

## FLEXURAL RIGIDITY AND ELASTIC CONSTANT OF CILIA

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### INTRODUCTION

Several investigators (cf. Holwill, 1966) have analysed the movements of cilia and flagella by hydrodynamic treatment to estimate some physical parameters of the movements, e.g. force, bending moment, work, etc. Flexural rigidity, which is one of the important physical properties of cilia and flagella in explaining the structure as well as the form of beating, cannot, however, be determined from hydrodynamic analyses of normally beating cilia and flagella, because it is not known whether their bending is due to the external force or to their own mechanical activity.

Yoneda (1960) first succeeded in measuring the force exerted by a single cilium of *Mytilus edulis* from the bending of a flexible glass needle which arrested it during the beat. In the present study the flexural rigidity of a ciliary shaft was measured at various phases of the beat cycle by a modification of Yoneda's method, whereby simultaneous records of the changes of curvature and bending moment due to the applied force were obtained by means of high-speed microcinematography (Baba & Hiramoto, 1970*a, b*).

### MATERIALS AND METHODS

The solitary large abfrontal cilia of *Mytilus edulis* were used as material. A single gill filament about 3 mm long was dissected out and held between two small pieces of coverslip stuck on the end of a glass rod supported by a micromanipulator, and was set

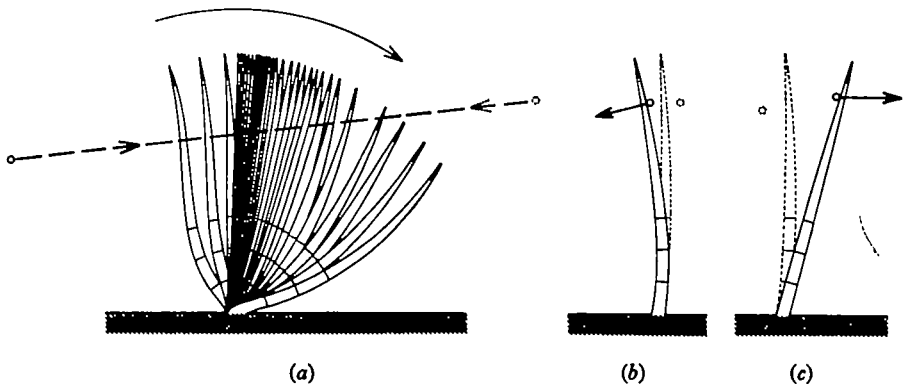


Fig. 1. Diagram showing the principle of determination of the flexural rigidity of the cilium. (a) The sequence of a part of a normal stroke (interval: 11 msec) and the path (dashed line) of the tip (circles) of a needle. (b) and (c) show that the change of the curvature of the ciliary shaft occurs in response to the force (arrows) applied to the cilium by the needle.

in a position such that a cilium could be observed beating in a plane perpendicular to the optical axis of a microscope (cf. Baba & Hiramoto, 1970*a*, *b*).

The elasticity (flexural rigidity) of the cilium was, in principle, determined from the force applied to the cilium by a micro-needle and the change in the curvature of the ciliary shaft in the following way. A flexible glass micro-needle supported vertically is moved abruptly in the direction of the effective stroke of the cilium (to the right in Text-fig. 1*a*) or *vice versa* by means of a piezo-electric ceramic bimorph driven by a train of square pulses. Because of the very short response time of the piezo-electric device the rigid base of the needle shifts almost instantaneously to the new position, whereas the flexible tip lags behind the base owing to the resistance of the surrounding sea water. In the course of its movement (indicated by the dashed line in Text-fig. 1*a*) the tip hits the cilium (by chance) at various stages of the stroke as shown in text-fig. 1*b* and *c*. The force ( $F$ ) applied to the cilium is the sum of the force due to the elasticity of the needle and the resistance of the medium to the needle. Thus,

