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LOCOMOTION OF FLAGELLATES WITH MASTIGONEMES

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Theoretical hydrodynamic analyses of the locomotion of flagellates with mastigonemes are presented and particular comparison is made within experimental data on *Ochromonas malhamensis*. The first part of the paper analyses locomotion assuming the mastigonemes are rigid and maintain a fixed and normal position relative to the flagellum. The predicted propulsive velocity of 60 μm/sec for *Ochromonas* agrees well with the observed values of 55–60 μm/sec. It is shown that the propulsive system of Ochromonas represents a compromise between the need for efficient rectilinear propulsion and the need to manoeuvre and accelerate. The effect of rigid mastigonemes which are maintained at non-zero angles to the flagellar normal is also calculated and demonstrates a significant degradation of performance when this angle is greater than about 10°.

The latter part of the paper investigates the more complex but more realistic situation in which the mastigonemes flex during the motion according to the instantaneous hydrodynamic forces imposed upon them. The cyclical flexing history of a mastigoneme with passage of a flagellar wave and the consequent velocity of propulsion are obtained for a variety of geometric configurations and structural mastigoneme stiffnesses. It is demonstrated that there exists a relatively small transition range in the values of mastigoneme flexibility below which the mastigonemes are essentially rigid and above which they become totally ineffective hydrodynamically so that the flagellum can be regarded as essentially smooth. Since the transition value of the modulus of elasticity is about 5 dynes/μm^2 (or stiffness of 3.5×10^{-16} dyne cm^2) for the mastigonemes of *Ochromonas* it would appear that the actual value must be in excess of this. Comparison is made with the structural properties of the micro-tubules in eukaryote cilia and flagella and with prokaryote flagella. The latter comparison suggests that the mastigonemes of *Ochromonas* are just rigid enough to produce the observed propulsive effect.

1. INTRODUCTION

During the past twenty years much progress has been made in the theoretical analysis of the locomotion of flagellated micro-organisms. Following the early work of Taylor (1951, 1952) and Hancock (1953), Gray and Hancock (1955) derived two very useful approximate formulae for calculating the tangential and normal forces, dF_n and dF_s, acting on element (length ds) of a long thin cylindrical filament moving through a viscous fluid with tangential and normal velocities, V_s and V_n, relative to the fluid. The relations are

$$dF_n = -C_n^f V_n ds, \; C_n^f = 4\pi\mu/\{(ln(2\lambda/R) - \tfrac{1}{2}\}$$
$$dF_s = -C_s^f V_s ds, \; C_s^f = C_n^f/2 \qquad (1)$$

where μ is the dynamic viscosity of the fluid, R is the filament radius and λ a wavelength of the flagellar motions. These formulae have been used by many authors including Gray (1958) and Carlson (1959) to predict the locomotion due to planar waves propagating along a flagellum. More recently Chwang and Wu (1971) have extended their use to investigations of flagella with helical waves.

The present paper is concerned with a distinctively different situation. It is known that the flagellum of many species have appendages in the form of thin, lateral projections called mastigonemes (Pitelka, 1963). The observations of Pitelka (1963) and Pitelka and Schooley (1955) on one such organism, *Ochromonas*, indicated that the mastigonemes are quite rigid and are solidly connected more or less normal to the flagella. Subsequently Jahn, Landman and Fonseca (1964) observed that *Ochromonas*, propagated planar waves along the flagella from base to tip in the manner indicated in Figure 1. The resulting propulsion was in the *same* direction as this wave propagation and hence contrary to the direction of propulsion expected in the absence of mastigonemes. Thus Jahn, Landman and Fonseca (1964) rejected Pitelka's (1963) suggestion that the mastigonemes merely supplemented the hydrodynamic effect of the flagellar wave and, in explaining the major propulsive effect of these appendages, qualitatively ascribed it to the rowing action of each mastigoneme as the flagellar wave passed by. One qualitative and approximate way of including the effect of the mastigonemes in a hydrodynamic analysis was suggested by Jahn, Landman and Fonseca (1964) and later implemented by Holwill and Sleigh (1967). This model considered that the role of the mastigonemes can be envisaged as increasing the effective tangential resistive coefficient, C_s^f, on the flagellum so that the effective ratio C_s^f/C_n^f is much larger than would occur for the basic "smooth" flagellum. The potential effect of such an increased value of C_s^f/C_n^f was demonstrated by Taylor (1951) in his pioneering paper. Holwill and Sleigh (1967) confirmed that propulsion would be in the same direction as the propagation of the flagellar wave when the effective C_s^f/C_s^f became greater than unity. Indeed they employed their measured swimming speeds in an inverse calculation to obtain an effective value of this ratio in the neighbourhood of 1.8; comparison of sessile and swimming organisms and other evidence also caused Holwill and Sleigh to conclude that the majority of the mastigonemes must be aligned in the plane of the flagellar wave.

