A Study of Spiral Movement in the Ciliate Infusoria

by

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(With 9 textfigures.)

Contents.

Introduction.

Probably the first record we have of the study of spiral movement in one-celled organisms is that of NÄGELI, in 1860, of the paths of flagellates and swarm spores. Later investigators reported spiral movement in various other protozoan organisms but they apparently were unable to get away from the idea that it was a purposeless reaction of no special importance. KENT (1882) mentions the occurrence of spiral movement in various ciliates but the spiral itself meant little or nothing to him. He did not concern himself with the question of why or how it occurred. It is only within the last twenty-five years that the question of spiral movement has been considered of sufficient importance in the life of the protozoan organism to merit special attention. JENNINGS (1898—1906) seems to be the first investigator to regard it as an important factor in the study of these animals. He contributed much valuable information to this subject which has served as a basis for the work of all succeeding investigators. In 1901 (p. 370—371) he regarded spiral movement as the only method by which these organisms could swim in a straight course, believing spiral swimming due to an adaptation of movement to shape of body. Later in the same paper (p. 372) he decided that unsymmetrical form was due rather to an adaptation to this method of swimming. In 1902 (p. 233) he found spiral swimming due to another cause, viz., the direction of contraction of the body cilia, since this same swerving continued regardless of size, shape, or mutilation of the body of the organism.

In 1917 D'ARCY W. THOMPSON thought movement of infusoria due to a sort of molecular bombardment slmilar to that of Brownian movement.

In 1920, SCHAEFFER found a great variety of organisms swimming in spiral paths and came to the conclusion that spiral movement was the most natural method of movement for all animals devoid of image-forming eyes or equilibrating organs. He blazed a new trail in breaking away from the idea that the reactions of these animals were due to tropisms or to chemical and physical stimuli. He believed there was a directive center in these organisms, a sort of automatic mechanism, which controlled their movements somewhat as the brain center controls the movements and reactions of the higher animals, so that when free from stimulation a spiral path was followed. He thought it very improbable that spiral swimming was an acquired habit but believed the cause for its existence was locked up in phylogeny.

Acknowledgments.

I wish to take this opportunity of expressing my deep appreciation particularly to Dr. A. A. SCHAEFFER for his helpful suggestions and criticism of my work throughout its entire period of preparation. It was at his suggestion and under his direction that this work was undertaken more than two years ago. I wish also to take this opportunity of expressing my appreciation to Dr. C. B. DAVENPORT for his help in making it possible for me to carry on this work at Cold Spring Harbor during the summers of 1922—1923 and I wish also to thank Dr. L. L. WOODRUFF for his kindness in contributing *Paramaecium calkinsi* WOODRUFF included in this study.

Materials.

The Infusoria studied in these experiments were collected in widely separated places as they appeared from time to time throughout the entire two years. Some came up in ordinary infusion cultures set up in the laboratory; others came from fresh water cultures collected from the swamps of Lonsdale and Middlebrook in the outskirts of Knoxville, and from Second Creek just north of the University campus; a few came up in sphagnum cultures set up in the laboratory from sphagnum shipped in from eastern Pennsylvania, and still others in salt water cultures set up in Knoxville from sea weed and sea water shipped in from Cold Spring Harbor. The majority, however, were found at Cold Spring Harbor during the summers of 1921, 1922 and 1923. These were collected from the surrounding fresh water lakes and pools, from floating eel grass gathered in both the outer and inner harbors, and from shells dredged up from the bottom of Long Island Sound just off Lloyds Neck. A few were also found in a salt marsh on the south side of Oyster Bay, while still others came from floating eel grass in Great South Bay. A great many were obtained from the brackish water marsh-pools on Gilgo Beach on the south shore of Long Island, where they occurred in great numbers. But most of the Cold Spring Harbor ciliates came from the Jones Marsh, at the south end of the inner harbor, and from the overflow pond near the engine room. Both the latter places were particularly good collecting places for all sorts of Protozoa. The distribution of the organisms studied is fairly wide, therefore, and it is believed that their reactions are representative.

Methods.

These animals were studied in watch glasses under a binocular microscope and the direction of spiral determined while they were swimming freely through the water. In doubtful cases the direction was determined while they were swimming directly toward or away from the surface film. Use was made of the high power objectives and oil immersion lenses of the compound microscope for determining structure. For identification, access was had to the papers of KENT, BÜTSCHLI, CONN, ENTZ, WRZESNIOWSKI, STEIN, PENARD, LACHMANN, ROUX, SCHEWIAKOFF, EHRENBERG, SAND, CALKINS, STOKES, and POCHE.

Spiral Movement in the Ciliates.

Relation of Taxonomy to Direction of Spiral.

(Table 2.)

My first observations on spiral movement were made on a group of 88 ciliates which I had studied up to the beginning of the summer of 1922. The results of these studies were such that this work was continued with the idea of studying a much larger number of species in order to determine whether these results were constant and characteristic or only accidental. Each one of these 88 ciliates swam in spirals when swimming freely through the water, and by the term spiral we mean rotation of the body on its own long axis and revolution of the body on the axis of progression. These two movements combined with forward movement compose the spiral path. JENNINGS 1906 p. 44 apparently uses these terms,

Table 2. Relation of Taxonomy to/ Direction of Spiral.

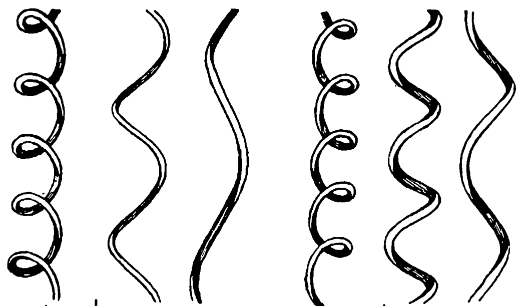
Groups	Infusoria studied at Knoxville previous to summer of 1922				Infusoria studied at Cold Spring Harbor during summer of 1922				Infusoria studied at Cold Spring Harbor summer of 1923				Total number Infusoria studied, including 24 not listed in other groups			
	Total number studied	Number rotating Left	Number rotating Right	With both species	Total number studied	Number rotating Left	Number rotating Right	With both species	Total number studied	Number rotating Left	Number rotating Right	With both species	Total number studied	Number rotating Left	Number rotating Right	With both species
Families																
Holotricha	10	5	1	4	5	2	1	2	4	—	2	2	12	4	2	6
Heterotricha	4	4	—	—	1	—	—	1	1	1	—	—	3	1	—	2
Peritricha	3	—	2	1	2	1	1	—	1	1	—	—	3	—	—	3
Hypotricha	5	3	—	2	5	4	—	1	5	2	2	1	6	3	1	2
Totals	22	12	3	7	13	7	2	4	11	4	4	3	24	8	3	13
Genera																
Holotricha	21	12	6	3	9	6	3	—	9	3	6	—	27	11	10	6
Heterotricha	7	7	—	—	2	2	—	—	1	1	—	—	8	6	1	1
Peritricha	8	3	5	—	6	3	2	1	1	1	—	—	12	5	4	3
Hypotricha	15	10	5	—	5	5	—	—	5	2	3	—	21	14	5	2
Totals	51	32	16	3	22	16	5	1	16	7	9	—	68	36	20	12
Species																
Holotricha	35	24	11	—	14	7	7	—	11	4	7	—	60	35	25	—
Heterotricha	14	13	1	—	2	2	—	—	2	2	—	—	18	16	2	—
Peritricha	11	4	7	—	13	6	7	—	1	1	—	—	36	14	22	—
Hypotricha	28	20	8	—	10	9	1	—	8	4	4	—	50	37	13	—
Totals	88	61	27	—	39	24	15	—	22	11	11	—	164	102	62	—

rotation and revolution, as synonymous, but in this paper rotation has reference to spinning on an axis while revolution has reference to moving in an orbit along the axis of progression. There was in all these 88 species only one complete rotation of the body in each complete revolution, and both were in the same direction: i. e., if rotation was over to the left, revolution was also over to the left. Moreover, the direction of this spiral was constant and characteristic for each species at all times. In no species did some of the individuals swim in spirals in one direction while others swam in spirals in the opposite direction, nor did the same individual in any case alternate from one to the other direction, although at one time there were two species (see below) which appeared to spiral in either direction, alternating from one to the other. Later observation, however, showed this to be an optical illusion and not a true direction.

Lembadion bullinum O. F. MÜLL. was first found at Cold Spring Harbor during the summer of 1921 and at that time the spiral appeared to be in either direction. Later, however, at two different times, this same species was found at Knoxville and the spiral studied carefully, but in every case the direction was to the right only. Since no others have been found spiraling to the left, the first apparent observation was undoubtedly an optical illusion, and the true direction of the spiral for this species is from left over to the right.

Urocentrum turbo O. F. MÜLL. was first observed at Knoxville in June, 1921, and the spiral path was seen distinctly to the right. But when the same species was observed later that same summer at Cold Spring Harbor, the direction of the spiral appeared both to the right and to the left. A great many individuals (25—50) were studied again but more critically, at Knoxville on January 3, 1922, 12—15 individuals were studied January 7, 1922, and 10—12 individuals were studied January 3, 1922, and in each instance in all these groups, the direction of the spiral was definitely over to the right at all times. The left-hand spiral apparently seen at Cold Spring Harbor, was without doubt another case of optical illusion. The true direction of the spiral in this species is considered, therefore, as from left to the right.

Although the direction of spiral was found to be constant and characteristic for each species, this direction was not found to be the same for all species. The 88 species did not all spiral in the same direction neither did they divide equally between the two directions right and left. Two out of every three swam in spirals over to the left. Sixty-one of the 88 species spiraled to the left while 27 spiraled to the right. By the terms over to the right and over to the left is meant, in the former, a direction similar to that of the movement of the hands of a clock when the observer is looking directly at its face in its normal position, and in the latter, a direction of movement opposite to that of the hands of a clock, the position of the observer being the same. These spirals may also be spoken of as clockwise and counterclockwise, or as right-hand spirals and left-hand spirals respectively. The right and left referring to the right and left of the organism as it moves through the water. Both kinds of spirals are shown below (Fig. 1).



Left-hand spirals. Right-hand spirals.

Fig. 1. Right and left-hand spirals.

No reason was found for this large preponderance of left spiraling over right spiraling, nor for the constancy of direction the spiral in the species, but it led to the idea that probably after of all this constancy of direction and preponderance of lefts did not end with the species but extended to the larger groups, — the genus and the family. It was thought that perhaps it might be related in some way with the taxonomy of the organism, the division on the basis of spiral swimming into left spiraling and but right spiraling, being closely connected with the division into the various taxonomic groups. Comparisons were then made of these groups, the genera and the families, with the following results.

Of the fifty-one genera represented in these 88 species, 49 were found to separate actually and definitely, on the basis of spiral swimming, into left spiraling and right spiraling in the proportion of 2 lefts to 1 right, as in the species; i. e., 33 of the 49 genera swam in spirals to the left and 16 in spirals to the right. But two genera *Trachelocerca* and *Lacrymaria*, contained both kinds of species, one left spiraling and one right spiraling in each genus, and could not be so divided. In an examination of the classification of the species of these two genera we found the two species of *Trachelocerca* very much alike in general appearance and were thought probably correctly classified, but the two species of *Lacrymaria* seemed to be generically different and were most likely incorrectly classified. The species *L. cohnii* S. K. appeared to be the species in this genus which was incorrectly classified.

In the families, 15 of the 22 represented, separated also on the basis of spiral swimming into left spiraling and right spiraling the proportion being, in this case, 4 to 1; twelve families being found to swim in spirals to the left and 3 in spirals to the right. A relation betwen division into taxonomic groups and division on the basis of direction of spiral, at least in this particular group, did actually exist, therefore, in 100 $^0/_0$ of the species, approximately 94 $^0/_0$ of the genera, and about 68 $^0/_0$ of the families.

The above figures, however, include all genera and families represented, whether this representation was by only one species or by more than one. Thirty-six genera were represented by only one species, while 5 families were represented by only one genus of only one species each. When these genera and families were eliminiated and only those of two or more species were considered, we had left 14 genera, of which 9 spiraled to the left, 2 spiraled to the right, and 3 contained both kinds of species. Eleven of the 14 genera or 78 $^0/_0$, with two or more species, therefore, showed a relation between direction of spiral and taxonomy, — the proportion being 4,5 lefts to 1 right. In the 16 families which contained two or more species, 8 spiraled to the left, 1 to the right, and 7 contained both species. Direction of spiral in 9 of the 16 families or 56 $^0/_0$, with two or more species, therefore, is apparently related to taxonomy in the proportion of 8 lefts to 1 right.

Now since one of the most important results in these comparisons, and in the study of these 88 ciliates, is this large proportion of left spiraling to right spiraling, and since, generally speaking, all later species were studied more or less in groups, it seemed desirable to present these groups as they were studied, rather than taxonomically as a whole. It is evident, that on account of their sporadic appearance, only a small number of all the known species of ciliates can be critically studied at any one time. If several large groups of species selected at random, however, give essentially the same results as that shown by all the groups when taken as a whole, it may then be presumed that the proportion of left spiraling found in the whole group of species studied, is the same as that existing in all known ciliates.

