A QUANTITATIVE STUDY OF THE MOVEMENT OF *PARAMECIUM CAUDATUM* AND *P. MULTIMICRONUCLEATUM* [1]

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A previous study of the effect of inert gases on oil-water emulsions suggested a mechanism whereby these gases could produce narcosis (Sears and Fenn, 1957). Extension of this research to a biological system was desirable. Reports that narcotics, *e.g.,* chloral hydrate, affected cilia and hence movement of paramecia (Alverdes, 1922) led us to investigate effects of pressures of inert gases on movement of these organisms. The theoretical work of Ludwig (1929) and the behavioral studies of Jennings (1923) presented factors involved in movement of paramecia. However, to use movement as a criterion of narcosis, these studies and others consulted did not yield sufficient quantitative information in the following aspects: (1) the three dimensional nature of the movement; (2) the basic measurements required to define the spiral path generated by the movement; (3) the most accurate method for estimating distances traveled; and, (4) whether measurements of movement of single paramecia or of groups would yield more reproducible data. Only by further characterization of paramecia movement was it possible to observe and quantitate narcotic action. This paper is a study of movement designed to supply the necessary quantitative information.

Data on speed were obtained from single individuals and groups of *Paramecium caudatum* and groups of *P. multimicronucleatum* under conditions which allowed description of typical speed, variability in speed during short time intervals, and change in mean speed over long periods of time. Individual differences among paramecia under the same experimental conditions were explored. Variations in measurements on single paramecia in a drop of media were compared with measurements in which the drop contained several paramecia. Data characterizing the spiral paths were obtained from experiments with *P. multimicronucleatum;* these data allowed us to test for a relationship between speed and shape of path. Finally, consideration was given to relative errors of one and two dimensional measurements of the three dimensional path.

Methods and measurements.—Hanging drop preparations of paramecia were used in most of the work. Pyrex discs were sufficient in size to permit observation of three drops during an experiment. Paths of free swimming paramecia were traced on paper using a *camera lucida* and timed with a stop watch. Lengths of these lines were determined with a map measurer. The length divided by the magnification gave an estimate of the distance traveled by the paramecium. A value for speed at a particular time represents a mean speed determined from at least five tracings of whatver paramecia appeared in the field during the two to three minutes usually required to make the tracings. Measurements were made alternately on the drops. Mean speed and standard deviation were calculated for each of these short periods of time. This procedure was used especially for measurements with single paramecia.

For comparison with these experiments, a chamber as designed by Ferguson (1957) was constructed. This stroboscopic dark field illumination method was used in experiments with *P. multimicronucleatum.* Paramecia paths were photographed and resulted in streaks on 35 mm film. The negatives were projected with a microfilm reader. A typical record for this type illumination is shown as figure 1. Due to the large num-

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Figure 1. Photograph of paramecia paths with stroboscopic dark field illumination.

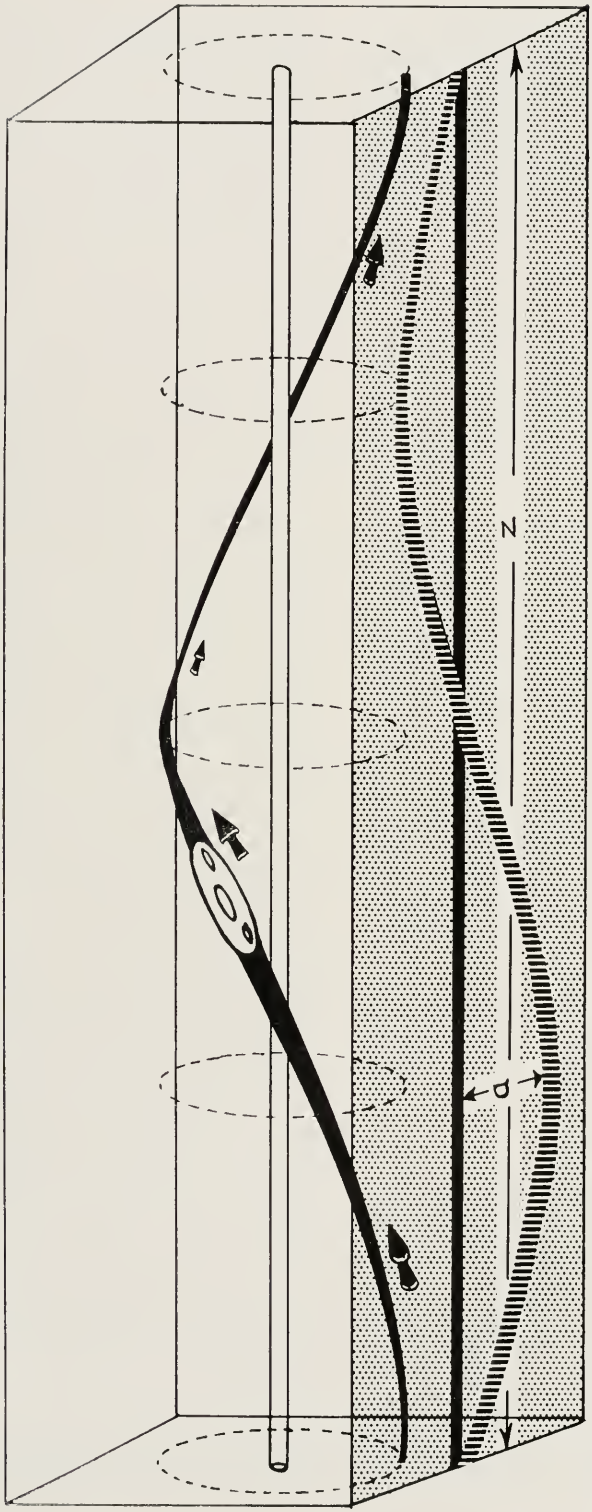

Figure 2. Schematic representation of the path of a paramecium. Measures of the length of one complete rotation, z, and the radius of the spiral, a, may be obtained from the two dimensional projection.

