

## FORCE EXERTED BY A SINGLE CILIUM OF *MYTILUS EDULIS*

### II. FREE MOTION

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A cilium can be stopped by applying the tip of a glass microneedle during the effective stroke. The force required to stop the cilium has been measured by the author by the displacement of a flexible needle on the basis of its compliance. This force was expressed in terms of a torque, at the base of the cilium, which was  $4 \times 10^{-7}$  dyne.cm. The second step would be to know the magnitude of the torque when the cilium is beating freely without constraint. Such a study would require a hydrodynamical treatment, as was given in the case of swimming spermatozoa (Taylor, 1951, 1952; Hancock, 1953; Gray & Hancock, 1955; Machin, 1958; Carlson, 1959).

In Part I of the present paper the form and velocity of the cilia in motion in media of various viscosities are reported, in Part II an equation for the torque at the base of the cilium is given, and in Part III the amount of the torque is calculated from the equation and the physiological significance is discussed.

#### PART I. ANGULAR VELOCITY AND PATTERN OF BEAT OF A CILIUM IN MEDIA OF VARIOUS VISCOSITIES

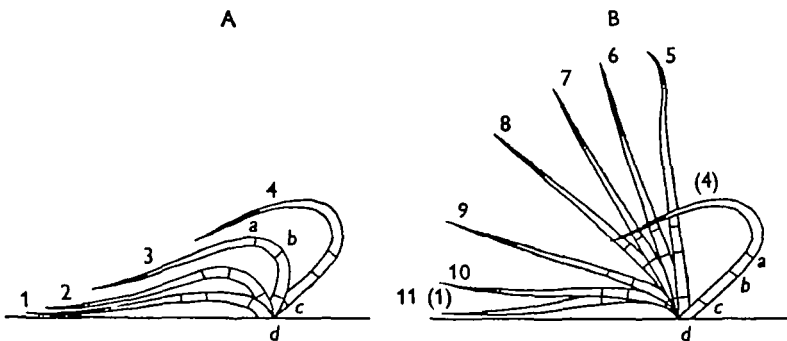
*Material and preparation.* Large abfrontal gill cilia of *Mytilus edulis* were used as described in the previous paper. The mean length of the cilia is about  $55 \mu$ , although individual length varies between 40 and  $90 \mu$ . In order to orient the abfrontal cilia so as to make them beat in the horizontal plane a gill filament was stretched across a trough, keeping about 0.2 mm. distant from the surfaces of a slide and a cover-glass. Thoroughness of exchange of media was assured, judging from the fact that the cilia were forced to bend down-stream during the changing of the medium.

*Preparation of viscous media.* 3 g. of sodium carboxymethyl cellulose was dissolved in 100 c.c. of sea water on water-bath and filtered through cheese cloth. To remove undissolved particles the filtrate was centrifuged for 30 min. at 26,500 g. Any effect of the remaining particles on viscosimetry and on ciliary beating is regarded as negligible, since the particles remaining in the supernatant were about  $2 \mu$  or less in diameter, and the concentration was of the order of 1 particle/8000  $\mu^3$ . This supernatant was used as stock solution. Employing an Ostwald viscometer, the viscosity of the stock solution was found to be 0.40 poise at 20° C. Examination by the capillary flow method revealed that the solution behaved as a Newtonian fluid at the maximum rate of shear of between 3 and 60 sec.<sup>-1</sup>. Less viscous solutions were prepared by diluting the stock solution with sea water. The colloid osmotic pressure of sodium

carboxymethyl cellulose is negligible, the stock solution being practically isosmotic with sea water using *Maetra* egg as an osmometer.

*Photographic recording of the cilium.* The track of the beat of the cilium was recorded photographically with exposure of  $\frac{1}{25}$  sec. with  $40\times$  objective and  $10\times$  ocular. By employing phase optics the track of the cilium during  $\frac{1}{25}$  sec. was recorded as a bright area against the dark background on the print. Such exposure was just enough for the cilium to cover  $10-50^\circ$  excursion during the effective stroke, from which the angular velocity of the stroke may be obtained, provided the shutter speed is reliably accurate. In the case of very small velocities  $\frac{1}{10}$  sec. exposure was employed. Calibration of the speed of the Copal Shutter no. 00 here employed revealed that standard error of the mean in ten measurements was 2 and 3 % respectively for  $\frac{1}{25}$  and for  $\frac{1}{10}$  sec. exposure.\*

*Pattern of the effective stroke.* Typical examples of records of the effective stroke are shown in Pl. 1. The general patterns were quite similar to the ciné-photographs published by Gray (1930, 1931) and by Kinoshita & Kamada (1939). It would, however, be appropriate to remind the reader of a few points of importance, in reference to the diagram of Kinoshita & Kamada reproduced in Text-fig. 1.