Species Studied During the Summer of 1922.

Thirty-nine additional species studied during the summer of 1922 were also found to swim in spiral paths and they contained approximately the same proportion of left spiraling to right spiraling and the same constancy of direction in the species. One other species, however, observed at Cold Spring Harbor during the summer of 1921, — *Paramaecium marina* S. K. — and found apparently spiraling to the right, was found in large numbers during the summer of 1922 in a brackish marsh, south side of Oyster Bay. The spiral in every individual was carefully investigated and found to be definitely to the left. The first observation is considered an optical illusion, therefore, and the true direction of the spiral in this species is considered as from right over to the left. One explanation for these mistaken observations in 1921 is the fact that the spiral in part of the species studied in 1921 had to be studied with a compound microscope, whereas, up to this time the spiral had been studied with a binocular microscope. One is much more easily deceived as to actual direction of the spiral with a compound than with a binocular microscope, and this fact may have been overlooked at the time. It is significant that all individuals of every species seen since that time spiral in the one direction only.

In the 22 genera of this group 21 were classified on the basis of spiral swimming into left spiraling genera and right spiraling genera in the proportion of 3 left spiraling to 1 right spiraling. And in the families, the direction of spiral of 9 out of 13 appeared related to taxonomy in the proportion of 3.5 lefts to 1 right, — 7 families spiraling to the left and 2 spiraling to the right. The four remaining families contained both kinds of species. The high degree of correlation between division into taxonomic groups, and into groups based on direction of spiral, found to exist in the species of the previous group, therefore, remained unchanged, but the 94 % relation in the genera increased to 95 %, and the 68 % in the families increased to 70 %.

Species Studied During the Summer of 1923.

Twenty-two other species were studied during the summer of 1923 and each one, as before, was found to swim in spiral paths. Again the direction was found to be constant in each species, but the preponderance of left spiraling found in the two preceeding groups, did not exist in this group. Eleven of the 22 species swam in spirals to the left and 11 in spirals to the right. This decrease in the number of species spiraling to the left is probably accounted for in the comparatively small number of species studied. The 16 genera represented in this group, separated completely into left and right spiraling genera in the proportion of about 1 left to 1 right, as in the species. Three of the families contained both kinds of species and of the other 8 families, 4 spiraled to the left and 4 to the right. Since, however, some of these genera and families are represented by only one species, these results are not significant by themselves, but are of interest in connection with the other groups already studied.

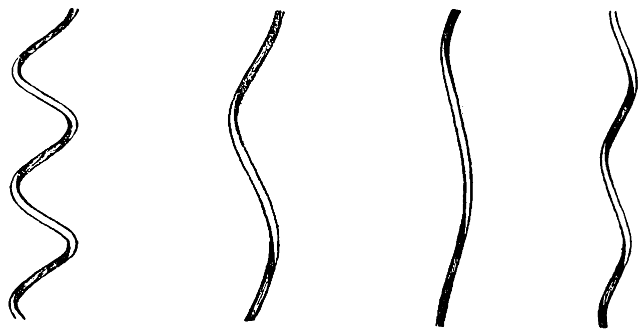
Total Number of Species Studied.

One hundred sixty-four ciliates and one suctorian have now been studied. Since the number is comparatively large, and since they came from widely separated places at various times during the year and under a great variety of conditions, they are believed to be representative and their reactions typical. Every one of the 164 ciliates swims in a spiral path when swimming freely through the water, the spiral, as stated previously, consisting of both rotation and revolution. Not one was found to swim in any other manner, although JENNINGS, for example, in 1900 (p. 248) reported *Bursaria truncatella* O. F. MÜLL. swimming forward for some time without revolving. This species is included in the 164 ciliates listed in this paper, however, and in no case was an individual found swimming freely without revolving in regular spirals. The only time it fails to revolve is when feeding along over the bottom or surface film, or on some debris. JENNINGS, in the same paper (p. 253), also stated that, "the Hypotricha do not revolve as they move through the water, as is done by most other infusoria, but run along the bottom with the ventral side below", although he had just previously stated that *Oxytricha fallax* STEIN swam freely through the water "revolving on its axis". Later, also in 1902 (p. 227), he reported free swimming and a spiral path in *Stylonychia*. But free swimming and a spiral path in the Hypotricha are not limited to *Stylonychia* and *Oxytricha*. The *Euplotidae*, *Lionotidae*, and all other members of this order swim freely equally as well, and when they do, they swim constantly in regular spirals. The factors of size, shape, and classification have nothing whatever to do with the cause or prevention of a spiral. It is followed in spite of them. Practically every variation in size and shape of body has been studied in these ciliates and no individual of any one of these species has been found free from this "spiral urge". The cylindrical *Prorodon*, *Coleps*, and *Didinium*; the flattened leaf-like *Loxophyllum* and *Loxodes*; the long cylindrical *Spirostomum*; the bugle-shaped *Stentor*; the colonial *Vorticellidae*, and the deep-grooved *Paramaecium*, all move in spiral paths in free swimming. SCHAEFFER (1920) makes the statement that "all moving organisms are subject to the tendency to move in spiral paths". So strong, in fact, is this spiraling tendency in these organisms that pieces of any size or shape, dissected from any part of the body, continue to swim in spiral paths similar to that of the original organism (JENNINGS 1902).

The spiral path of a free swimming ciliate, therefore, bears a definite relation to this free swimming, and this relation is absolute so far as the spiral is concerned. But it is not absolute to the extent that if one occurs the other occurs. Free swimming never occurs without spiraling, but spiraling may occur without free swimming. Decreasing the temperature of Paramecia decreases the speed and at the same time increases proportionally the number of spiral turns of the body (SCHAEFFER 1920). Forward movement may cease altogether in some ciliates and the organism continue to spiral. *Urocentrum turbo* O. F. Müll. and one species of *Strombidium* frequently cease swimming through the water and attach themselves to some debris. At such times they spin around on the body axis and at the same time revolve in an orbit.

The width of this spiral in free swimming also appears to be regular for each species. It may be narrow or it may be wide for any particular species, but this width once determined seems to remain fairly constant. It is characteristic of the species and varies, if it varies at all, within rather narrow limits. The number of spiral turns of the body, however, may be many or few, increasing or decreasing with an increase or decrease of speed, respectively, but in normal free swimming this change is so small that even it may be considered characteristic. Some ciliates, such as, *Urocentrum*, *Strombidium*, *Vorticella*, *Halteria*, *Mesodinium*, and *Didinium*, etc., are characterized by a wide spiral; others, such as, *Frontonia*, *Loxophyllum*, and *Loxodes*, are characterized by a spiral of medium width. Paramecia swim usually in very narrow spirals with long spiral turns, while *Euplotes*, *Stylonychia*, and *Oxytricha* swim in narrow spirals with short spiral turns.

Since both rotation and revolution combine to form the spiral path of these organisms, the direction of both must be the same at all times for each particular species. If the swerving, and its consequent revolution in the axis of progression, is to the left, rotation on the long axis of the body is also to the left, and vice versa. No ciliate swims by revolving to the left and rotating to the right. Both must be to the right or both to the left and there ist no changing. This relation is definite and absolute. KOFOID and SWEZY (1921), howewer, in a study of the Unarmored Dinoflagellata have reported in three species of these organisms the extremely peculiar condition of an occasional spiral path made up of rotation on the long axis to the one direction and spiraling in the orbit to the other direction.



Strombidium No. 2. *Frontonia leucas.* *Paramaecium aurelia.* *Euplotes patella.*

Fig. 2. Spiral paths of different types of ciliates.

Both rotation and revolution in spiral swimming, in addition to moving in the same direction, move together and at the same rate of speed, so that only one rotation on the body axis is completed in one revolution in the orbit. And at no time does one occur without the other. It is this combined movement which gives the spiral its peculiar appearance.

Now, since there is only one rotation on the body axis to one revolution in the orbit, and since the direction of each is the same, the same side of the body of the organism must necessarily be kept to the same side of the spiral, i. e., either to the outside or to the inside of the spiral. This bears out JENNINGS, (1901 p. 369) statement that, "the body of the organism bears a constant relation to the axis of the spiral". The body turns on its axis only as it moves around in its orbit. In this manner the number of rotations is alwavs equal to the number of revolutions. Moreover, the same side of the body, from the point of view of the observer, appears each time at the same relative place in the same side of each spiral turn. This side of the body is constant and characteristic and is definable by some structural or other modifications, e. g., the oral groove in Paramecia, and the oral or aboral side of *Euplotes*, *Oxytricha*, etc. In *Prorodon* and some other ciliates with smooth symmetrical bodies, however, the determination of this side is sometimes difficult. And although this side is structurally definable, all species do not maintain the same side of the body to the same side of the spiral. Some species maintain one side while other species maintain the opposite side to the outside of the spiral. JENNINGS (1900) found *Colpidium colpoda* EHRBG., *Microthorax sulcatus* ENGELM., *Dileptus anser* O. F. MÜLL., and *Loxodes rostrum* O. F. MÜLL., swerving toward a structurally definable side and consequently maintaining this side of the body to the outside of the spiral. Two, however, *M. sulcatus* ENGELM., and *L. rostrum* O. F. MÜLL., kept the oral groove to the inside of the spiral while the other two, *C. colpoda* EHRBG., and *D. anser* O. F. MÜLL., kept the oral groove to the outside of the spiral. In this study, *Paramecium*, *Euplotes*, *Stylonychia*, *Oxytricha*, *Strombidium* no 2, and *Frontonia* no 3, have been found swimming with the oral groove maintained constantly to the inside of the spiral, and the dorsal side of the body always to the outside of the spiral. On the other hand, *Amphileptus*, *Lembadion*, *Colpidium*, *Chlamydodon*, and *Aspidisca*, swim with the oral groove alw ys to the outside of the spiral and the convex side of the body always pointing in toward the center of the spiral. It is not known why the species should differ as to the side of the body maintained to the outside of the spiral. It evidently does not correspond with the structure of the body since ciliates of widely varying types of body structure keep the same side of the body to the outside of the spiral, while other ciliates with practically the same body structure, e. g., *Euplotes* and *Aspidisca*, differ in the side of the body kept to the outside of the spiral. *Euplotes* swims constantly with the dorsal or convex side of the body to the outside of the spiral while *Aspidisca* keeps the flattened or ventral side of the body to the outside of the spiral. Furthermore, this difference does not vary with the direction of spiral path of the organism, since we find ciliates spiraling in the same direction keeping opposite sides of the body to the outside of the spiral, e. g., *Euplotes*, and *Aspidisca*, while other ciliates spiraling in different directions maintain the same side of the body to the outside of the spiral, e. g., *Oxytricha* and *Euplotes*.

This variation, however, does not exist in the individuals of a species. All individuals of any one species maintain the same side of the body constantly to the same side of the spiral. They do not alternate from one side to the other.

Now, although no reason is seen for this variation in the side of the body kept to the outside of the spiral, at the same time no reason is known why one side of the body, in preference to the other, should be "selected" for this position. It would appear that one side might be just as satisfactory as the other. It probably means that, in the evolution of a new species, this side is determined at the time of its origin either in the species itself or in the genus to which the species belongs. Apparently either side may be "selected" and with equally as good results, but once this "selection" is made there is no changing. It becomes absolute. The side of the body of these organisms maintained to the outside of the spiral, therefore, is undoubtedly of absolute specific value and no doubt of some generic value.

The direction of this spiral remains constant and characteristic fo each species, being either over to the left or over to the right. And by over to the left and over to the right we mean here the same as in the preceding part of this paper. The direction never varies from one to the other, but is always either to the one side or to the other. No individuals of any species have been found swimming in spirals in opposite directions, nor has the same individual in any one species been seen alternating from one to the other direction. The direction is constant for all individuals of the same species at all times and in all places. KONSULOFF (1922), however, claims to have seen *Opalina ranarum* PURK., from *Rana temporaria*, rotating in first one direction and then in the other. But a species of *Opalina*, resembling *Opalina ranarum* PURK., but found in the intestine of the American "Bull frog", *Rana catesbiana*, is included in this paper and the spiral studied carefully in a few individuals, but in no case was it found to be first in the one and then in the other direction. The direction was constantly to the right. Since no *Opalina* is known to have been found in *Rana catesbiana*, however, this species may probably be a new one but this is not believed likely. It is believed that what probably appeared to KONSULOFF as a change of direction must undoubtedly have been an optical illusion. This organism is very much flattened, slightly cupped, and more or less transparent, and for this reason it is very easy to believe that the spiral is first in the one direction and then in the other. When the animal is swimming in a horizontal plane, one can close his eyes momentarily and imagine the spiral to either the left or right, and then upon opening his eys and looking quickly at the organism, actually see that which he imagined. This is not a true direction, however; it is an optical illusion but is sometimes taken for the true direction. In these flattened, more or less transparent forms it is sometimes impossible to determine which is the actual direction until the animal is seen swimming directly toward or away from the observer.

