeland, 1919, 1922; Gersch, 1934; Olmsted, 1917); (ii) swimming through parapodial movement as seen in *Thysanozoon* and *Aplysia*; and above all (iii) muscular locomotion for sliding over more or less solid surfaces.
This latter mode shows a great variety of coordination in gastropods, and it is interesting to note that an alternation of the locomotory activity of the right and left halves is found in certain marine Polyclades (Olmsted, 1922). This type of creeping locomotion differs, however, in some respects fundamentally from the type of locomotion exhibited by an annelid worm (Gray & Lissmann, 1938): (i) in that the areas of fixation are wide and represented by zones of longitudinal muscular relaxation; (ii) the parts in motion are short and longitudinally contracted; (iii) the propagation of waves takes place in postero-anterior direction. The significance of these facts could perhaps be more fully appreciated if the forces set up during one complete locomotory cycle were better known.

**SUMMARY**

1. The modes of progression of Helix, Haliotis, and Pomatias are described.
2. In all three species waves of longitudinal muscular contraction, followed by relaxation, pass over the foot in postero-anterior direction.
3. Typically, any point on the sole shows during one locomotory cycle a phase of forward movement and a phase of rest. Minor variations depend on external conditions, and on the location of such a point on the sole.
4. In all three species the longitudinally contracted areas are lifted off the ground and move forward, whilst the elongated areas remain stationary.
5. The length of a step is essentially determined by the difference between the length of the musculature comprising the contraction phase of one locomotory wave, and the length of this musculature when it is fully relaxed (Fig. 6).
6. The difference between the three species consists in a difference of wave length relative to the total length of the foot. In Haliotis and Pomatias there is a functional alternation of locomotory phases of the right and left halves of the foot.

I am greatly indebted to Prof. J. Gray, F.R.S., for his interest and help in the course of these investigations. Part of the work was done while holding the Cambridge University Table and a grant from the Bidder Fund at the Stazione Zoologica in Naples. I wish to express my thanks to the Director and staff for the facilities they gave me.

**REFERENCES**


**EXPLANATION OF PLATE 1**

Successive cinema-photographs showing the ambulation of Pomatias elegans. The transverse lines indicate a distance of 5 mm., the figures the time in 1/10 sec. Note that the contraction starts at the hind end and spreads anteriorly. At 28 it involves the whole length of the left half, and at 88 of the right half of the foot, which at these stages are lifted off the ground and brought from a more posterior position to the level of the stationary relaxed half of the foot. Relaxation sets in at the posterior end (56 and 96); the foot is first lowered at the posterior edge, thereby establishing a posterior point d’appui against which the anteriorly situated parts move forward as relaxation and elongation proceeds. In the long interval between 40 and 68 no forward motion occurs, but a very significant change in the adhering surface area of the two halves is noticeable which takes place in preparation for the next step.