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THE MECHANISM OF LOCOMOTION IN GASTROPODS

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INTRODUCTION

The snail's foot in locomotion is so striking and so easily observed that it has excited the interest of naturalists for a long time and yet a complete solution of even the mechanical problems connected with its action seems not to have been attained. Within recent times a number of investigators have attacked the problem of locomotion in snails, but their efforts have been directed chiefly toward the elucidation of the action of the neuromuscular mechanism rather than toward an understanding of the external mechanical conditions that accompany locomotion. It is the object of this paper to consider, in the light of the more recent investigations and from the standpoint of renewed observation, the external mechanical factors involved in the movements of the gastropod foot.

The observations recorded in this paper were made partly at the Bermuda Biological Laboratory, at the Harvard Zoölogical Laboratory, and at the Biological Laboratory of the United States Bureau of Fisheries at Woods Hole. I am under obligations to the directors of the laboratories mentioned for the materials and opportunities for carrying on these studies.

TYPES OF MOVEMENT

When the locomotor movements of the foot in many species of gastropods are compared, a surprising diversity is found. These different types of movement have been well classified by Vlès

('07) and are apparently characteristic not only for species but for larger groups of gastropods. In the majority of species thus far examined, the pedal waves course forward over the foot, thus agreeing in direction with the animal's locomotion. Vlès has appropriately designated this type of movement as the *direct* type and has given the following gastropods as examples; the pulmonates (including Onchidium), Aplysia, Aeolis, Doris, Haliotis, Trochus, Cyclostoma, and certain small species of Littorina. I can confirm this statement for such of these molluscs as I have examined, namely, many pulmonates, including Onchidium, and I can add to this list Crepidula fornicata. In other gastropods the waves pass over the foot from anterior to posterior and this type has been designated by Vlés as *retrograde.* As examples he has given Acanthochites fascicularis, Littorina littorea, and L. rudis. Besides confirming Vlès' observation on Littorina littorea, I can add to this list Dolabrifera virens Verrill, Tectarius nodulosus Gmel., Nerita tessellata Gmel., and Chiton tuberculatus Linn. According to the observations of Jordan ('01, p. 99) Aplysia belongs under this head and not under that of the direct type as given by Vlès.

In both chief types of movement several subtypes can be distinguished as determined by the lateral extent of the pedal waves. In some gastropods each wave extends over the functional width of the foot and thus the foot is occupied by only a single series of waves. This subtype has been termed by Vlès *monotaxic,* and is exemplified by the pulmonates and chitons. In addition to these gastropods, Dolabrifera virens also has a monotaxic wave. In other gastropods the foot is functionally or even structurally divided along the median plane and exhibits a double system of waves, one right and the other left. This subtype has been designated *ditaxic* by Vlès and is exemplified by Haliotis, Trochus, and Cyclostoma among the direct types, and by Littorina littorea among the retrograde types. Besides confirming Vlès' statement as to Littorina littorea, I can add Tectarius nodulosus and Nerita tessellata as ditaxic gastropods. In Tectarius the waves on the two sides of the foot usually alternate and they are so extensive that never more than two waves can be seen on one side of the foot at once. The foot, therefore, moves forward in alternate steps, first on the right side and then on the left, the motion resembling that of a person in a sack walk. In Nerita the wave begins anteriorly as a single wave whereupon it breaks and passes down the right and left sides of the foot to unite as one wave again at the posterior margin. These two conditions of *alternate* waves, as in Tectarius, and *opposite* waves, as in Nerita. will probably be found exemplified in other ditaxic gastropods. In certain small species of Littorina with direct movements, Vlès has described four parallel sets of waves, fulfilling the requirements of a tetrataxic subtype. This occurs, according to Vlès, only in connection with the retrograde type of movement. I have seen no example of it.