Although the direction of this spiral is constant and characteristic for these 164 species, the direction itself is not the same for all species. Some species swim in spirals to the left and others in spirals to the right. But on the other hand, they do not divide equally between the two directions. The majority swim in spirals to the left. In the first 88 species studied this proportion of left spiraling to right spiraling was as 2 to 1, but it has decreased in the totals to 1,6 to 1. In other words, where 20 ciliates in the first group swam in spirals over to the left to every 10 swimming in spirals to the right, 16 in the totals swim in spirals to the left to every 10 swimming in spirals to the right. One-hundred-two of the 164 species swim in spirals to the left and 62 in spirals to the right. Although the apparent number of species spiraling to the left has decreased, this decrease is so small that the preponderance of left spiraling over right spiraling is taken as characteristic for all species. Left spiraling is more characteristic, and probably a more fundamental direction of movement in the ciliates, therefore, than is right spiraling. And as new species are discovered, the majority will probably be found to swim in spirals to the left.

Spiral Swimming in the Genera.

It has been stated above that 51 genera were studied in the first group, 22 in the second, and 16 in the third, but when these were combined, it was discovered that only 68 different genera had actually been studied. The other 21 were repetitions, the same genera but represented by different species, studied at another time, and arranged in a different group. It was also discovered, when these groups were combined, that some genera were represented in one group by a species swimming in spirals to the right, and in the other by a species swimming in spirals to the left. Thus the genera including both species increased in number, while the

Table 3. Comparison of Genera with Direction of Rotation.

Order	Rotating Left	Rotating Right	Genera with both species	No. sp. studied Rotating Left	Right
Holotricha					
	Prorodon			3	
	Nassula			5	
	Coleps			2	
	Tillina			1	
	Loxophyllum			4	
	Ophryoglena			2	
	Colpidium			1	
	Uronema			1	
	Lembus			1	
	Gen.?			1	
		Enchelys			1
		Choenia			1
		Trachelius			1
		Amphileptus			2
		Lembadion			1
		Plagiopyla			1
		Pleuronema			2
		Cyclidium			2
		Opalina			1
		Gen.?			1
			Paramaecium	4	1
			Holophrya	1	1
			Colpoda	2	1
			Trachelocerca	1	3
			Lacrymaria	2	3
			Frontonia	2	2
			Spathidium	2	1
Heterotricha					
	Bursaria			2	
	Metopides			1	
	Spirostomum			3	
	Condylostoma			4	
	Apgaria			1	
	Stentor			3	
		Gen.?			1
			Metopus	2	1

Table ~~4.~~ 3 Comparison of Genera with Direction of Rotation

Order	Rotating Left	Rotating Right	Genera with both species	No. sp. studied Rotating Left	No. sp. studied Rotating Right
Peritricha					
	Halteria			1	
	Strombidium			6	
	Mesodinium			2	
	Caenomorpha			1	
	Dinophrys			1	
		Urocentrum			1
		Carchesium			1
		Epistylis			~~11~~ 2
		Cothurnia			1
			Didinium	1	1
			Vorticella	1	12
			Zoothamnium	1	3
Hypotricha					
	Lionotus			8	
	Chlamydodon			3	
	Chilodon			1	
	Loxodes			1	
	Peritromus			1	
	Kerona			1	
	Urostyla			1	
	Amphisia			1	
	Plagiotricha			1	
	Stichochaeta			1	
	Uroleptus			3	
	Stylonychia			3	
	Microthorax			1	
	Styloplotes			1	
		Dysteria			1
		Aspidisca			2
		Glaucoma			2
		Uronychia			1
		Euplotes			4
			Holosticha	1	1
			Oxytricha	9	2

percentage in which there was an apparent relation between classification and direction of spiral decreased proportionally. Those genera containing both species increased from 4 to 13 while the percentage of taxonomically related species decreased from 95 % to approximately 81 %. And of the 55 genera representing this 81 %, 35 swam in spirals to the left and 20 swam in spirals to the right — a proportion of approximately 1,8 lefts to 1 right.

It is interesting to note, in this connection however, that these 13 genera which contain both species may be divided into three groups; one made up of 5 genera in which a majority of the species spiral to the left, the second with 4 genera in which a majority of the species spiral to the right, and the third composed of 4 genera in which the species are equally divided between right and left spiraling.

Table 4. Genera containing both right and left spiraling species.

Group I. Genera containing a preponderance of left spiraling species.

Name	Number of species L	R
Paramaecium	4	1
Spathidium	2	1
Colpoda	2	1
Metopus	2	1
Oxytricha	9	1
Total species	19	5

Group II. Genera with preponderance of right spiraling species.

Name	L	R
Tracheloccrca	1	3
Lacrymaria	2	3
Vorticella	1	12
Zoothamnium	1	3
Total species	5	21

Group III. Genera in which the species are divided equally into left and right spiraling.

Name	L	R
Holophrya	1	1
Frontonia	2	2
Didinium	1	1
Holosticha	1	1
Total species	5	5

Althoug these 13 genera can not be separated absolutely into genera spiraling to the left and other genera spiraling to the right, eight of these do have a preponderance of either right or left spiraling species, and only the other 4 genera have an equal division of species into left spiraling and right spiraling. Of these four, only one, *Frontonia*, has more than one species to the left and one species to the right. In group I, no genus contains more than one right spiraling species. All the other species are left spiraling. In the genus *Paramaecium*. this right spiraling species is *P. calkinsi* WOODRUFF. In *Colpoda* the right spiraling species is unidentified and is given as *C.* sp. no. *1*, but the classification is believed correct. In *Spathidium*, the right spiraling species is *S. spathula* and appears correctly classified. The right spiraling species of *Metopus* is a new species and is listed as *M.* sp. no. *1*, but it is also believed correctly classified. In the *Oxytricha*, however, the right spiraling species is a new species of marine *Oxytrichidae* and was believed to belong to the genus *Oxytricha*, but there is a possibility of its being a new genus.

In group II, only one genus contains more than one left spiraling species. In the genus *Trachelocerca*, the left spiraling species is *T. tenuicollis* Quenn., and its classification appears correct. In *Lacrymaria* the species *cohnii* S. K., and a new species, given here as *L.* sp. no. 1, spiral to the left, and of these two, *L. cohnii* S. K. already mentioned, appears incorrectly classified. The left spiraling *Vorticella* is a new one listed as *V.* sp. no. 3, but its classification appears correct. The left spiraling *Zoothamnium* is *Z. marinum* MERESCHK., and the direction given is that of the colony while swimming with the pedicle in front. Since the individual zooids may face either backward or forward, back toward the pedicle or away from it toward the front, and since the direction of movement is determined by the direction in which the majority of these zooids face, movement in either direction, — toward or away from the pedicle, is considered as forward movement and the direction of the spiral determined accordingly. Most of these colonial forms, however, especially where the colonies are very large, swim with the compound pedicle in front, and this condition has not been found to vary from one to the other within any one species. All species in group III, appear to be correctly classified.

Spiral Swimming in the Families.

The total number of families represented in the 164 species increased also but very slightly over the number represented in the first 88 species. Only 2 additional families have been studied since that time, making a total of 24. The other families listed by number in the three groups, are only repetitions by different species,

Table 5. Comparison of Families with their Direction of Rotation.

Order	Families Rotating to Left	Families Rotating to Right	Families with both species	No. spec. studied Rotating Left	No. spec. studied Rotating Right
Holotricha					
	Colepidae			2	
	Lembidae			1	
	Fam.?			1	
		Opalinidae			1
		Fam.?			1
			Paramaeciidae	4	1
			Prorodontidae	9	1
			Enchelyidae	3	2
			Trachelocercidae	3	7
			Tracheliidae	4	3
			Ophryoglenidae	7	5
			Pleuronemidae	1	4
Heterotricha					
	Stentoridae			3	
			Bursariidae	5	1
			Spirostomidae	8	1
Peritricha					
			Halteriidae	10	1
			Gyrocoridae	2	1
			Vorticellidae	2	20
Hypotricha					
	Lionotidae			8	
	Chlamydodontidae			5	
	Peritromidae			1	
		Dysteriidae			1
			Oxytrichidae	21	3
			Euplotidae	2	9

as in the genera. The spiral in only 10 of these 24 families may be said to bear a definite relation to taxonomy, and of these 10, only 4 contain more than one species each, — *Colepidae* 2 species, *Stentoridae* 3 species, *Chlamydodontidae* 5 species, and *Lionotidae* 8 species. Each of these 4 families spirals to the left. The 14 families containing both species are made up of three classes of genera, left spiraling, right spiraling, and genera with both kinds of species, — 26 genera with 52 species spiraling to the left, 17 genera with 26 species spiraling to the right, and 12 genera with 22 left spiraling and 31 right spiraling species. Although the direction of spiral swimming in these 14 families is apparently unrelated to the taxonomy of the organism, 9 of the 14 families, *Parameciidae*, *Prorodontidae*, *Pleuronemidae*, *Bursariidae*, *Spirostomidae*, *Halteriidae*, *Vorticellidae*, *Oxytrichidae*, and *Euplotidae*, do, however, contain each four or more times as many species spiraling in one direction as in the other. That is, each of these 9 families is either strongly right spiraling or strongly left spiraling, — 6 containing 4 or more times as many left spiraling species as right spiraling species, and the other 3 containing 4 or more times as many right spiraling as left spiraling species.

Direction of the spiral path in free swimming, therefore, is of undoubted generic value and probably of sub-family value, and must be taken into consideration hereafter in any revision of the classification of these animals. Thus a left spiraling individual belongs absolutely to a left spiraling species, and in approximately 81 % of the cases this species itself will belong to a left spiraling genus. It would appear from this that the line of division separating the individuals into the various taxonomic groups, corresponds closely with the line of division into right spiraling and left spiraling groups.

Relation of Oral Groove to Direction of Spiral.

Many ciliates have a deep and prominent oral groove extending from the anterior extremity, diagonally across the body of the organism to its mouth, e. g. *Paramaecium*, and *Lembadion*. Jennings (1901, p. 371) gave the oblique position of this groove or peristome as one of the mechanical causes of revolution on the axis of progression. In 1902 (p. 233) however, in experimenting with pieces of infusoria, he decided that the oral groove had nothing to do with causing revolution, since pieces of ciliates without a groove revolved equally well. But, nevertheless, in 1906 (p. 45) he still held the idea that the oral groove had some influence upon the direction of spiraling. He believed that the oral cilia, probably by beating more effectively than the body cilia, caused the organism to swerve, and this swerving combined with rotation and forward movement, produced a spiral path. Schaeffer (1920 p. 133) thought there were numerous animals in which a correspondence existed between the axis of the structure and the spiral path of the organism, having in mind the curved form of the body of certain ciliates and the oral groove of Paramaecia. In view of this fact, and since a great many of the 164 ciliates listed in this paper have a prominent oral groove, a comparison was made of the direction of this groove with the direction of the spiral in order to determine, if possible, just what effect the groove did have in determining the direction of the spiral.

One would ordinarily suppose, according to the laws of mechanics, that an animal would spiral in the same direction as that of a groove running obliquely across its body. If this groove extended from left to right, we would expect the animal to swim in spirals from left to right. This would appear to be the direction which would offer least resistance to the forward progress of the organism. That this is true, can be demonstrated with a Paramaecium modeled out of some light material such as paraffin, being careful to have the groove correctly placed and the animal properly balanced. If a thread is now attached to the center of the anterior end of this model and pulled rapidly through the water, it will rotate in the direction of the oral groove. The same thing can be shown with a Paramaecium modeled out of corn pith, a needle carefully run trough the center as an axis, and the points of the needle placed in sockets which leave it free to rotate easily. If now one blows directly down this groove from the anterior end of the animal, the model will spin around in the direction of the groove as before. The force of the air against the groove compels rotation in this direction. This would seem to be an exact duplicate of that which should occur in a free swimming Paramaecium. It should make no difference whether the water is forced through the groove of the Paramaecium or whether the Paramaecium forces itself through the water. The results should be the same in either case.

Sixty-seven of the 164 species of ciliates studied in this paper were found to have a distinct oral groove, e. g., *Paramaecium Lembadion, Euplotes, Spirostomum, Condylostoma*, etc. The direction of this groove is the same for all these sixty-seven species. It extends in every case diagonally across the animal's body from left to right. By the terms from left to right we mean, e. g., in a *Paramaecium*, beginning at the mouth near the center of the left ventral side of the body of the organism, and extending diagonally across the body to the right, near the anterior extremity, having in mind the ventral side of the animal and the left and right of the observer. (Fig. 3.)

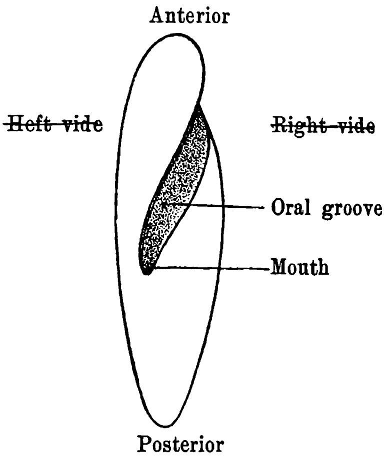


Fig. 3. Oral groove of *Paramaecium*.