bers of measurements, the data were processed with the IBM 650 computer.[2]

The shape of paramecia paths.—The shape of a paramecium path has been described as helical (Ludwig, 1929). Determination of the three dimensional distance traveled may be derived from the parametric equation for a helix:

$$z = a\theta$$
$$x = a\cos\theta$$
$$y = a\sin\theta$$

As shown on figure 2, the width of the spiral is 2a, and the progression is assumed to be along the z axis of a Cartesian coordinate system. If L_3 represents the distance a paramecium travels in three dimensions for one complete rotation, *i.e.*, θ going from 0 to 2π, then

$$L_3 = \sqrt{(2\pi a_0)^2 + z_0^2}$$

Obviously when $a = 0$, $L_3 = z$. Both z and a are available from sketches of paramecia paths or from photographs.

From these two measurements (z, a) the helix can be completely described. Thus the angle of progression (α) is given by

$$\tan\alpha = \frac{z}{\theta a}$$

The tangent of this angle is the ratio of the distance along the major axis of the helix to the circumference of the cylinder about which the rotation occurs. The curvature K of the path at every point on the helix is

$$K = \frac{\cos^2\alpha}{a}$$

when α is 90°, cos α is 0 and the paramecium is swimming in a straight line. Torsion T in terms of α was given by Ludwig as:

$$T = \frac{\sin 2\alpha}{2a}$$

when the torsion is equal to curvature, the length of the spiral z is equal to the cylinder circumference about which the spiral is wound.

It has been reported (Walton, 1916, Ebbecke, 1935, and Sears, 1957) that rotation about the longitudinal axis of the organism or the curvature of the path changes under various conditions. This was the predominant effect determined for the response of paramecia to high pressures of argon (Sears, 1957).

Errors in the measurement of distance.—As already stated, we can calculate the three dimensional distance, L_3, by measuring the length of the major axis of the helix z and its radius a. Also it is possible to measure the distance L_2 with a map measurer following along the curve obtained from the tracing or photograph of the path. Finally z may be measured with a ruler.

In our early experiments we determined the L_2 distances and reported these in the majority of cases. L_2 measurements give more accurate results than straight line distances and allow easy estimates of rotation (see appendix). The availability of a computer made calculations of L_3 feasible in our recent experiments. The ratio of mean width to mean length of a spiral for *P. multimicronucleatum* was 0.041. Therefore the error as a proportion of L_3 when the distance is estimated by L_2 would be about one percent. However, the estimate obtained from *z* measurements would give a three percent error compared to L_3.

Determination of speed.—Primarily we sought to describe a pattern of movement of paramecia over time periods. There is possibility for variation in this pattern due to different experimental situations; differences in species, media, temperature, age, or pH. These sources of variation are fairly easily controlled. There are other variations, however, which are not amenable to external control. A simple paramecium will vary its speed during even short periods of observation. Therefore, it is desirable to report the mean and standard deviation of speed measurements for these short intervals of time. There is variation: (1) between speeds of single paramecia in the chamber at the same short time interval but in different drops; (2) in patterns of movement of two different paramecia over a long time interval; and, (3) variation between experiments (between single paramecia and between groups of paramecia). In an attempt to study external factors which might cause variability in speed, we measured speed of single individuals and groups of *P. caudatum* in tap water, lettuce media, malt media, and in a solution recommended by Chalkley (1930). This

[2] We are indebted to Mr. Bill Nettleton, Tulane Computer Center, for his assistance in programming and will gladly make this program available to any investigator.

solution contained NaCl (0.1 grams), $CaCl_2$ (0.006 grams), KCl (0.004 grams), $NaHCO_3$ (0.004 grams) in one liter of water.

Basic variability.—Figure 3 illustrates experimental data for single individuals of *P. caudatum*. One paramecium was placed in each of three hanging drops in the chamber. Four short interval sets of measurements were made on each drop. The five measurements made on each paramecium during each short interval are plotted, and we see that during a period of 2 minutes a paramecium may change its speed by a factor of two, although this is unusual. The extent to which the three paramecia differed in their pattern of speed with time is also illustrated. The set of data available for single *P. caudatum* was obtained from experiments in-

