

## THE MECHANISM OF LOCOMOTION IN GASTROPOD MOLLUSCS

## II. KINETICS

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(With Thirteen Text-figures)

As is the case in all terrestrial animals, the progression of a snail or other gastropod depends on the exercise by the animal of an adequate force directed posteriorly against the ground; in an animal moving horizontally and at constant speed, this force overcomes the frictional resistance encountered by the parts which are gliding forwards. The movements of the pedal surface of some gastropods have been discussed in a previous paper (Lissmann, 1945). The experiments described below were designed to correlate these movements with the forces set up during locomotion. The salient point which appears to be established is that during progression the foot exhibits (i) areas of forward motion, coinciding with phases of longitudinal muscular contraction, followed by extension; (ii) areas at rest, which remain essentially elongated. However, the state of the muscles is no indication of the tensions they may set up within the body, nor of the propulsive force they may exert; it is by no means obvious how the external forces are produced, or how they lead to progression.

The musculature of the gastropod foot is complex in structure, and there is no general agreement as to how it produces the necessary cycles of longitudinal shortening and elongation on the foot. Whilst there can be little doubt that the process of shortening is effected by the contraction of longitudinal muscle fibres, the subsequent process of elongation is more controversial. According to Jordan (1901), this process is effected by the elastic properties of walls of cavities containing fluid, whilst Trappmann (1916) suggested that transverse muscle fibres were involved. Jordan based his view on experiments with *Aplysia*. He found that vesicles containing body fluid under pressure protruded from isolated pieces of the foot when the latter were made to contract through stimulation. As soon as stimulation ceased the vesicles disappeared and the pieces elongated to their normal length. When the vesicles had been punctured, however, these pieces failed to elongate after stimulation had been discontinued, although the muscles became soft and did not resist passive stretch.

So far as locomotion is concerned *Aplysia* differs markedly from the gastropods discussed here. No

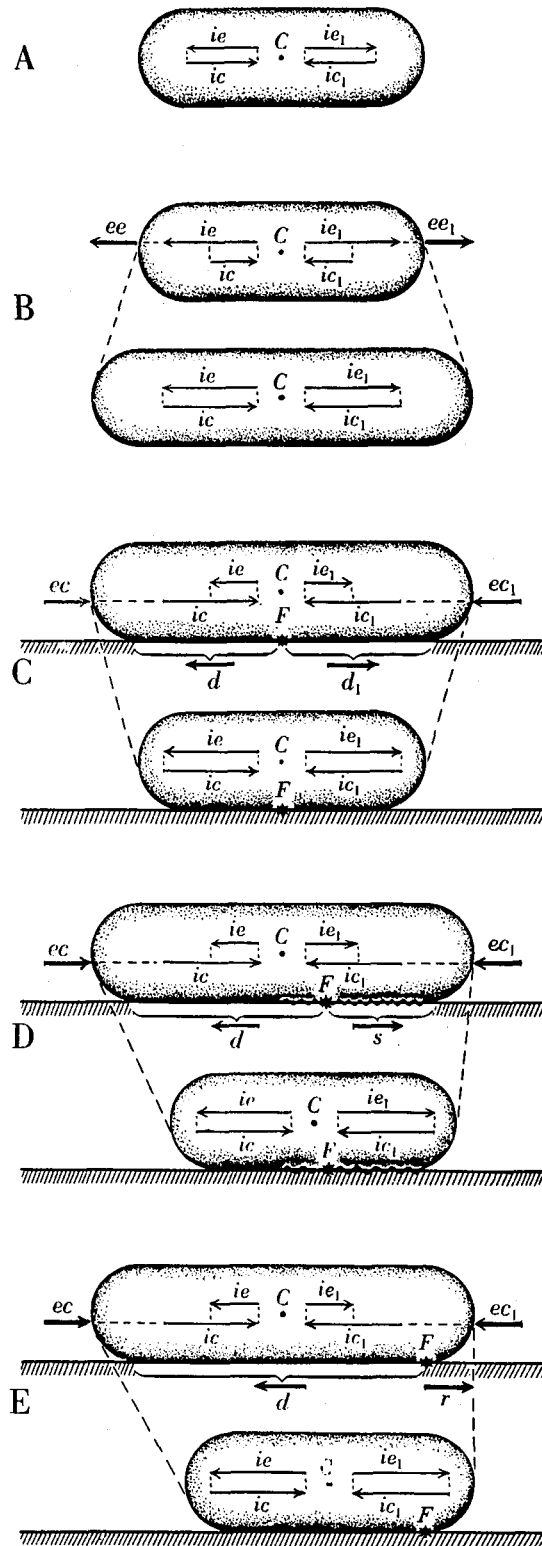
attempt has been made in the course of the present investigation to elucidate experimentally the internal mechanism, but some conclusions can be drawn from the observations reported below. With regard to the external mechanics of movement it is immaterial whether antagonism to the longitudinal fibres is effected by hydrostatic pressure, elasticity of connective tissue, or by a set of transverse muscles; the existence of two antagonistic forces—one leading to elongation, the other to longitudinal contraction—is essential, since longitudinal shortening cannot effect a forward movement of the anterior end of the foot, whilst elongation alone cannot produce a forward displacement of the hind end of the foot. Therefore, if the foot as a whole is in steady progression and retains a constant length, both these forces must be operative, and all endeavour to explain locomotion as being due to either one of them alone must fall short of supplying a complete answer.

MECHANICAL PRINCIPLES AND  
TERMINOLOGY

Before considering the movements of a body which, like that of a snail is without rigid skeletal elements, it is profitable to recall some elementary mechanical principles applicable to such a system. An inflated rubber balloon may conveniently serve as an illustration, especially if Jordan's picture of antagonism between hydrostatic pressure and longitudinal contraction be accepted.

Only forces acting parallel to the long axis of the body will be taken into account, and the following abbreviations be used in the text below:

Internal force of contraction	$ic, ic_1$
Internal force of extension	$ie, ie_1$
Internal friction	$f$
External force of contraction	$ec, ec_1$
External force of extension	$ee, ee_1$
Reactions from the ground:	
(1) External sliding friction (drag)	$d, d_1$
(2) External sliding friction (slip)	$s$
(3) Static reaction from the ground	$r$
Point of frictional equilibrium	$F$



If an inflated balloon be freely suspended the pressure inside ( $ie$ ,  $ie_1$ ) and the elastic force of the outer membrane ( $ic$ ,  $ic_1$ ) are equal and opposite (Fig. 1 A), and as long as both forces increase or decrease in the same sense and proportion no outward movement will occur. However, as soon as only one of these forces is changed a deformation of the body will become apparent. When  $ie$ ,  $ie_1$  is increased, or if  $ic$ ,  $ic_1$  is decreased, elongation will take place; when  $ic$ ,  $ic_1$  is increased, or  $ie$ ,  $ie_1$  decreased, the body will shorten longitudinally. It is assumed that there is a sliding readjustment of the two antagonistic forces, and whenever a change of one of them causes movement, the other automatically undergoes a corresponding change, e.g. if the internal pressure of the balloon be increased, the resultant expansion thereby increases the tension of the outer membrane until a new state of equilibrium is reached (Fig. 1 B). Thus an external force of contraction ( $ec$ ,  $ec_1$ ) can be expected to operate as long as the resultant vectors converge within the body ( $ic > ie$ ); an external force of extension must exist whenever the vectors point outwards ( $ie > ic$ ). In a complex system like the body of a snail these changes must be significant enough to overcome any internal friction ( $f$ ) which might impede the spreading of the effective force throughout the system. The external forces are therefore

$$\begin{aligned} \text{Longitudinal contraction} & \quad ec = ic - (ie + f) \\ \text{extension} & \quad ee = ie - (ic + f) \end{aligned}$$

