

THE PEDAL LOCOMOTION OF THE SEA-HARE *APLYSIA CALIFORNICA*

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ONE FIGURE

The way in which snails use the foot in locomotion is by no means clear, and the discussion of this subject has led to a number of diverse views. The cilia found covering the foot of some gastropods have been supposed by a few investigators to be the means of locomotion, but the majority of students have maintained that the pedal muscles are the organs concerned with this form of movement. These muscles usually act in rhythmic fashion producing a series of waves that course over the foot, and by this means it is believed that the snail is enabled to move from place to place. The pedal waves of most snails are of small dimensions and the exact way in which they serve in locomotion cannot easily be seen. In the large California sea-hare, *Aplysia californica* Cooper, these waves are of very unusual size and progress at such a rate that they give ample opportunity for the examination of many details which in most snails are quite hidden. I have had the opportunity of studying this animal at the Scripps Biological Institute, La Jolla, California, to the staff of which I am under obligations for many courtesies.

Aplysia californica is found in considerable numbers among the rocks at low tide on the beach to the north of the Scripps Laboratory. Full grown individuals average about 25 cm. in length. In such specimens the foot proper is represented by a band running lengthwise the ventral surface and about 23 cm. long by 2 cm. wide. This band, however, is capable of contracting to at least one-half its original length. The locomotor waves, which reach across the whole width of the foot, begin at the anterior

end of that organ and sweep over it posteriorly¹; they involve not only the pedal muscles proper, but more or less of the musculature of the adjacent body wall. In consequence of the direction and extent of these waves they may be designated as retrograde monotaxis, to use terms introduced by Vlès ('07).

In *Aplysia californica* as a rule there is present on the foot only one wave at a time (fig. 1, *B*), and as this wave dies out at the posterior end, a new one starts at the anterior end (*A*). Occasionally a wave on approaching the posterior limit of the foot decreases its rate of progress and before it has disappeared at the hind end, a second wave makes its appearance at the anterior end thus giving rise to a condition in which two whole waves may be represented on the foot at the same time. This condition, however, is distinctly exceptional, for as a rule not more than one wave can be seen on the foot at any one moment.

In an *Aplysia* whose length of body was about 23 cm., 19 waves passed over the foot in 2 minutes and the animal progressed in that time 124 cm.; or, expressed in averages, a wave appeared every 6.3 seconds and the snail progressed with each wave 6.5 cm. In another *Aplysia* 26 waves passed over the foot in 225 seconds, during which time the snail went forward 135 cm.; or, again expressed in averages, a wave occurred every 8.7 seconds and the animal advanced 5.2 cm. with each wave. It is thus clear that in the ordinary locomotion of *Aplysia californica* wave follows wave about every 6 to 8 seconds and with each wave the snail progresses 5 to 6 cm. In some instances, however, progress was much more marked than these figures indicate; thus an *Aplysia* with a length of body of 23 cm. was seen to advance 8 to 10 cm. for each wave and on one occasion as much as 13 cm. or a little more than half the length of its body. When one compares waves of these dimensions and effectiveness with the small ripple-like movements seen on the foot surfaces of most gastropods, the advantages offered by *Aplysia* for the study of pedal locomotion are evident.

¹ My observations on the direction taken by the pedal waves in *Aplysia californica* agree with those of Jordan ('01, p. 199) on *A. limacina*. Vlès' ('07, p. 277) general statement that in *Aplysia* the pedal waves appear to run from posterior to anterior is very probably inaccurate.

In discussing the locomotion of gastropods two important questions must be considered: first, what part of the foot is at any moment concerned with locomotion, and, secondly, where and how is the foot anchored. On both these questions impor-

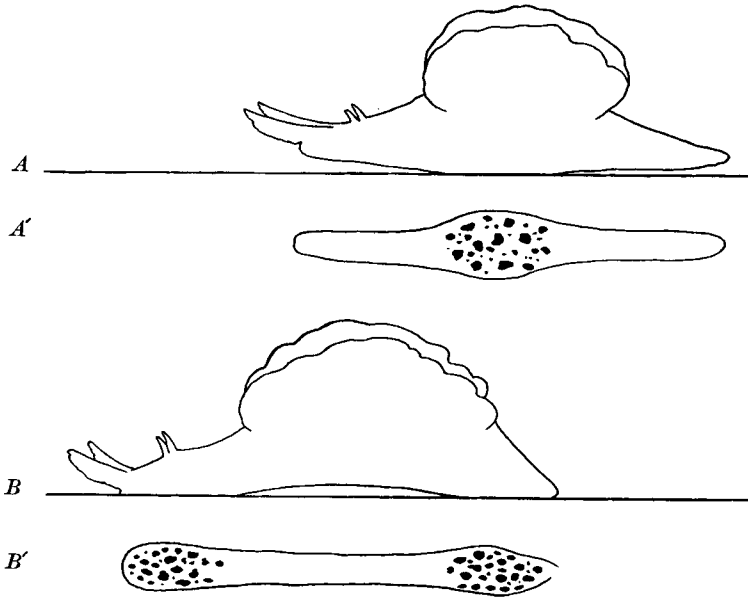


Fig. 1 A, side view of an *Aplysia* at the moment the anterior end is raised from the substrate as the initial step in the formation of a wave; the middle of the foot is attached and a wave is disappearing at the posterior end. A', ventral view of the foot, narrow at the two free ends and broad at the attached middle, where fragments of pebbles and fragments of shell are held by suction. B, side view at the moment the two ends are attached and the wave has reached the middle. B', ventral view of the foot, showing the narrow free middle and the broad attached ends, to which pebbles and fragments of shells are held by suction.

tant evidence can be had from *Aplysia*, and in dealing with the first of them direct observation is all that is necessary.