Text-fig. 1. Normal beating of the cilium, reproduced from the diagram of Kinoshita & Kamada (1939). A. Recovery stroke. B. Effective stroke.

Gray defined the effective stroke as from phase 6 to 10 of the diagram in Text-fig. 1, when the cilium remains straight (phases 1-5 are recovery stroke). At the transition from the recovery to the effective stroke (phases 5-6), when the cilium becomes completely straight, the motion becomes momentarily distinctly slower. In fact, even at  $\frac{1}{10}$  sec. exposure, the cilium often appears to be motionless at the transition. Thereafter the cilium moves rapidly with an almost uniform velocity to the end of the effective stroke (phase 10 in Text-fig. 1). In the paragraphs to follow, this rapid and uniform phase of the effective stroke will be dealt with exclusively, for the sake of simplicity in analysis. Force exerted or work done by the cilia which will be calculated later should therefore be considered as the highest value within the beating cycle of the cilium.

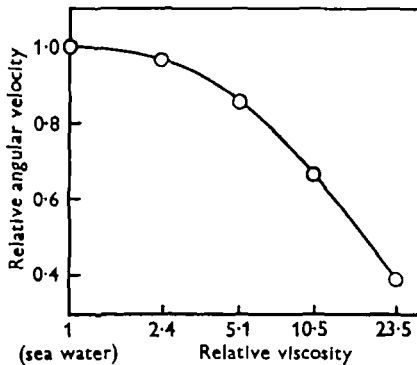
From measurements made on the photographs the mean angular velocity in sea water for thirty-five individual cilia was found to be 11.4 rad./sec., with a standard error of 3.1 rad./sec.

\* The author is indebted to Mr Toshio Nakatsubo of The Olympus Optical Co. for the calibration.

Effect of viscosity on pattern of beat and on angular velocity. Angular velocities between phases 6 and 10 in media of various viscosities are shown in Text-fig. 2. Gradual decrease in the angular velocity is evident as the viscosity increases to a relative viscosity of 23.5, i.e.

$$\frac{\text{viscosity of test solution}}{\text{viscosity of sea water}} = 23.5.$$

On the other hand, the curvature of the cilium, which in normal sea water is very small or non-existent, increases slightly as the viscosity rises. The critical inclination of the cilium when the effective stroke begins is not affected by change in viscosity. When the relative viscosity increases as far as 40, damping of the distal part of the cilium is so great that only the proximal part oscillates. The pattern of beating then becomes too complicated and unstable to be analysed.



Text-fig. 2. Angular velocities of the effective stroke of the cilium in media of different viscosities. Abscissa on logarithmic scale.

PART II. HYDRODYNAMICAL CONSIDERATIONS AND MODEL EXPERIMENT

The main object of this paper is to obtain the force exerted during free motion of the cilium. As far as the large abfrontal cilia of *Mytilus* are concerned the only part which bends actively is the extreme base (Yoneda, 1960). In the following sections the force will therefore be expressed in terms of a torque around the base of the cilium.

*Theoretical considerations.* Both size and velocity of the cilia are so small (i.e. low Reynolds number) that inertial force is considered to be negligible as compared with viscous force. Thus the problem is reduced to calculation of the amount of viscous reactive force of the medium when a cilium of a given size is beating with a given angular velocity in a medium of a given viscosity.

For the purposes of calculation some simplifying assumptions are needed, which are as follows: (a) the cilium remains straight during the effective stroke; (b) the cilium beats in a stationary medium. (The two conditions do not always hold true. An estimate of the error arising from these simplifications will be given in the Appendix.)