Among those snails that I have examined, one species, Ilyanassa obsoleta (Say), seems to find no place in Vlès' classification. This snail is a vigorous, active creeper. Its foot covers a large area compared with the size of its body. Anteriorly the foot is truncated and auriculate; posteriorly it is bluntly rounded. Its ventral surface is whitish, flecked over with irregular grayish splotches. In resting, the snail uses chiefly the posterior part of the foot, the anterior part being sometimes more or less withdrawn into the shell. In locomotion the anterior part seems to be the more active. Notwithstanding the fact that this snail is very easily observed in active creeping and that its foot is marked in a most favorable way for exhibiting wave-like movements, I have never been able to discover any evidence of such movements. When in locomotion, the whole foot seems to glide at a uniform rate over the surface of attachment such as that of a glass plate. Only along the anterior edge and over a small portion of the anterior ventral surface of the foot, can slight variations in the rate of movement be discovered and these variations are so local and scattered that they can in no sense be regarded as forming a wave. The movement of the foot of Ilyanassa has a most striking resemblance to that of the foot of a planarian in which cilia may be the chief motor organs, but on testing the foot of Ilyanassa with carmine suspended in seawater, not the least evidence of cilia could be discovered. I therefore believe that Ilyanassa moves by a form of muscular activity that does not appear as pedal waves and it is not improbable that other gastropods will be found that have the same peculiarity. That Vlès recognized something of this kind may be inferred from his statement that no changes in color can be seen in the creeping foot of Nassa, Buccinum, Aeolis, etc., and that the direction of the waves in these instances can be judged only by the deformations produced at the edge of the foot. As Vlès makes no further mention of Nassa in his subsequent account, I suspect that it is more or less like Ilyanassa and is capable of little or no pedal-wave movement. The locomotion of such gastropods I should designate as due to *arhythmic* pedal movements as contrasted with *rhythmic* pedal movements, such as have been fully classified by Vlès.

It is a significant fact that all gastropods, irrespective of their type of movement (direct or retrograde), are restricted to forward locomotion. None, so far as I am aware, can reverse and move backward as, for instance, an earthworm can. Whatever differences these various types of pedal movements possess, they still lead to but one result, the forward locomotion of the snail.

THE GASTROPOD FOOT AS A HOLDFAST

The snail's foot subserves the double function of attachment and locomotion. As means of attachment snails secrete a bed of mucus, and use the foot as a sucker. Both methods are commonly employed by the same species, but in a given form one method is usually developed much in excess of the other. For instance, in Helix pomatia, Limax maximus, and other allied species, the moist surface of the expanded foot will stick with some tenacity to glass. But if such an animal be allowed to creep its length over a glass surface and thus spread a bed of mucus on which it can rest, it will be found to have multiplied the strength of its attachment many times. The mucus adheres to the glass and the surface of the foot to the mucus very much more power-fully than the foot alone can adhere to the glass. That this attachment is due chiefly to the adhesive properties of the mucus and not to the sucking action of the foot, is seen from the fact that the attachment can be completely accomplished over a minute hole in a plate of glass. When a snail in such a position is seized and drawn off, air is sucked in through the hole in the glass as the middle of the foot rises, showing that under these extreme circumstances, the foot does act as a sucker, but in the ordinary resting state of the snail no such suction is exerted. All snails with which I am acquainted deposit more or less mucus and though this is sometimes so small in amount that it can be demonstrated only by means of powdered carmine, it serves, I believe, in so far as it is present, as a means of attachment. This production of mucus is highly developed in the pulmonates. Its relation to creeping on the surface-film of water, as exhibited by many fresh-water snails, has long been recognized.

In some snails the foot serves as an organ of attachment chiefly through its power of suction. The general surface of the foot is applied closely to the substrate after which the central portion is lifted thus converting the foot into a sucker. This kind of attachment is well exemplified in Patella, Crepidula, etc. Crepidula fornicata can be made to creep over a surface of glass and can move with ease and security over a minute hole in the glass. If, however, the snail is disturbed by being touched several times when its foot is over the hole, it will actually dislodge itself by endeavoring to suck firmly to the glass, for in so doing it will fill to repletion the forming concavity on the underside of its foot by sucking water through the underlying hole. When one contrasts the difficulty with which Crepidula is dislodged from its natural surface of attachment, particularly after it has been induced to exert full suction, with the ease with which it can be made to dislodge itself when over a small hole, the magnitude of its power of suction becomes apparent. The action of the foot of Aplysia as a suction apparatus has already been demonstrated by Jordan ('01). These two methods of attachment, suction, and adhesion through mucus are the chief means by which snails hold to the surfaces on which they creep.