We would expect, according to the reactions of the models, that the direction of the spiral in all 67 of these ciliates would be from left to the right, but this is not the case. Forty-eight swim in spirals in the opposite direction. Only 19 species swim in spirals in the direction of the groove. More than two out of every three ciliates with an oral groove, therefore, swim in spirals in a direction directly contrary to that considered as requiring least effort. But on the other hand those species without an oral groove divide about equally into left spiraling and right spiraling, — 54 swimming in spirals to the left and 43 in spirals to the right. This increased tendency to spiral to the left in those species having an oral groove, would appear to support Jennings, (1906 p. 45) idea that the cilia in the oral groove beat more effectively than those elsewhere, thus causing the body to swerve or revolve in a direction opposite to that of the groove. This might be taken as a satisfactory explanation of a left-hand spiral, but it cannot explain either the cause or direction of a spiral to the right. Neither can it account in any way for the cause or direction of a spiral in those 97 species which have no groove. This explanation would mean simply that those ciliates without a groove could not swim in spirals. But since all ciliates do swim in spirals regardless of whether a groove is present or absent, this explanation is not sufficient. Any explanation, to be satisfactory must account for both right and left spiraling in both classes of ciliates, — those without a groove as well as those with a groove.

Moreover, if the stronger beating of the oral cilia caused the organism to swerve away from the groove instead of with it, we would expect to find the greatest swerving and consequently the widest spiral, in those ciliates having the strongest and most prominent oral cilia. But we find instead, that those ciliates having the most prominent oral groove, in which we would expect to find the strongest oral groove cilia, swim in the narrowest spirals. *Paramaecium*, and *Euplotes* are examples of ciliates with a prominent oral groove swimming in this manner. *Paramaecium* has probably the most prominent oral groove of any of the ciliates, and it apparently swims in the narrowest spirals. *Euplotes*, also with strong oral cilia swims in narrow spirals and at the same time this spiral is in the direction of the groove. We find the widest spirals in those ciliates without an oral groove. *Urocentrum* and *Didinium* with apparently no oral cilia swim in extremely wide spirals. The oral groove, therefore, appears to have no influence whatever upon either the cause or the direction of a spiral.

Jennings (1906, p. 45), on the other hand, believed that the body cilia themselves were partly responsible for the swerving in these organisms. He believed swerving due to "a peculiarity in the stroke of the body cilia, by which on the whole they strike more strongly toward the oral groove than away from it, thus driving the body in the opposite direction". He thought the body cilia to the left of the oral groove, which strike normally toward the left, or away from the groove, changed direction of contraction so as to strike to the right or toward the groove, the result being to oppose rotation to the left, and to increase swerving. This sort of explanation would necessitate a frequent slowing down, and probably a complete cessation of both rotation and forward movement, and a frequent change in the width of the spiral, for as Jennings, continuing, says: "The width of the spiral, or the final complete cessation of rotation on the long axis which sometimes occurs, depends upon the number and effectiveness of these cilia on the left side that beat toward the groove." But we have seen already that in normal free swimming both rotation and revolution are continuous processes unbroken by frequent stops. Moreover, we have found the width of the spiral to be fairly constant and characteristic for each species and it does not alternate from a wide toa narrow spiral at frequent intervals. We strongly doubt, therefore, that this is the method of contraction of the body cilia which is responsible for the swerving, and consequently for the revolution in these organisms.

JENNINGS also in 1906 (p. 46) in speaking of the movements of the cilia in Paramaecia, says. "The same movements of the cilia which carry the animal through the water also bring it its food. The oral cilia cause a current of water to flow rapidly along the oral groove. In the water are the bacteria upon which the *Paramaecium* feeds; they are carried by this current directly to the mouth." But in these experiments no such current has been found to exist in free swimming. That there is no current down the oral groove at this time, may be shown by the action of particles along the path of the organism. These particles are found to remain immobile as the organism passes regardless of whether the particles are on the groove side of the animal or on the opposite side. Now if there was a feeding current at this time these particles would be drawn rapidly toward the animal as it approached, and would pass rapidly to the rear as it passed. But this has not been seen to occur. The feeding current is set up after free swimming ceases. The beginning of this feeding current can be distinctly seen e. g. in *Paramaecium calkinsi* WOODRUFF, after free swimming has ceased. Moreover, if there was a feeding current down the oral groove in free swimming, strong enough to carry bacteria and other food material to the mouth of the organism, the supposition is that the force of this current would be strong enough to influence the direction of the spiral toward that of the groove. But since 48 species of ciliates, out of 67 which have a distinct oral groove, revolve in a direction opposite to that of the groove, we are strongly inclined to doubt the presence of a feeding current in any ciliate during free swimming.

On the other hand, in connection with this study of the oral groove, a few ciliates have been observed curving the body in such a way as to form one or more segments of a spiral, and then to follow the direction of this curve in spiraling. The following ciliates have been seen to swim in this manner: *Lionotus wrzesniowskii* S. K., *Lionotus* sp. no 4, *Chlamydodon* sp. no 1, *Choenia teres* DUJ. and *Trachelocerca* sp. no 1.

Relation of Size and Shape of Body to Direction of Spiral.

Ciliates of a great variety of sizes and shapes have been studied, but size and shape have not been considered as factors in spiral swimming in the preceding part of this paper. JENNINGS (1901, p. 371) gives unsymmetrical form of body as one of the mechanical causes of revolution, but later in the same paper says: "The unsymmetrical form seems rather an adaptation to this method of swimming — a consequence of it." In 1902 (p. 233), however, he found the spiral not due to geometrical form or peculiarity of the shape of body, but rather to the direction in which the cilia strike. SCHAEFFER (1920, p. 132) in a very convincing argument states that shape of body has nothing to do with causing the spiral path.

The sizes of these 164 species of ciliates range from 34 to 1140 μ in length, and from 17 to 308 μ in width. The 102 ciliates spiraling to the left vary from 34 to 1140 μ in length and from 21 to 308 μ in width. The 62 spiraling to the right vary from 26 to 492 μ in length and from 15 to 174 μ in width. This looks as if all the larger species spiral to the left and the smaller ones to the right. But there are some small ones swimming to the left and some large ones swimming to the right so that when the sizes of each group are averaged, the length is found to be nearly the same for both groups. Those species spiraling to the left have an average length of 181 μ and those spiraling to the right have an average length of 167 μ. There is apparently a slight preponderance of left spiraling in the larger ciliates. This preponderance is shown in table 9.

Almost every imaginable body form has been included in this study and the results of a comparison of the various types are as follows:

Now if the spiral path was determined or influenced by the shape of the body, we would expect all species of a given general type of body structure to spiral in the same direction. But *Coleps* and *Stentor* are the only genera of more than one species in table 6 in which all members spiral in the same direction. Moreover, if shape of body determined direction of spiral, we would expect to find the greatest difference in this direction in those species having the most pronounced difference in body structure. The majority of each of these groups, however, except for the family *Vorticellidae*, regardless of shape of body, swim in spirals to the left. Ten out of eleven Vorticellas spiral to the right. The *Vorticellidae* and the *Halteriidae* are very much alike except for the pedicle, and they are placed here in the same general class, and we would expect the least difference in these two in the direction of spiral. We find, however, the most pro-

Table 6.

Correspondence between general shape of body and the direction of the spiral path.

Type of body	No. of species spiraling to Left	to Right
1. With prominent oral groove *Paramaecium, Lembadion, Colpoda* etc.	48	19
2. Flattened body		
Frontonia	2	2
Loxophyllum	4	1
Loxodes	1	—
Apgaria	1	—
Chilodon	1	—
Oxytricha	21	3
3. Cylindrical		
Prorodontidae	9	1
Coleps	2	—
Enchelys		1
4. Short cylindrical to spherical		
a) with pedicle *Vorticellidae*	2	20
b) without pedicle *Halteriidae*	10	1
5. Bugle-shaped *Stentoridae*	3	—

nounced difference. Ten out of eleven *Halteriidae* spiral to the left whereas ten out of eleven *Vorticellidae* spiral to the right. It is not conceivable how this difference could be caused by the pedicle alone.

On the other hand we would expect those groups having the most nearly symmetrical form of body to be on the borderline between left spiraling and right spiraling, i. e., we would expect approximately as many species spiraling to the right as to the left. The *Prorodontidae* is a good example of such a group, but instead of dividing equally into the two directions, 9 out of every 10 spiral to the left. This analysis shows again that the general shape of the body of a ciliate, has no influence upon the direction of the spiral path followed by these same organisms.

We do find, however, that where all the species of any one genus or family have a distinct, clear-cut, structural plan of organization, that a much closer correspondence exists among the species within these genera and families, in the direction of their spiral paths. The family *Halteriidae*, e. g., is composed of species having the same general structure and organisation, and all except one out of eleven species spiral to the left. The *Vorticellidae* have the same general structural plan running throughout the species and the direction of the spiral in 20 of the 22 species is over to the right. The structure of all members of the family *Oxytrichidae* is based upon the same general plan and 19 out of 22 spiral to the left. In the *Euplotidae*, with the general form and structure of all members the same, 9 out of 11 spiral to the right. Not enough difference is seen in the shape and structure of *Oxytricha* and *Euplotes* to warrant this difference in direction of spiral. The members of the family *Lionotidae* have the same general type and all swim in spirals to the left. The bugle-shaped stentors all spiral to the left.

But let us now in contrast, examine that heterogeneous family, the *Ophryoglenidae*. This family is clearly the dumping ground for all species which fail to fit in elsewhere. There is no clear-cut structural plan but rather a mixture of plans, and the spiral in 7 species out of 11 is over to the left, while the spiral in the other 5 is over to the right.

Relation of Speed to Spiral Swimming.

SCHAEFFER (1920, p. 135), found that lowering the temperature of Paramaecia decreased forward movement and increased the number of spiral turns. This relation of speed to number of spirals has been found by another method, in the various types of cilliates considered in this paper. Speed of swimming and length of spiral have been determined in 29 different species, and when speed of an organism is compared with length of its spiral, we find that a definite relation exists between these two.

Increasing the speed decreases the number of spirals within a given distance, and decreasing the speed increases the number of spirals. Great speed is associated with long spirals and few spiral turns, while slow movement is associated with short spirals and many spiral turns. Those ciliates moving with greatest speed swim in open spirals, with the fewest spiral turns, while those ciliates moving with least speed swim in close spirals with many spiral turns. In general, therefore, we may say that the length of spiral varies as the speed of swimming. The greatest uniform speed observed is that of *Paramaecium caudatum* EHRBG., swimming 2647 microns per second and moving in a spiral 1731 microns in length. The slowest swimming ciliate observed was *Kerona polyporum* EHRBG., having a speed of 488 microns and a spiral of only 222 microns. There is in fact a gradual increase in length of spiral, from the slowest moving ciliate to the swiftest ciliate. This is shown in the following table.

Table 7.

Relation between speed of swimming and length of spiral turns.

Name	Speed in microns	Length of spiral in microns
Slow moving		
Kerona polyporum EHRBG.	488	222
Euplotes charon O. F. MÜLL.	1050	282
Trachelocerca tenuicollis QUENN.	1111	303
Urocentrum turbo O. F. MÜLL.	700	333
Swiftly moving		
Frontonia sp. no. 1	1634	1000
Stentor coeruleus EHRBG.	1500	1140
Nassula ambigua STEIN	2004	1185
Paramaecium aurelia O. F. MÜLL.	2000	1500
Paramaecium caudatum EHRBG.	2647	1731

In addition to this relation between speed and length of spiral, there is an apparent relation also between left-hand spiraling and great speed. All the rapidly moving ciliates listed above swim in spirals to the left and of the slower ones, half swim in spirals to the right and half in spirals to the left. The speed of the left spiraling ciliates ranges from 285 microns per second to 2647 microns per second, while speed for right spiraling ciliates ranges from 526 microns to 1250 microns per second. Distance traveled in one complete spiral measured in body lengths, varies from 1,27 body lengths to 7 body lengths for left spiraling species and from 1 to 5,25 body lengths for right spiraling species. Measured in microns the length of spiral varies from 222 microns to 1731 microns for left spiraling species and from 282 microns to 840 microns for right spiraling species.

Although there is a relation therefore, between left-hand spiraling and speed of swimming, speed being apparently linked up in some way with this direction, this relation cannot be said to be absolute since several slow moving ciliates swim in spirals to the left and some rapidly moving ones spiral to the right. These swiftest ciliates will also, in general, be found to be the largest ciliates, and since we have already found that the largest ciliates swim usually in spirals to the left, it would appear that speed, large size, and left spiraling are all three linked up together in some way. Large size, therefore, is a more perfect expression of evolutionary tendency in the ciliates than small size, and great speed is the most perfect expression of locomotion in the ciliates. See tables 8, 9, and 10.

The conclusions, however, are based on a relatively small number of species. Speed should be determined for a much larger number of species. It was not determined in more species in this paper for several reasons. The determination of speed of an organism was made with a stop watch while the animal was swimming freely and entirely across a field of a given diameter. In many cases this was overlooked at the time the other information was collected and when a later attempt was made the reactions of the organism were not satisfactory. In some cases the stop watch was out of order, in other cases it was impossible to induce sufficient free swimming to make satisfactory tests.

