THE LOCOMOTION OF LIMAX.

II. VERTICAL ASCENSION WITH ADDED LOADS.

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The inner mechanism of the pedal creeping organ of *Limax* responds so exactly to the action of temperature (Crozier and Pilz, 1923–24) that it has seemed desirable to study also the effect of varying the load to be moved by the pedal waves. It has been shown that the speed of vertically upward creeping, at constant temperature, is directly proportional to the frequency of pedal waves, to the advance produced by a single wave, and to the velocity with which the waves traverse the sole of the foot. When the temperature is varied, the frequency of the pedal waves required to lift the body vertically at given speed is proportional to the exponential of $\frac{1}{T}$, in which $T$ is the absolute temperature.

With the technique described in the preceding paper (Crozier and Pilz, 1923–24) the efficiency of creeping was measured when the slug was forced to carry additional masses. Lead weights were attached by means of a thread to a bent pin inserted in the apex of the slug's dorsum. The pin, without weights, was present in control experiments, and was found to be without influence. The thread was long enough to prevent contact between the bit of lead and the body of the animal. In order to obviate the influence of phototropism the animals in some experiments were de-eyed.

The negative geotropism of *Limax* is as a rule precise. When the animal is placed at the bottom of a glass cylinder it begins to creep, encounters the wall, and orients upward. A number of instances appeared in which the orientation was not exactly vertical.
It was easy to show that if added traction be applied to the body muscles, by hanging a weight upon the hook inserted in the animal's back, orientation instantly became exactly upward. Thus a Limax with small lead mass attached by the thread might creep upward at an angle of about 45° upon the vertical wall of a cylinder, until the attached weight began to be lifted; the head end then immediately turned upward, and the vertical orientation was thereafter maintained. This probably proves that tension of the body muscles, produced by the pull of the animal's weight, is proprioceptively concerned in effecting geotropic orientation (as suggested for Chiton, which lacks statocysts (Arey and Crozier, 1919, a)). The experiment is of interest as demonstrating that the orientation of the anterior end is an active process.

As the loaded slug creeps vertically the speed of progression changes; it generally becomes at first faster, then slower; or it may change erratically. The effect is partly a function of the amount of additional mass. For our purpose the necessary information was obtained by measuring the time and counting the number of waves disappearing at the anterior end of the foot while moving upward over a known small distance (1.5 cm. or less) marked on the glass wall of the cylinder.

Fig. 1 demonstrates that while the velocity of spontaneous vertical ascension may be altered by added loads, the linear relation between this velocity \( V \) and the frequency \( F \) of the pedal waves is not affected; nor is the magnitude of the relation between the mean advance \( A \) due to a single wave and the speed (Fig. 2).

These results permit the conclusion that for equal rates of creeping the activity of the pedal organ is independent of the added loads. This is consistent with the view that the activities of the pedal organ are determined by its intrinsic neuromuscular structures; the nervous elements (nerve net) in the foot are only secondarily under the control of the central ganglia. In this respect the foot of Limax is comparable to the gill-crown of the nudibranch, Chromodoris (Crozier, 1918–19; Crozier and Arey, 1919 a, b).

It is of interest that small additional weights usually tend to accelerate the speed of spontaneous creeping; while large weights are carried only very slowly, and the slug soon stops creeping. The
Fig. 1. Typical results illustrating the relation between wave frequency ($F$) and velocity of creeping ($V$). The three individuals (2, 5, 14), weighing respectively 9.8, 3.3, and 5.0 gm., were each in different trials loaded with extra weights as indicated. Variation results in part from errors of observation, in part from fluctuations in the velocity with which the individual waves traverse the sole of the foot. Within the limits of this variation the carrying of additional masses does not disturb the relation between wave frequency and speed of progression.
latter effect is probably due in part to the action of tension upon the skin and muscles of the body wall. But a gross direct effect upon the foot must also be recognized. The pedal surface of *Limax* is functionally divisible into two portions, an axial portion, about one third of the total area, upon which locomotor waves appear; and the lateral margins of the foot, which are adhesive. Excessive weights make adhesion difficult, so that the slug comes to attach more and more vigorously to the glass. After forward motion has ceased, modified pedal waves are still visible on the median area. The modification consists in the suppression of a part of the normal creeping wave. The pedal wave in active progression shows a narrow whitish band succeeded by a darker space (Parker, 1911). When
waves appear which do not move the animal they are white only, lacking the dark band, and they are usually faster than the truly locomotor waves. It is supposed that the white bands represent the "peristaltic" action of only one of the two sets of locomotor muscles in the foot. Incomplete waves of this type may appear on the foot of a stationary slug to which no loads are attached.

Aside from this direct effect upon the foot as an organ of attachment, added loads do not influence the rules for intrinsic activity of the creeping organ, but appear to act upon the central reflex machinery which inhibits or releases the pedal waves. It was shown previously that larger animals evidence a greater advance (A) per single wave, at given temperature and for a given velocity of movement, than do smaller ones. But in a given individual the proportionality of speed to wave size and to wave frequency is not affected by magnitude of the load carried. Therefore, the variation of A with weight of the individual must be due merely to the size of the locomotor elements in the foot.

SUMMARY.

In Limax the lifting of additional loads during vertical ascension does not alter the law of linear proportionality between speed and frequency of pedal waves, or that between speed and dimensions of the single waves; for equal velocities of progression these quantities are the same, regardless of the mass lifted. The pedal organ of the slug, although under the control of central impulses, is thus essentially an independent effector.

CITATIONS.

Parker, G. H., 1911, J. Morphol., xxii, 155.