THE GASTROPOD FOOT AS A LOCOMOTOR ORGAN

Locomotion by the gastropod foot, is not dependent upon ciliary action but is a muscular operation as shown by Dubois and Vlès ('07). The precise way in which the movements of locomotion are accomplished can best be made out by examining good examples of direct and retrograde movement. The first is well exemplified in Helix pomatia and Limax maximus; the second in Chiton tuberculatus and Dolabrifera virens.

In an expanded and actively creeping Helix pomatia, the foot may measure as much as seven to eight centimeters in length by two and a half in width. Over this a succession of transverse, dark-brownish waves run from posterior to anterior. At any instant there may be as many as ten or a dozen such waves on the foot. Each wave is separated from its neighbor by a space equal to about three-times its own thickness. The waves travel over the foot in about thirty seconds, or at a rate of a centimeter in seven to eight seconds. These records, taken from a normal individual, agree fairly well with those given by Bohn ('02) and by Biedermann ('05).

As the snail creeps, it spreads from the mucous gland at the anterior edge of its foot a broad path of slime over which it makes its way. An active snail marks its course in this manner by a long track of slime. A somewhat exhausted snail, when placed upon an appropriate substrate, will almost always creep far enough to lay a mucous path that will subtend the whole of its foot, after which it will cease creeping. If it is removed to another position, it will usually repeat this operation, but it will seldom creep farther. This habit is doubtless connected with the effectual attachment of its foot to the substrate.

Locomotion in Helix, like that in other pulmonates (Künkel, '03), is apparently inseparable from the wave movement of its foot. When a snail is placed upon a glass plate preparatory to creeping, it lengthens and expands its foot; almost immediately thereafter pedal waves appear and the animal begins to move forward. Such a snail will creep over a perforation in a glass plate without sucking air through the perforation, thus demonstrating that its attachment in locomotion, as in rest, is due to adhesion and not to suction. In fact in a creeping Helix the foot not only does not suck but actually presses on the substrate. If, as the snail creeps, a bubble of air is introduced under it by a capillary tube or other means, this air will usually escape at the edge of the foot in such a way as to show that it was under considerable pressure. The action of such bubbles demonstrates that the foot as a whole is firmly attached to the mucous substrate, in fact presses against it. Locomotion in Helix pomatia, then, has to overcome under ordinary circumstances only the adhesion of the foot and this is accomplished apparently by the pedal waves. In snails in which the attachment is due to suction as well as to adhesion, locomotion requires that both attractive forces shall have been overcome, but, as suction is muscular, it seems likely that this would be relaxed somewhat, as seems to be the case in Crepidula, before locomotion begins.

How the pedal waves accomplish locomotion is still a disputed question. According to von Uexküll ('09, p. 181), who has followed Jordan ('01) and Biedermann ('05) in many particulars, each pedal wave is formed by the contraction of the longitudinal muscles of the foot and takes the form of a slight swelling on the underside of the organ. Such a wave, as von Uexküll rightly remarks, would effect nothing by way of locomotion unless some portion of the foot were fixed. Von Uexküll ('09, p. 187) believes that the foot is provided with some such mechanical device as the setae of the earthworm, which, resist backward movement while they allow forward motion and that, therefore, the region in front of each wave may be regarded as a fixed region. Hence the contraction waves would always draw that portion of the foot where they temporarily were forward over the substrate toward the fixed point in front and as a result forward locomotion would be accomplished.

Although this explanation is free from mechanical objections, it is doubtful whether it really applies to the case in hand. Von Uexküll has maintained in support of this view, that a snail can be slipped over a glass plate more easily forward than backward, just as an earthworm can be drawn over an appropriate surface more easily headward than tailward. I must confess that I have not been able to convince myself that there is any difference in this respect in Helix pomatia or Limax maximus; both seem to slip over the glass forward and backward with equal ease.