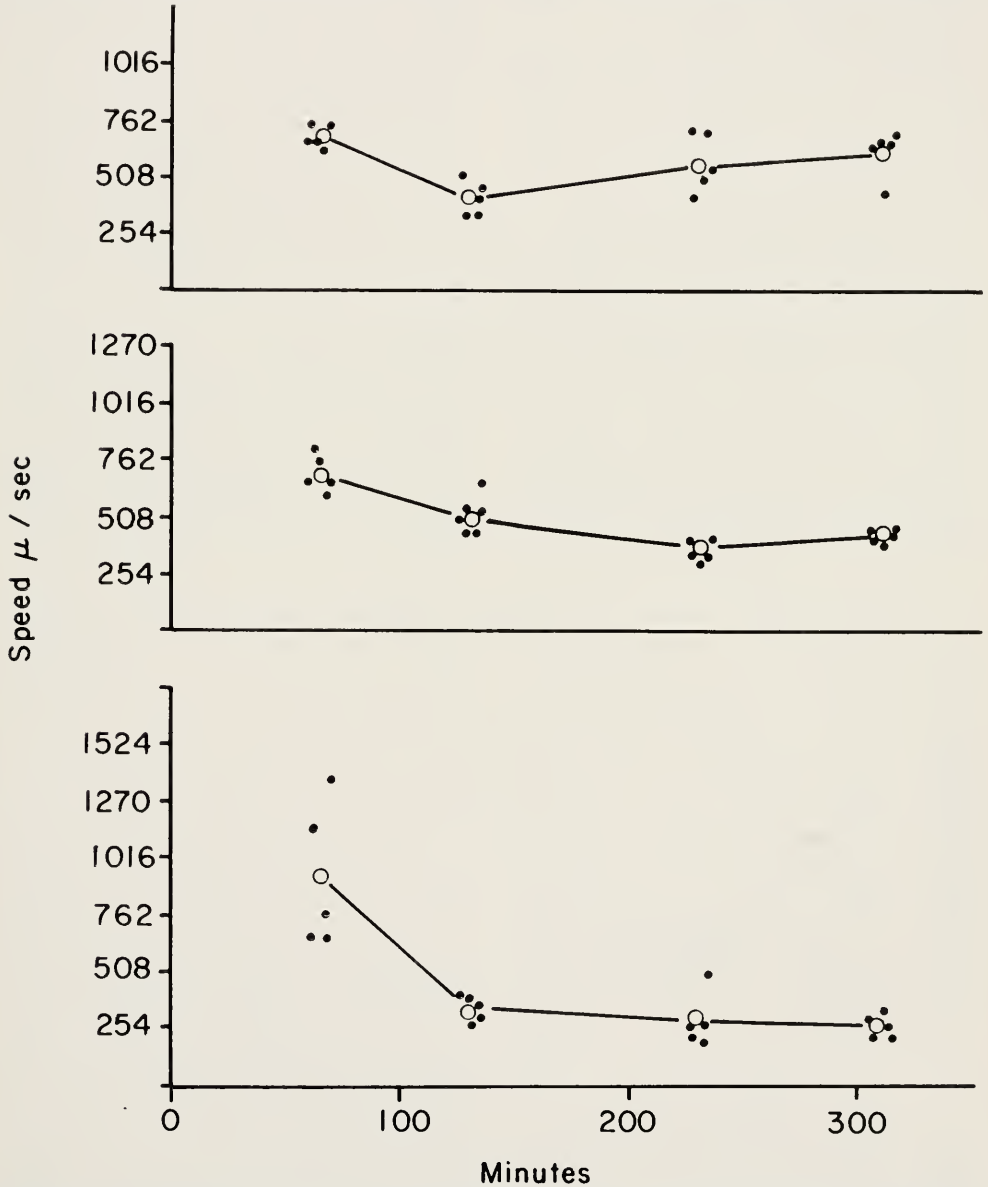

Figure 3. Variation in speed and mean speed of three single organisms (*P. caudatum*) in three different drops observed alternately. The small black dots represent single observations. Circles represent mean speed. (Note: 254 μ/sec = 0.01 inches/sec).

volving 80 drops each containing a single paramecium and involved a total of 219 sets of two or three minute intervals, taken from two minutes to 30 hours after the paramecia were placed in the chamber. The vast majority of measurement intervals were during the first 8 hours. Several media were used. Means and standard deviations of the five (or more) measurements made during the short intervals were studied.

Speed of single P. caudatum.—Standard deviations were computed for each of 219 two-to-three minute intervals, and differed greatly. Even within subgroups of the same media, temperature, pH, and time, differences corresponding to a factor of ten were observed. Distributions of these short interval standard deviations for Chalkley and other media (malt, lettuce, and tap water suspensions of paramecia) are illustrated in figure 4. Shown also are distributions of short interval standard deviations for drops containing more than a single paramecium. With several paramecia in the drop, standard deviations were only slightly larger than those for measurements made on single organisms. *With respect to speed measurements little is to be gained by limiting experiments to a single organism per drop.*

Speed of P. caudatum and P. multimicronucleatum.—In general, speed of both species decreases from the beginning of experiments but tends to approach equilibrium by the end of the third hour (fig. 5). This equilibration time seems to be characteristic of hanging drop preparations. Ferguson (1957) did not report any such long equilibration required to attain a mean speed when his chamber is used, and our experiments with his chamber bear this out. We suspect that variation in CO_2 tension of the drop makes equilibration necessary; we are now investigating this possibility.