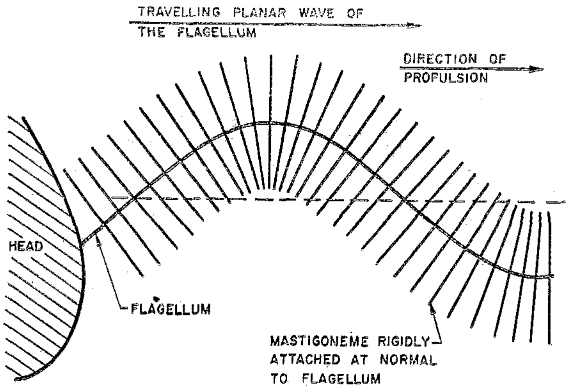

Figure 1. The flagellar/mastigoneme propulsion system.

FIGURE 1 The flagellar/mastigoneme propulsion system.

The objective of the present paper is to present, first, a more detailed fluid mechanical analysis of the mastigoneme/flagellar system of propulsion and to evaluate this system and its optima in the light of previous experimental observation. This analysis will then be modified to allow study of the structural requirements on the mastigonemes which are necessary for propulsion. It will be demonstrated that mastigonemes must be quite rigid with a fairly large modulus of elasticity, E, in order to achieve the observed propulsive velocity. Theoretically, smaller values of E would cause the deflections of the mastigonemes under the applied hydrodynamic load to be quite large with a consequent reduction in performance of the propulsion system and eventually a reversion to an effectively smooth flagellum.

2. HYDRODYNAMIC VELOCITIES AND FORCES ON THE MASTIGONEMES

We concentrate attention on the motion of a pair of mastigonemes in a frame of reference (x, y) in which the head of the organism is fixed (Figure 2). The wave number, wave velocity and amplitude of the wave propagating along the flagellum in the $+$ve x direction are denoted by $k(=2\pi/\lambda)$, c and a respectively. It follows that lateral motion of a general material point, B, on the flagellum at $x = x_0$ is given by

$$y_0 = a \sin k(x_0 - ct) = a \sin \theta \tag{2}$$

where t is time and $k(x_0 - ct)$ is denoted for convenience by θ. Assuming that a mastigoneme remains attached at a normal to the flagellum at the point B the coordinates of a general material point C on the mastigoneme, distance s from B, are denoted by x_c, y_c where

$$\begin{aligned} x_c &= x_0 - s \sin \varphi \\ y_c &= a \sin \theta + s \cos \varphi \end{aligned} \tag{3}$$

where φ is the slope of the tangent to the flagellum at B so that

$$\tan \varphi = ka \cos \theta \tag{4}$$

and hence φ defines the angular inclination of the mastigonemes. It follows that the velocities of the material point C in the x and y directions are respectively

$$u_c = -\frac{sk^2ac \sin \theta}{[1 + k^2a^2 \cos^2 \theta]^{\frac{3}{2}}} \tag{5}$$

$$v_c = -kac \cos \theta - s\frac{k^3a^2c \cos \theta \sin \theta}{[1 + k^2a^2 \cos^2 \theta]^{\frac{3}{2}}} \tag{6}$$

If in addition the organism is propelling itself with velocity V in the positive x direction then, in the above frame of reference, the fluid has an additional velocity V in the negative x direction. Consequently the velocities of an element of mastigoneme, length ds, relative to the fluid are $(u_c + V)$ and v_c. By resolving these into components normal and tangential to the element, employing viscous resistive