Now let us consider a small cylindrical element (of length  $dx$ ) of the cilium a distance  $x$  from the base (Text-fig. 3). Granted assumption (a) above, the viscous

reactive force is directed normal to the axis of the element and the force ( $dF$ ) can be written as

$$dF = f(R, x/l)v\eta dx, \quad (1)$$

where  $l$  is the total length of the cilium, and  $f(R, x/l)$  is a dimensionless coefficient of viscous force, dependent on Reynolds number ( $R$ ) of the system and on  $x/l$ , which denotes the level of the element on the cilium;  $v$  is the translational velocity of the element, and  $\eta$  is viscosity of the medium. Such viscous force should give rise to a torque around the base of the cilium, which is

$$x dF = f(R, x/l)v\eta x dx = f(R, x/l)\omega\eta x^2 dx, \quad (2)$$

where  $\omega$  is angular velocity ( $v = \omega x$ ). Since the force exerted by the cilium, expressed in terms of a torque at the base ( $I$ ), balances the net viscous force acting over the length of the cilium,

$$I = \int_0^l f(R, x/l)\omega\eta x^2 dx. \quad (3)$$

By transforming  $x$  to a dimensionless variable,  $t = x/l$ , equation (3) becomes

$$I = \omega\eta l^3 \int_0^1 t^2 f(R, t) dt, \quad (4)$$

or it can be written as

$$I = \omega\eta l^3 F(R). \quad (5)$$

Equation (5) holds not only for a cilium, but for any model of a geometrically similar figure moving in the manner of a cilium. By definition Reynolds number ( $R$ ) is

$$R = (\text{size}) \times (\text{velocity}) \times (\text{density}) / (\text{viscosity}).$$

Let us use  $l$  to represent the size of the system and the translational velocity of the ciliary tip ( $V$ ) to represent the velocity of the system. Since  $V = \omega l$ ,

$$R = V\rho l/\eta = \omega\rho l^2/\eta, \quad (6)$$

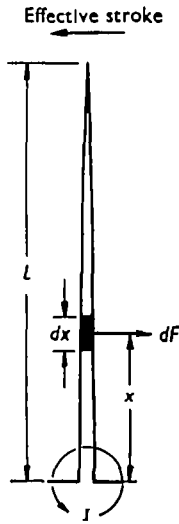
where  $\rho$  is the density of the medium. By putting values measured in Part I (Text-fig. 2) for  $\omega$ ,  $\eta$ ,  $l$ , the torque in free motion can be calculated by equation (5), provided  $F(R)$  is known (which will be determined by a model experiment to be described below).

*Model experiment.* The average thickness of the cilia at various levels was determined from photographs (Table 1 and Text-fig. 4). Assuming that the shape of the cilium is a solid of revolution of such optical section, a model of the cilium can be constructed with considerable fidelity as to shape. The arrangement for the model experiment is shown in Text-fig. 5. A symmetrical pair of model cilia ( $M$ ) continuous at the base, each being 4 cm. in length and 1.6 mm. in diameter at the base, was carved from a bamboo rod. This was pierced through with a needle ( $N$ ) at the centre (base). The needle with the model was hung by a piano wire ( $W$ ) which would serve as a torsion balance. Torque can be calculated from the torsion of the wire, as recorded by lamp-mirror-scale system ( $m$ ), the factor being 0.344 dyne.cm per degree. A cylindrical vessel ( $C$ ) of diameter 12 cm., filled with glycerol, was brought beneath the assembly and centered visually. The model was then submerged 1.5 cm. below the surface of

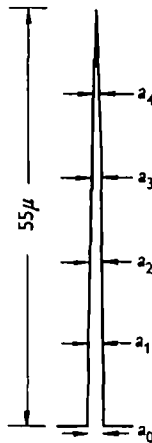
glycerol and 2.5 cm. above the bottom of the vessel. The vessel could be rotated by a simple belt-drive at speeds of from 0.002 to 0.5 rad./sec.

**Experiment and result.** By rotating the vessel at a constant angular velocity, the cilium was deflected, twisting the piano wire till it reached a position of equilibrium. If the rod represents a pair of cilia, the measured torque ( $T$ ) should be divided by  $\omega$ , or

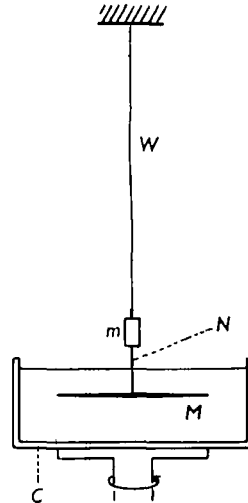
$$F(R) = T/(\omega\eta L^3), \quad R = \omega\rho L^2/\eta, \quad (7)$$



Text-fig. 3.



Text-fig. 4. Standardized shape of the abfrontal cilium.



