

THE PHYSIOLOGY OF LOCOMOTION IN
GASTEROPODS.

A REPLY TO A. J. CARLSON.

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In No. 2 of Vol. VIII., of this BULLETIN, A. J. Carlson publishes a note on locomotion in gasteropods. He, at first, tries to show that my opinion concerning the mechanics of locomotion in *Aplysia*¹ is wrong. On page 87 he says: "Jordan (1901) rejects the theory of 'extensile Muskulatur' in accounting for the locomotion in the marine gasteropod *Aplysia*, and ascribes the relaxation or extension of the longitudinal muscle of the foot to the pressure of isolated bodies of the visceral fluid or blood. As evidence Jordan points to small reservoirs or lakelets of plasma in the strongly contracted foot. These lakelets are constricted off from the visceral cavity by the contraction of the muscular septa. A body of liquid thus cut off from the visceral cavity may serve to produce extension of the longitudinal muscle at its anterior border by the force of contraction of the oblique and transverse muscles at its posterior end. In this way we would have as many isolated bodies of blood being gradually pushed from behind forwards in the foot as there are areas of relaxation on the sole of the foot. The presence of isolated bodies of liquid in the strongly contracted foot is not a sufficient evidence that they are the factors in producing the waves of locomotion, as similar isolated bodies of liquid are also found in the musculature of the contracted mantle (*Aplysia Pleurobranchæa*). . . . Simroth and Jordan missed the true explanation by not taking into account the part played by the musculature of the dorsal and lateral walls of body cavity."

Carlson then describes a mode of locomotion, which he observed only in *Helix dupetithouarsi*. Instead of the ordinary locomotion by waves in the foot, this snail is able to lift up its

¹ *Zeitschr. Biolog.*, XLI., p. 196.

head and to push it forward ; it repeats the same movement with the rest of its body, forming in this way two or three waves of the whole body. It is unnecessary to continue the explanation of this mode of locomotion : it is identical with the locomotion in many worms and caterpillars. I say identical, because it is immaterial how many waves there are.

"Nevertheless," Carlson says, at the very end of his note, "the peculiar mode of progression in the snail just described is probably only an exaggerated form of the ordinary locomotion."

I am sorry to be obliged to declare that Carlson did not know or understand my publication at all. Therefore I must repeat the passages in question, and I will try to translate them into English, in order to prevent a second misunderstanding.

Page 199 (*l. c.*) I say : The movement of the foot is formed by waves. To understand this kind of movement we must imagine the sole divided into several parts (Fig. 1). The wave

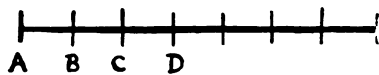


FIG. 1.

begins through the extension of the first division *AB* in the direction *A*, and by adhering to the ground at *A*. Then the same part contracts, so that *B* approaches *A*. At the same time *BC* leaves the ground, extends, until *B* adheres, then *BC* contracts, *CD* extends and *C* adheres, etc. In this way we have waves advancing — when the foot is lifted from the ground — from the anterior to the posterior part of the body. (In *Helix*, *Limax*, etc., the waves advance in the opposite direction.) All these waves must be combined with appropriate adhesion in order to produce locomotion in the posterior-anterior direction.

The snail is able to change this mode of locomotion spontaneously, thus, for instance, *Aplysia* can execute movements similar to caterpillars of geometridæ (Spannerräupen). I think this explanation should suffice, for this mode of locomotion is known (the mode now described by Carlson for *Helix*). In part 3 of the introduction of my work, page 200, I try to explain how extension is possible. This, I think, is the only part that Carlson read ; perhaps without understanding it. For in this chapter there is almost no question of waves of locomotion. The whole snail as

well as its single parts is able to extend completely, therefore without coincident contraction of other muscles. This question was studied with pieces of the musculature, and I found that the extension of the relaxed muscle was performed by means of the pressure of the blood. *Under the conditions I observed*, the blood had been pressed into lacunæ beneath the snail's skin (*l. c.*, Pl. II.), and I showed that it was pushed back into the musculature by the extended collagenous tissue, extending it in this way. These lakelets may *sometimes* be completely "isolated."

Concerning the waves of locomotion I say, p. 236: when contraction takes place, water ("blood") is driven into the confined part, which thereby is extended; by this extension tonus is diminished, etc. It will be seen, that I never spoke of "as many isolated bodies of blood being gradually pushed from behind forwards in the foot as there are areas of relaxation on the sole of the foot."

Where is the difference between my opinion and that of Carlson?

Carlson thinks that every extension is produced by blood and organ-pressure, following the contraction of other muscles. According to my opinion, this mode is assumed in normal locomotion, *while the lakelets produce complete or partial extension*. (Perhaps first extension in locomotion also.) Carlson thinks that the special kind of locomotion is nothing else than an exaggerated normal one, consequently also produced by contraction of the "musculature of the dorsal and lateral walls of the body cavity."¹ *This opinion is wrong because, if this musculature is removed, the foot is able to produce normal locomotory waves.*

In conclusion: The opinion Carlson ascribes to me, is in reality not my opinion. My work of 1901 contains all that Carlson publishes as new in 1905, so far as the latter is true. The two modes of locomotion are quite different: in the normal one the blood, which is contained in the lacunæ (not in isolated lakelets!) of the foot, extends the musculature; in the fast one this rôle is performed by the contents of the body cavity, with the aid of the muscles of the dorsal and lateral sides of the body.

ZÜRICH, March, 1905.

¹ This ought to be regarded as the chief result of Carlson's note, because otherwise he would have done nothing to explain *normal* locomotion.