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Helical Nature of the Ciliary Beat of Colpidium striatum

Our knowledge of the normal movement of individual body cilia of free-swimming protozoan ciliates has been derived from studies that have utilized six basic methods.

2. Rapid fixation techniques as developed by Párducz (1967 and earlier), and modified by Grębecki (1964).
6. High speed cinemicrographs of swimming organisms where ciliary movements are observed in two planes of reference – on the cell surface and on the periphery of the cell (Kuźnicki et al. 1968 a, 1968 b, 1970).

The development of these various methods was prompted by the fundamental problem that when functioning normally, cilia cannot be directly observed under the microscope due to their small size, rapid movement, optical properties which are almost identical to the cytoplasm of the cell and the dense number of cilia normally found covering many ciliates (Párducz 1967, Preston 1972, Kuźnicki 1970, Kuźnicki et al. 1970).

The methods of Párducz (1967) and Tamm (1972) attempted to overcome the above-mentioned problems by analyzing fixed specimens. When analyzing fixed specimens there is no guarantee that the actual form of the beat observed in the living specimen is preserved in the processes of fixation, dehydration or embedding. As pointed out by Kuźnicki (1970), a technique which involves fixation may lead to the production of artifacts. Methods 1, 3, and 4 are concerned primarily with analyses of peripheral cilia. When only peripheral cilia are analyzed, the optical illusion created

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when the cilia bend out of the plane of focus may lead to erroneous interpretations (Kuźnicki et al. 1970).

Method (6), which analyzes the ciliary beat of freely-swimming organisms in two planes of reference does not appear to be plagued with the shortcomings mentioned for the other five methods. It would appear, therefore, to be the method of choice for the analysis of ciliary beating in free swimming protozoans.

The advantages of using method six, as compared to the other methods mentioned above, have been exhaustively discussed previously by Kuźnicki (1970) and Kuźnicki et al. (1970) (and references contained therein). These papers contain a more detailed account of the advantages and methodology involved in the analysis of ciliary beating using this method.

Párducz (1967), Sleigh (1962, 1966, 1968), Machemer (1972, 1973) Tamm (1972) and other investigators, who have utilized methods 1-5 mentioned above, generally agreed that the ciliary beats of *Tetrahymena pyriformis*, *Opalina ranarum*, *Paramecium multimicronucleatum*, *Balantidium coli* and most other ciliates that they have studied, conform to either a "classical" planar discontinuous effective and recovery stroke as described by Gray (1922, 1928, 1930, 1953) or a three-dimensional effective and recovery stroke as described by Párducz (1967).

Recently evidence has been accumulating that not all ciliary organelles beat with the classical effective and recovery phases. Sleigh (1968) has shown that the caudal cirri of *Stylonychia mytilus* may show a helical beat and Párducz (1967) and Kuźnicki et al. (1970), working with the body cilia of *Paramecium* or *Colpidium*, have shown that in stationary organisms the cilia may show a conicoidal beat.

The best evidence to date showing that not all cilia beat with a classical discontinuous stroke has been obtained by Kuźnicki, Jahn and co-workers. Analyzing some of the same species of ciliates as were used by Párducz, Sleigh and other investigators, they have shown that the body cilia of *Paramecium multimicronucleatum* (Kuźnicki et al. 1970, Kuźnicki 1970), *Tetrahymena pyriformis* (Preston et al. 1970, Preston 1972), *Opalina ranarum* (Cheung et al. 1973, Cheung 1973) and *Colpidium striatum* (Wilson et al. 1974), beat with a helical wave traveling from base-to-tip. Unlike the work of other authors, high speed cinemicrographic techniques were always employed to make observations of ciliary beating of living organisms utilizing method six.

In the present paper the ciliary beat of free-swimming and stationary *Colpidium striatum*, and the process of ciliary reversal were analyzed using the methods of Kuźnicki, Jahn and co-workers. The results of the analyses are presented in detail and the normal motor responses and pattern of ciliary metachrony shown by *Colpidium* are described.
Materials and Methods

Cultures of *Colpidium striatum* were grown agnotobiotically in Pringsheim's wheat grain medium\(^2\) or in Cerophyl sodium phosphate medium\(^3\) to concentrations of \(10^5\) or \(10^4\) per milliliter, respectively. The organisms were then transferred in their media to a slide. All of the preparations examined were prepared as vaseline mounts to prevent evaporation, and to insure a sufficient distance between the slide and coverslip (about 720 \(\mu\)m) to allow full freedom in swimming.