$$F = KD + R (dD/dt), \quad (1)$$

where  $D$  is the distance of the tip of the needle from its final steady position,  $dD/dt$  is the velocity of the tip,  $K$  and  $R$  are elastic and viscous constants, respectively. The constant  $K$  was determined by the method similar to Yoneda's (1960) and the constant  $R$  was determined from the analysis of the movement of the tip of the needle free from obstacles, which is given by  $D = D_0 e^{-(K/R)t}$ , where  $D_0$  is the distance of the tip from the final point at  $t = 0$ . In several needles used in the present study the values of  $K$  lay in the range of  $1-5 \times 10^{-6}$  dyne/ $\mu\text{m}$ ; those of  $R$ ,  $5-8 \times 10^{-8}$  dyne.sec/ $\mu\text{m}$ ; and those of  $R/K$  which represents the time constant of the response of the tip, 10-70 msec. The movement of a single cilium and of the tip of the needle was recorded by 16 mm high-speed microcinematography similar to that reported previously (Baba & Hiramoto, 1970*a*, *b*).

The bending moment about a given point on the cilium was calculated from the force of the needle, which was determined from equation (1) using  $D$  and  $dD/dt$  obtained from ciné records, and the resistance of the medium acting on the different parts of the ciliary shaft (cf. Baba & Hiramoto, 1970*b*).

The curvature ( $\gamma$ ) of a ciliary axis is defined by  $\gamma = d\phi/ds$ , where  $\phi$  is the angle formed by the tangent at the point in question to the axis of the cilium and a fixed reference line and  $s$  is the distance measured along the axis. In practice,  $\gamma$  was obtained from the difference of  $\phi$  at the two points 2.5  $\mu\text{m}$  or 5  $\mu\text{m}$  apart from the point in question in opposite directions (one distal and the other proximal) along the axis divided by the distance (i.e. 5  $\mu\text{m}$  or 10  $\mu\text{m}$ ) between the two points.

The measurements of the flexural rigidity, which is the ratio of the bending moment to the corresponding change of curvature, were made using cilia normally beating in sea water as well as cilia which were immobilized, maintaining the posture at the beginning of the effective stroke by treatment with sea water containing acetic acid (pH 4).

For counting the number of component cilia in large abfrontal cilia, the optical cross-section of the cilia whose beating was stopped at the end of the effective stroke in sea water containing acetic acid (pH 4.5) was observed and photographed through

a Zeiss Nomarski interference microscope using a  $\times 100$  oil-immersion objective following Dr Thurm's personal suggestion. For observation by electron microscopy, gill filaments were fixed with 2.5% glutaraldehyde in sea water, stained with 20% phosphotungstic acid in methanol after dehydration, and embedded in Epon. The cross-section of the cilia was examined with an electron microscope (JEM-T8).

## RESULTS

Fig. 2 (open circles) shows the changes in the curvature of the part at  $20\ \mu\text{m}$  from the base when a force is given by a glass micro-needle in the early effective phase (stage A in Fig. 4). The change of the curvature of the normal beat of the same cilium

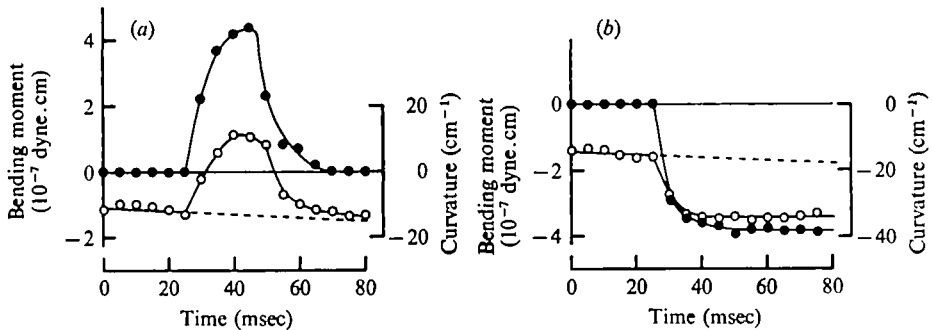


Fig. 2. Changes in the curvature of the ciliary shaft at  $20\ \mu\text{m}$  from the base by the application of force with a micro-needle. Open circles indicate the curvature and closed circles the bending moment in the early effective phase (stage A in Fig. 4). Dotted lines show the changes of the curvature in the same stage of a normal beat.  $24.5\ ^\circ\text{C}$ .