Moreover, the view advanced by von Uexküll is based upon what I believe to be a somewhat erroneous conception of the pedal wave. Biedermann ('05, p. 11) pointed out that the foot of Helix pomatia has great advantages over that of many other gastropods for studies of this kind because of the numerous small specks contained in its outer layer. These specks can be discerned clearly by means of a hand lens and they give a true picture of the movements of the foot. As watched through a plate of glass over which the animal is creeping, they can be seen, as Biedermann has described, to move momentarily forward, then come to rest, and then again to move forward. This is best demonstrated on a sheet of glass on which there are numerous scratches. Such scratches serve as landmarks and by them it can be seen that the minute specks in the foot do remain essentially fixed in position and then momentarily move forward to assume again for a brief period a position of rest. When this motion is examined in relation to the foot as a whole, it is evident that the forward motion takes place in the dark waves and that quiescence is characteristic of the intermediate lighter portions of the foot. Each wave, then, is a pulse of forward motion and the rest of the foot is momentarily quiescent. The area covered by the waves is probably a fourth or a fifth of the total area of the foot. At any moment, therefore, about three-fourths to four-fifths of the surface of the foot is stationary and about one-fourth to one-fifth is moving forward. In other words the snail stands on the greater part of its foot while it moves forward with a much lesser part.

Essentially the same conditions as have been described for Helix pomatia can be demonstrated in Limax maximus. If particles of carmine be driven into the substance of the median, active band of the foot of this slug, they can be seen to exhibit exactly the same type of movement as has been described for the specks in the foot of Helix. In Limax the waves, however, are light in color, instead of being dark as in Helix, and their surfaces, .as seen in the air, are marked with fine wrinkles transverse to the longitudinal axis of the animal. These wrinkles show that the waves are regions of longidudinal contraction, as has been maintained by most recent writers on this subject.

The chief error in most previous accounts of the locomotion of the gastropod foot is found in the physical configuration ascribed to the underside of this organ. Biedermann ('05, pp. 10, 17) states that the waves are convexities on the surface of the foot and that they press more firmly against the substrate than does the rest of the foot. This view was adopted by von Uexküll ('09, p. 187) in his discussion of gastropod locomotion. In Helix pomatia it is by no means easy to determine whether the waves are convexities or not, for the reason that they are at most only very slightly different in level from the general surface of the foot. On inspecting by reflected light the free ventral surface of a part of a Helix foot over which waves were running, I was unable to tell with certainty whether the surfaces of the waves were convex, concave, or flat. If, however, the creeping foot be closely studied through glass, evidence of a conclusive kind can be found. If, under these circumstances, a very minute air bubble entangled in the mucus under the snail is watched, it will be seen to change its form and position slightly as each wave passes over it. As the wave approaches it, it will elongate slightly on its face next the wave and at times move a little towards the wave, and as the wave leaves it, it will elongate slightly in the opposite direction and at times follow slightly the retreating wave. The motions of the bubble are exactly those that should be expected provided the wave exerted a slight suction in its passage and the reverse of what would occur supposing the wave pressed upon the bubble. The evidence, though slight, is clear and I, therefore, believe that each wave on the underside of the foot of Helix pomatia is a slight concavity.