A Red Lake Locam high speed movie camera, model 1624DC, was used to film all the sequences. Eastman Ektachrome Commercial No. 7255 (ECO) film was used for color photography while black and white filming was done with Eastman 4\( \times \)negative No. 7224 (4\( \times \)N). A 100W tungsten-halogen light source was used. Framing rates of 200 to 400 fps were used with 4\( \times \)N film and 16 fps with ECO. The framing rate was determined for each film by an internal timing light which marked the edge of the film.

The movie camera was attached to a Zeiss Universal Research Microscope, equipped with phase and Nomarski differential interference contrast optical systems. In this study the best cinemicrographs were obtained using oil immersion phase contrast optics (650\( \times \)magnification) at a film rate of 200 fps. with the organisms freely swimming in a medium of normal viscosity.

Analysis of the high speed cinemicrographs was accomplished using a flickerless L. W. photo-optical analyzer employing projection rates between 1 and 16 fps. Selected sequences were traced or printed to confirm conclusions gained from repeated low speed analysis of the cinemicrographs.

Observations of cilia on the cell surface in addition to those of peripheral cilia of freely swimming and stationary *Colpidium* were made, using procedures similar to the pioneer high speed cinemicrographic studies of Kuźnicki et al. (1968 a, 1969 a, 1970) on the ciliary beat of *Paramecium multimicronucleatum*, which were done in this laboratory.

Results

General Description of *Colpidium striatum*

*Colpidium striatum* is a holotrich ciliate classified in the order *Hy- menostomatida* (Corliss 1961, 1967). It is related to both *Paramecium* and *Tetrahymena*.

The organism is generally 60 to 90 \(\mu\)m long and 20 to 30 \(\mu\)m wide. The cilia are arranged in rows which run the length of the body (anterior to posterior). There are 27 to 30 rows on the organism. The rows are spaced at intervals of between 0.8 and 1.8 \(\mu\)m, while the cilia in each row are spaced at intervals between 2.4 to 3.0 \(\mu\)m. The cilia are more closely

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\(^2\) Pringsheim's medium: 1 part 0.2 g K\(_2\)HPO\(_4\) and 0.2 g NaCl in 500 ml H\(_2\)O; 1 part Ca(NO\(_3\))\(_2\), 2.0 g; MgSO\(_4\), 2.0 g; and FeSO\(_4\)·7 H\(_2\)O, 2.0 g in 500 ml H\(_2\)O; and 20 parts H\(_2\)O. To 125 ml of this solution 40 boiled wheat grains were added.

\(^3\) Cerophyl sodium phosphate medium: 2.5 g Cerophyl (Cerophyl Laboratories, Inc. Missouri) per 1000 ml H\(_2\)O. Boil, filter and autoclave, then add 1.0 g Na\(_2\)HPO\(_4\)·12 H\(_2\)O per 1000 ml.
packed at the anterior end than the posterior end, for the distance between rows increases slightly as they progress posteriorly. The cilia are approximately 10 μm long and 0.27 μm in diameter.

General Patterns of Movement and Metachrony

When freely swimming Colpidium is observed to exhibit motor responses similar to those of Paramecium, as described by Dryl and Grębecki (1966) and Kuźnicki (1970) (forward movement with left or right spiralling (FLS or FRS), continuous ciliary reversal (CCR), periodic ciliary reversal (PCR), and partial ciliary reversal (PaCR)). Among the five basic motor responses noted above, LFS and PaCR are the patterns most commonly observed for Colpidium.

When Colpidium is freely swimming and the cilia are working in a coordinated manner, the somatic ciliature of Colpidium shows a "dexioplectic metachronism". The Knight-Jones (1954) classification of metachronal coordination, defines dexioplectic metachrony as metachronal coordination in which the effective stroke of the cilia is directed rightward from the propagation of the metachronal waves. The cilia of Colpidium, as will be described shortly, do not have a classical planar discontinuous beat as described by Gray (1922, 1928, 1930, 1953) or a three-dimensional effective and recovery stroke as described for the cilia of some protozoa by Párducz (1967), Sleigh (1968), and Machemer (1972). Rather, the cilia of Colpidium beat with the form of a three-dimensional traveling helical wave propagated from base to tip, which is similar to the form of beat described for Paramecium multicornucleatum Kuźnicki 1970, and Kuźnicki et al. 1970) and Tetrahymena pyriformis (Preston et al. 1970, Preston 1972). Instead of saying that the effective stroke of the cillum is directed rightward in relation to the propagation of the metachronal wave, we must say that the traveling helical wave of each cillum is directed toward the right from the longitudinal axis of the organism and that the metachronal wave moves anterior to posterior following a course down the longitudinal axis of the organism. As shown in plate I, the cilia beat at an angle of about 30° to the right of the propagation of the metachronal waves when the organism is moving forward with left spiraling (FLS).