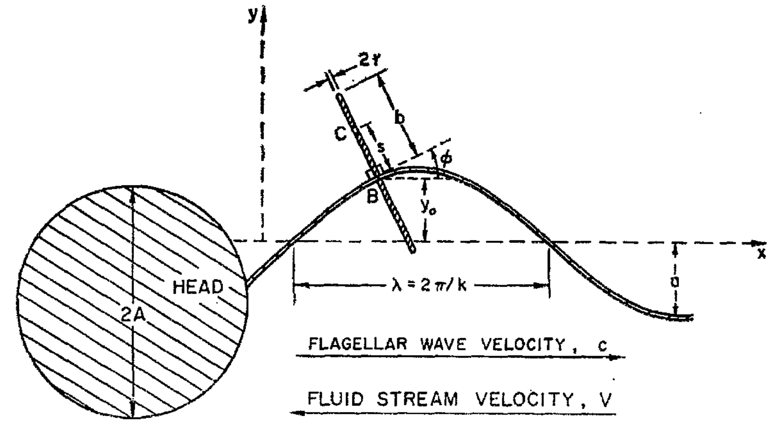

FIGURE 2 Geometric and hydrodynamic variables in the model of the flagellar/mastigoneme propulsion system.

coefficients for the mastigoneme C_n^m and C_s^m describing the elemental forces in those directions and resolving the forces on the element back into components in the x and y directions, dF_x and dF_y we find

$$\begin{aligned} dF_x &= C_n^m[-(u_c+V)\{1-(1-\gamma)\sin^2\varphi\} \\ &\qquad -v_c\sin\varphi\cos\varphi(1-\gamma)] \\ dF_y &= C_n^m[-(u_c+V)(1-\gamma)\sin\varphi\cos\varphi \\ &\qquad -v_c\{1-(1-\gamma)\cos^2\varphi\}] \end{aligned} \tag{7}$$

where $\gamma = C_s^m/C_n^m$. The resistive coefficients which seem to be most appropriate to this situation are those developed by Burgers (1938) and more recently by Chwang and Wu (197~~4~~5) for long thin ellipsoids of length $2b$ and radius r, namely

$$C_n^m = 4\pi\mu/(ln(2b/r)+\tfrac{1}{2}) \tag{8}$$

$$C_s^m = 2\pi\mu/(ln(2b/r)-\tfrac{1}{2}) \tag{9}$$

Unnecessary complexity in the present case is avoided by observing that $b/r \gg 1$ for a pair of mastigonemes where b and r are respectively the mastigoneme length and radius so we may set $\gamma \simeq 1/2$ without introducing significant error. Substituting this and the expressions for u_c and v_c, Eqs. (7) become

$$dF_x = C_n^m\left[-V+\frac{(V+c)k^2a^2\cos^2\theta}{2[1+k^2a^2\cos^2\theta]} + \frac{sk^2ac\sin\theta}{[1+k^2a^2\cos^2\theta]^{\frac{3}{2}}}\right] \tag{10}$$

$$dF_y = C_n^m\left[kac\cos\theta-\frac{(V+c)ka\cos\theta}{2[1+k^2a^2\cos^2\theta]} + \frac{sk^3a^2c\cos\theta\sin\theta}{[1+k^2a^2\cos^2\theta]^{\frac{3}{2}}}\right] \tag{11}$$

Integrating (10) from $s = -b$ to $s = +b$, that is over the length of the pair of mastigonemes emanating from B on either side of the flagellum we obtain the total instantaneous force in the positive x direction, $2F_x$, on this mastigoneme pair as

$$2F_x = 2bC_n^m\left[-V+\frac{(V+c)}{2}\,\frac{k^2a^2\cos^2 k(x_0-ct)}{[1+k^2a^2\cos^2 k(x_0-ct)]}\right] \tag{12}$$

Finally integrating over one cycle in time, $2\pi/kc$, the average force in the positive x direction per mastigoneme pair, $2F_m$, becomes

$$2F_m = bC_n^m\left[-V+c-\frac{(V+c)}{(1+k^2a^2)^{\frac{1}{2}}}\right] \tag{13}$$

3. FORCE BALANCE ON THE ORGANISM AND VELOCITIES OF PROPULSION

It remains to evaluate the forces on the other components of the organism, before we can construct the condition of zero total force and thus obtain an expression for the propulsive velocity, V. The force on the flagellum, F_f, can be assessed in the conventional manner mentioned in the introduction; it corresponds precisely with Holwill and Sleigh's (1967) result for a smooth flagellum with $C_m^f/C_s^f = 2$, i.e.

$$F_f = C_n^f L\left[-\left(V+\frac{c}{2}\right)+\frac{(V+c)}{2[1+k^2a^2]^{\frac{1}{2}}}\right] \tag{14}$$

where L is the length of the flagellum and C_n^f is given by (1). When the ratio of the mastigoneme length to their separation distance is large we shall see that this flagellar force contributes negligibly to the results. Though this is often the case, the force