Relation of Salt Water Habitat to Spiral Swimming.

At the beginning of this work there appeared to be a difference in the direction of the spiral of fresh water ciliates as compared with that of salt water ciliates. In a few instances where genera e. g. *Trachelocerca*, *Oxytricha*, and *Euplotes* could not be classified as either right or left, the difficulty was due in each case to a single species rotating in the opposite direction, and these species were from salt water. In order to find out what influence, if any, the culture medium itself had upon the direction of spiral, comparisons were made of the spiral paths of fresh water ciliates with those of salt water ciliates. There are 92 fresh water ciliates and 72 salt water ciliates in the entire list of 164 species. Fifty-three of these 92 from fresh water, or 57 %, spiral to the left, while 49 of the 72 from salt water or 69 % spiral to the left. According to these figures 2 out of every 3 salt water ciliates swim in left-hand spirals while the fresh water ciliates divide about equally between the two directions. If the salt water itself, however, had any direct influence in determining the direction of the spiral, we would expect some fresh water species transferred to it, if such transfer could be made, to change direction from the right over to the left. Several ciliates have been reported found in both fresh water and salt water, but attempts to transfer them from one to the other have not been successful in most cases. In the few ciliates which it has been possible to transfer from fresh water to salt water without injury to the organism, however, the spiral has remained constant. *Frontonia leucas* EHRBG. was transferred into as high as 25 % sea water without changing the direction of spiral. *Euplotes patella* EHRBG. was transferred gradually from fresh water to pure sea water but the spiral remained the same. Another Hypotrichan unidentified, was transferred back and forth from fresh water to sea water with no change in spiral. *Euplotes charon* O. F. MÜLL. has been found in both sea water and fresh water, and seems to live equally well in either. Now if either sea water or fresh water in itself, had a tendency to influence direction of spiral, we would not be surprised to find this species of Euplotes spiraling to the left in sea water and to the right in fresh water. But this does not occur. The direction of the spiral is the same in both. It does not change when the organism is transferred from one to the other. The culture medium itself, therefore, has no direct influence upon the direction of the spiral path of the ciliates. But since left spiraling, as we have already seen, is a more characteristic direction of movement in these organisms, we may say, based upon this fact, that left spiraling is a more perfect expression of movement in the ciliates than is right spiraling. The larger proportion of left spiraling in sea water as compared with fresh water, may indicate that the ciliates probably originated in sea water. Or, assuming that left spiraling and right spiraling are evolved equally often in phylogeny, sea water forms which are largely left spiraling are better coordinated than the fresh water forms where right spiraling species still exist in greater numbers.

Relation of Temperature to Spiral Swimming in Paramaecia.

JENNINGS (1901 p. 370), in attempting to find a solution to the question of how an unnsymmetrical organism without eyes or sense organs to guide it by the position of objects at a distance, was able to maintain a definite course through the trackless water where it might vary from the path to the right, left, up, or down, or in any intermediate direction, says: "One of these organisms, as, for example, *Loxodes* or *Paramaecium*, 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. To obviate this difficulty, revolution on the long axis is combined with forward movement of the organism." He believed rotation (he uses the word revolution), on the long axis was a device found generally among smaller water organisms for enabling an unsymmetrical animal to follow a straight course. He thought rotation, by turning the body in successive directions caused an exact compensation of the swerving from the course in any given direction, by an equal swerving in the opposite direction. In 1906, p. 44, JENNINGS stated that this swerving — this continual turning of the anterior end away from the oral side — was due to the more effective beating of the oral cilia rather than to unsymmetrical form. In the same paper (p. 46), he stated that the device of rotation on the axis was "marvelously effective, since it compensated with absolute precision for any tendency or combination of tendencies, to deviate from a straight course in any direction whatsoever".

Now if this rotation compensated, as JENNINGS says, with absolute precision for any tendency to deviate from a straight course, we would expect a *Paramaecium*, or any other ciliate for that matter, in normal free swimming, to proceed through clear water in a straight course with no marked deviation whatsoever to the right, left, up, or down, neither in gentle curves nor in abrupt changes of direction. The organism would be compelled to move in straight paths in all free swimming. Rotation would permit no other kind of paths. And under such conditions it would be nesessary for free swimming to cease before a change of direction could be effected. But do these organisms swim in this manner? Is it a fact that they swim in straight paths only? Or are not these straight paths broken into by gentle curves and abrupt turns?

Now taking up the question of the effect of rotation upon these paths, would rotation itself produce straight paths and prevent swimming in circles? Let us now recall, in this connection, that there is only one rotation of the body on its axis to each revolution of the body in its orbit; that both rotation and revolution move together and at the same rate, thus causing the same side of the body to be constantly to the same side of the spiral, i. e., either to the outside or to the inside. Now the side of the body toward which an animal swerves is constantly to the outside of the spiral, since it is this swerving which produces the spiral. This swerve may be likened to a "pull" on the outside of the body, and would continue as long as free swimming continued, since the cilia causing it would undoubtedly continue to beat. According to JENNINGS explanation, however, this swerve would continue in any one path only until a certain width of spiral was reached and then it would cease. After that this width would be maintained without any additional swerving.

But in the ciliates this pull is not a discontinuous process. It is continuous, and would tend constantly to pull the anterior end of the organism away from the center of the spiral. The width of the spiral therefore, would increase with each spiral turn. The fact that the organism is swimming in a forward direction at the same time would not alter the situation. JENNINGS (1906, p. 44) compared this swerve to the action of a boat pulled stronger on one side than on the other, which as a result, would move in circles. But, however, if the stronger pull of the boat be switched to the other side, the boat would move back in the opposite direction. Now if this stronger pull should be switched from side to side at regular intervals, the path of the boat would be a series of alternating curves to the right and left, somewhat like that shown in Fig. 4. In this manner the boat would move forward in

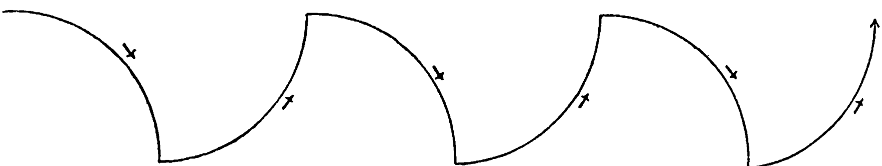


Fig. 4. Path of a boat pulled ~~lardo ou sur~~ stronger on one side, and this stronger pull alternated from side to side.

a path along a relatively straight general axis. Now JENNINGS believed rotation had the same effect upon the path of a ciliate as the change of stroke has upon the path of a boat, except that a ciliate is a ble to move in three dimensional space and rotate on the body axis, while the boat can move only in a horizontal plane.

But this swerve in the ciliates does not change as the change of stroke in the pull of a boat. The swerve does not alternate from the outside of the spiral to the inside. It is always to the outside and could be represented by a boat only if it were possible for this boat to move in three dimensional space. Supposing this were possible and this boat should be pulled stronger on one side than on the other; if this pull were continued on this same side, we would have exactly the same situation as in the ciliates. The boat would move forward under such conditions, in a spiral of a constantly increasing width. So it is in the ciliates. They would swim in a spiral which would become wider and wider as the anterior end of the organism pointed more and more away from the direction of forward progression. Very soon the body of the organism would point out at an angle of 90 degrees from the original direction and the animal would then move out in wide circles. See Fig. 5. Rotation could not compensate, therefore, in the ciliates for the tendency to swim in circles. They would swim in circles in spite of rotation.

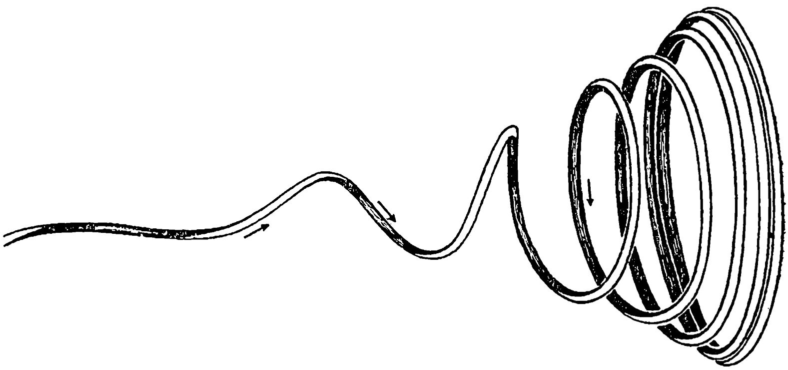


Fig. 5. Representation of the path of a *Paramaecium* having a stronger contraction of the oral cilia.

Moreover, some ciliates swim with the oral cilia constantly maintained to the outside of the spiral, as we have already seen, e. g., *Amphileptus, Lembadion, Chlamydodon.* Now if, as JENNINGS believed, the oral cilia caused the swerve in these organisms, these particular species, at least, would swerve in a direction away from the side on which the groove is located, which would be in toward the center of the spiral. But they do not swerve in toward the center but out from the center and toward the oral cilia instead of away from them. It is difficult to believe these oral cilia would cause some ciliates to swerve toward the oral groove and others to swerve away from it.

Furthermore, since many ciliates which possess no oral groove and no distinctive oral cilia swim nevertheless in spirals, swerving out away from the center, e. g., *Prorodon,* similar to the swerving of those ciliates with a groove, the cause of spiral movement is not generally related to the possession or absence of either oral cilia or oral groove.

It is therefore, gratuitous to assume in *Paramaecium,* or any other ciliate that the oral cilia are in any way connected with causing a spiral without actual and definite proof. As they stand, the facts derived from the study of a large number of ciliates speaks against such a conclusion.

It must be assumed, therefore, that ciliates spiral in spite of the absence of oral cilia. JENNINGS (1902) found by operative procedure that pieces of ciliates of any shape or size, dissected from either the anterior part of the body with part of the oral groove, or from the posterior part of the body where there was no groove, continued so swin in spirals similar to the original organism regardless of the presence or absence of a groove. The groove had no part in determining the spiral path. Moreover, one can often see a dividing *Paramaecium* or a pair of conjugating Paramaecia, and in every case they swim in spirals in the same manner and in the same direction as the normal organism.

What then is the cause of the spiral? No definite answer can yet be given. Spiraling in ciliates is too uniform a phenomenon to be caused by a variety of heterogenous morphologies, differentiation of body or motile organs. It is altogether improbable that spiraling is due now to a stronger beat of the oral cilia, now to a weaker beat of oral cilia, now to assymetrical body, etc. When it is seen that species occur in symmetrical ciliates devoid of oral cilia, it is probable that so important a phenomenon as spiraling has the same fundamental cause in all cases.

SCHAEFFER (1920) found that he could reduce the length of stretches of straight lines in the paths of Paramaecia by lowering the temperature. The organism then swam in short broken paths. He also found that man, when blindfolded, walked and swam always in large circles.

The question, therefore, arose whether after all, Paramaecia, and the other infusoria, did actually swim in straight paths only, in all free swimming, as JENNINGS (1906, p. 46) thought, due to rotation on the body axis, or whether they did not also move in large circles outside of and in addition to the spiral caused by rotation on the axis and revolution in the orbit, somewhat similar to the circles in which animals limited to two-dimensional space moved. In an attempt to find an answer to this question a study was made of a large number of paths of Paramaecia at various temperatures in a large dish.

Table 8.