When either of these two forces operates while the body rests horizontally on solid substratum, the situation is changed owing to the interactions between the body's surface and the ground. These interactions can be expressed as forces acting tangentially against the ground and the surface of the body, i.e. as friction ( $d$ ) which opposes the external force. If the body rests uniformly on the ground and undergoes a uniform contraction, both ends will tend to approach the centre of gravity (Fig. 1 C), and the farther away from the centre of gravity a point is situated, the greater will be its excursion,

Fig. 1. Model illustrating the relationship between the internal forces, the external forces, and the reactions from the ground. A. An inflated balloon; the internal forces of extension ( $ie$ ,  $ie_1$ ) and of contraction ( $ic$ ,  $ic_1$ ) are balanced. B. Increase of  $ie$ ,  $ie_1$  causes the appearance of an external force of extension ( $ee$ ,  $ee_1$ ), and a movement will result until a new state of equilibrium is reached between the internal forces. C. Through increase of  $ic$ ,  $ic_1$ , while the model rests on the ground, an external force of contraction ( $ec$ ,  $ec_1$ ) emerges, causing displacement of the surfaces towards  $F$  (point of frictional equilibrium). The external forces act against symmetrical external friction ( $d$ ,  $d_1$ ). D. As in C; through asymmetrical external friction (rough ground under one half),  $F$  is shifted towards the area of higher friction, which causes a differential excursion of the two ends (drag =  $d$ ; slip =  $s$ ). E. Absolute fixation at one end ( $F$ ) produces a static reaction from the ground ( $r$ ) under  $F$ , and a displacement of the rest of the body towards  $F$ .

the greater its velocity. Only the area vertically beneath the centre of gravity will remain fixed; this point may be termed the point of frictional equilibrium ( $F$ ).

If during the contraction phase the degree of shortening is uniform, the force exerted by any contracting unit varies more or less inversely with its distance from the point of frictional equilibrium, for the force exerted by the section nearest to  $F$  has not only to overcome the friction accompanying its own deformation, but must also exert a tractive force on the more distal parts.

The body will behave similarly when exposed to a force of extension ( $ee$ ), but this time both ends will tend to move away from  $F$ , as in Fig. 1 B.

The following general relations between the external forces ( $ec$ ,  $ee$ ) and the external friction ( $d$ ) can be expected: (i) no displacement will occur when  $ec < d$ , or  $ee < d$ , because the external force is insufficient to overcome the initial static friction; (ii) acceleration will result when  $ec > d$ , or  $ee > d$ . The component vectors of each force, of  $ec$  and  $ec_1$ , and of  $ee$  and  $ee_1$ , must under all circumstances be equal and opposite, as must be  $d$  and  $d_1$  (external friction), and in the case discussed above, the nature of the surfaces and the equal distribution of weight make for a symmetrical appearance of friction and displacement.

If the body undergoes the same deformation as before, while the substrate under one half is smooth and under the other rough, or if the body is fitted with devices which increase the friction under one half, then the point of frictional equilibrium will no longer coincide with the position vertically beneath the centre of gravity, but will be shifted towards the area of higher friction (Fig. 1 D). As before,  $F$  will remain stationary and the degree of displacement of any point on the body will vary directly with its distance from  $F$ . Since one of the two ends is now farther away from  $F$  than the other, it will execute a larger movement. The friction accompanying the larger movement may be termed 'drag', while the smaller excursion at the opposite end is known as 'slip' ( $d$  and  $s$  in Fig. 1 D).

In the extreme case when friction becomes infinitely great at one end of the body, whereby this remains fixed to the ground, the whole body will tend to approach this area of fixation when a longitudinal contraction takes place (Fig. 1 E), and will tend to move away from it in case of elongation. In both cases the maximum distance of displacement will be twice that of the original movement when the point of frictional equilibrium was situated midway between the two extremities, because  $F$  is now situated twice as far away. In other words, one of the two component vectors of  $ee$ ,  $ee_1$  or  $ec$ ,  $ec_1$  has become completely neutralized by a static reaction from the ground ( $r$ ), and the displacement has become unidirectional.

So far tensions and thrusts have been conceived

as developed between two surfaces exerting sliding friction, or between one such area and a fixed point. Additional forces can also be set up between two fixed points; such instances will be considered later (p. 42).

In gastropods the external forces, which are the actual propulsive agents, are derived from an interplay of internal forces generated through co-ordinated muscular activity. At any one moment the magnitude and direction of the external forces must be essentially considered as a balance between the horizontal longitudinal components of the internal forces of extension and of contraction, reduced by a certain amount of internal friction.

Fixation to the ground is assumed to be effected by adhesion of longitudinally relaxed parts of the sole by means of mucus (Parker, 1911). Unlike the instances discussed above, or unlike the leech, the whole area of fixation is not static; each point within that area remains stationary relative to the ground for a brief period, but the central point of the area of fixation shifts continuously and with the same velocity as that of the preceding (anterior) and the following (posterior) longitudinal contraction.

Detachment and reduction of friction may be aided—as Rotarides (1927) suggests—by expulsion of mucus from the numerous glands usually distributed on the sole. This may be caused directly through the muscular contraction. The mucus may therefore play a double role; as adhesive and as lubricant. Frequently a simultaneous contraction of longitudinal and dorso-ventral fibres is taken for granted, because the regions of longitudinal contraction are lifted off the ground. There is no need for this assumption on mechanical grounds; any local increase in tension through muscular contraction will produce the same effect, while a reduction in tension will produce a bulge, just as a bulge will appear on the weakest part of a tyre under high pressure.

It is tempting to attribute the internal pressure to the longitudinal contractions. However, while these contractions undoubtedly have an effect, it must be remembered that the internal pressure of the system cannot be greater than the weakest point of the balancing tension of the enclosing walls. Whether the walls of the system are exclusively represented by the 'vesicles' described by Jordan, or whether there is a general pressure or pressure gradient within the body spaces remains doubtful. This point is of importance in considering the internal friction.

#### RELATIONSHIP OF INTERNAL AND EXTERNAL FORCES AS DEDUCED FROM *POMATIAS ELEGANS*

The foregoing considerations can now be exemplified by a concrete case. From a mechanical point of view

the conditions in *Pomatias elegans* appear reasonably clear. Although this species presents problems of its own and does not lend itself readily to experimental enquiry, it is more suitable than the snail for illustrating the general distribution of forces, and may thus serve to elucidate the somewhat complex phenomena discussed in the subsequent analysis of *Helix*. As has been suggested previously the physiology of locomotion of the two genera reveals some fundamental similarities despite a strikingly different appearance.

When an animal like *Pomatias* is at rest it can be assumed that the muscular tone is balanced, and whatever the magnitude of the internal forces ( $ic$ ,  $ie$ ) may be, they must be either equal and opposite

posteriorly directed force ( $ec_1$ , Fig. 2 B) generated by these muscles is resisted through interposition of a zone of relaxed tissue, by an equal and opposite reaction from the ground ( $r$ ). The anteriorly directed component of the contraction ( $ec$ ), on the other hand, accounts for (i) a forward acceleration of mass (quantitatively negligible); (ii) any frictional resistance that the forward gliding posterior end may have to overcome, including any adhesive forces ( $d$  in Fig. 2 B). It can also be assumed that this contraction exerts a pressure on the body fluid and contributes to driving it into the other stationary half of the foot.

As the contraction passes forward the area of the anteriorly situated adhering surface is reduced (partly by detachment and partly by reduction of its transverse expansion); eventually the area of the adherent region is insufficient to resist the force of longitudinal muscular contraction. At this stage a backward slip of the anterior end occurs. When the phase of contraction occupies one half of the whole foot the complete half foot is, as a rule, lifted off the ground in a fully contracted state (Fig. 2 C). Simroth (1882) suggested that after the half foot had been lifted from the ground it was advanced relative to the head of the animal by the contraction of caudal muscles. This would however involve a reaction against the ground by the other adherent half foot or by the proboscis, since these now carry the whole load. Simroth's assumption, however, does not seem legitimate in view of the fact that the raised half of the foot is merely brought alongside the relaxed half, and is in no way protracted.