F_f will nevertheless be included for the purposes of completeness. Finally the force on the head, F_h, is assessed by assuming a roughly spherical shape of radius A so that $F_h = 6\pi\mu VA$. Then setting $F_h + F_f + NF_m = O$ where N is the number of mastigonemes, the velocity of propulsion, V, becomes

$$\frac{V}{c} = \frac{[(1+k^2a^2)^{\frac{1}{2}}-1]}{\left[\frac{(1+2\alpha+\beta)}{(\beta-\alpha)}[1+k^2a^2]^{\frac{1}{2}}+1\right]} \qquad (15)$$

where $\alpha = C_n^f L/12\pi\mu A$, $\beta = C_n^m bN/12\pi\mu A$. Hence it is clear that if $bN \gg L$ the force on the flagellum can usually be neglected and α set equal to zero in the relation (15).

Eq. (15) in combination with the definitions (8) and (1) for C_n^m and C_n^f therefore allows evaluation of the propulsion of a flagellated organism with mastigonemes once the geometric lengths λ, a, b, c, r, L, A, R, the number of mastigonemes, N, and the flagellar wave velocity, c, are known. The result clearly shows why propulsion with mastigonemes is generally opposite in direction to that without mastigonemes since when $\beta > \alpha$, V/c is positive whereas when $\beta = O$, V/c is negative.

The optimizations of V/c with regard to α, β are quite simple since the latter quantities must always be positive. It is readily established that maximum negative propulsion is provided when $\beta = O$ and α is as large as possible; that is with a long smooth flagellum and no mastigonemes. On the other hand maximum positive propulsion is established when α is as small as possible and β as large as possible; this corresponds to a thin flagellum with as many long mastigonemes as possible. The latter condition must however be qualified by uncertainty in the validity for the resistance coefficient approach when the mastigonemes are tighly packed. Such simple optima are clearly a result of the fact that the net flagellar force is always in the negative x direction whereas the net mastigoneme force is always positive. It follows that all intermediate physiologies are less effective from a propulsion standpoint.

TABLE I. Measurements on Ochromonas malhamensis by Pitelka and Schooley (1955), Jahn, Landman and Fonseca (1964) and Holwill and Sleigh (1967).

Quantity		Pitelka and Schooley (1955)	Jahn, Landman & Fonseca (1964)	Holwill and Sleigh (1967)
Average Head Radius, A (μm.)			3.5	
Flagellar Length, L (μm.)			8	19.8
Flagellar Radius, R (μm.)				0.125
Flagellar Wavelength, λ (μm.):	Basally			4.0
	At tip			9.0
	Average		4	7.0
Flagellar Wave-amplitude, a (μm.):	Basally			0.65
	At tip			1.25
	Average		0.8	0.95
Flagellar Wave-frequency, (Hz)			50	68.4
Flagellar Wave Velocity, c (μm/sec)			200	480
Mastigoneme length, b (μm.)		1.3		1.1
Mastigoneme radius, r (μm.)		0.0075		0.01
Number of mastigonemes per μm of flagellum		10		16.4
Number of mastigonemes, N			80	320
Propulsive velocity, V (μm/sec)				55 - 60
ka:	basally			1.02
	at tip			0.87
	average			0.95
kb:	(average)			1.0
α				0.79
β				5.05
Γ				0.2
V/c				0.114→0.125

4. OCHROMONAS

Numerical values quoted by Pitelka and Schooley (1955), Jahn, Landman and Fonseca (1964) and Holwill and Sleigh (1967) enable a theoretical estimate to be made for the propulsive velocities of *Ochromonas malhamensis*. Table 1 lists these values together with the resulting non-dimensional quantities ka, kb, α, β and V/c. Only Holwill and Sleigh (1967) present data which is sufficiently complete for the purposes of comparison with theory and hence the present paper will utilize those values. (It should, however, be noted that comparison of some of the data reveals significant differences.)

The predicted value of V/c based on the observed values of ka (average) kb, α and β is 0.125 (see Figure 3). The corresponding propulsive velocity, V, would be 60 μm/sec which compares most favourably with the observed swimming speed of 55→60 μm/sec.