A close inspection of the movements of the foot of *Aplysia* is best made on a specimen creeping in a large glass aquarium accessible to observation from several sides. In a specimen so situated each pedal wave can be seen to start at the anterior

end of the foot, as already described, and sweep steadily over this organ to its posterior end, the snail meanwhile making a relatively gigantic forward stride, as Carlson ('05) has described for *Helix dupetithouarsi*. As one wave disappears at the posterior end, another appears anteriorly. At the initiation of locomotion the head of the snail together with the subjacent portion of the foot is lifted well off the substrate (fig. 1, *A*) and projected forward narrowing as it extends till it has been advanced a distance equal to a fourth, a third, or even a half the length of the animal. Then the anterior edge of the foot is brought down on the substrate and attached while the foot posterior to this part forms an arch reaching back to the hind end of the snail (*B*). This end, though still attached to the substrate, is just about to be freed, being in fact the vanishing traces of an area of attachment such as is now established at the front end. The anterior portion of the arch of the foot now crowds forward and attaches itself behind the attached anterior edge and thus the arch itself seems to move backward till the posterior portion of the animal is released from the substrate and is crowded and carried forward a distance equal to that over which the head was advanced. With the disappearance of this wave at the hind end of the snail, a new wave starts at the anterior end and so on in regular succession.

Where on the foot of the creeping gastropod locomotion is actually accomplished, has been a matter of uncertainty. In *Aplysia*, however, there can be not the least doubt that the anterior part of the arch of the foot is the portion that moves forward. The advance of this region and the consequent crowding together of its parts is easily observable, and these changes occur in no other area of the foot. All this is easily seen in *Aplysia*, not only because of the large size of its pedal wave but in consequence of the relatively great height to which the arched portion of its foot is momentarily lifted. In many snails it is very difficult to demonstrate that the moving portion of the foot is lifted at all from the substrate; in fact Biedermann ('05, p. 10), who studied *Halix pomatia* with much care, was erroneously led to believe that this part was actually pressed on

the substrate. But in *Aplysia californica* the arch of the foot is sometimes lifted as much as 1.5 cm. above the surface over which the snail is moving thus enabling an observer when in a favorable position to see completely under the animal. Hence it is perfectly easy to observe that the region of the foot that moves forward is the elevated region and that the most active part of this region is the anterior part.

The second question of importance in the locomotion of gastropods is where and how the foot is attached to the substrate during locomotion. Two methods of attachment have long been known; either the snail holds to the substrate by suction, or a bed of mucus is laid which on the one hand adheres to the substrate and on the other to the animal's foot. In *Aplysia*, as in all other gastropods, the portion of the foot that serves as a holdfast is of course within the limits of the area temporarily applied to the substrate. That part of the *Aplysia* foot temporarily in contact with the ground is formed, as already indicated, by the crowding together of the anterior region of the arch. In consequence of this crowding the part of the foot applied to the substrate is always broader than the portion that is momentarily free from contact. At the moment the middle of the foot is attached and the two ends are free, the foot has the form shown at *A'*, figure 1, broad in the middle and narrow anteriorly and posteriorly. On the other hand, at the moment the middle of the foot is free and the two ends are attached it has the form shown at *B'*, narrow in the middle and broad at the two ends. Thus in the progress of the waves from the head to the tail of *Aplysia* the area including the region of attachment is marked by considerable breadth, whereas that portion of the foot that is free is always narrow.

The means of attachment in the widened portion of the foot can be demonstrated very clearly on an *Aplysia* that is creeping over a shelly or gravelly beach. If such an animal is quickly inverted, the momentarily narrow part of the foot will be found to be quite clean, whereas the broadened part will be seen to be covered with a great number of fragments of shell and gravel, all of which drop off as soon as the region of the foot to which

they are attached narrows. If a fragment of shell or gravel is taken hold of by forceps before it is naturally released, it is found to be held not by its whole surface but by a limited area and with such force as to give the impression that it is held by well localized suction. This view is fully confirmed by the simple experiment of applying one's finger to the widened portion of the foot of an inverted *Aplysia*, whereupon the finger is taken hold of by the foot at several spots and the experimenter has the sensation of strong but local suction at these spots. Since the foot of *Aplysia* is practically free from mucous, it is evident from these observations that its means of attachment is by suction and that this suction is not by the foot as a whole, as in *Crepidula* or *Patella*, but is produced locally.

How local this suction is can be judged from the smallness of the particles of shell or gravel that are found attached to the foot. When an *Aplysia* is picked up from a shelly beach and gently shaken in water, the largest fragments found attached to its foot measure about 1 cm. in diameter. The smallest pieces that are firmly held there have a diameter of approximately 2 mm., thus demonstrating that the suction areas must be of very limited extent. Judging by the distribution of the bits of shell and of gravel, suction may appear anywhere on the full width of the foot and it ordinarily does appear over all that part of the foot that widens in the course of locomotion. In *Aplysia*, then, the widened part of the foot is the part that momentarily serves as a holdfast, and the foot is so organized that its surface can temporarily and locally resolve itself into many sucking organs capable of holding bodies whose diameters are not above 2 mm. Doubtless this local suction is dependent upon the activity of the perpendicular muscle strands in the foot, as surmised by Jordan ('01, p. 197).

In conclusion it may be stated that pedal locomotion in *Aplysia* is due to monotaxic retrograde waves, which lift the foot locally and temporarily from the substrate enabling it thus to move forward with freedom while the rest of the foot for the time being holds the snail in place by many small areas of local suction. The observations on which these conclusions are based

are entirely in accord with the view I have elsewhere expressed as to the mechanics of gastropod locomotion (Parker, '11).

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