Text-fig. 5. Arrangement for model experiment. C, Cylindrical vessel; M, a pair of models; m, mirror; N, needle; W, steel wire as torsion balance.

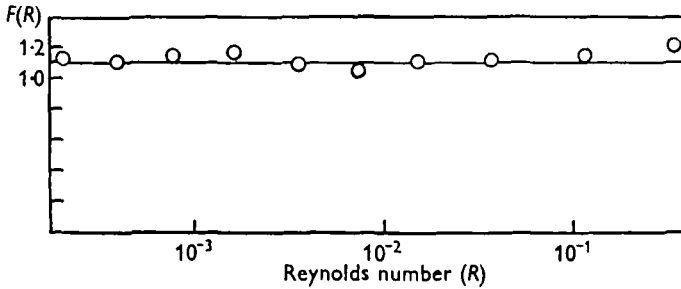
Table 1. Standardized size of the large abfrontal cilium

Distance along the cilium ( $\mu$ )	Diameter of the cilium ( $\mu$ )
0 (base)	2.16 ( $a_0$ )
11	1.93 ( $a_1$ )
22	1.67 ( $a_2$ )
33	1.36 ( $a_3$ )
44	0.96 ( $a_4$ )
55 (tip)	0

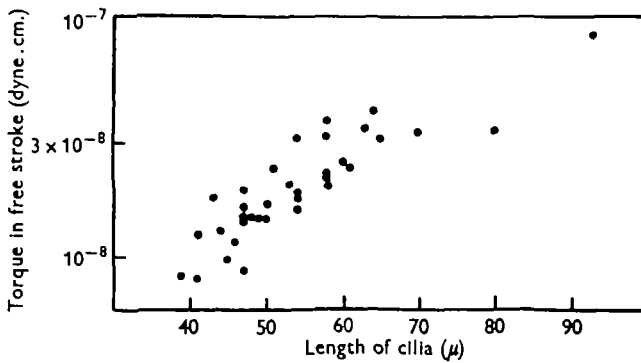
where  $\omega$  is the angular velocity of the vessel,  $\eta$  is the viscosity of glycerol (0.4–60 poise), the density (1.23–1.26 g./cm.<sup>3</sup>) and  $L$  is 4 cm. Values of  $F(R)$  obtained by equation are shown in Text-fig. 6. Clearly  $F(R)$  is constant over values of  $R$  ranging from 0.4 to 0.1, as might be expected from the generally low value of  $R$ . In the case of primary activity referred to in Part I  $R$  was fully covered by this range.  $F(R) = 1.1$  probably be an appropriate value to apply to the condition considered in Part I,

$$I = 1.1 \times \omega\eta l^3. \quad (8)$$

Before going further reference should be made to a laborious model experiment by Ludwig (1930). He found the relationship  $I \sim \omega l^3$  when  $\eta$  is kept constant, or in other words  $F(R)$  is constant within the present range of  $R$ . Unfortunately he failed to give the absolute value of  $F(R)$ , since his model of the cilium was a thin tin plate, which differs greatly from a real cilium in shape.



Text-fig. 6.  $F(R)$  plotted against  $R$ . Abscissa on logarithmic scale. Note constancy of  $F(R)$  ( $= 1.1$ ).



Text-fig. 7. Torques in free motion calculated by equation (8), plotted against length of individual cilia. Ordinate on logarithmic scale.

### PART III. CALCULATION AND DISCUSSION

The torque generated by a single cilium in sea water was calculated by equation (8). From Text-fig. 7 it can be seen that larger cilia will exert stronger torques. On the average, for a cilium of  $55 \mu$  in length and mean angular velocity of  $11.4$  rad./sec. the calculated torque is  $2.2 \times 10^{-8}$  dyne.cm.\* In the previous paper the torque exerted by the cilium when it was arrested was found to be  $4 \times 10^{-7}$  dyne.cm., a higher value than that in the normal environment; that is, in free motion a force of only one-twentieth of the maximum is developed.