Speeds measured in all experiments on both single or many organisms in a drop were averaged for each 100 minute interval. The time interval extends to 700 minutes. Scattered measurements at more than 2,000 minutes confirm the tendency to an equilibrium speed reached after about 300 minutes. Initial high mean speeds were frequently accompanied by large standard deviations.

The relationship between short interval means and standard deviation was examined graphically. For mean speeds in excess of 900 microns per second the standard deviations were, in the large majority of cases, also large. For moderate speeds, typical after three hours (254 to 635 μ/sec), no relation-

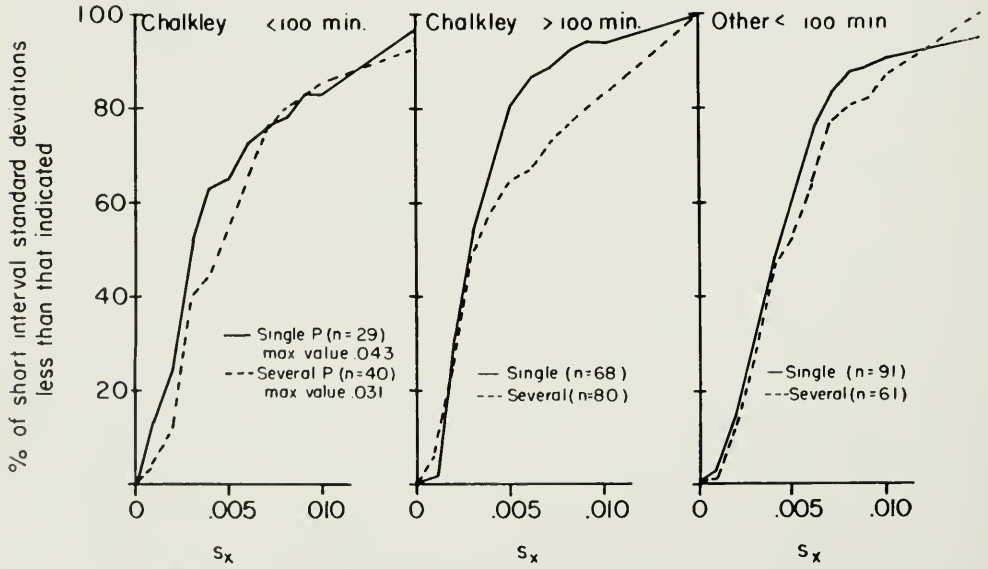

Figure 4. Standard deviations of measurements of short intervals speed grouped according to observations on single and many paramecia in a drop and in different media. Other media include tap water, lettuce media, and malt media. The values for standard deviation are in inches per second and must be multiplied by 25,400 to convert into μ/sec.

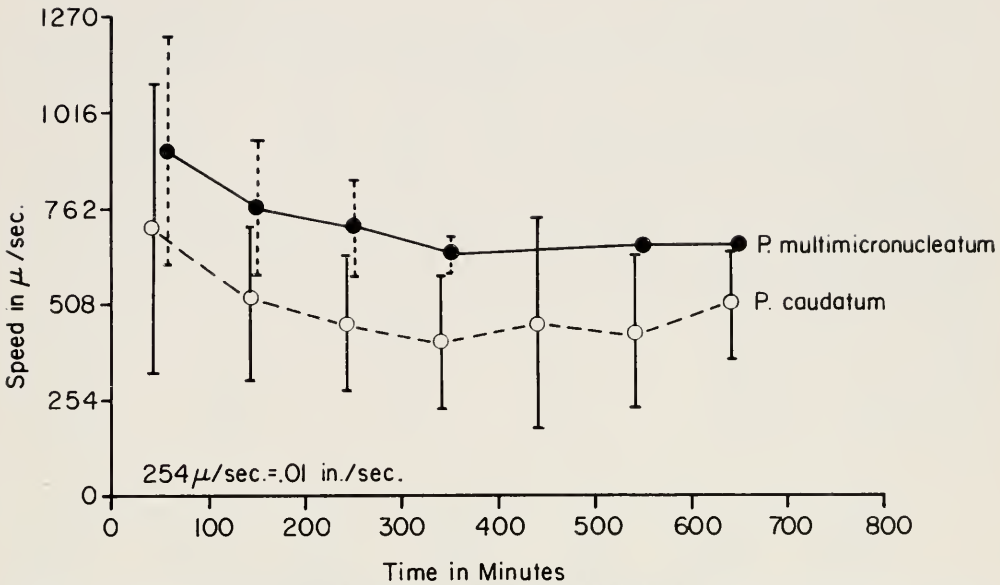

Figure 5. Speed of *P. caudatum* and *P. multimicronucleatum*. Bars through each point indicate standard deviations rather than standard errors of the mean since the great variability in speeds is of fundamental interest. Circles refer to *P. caudatum* and dots show mean speed for *P. multimicronucleatum*.

ship between short interval mean and standard deviation was detected.

Ferguson (1957) reported that thirty measurements are required for computation of a mean average velocity. From our measurements we estimate that mean speed of *P. caudatum* at 500 μ/sec with a standard deviation of 127 μ/sec. At least 70 speed measurements are required to reduce the error of the mean to three percent, and 625 are required for a one percent error. Thirty measurements lead to nearly 5% error of the mean from these values. This may be another difference in hanging drop preparations and the closed Ferguson chamber.