Form of the Ciliary Beat in Swimming Colpidium

Repeated low speed (2–16 FPS) and frame by frame analysis of selected sequences from high speed movies of freely-swimming Colpidium, revealed that the cilia of Colpidium beat with a continuous traveling helical wave propagated from base to tip.
Plates II and III present a typical picture of the beat of the body cilia of *Colpidium*, as observed on the cell surface. Eighteen successive frames are shown. The frame rate was 200 per second and the original magnification was 650×. The cilia are beating with a frequency of about 25/sec. As is shown, the cilia beat with a continuous undulatory wave which is propagated from base to tip. In the eighteen frames presented, the cilia pass through about 21/2 cycles, but notice that a return stroke is never observed.

Plate IV presents the ciliary beat of *Colpidium* as observed in lateral view on the cell periphery. As in Plates II and III, the cilia beat with a continuous traveling undulatory wave, and no return stroke is ever observed. The cilia in Plate IV were filmed at 200 FPS and the ciliary beat is about 25/sec (as in Plates II and III).

Since the beat is seen as an undulatory wave in both surface and profile views (Plates II-IV), the wave can actually be described as a 3-dimensional traveling wave and approximates a traveling helical wave (Kuźnicki et al. 1970). Figure I shows a diagram of the traveling helical wave as it appears in an individual cilium of *Colpidium* when it is beating at a frequency of about 15-25/sec. The wave is composed of 2 undulatory traveling waves at right angles to each other and 90° out-of-phase. If the undulatory waves are sine waves the combination is a perfect helix. The cilium does not rotate on its axis but merely undulates in 2 planes simultaneously, 90° out-of-phase (Jahn and Bovee 1968, Kuźnicki et al. 1970). The simultaneously undulation of the two waves causes the cilium to appear to rotate or gyrate about its axis.

Fig. I. Diagramatic illustration of the traveling helical ciliary beat as observed in freely swimming *Colpidium striatum* (Plates II-IV). The large arrow indicates the direction of movement of the organism. The dotted arrow indicates the movement of the continuous traveling helical wave (base-to-tip). The cilium appears to gyrate about its axis (as indicated by the dotted arrow near the base of the cilium) as the helical wave propagates from base to tip, however, this gyration is more apparent than real. Based on the drawing by Kuźnicki (1970) of the traveling helical wave in an individual body cilium of swimming *Paramecium*.
When the cilia of *Colpidium* are beating quickly (15–25 beats per sec) there are about 1 to $1\frac{1}{4}$ wave lengths present along the length of the cillum at any one given time. The ratio of amplitude to wave length is about 1:4. The ciliary wave of *Colpidium* is not a true sine wave but it does have a symmetrical form and as seen in the motion picture (Wilson et al. 1974) and Plates II–IV, the waves do travel from base to tip.

The Ciliary Beat in Slow-Moving *Colpidium*

When the ciliary beat of *Colpidium* drops below 10 per second, as in slow-moving organisms, the basic form of the helical beat changes. The amplitude greatly increases and the ratio of amplitude to wave length changes from about 1:4 to about 1:2. Because it is moving slowly the illusion that the cillum is rotating is even more apparent. At times it may even appear to look like a spiral.