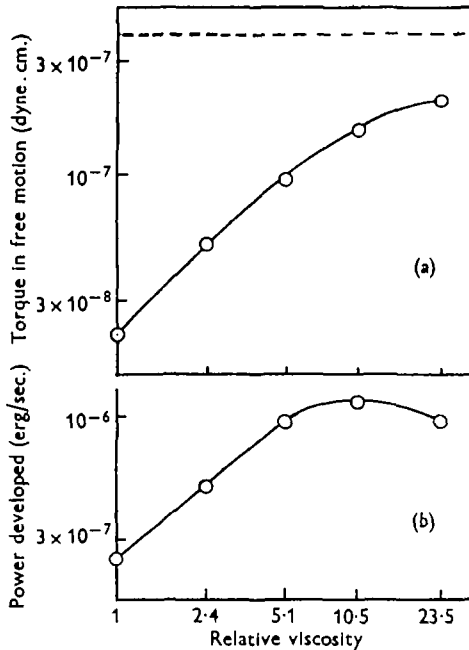
The effect of viscosity on the torque developed is summarized in Table 2 and illustrated in Text-fig. 8(a). A tendency for the torque to increase with increase in viscosity, up to a maximum when the cilium is arrested, suggests that some sort of

\* This figure may become smaller (at the most by 30%) if due corrections are made for bending of the cilium and for the current caused by small cilia (see Appendix).

machinery analogous to that of muscle must be involved in ciliary movement. According to Sleight (1956) peristomial cilia of *Stentor* resemble the abfrontal cilia of *Mytilus* in this respect. Despite viscosity increase of up to 3.5 times, the frequency of beat of the *Stentor* cilia maintained the level of 70% of its initial value with no change in amplitude. In Sleight's data, since the frequency is proportional to the mean velocity

Table 2

Relative viscosity (value of sea water taken as unity)	Relative angular velocity (value in sea water = 1)	Torque in free motion ( $\times 10^{-8}$ dyne. cm)	Reynolds number ( $\times 10^{-2}$ )	Power developed ( $\times 10^{-7}$ erg/sec.)	No. of determinations
1 (sea water)	1	2.2	3.22	2.5	35
2.4	0.97	5.1	1.43	5.6	6
5.1	0.86	9.6	0.73	9.5	7
10.5	0.67	15.5	0.17	11.8	5
23.5	0.40	20.7	0.05	9.4	6



Text-fig. 8. (a) Relation between the torque developed and the viscosity of the medium. Both axes on logarithmic scales. Horizontal broken line indicates the level of the torque which the cilium can develop when it is arrested ( $= 3.9 \times 10^{-7}$  dyne.cm., Yoneda, 1960). (b) Power developed by the cilium in media of different viscosities. Both axes on logarithmic scales.

of the stroke, increase of the torque of the peristomial cilia by 2.5 times ( $= 3.5 \times 0.7$ ) is obtained for 3.5-fold shift in viscosity according to equation (8). Papers by Gosselin (1958) and Aiello (1960), both working on the influence of viscosity on the motion of molluscan cilia, cannot be used for comparison owing to lack of information necessary for calculation.

Results by Pigoń & Szarski (1955) on the swimming speed of *Paramecia*, however, suggest the contrary. The speed was found to be inversely proportional to the viscosity within the range of relative values from 1 to 15. Since Stokes's law implies that the force required to move a *Paramecium* is proportional to the product of velocity and viscosity, it can be concluded that the net force exerted by the cilia of *Paramecium* is unchanged, regardless of change in viscosity. Such discrepancy cannot be explained at present.

The power, or the rate of doing work, of a single cilium of *Mytilus* can be calculated from the equation:

$$(\text{power}) = (\text{torque}) \times (\text{angular velocity}).$$

Text-fig. 8(b) and Table 2 indicate that the calculated power has a maximal value of as much as  $1.18 \times 10^{-8}$  erg/sec. Since the abfrontal cilium consists of several subunits, each capable of beating independently, strictly speaking this figure should be divided by the number of subunits. Although the exact number of the subunits is unknown it is considered to be between 10 and 30. Assuming the number is 20, the maximal power of one subunit is  $6 \times 10^{-8}$  erg/sec. The wide variation in torque shown in Text-fig. 7 might be due to variation in the number of subunits in each cilium.

Using Gray's (1955) data Carlson (1959) calculated the power developed by a swimming spermatozoon of the sea urchin, *Psammechinus miliaris*, which was  $2.92 \times 10^{-7}$  erg/sec., being roughly comparable to, but definitely higher than, the value ( $6 \times 10^{-8}$  erg/sec.) for one subunit of the abfrontal cilium of *Mytilus*. Gray (1955) and Machin (1958) concluded that any part of the sperm tail can bend actively, while in the case of the abfrontal cilium, only the proximal part bends actively (Kinosita & Kamada, 1939; Yoneda, 1960). The difference in power developed by these two structures might be explained on this same basis.