There is no evidence to suggest that in *Pomatias* there may exist a direct antagonism between longitudinal and transverse fibres, because the longitudinal contraction occurs simultaneously with the transverse contraction. This, quite to the contrary, probably means that whilst a simultaneous contraction of longitudinal and transverse fibres takes place in one half foot, a corresponding relaxation of both sets of muscles occurs in the other half. The significance of this suggestion should not be exaggerated, since it must be remembered that in *Haliotis* the conditions appear to be reversed. It may be that in *Pomatias* these synchronous contractions involve a movement of the common centre of gravity towards the middle line of the stationary half foot; this would increase the stability of the animal, just as a bipedal vertebrate tends to shift the centre of gravity towards the supporting limb during slow ambulation.

When one half foot of *Pomatias* is lifted, relaxation begins posteriorly, and the posterior edge of the foot is lowered. As soon as this process has brought a sufficient area of surface into contact with the ground, adhesion to the ground is firmly established (Fig. 2 D). Internal pressure, or other force of elongation ( $ie$ ,  $ie_1$ ) now increases while the force of longitudinal contraction ( $ic$ ,  $ic_1$ ) decreases; in this

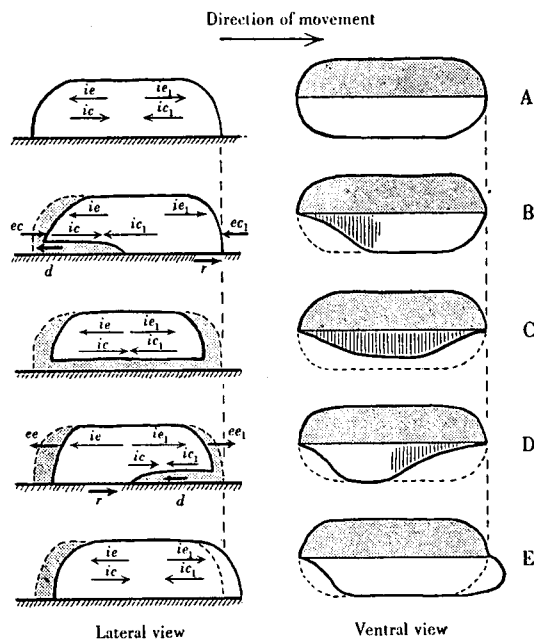


Fig. 2. Diagrammatic representation of the forces leading to locomotion in *Pomatias elegans*;  $ie$ ,  $ie_1$  internal pressure;  $ic$ ,  $ic_1$  longitudinal contraction;  $ec$ ,  $ec_1$  and  $ee$ ,  $ee_1$  external forces of contraction and extension;  $d$  = dynamic friction;  $r$  = static reaction from the ground.

(Fig. 2 A), or their difference must be smaller than the external friction between the animal and the substrate:

$$ie = ic, \text{ or}$$

$$\begin{array}{l} ie - ic = ee < d \text{ (long. thrust)} \\ ic - ie = ec < d \text{ (long. tension)} \end{array} \left. \begin{array}{l} \text{stress on substrate} \\ \text{without displacement.} \end{array} \right\}$$

When a wave of contraction starts at the posterior end of the foot, this region of contraction is lifted from the ground and, owing to the shortening of the muscles, it is drawn forward towards the anterior regions which, being still relaxed, adhere firmly to the ground. The tension set up between the adherent and non-adherent regions is undoubtedly due to a contraction of longitudinal muscles. The external

when the foot regains its original length. The position of the foot relative to the ground is however changed; the posteriorly directed component of the external forces ( $ee$  in Fig. 2 D) is resisted by the adhesion to the ground of the posterior edge ( $r$ ), whereas the

posterior surface of application, and the contraction must be considered as a necessary preparatory act.

The difference between the initial short step and a full step during normal ambulation is diagrammatically shown in Fig. 3. In the latter case the

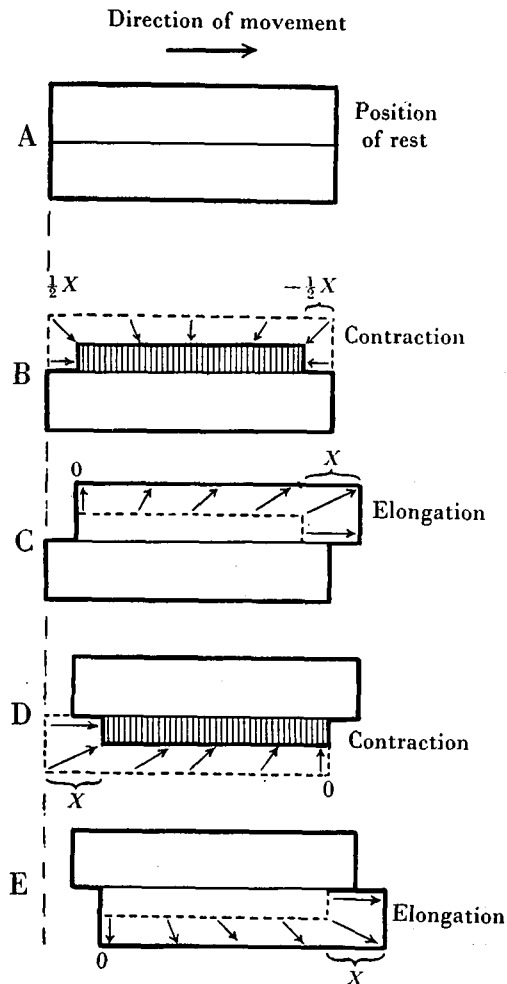


Fig. 3. Diagram showing the difference between the initial short step (A-C), and a step in normal ambulation (C-E) in *Pomatias elegans*.  $X$ =length of one step.

partially contracted anterior region, being out of contact with the ground, is pressed forward, overcoming (by the component  $ee_1$ ) any frictional resistance ( $d$ ) it may encounter with the substratum.

It will be noted that during this initial short step the mass of the half foot as a whole is not moved forward by energy derived from longitudinal muscular contraction. During this phase the posterior end moves forward, whilst the anterior end moves backwards, i.e. the foot merely shortens. The short step forward is executed exclusively through the force of extension acting against a

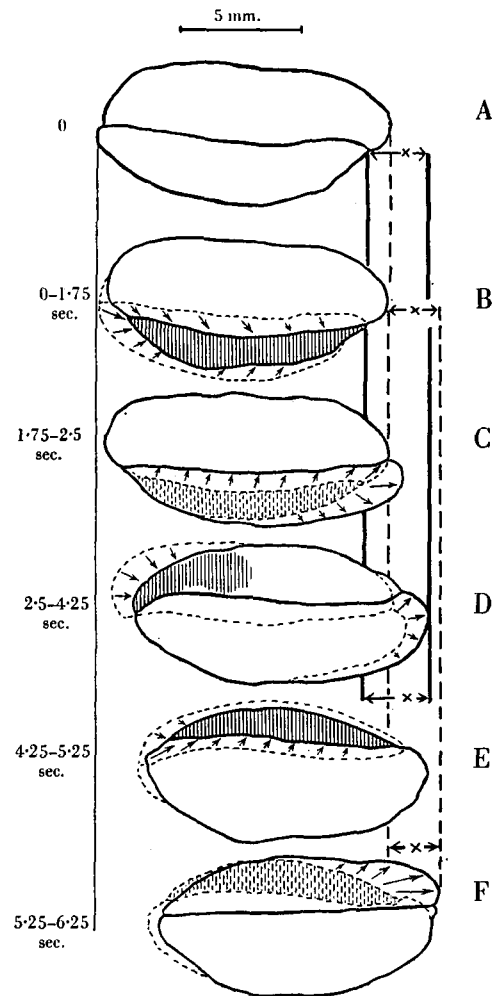


Fig. 4. Ambulation of *Pomatias elegans* (ventral aspect) as recorded by cinematography. The interrupted outline shows the immediately preceding position of the sole. The arrows indicate the direction of movement of the surface; any friction operates in the opposite direction. In D the final phase of elongation is shown anteriorly on the left half foot, and the beginning of the contraction phase on the posterior end of the right half, indicating that the waves of activity spread over the sole in a postero-anterior direction.  $X$ =length of one step.

contraction of longitudinal fibres moves the whole mass of the foot from a posterior position to the level of the stationary half foot, while the force of extension drives it an equal distance forward, as is shown in Fig. 4. Obviously so far as locomotion of this type is concerned, the end from which the

contraction spreads over the foot is of little consequence provided the stationary half foot is firmly fixed to the ground. Forward motion, however, can only be achieved when relaxation begins at the hind end.