Characteristics of the path of P. multimicronucleatum.—From photographic tracings we were able to measure length z as the distance from one peak to the next, and width a as half the depth of the valley of the track, (see fig. 1). We analyzed the length and width of the spiral only for *P. multimicronucleatum*. There were many paramecia in each drop under observation. Photographic tracings of movement were measured at 173 × magnification. Length and width of one complete spiral turn were studied in relation to corresponding speed. The data covered a wide time interval and several temperatures. The greatest number of measurements were made at 20° C. As many as 10 measurements of the spiral were obtained at each short time interval. Measurements of a, z and speed were made on a total of 334 paths.

The set of 334 paths studied were first ordered on speed. In studying change in the mean values of a and z with speed, speeds were grouped in intervals of 130 μ/sec (0.005 inches/sec). Means are plotted in figure 6. Of the three variables, a, z, and speed, the diameter of the spiral, a, had much the largest relative variability. Part of this effect may be due to the fact that, in relative terms, measurement error in a was larger than in z or in speed. It will be seen from figure 6 that there was little change in average length or width of the spiral over the speed range. If a relationship exists it would be a tendency for z to increase with speed.

The relationship of a to z was examined by plotting (a, z) pairs for paths corresponding to the 120 lowest speeds (281 to 635 μ/sec) and for the 120 highest speeds (889 to 1651 μ/sec) (fig. 7). In each of the two groups correlation between a and z

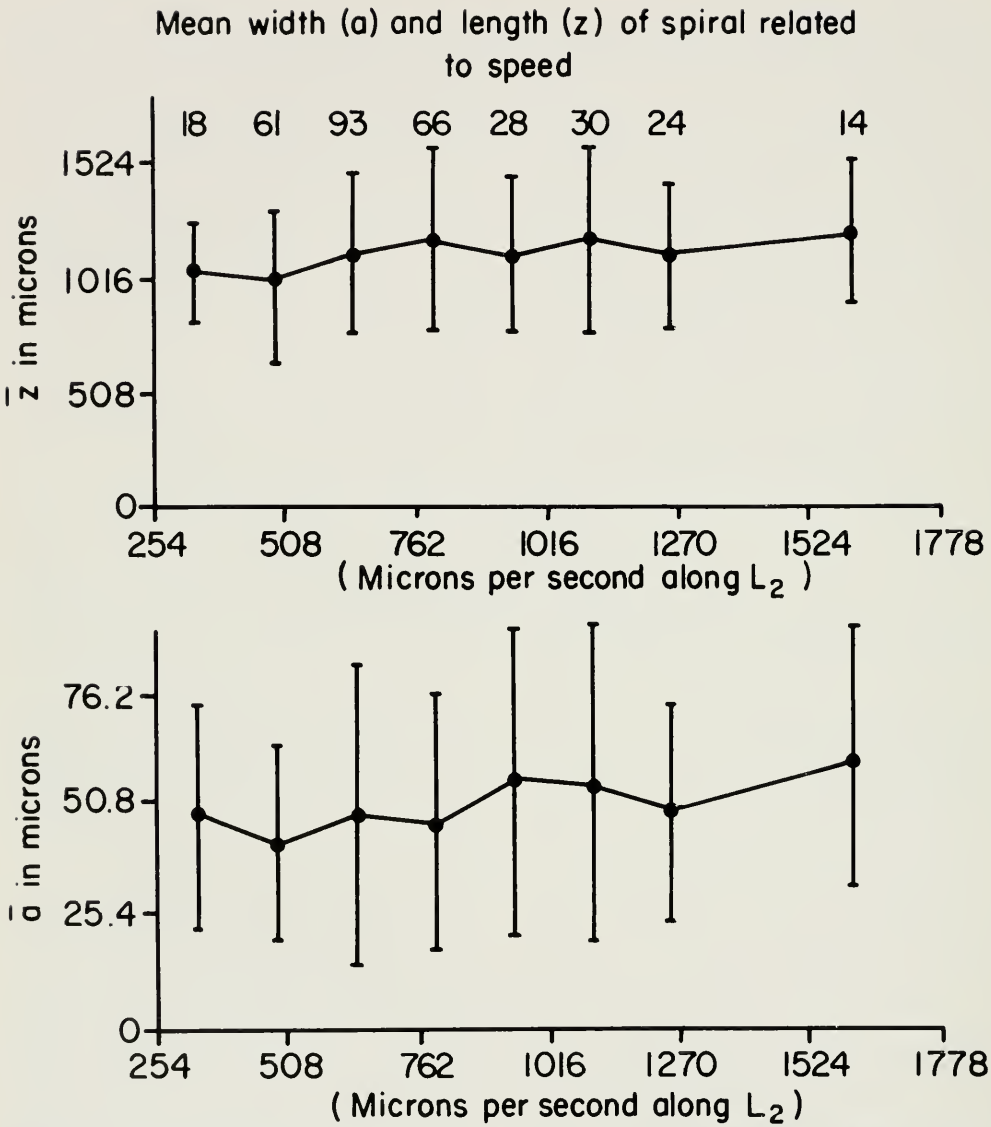

Figure 6. Mean width a and length z of the spiral of *P. multimicronucleatum* related speed. At the top of the figure are the numbers of obseravtions for each speed grouping.

was weak but positive. There was some tendency for large values of a and z to occur together, and this tendency was stronger at high speeds than low.