is relatively slow at this stage as represented by dotted lines in Fig. 2. The force is applied to the cilium in the direction of the effective stroke in Text-fig. 2a (cf. Text-fig. 1c) or in the opposite direction in Fig. 2b (cf. Text-fig. 1b). In either case the curvature (open circles) changes approximately in parallel with the bending moment (closed circles) in its rising phase as well as in its falling phase and/or in its final state. The curvature recovers its initial value as the bending moment comes to zero again by the release of the cilium from the needle. The parallelism of stress (bending moment) and strain (curvature) suggests that the deformation of the cilium in the present case is regarded as an elastic one.

A typical example of the relations between the bending moment and the curvature at  $20\ \mu\text{m}$  and  $30\ \mu\text{m}$  from the base of the cilium is presented in Text-fig. 3. It should be noted that both the relations at these two different parts of the shaft are linear with almost the same slope of  $7.5 \times 10^{-9}$  dyne.cm<sup>2</sup>, although the values of curvature (intrinsic curvature,  $\gamma_i$ ) when the bending moment is zero are different. In other words, the magnitude of the change of curvature as a response to the same change of external bending moment is nearly constant irrespective of the sign of bending moment and of the regions of the shaft, i.e. the elastic deformation due to the external bending moment ( $M$ ) is expressed by a simple formula  $M = k(\gamma - \gamma_i)$ , where the constant  $k$  represents the flexural rigidity of the cilium.

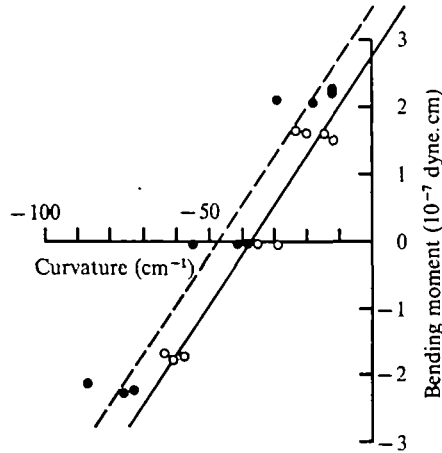


Fig. 3. Responses of the curvature at  $20\ \mu\text{m}$  (closed circles) and at  $30\ \mu\text{m}$  (open circles) from the base of a cilium to the bending moment due to the external force. The force acts on the cilium, either in the direction of the effective stroke or in that of the recovery stroke. Slopes of the straight lines represent the flexural rigidity of the cilium.  $24\ ^\circ\text{C}$ .

Text-fig. 4 shows an example of the relation between the bending moment and the curvature at  $20\ \mu\text{m}$  from the base at various stages (A, B and C in inset) in the effective phase of the cilium. As shown in this figure, the flexural rigidities at various stages of the effective phase are almost constant, while the values of the intrinsic curvature mentioned above vary in different stages. The values of the flexural rigidity of the cilium determined in different cilia are shown in Table 1.