The spread of the phase of contraction from the posterior end is probably more advantageous since it tends to relieve at an earlier moment any stress caused by the asymmetrical posture, and permits a larger anterior area of the foot to remain fixed to the ground while the posterior end is brought forward. It seems likely that the asymmetrical position of the two half feet involves stresses between them because the movement of the active half foot affects, to a small extent, the stationary half foot; e.g. the contraction of the active half foot protracts somewhat the posterior edge of the relaxed half foot (Fig. 4 B), while relaxation of an active half foot tends to move forward the anterior margin of the other half foot (Fig. 4 D). It also seems likely that the inactive half foot assists the active half foot in some phases of contraction and extension by enlarging the anterior (or posterior) area of fixation.

#### ANALYSIS OF FORCES IN *HELIX*

The sole of the snail (*Helix pomatia*) in locomotion has an average surface area of 15.75 cm.<sup>2</sup> and measures 7.5 cm. in length.\* It is divided transversely by eight to ten distinct phases of muscular activity, each of which is separated from the succeeding one by a stationary elongated region. Thus each zone of fixation is bordered anteriorly by an area undergoing extension, while behind it is an area of muscular contraction, and the whole pattern shifts continuously forward. So far as the state of the muscles is concerned any one of the functional units may be considered as comparable to the system described above for *Pomatias*; the simultaneous existence of more than one area of fixation however makes it illegitimate to consider the tensions and thrusts as being solely developed between an area of fixation and an area exerting sliding friction. In the snail, additional forces may be developed between adjacent fixed points. Displacement of a localized area between two fixed points can be effected in a number of ways by different combinations of forces (*ec* and *ee*); these possibilities are illustrated in Fig. 5. But as in all types of animal locomotion where at any one time some part of the body remains fixed to the ground, both the force of extension and the force of longitudinal contraction in the snail must necessarily contribute in equal measure to the distance of forward displacement of either the whole animal or some of its parts. The magnitude of the two forces, however, need not be the same, and will probably depend largely on the position of the point of frictional equilibrium, and the centre of gravity.

\* Corresponding values for *H. aspersa*: 4.1 cm.<sup>2</sup> and 5 cm. length.

If these assumptions and the picture given above for *Pomatias* are correct, and are applicable to the snail, it should be possible to demonstrate experimentally four and possibly five forces: (1) an external force leading to elongation; (2) an external force leading to longitudinal contraction; (3) sliding friction (drag), acting in a posterior direction and developed by regions of the foot which are in forward

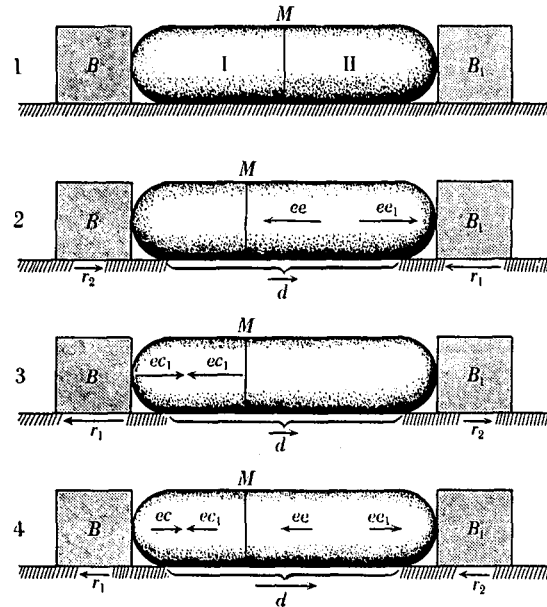


Fig. 5. Model illustrating three different modes of distribution of forces during an active forward displacement of a localized area, situated between an anterior and a posterior area of fixation (*B*, *B*<sub>1</sub>). (1) A rubber balloon consisting of two chambers (I, II) separated by a median wall (*M*) is attached to two blocks *B*, *B*<sub>1</sub> which rest firmly on the ground; no longitudinal forces are exerted. (2) If chamber II is inflated, it will elongate, thereby compressing chamber I, and developing a longitudinal thrust between *B* and *B*<sub>1</sub>. *M* will be displaced towards *B*. (3) If chamber I is deflated it will contract, thereby extending chamber II, and setting up a tension between *B* and *B*<sub>1</sub>. *M* will be displaced towards *B*. (4) If chamber I is deflated to the same degree and simultaneously as chamber II is inflated, a similar displacement will take place, and both areas of fixation will produce static reactions from the ground acting in the same direction; these two forces balance the friction resulting from the displacement.

motion; it is independent of the nature of the propulsive force; (4) a static reaction from the ground, acting in an anterior direction under the areas of fixation; (5) possibly static tensions and thrusts developed between successive areas of fixation.

**External forces.** An indication of the nature and magnitude of the forces existing at any one region of the pedal surface of a snail can be obtained by

parts of an apparatus previously described (Gray & Lissmann, 1938) which consists essentially of a fixed platform separated by a narrow gap from a movable bridge, the latter being mounted on knife-

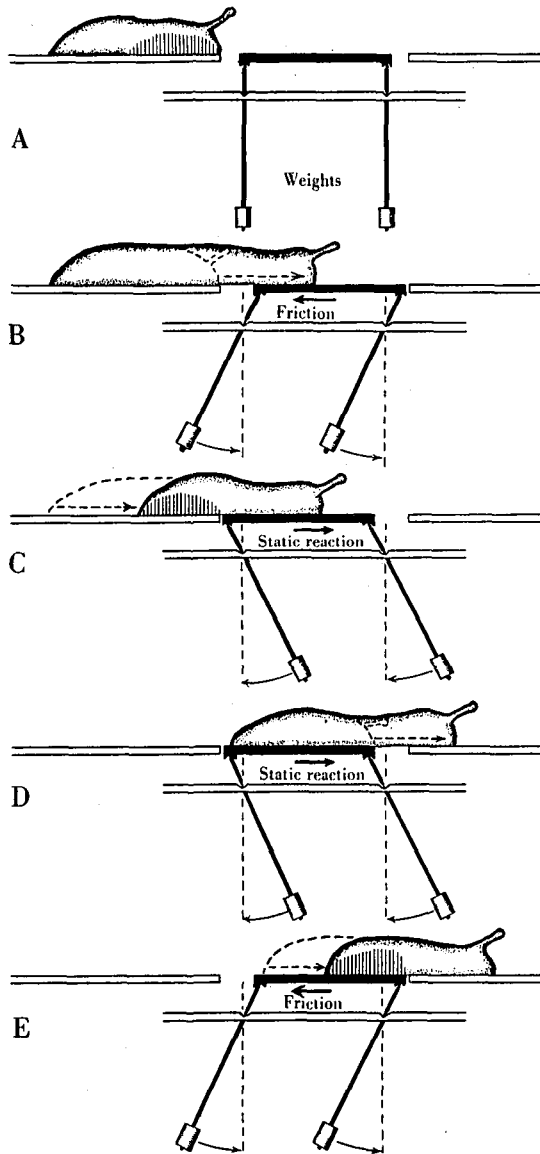


Fig. 6. Diagram illustrating the recording mechanism in some characteristic stages. The displacing force which is applied to the movable bridge reaches a position of equilibrium when the applied force is equal and opposite to the restoring couple of the weights which tend to return the bridge to the position shown in A.

edges in such a way as to record either tensions or thrusts acting between the platform and the bridge while the snail traverses the gap. It is obvious that only a force of extension can lead to a widening of the gap, and only a force of longitudinal contraction

can narrow the gap. This is illustrated diagrammatically for four characteristic stages of progression in Fig. 6, each of which corresponds to the changes indicated in Fig. 2 from position A to B, and from position D to E. Interpreted in terms of the foregoing analysis of movement of *Pomatias elegans* this means that when the snail moves from the fixed platform on to the bridge: (i) the gap widens (Fig. 6 B); this can only be due to a force of extension acting against a posterior surface of application; the force recorded represents sliding friction between the part of the animal which is thrust forward and in contact with the bridge; (ii) the gap narrows (Fig. 6 C); this is an indication of a force which leads to longitudinal shortening. The force thus recorded signifies that anteriorly the ground has to resist a backward displacement (static reaction) when the animal has established an anterior fixed point against which posteriorly situated parts are protracted. When the animal moves from the bridge on to the fixed platform: (iii) a static reaction from the ground under a posteriorly established point d'appui is recorded (Fig. 6 C); (iv) Fig. 6 E shows the recording of friction exerted by the posterior part of the body sliding forward.