Sets of measurements made on the same drop during a short period of time were also studied. Short intervals means ($\bar{a}$, $\bar{z}$) were plotted against each other. Again positive, but weak, correlation was observed. The times covered ranged from 5 to 422 minutes after paramecia had been put into the chamber. These times seemed to bear no relation whatever to $\bar{a}$ or $\bar{z}$ values.

From experiments carried out at 20° C, four short interval sets of measurements made during the first hour after putting paramecia into the chamber were analyzed, and compared with four short-interval sets of measurements made after 172 minutes. Coefficients of variation were as follows:

Time (in minutes)	5	7	43	45	172	233	289	388
No. measurements	9	12	6	19	12	10	5	10
Coeff. of Var.								
z	35	20	12	29	29	37	23	30
a	50	39	41	53	44	69	70	49
speed	47	16	21	27	21	22	21	22

Data presented here were characterized by great variability in a and z even in the same drop during a short period of time. For example at 20° C and 289 minutes after paramecia were placed in the chamber five paths gave the following measurements:

Speed (μ/sec)	z (μ)	a (μ)	α	Curvature K (μ^{-1})	Torsion T (μ^{-1})
584	1097	116	56°	0.0026	.0040
279	810	29	77°	0.0017	.0076
610	1128	58	72°	0.0017	.0051
356	1504	116	64°	0.0017	.0034
610	1011	17	84°	0.0059	.0062

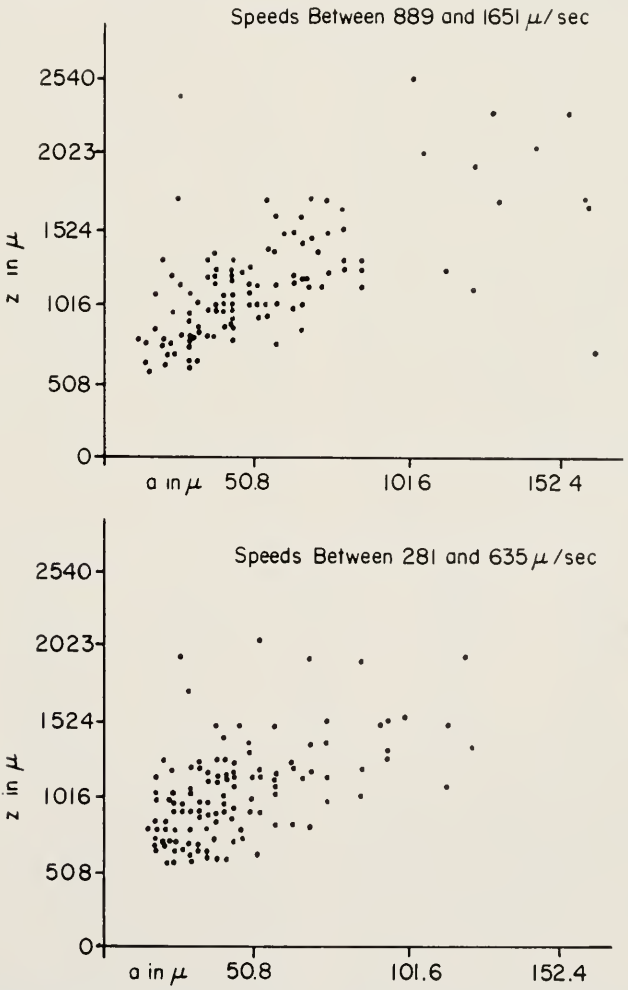

Figure 7. Relation between length of spiral z and width of that spiral a. Upper plot of distance related to the ratio of a to z.

Since there were many (perhaps 10 to 12) paramecia in each drop studied, we cannot, on the basis of these data, say what part of the variability observed is a reflection of difference between paramecia. We have only begun to study the variability in spiral shapes of single paramecia.

An interpretation of the spiral movement.—A theoretical study of spiral movement of ciliates was reported by Ludwig. He stated that two forces are responsible for the spiral path: one, a force which alone would cause the organism to go in a circle; the other, a force which causes the organism to rotate about its longitudinal axis. A canoe, if paddled on one side more strongly than the other, will travel in a circle with the side having the greatest force applied directed outward. Ludwig stated that force exerted by cilia of paramecia on the aboral side normally exceeds that applied by the oral side. This causes the organism to make a basic circle. There is a rotation component to the force which cilia are supplying which causes the organism to rotate about its longitudinal axis. This rotatory movement has been attributed to the oblique direction of the cilia beat from left backward, toward the right.

The organism, therefore, may start moving in a circle to the right, but due to accompanying rotation of the organism, the circle changes to be directed upward, then to the left, downward, and finally to the right again. Thus, a spiral results.

Ludwig stated that characteristics of the spiral are affected by changes in curvature (arising from differences in force applied on the oral and aboral surfaces) and changes in torsion (arising from differences in direction of cilia beat). Consideration of these changes led him to three generalizations:

(1) If the curvature remains constant, increasing torsion (rotation) would result in a steeper and more narrow spiral. (That is, a large value for z and smaller for a).

