ON THE SIGNIFICANCE OF THE SPIRAL SWIMMING OF ORGANISMS.[1]

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It is a well-known fact that many of the lower organisms swim in a spiral path, but the real significance of this fact has never been pointed out, I believe, until recently. Swarm-spores, flagellate and ciliate infusoria, rotifers, and many other lower organisms as they pass through the water revolve on their long axes, and thus follow a course that takes the form (as a rule) of a spiral. Extended discussions of this fact are to be found in many works, as in Bütschli's "Protozoen" in Bronn's *Klassen und Ordnungen des Thierreichs*, and in many special papers. These discussions usually confine themselves to a description of the facts, — so far as these were made out, — and to a discussion of the mechanical factors involved in producing the spiral movement, without any attempt to show the biological significance of the phenomenon. To understand the significance of this method of swimming was indeed perhaps impossible until the relation between it and the method of reaction to a stimulus in these organisms was known, and especially until it was recognized that *the body of the organism bears a constant relation to the axis of the spiral*, — that is, that the same side of the organism is always directed toward the outside of the spiral (as in Fig. 1). These relations were first pointed out by the present writer in Nos. II and V of his "Studies on Reactions to Stimuli in Unicellular Organisms," [2] where they were shown to hold for a considerable number of Flagellata and Ciliata.

[1] The substance of this paper was presented at the meeting of the Western Naturalists in Chicago, Dec. 27, 1900.

[2] II, The Mechanism of the Motor Reactions of Paramecium, *Am. Journ. of Phys.*, vol. ii (1899), p. 323; V, On the Movements and Motor Reflexes of the Flagellata and Ciliata, *Am. Journ. of Phys.*, vol. iii (1900).

The exact purpose that is served by this method of swimming is a point deserving of further emphasis and fuller discussion. The Flagellata and Ciliata are as a rule unsymmetrical in form. One of these organisms, as, for example, Loxodes (Fig. 2), or Paramecium (Fig. 3), when it leaves the bottom and starts to swim freely through the water, cannot go in a straight line, but owing to its lack of symmetry continually swerves toward one side, so that it tends to describe a circle. If no method is taken of compensating this deflection, the circles described are frequently very small, and of course the animal makes no progress by swimming in this way. Paramecium and Loxodes thus tend to circle toward the aboral side, Chilomonas (Fig. 4) toward its "lower lip," all the Hypotricha to the right, etc.

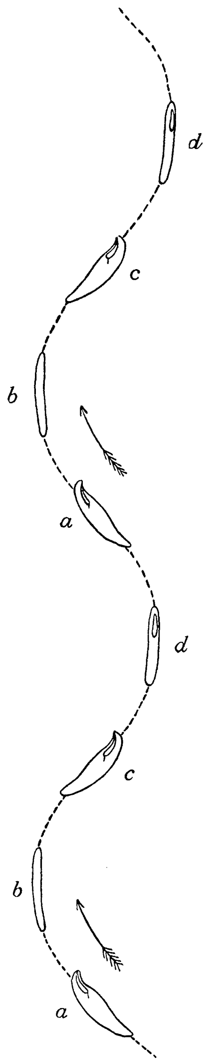

FIG. 1. — Diagram of spiral course of Loxodes when swimming freely through the water. If *a* and *c* are conceived as being in the plane of the paper, then *b* is above and *d* below this plane.

To obviate this difficulty, revolution on the long axis is combined with the forward movement of the organisms. By this means the continual swerving toward one side is compensated, since this side is continually turned in a new direction. Thus, if Loxodes is swimming (freely through the water) away from the observer, and the aboral side is at first to the observer's left (Fig. 1, *a*), the organism at first swerves to the left; but as it revolves the aboral side soon comes to be the upper side, and the animal now swerves up (*b*). By continued revolution the aboral side is brought to the right (*c*), so that the animal swerves to the right. Next, of course, it swerves down and the process is continued, the animal swerving successively to the left, up, right, down, etc. These movements, of course, compensate each other, so that only the forward component of the motion is effective; the animal thus moves forward as if on a straight line, — the actual path being a spiral with a straight axis. The principle is the same as that by which a rifle bullet is given a straight course by making it revolve in the axis of flight.