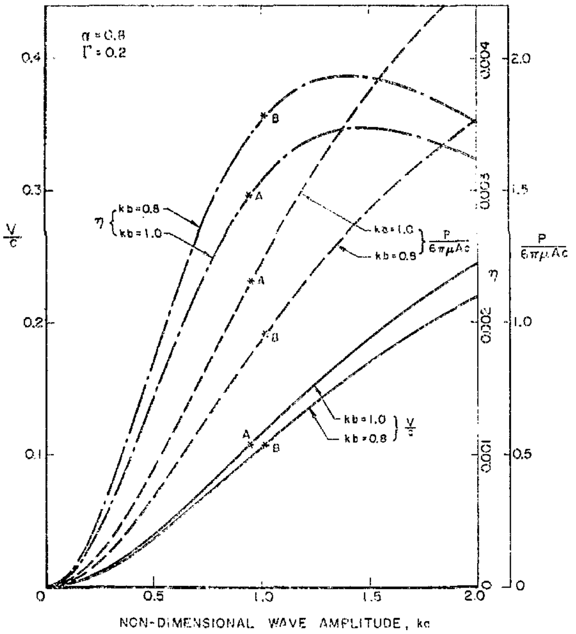

FIGURE 3 The propulsive velocity, V, efficiency, η, and zero velocity thrust, P, as functions of the non-dimensional wave amplitude, ka, for $\alpha = 0.8$, $\Gamma = 0.2$, $kb = 0.8$ and 1.0. The point A is apparently the operational mode for *Ochromonas malhamensis*; B is a modified operational point discussed in the text.

In evaluating this result it should be noted that $L \ll bN$ and hence $\alpha \ll \beta$ for *Ochromonas*; thus the contribution of the flagellar forces is small and the result would be little changed by setting $\alpha = O$. In addition the value of β is not particularly sensitive either to r or the factor $\frac{1}{2}$ in the denominator of the definition of C_n^m. Furthermore the resulting value of V/c is most sensitive to the value of ka and relatively insensitive to the accuracy in computing β. Thus one must note that agreement between experiment and theory is really limited by the accuracy with which one can estimate ka; a rough estimate of all the other geometric lengths is all that is necessary. In this regard it is worth observing that according to the observations Holwill and Sleigh, the value of ka varies much less than either k or a as one progresses from the base to the tip of the flagellum.

5. ENERGY EXPENDITURE

It is clearly of importance to establish the rate at which an organism must do work on the fluid in order to move at the propulsive velocity, V. The instantaneous rate of working of the mastigoneme element, ds, of section 2 is given by dW, where

$$dW = -(u_c + V)dF_x - v_c dF_y \qquad (16)$$

which upon substitution for u_c, v_c, dF_x and dF_y, integration over a mastigoneme pair and then over one cycle in time yields the following mean rate of work done by a mastigoneme on the fluid, W_M, as

$$W_M = \frac{C_n^m b V^2}{2}\left[2 - \left(1 + \frac{c}{V}\right)^2 [1 - (1 + k^2a^2)^{-\frac{1}{2}}] + k^2a^2\left(\frac{c}{V}\right)^2 + \frac{k^2a^2k^2b^2}{3(1 + k^2a^2)^{\frac{1}{2}}}\left(\frac{c}{V}\right)^2\right] \qquad (17)$$

where V/c is given by the Eq. (15).

Similarly the mean rate of expenditure of energy by the flagellum is

$$W_F = \frac{C_n^f L V^2}{2}\left[1 + \left(1 + \frac{c}{V}\right)^2 [1 - (1 + k^2a^2)^{-\frac{1}{2}}] - \frac{k^2a^2}{2}\left(\frac{c}{V}\right)^2\right] \qquad (18)$$

and that of the head is $W_H = 6\pi\mu A V^2$. Thus the total rate of work done on the fluid and hence the energy expenditure by the organism, W_T, is readily computed. Since a primary objective of the propulsion system is to move the head, it is both convenient and instructive to present this as an efficiency, η, defined as the ratio of the work done in moving the head, W_H, to the total work done,

W_T. This may be written in terms of ka, kb, α and β as

$$\frac{1}{\eta}=\frac{W_T}{6\pi\mu AV^2}=(1+\alpha+2\beta)+(\beta-\alpha)\left(1+\frac{c}{V}\right)^2\{(1+k^2a^2)^{-\frac{1}{2}}-1\}+(2\beta-\alpha)\left(\frac{c}{V}\right)^2\frac{k^2a^2}{2}+\frac{\beta k^2a^2k^2b^2}{3(1+k^2a^2)^{\frac{1}{2}}}\left(\frac{c}{V}\right)^2$$