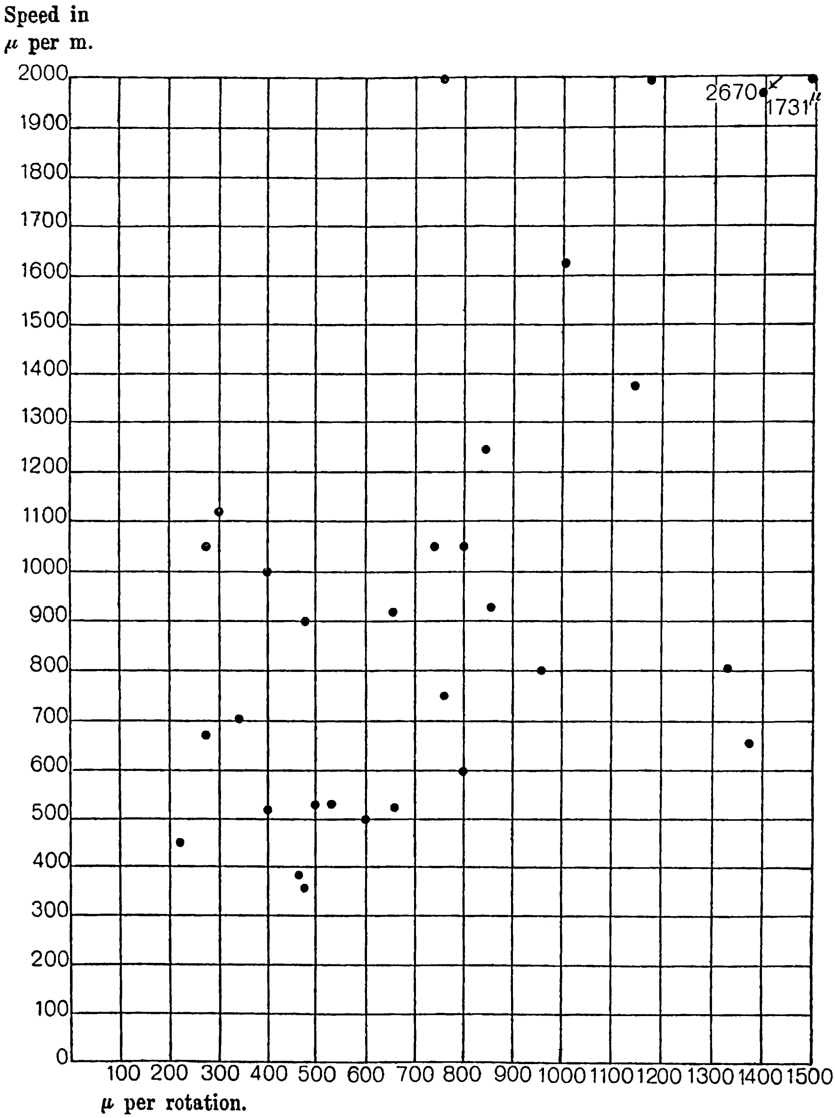
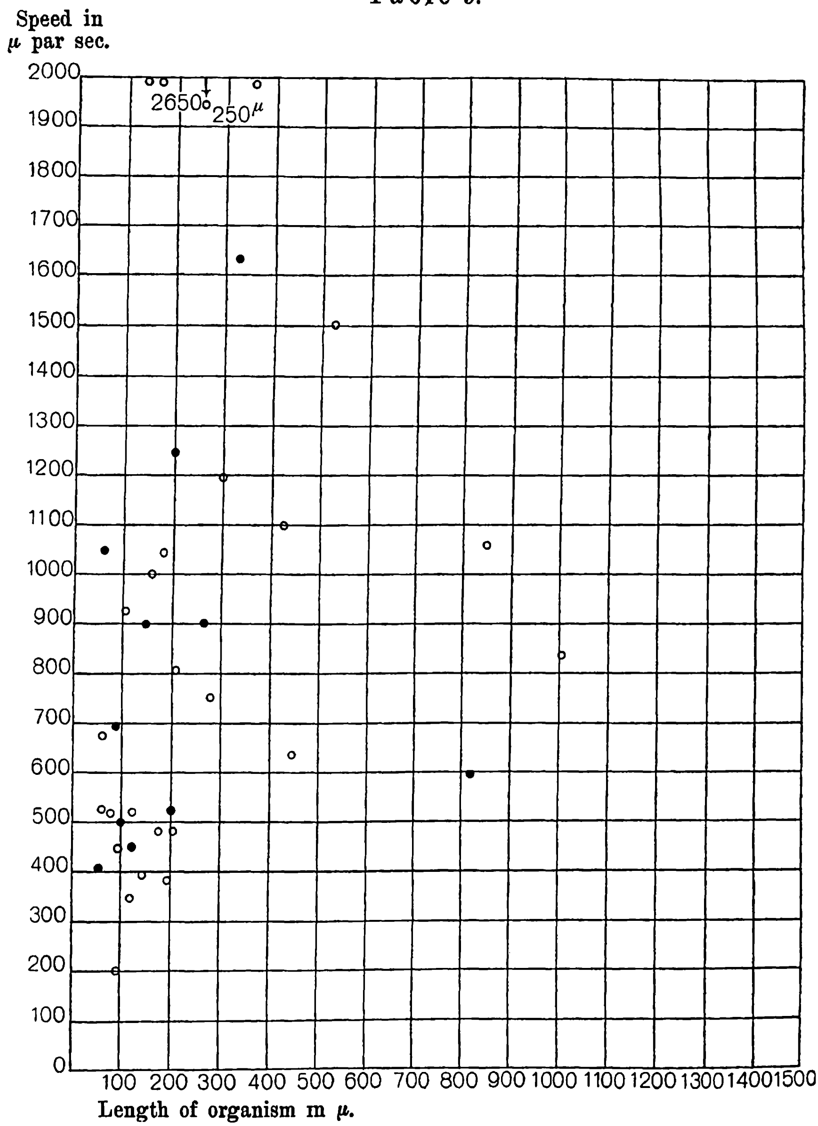


Table 8. Correlation between great speed and length of spiral turns.

Materials and methods.

A special dish constructed of a sheet of plate glass, 2 feet by 3 feet, onto the sides and ends of which strips of glass about 4 inches high were sealed with a preparation of resin, was made up

Table 9.



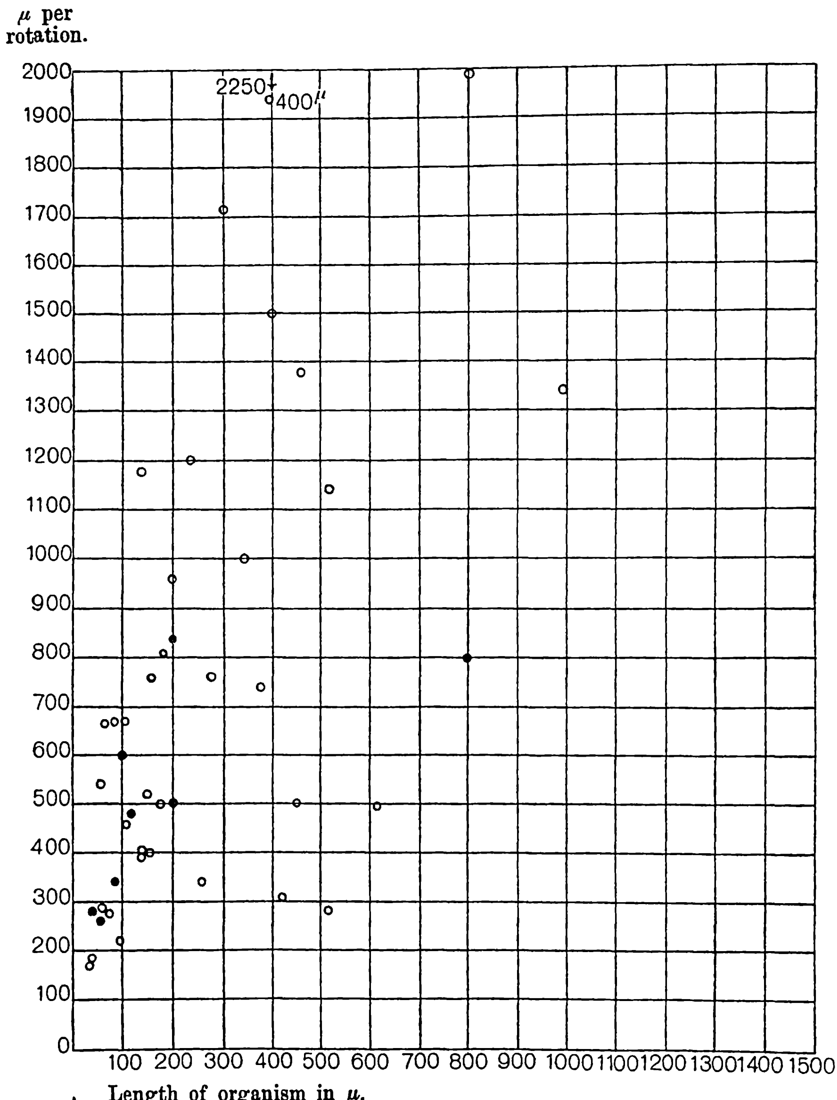
○ = Left spiraling.

● = Right spiraling.

Table 9. Correlation between great spred. and large size, gread speed. and left spiraling, and large size and left spiraling.

for this work but a large petri dish 15,5 inches in diameter by 4,5 inches deep was later found to give satisfactory results and

Table 10.



○ = Left spiraling.

● = Right spiraling.

Table 10. Correlation between length of spiral, size of body, direction of spiral, and speed of swimming.

was much easier to handle. The bottom of the dish was covered with carbon paper in order to make the Paramaecia more easily seen. An ordinary sixty watt electric light bulb was aranged on the side of the dish opposite to that of the observer in such a way as to throw horizontal beams of light through the culture medium. The dish was then filled with distilled water into which some boiled hay infusion was dialyzed. This dialyzing was done in order to keep the infusion free from all particles of hay and dirt and at the same time have a solution as nearly normal as possible. The culture medium was later found to be just as satisfactory when filtered through ordinary filter paper. The Paramaecia were discharged from a small pipette into this solution and their paths traced with a pantograph, the paths being followed with the naked eye looking through a small glass tube inserted in the end of one arm of the pantograph, while the path, reduced one half, was traced by a pencil inserted in the end of the opposite arm of the pantograph.

Tests were made at various degrees of temperature from 11° C to 40° C. One hundred and fifteen separate paths of varying lengths were traced. These had a total length of more than 36 meters, of which 14,9 m. were stretches of straight lines.

11° C. At 11° C the Paramaecia moved rapidly in short broken lines, darting here and there and crossing their paths several times. In no case did they get far away from the starting point but were usually lost in a short time near the side of the dish or on the bottom, thus ending the experiment. Seven paths were traced at this temperature having a total length of 124 centimeters, the longest single path measuring 35 centimeters, being very irregular, and containing 9 loops. The longest single stretch of straight line at this temperature measured 7,5 cm. Twenty-two distinct changes of direction were made in this path, 9 to the right and 13 to the left. By change of direction is meant a deviation from a straight line, or a deviation from the projection of the original direction, by at least 22,5 degress and continued for at least twenty body lengths. The 22,5 degress is an arbitrary selection made because this angle is easy to use, since it is half of 45 degress and exactly divisible into 360 degrees. Another angle either smaller or larger might have been used with probably as satisfactory results.

If a *Paramaecium*, therefore, deviated from its original direction by as much as 22,5 degrees, the two paths, — before and after the change should certainly not be considered as one straight line. The only place where such a path might be considered a straight line is a deviation which is not continued for a sufficient distance.

Twenty body lengths, equal to about 4 spiral turns, was selected as a distance entirely sufficient for this purpose. If, therefore, an organism deviated from the original direction by as much as 22,5 degrees, and continued this course for approximately twenty times its own body length, this was considered a change of direction. The Paramaecia show no tendency at this temperature to swim in circles, but there is a marked tendency to frequently change direction of swimming.

Table 11.

Effect of temperature upon the spiral path of Paramaecia.

	11° C	20° C	Room temp.	22° C	25° C	29° C	Total
Number of paths	7	10	47	23	21	7	115
Total length of paths, in cm	124	247	1060	802	1130	251	36 m
Average length of paths	17,5	24,7	22,5	35,5	54,5	33	
Longest single path	35	46	51	63	183	78	
Longest single distance in a relatively straight line in one path	3	25	31	25	20	28,5	
Total distance in straight lines	3	165	640	333	312	35	1493 cm

Number and direction of turns		11° C LT	11° C RT	20° C LT	20° C RT	Room temp. LT	Room temp. RT	22° C LT	22° C RT	25° C LT	25° C RT	29° C LT	29° C RT	Total LT	Total RT
	Near surface	24	14	9	4	20	24	48	71	83	85	—	—	186	198
	Midway	8	1	0	4	26	23	8	8	—	—	18	10	46	660
	On bottom	3	7	2	3	21	33	10	13	18	65	30	29	84	150
		35	22	11	11	67	80	66	92	101	150	46	39	330	394

LT = left turn. RT = right turn.

The above figures do not take into consideration the up and down deviations from the straight line, since the general direction of movement from the point of view of the observer, remained the same. Supposing now that these up and down turns were as frequent as those to the left and right, the number of turns would be greater in all cases by from, say, 25 % to probably as much as 50 %.

20° C. At 20° C the Paramaecia moved freely, swimming in long straight lines. All the paths are characterized by the almost complete absence of curves and sharp turns. Ten paths were traced at this temperature having a total length of 247 cm of which 158 cm are stretches of straight lines, each one of which measured at least 2,5 cm in length, since none were considered under this length. The longest single straight line measured 25 cm out of a total length for the path of 44 cm. Here again we find no tendency to swim in large circles and only a negligible tendency to swerve to the one direction rather than to the other. There is a greater tendency to swim in straight lines.

Room temp. At room temperature, by which is meant a temperature ranging from about 20 to 25 degrees centigrade, no temperature readings being taken, we find more turns and loops than at 20° C. There is also a tendency to shorter paths at this temperature. Forty-seven paths were traced, having 13 loops, 147 turns, — 80 to the right and 67 to the left, and a total length of 1060 cm. Of this 1060 cm 640 cm were stretches of straight lines, the longest single straight line measuring 31 cm or approximately 1000 times the length of the body of the organism or 200 spiral turns. It is very noticeable, that increasing the temperature from 11° C. to room temperature has been accompanied by an increase in the length of the stretches of straight lines. At 11° C we found one straight line measuring 7,5 cm, one measuring 25 cm at 20° C, and one of 31 cm at room temperature. This is the longest single straight line in the whole set of experiments, the length gradually decreasing as the temperature is increased above that of the ordinary room.