In the Hypotricha a similar course is followed, save that the swerving is to the right; in Chilomonas (Fig. 4) it is toward the lower lip (*a*). Such a spiral path is known to be followed by most of the free-swimming Protista, — by swarm-spores, flagellates, and ciliates in general; by Volvox, Eudorina, Pandorina, Platydorina, etc. In some of these organisms the course followed becomes almost an actual straight line, owing to the fact that the body is symmetrical, so that there is no pronounced swerving toward one side. Such is the case, for example, in Volvox. Here the revolution on the long axis probably serves merely to compensate for any accidental deviations that may occur through injury, unequal development, and the like. Such cases are comparatively rare, however, most of these organisms being markedly unsymmetrical.

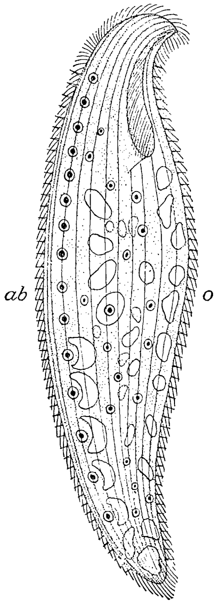

FIG. 2.

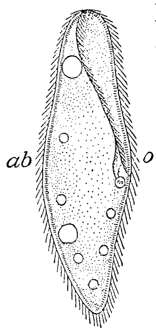

FIG. 3.

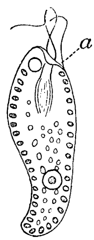

FIG. 4.

FIG. 2.—*Loxodes rostrum*, after Bütschli, showing the unsymmetrical form. *ab*, aboral side; *o*, oral side.

FIG. 3.—*Paramecium caudatum*. *ab*, aboral side; *o*, oral side.

FIG. 4.—*Chilomonas paramecium*, after Bütschli. *a*, "lower lip."

The mechanical cause of the revolution on the axis of progression has often been discussed. In the Ciliata there seem to be three possible factors: (1) an oblique stroke of the cilia; (2) the oblique position of the peristome; (3) the unsymmetrical form of the body, which is often of such a shape as to favor rotation in a given direction. That the first factor is the primary one is indicated by the fact that the direction of revolution may be reversed in many of these organisms, even when the form of the body is such as to oppose this reversal. The unsymmetrical form seems rather an adaptation to this method of swimming, — a consequence of it. Many of these organisms are so shaped that the body forms part of a spiral; this is to a certain degree the case, for example, in Paramecium (Fig. 3). In some others this is much more marked. Phacus, for example, is frequently strongly spiral. Some of the bacteria swim in this same manner, and among these, Spirillum forms, as is well known, a sort of animated corkscrew. The prevailing asymmetry in the unicellular organisms is closely correlated with this method of swimming.

When creeping along the bottom (as Loxodes usually does), or when in contact with any solid object, these same organisms exhibit no such rotation. When moving along a surface there are, of course, only two chances to err from the straight line, either to the right or to the left. When swimming freely through the water, on the other hand, the chances of deviation are indefinitely numerous, since the organism may swerve to the right or left, or up or down, or in any intermediate direction. Moreover, when in contact with a surface, this usually presents numerous stimuli, which serve as directives of motion, while in the free water such stimuli are lacking. Hence the necessity of some special device for keeping the straight course in the latter case. The movements and reactions of organisms differ greatly when they are moving along a surface from those exhibited when passing freely through the water. (Pütter[1] has recently published a valuable paper on this subject.) Both flagellates (*e.g.*, Peranema) and ciliates move without rotation when in contact with a surface. Yet even then they usually cannot travel in a straight line; Colpidium and Oxytricha, for example, follow a much curved course.

As the present writer has fully set forth in his "Studies on Reactions to Stimuli" (*loc. cit.*), this method of locomotion is closely related with the usual method of reaction to a stimulus. In addition to swerving toward a structurally defined side in

[1] Pütter, August. Studien über Thigmotaxis bei Protisten, *Archiv f. Anat. u. Phys.*, Physiol. Abth., Supplement Band (1900), pp. 243–302.

their locomotion, these unsymmetrical organisms respond to a stimulus by turning toward a structurally defined side.