These four stages show the maxima of tensions and thrusts. As the waves of muscular activity pass over the gap, the magnitude of the forces acting across the gap decreases, corresponding to the decrease of external resistance.

Additional forces developed as static reactions between successive fixed points in *Helix* can be revealed by the same method.

Typical illustrations of records made by the passage of snails (*Helix pomatia* and *H. aspersa*) are shown in Fig. 7. It will be noticed that the passage of the anterior end of the foot on to the bridge is accompanied by a forward thrust from the region of the foot still in contact with the fixed platform—the gap widens. Subsequent to this, however, the tracing rises above the base line and remains so not only while the rest of the animal is moving on to the bridge but also after the whole animal has passed over the gap, thus indicating a tension across the gap—which narrows. The existence of a residual tension after the whole animal is on the bridge is due to the presence of a film of mucus acting across the gap, and introduces a complication in the interpretation of the whole tracing. It is, however, clear that, after the initial thrust, and, as long as the central and posterior regions of the pedal surface pass over the gap, definite tensions are acting between the bridge and the platform. If it be assumed that the tension of the slime band remains constant throughout the whole tracing, this mucus tension must increase any apparent muscular tensions across the gap and must act in opposition to any thrust developed between the bridge and the platform. Therefore, for a true representation of external muscular forces the base line must be

adjusted by an amount equal to the mucus tension recorded after the passage of the animal (Fig. 7). The general conclusion to be drawn from tracings of this type is that the propulsion of the front end of the animal is effected by regions of the foot lying posterior to itself, whereas the hind end is being aided by a pull from regions lying more anteriorly. A continuous but fluctuating thrust acts between the anterior region and the central region, and a continuous tension is developed between the central region and the hind end. The longitudinal muscular contractions (dark waves) which occur throughout the whole length of the foot coincide with these fluctuations. Their effects are usually clearly superimposed on the thrust-tension curve, although they

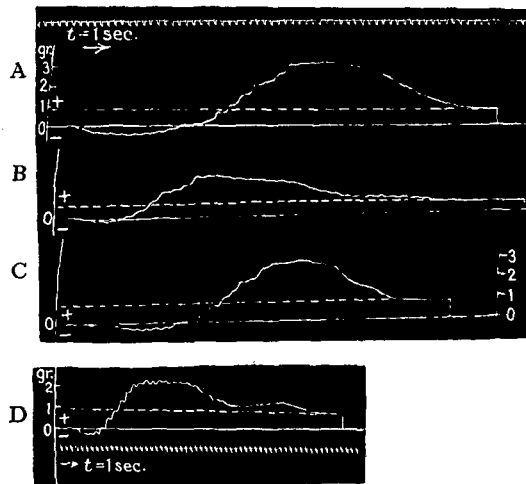


Fig. 7. Tracings showing direction and magnitude of the forces (—forward thrust; +tractive force) recorded by (A–C) *Helix pomatia*, (D) *H. aspersa* moving from a horizontal glass plate on to the recording bridge. Note that after the snail has moved over the gap an appreciable tension persists, which is caused by the mucus band deposited on the track; the interrupted line indicates the magnitude of the mucus tension at the posterior end of the animal. In *H. pomatia* tension and thrust amount to about 2.5 g., in *H. aspersa* about 1 g.

do not affect the direction of the resultant force. Consequently they appear isotonic anteriorly and isometric posteriorly. It follows that those parts of the anterior regions which glide forward are pushed from behind; this thrust not only compresses these parts which shorten isotonically, but also involves a static reaction by the preceding area of fixation (Fig. 5, 2). Similarly the tensions under the hind end not only overcome the frictional resistance of the forward gliding parts but also exert a tension between two succeeding fixed points (Fig. 5, 3). This conclusion is supported by the observation that the regions of the foot lying posteriorly may be in continuous forward motion, whereas the central and slightly more anterior regions exhibit occasionally a

backward slip. The exact proportion of these regions may possibly depend on whether the animal moves vertically or horizontally, and may, during horizontal movement, also depend on the position of the shell, which is not always constant. The relatively complex system thus recorded can best be illustrated by means of a model (Fig. 8). An inflated elastic balloon rests on the ground, adhering firmly by its central region; if then either the hind end (*BM*) contracts, or the front end (*AM*) relaxes, or if both these processes take place simultaneously, the whole surface of the balloon which is in contact with the ground will glide forward with the exception of the central, fixed area. Anteriorly a thrust will be developed, while posteriorly a tension exists between the area of fixation and the forward gliding parts. If

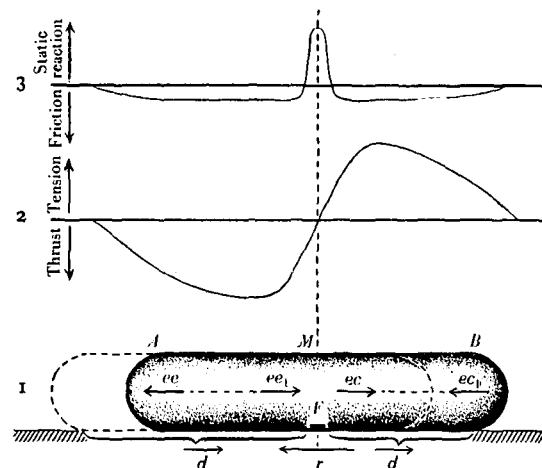


Fig. 8. Model illustrating the mechanical effects of the snail's foot. A rubber balloon rests on solid substrate with its central region firmly attached. If the posterior end (*BM*) contracts, or the anterior end (*AM*) relaxes, a movement will occur leading to the position indicated by the dotted outline. During this process the thrust-tension curve would be essentially similar to that recorded by the snail.  $F$  = area of fixation.

measured with the apparatus described above a thrust-tension curve can be expected similar to that shown in Fig. 8, 2; the curve crosses the base line through the area of fixation. The regions behind and in front of the area of fixation exert a sliding friction ( $d$ ) against the ground, while the ground resists a backward displacement with a static reaction ( $r$ ) under the area of fixation itself (Fig. 8, 3).

**Reactions from the ground.** The existence of static and dynamic reactions from the ground ( $r$  and  $d$ ), opposite in direction, can be demonstrated under the sole of a snail in locomotion. As in the model, the former are set up under regions of fixation, the latter under the parts in forward motion.

In both species of snail the areas of fixation on the sole (light transverse bands) are about 5–8 mm. wide. It is therefore possible to demonstrate the static



reaction under these regions by replacing the movable bridge by a glass strip 5–8 mm. wide; maximum backward displacement being obtained—as in the model—at the point where the thrust-tension graph crosses the base line. This was found to be the case for both species (Fig. 9).