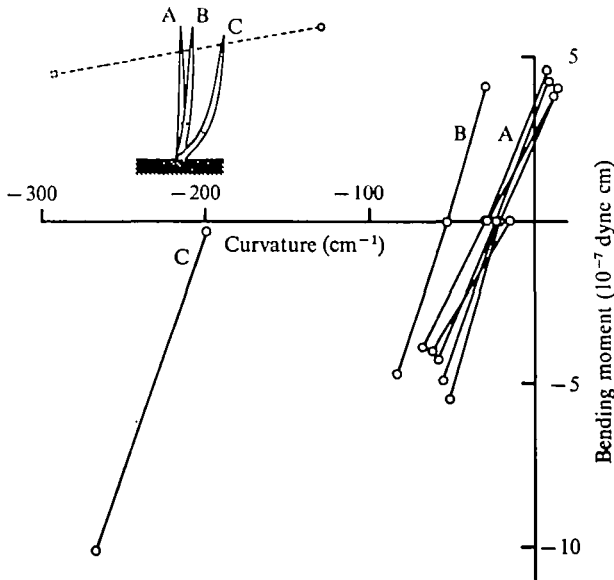


Fig. 4. Responses of the curvature at  $20\ \mu\text{m}$  from the base of a cilium to the bending moment due to the external force at various stages (A, B and C in Inset) of the effective stroke.  $24.5\ ^\circ\text{C}$ .

Table 1. *Flexural rigidity of large abfrontal cilia of Mytilus edulis*

| Length of the cilium ( $\mu\text{m}$ ) | Diameter* of the cilium ( $\mu\text{m}$ ) | Flexural rigidity $\pm$ s.d. (number of determination)<br>( $10^{-9}$ dyne. $\text{cm}^2$ ) |   | Distance from the base ( $\mu\text{m}$ ) |
|--|---|---|---|--|
|  |   | Effective phase   | Recovery and preparatory phases                         |  |
| 82                                     | 3.6                                       | $9.5 \pm 3.3$ (17)  | [11.0 ( $\gamma_t = 40$ )], [6.0 ( $\gamma_t = 260$ )]  | 20                                       |
|  |   | $9.6 \pm 3.4$ (17)  | [10.8 ( $\gamma_t = 20$ )], [7.4 ( $\gamma_t = 160$ )]  | 30                                       |
| 80                                     | 3.6                                       | $13.3 \pm 3.5$ (12)   | —   | 20                                       |
|  |   | $12.9 \pm 2.3$ (12)   | —   | 30                                       |
| 80                                     | 3.2                                       | $8.7 \pm 2.9$ (6)   | —   | 20                                       |
|  |   | $9.0 \pm 2.5$ (6)   | —   | 30                                       |
| 75                                     | 3.0                                       | $8.9 \pm 2.3$ (15)  | [10.3 ( $\gamma_t = 1800$ )], [8.5 ( $\gamma_t = 50$ )] | 10                                       |
|  |   | $8.9 \pm 2.8$ (15)  | —   | 20                                       |
|  |   | $7.9 \pm 3.0$ (15)  | [6.1 ( $\gamma_t = 140$ )], [7.2 ( $\gamma_t = 1800$ )] | 25                                       |
| 72                                     | 2.3                                       | $3.6 \pm 0.6$ (9)   | [2.0 ( $\gamma_t = 1450$ )], [4.1 ( $\gamma_t = 100$ )] | 10                                       |
|  |   | $4.5 \pm 1.8$ (9)   | —   | 20                                       |
|  |   | $4.3 \pm 1.2$ (5)   | [3.1 ( $\gamma_t = 30$ )], [3.0 ( $\gamma_t = 1500$ )]  | 25                                       |
| 59                                     | 2.4                                       | $4.9 \pm 1.9$ (13)  | —   | 20                                       |
|  |   | $4.4 \pm 1.2$ (13)  | —   | 30                                       |

\* The diameters are measured at  $20 \mu\text{m}$  from the base.

Brackets indicate that the pair of values at different parts of a ciliary shaft are measured at the same moment.

$\gamma_t$  is intrinsic curvature ( $\text{cm}^{-1}$ ), see text.

$23.5\text{--}24.5^\circ\text{C}$ .