#### SUMMARY

1. Angular velocities of the large abfrontal cilium of *Mytilus* beating in media of various viscosities were measured.
2. An equation for the force produced by a single cilium in free motion was derived by hydrodynamical methods. Expressing the force in terms of torque referred to the base of the cilium:

$$\text{Torque} = \text{angular velocity} \times \text{viscosity} \times (\text{length of the cilium})^3 \times \text{constant}.$$

The constant appropriate to the effective stroke of the large abfrontal cilium was found by a model experiment to have a value of 1.1.

3. The torque exerted by the cilium in normal sea water was  $2 \times 10^{-8}$  dyne.cm. Increase of viscosity resulted in increase in the torque.

4. The maximum power developed by the cilium was calculated to be  $1.2 \times 10^{-6}$  erg/sec. Assuming that a single cilium is made up of 20 subunits, the power developed by a single subunit is  $6 \times 10^{-8}$  erg/sec., which is of the same order of magnitude as the power developed by a single spermatozoon of a sea urchin (Carlson, 1959).

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REFERENCES

- AIELLO, E. L. (1960). Factors affecting ciliary activity on the gill of the mussel *Mytilus edulis*. *Physiol. Zool.* **33**, 120-35.
- CARLSON, F. D. (1959). The motile power of a swimming spermatozoon. *Proceedings of the First National Biophysics Conference*, pp. 443-9.
- GOSSELIN, R. E. (1958). Influence of viscosity on metachronal rhythm of cilia. *Fed. Proc.* **17**, 1468.
- GRAY, J. (1930). Photographic and stroboscopic analysis of ciliary movement. *Proc. Roy. Soc. B*, **107**, 313-32.
- GRAY, J. (1931). *Experimental Cytology*. Cambridge University Press.
- GRAY, J. (1955). The movement of sea-urchin spermatozoa. *J. Exp. Biol.* **32**, 775-801.
- GRAY, J. & HANCOCK, G. J. (1955). The propulsion of sea-urchin spermatozoa. *J. Exp. Biol.* **32**, 802-14.
- HANCOCK, G. J. (1953). The self-propulsion of microscopic organisms through liquids. *Proc. Roy. Soc. A*, **217**, 96-121.
- KINOSHITA, H. & KAMADA, T. (1939). Movement of abfrontal cilia of *Mytilus*. *Jap. J. Zool.* **8**, 291-310.
- LUDWIG, W. (1930). Zur theorie der Flimmerbewegung. *Z. vergl. Physiol.* **13**, 397-504.
- MACHIN, K. E. (1958). Wave propagation along flagella. *J. Exp. Biol.* **35**, 796-806.
- PICOŃ, A. & SZARSKI, H. (1955). The velocity of the ciliary movement and the force of the ciliary beat in *Paramecium caudatum*. *Bull. Acad. Pol. Sci.* **3**, 99-102.
- SLEIGH, M. A. (1956). Metachronism and frequency of beat in the peristomial cilia of *Stentor*. *J. Exp. Biol.* **33**, 15-28.
- TAYLOR, G. (1951). Analysis of the swimming of microscopic organisms. *Proc. Roy. Soc. A*, **209**, 447-61.
- TAYLOR, G. (1952). The action of waving cylindrical tails in propelling microscopic organisms. *Proc. Roy. Soc. A*, **211**, 225-39.
- YONEDA, M. (1960). Force exerted by a single cilium of *Mytilus edulis*. I. *J. Exp. Biol.* **37**, 461-8.

APPENDIX

In the application of hydrodynamics to the problem of ciliary activity, two simplifications have been made; the extent of error introduced by these assumptions will be estimated.