When the snail moves over a movable glass strip of appropriate dimensions, mounted between two fixed platforms, and its anterior region has reached the second platform the strip is continuously pushed

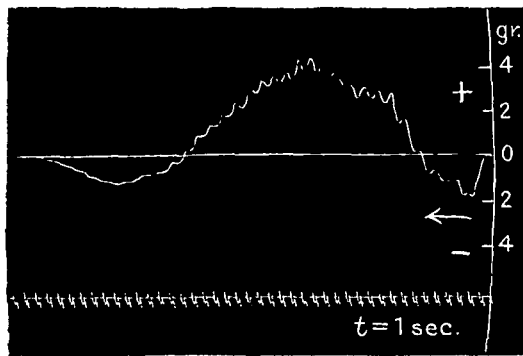


Fig. 9. Typical tracing showing the forces exerted by the foot of *Helix pomatia* on a recording glass strip 7 mm. wide. Note that the maximum force of backward displacement (static reaction +) acts in the central regions of the foot.

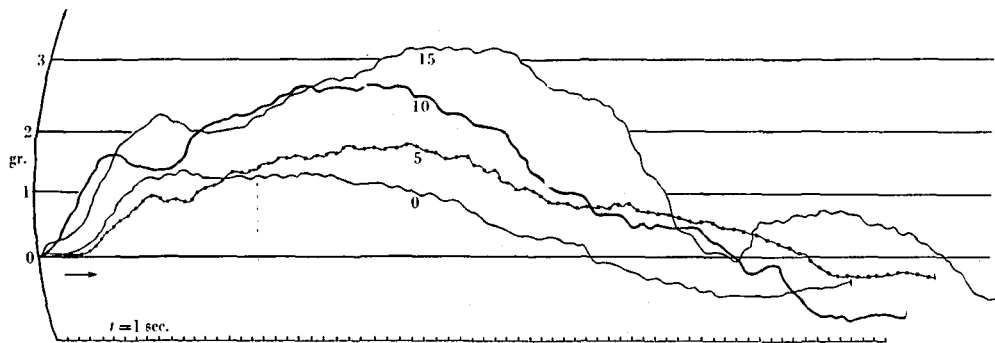


Fig. 10. Tracings showing the force with which a 5 mm. wide recording strip is pushed backwards under the central parts of the sole of *Helix pomatia* and the increase of this 'static reaction from the ground' by letting the animal lift a load while crossing the recording mechanism. The figures 0, 5, 10, 15 indicate the load in grams.

backwards; the force of displacement reaches its maximum when the central region of the foot is on the strip; thereafter the force gradually decreases. During the initial stages, when the snail moves on to the glass strip, the record does not differ markedly from the initial part of the tracing obtained in the bridge experiment, i.e. the strip is pushed forward. Similarly, the strip is pulled in the direction of the animal's motion when its posterior tip moves off the strip, with its anterior and central parts well on the second platform. However, after the animal has crossed the second gap, there is usually no sign of

a residual tension, owing to the formation of a mucus band connecting the glass strip on either side with a fixed platform, thus producing symmetrical tensions.

An indication of the accuracy of this experiment can be gained by demonstrating the dependence of the magnitude of the static reaction on the degree of external resistance which the animal has to overcome. This external resistance can be increased by a known amount by allowing the animal to move horizontally over the recording glass strip while at the same time it is made to lift a weight over a pulley attached by a string to its shell. Apart from the propulsive forces required to move the animal along, the forces must be increased in order to lift the weight against gravity. This additional force is applied through the areas of fixation and must increase the tangential static reaction from the ground. The greater the load, the greater the reaction (Fig. 10), and the increase of work done under different loads can be calculated from the area of the tracings; it agrees, to a surprising extent, with the theoretical requirements. However, the exact quantitative estimation of the external work which the unloaded animal has to do while creeping horizontally, is considerably complicated by mucus tensions and other factors; it will be referred to in a subsequent publication.

The absence in the central part of these tracings of any sign of the sliding friction (opposite in direction

to the static reaction) which can be clearly demonstrated by a similar experiment in the earthworm, may appear puzzling at first sight. But contrary to the conditions in the earthworm the areas fixed to the ground are, in the case of the snail, wider than the forward gliding parts. If the glass strip is 5–8 mm. wide, there will be no stage at which an area of fixation does not either occupy the whole width of the strip or when it does not connect the strip to one of the two fixed platforms. In the former case the strip is displaced backwards, in the latter it remains stationary.

The width of the forward gliding parts is normally 1.5–4 mm. If a movable glass strip of this width is mounted between the two fixed platforms, and its displacements recorded while a snail moves across it, the tracing is of an entirely different character as compared with those obtained with a wider strip: whenever a dark wave at any point along the foot

Bonse (1935). Snails were made to creep over a glass roller of 2 mm. diam. mounted between two glass plates, and the movements of the roller were recorded. The interpretation of these oscillations is, however, based on a number of misconceptions. Neither of the authors recorded the base line, but from the available data it seems legitimate to conclude that they too

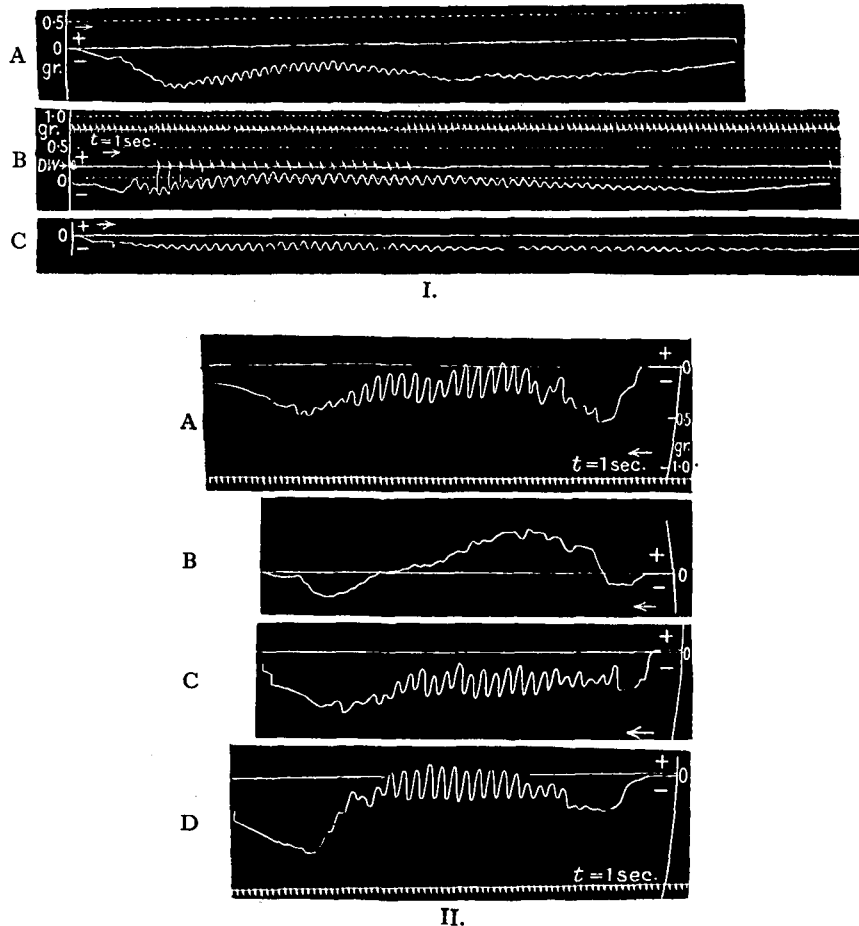


Fig. 11. Tracings obtained from two snails (I, II) crossing a narrow strip. As long as the recording strip over which the snails move is about 1.5–4 mm. wide it will be essentially displaced in the direction of the animals motion (—). The displacing force appears greatest during, or just prior to, the passage of the dark waves (regions of forward motion), and is therefore assumed to represent friction. I. Successive records from one specimen of *Helix pomatia* moving slowly across a recording strip (A) 1.9 mm.; (B) 3.2 mm.; (C) 1.9 mm. wide. Note that the whole tracing is beneath the base line in A and C. In B the passage of the dark waves over the recording strip was marked with a tapping key (DW). II. Another animal (moving fast) crossing a recording strip (A) 4 mm.; (B) 7.5 mm.; (C) 4 mm.; (D) 4 mm. wide. Note the appearance of a static reaction (+) in B.

traverses the strip, the latter is dragged in the direction of motion, returning after the passage of the wave more or less to the base line, but more often the whole tracing is beneath the base line (Fig. 11). It appears evident that these displacements are due to sliding friction. Similar experiments, designed to demonstrate the propulsive forces, have been carried out by ten Cate (1922) and repeated by

recorded the sliding friction of the forward gliding parts. Both authors noticed that the recorded deflections do not coincide exactly with the phases of the waves passing over the roller: the explanations offered are, however, in no way convincing. Moreover, the fact that the whole tracing is usually beneath the base line requires an explanation.