The determination of the flexural rigidity of cilia during the recovery and preparatory phases (cf. Baba & Hiramoto, 1970*b*) is interesting in connexion with the analysis of the mechanism of ciliary movement. At present, only a few data have been obtained because chances of measurement were few since these phases occupy only a small fraction of the beat cycle. The speed of the change of curvature during these phases makes it difficult to evaluate the exact value with the present technique. However, the results so far obtained (Table 1, Pl. 1) suggest that the flexural rigidity of the cilium in the recovery and preparatory phases is similar to that in the effective phase.

Table 2. *Flexural rigidity of large abfrontal cilia of Mytilus edulis immobilized by acetic acid treatment*

| Length of the cilium ( $\mu\text{m}$ ) | Diameter of the cilium ( $\mu\text{m}$ ) | Flexural rigidity $\pm$ s.d. (number of determination)<br>( $10^{-9}$ dyne. $\text{cm}^2$ ) |
|--|--|---|
| 89                                     | 3.1                                      | $8.7 \pm 4.1$ (6)   |
| 81                                     | 3.8                                      | $5.5 \pm 0.6$ (6)   |
| 79                                     | 3.4                                      | $4.9 \pm 1.4$ (8)   |
| 69                                     | 2.4                                      | $3.0 \pm 1.1$ (4)   |

The flexural rigidities and the diameters are measured at  $20 \mu\text{m}$  from the base.  
 $24.5^\circ\text{C}$ .

In sea water containing acetic acid (pH 4) large abfrontal cilia are immobile in the position normal to the gill surface. Table 2 shows the flexural rigidity of such immobilized cilia, whose values are not significantly different from those of actively beating cilia as shown in Table 1.

The cross-section of large abfrontal cilia was examined with Nomarski optics in living material and with an electron microscope in fixed and sectional material. It was found that these compound cilia consist of a number of component cilia of  $9+2$  pattern, which are separately enclosed with a membrane, lacking any visible connexion with their neighbours and arranged in an approximately hexagonal array as observed by Thurm (1968).

The cross-sections of the compound cilia are regarded as circles or ellipses of various sizes and axial ratios. Text-fig. 5 shows the relation between the number of component cilia in a single large abfrontal cilium and the area of its cross-section. As shown in this figure, the number of components is approximately proportional to the area of the cross-section, the density of components being  $4.3 \mu\text{m}^{-2}$ .

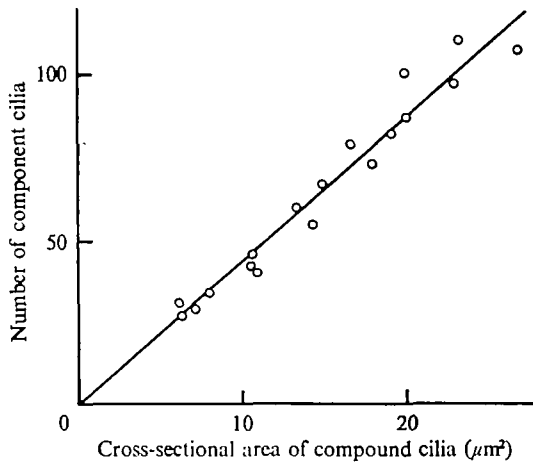


Fig. 5. Relation between the number of component cilia and the area of cross-section of large abfrontal cilia of *Mytilus edulis*. The measurements were made on the photographs taken through a Zeiss Nomarski interference microscope using living material.

#### DISCUSSION

The large abfrontal cilia are known to be compound cilia constituted of a number of single cilia which normally beat in unison. For the calculation of the elastic constant of component cilia it is essential to estimate the degree of their binding. If they unite tightly with one another, the flexural rigidity of the cilia of various sizes should be proportional to the fourth power of the diameter. If the binding force of the components is negligible, the flexural rigidity should be proportional to the number of the components, and consequently to the square of the diameter of the compound cilium. It seems likely that the connexion among the component cilia is relatively loose since the flexural rigidity is roughly proportional to the square of the diameter rather than to the fourth power as shown in Text-fig. 6. Thus the flexural rigidity of the component cilia is obtained from that of the compound cilium divided by the number of components. From the results in Text-figs. 5 and 6, the value of flexural rigidity of the component cilia is estimated to be  $3 \times 10^{-10}$  dyne.cm<sup>3</sup>. A similar value ( $2 \times 10^{-10}$  dyne.cm<sup>3</sup>) was obtained from the data of the cilia immobilized with acetic acid (in Table 2). The difference between these values might be due to uncertainty in the

estimation of the number of components of the compound cilium owing to the variation in the shape of the cross-section.