It is important not to misunderstand the nature of this spiral motion. If one of these swimming organisms is viewed from above with the ordinary microscope, the path of the organism seems to swerve merely first to the right, then to the left. This is of course because the upward and downward part of the path is lost from view with the ordinary microscope which sees approximately in a single plane; with a stereoscopic binocular the real nature of the path is evident. If the constant relation of the body of the organism to the axis of the spiral is likewise overlooked, a peculiarly false conception of the movements of these organisms is obtained, which seems to be somewhat widespread. This is the conception that the organism swerves as it swims, first toward one side, then toward the other.

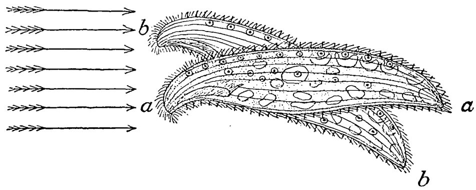

FIG. 5.— Diagram to illustrate supposed oscillation of an unsymmetrical organism when oriented by lines of force (represented by the arrows).

For example, Loxodes or Paramecium, according to this view, would swerve first toward the aboral side, then toward the oral side. This supposed movement has even been given a high theoretical significance, as being the natural result of the orientation of an unsymmetrical organism by lines of force, such as rays of light, or the path of diffusing ions. Thus, in Fig. 5, in the position *a–a*, in which the axis of the organism is parallel with the lines of force, more lines of force impinge on the convex side of the organism; hence the locomotor organs on that side act more (or less) strongly than those on the concave side. As a result of this differential action, the organism swings (supposedly) to the position *b–b* (that is, it swings toward the aboral or convex side). Now more lines of force impinge on the concave side; the locomotor organs act more (or less) strongly on this side, and the organism swings again (now toward the oral or concave side) into the position *a–a*. This continues, and, combined with the forward motion, supposedly accounts for the sinuous path of these organisms. It should be clearly stated that the actual movements of these creatures lend no support to this account, but are, on the contrary, quite incompatible with it. The organisms swerve always toward the *same* side, not first to one side, then to the other.

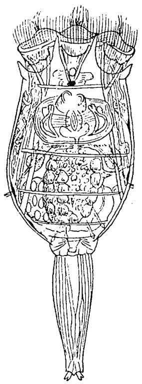

FIG. 6. — Dorsal view of a rotifer (*Brachionus pala*, after Weber) to show the similarity of the two sides.

But it is well known that it is not only unsymmetrical organisms that swim in a spiral, but that the same is true for many bilateral organisms also, — as, for example, the Rotifera. Since the two sides are alike in these animals (see Fig. 6), there is no reason for swerving to the right rather than to the left, and the spiral path calls for some further explanation. The significance of the spiral path in such cases is clearly seen when the movements of these animals are carefully studied. When creeping on the bottom or the surface film, there is no rotation. Here the only possibilities of deviation from the straight line are either to the right or to the left, and since the two sides are alike there is no reason for swerving in either direction. But the dorsal and ventral sides are not alike (see Fig. 7), and in swimming freely through the water the animal might err by turning toward the dorsal or toward the ventral side, or in any intermediate direction. As a matter of fact, careful observation shows that most rotifers do swerve toward the *dorsal side* as they swim freely through the water. This tendency seems traceable to the fact that the rotifers are primitively creepers on the bottom, and most of them still retain this habit. In order to rise from the bottom into the free water, the animal must necessarily move toward the dorsal side (as in Fig. 7). The cilia which bring about the free-

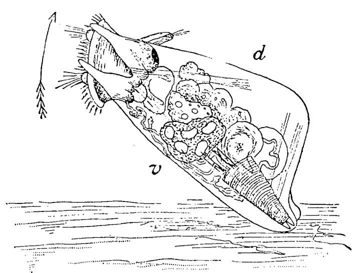

FIG. 7. — Rotifer (*Brachionus pala*, modified from Hudson and Gosse), side view, showing the turning toward the dorsal side when rising from the bottom. *d*, dorsal side; *v*, ventral side.