22° C. At 22° C the Paramaecia swam in longer paths, — the average being 35,2 cm as compared with 22,5 cm at room temperature and 25,5 cm at 20° C. Twenty-three paths were traced at this temperature with a total length of 802 cm of which 333 cm are stretches of straight lines. The longest single straight line measured 25 cm. There are no indications of swimming in large circles at this temperature although 14 loops were described in these 23 paths. There were however, 156 distinct changes of direction, — 92 to the right and 66 to the left.

25° C. Twenty-one paths were traced at 25° C temperature, having a total length of 1130 cm and an average length of 54,5 cm. This is the longest average length of path in the whole group of experiments. The longest single path in this test, and also in the whole group, including both curves and stretches of straight lines, measured 183 cm. This path extended almost twice acress the dish, with four main changes of direction. Seventy-nine centimeters of this path were stretches of straight lines, the longest single one measuring 20 cm, which was also the longest single straight line at this temperature. There were 251 changes of direction at this temperature in all paths.

29° C. Only seven paths were traced at a temperature of 29° C. These had a total length of 251 cm and the longest single path measured 78 cm and included 28,5 cm of straight lines. The Paramaecia moved more rapidly at this temperature, darting here and there, making 80 changes of direction.

40° C. No paths were traced at a temperature of 40° C, the Paramaecia darting quickly back and forth from a point near the surface to the bottom of the dish and back again, but never quite reaching the surface probably because of the higher temperature at the surface. These reactions lasted for only a very short time, the Paramecia soon settling to the bottom of the dish apparently killed by the excessive heat.

In these experiments with Paramaecia, consisting of a study of 115 separate paths, and having a total length of 36 meters, of which 14,9 meters are stretches of straight lines, we have found no tendency for Paramaecia to swim in large circles in addition to the spirals caused by rotation of the body on its axis, and revolution of the body in an orbit. But on the other hand, we have not found rotation to give "absolute compensation" for any tendency or combination of tendencies to deviate from a straight course. Rotation does not compensate with absolute precision for such deviation. Paramaecia do not swim in straight paths only, in normal free swimming. They swim in curved and broken paths as well as in straight paths, and they change from one to the other by either gentle curves or abrupt changes, to the left, right, up, or down. In these 115 paths of 36 meters, although including 14,9 meters of straight lines, there are 724 changes of direction, — 330 to the left, and 394 to the right.

Spiral movement in the suctorians.

Podophrya collini ROOT.

Spiral movement has been studied in only one suctorian due to the fact that the free swimming embryos of only this one species were found. Since only the ciliated embryos swim freely through the water, direction of spiral could not be determined for the matured individuals of the other species found. The species studied was identified as *Podophrya collini* ROOT and has been seen at various times during the past two years in Second Creek, just north of the Tennessee University campus.

ROOT (1914) claims to have seen this organism spiraling both to the right and to the left, alternating from one to the other direction in approximately every 6—15 rotations. He states also that only some of the individuals swam this way. Others swam in spirals in a single direction as long as followed. He states that some of these latter swam in spirals constantly to the left and others swam in spirals constantly to the right. From 300—400 individuals of this species of suctorian were studied at Knoxville during the past several years, being first observed Oct. 24, 1921. No note was made as to the probable number observed at this time but the direction of spiral in all cases was to the left. Some (15—25) half-grown, flat and clear embryos, and one fat, granular embryo almost grown, were studied Jan. 16, 1922, until they all attached themselves to the bottom of the watch glass, but in every individual the spiral was over to the left. More than a hundred individuals were observed Jan. 17, 1922, in apparently all stages of development, which gave the same results. Another group of at least one hundred were observed for more than an hour and in this time not one was seen to vary the direction of spiral. ROOT states that this change of direction which he noted occurred immediately after "butting" into another *Podophryan* or into some particle. In these experiments, however, the writer followed one individual across the watch glass six times without a change of direction of rotation occurring. On one trip across the watch glass it swam directly into another individual, was apparently stunned for an instant, then turned and shot off in a new direction with no change in direction of the spiral. Fifty to one hundred individuals were again observed Oct. 1923 and in all cases the spiral was to the left. These embryos are very flat and usually very clear, and due to this fact it is sometimes difficult to determine just what is the actual direction of spiral. One can very easily make oneself believe this spiral is to the right when it is actually to the left, just as was seen to be the case with some of the ciliates. And although ROOT is very positive in his statements of his observations it is nevertheless believed that he too fell under the spell of this optical illusion. These organisms must sometimes be seen swimming directly toward the observer in order to determine what is the actual direction of spiral. It is not believed that only one strain has been found in these successive periods and that this strain differs from the one described by ROOT. We must conclude, therefore, that *Podophrya collini* ROOT does not swim in spirals in both directions, varying from one to the other, but that it swims in spirals constantly to the left.

Significance of spiral swimming.

In the examination of the various explanations given for the cause and direction of a spiral path, heretofore, we have found no explanation entirely satisfactory for either cause or direction. JENNINGS (1901) thought spiral swimming due probably to several factors; (1) unsymmetrical form of body, (2) oblique position of oral groove, and (3) the oblique stroke of the body cilia. We have already seen that unsymmetrical form has nothing whatever to do with either the cause or the direction of a spiral. Neither is the spiral due to, or influenced by, the oral groove. We have also already seen that JENNINGS' (1906, p. 44) idea that the swerving, and consequently the spiral path was due to the stronger beating of the oral cilia, explains neither the cause of a spiral nor its direction. The idea of the oblique stroke of the body cilia we shall examine later. In 1917, D'ARCY W. THOMPSON considered movement in the Infusoria a sort of bombardment similar to that of Brownian movement. In speaking of what he terms Brownian movement in the actions of flies darting here and there on a summer morning, he says: "Again the same phenomenon may be witnessed under the microscope in a drop of water swarming with Paramaecia." Then he quotes PRZIBRAM (1912) as stating that the range of motion of these little active organisms, whether they were gnats or Infusoria, was vastly greater than that of minute particles. Nevertheless he believed even the comparatively large Infusoria small enough for the molecular bombardment of the nucleus to be a stimulus to their irregular and interrupted movements.

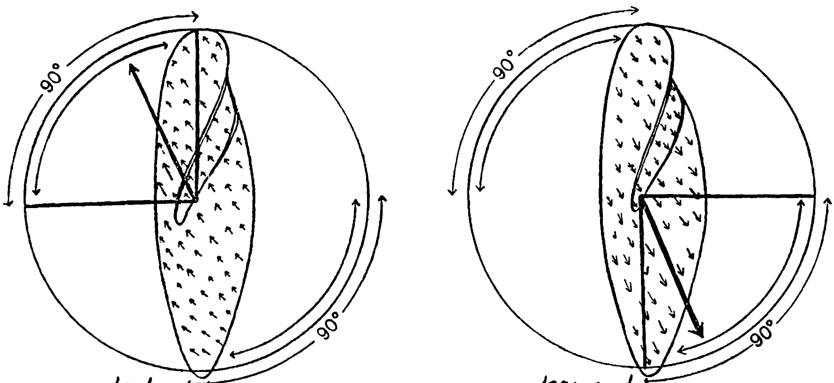
If these statements were true, how could the one stretch of straight path in Paramecia recorded in this paper, measuring 31 centimeters or approximately 1000 times the animals own body length, be accounted for? Or how could this explain the great number of other stretches of straight paths having a combined length of 14,9 meters, none of which measure less than 2,5 centimeters in length, or approximately 75 times the animal's own body length? These paths simply cannot be explained on this basis. There is absolutely no such movement in these organisms. Their movements are not, nor could they be in any way considered as caused by a sort of molecular bombardment, or Brownian movement. These organisms swim around through the culture medium, going here and there in stretches of straight lines, broken lines, and curved lines, changing from one to the other and back again to the left, right, up, or down, with no apparent effort, and apparently caused by no outside influences. These animals when in search of food, appear to move just as the higher animals do, moving here and there selecting some substances and leaving others. Certain substances "wanted" are eaten readily while others not "wanted" are rejected and left alone, SCHAEFFER (1920).

YOCOM (1918) found what he terms a motorium, or a sort of directive center connected with the moter apparatus of *Euplotes patella*, and SCHAEFFER (1920) came to the conclusion that all animals without orienting senses or equilibrating organs, moved in orderly paths due to possession of an automatic directive mechanism.

We must conclude therefore, as JENNINGS once thought (1901) that the spiral path of the Infusoria is not due to the action of any particular group or set of cilia, but it is due instead, to the oblique stroke of all the body cilia working together and striking in the same general direction. This holds for all Infusoria regardless of size, shape, classification, or mutilation of the body.

Now, since the direction of the spiral of these organisms is constant and characteristic for absolutely 100 % of the species, and for approximately 81 % of the genera, the direction of the stroke of the cilia responsible for the direction of this spiral path, must therefore, also be constant and characteristic. But JENNINGS (1906) thought there was a wide variation in the direction of contraction of the body cilia, and SCHAEFFER (1920) found that by reducing the temperature of *Paramaecium* he could decrease forward movement and correspondingly increase the number of spiral turns. In other words by decreasing the temperature he was able to actually change the direction of beat of these cilia from a direction almost directly backward to a direction approaching a perpendicular to the forward movement of the organism. But this variation is not unlimited. It has limits. In left spiraling Infusoria, the cilia can contract in only two general directions, — obliquely backward to the right.

producing forward movement, and obliquely forward to the left, producing backward movement. Either of these general directions may approach a variation of as much as 90 degrees or the fourth part of a circle, but the variation cannot exceed this amount without changing direction of the spiral (see fig. 6).



In ~~forward~~ backward movement. In ~~backward~~ forward movement.

Fig. 6. Direction of contraction of body cilia in a left spiraling ciliate.

New species of ciliates.

Forty-eight species of ciliates have been found in these studies which are still unidentified and are believed to be undescribed. A few, 4—6, may be marine varieties of the regular fresh water species, but the majority are believed to be new. The entire 48 are listed in Table 1 by number only. No description, drawings or other information, other than that contained in this table, is given in this paper. Names, drawings, and descriptions, of the entire group will appear at a later date.

Summary and conclusions.

In this study of 164 ciliates and one suctorian we have arrived at the following general conclusions.

1. All ciliates swim in spiral paths while swimming freely regardless of size, shape, or classification.

2. The kind of spiral followed is characteristic for each species in normal free swimming, as to width of spiral, length of spiral turns, etc.

3. The side of the body of the organism bears a constant relation to the spiral path, rotation on the axis and revolution in the orbit moving together, at the same rate, and in the same direction, the body turning on its axis only as it turns in its orbit. This side of the body is structurally definable.

4. The direction of this spiral is constant and characteristic in all species and in approximately 81 % of the genera.

5. The direction of this spiral is more often over to the left than over to the right. Left spiraling, therefore, is a more characteristic direction and a more perfect expression of movement in the ciliates than right spiraling.

6. The direction of spiraling is closely related to the taxonomy of the organism, being of pronounced generic value, and must be taken into consideration hereafter in any revision of classification of these organisms.

7. Neither the oral groove itself, its oblique position, nor the stronger beating of the oral cilia, have any influence upon either the direction or the cause of a spiral.

8. Large size in ciliates is more closely related to left spiraling than to right spiraling, e. g., large ciliates most often swim in spirals to the left. Large ciliates are also generally the swiftest. Large size is therefore a more perfect expression of evolutionary tendency in the ciliates than small size.

9. Shape of body has no influence upon direction of spiral. There is, however, a much closer correspondence in direction of spiral in those species built upon the same general structural plan, i. e., specialized ciliates as against generalized.

10. Speed of swimming is directly related with the number of spiral turns. Increasing the speed increases the length of spirals. Speed of swimming is also closely related to left-hand spiraling; ciliates with greatest speed generally swim in spirals to the left. Great speed is also closely associated with large size, since the largest ciliates are usually the swiftest. Great speed, therefore, is the most perfect expression of locomotion in the ciliates.

11. The nature of the culture medium itself has no influence whatever upon either the cause or direction of spiral swimming. But the fact that a greater number of left spiraling species have been found in salt water seems to indicate that the salt water ciliates are the oldest, or are better coordinated than the fresh water forms where right spiraling species are still found in greater numbers.

Table 12. List of the Ciliates studied.