The Conical Beat of Cilia in Stationary *Colpidium*

In stationary *Colpidium* the cilia show a conicoidal or rotational form of movement. Plate V and Fig. 2 show what this form of beat looks like when a cillum is viewed in profile near the cell periphery. As shown, the cillum rotates slowly in a counter-clockwise fashion (about 7 rotations per second), and never acquires a straight line appearance in any plane. Coni-

![Fig. 2. Diagram showing the conicoidal ciliary beat in stationary *Colpidium striatum*. The cillum shown is indicated by the arrow in plate V. The cillum is rotating counter clockwise at 7 rotations per second. The solid parts of the cillum indicate the sections of the cillum which are in focus in the frame indicated. The dotted parts indicate those parts of the cillum which are out of focus. The cillum sequentially rotates out of the focal plane and then in again (Frame 1–27, Plate V)](image-url)
Cilioidal movement or "rotational" movement is not simply a pre-mortal symptom or pathological symptom as originally felt by Párducz (1954, 1967) when he observed it for cilia on hyaline blebs of stationary Paramecium or on intact Paramecium, Colpidium, Didinium and Opalina, when the organisms were treated with a harmful substance (narcotics, inorganic salts, etc.). Rather, cilioidal ciliary movements are normal phenomena observed in stationary protozoan ciliates. This has been well documented for Paramecium multimicronucleatum by Kuźnicki et al. (1970) and Kuźnicki (1970). In this study, Colpidium, which when stationary showed cilia performing a cilioidal beat (Plate V, Fig. 2), subsequently many of these organisms began to move in a normal fashion. This indicates that cilioidal ciliary movement in Colpidium is merely a transitory state accompanying a condition in which the organism is stationary. When the organism begins to move a normal continuous traveling helical ciliary form of beat is observed.

Ciliary Reversal in Colpidium

During turning movements and complete ciliary reversal in Colpidium, each cilium rotates about its point of attachment to the cell. The reversal or turning movement may occur in either direction dependent upon the new direction of movement. In ciliary reversal the cilia are observed to travel 180° from their previous positions, thus causing the organism to move in the opposite direction.

The process of ciliary reversal in Colpidium is shown in Plate VI. Plate VI presents every sixth frame in a series of 179 frames taken from a high speed movie shot at 200 FPS. The cilia are shown on the surface as viewed from above the organism (650 × magnification). Prior to frame 1 and after frame 179, the cilia were observed to beat with a continuous helical wave. As shown, successive rows rotate 180° until all the cilia have changed direction.

Figure 3 presents a diagramatic representation of the successive stages of a cilium during reversal. As shown in Plate VI and Fig. 3, the cilia change position following a course which is quite analogous to the recovery phase of a planar discontinuous ciliary beat (Gray 1928). As can be seen in Plate VI, the entire cilium is always in the same plane of focus, which indicates the relative planar nature of the reversal process.

As shown in Fig. 3, the process of reversal occurs with an active bending and rotation starting at the basal part of the cilium (position 2). The basal part sequentially rotates and the bend progressively encompasses the entire cilium as the distal part of the cilium is "dragged" by the basal part (positions 2-5). The cilium then straightens out and the reversal sequence is completed (positions 6 and 7).
Fig. 3. Diagram showing ciliary reversal in *Colpidium striatum* as seen on the cell surface. The large arrows indicate the direction of movement of the cilium prior to and after reversal has occurred. Seven stages of the reversal process are shown. The direction of reversal is indicated by the dotted arrow. The entire cilium is always in the same focal plane, indicating the relatively planar nature of the reversal process.

The high speed movies of the reversal progress in *Colpidium* were compared to the original movies obtained by Kuźnicki et al. (1969 a, b) on *Paramecium*. Comparison of the reversal process as shown by these two ciliates demonstrated that they are nearly identical. Refer to Kuźnicki (1970) for some cinemicrographs showing reversal in *Paramecium*. It should be noted that in *Colpidium* regardless of the speed with which the cilia undergoes reversal, the basic stages of ciliary reversal as shown in Fig. 3 remain the same.

**Discussion**

Observations of the ciliary beat in free-swimming *Colpidium striatum* have never before been attempted. The only descriptions of the ciliary beat of *Colpidium* are those of Párducz (1967). Párducz observed specimens of *Colpidium* which had been fixed with osmium tetroxide and subsequently stained and at times even dehydrated and mounted in balsam. Using fixed specimens obtained in this manner he postulated and described a three-dimensional discontinuous beat for the cilia of *Colpidium*, *Opalina*, and *Paramecium*. Very little analysis was actually done on specimens of *Colpidium*, instead Párducz simply drew analogies to the form of beat he had worked out for *Paramecium*. 
In this study we have used the methods of Kuźnicki, Jahn and co-workers (Kuźnicki et al. 1968 a, b, 1970; Kuźnicki 1970: Preston et al. 1970; Cheung et al. 1973; Boggs et al. 1970) to study the ciliary beat of *Colpidium striatum*. Using these methods we have determined that:

1) The ciliary beat of *Colpidium* is a traveling helical wave similar to that observed for *Tetrahymena pyriformis* (Preston et al. 1970, Preston 1972) and *Paramecium multimicronucleatum* (Kuźnicki 1970, Kuźnicki et al. 1970). The wave is distally directed and thus exerts a locomotory force from base to tip which pushes the organism in a direction opposite to the movement of the wave (Plates II-IV, Fig. 1).