Brokaw (1966) estimated the stiffness of a single cilium to be  $5 \times 10^{-12}$  dyne.cm<sup>2</sup> assuming that the bending of the distal portion of the cilium during the effective stroke is solely due to the bending moment by the viscous resistance of the medium. Rikmenspoel (1965, 1966) and Rikmenspoel & Sleight (1970) calculated the stiffness of a

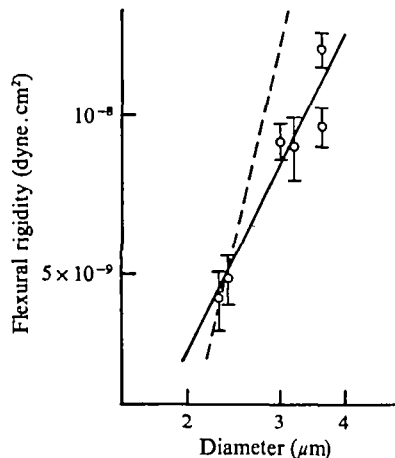


Fig. 6. Relation between flexural rigidity and diameter in large abfrontal cilia of *Mytilus edulis*. Each point is the mean of several measurements for a cilium, with vertical bars representing the standard error of the mean. The slope of the solid line is 2 and that of the dashed line is 4. The diameters are measured at 20  $\mu\text{m}$  from the base. 23.5–24.5 °C.

flagellum or a cilium using their passive model similar to Machin's (1958) and obtained the values of the order of  $10^{-12}$ – $10^{-14}$  dyne.cm<sup>2</sup>. These values are considerably lower than those of the flexural rigidity, i.e. the stiffness, of a single cilium in the present paper, because the latter were directly obtained with a microtechnique, whereas the former were derived on the basis of equivocal assumptions as to the mechanical activity of the cilium or flagellum.

The structure which could constitute the elastic elements within the cilium is so far uncertain in spite of the efforts by several investigators (Harris, 1961; Rikmenspoel, 1965, 1966; Rikmenspoel & Sleight, 1970; Holwill, 1965) owing to their indirect methods of estimation. It is interesting to estimate the Young's modulus of microtubules constituting the cilium since the microtubule is a highly ordered protein fibre resembling muscle actin (Mohri, 1968; Renaud, Rowe & Gibbons, 1968; Stephens & Linck, 1969; Stephens, 1970). The flexural rigidity, namely the bending moment required to produce unit curvature, is given by  $QSK^2$  for uniform structure, where  $Q$  is the Young's modulus and  $SK^2$  the second moment of area of the cross-section. If it is assumed that the nine outer doublets and the two central singlets act as the elastic elements without any connexion among one another, the value for  $Q$  is  $2 \times 10^{13}$  dyne/cm<sup>2</sup> using the value of  $SK^2$  ( $13.2 \times 10^{-25}$  cm<sup>4</sup>) for each doublet given by Holwill (1965). This value is improbably high for the  $Q$  of protein fibres since the Young's moduli of various protein fibres are known to be of the order of  $10^{10}$ – $10^{11}$  dyne/cm<sup>2</sup> (cf. Mason, 1965, 1967; Meredith, 1958). If the nine outer doublet fibrils have a mechanical

connexion with one another by some transverse structures such as radial links, arms etc.,  $SK^2$  is given by