swimming movement seem to have this tendency, to strike so as to turn the animal toward the dorsal side, strongly ingrained. Many of these animals cannot rise from the bottom so long as the dorsal side is down. In such a case the dorsal side of the head repeatedly strikes the bottom until, by revolving on the long axis, the dorsal side is turned toward the free water; the animal then swerves off the bottom in that direction. Some

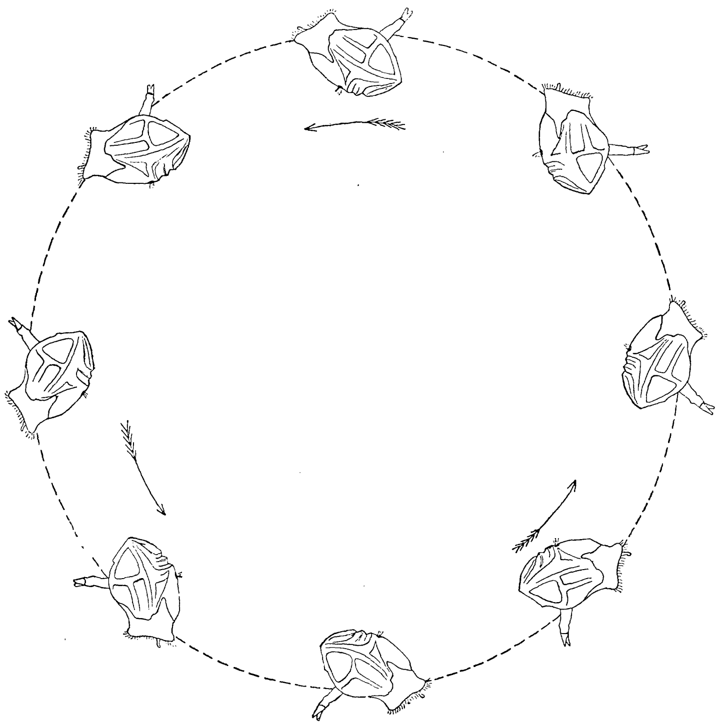

FIG. 8.— Diagram showing course followed by Plœsoma when swimming without revolving on the long axis. The animal continually swerves toward the dorsal side, hence follows a circular path.

of the rotifers, if they attempt to swim freely through the water without revolving on the long axis, turn backward somersaults, over and over, describing thus small circles. I have seen Plœsoma thus describe circles (Fig. 8) for considerable periods. But as soon as the animal begins at the same time to revolve on the long axis, without otherwise changing its movement, the effect is striking. The purposeless circular movement

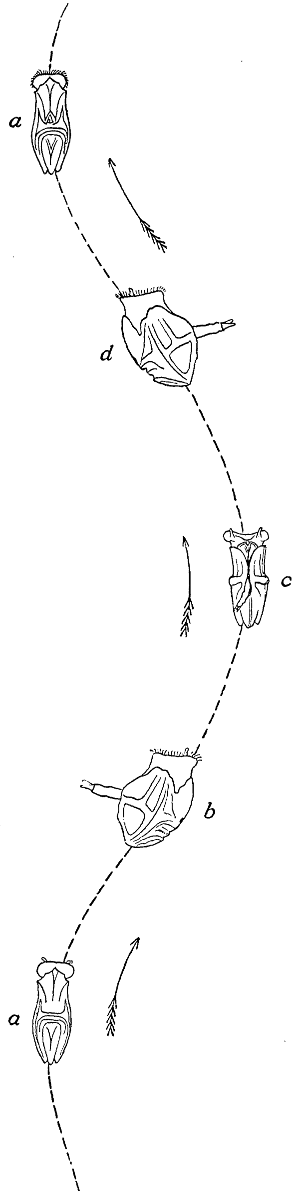

FIG. 9. — Diagram showing the course of Plœsoma as soon as it begins to revolve on the long axis (*a* and *c* are higher and lower, respectively, than *b* and *d*, which lie in the same plane). This spiral course, with the dorsal side to the outside of the spiral, is characteristic for many Rotifera.