2) In slow-moving organisms the ciliary beat may appear to take the form of a spiral because of an increased amplitude and apparent gyration about the base of the cilia as the wave is propagated toward the tip. This gyration is more apparent than real.

3) In stationary *Colpidium* the ciliary beat is conicoidal (Plate V, Fig. 2).

4) *Colpidium* shows motor responses similar to those observed in freely swimming *Paramecium* (Kuźnicki 1970).

5) *Colpidium* when swimming normally shows a dexioplectic form of metachrony.

Dexioplectic metachrony as used in reference to the ciliary beat of *Colpidium* is defined in this paper as a form of metachronal coordination in which the traveling helical wave of each cilium is directed toward the right from the longitudinal axis of the organism while the metachronal wave moves anterior to posterior following a course down the longitudinal axis of the organism (see Results, Plate I). That a coordinated type of ciliary movement can occur and result in metachrony when cilia (or flagella) are beating with traveling undulatory waves (helical waves) is supported by the work of Cleveland and Grimstone (1964) on *Mixotricha paradoxa*, by the papers of Jahn and Bovee (1968) and Jahn and Landman (1965) and by the theoretical papers of Machin (1958, 1963).

The locomotion of *Mixotricha* is primarily caused by symbiotic spirochetes. Each spirochete swims by means of a traveling helical wave as described for *S. cristispira* and *S. plicatilis* by Jahn and Landman (1965), and which is similar to the ciliary beat of *Colpidium* and *Paramecium* (Kuźnicki et al. 1970). As shown by Cleveland and Grimstone (1964), the thousands of spirochetes attached to *Mixotricha* can beat with absolutely perfect metachronal waves. The papers of Machin (1958, 1963) describe a plausible theory on how synchronization or coordinated beating (metachrony) of flagellar or ciliary organelles occurs.

The results obtained in this present investigation and the work of Kuźnicki et al. (1970), and Kuźnicki (1970) on *Paramecium*, Preston et al. (1970, 1972) on *Tetrahymena* and Cheung et al. (1973) on *Opalina*, demonstrate that the ciliary beat in some ciliates is helical in form. Not all
cilia show a planar effective and recovery stroke as originally postulated by Gray (1922, 1928, 1930, 1953), or a three-dimensional effective and recovery stroke as described by Pârducz (1967), Tamm (1972), Sleigh (1962, 1966, 1968) and Machemer (1972, 1973). It has been demonstrated by Boggs et al. (1970), using the high speed cinemicrographic methods of Kuźnicki, Jahn and co-workers, that the somatic cilia of Spirostomum do beat with an effective and recovery stroke. This finding indicates strongly that the methods of Kuźnicki, Jahn and co-workers are quite valid, and that the helical form of ciliary beat is authentic. If the helical form of ciliary beat were merely an artifact resulting from abnormal ciliary behavior caused by the methods employed or from erroneous interpretations of the results, one would expect all ciliates analyzed to show this type of beat when treated in an identical manner. The study of Boggs, Jahn and Fonseca (1970) shows that the helical form of ciliary beating is not observed for all ciliates when the methods of Kuźnicki, Jahn and co-workers are used, but only in those protozoans which actually do swim by means of a continuous traveling helical ciliary beat.

It has been shown that the flagella of different protozoan flagellates may beat differently, although they are structurally identical (Jahn and Bovee 1967). Some flagella beat with planar undulatory waves (Ceratium and Prymnesium), some with traveling helical waves (Trachelomonas) and some with a spiral wave (Peranema). Some flagella even beat with a latero-posterior beat (Trichomonas and Entosiphon) (Jahn and Bovee 1967, Jahn and Votta 1972) which is somewhat similar to the form of beat postulated by Gray (1922, 1928, 1930, 1953) and others (Pârducz, 1967, Sleigh 1968, Tamm 1972, Machemer 1972) for most cilia.