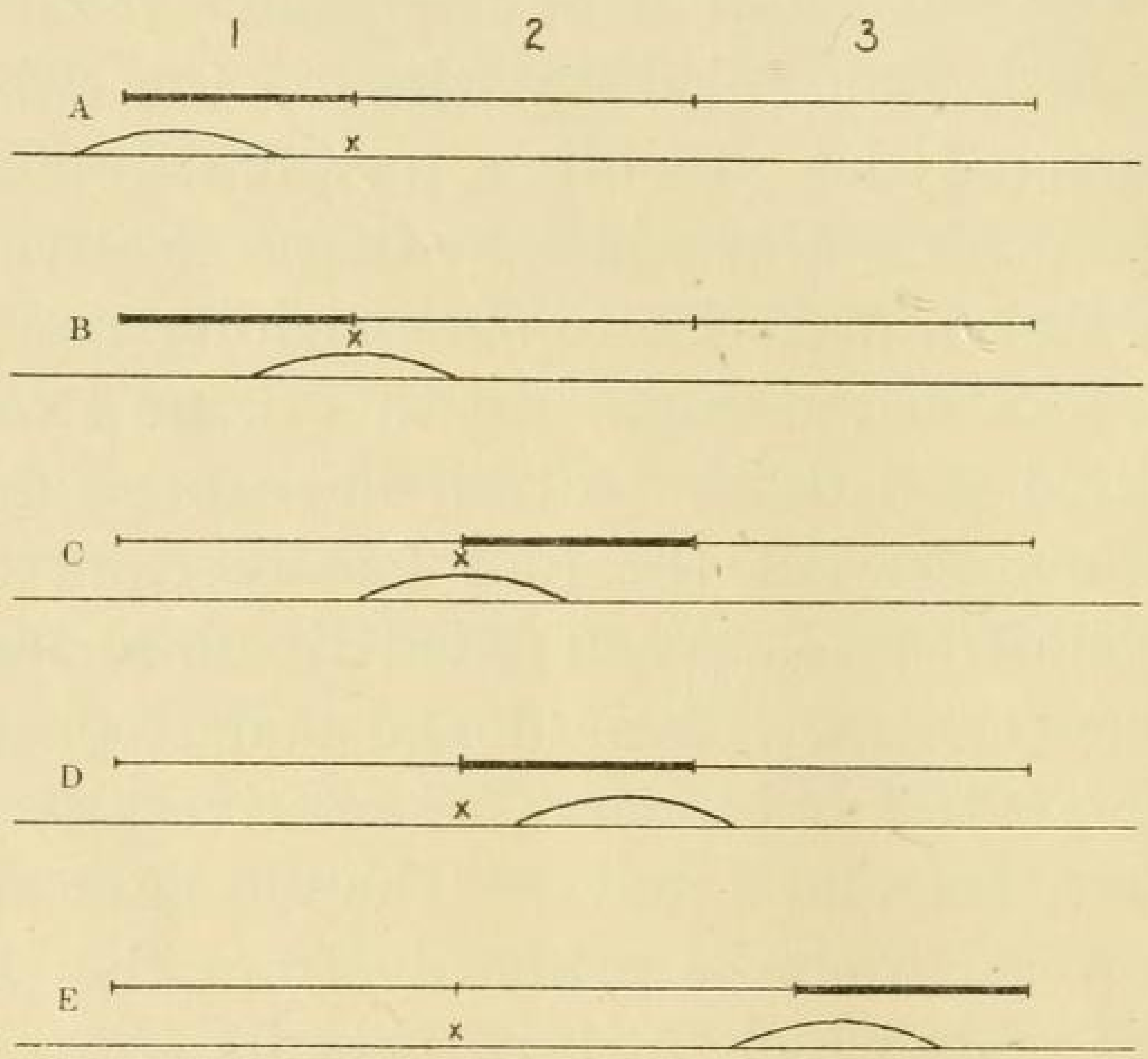
Although the configuration of the surface of the wave in Helix pomatia could be determined only indirectly, in Limax maximus it can be seen with distinctness. If the anterior part of the foot of this slug be applied to a glass surface, the pedal waves appear quickly over the whole foot. On inspecting the portion of the foot not yet in contact with the glass, the waves can be identified as dark bands alternating with light areas. On examining from the side the portion of the foot not yet in contact with the glass, it can be clearly seen that the waves are concavities in the foot as compared with the areas between the waves. I am, therefore, entirely convinced that, contrary to the opinion expressed by Biedermann and others, the pedal waves of the gastropods are concavities and not convexities on the foot. In these concavities, which are probably filled with the more fluid portion of the mucus, the foot moves forward, the rest of this organ being temporarily at a standstill.