(2) If the torsion remains constant but the curvature increases, the spiral line becomes fatter (z would decrease) and the width a would increase until the paramecium makes an angle of 45° with the XY plane (assuming progression along the Z axis). As the angle decreases toward zero, the width of the spiral would then decrease.

(3) Asymmetry in rotatory force components causes a widening and flattening of the spiral path.

Ludwig (1929) and Bullington (1925) attempted to determine whether characteristics of spiral patterns would aid in classification of ciliates. Bullington concluded that among species "speed of swimming is directly related with the number of spiral turns. Increasing the speed increases the length of the spiral". It was this statement and the first rule of Ludwig's which caused us to investigate whether, in order to increase their speed, paramecia of the same species alter the spiral paths which they follow.

Three values for curvatures given above are constant (0.0017 μ^{-1}). The torsion changes and in this case, in agreement with Ludwig's generalization, the radius, *a*, varied inversely with the torsion; the length of the spiral increased. The question arises to what extent a single paramecium can produce these changes. The following values were obtained from a single *P. multimicronucleatum* in a hanging drop:

Minutes	Speed	z	a	*a*	Curvature K (μ^{-1})	Torsion T (μ^{-1})
20	600	1300	38	80°	0.0009	0.0045
20	1000	1850	145	64°	0.0013	0.0027
20	900	1330	72	71°	0.0014	0.0043
20	1500	1965	214	56°	0.0015	0.0022
78	900	1156	58	73°	0.0016	0.0048
157	400	1450	72	73°	0.0013	0.0039
221	700	1127	43	77°	0.0012	0.0051
221	600	1272	72	70°	0.0016	0.0044
392	300	867	101	54°	0.0034	0.0047

Characteristics of the rotation could be measured from only about a fourth of the photographs of the paths. In many cases the paramecium swam in a straight or nearly straight line. Although rotation about the longitudinal axis occurred, no radius, *a*, could be measured. Where measurable rotation occurred the curvature remained fairly constant. Since curvature is related to the bal-

ance of forces on the oral and aboral sides, we may conclude that this ratio of forces was generally maintained. The torsion indicates the variation in direction of the cilia beat. There is a weak relationship obtainable from the extremes of the speeds that indicates that the length of the spiral increases with increase in speed. However, the middle speed values do not show any clear evidence for such a relationship.

As we have shown, there is much variation in the shape of paths which paramecia follow. However, our mean path length and width agree closely with those found by Bullington for *P. multimicronucleatum.*

paths of paramecia is illustrated in the following data (25° C).

Experiments	No. of z measurements	z (μ)
Control (1)	403	1607± 51
Control (2)	186	1543± 30
Added CO_2 (1)	218	1688± 94
Added CO_2 (2)	82	1673± 86
Ethyl alcohol 2.58	43	2267±157

Mean z values for *P. multimicronucleatum* placed in the Ferguson chamber in the culture media differ little (about 3%) between the two experiments. Bubbling 100 percent

Reference	Mean z	Range	Mean a	Range
Bullington, 1925	1290μ	833-1666μ	—	143-200μ
Our data	1121μ	402-2540μ	46μ	11.5-162μ

We also measured the length along L_2 corresponding to a single rotation for *P. caudatum.* The mean length of the spiral path of this species so measured (not calculated from z and a is 784μ. We did not measure widths of paths. Bullington's value for length of the spiral of *P. caudatum* were from 900 to 2250 microns.

Results presented are for many different paramecia and do not show what happens to an individual path as a paramecium increases its speed. (See fig. 6) But we expected that in the study of 334 paths any decided tendency to change either length or width of spiral with increasing speed would have been discernible. We can only say that in the hanging drop preparation the tendency for length of the spiral to increase with speed is weak but if a real relationship exists it is indeed that both increase together.

Again there was a difference in the values obtained depending upon the nature of the preparation. The mean z values reported above from our studies were taken from the hanging drop preparation. Using the Ferguson chamber where the paramecium's path is not restricted to the diameter of a drop, the mean z is greater, about 1660μ. Using the data obtained from this chamber we plotted the mean lengths of rotations z against speed and found an indication that speed and length of rotation increase together. However, the scatter was great.

The use of z to indicate changes in the CO_2 in the media caused no significant change. However 2.58 volumes percent ethyl alcohol produced a significant change. This amount of alcohol was not lethal to the paramecia.

Four concentrations of CO_2 were used: 10%, 50%, 90% and 100% of one atmosphere. The mean z values with added CO_2 were little different from experiments with adding CO_2. However, the mean a value for the experiments with CO_2 (300 measurements) was 126 μ compared to 195 μ where CO_2 was not artificially raised. The lowest a values were associated with the 90 percent CO_2 experiments. With no essential variation in z this indicates a straightening of the paramecia paths as the concentration of CO_2 increased. We therefore propose the use of orientation (the angle α) to indicate a positive attraction to the gradient of a chemical.

Experimental design.—Relating this investigation to experimental design, we find little difference in basic variability of speed measurements whether observations are made at controlled temperatures in lettuce media, malt media, tap water, or a salt solution at pH 6.8. Observations on single paramecia gave smaller standard deviations, but the difference compared to observations made on groups of paramecia was small. Equilibration after the organisms were placed in the hanging drop, gave smaller standard deviations and also a more stable mean speed.