Names	Direction of rotation				Direction of Oral Groove	Speed		Body Lengths per rotation	Temp.	Size	
	Fresh water		Salt water								
	to Left	to Right	to Left	to Right		µ per sec.	µ per rotation		C.	Length in µ	Width in µ
Holotricha											
Fam. Paramaeciidae S. K.											
Paramaecium aurelia O. F. Müll.	L				LR	2000	1500	4,5	21	300—390	60—120
Paramaecium caudatum Ehrbg.	L				LR	2647	1731	7,0	22,5	237—281	65
Paramaecium bursaria Ehrbg.	L				LR	1000	400	3,4	25	100—200	60
Paramaecium marinum S. K.			L		LR	930	666	5,6	19	115	49
Paramaecium calkinsi Woodruff		R			LR	500	600	5,0		107—128	43
Fam. Prorodontidae S. K.											
Prorodon teres Ehrbg.	L					1066	800	5,0		175	160
Prorodon griseus C & L.	L						1200		18	237	132
Prorodon marinus C. & L.			L							214–296	86—174
Holophrya saginata Penard			L							113	68
Holophrya sp. No 1		R								122	86—104
Nassula ambigua Stein			L			2004	1185		19,5	118—168	59—79
Nassula ornata Ehrbg.	L					750	761			282	90
Nassula rubens C. & L.	L						500		22,0	171–192	69—85
Nassula lateritia C. & L.	L								19,5	174—204	104
Nassula sp. No 1			L							139—348	87—157
Fam. Colepidae Ehrbg.											
Coleps hirtus Ehrbg.	L					686	286	4,0		66	30
Coleps sp. No 1			L			523	666			78	35
Fam. Enchelyidae S. K.											
Enchelys farcimen Ehrbg.		R					256	4,0	19,0	64	28
Colpoda cucullus Ehrbg.	L				LR		266	4,0		68	45
Colpoda parvifrons C. & L.	L				LR				21,0	57—70	30—40
Colpoda sp. No 1		R			LR					52	17—35
Tillina magna Gruber	L				LR	2000	759	3,5—5,0	25,0	150—175	75—90

Fam. Trachelocercidae S. K.											
Trachelocerca olor O. F. Müll.		R				900				235—300	35—40
Trachelocerca tenuicollis Quenn.			L			1111	303			432	43
Trachelocerca phoenicopterus Cohn				R							
Trachelocerca sp. No 1.		R								405—1575	45—67
Lacrymaria cohnii S. K.			L						24,5	180—196	66
Lacrymaria lagenula C. & L.				R		909	474		26,0	142	45
Lacrymaria sp. No 1			L							251	51
Lacrymaria sp. No 2				R						128	17
Lacrymaria sp. No 3				R						170	68
Choenia teres Duj.				R						102—204	15—20
Fam. Tracheliidae Ehrbg.											
Trachelius ovum Ehrbg.		R					2000				
Loxophyllum meleagris Ehrbg.	L								21	270	150
Loxophyllum rostratum Cohn			L							261—435	104
Loxophyllum setigera Quenn.			L							255	51
Loxophyllum sp. No 1			L							348	87
Amphileptus gigas C. & L.		R				608	800			808	136
Amphileptus meleagris Ehrbg.		R								102—348	87
Fam. Ophryoglenidae S. K.											
Ophryoglena acuminata Ehrbg.	L						400	2,3	24	90—174	68—121
Ophryoglena sp. No 1	L									119—170	26—34
Lembadion bullinum O. F. Müll.		R			LR	415				43	36
Colpidium colpoda Ehrbg.	L				LR					104	35—51
Plagiopyla nasuta Stein		R			LR					85—104	43
Frontonia leucas Ehrbg.		R							21,5	188	141
Frontonia sp. No 1	L					1632	1000	3,5	21,5	282—475	141—285
Frontonia sp. No 2			L							170—346	85—130
Frontonia sp. No 3				R						102—104	62—68
Spathidium spathula Duj.		R				526	500			172—237	21—43
Spathidium sp. No 1			L							120—140	30
Spathidium sp. No 2			L								
Fam. Pleuronemidae S. K.											
Pleuronema marina Duj.				R	LR					104	43
Pleuronema chrysalis Ehrbg.				R	LR					85—153	34

Table 12. List of the Ciliates studied. (Continued.)

Names	Direction of rotation				Direction of Oral Groove	Speed		Body Lengths per rotation	Temp. C.	Size	
	Fresh water		Salt water								
	to Left	to Right	to Left	to Right		μ per sec.	μ per rotation			Length in μ	Width in μ
Holotricha											
Fam. Pleuronemidae S. K.											
Uronema marinum Duj.			L				172			35	17
Cyclidium sp. No 1				R						35—70	26
Cyclidium citrellus Cohn				R						43	25
Fam. Lembidae S. K.											
Lembus velifer Cohn			L		LR	200				87	17
Fam. Opalinidae Stein											
Opalina ranarum Purk.		R								107	87
Fam.? Gen.? Sp ?				R						34	
Fam.? Gen.? Sp.?	L						818			142—380	95—128
Heterotricha											
Fam. Bursariidae Stein											
Bursaria truncatella O. F. Müll.	L				LR		2250	5,2	19	388—432	254—259
Bursaria sp. No 1	L				LR			8,6		302	216
Metopus sigmoides O. F. Müll.	L				LR			4,0		110	50
Metopus sp. No 1		R			LR			1,3		121—191	69—70
Metopus sp. No 2	L				LR					87	43—52
Metopides contorta Quenn.			L		LR	359	468			115	33
Fam. Spirostomidae S. K.											
Spirostomum ambiguum Ehrbg.	L				LR	810	1333			950—1140	95
Spirostomum teres C. & L.	L				LR	640	1380			300—600	50—60
Spirostomum sp. No 1			L		LR						
Condylostoma patens O. F. Müll.			L		LR	1061	738	2,0	20	371	102
Condylostoma sp. No 1			L		LR				20	756—864	86

Condylostoma sp. No 2			L		LR		500			450	
Condylostoma sp. No 3			L		LR					415—595	145—170
Apgaria undulans Stokes	L									226	139
Gen.? Sp.?				R						492	49
Fam. Stentoridae Stein											
Stentor polymorphus O. F. Müll.	L				LR	817	966			208	152
Stentor igneus Ehrbg.	L				LR					175	
Stentor caeruleus Ehrbg.	L				LR	1500	1140			420—637	139—308
Peritricha											
Fam. Halteriidae C. & L.											
Halteria grandinella O. F. Müll.	L					533	533	9,0		60	50
Strombidium claparedi S. K.	L					3740			18	64—75	43
Strombidium urceolare Stein			L							69—121	35 - 52
Strombidium turbo C. & L.			L							87	35—61
Strombidium typicum Lankester			L						29	52	17—35
Strombidium sp. No 1			L					4,4		82—86	49—65
Strombidium sp. No 2			L					4,0		135	90—102
Mesodinium acarus Stein	L								18	32—52	21—43
Mesodinium pulex C. & L.			L								35
Didinium nasutum O. F. Müll.		R				464			20	107—145	64—107
Didinium sp. No 1			L							174	104—121
Fam. Gyrocoridae Stein											
Urocentrum turbo O. F. Müll.		R				700	333	3,7	28,5	90	60
Caenomorpha medusula Perty	L				LR			5,0		100—120	65—70
Dinophrys lieberkühni Bütsch.	L								20,5	142	71
Fam. Vorticellidae Ehrbg.											
Vorticella nutans O. F. Müll.		R								121	69
Vorticella nebulifera From.		R								78 -122	60—69
Vorticella campanula Ehrbg.		R								400	87—104
Vorticella cratera S. K.		R								139	104—174
Vorticella alba From.		R						7,0		104	69—87
Vorticella citrina Ehrbg.		R								87	35—69
Vorticella striata Duj.				R						43—174	35
Vorticella fasciculata O. F. Müll.		R								122—239	104

Table 12. List of the Ciliates studied. (Continued.)

Names	Direction of rotation				Direction of Oral Groove	Speed		Body Lengths per rotation	Temp. C.	Size	
	Fresh water		Salt water								
	to Left	to Right	to Left	to Right		μ per sec.	μ per rotation			Length in μ	Width in μ
Peritricha											
Fam. Vorticellidae Ehrbg.											
Vorticella sp. No 1				R						87	52—69
Vorticella sp. No 2				R						104—87	87
Vorticella sp. No 3	L									87	52
Vorticella sp. No 4		R								52—87	35
Vorticella sp. No 5		R								87—104	52
Zoothamnium nutans C. & L.				R						139	17—69
Zoothamnium arbuscula Ehrbg.		R								107	84
Zoothamnium marinum Mereschk.			L						25,5	85	43
Zoothamnium sp. No 1		R									121
Carchesium polypinum Linn.		R							25,5		
Epistylis flavicans var. *decumbens* S. K.		R								186	93
Epistylis plicatilis Ehrbg.		R								141—209	52
Cothurnia nodosa C. & L.				R						130	52
Opercularia nutans Ehrbg.		R								191	35—52
Hypotricha											
Fam. Lionotidae S. K.											
Lionotus wrzesniowskii S. K.			L				500			312—935	20—41
Lionotus fasciola Ehrbg.	L							2,0		235—282	47
Lionotus grandis Entz			L							174—278	69
Lionotus sp. No 1			L							122—148	35—43
Lionotus sp. No 2			L								
Lionotus sp. No 3			L								
Lionotus sp. No 4			L							261—348	64—87
Lionotus sp. No 5			L							104—208	20—34

Fam. Chlamydodontidae S. K.											
Chlamydodon cyclops Entz			L							95	71
Chlamydodon mnemosyne Ehrbg.			L					3,0		104	62
Chlamydodon sp. No 1			L							85—204	34—85
Chilodon cucullus O. F. Müll.	L						333	1,3		261	69
Loxodes rostrum Ehrbg.	L									330	60
Fam. Dysteriidae S. K.											
Dysteria armata Huxley				R						102—119	52
Fam. Peritromidae Stein											
Peritromus emmae Stein			L							139—174	87
Fam. Oxytrichidae Ehrbg.											
Kerona polyporum Ehrbg.	L				LR	465	222	2,0		107	64
Urostyla grandis Ehrbg.	L				LR				24,5	180—300	100—120
Amphisia pernix Wrz.			L		LR				17	104	34—52
Holosticha flava Cohn				R	LR					226	69
Holosticha sp. No 1			L		LR					197—285	65
Plagiotricha sp. No 1			L		LR					93—174	24—34
Stichochaeta pediculiformis Cohn			L		LR				24	129—255	24—32
Uroleptus piscis O. F. Müll.	L				LR	487			22	203	52
Uroleptus rattulus Stein	L				LR	385	465	2,1	21		
Uroleptus agilis Engelm.	L				LR				24,5	214—238	71
Oxytricha fallax Stein	L				LR			2,3	18	174	69
Oxytricha ferruginea Stein	L				LR	400				150	64
Oxytricha platystoma Ehrbg.	L				LR	520	400			120—140	40—60
Oxytricha bifara Stokes	L				LR	1210				235—329	94
Oxytricha sardida Entz	L				LR					120—140	40
Oxytricha saltans Cohn			L		LR					104—122	35
Oxytricha sp. No 1			L		LR						
Oxytricha sp. No 2				R	LR						
Oxytricha sp. No 3	L				LR						
Oxytricha sp. No 4	L				LR					261—348	120
Oxytricha sp. No 5				R	LR					348	104

Table 12. List of the Ciliates studied. (Continued.)

Names	Direction of rotation				Direction of Oral Groove	Speed		Body Lengths per rotation	Temp.	Size	
	Fresh water		Salt water								
	to Left	to Right	to Left	to Right		μ per sec.	μ per rotation		C.	Length in μ	Width in μ
Hypotricha											
Fam. Oxytrichidae.											
Stylonychia mytilis Ehrbg.	L				LR		530			141—191	47—87
Stylonychia pustulata Ehrbg.	L				LR				21	120—140	60
Stylonychia sp. No 1	L				LR	475			22	167	86
Fam. Euplotidae Ehrbg.											
Aspidisca costata Duj.		R			LR				22,5	26—64	21—34
Aspidisca polystyla Stein				R	LR					51—68	34—42
Glaucoma pyriformis Ehrbg.		R			LR					87	61
Glaucoma scintillans Ehrbg.		R			LR			5,2	24	87	61
Microthorax sulcatus Engelm.	L				LR		172			34—52	23—34
Uronychia transfuga O. F. Müll.				R	LR		666		24	86	43
Euplotes patella Ehrbg.		R			LR	1250	840	5,2		143—261	91—156
Euplotes harpa Stein				R	LR				24	118—139	59
Euplotes charon O. F. Müll.		R		(R)	LR	1053	282		19	49—83	34—69
Euplotes plumipes Stokes		R			LR					323	243
Styloplotes appendiculatus Ehrbg.			L		LR		317			49—57	26—38
Tentaculifera-Suctoria											
Fam. Acinetidae											
Podophrya collini Root	L								25	53—121	43—69

12. The ciliates do not swim in large circles, neither do they, in free swimming, proceed continually in relatively straight paths. They move in straight paths, curved paths, and broken paths, changing from one to the other, to the right, left, up, or down. These paths are more broken at the higher and at the lower temperatures. Rotation is not a device, therefore, for enabling these organisms to move in perfectly straight paths.

13. From the study of 300 to 400 individuals of *Podophrya collini* Root, although it included only the one species, we are inclined to believe that the same factors which influence spiral paths in the ciliates also influence the spiral paths of suctorians. It is believed that the same factors apply equally well to all free swimming Infusoria.

14. The cause of both rotation on the body axis and the revolution on the axis of progression is the combined action of all the body cilia and is not due to the action of any one particular group of cilia. The direction of the beat of these cilia is obliquely backward to the right for forward movement in normal free swimming in a left spiraling ciliate, and obliquely forward to the left for backward movement.

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