The mechanical advantage of this arrangement must be obvious. The snail is attached to the substrate chiefly by adhesion to the denser mucus. This attractive force is overcome by drawing certain parts of the foot, the region of the waves, away from the substrate. These parts are then in a position to move with reduced resistance and are momentarily shifted forward while the snail supports itself on the rest of its foot. As this release from adhesion is propagated as a wave over the whole of the foot, this whole organ, together with the rest of the snail, is eventually moved forward. At first thought it might seem that such a wave movement could not produce so uniform a motion as snails show, but it must be remembered that the uniformity of this movement is seen only in parts of the animal some distance from the foot. On the foot itself the operation is alternate movement and rest, which becomes more and more continuous motion as points on the body more and more distant from the foot are reached. The locomotion is in many fundamental respects like that of the human being. In our locomotion each foot is alternately at rest and in motion and yet distant parts of our body, like the head, show a motion which in comparison with that of our feet is almost continuously uniform. In fact, a ditaxic gastropod with alternate, direct, single waves on the foot would almost exactly reproduce the method of locomotion found in the human being.

Tectarius, as already noted, practically fulfills these conditions except that its waves are retrograde. This general theory of the mechanics of gastropod locomotion is an elaboration of the views already set forth by Jordan ('01).

It is not my purpose in this paper to enter into an account of the musculature by which the movements already described are carried out, for I have made no observations on this part of the subject. It is, however, pertinent to show that the elements of motion implied in the preceding description are not inconsistent with the general structure of the snail's foot. The work of Jordan ('01), Biedermann ('05), and others shows conclusively, I believe, that the musculature of the snail's foot works against the elastic-walled, fluid-filled cavities of the animal's interior and that these cavities are often temporarily closed from one another. It is these spaces which, acting collectively as a vacuolated, erectile tissue, give rise to such rigidity as is possessed by the expanded foot of the snail. In this tissue two sets of muscles, longitudinal and dorso-ventral, have been identified. The dorso-ventral muscles lift the foot locally from the substrate. They are imbedded in the vacuolated tissue already mentioned and when they contract, their dorsal ends, being more firmly set than their ventral ones, serve as relatively fixed points and the ventral ones, therefore, move. The mechanical support that these muscles receive comes primarily from the tissue adjacent to their dorsal ends which in turn gets its support from other tissues reaching to the parts of the foot fixed on the substrate in front and behind the region of elevation. The action of the ventral end lifts the foot locally and overcomes adhesion in the given region. When the muscle relaxes, the portion of the foot that was elevated is returned to its former level chiefly by the elastic action of the vacuolated tissue and the muscle recovers its original length and position. This action of the dorso-ventral muscles takes place in sequence from behind forward and thus a concave wave runs on the surface of the foot from tail to head.

The second element in the pedal wave is the forward movement of that portion of the foot which is temporarily lifted from the substrate. This must be accomplished by the contraction of the longitudinal muscles and can be best pictured by reference to the accompanying diagrams. These diagrams represent steps in the passage of a concave wave over the foot of a snail from an anterior position to a posterior one (left to right in the diagram) whereby the point x is temporarily released from full adhesion to the mucous surface, moved forward, and brought to full adhesion again. The point x is supposed to be associated with a particular longitudinal muscle fiber, number 2, through whose action it is moved. In *A*, this fiber is shown in its relaxed condition with the wave approaching. In *B*, the wave has released the point x from full



adhesion. In *C*, fiber 2 has contracted and since the posterior end of it is over a released part of the foot and the anterior end over a fixed part, the posterior end with the underlying point x has been moved anteriorly. In *D*, the fiber remains contracted and the point x has come again to adhere to the substrate. In *E*, the wave has reached the next longitudinal fibre anterior, number 3,which has contracted and drawn out the relaxing fiber, number 2, to its original length and position in reference to point x. The contraction of each longitudinal fibre then serves two purposes: it moves the foot forward as the releasing wave passes over the region and it extends the relaxing posterior fiber. In this way each point on the foot is lifted, moved forward, and set down again and thus the foot, and with it the animal as a whole moves forward. From this theoretic consideration, it is evident that the theory of pedal-wave action advanced in the preceding paragraphs is entirely consistent with such an arrangement of muscles as has long been known to occur in the gastropod foot.