The mean speeds obtained here agree closely with those obtained by other investigators and lend support to the use of the change in mean speed as an index of response in certain experimental situations. However, complete characterization of the spiral path is desirable to give information about the force and direction of the cilia activity.

Summary

(1) Three measurements are necessary to characterize movement of a paramecium; length of the spiral, width of the spiral, and speed of the organism progressing along this path.

(2) Of the three methods of estimating the actual distance traveled by a paramecium per unit of time, calculating the three dimensional path length (L_3) is the most accurate. The distance measured along the two dimensional projection of the path may be expected to give an error of about 1% compared with L_3; the straight line distance underestimates L_3 by about 3%.

(3) Hanging drop preparations of paramecia are characterized by rapidly changing mean speeds during early periods after formation (time $<$ 180 minutes). After equilibration more stable mean speeds are obtained.

(4) The mean speed of *P. caudatum* at 25° is between 400 and 500 μ/sec. For *P. multimicronucleatum* this mean is between 600 and 700 μ/sec.

(5) Measurements of mean length and width of the spiral of *P. multimicronucleatum* in hanging drops give: length $z = 1121\ \mu$, width $a = 46\ \mu$.

(6) There is little advantage in measuring speed on many single paramecia individually as compared to groups.

Appendix

Error Involved in Measurement of Distance

The actual distance traveled by a paramecium may be calculated if one assumes that the organism swims along a perfect helix. There are two other measures of distance traveled which are considered less accurate estimates. One is the length of the curved two dimensional projection of the path, the other is the straight line distance from start to finish (z on fig. 2).

The three dimensional distance traveled may be derived from the parametric equations for a helix:

$$z = a\,\theta$$
$$x = a\cos\theta$$
$$y = a\sin\theta$$

If L_3 is the arc length the paramecium travels during one complete rotation (θ doing from 0 to 2π) then

$$L_3 = \sqrt{(2\pi a)^2 + z^2}$$

where a is the radius of the helix and z is the distance traveled in the direction of the major axis during one rotation.

If one measures the two dimensional projection of the path as shown in figure 2, the accuracy of this estimate is between z and L_3. Comparison of the length of the two dimensional path, L_2 with L_3 may be made by also determining this length from a and z as was done for L_3. If

$$b = \frac{z}{2\pi}$$

then the two dimensional arc length corresponding to one complete rotation, L_2 is given by

$$L_2 = \int_0^{2\pi} (b^2 + a^2\cos^2\theta)^{1/2} d\theta$$

$$= 4(a^2 + b^2)^{1/2} \int_0^{\pi/2} (1 - K^2\sin^2\theta)^{1/2} d\theta$$

where

$$K^2 = \frac{a^2}{a^2 + b^2}$$

Here the elliptical integral will not simplify therefore, it must be evaluated for each value of z and a from tables. (Mathematical Tables from the Handbook of Chemistry and Physics, Ed. 9, page 238.)

The relative errors, $\frac{L_3 - z}{L_3}$ and $\frac{L_3 - L_2}{L_3}$ can both be expressed as functions of the ratio a/z:

$$\frac{L_3 - z}{L_3} = 1 - ((2\pi a/z)^2 + 1)^{-1/2}$$

$$\frac{L_3 - L_2}{L_3} = 1 - (2/\pi)E$$

where E is

$$\int_0^{\pi/2} (1 - K^2\sin^2\theta)^{1/2} d\theta$$

These relative errors are shown graphically in figure 8.

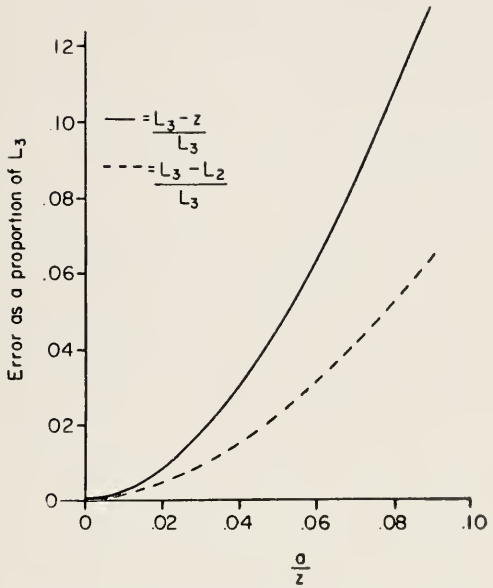

Figure 8. Magnitude of error is measure of distance related to the ratio of a to z.

In data studied here the ratio a/z exceeded 0.06 for less than ten percent of the paths studied, and exceeded 0.07 in only four percent of these paths. This means the relative error in using distance along L_2 rather than along L_3 is small.

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Abstract

The investigation reports experimental methods for determination of speed and rotation of paramecia. Three measures are necessary to characterize movements of paramecia: speed of the organism, and the length and width of the path along which movement is occurring. Mean speeds of *P. caudatum* at 25°C are between 400 and 500 microns per second (time>180 minutes). For *P. multimicronucleatum* these means are between 600 and 700 μ/sec.

For *P. multimicronucleatum* the mean length of a complete rotation about the longitudinal axis is 1121 microns, the radius of the spiral 46 microns.

Several factors involved in the design of experiments on movement of paramecia were discussed.