While the details of these recorded effects may be

is perfectly understood, the following considerations should be taken into account. The surface of a snail's foot alternately glides over the glass strip and then rests, etc. When a similar experiment is performed by towing an inactive body intermittently over the recording strip between two fixed platforms, the following points emerge: when the body is placed across the strip no horizontal force is recorded. As soon as it is being passively pulled, initially a large 'static friction' is recorded, i.e. a critical value of tension must be reached before the two surfaces (strip and body) begin to glide past each other. When this point has been passed a smaller 'sliding friction' will persist as long as the body is in motion. When the towing is interrupted, a force corresponding more or less to the sliding friction will still be indicated. In the next phase, when the body is pulled again, the 'static friction' will reappear. In this case, too, the whole tracing is beneath the base-line, and the fluctuations merely represent a difference between sliding and static frictions. The larger 'static friction' is recorded just before the body begins to move, not unlike the observations reported by ten Cate and Bonse. While this interpretation may appear plausible in case of passive towing, considerable complications must arise in the case of the snail owing to the visco-elastic properties of the mucus, the vertical displacements of the pedal surface, and the gradual spreading of regions of static and sliding friction on to the recording surface, both of which are preceded and followed by stationary regions exerting forces between them.

In considering the mechanical effects of the snail's foot on the substrate we may conclude from these two types of experiment that the sole is subdivided into narrow transverse regions each exerting friction against the ground, and each bordered in front and behind by wider stationary transverse areas which exert static reactions against the ground; these latter forces, however, vary in magnitude and direction under the various parts of the sole. The difference in width of the two functional regions makes it difficult to record the opposite effects of friction and static reaction in a single experiment. When the recording strip is sufficiently narrow it registers only the sliding friction exerted by the narrow, dark bands. When the width of the strip exceeds a minimum value the friction of the narrow dark bands is not recorded, because the strip is locked to both the fixed platforms by areas of the foot which are in the relaxed state.

By careful adjustment of the width of the recording strip (usually 2.8–5 mm.) it is possible to obtain an intermediate condition under which both sliding friction and static reaction can be recorded. Under such conditions small oscillations appear on the tracing above and below the base line; backward displacement of the strip occurs during the passage of light, relaxed bands. This is particularly obvious when records are made from regions halfway along

the foot (Fig. 11, I, B). When the anterior end of the animal passes over the recording strip the records show an alternation between sliding friction and forward thrusts, whilst records from the hind end of the animal indicate sliding friction and static tension.

In all cases the static and dynamic ground reactions as shown in the records must be corrected for the disturbance due to mucus tension acting between the fixed platforms and the recording strip.

## DISCUSSION

As the longitudinal contractions on the sole of the snail are the most conspicuous phenomena during locomotion, it is tempting to suggest that these contractions, as they move anteriorly, squeeze the body fluid in that direction, thereby producing a high internal pressure in the anterior region. Such high pressure would tend to elongate the anterior regions. As long as these regions adhere to the ground, the force of extension will merely produce a longitudinal thrust and a corresponding static reaction from the ground. However, when the longitudinal contractions pass forward and thus involve detachment of localized regions in the anterior half, the latter elongate and are displaced forward. The building up of a pressure gradient against internal resistance may be achieved gradually, because when the snail begins to move, the first waves appear at the anterior end and the pattern spreads in a posterior direction over the foot. The protraction of the posterior half of the foot through the longitudinal muscular contractions offers no difficulty. The elongation of longitudinally contracted fibres is apparently being aided in this part of the foot by the preceding contraction phase, acting partly against friction and partly against a posterior fixed point. The conditions as pictured here for the anterior and the posterior end of the animal are only possible, if at the same time an effective fixation to the ground of the central region is established. This presents no difficulty as long as the central region is occupied by an area of relaxation. When this area is being detached, it can be imagined that it is being propelled forward between the two adjacent areas of fixation in the manner diagrammatically represented in Fig. 5, 4, while the anterior and posterior regions correspond to Fig. 5, 2 and 5, 3 respectively. These suggestions concerning the internal mechanism, however, can only be regarded as tentative, and will require further consideration.

There does not appear to exist any fundamental difficulty in imitating by means of a model the kinematic and kinetic effects of the external mechanism as observed on the sole of the snail. The musculature of the foot may be represented by a series of inflated rubber balloons attached to each other. The mechanical effect of longitudinal contraction can be achieved by deflation, and extension by inflation of

the balloon. An inflated balloon will rest firmly, with a large surface on the ground; while a deflated balloon, when situated between two inflated ones, will be lifted off the ground.

The displacement of the whole chain of balloons under the influence of successive deflation, followed by inflation of the individual balloons, spreading in postero-anterior direction over the whole series is shown in Fig. 12. To reproduce the kinetic effects of the snail's foot it would be necessary for posterior deflation in one balloon to precede slightly the

will remain the same throughout, and independent of whether the forward motion is effected by push or by pull.

It is essential in animals like the earthworm or the snail, which creep over a solid substrate through locomotory waves of a peristaltic nature, that the regions of fixation to the ground should undergo the least possible deformations so as to ensure a good hold. If the changes of contraction and elongation are smooth and of a sinusoidal character, the turning points of muscular activity are more