(Fig. 8) becomes at once a well-ordered progression in a spiral path (Fig. 9). No one who has seen this sudden change from random circles to a path having all the essential qualities of a straight line can fail to appreciate the biological significance of the rotation on the long axis in compensating the tendency to swerve in a given direction.

This tendency to swerve toward the dorsal side seems present in the majority of the free-swimming Rotifera, and is compensated almost universally by the revolution on the long axis, causing the resulting path to be a spiral with the dorsal side directed toward the outside of the spiral (Fig. 9). All rotifers observed by the writer revolve to the right, and no reversal of the direction of revolution was ever seen.

In some of these primitively bilateral animals this spiral method of swimming has resulted in the production of an unsymmetrical form analogous to that of the infusoria. In the small aberrant family of Rattulidæ this adaptation to a spiral movement is most striking. *Rattulus tigris*, for example, has a twisted body, forming actually a segment of a spiral, and there is in addition a high spiral ridge on one side. This ridge begins behind the middle, near the mid-dorsal line, and passes forward, at the same time curving over to the right side. The animal swims in a spiral of which this ridge and its own twisted body form a part.

Asymmetry appears sporadically in many different groups of the Rotifera; possibly it may in every case be brought into relation with the spiral method of swimming.

The Rotifera are a group of organisms excessively varied in form and movements, furnishing a most excellent opportunity for studies on the interdependence of structure and function. Some species (*e.g.*, certain species of Diaschiza) have the body so curved ventrally that the tendency to turn toward the dorsal side is more than compensated, and the animal tends instead to curve continually toward the ventral side. This tendency is of course likewise corrected by the revolution on the axis of progression, the path taking here the form of a spiral with the ventral surface to the outside. Some few rotifers have become so modified that revolution on the long axis has become unnecessary for keeping a straight course. Thus *Euchlanis triquetra* (a view of which from the rear is shown in Fig. 10) has developed three great keels, one dorsal and two lateral, which tend to prevent swerving in any direction; so this animal frequently swims freely for long stretches without revolving, while the closely related *Euchlanis oropha* (having no keels) almost continually revolves as it passes through the water.

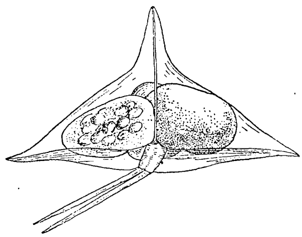

Fig. 10. — View of a swimming *Euchlanis triquetra* from behind (after Ehrenberg) to show the three keels.

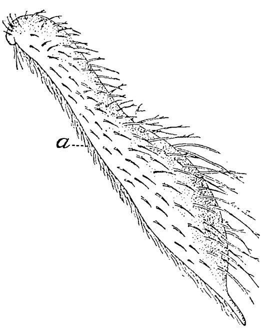

Fig. 11. — One of the Gastrotricha (*Chætonotus macrochætus*, after Zelinka), showing the position of the cilia (*a*) on the ventral side.

Revolution on the long axis, with the resulting spiral path, is common also in many other animals. In the Gastrotricha (*e.g.*, Chætonotus, Fig. 11) the locomotor organs (cilia) are confined to a strip on the ventral side, (*a*) which necessarily results in giving the organism a tendency to turn toward the dorsal side. The revolution on the long axis is therefore of great importance for producing an effective forward movement.

Revolution on the long axis is also to be observed in many rhabdocœls. It is indeed one of the commonest features in the locomotion of small fresh-water organisms, and doubtless occurs in salt-water forms in the same way.

On the whole, then, it is clear that revolution on the long axis, with the resulting spiral path, is of high biological significance. Only through this device are many organisms enabled to follow a course which is practically a straight one; without such revolution many creatures merely describe small circles, making no progress whatever. By means of this revolution on the long axis, any organism, no matter how misshapen and irregular, may follow a course which is, in effect, equivalent to a straight line. The simple device of revolving in the axis of progression is surprisingly effective, in that it compensates with absolute precision for any tendency or combination of tendencies to deviate from a straight course in any direction whatsoever.

ANN ARBOR, MICH., January 5, 1901.