$$SK^2 = S_d \sum_{i=1}^9 K_i^2, \quad (2)$$

where  $S_d$  is the cross-section of each doublet and  $K_i$  is the radius of gyration of the  $i$ th outer doublet about a line through the central pair and perpendicular to the plane of bending.  $SK^2$  is calculated to be  $3 \times 10^{-21} \text{ cm}^4$  from equation (2), if it is assumed that the nine outer doublets are equally spaced on circumference of a circle of radius  $0.1 \mu\text{m}$  and that the cross-section  $S_d$  is  $6.5 \times 10^{-13} \text{ cm}^2$  (calculated from the outside diameter of  $250 \text{ \AA}$  and the wall thickness of  $60 \text{ \AA}$  for the outer singlet; cf. Holwill, 1966). In this case the estimated Young's modulus for outer doublet microtubule is  $5-9 \times 10^{10} \text{ dyne/cm}^2$ , which is reasonable for protein fibres as mentioned above. The absence of any drastic change in the flexural rigidity during the beat cycle and the similarity in the flexural rigidity between actively beating cilia and immobilized cilia suggest that the transverse connexion among outer doublets is maintained throughout the whole course of the ciliary movement and irrespective of the presence or absence of the mechanical activity of the cilium.

Other possibilities are the membrane or the matrix. If the membrane has elasticity of the same order of magnitude as that of the surface structure of the sea-urchin egg (i.e. the cell membrane and the cortex; cf. Hiramoto, 1970), the fraction of the flexural rigidity due to the membrane would be of the order of  $10^{-18} - 10^{-15} \text{ dyne.cm}^2$ , which is negligibly small as compared with the flexural rigidity of a single cilium in the present paper. The matrix would contribute much less than the membrane.

The movement of cilia is asymmetrical, differing from the ordinary movement of many flagella, i.e. they move through their effective stroke as rigid rods and through their recovery stroke as though they were readily flexible (Gray, 1922; Carter, 1924). Gray (1930) foresaw the possibilities that the difference is due to an active change in the elastic properties of the cilium and/or to permanent structural organization. The fact that the flexural rigidity of the cilium is not different in various phases and in relation to the direction of action of the force may indicate that the difference is mainly due to an active bending and unbending of the cilium and that the asymmetry in the movement is of the nature of the active bending system in the cilium.