Vlès ('07) has called attention to the fact that the majority of theories as to the locomotor action of the gastropod foot apply only to the direct type of movement and do not take into account the retrograde type. The theory put forward in this paper is believed to apply equally well to both types. Among retrograde gastropods, Chiton tuberculatus is an excellent example. This mollusc uses its foot as a sucker, but nevertheless can creep with considerable rapidity. It exhibits, as a rule, not more than two waves on the foot at a time; these course posteriorly at the rate of about a centimeter in five seconds. In a Chiton creeping over a glass plate, the wave when viewed from the side can be seen to be an area lifted well off the substrate. This feature is much more conspicuous in Chiton than in any other mollusc that I have examined. As in the pulmonates, the surface of the Chiton foot in direct contact with the substrate is motionless; that in the wave area moves forward. At any moment about one quarter of the Chiton foot is moving forward while the animal supports itself on the remaining three quarters.

In Dolabrifera the foot is pear-shaped in outline with the rounded end posterior. It is about 8 mm. in length. In creeping, one to two waves can be seen on its surface at once; each wave sweeps the length of the foot in about seven seconds. As in Chiton, the waves can be clearly seen to be areas in which the foot is lifted completely from the substrate to which the rest of the foot is firmly applied. The pedal surface is mottled and in the wave area it can be seen to be moving forward, whereas on the rest of the foot it is motionless. The total wave area is about one-half the total area of the foot.

The conditions in Chiton and in Dolabrifera are essentially similar to those in the pulmonates, except that the pedal waves progress posteriorly instead of anteriorly, *i.e.*, the dorso-ventral muscles contract in sequence from the anterior to the posterior end instead of the reverse and the longitudinal muscles follow the same sequence; otherwise they act as they do in the direct type. It is evident from this brief discussion of the nature of the waves in the retrograde type that the theory developed in connection with the direct type applies perfectly to this second type.

It remains still to point out that what I have called the arhythmic form of pedal locomotion, a form well exemplified in Ilyanassa, may be explained on the same general basis as that which has just been given for the two types of arhyhmic locomotion. If the foot of such a snail as Ilyanassa be thought of as composed of a multitude of small areas, each one of which can be lifted from the substrate, moved forward, and set down again separately, and that this action takes place irregularly and without reference to any sequence, it can easily be seen how the animal could move forward but without the formation of pedal waves. It is my belief that this is the condition in the foot of the arhythmic gastropods, but because of the small size of Ilyanassa, I have not been able to subject this opinion to experimental test.

Before closing this paper, I wish to add a word concerning the very remarkable method of locomotion observed by Carlson ('05) in Helix dupetithouarsi. The movement carried out by this snail is appropriately described as a gallop, both from its rate and configuration. The snail on strong provocation lifts the head and projects it forward, and eventually brings it to the ground, thus initiating a giant wave which proceeds backward over the length of the body. Several such waves may be present at once. Carlson suggests that this movement is only an exaggerated form of the ordinary locomotion, but I am inclined to agree with Jordan ('05, p. 104) that this is probably an entirely different type of locomotion and I suspect that this snail also possesses the typical pedal wave. In fact it seems to me likely that the gallop was, so to speak, superimposed on the pedal wave system and, had the snail when in gallop been examined from below, the pedal waves would have been seen in operation in conjunction with the body waves. I am the more inclined to the view that the gallop is an independent form of locomotion as compared with the pedal waves, because in the gallop the body waves of this species, as reported by Carlson, were *retrograde* whereas the pedal waves in all Helices thus far reported are *direct*.

SUMMARY

Ordinary gastropod locomotion is accomplished either without pedal waves (arhythmic) or with pedal waves (rhythmic). In rhythmic locomotion the waves may run from posterior to anterior (direct) or the reverse (retrograde). The foot may exhibit one (monotaxic), two (ditaxic), or four (tetrataxic) series of waves. In the ditaxic foot the waves may be alternate or opposite.

The gastropod foot is an organ of attachment through adhesion (mucus) or suction, or both.

The pedal wave is an area of the foot that is lifted off the substrate as compared with the rest of the foot and thereby freed more or less from adhesion. It is also the region of the foot that moves forward, the rest of the foot remaining temporarily stationary. Locomotion is the cumulative result of local forward motion on the part of one section of the foot after another till the whole foot has been moved. The same type of muscular movement as that seen in rhythmic locomotion can be present in a diffuse form (not wave-like) in a gastropod foot and will result in locomotion.

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