It has also been rather well documented that flagella and cilia are nearly identical biochemically, structurally and metabolically (Afzelius 1959, 1969; Allen 1967, 1968; Grimstone 1966, Pitelka 1963, Pitelka and Child 1964). Therefore it should not be too difficult to conceive that they may function in similar ways. The existence of the traveling helical form of ciliary beat in some protozoa and the variations of the effective and recovery type of ciliary beat shown by other protozoans, suggest that ciliary organelles may function identically to flagella.

**Summary**

The ciliary beat of free-swimming and stationary Colpidium striatum and the process of ciliary reversal were analyzed using the high speed cinemicrographic methods of Kuźnicki, Jahn and co-workers with Colpidium in medium of normal viscosity. In addition the normal motor responses and pattern of ciliary metachrony shown by Colpidium were ascertained.
Using the above methods the following was determined:

1. The ciliary beat of freely swimming *Colpidium* is a continuous traveling helical wave propagated from base to tip.
2. In stationary *Colpidium* the ciliary beat is conicoidal.
3. *Colpidium* shows motor responses similar to those observed in freely swimming *Paramecium* (Kuźnicki 1970).
4. *Colpidium* when swimming freely shows a dexioplectic form of metachrony. “Dexioplectic metachrony” is redefined to apply to helical forms of ciliary beating.

**RÉSUMÉ**

On a analysé le battement ciliaire chez le *Colpidium striatum* en nage libre est en arrêt, en conditions de la viscosité extérieure normale. par la méthode de la cinématographie à cadence accélérée de Kuźnicki, Jahn et collaborateurs. En plus, on a contrôlé les réactions motrices normales et le pattern de la métachronie du travail des cils du *Colpidium*.

Les techniques employées ont permis d’établir que:

1. Le battement d’un cil d’un *Colpidium* en nage libre représente une onde helicoidale continue se déplaçant de la base du cil à son extrémité.
2. Chez un *Colpidium* en arrêt le battement ciliaire est conicoidal.
4. Le *Colpidium* en nage libre montre une métachronie dexioplectique. On présente une nouvelle définition de le “métachronie dexioplectique” applicable au battement ciliaire de forme helicoidale.

**REFERENCES**


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EXPLANATION OF PLATES I-VI

Plate I: Two successive frames showing ciliary metachrony as observed on the surface of freely swimming Colpidium striatum. The metachrony is "dextroplectic". The direction of the helical ciliary beat (H) is 30° to the right from the direction of the metachronal waves (M). The metachronal waves move anterior to posterior and the helical ciliary beat progresses base to tip on each cilium. The net result is a FLS form of movement. The organism is moving upward (indicated by the arrow). The cinemicrographs were taken at 400 FPS with Nomarski differential interference contrast microscopy (200 x original magnification).

Plates II and III: Eighteen successive frames showing the form of the ciliary beat in a swimming Colpidium as observed on the cell surface. The arrow in frames 1 and 10 indicates the direction of movement of the organism. The frame rate was 200 FPS and the original magnification was 650 x (phase contrast microscopy). The cilia are beating at about 25 cycles per second (CPS). About 21/2 cycles of beating are shown in frames 1-18. Notice that a return stroke is never observed and that the undulatory wave proceeds from base to tip.

Plate IV: Twelve successive frames of the same group of cilia as observed on the periphery of a freely swimming Colpidium. The frame rate was 200 FPS and the original magnification was 650 x (phase contrast microscopy). Approximately two cycles of beating are shown. A typical cilium (indicated by the arrow) can be followed through each of the 12 successive frames. As in plate II and III, the ciliary beat appears as an undulatory wave, and no return stroke is ever observed.

Plate V: The conicoidal beat of the body cilia of a stationary Colpidium, as observed near the cell periphery. Alternate frames of 29 successive frames are shown. The cilium indicated by the arrow can be followed through one entire rotation (frame 1 to frame 29). The cilium is rotating in a counter-clockwise fashion at about 7 rotations per second. (This rotation is shown diagrammatically in Fig. 2). As the cilium rotates parts of it go out of focus and the cilium never obtains a straight line appearance in any plane. The cinemicrographs were taken at 200 FPS with phase contrast microscopy (650 x - original magnification).

Plate VI: Ciliary reversal in Colpidium as observed on the cell surface. Every sixth frame of 179 successive frames are shown. The arrows in frame 1 and 179 indicate the direction of movement of the organism just prior to and after reversal has occurred. The framing rate was 200 FPS, and the original magnification was 650 x (phase contrast microscopy).