(1) *Correction for bending of the cilium during the effective stroke*

As seen in Pl. 1, the cilia are sometimes bent backwards, which will reduce the viscous resistance. Assuming the shape of the curved cilium to be expressed by a logarithmic spiral (Text-fig. 9) the decreasing curvature passing distally along the cilium can be expressed by the following relation (in polar co-ordinates):

$$r = C \exp(\theta/\tan \phi), \tag{9}$$

where  $C$ ,  $\phi$  are constants. Thus if a small cylindrical element of the cilium,  $dx$ , is at a distance  $x$  from the base (measured along the curve) its distance from the base (in a straight line) is  $r = x \cos \phi$ . The direction of the movement of the element  $dx$  is now inclined to the direction normal to its axis by the angle  $\phi$ . Two components of the viscous force, one ( $dFt$ ) acting along, and the other ( $dFn$ ) normal to, the axis, are

$$\left. \begin{aligned} dFn &= Cnv\eta \cos \phi dx = Cn\omega r\eta \cos \phi dx, \\ dFt &= Ctv\eta \sin \phi dx = Ct\omega r\eta \sin \phi dx, \end{aligned} \right\} \tag{10}$$

where  $C_n$ ,  $C_t$  are dimensionless coefficients of viscous force. Torques resulting from these forces are then

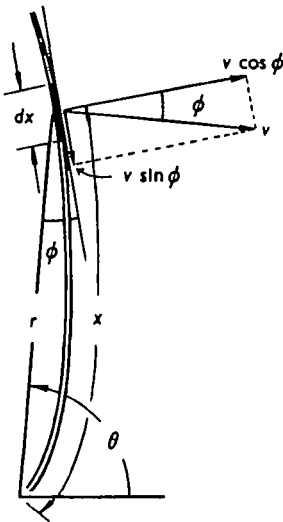
$$\left. \begin{aligned} dI_n &= r \cos \phi dFn = C_n \omega r^2 \eta \cos^3 \phi dx, \\ dI_t &= r \sin \phi dFt = C_t \omega r^2 \eta \sin^3 \phi dx. \end{aligned} \right\} \quad (11)$$

Letting  $C_n = 2C_t$  (following Hancock, 1953), and substituting  $x \cos \phi$  for  $r$ , net torque ( $dI$ ) is

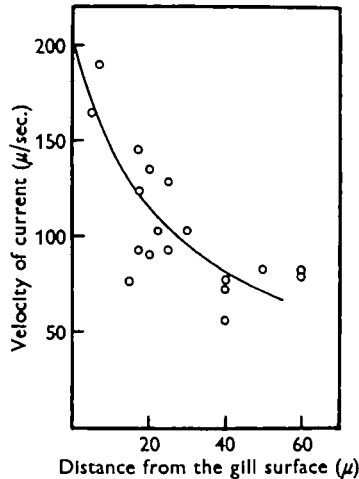
$$dI = dI_n + dI_t = C_n (\cos^2 \phi + \frac{1}{2} \sin^2 \phi) \cos^3 \phi \omega \eta x^2 dx. \quad (12)$$

For small values of  $\phi$ ,

$$(\cos^2 \phi + \frac{1}{2} \sin^2 \phi) \cos^3 \phi = 1 - \frac{3}{2} \phi^2.$$



Text-fig. 9. Logarithmic spiral. For explanation, see text.



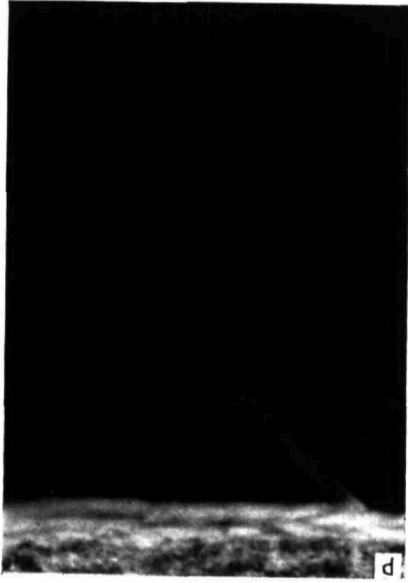
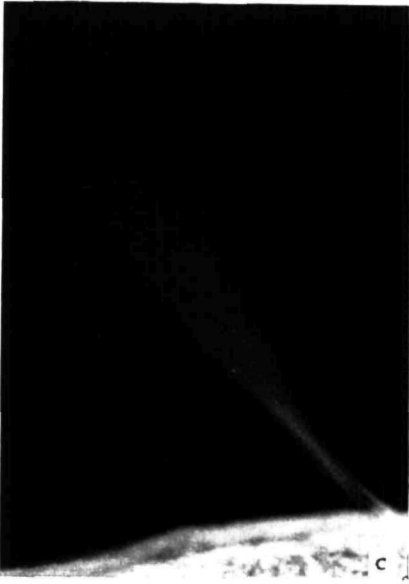
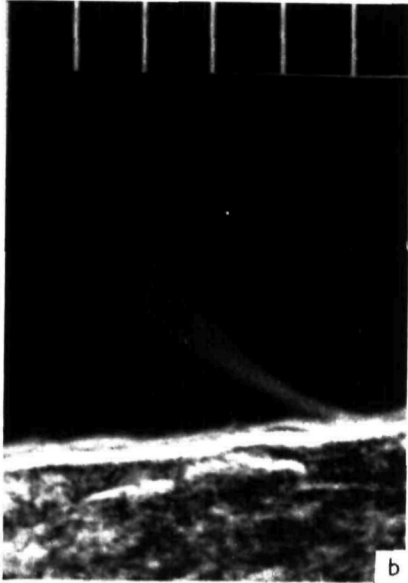
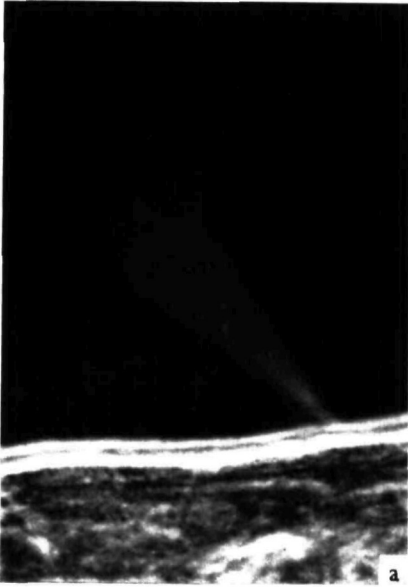
Text-fig. 10. Distribution of velocity in the current near the gill surface caused by the activity of small cilia.