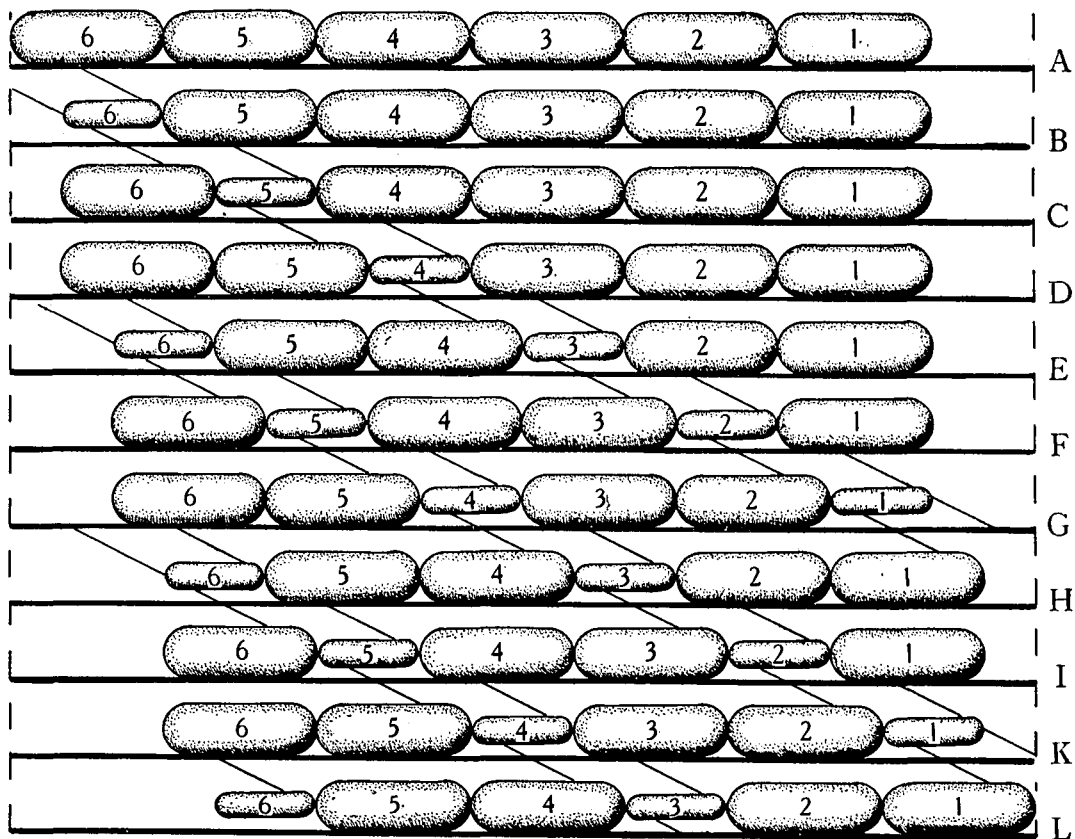


Fig. 12. Model illustrating the mechanism of locomotion in the snail. Beginning from the posterior end the balloons are successively deflated and re-inflated as shown in the figure. Deflation corresponds to longitudinal contraction, inflation to elongation. The oblique lines indicate the passage of waves of activity.

inflation of the one behind, e.g. the change from position C to position D should be made so that the process of deflating balloon 4 is somewhat in advance of the inflation of balloon 5. Thereby a tension will be set up between balloons 3 and 6. If, on the other hand, in the change from position E to F, inflation of balloon 3 precedes deflation of 2, a longitudinal thrust will exist between balloons 4 and 1. Under these conditions the maximal static reaction from the ground must be expected under the inflated balloon nearest the central point of the chain, while sliding friction under two adjacent active balloons

suitable than any other to be used as anchors, i.e. fixation should be effected either (i) during the state of maximal longitudinal contraction, or (ii) during the state of maximal elongation. Both types of fixation involve some fundamental differences in the whole locomotory mechanism. The former is realized in the earthworm, the latter in the snail. If fixation is achieved through adhesion, its effectiveness will depend on a large and smooth surface area, and the elongated regions are more profitably used; this type of locomotion is suited for movement over smooth surfaces. It is imperative in this type of

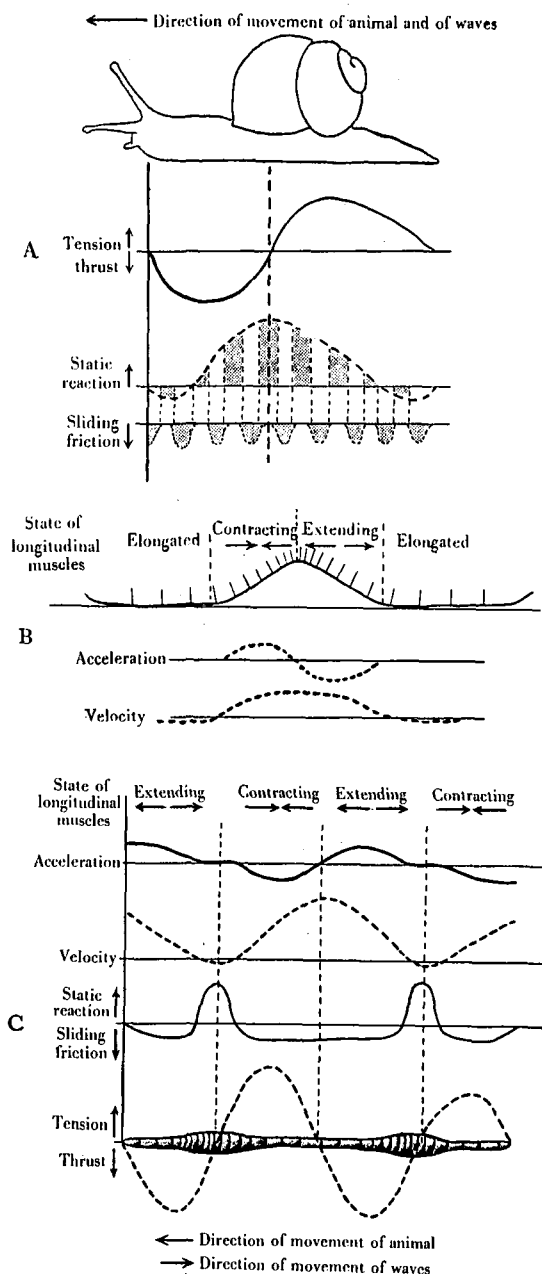


Fig. 13. Diagrammatic summary of kinematic and kinetic effects as observed on the sole of the snail in comparison with the earthworm. A. Kinetic effects of the foot as a whole; B. Kinematics of an individual locomotory wave; C. The same in the earthworm.

locomotion that acceleration of the sole should coincide with the phase of longitudinal contraction, as a result of which the locomotory waves must travel in postero-anterior direction.

In the earthworm, on the other hand, fixation through setae is restricted to the longitudinally

contracted segments, and acceleration of the segments coincides with the phase of elongation, i.e. the locomotory waves move posteriorly. These differences are graphically summarized in Fig. 13 which also shows that, while in the earthworm each individual locomotory wave can be considered as an independent mechanical unit, this is not the case with the snail, because so far as the reactions from the ground are concerned, the anterior and the posterior regions represent liabilities for the central region. This may possibly bring about a more diffuse distribution of the adhering surface.

The profound bearings which such differences in the kinetics of movement must have with regard to the whole reflex life of different animals will be discussed elsewhere, but it may be indicated that if a snail encounters an exceptional resistance during progression, it will have to increase its hold on the ground, and it can do so only by relaxing longitudinal fibres on the sole, whereas the earthworm, to achieve a similar effect, must respond by longitudinal contraction. Moreover, the problem of proprioceptive control or regulation of so uniform a locomotory pattern as exhibited in the snail is of special interest, as the mechanical conditions under the anterior and the posterior regions of the foot appear reversed. Whether one is to infer from this that local reflexes operate differently at the two extremities of the snail's foot, or whether any proprioceptive activity on the pedal surface is dependent on the deformation of the muscles rather than the development of tension, only future work can decide.

## SUMMARY

1. An attempt has been made to analyse the kinetic effects as observed on the sole of a gastropod in locomotion, and to illustrate these effects by analogy with mechanical models.

2. The internal mechanism involves during locomotion an internal force of longitudinal contraction, and an internal force of extension: the former is considered to be represented by the contracting longitudinal muscles, the latter is probably produced by hydrostatic pressure.

The external forces acting on the animal at any one moment represent the balance of the two antagonistic internal forces.

3. During normal ambulation in *Pomatias elegans* the posterior margin of the foot is exclusively protracted by the longitudinal contraction of the musculature of the foot; the anterior margin is propelled forward exclusively by the force of extension.

4. There is no evidence in favour of an antagonism of longitudinal and transverse fibres in *Pomatias elegans*; both sets of muscles appear to contract and relax synchronously in one half of the foot and to act antagonistically with both sets of muscles in the other half.

5. The external forces in *Pomatias* are set up between one area of fixation and an area of dynamic friction.

6. An experimental analysis of the snail showed the existence of an external force of extension (longitudinal thrust) acting between the anterior and the central region of the sole. A similar force of longitudinal contraction (tension) acts between the central and the posterior end. Both forces are of the order of 2.5 g. in *Helix pomatia*, and about 1 g. in *H. aspersa*.

7. A static reaction from the ground has been demonstrated to exist under the relaxed parts of the sole. This force reaches a maximum at a point near the central region of the foot.

8. Dynamic friction has been recorded under the forward gliding zones of contraction.

9. Static thrusts are developed between successive areas of fixation in the anterior region, while similar tensions can be observed posteriorly.

10. The foot of the snail as a whole must be considered as a mechanical unit; the individual locomotory waves do not represent mechanically balanced systems.

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