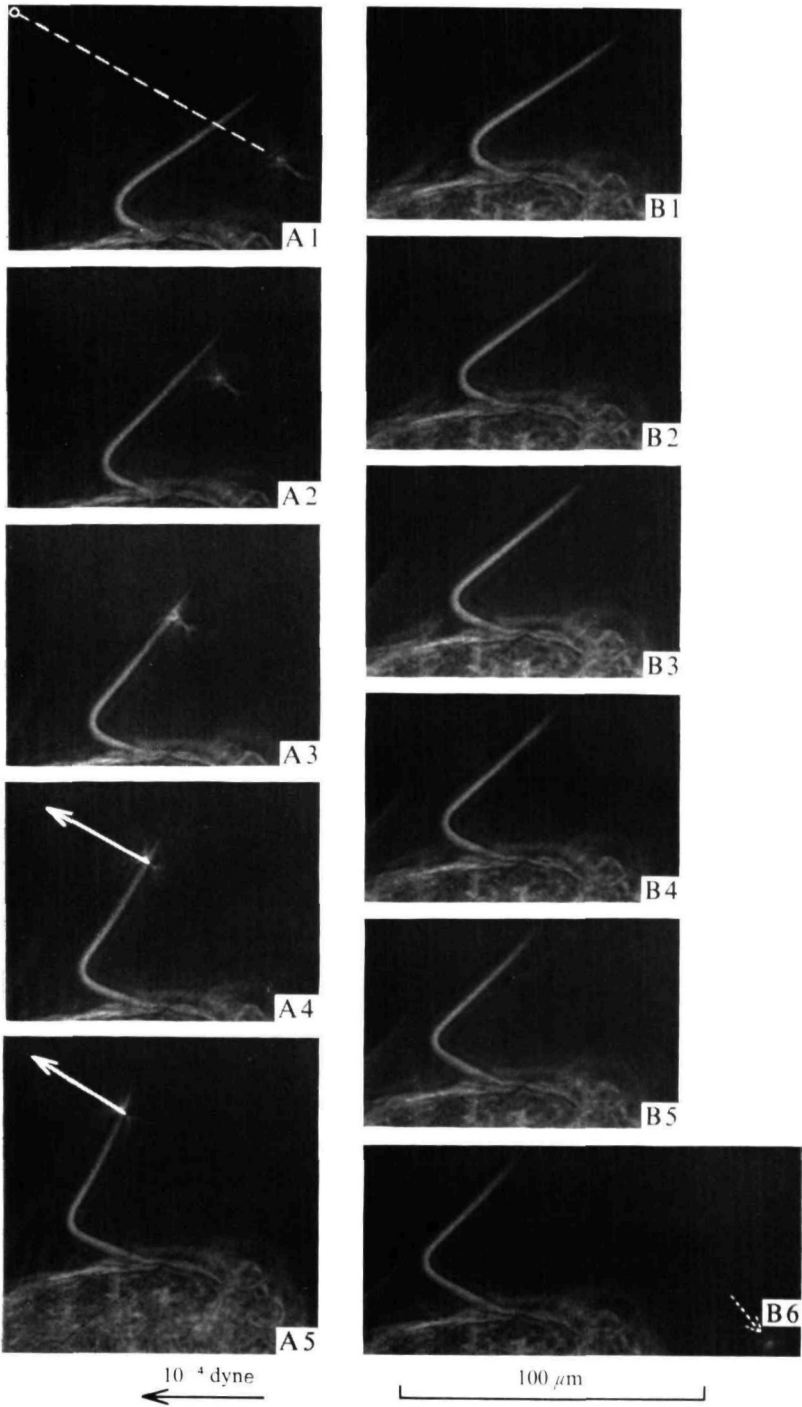
In conclusion, the cilia alter their intrinsic curvature throughout the beat cycle while they keep their flexural rigidity, which might be due to outer microtubules connected with one another, nearly constant. The nature of intrinsic curvature and the mechanism of its regulation are to be investigated in future.

#### SUMMARY

1. The flexural rigidity of the large abfrontal cilia of *Mytilus* has been measured with a flexible glass micro-needle.
2. The same cilium has similar values to the flexural rigidity irrespective of the phases of beat cycle (including the recovery phase) and of the direction of force applied.
3. The values of  $3-13 \times 10^{-9} \text{ dyne.cm}^2$  have been obtained for the flexural rigidity of compound cilia of various sizes;  $2-3 \times 10^{-10} \text{ dyne.cm}^2$  for that of the component cilia.







4. The Young's modulus of the microtubule is estimated to be  $5-9 \times 10^{10}$  dyne/cm<sup>2</sup> on the basis that the outer doublet microtubules are tightly connected with one another.

It is my great pleasure and privilege to offer this work to Professor H. Kinoshita of the University of Tokyo as a part of the celebration of his sixtieth birthday. I would like to thank him for his helpful suggestions during the course of this work and for his critical reading of the manuscript. I am also very grateful to Dr Y. Hiramoto for his careful discussion of the problems that were encountered in this work.

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## EXPLANATION OF PLATE I

PLATE 1. Measurement of the flexural rigidity of a cilium in its recovery phase. A1-5 is a sequence of the response of the cilium in the experiment and B1-6 corresponding part of a normal beat. The interval between successive frames is 3.1 msec. The tip of the needle that was first located at the position indicated by the dotted arrow in the lower-right corner of B6 moves to its final position (circle in A1) along the course represented by the dashed line in A1. In the course, the tip hits the cilium (A4) and exerts a force (shown by arrows in A4 and A5) on the cilium. 24 °C.