As measured from the photographs,  $\phi$  was below  $5^\circ$  in sea water, and even in viscous media  $\phi$  did not exceed  $15^\circ$ .  $15^\circ$  being  $0.26$  radian,  $\frac{3}{2} \times \phi^2$  is  $0.10$ , or reduction in torque as a result of bending did not exceed  $10\%$ .

(2) Correction for the movement of the medium caused by small cilia

Besides the large abfrontal cilia, which are sparsely distributed, the abfrontal gill surface bears numerous minute cilia. Such small cilia are sometimes so vigorous that a continuous current of water is generated near the gill surface, the direction coinciding with that of the effective stroke of the large abfrontal cilia. One should therefore subtract the velocity of this current from the observed velocity of the large cilium, in order to obtain the actual value of the torque exerted by the large cilium.

By suspending minute chalk granules in the medium, and by measuring the tracks of the granules photographically, the velocity profile of the current as a function of the distance from the gill surface was obtained as shown in Text-fig. 10. To take



account of the effect of the current, equation (2) should be modified, by substituting  $v - v_m$  for  $v$  as follows:

$$dI = f(R, x/l)(v - v_m)x dx, \tag{13}$$

where  $v_m$  is the velocity of the current at the relevant distance from the gill surface. Thus the relative decrease ( $r$ ) in torque as a result of taking account of the current is

$$r = \frac{\int f(R, x/l)v_m x dx}{\int f(R, x/l)\omega x^2 dx} \tag{14}$$

For simplicity, let us assume that  $f(R, x/l)$  is independent of  $x$ . Then

$$r = \frac{\int v_m x dx}{\omega \int x^2 dx} \tag{15}$$

Taking the length of the cilium as  $55 \mu$  and  $\omega = 11.4$  rad./sec., and putting the data in Text-fig. 10 into equation (15),

$$r = \frac{\int v_m x dx}{\omega \int x^2 dx} = \frac{1.36 \times 10^{-7} \text{ cm.}^3/\text{sec.}}{6.39 \times 10^{-7} \text{ cm.}^3/\text{sec.}} = 0.21.$$

Summing up the two corrections here considered, it is safe to say that the error does not exceed 30%  $((1 - 0.1) \times (1 - 0.21) = 1 - 0.29)$ .

#### EXPLANATION OF PLATE

Tracks of cilia in the effective stroke during exposure of  $\frac{1}{17}$  sec. exposure. One division in the upper right scale denotes  $10 \mu$ .

- (a) A cilium in normal sea water.
- (b) The same cilium as (a) in a medium of viscosity 10.5 times higher. Decrease in angular velocity and slight increase in curvature will be noted.
- (c) Another cilium in normal sea water.
- (d) The cilium of (c) in a medium 23.5 times more viscous.