Let us examine how this efficiency will change with properties of the propulsion system. Specifically we will first consider its variation with the wave amplitude, a (or ka), and the length of the mastigonemes, b (or kb), while the other properties of the system (A, C_n, b/r, N, k, α, etc.) retain some given value. Since β involves b it must be replaced in (19) by kb/Γ where $\Gamma = 12\pi\mu Ak/NC_n^m$. Figure 3 then demonstrates how the propulsive velocity, V/c and the efficiency, η, vary with ka and kb for the case of $\Gamma = 0.20$ and $\alpha = 0.80$ values appropriate to *Ochromonas malhamensis*. First of all one must remark that the efficiencies, η, are very small, even in comparison with other means of micro-organism locomotion (*cf.* Chwang and Wu, (1971)). It is however notable that for a given kb there exists a value of ka for which the efficiency has a maximum value. In particular when $kb = 1.0$ (a value appropriate to *Ochromonas malhamensis*) maximum efficiency occurs at about $ka = 1.5$. But this organism does not appear to operate at such a point of optimum efficiency. Instead the data indicates that it operates at the point A, Figure 3, with a value of ka of about 0.95 and thus the propulsion system would appear to be somewhat inefficient in this regard. To illustrate this one need only observe that the same forward velocity may be obtained at an operational point such as B of Figure 3 with a significantly increased efficiency simply by an increase in ka and a corresponding decrease in kb. The answer to this apparent dilemma may lie in the rather limited view we have taken of the duties which the propulsion system may be called upon to perform. More specifically, maximum steady translational velocity may *not* be the most important feature of propulsion for the organism. The ability to manoeuvre and accelerate may be of comparable importance. Now a measure of this ability is clearly implied in the thrust which the mastigonemes can develop when the organism is held at rest. This thrust, P, is immediately obtained from the equations of section 2 by setting $V = 0$; then

$$\frac{P}{6\pi\mu Ac}=(\beta-\alpha)\left[1-(1+k^2a^2)^{-\frac{1}{2}}\right] \tag{20}$$

Values of this non-dimensional thrust are also plotted in Figure 3. Now observe the consequences of the modification of the propulsion system from A to B; though this results in somewhat more efficient rectilinear propulsion it also causes a significant reduction in the thrust, P, and hence a reduced ability to manoeuvre and accelerate. It would thus appear that the propulsion system of *Ochromonas* represents a compromise in achieving not only a fairly efficient means of rectilinear translational motion but also a substantial ability to manoeuvre and accelerate. It is however necessary to qualify such purely hydrodynamic arguments by noting that important biological constraints should be included in any complete study of the optimization of the propulsion system.

6. MASTIGONEMES NOT PERPENDICULAR TO THE FLAGELLUM

Since mastigonemes may not be precisely normal to the flagellum it is clearly important to establish the sensitivity of the results to deviations from this geometry. First we examine the effect of mastigonemes which are not perpendicular to the flagellum but are held at a *fixed* angle, δ, to the flagellar normal. Proceeding through an analogous calculation for such a case and neglecting the force on the flagellum for simplicity the propulsive velocity V becomes

$$\frac{V}{c}=\frac{[(1+k^2a^2)^{\frac{1}{2}}-1]}{\left[\frac{\left(3+\frac{2}{\beta}-\cos 2\delta\right)}{2\cos 2\delta}(1+k^2a^2)^{\frac{1}{2}}+1\right]} \tag{21}$$

Hence deviations, δ, in either direction, i.e. away from or towards the head, have the same effect. Using the values of β and ka for *Ochromonas*, this result indicates that the ratio of the velocities of propulsion for $\delta = 10°$, $20°$ and $30°$ to the velocity of propulsion when the mastigonemes are normal to the flagellum are respectively 0.87, 0.76 and 0.56. It follows that if the mastigonemes were held rigidly at an angle of more than about 10° from the local normal to the flagellum the organism would experience a significant degradation in its propulsive ability. One should point out that the validity of the result (21) may be doubtful for larger values of δ due to the resulting structural and fluid mechanical interference between the mastigonemes.

7. FLEXIBLE MASTIGONEMES

In the real physical situation the hydrodynamic forces on each mastigoneme will cause these organelles to bend and to flex at their junction with the flagellum. Little evidence exists of any active mechanism controlling the motion of the mastigonemes themselves and hence we shall assume that the response of each mastigoneme to these hydrodynamic forces is a purely passive one, depending only on the elastic properties of the organelle and the junction. Then, since the forces vary with time the orientation or angle of the mastigoneme to the flagellum will change during the passage of a flagellar wave. In the present section we will attempt to determine the effect of such flexibility on the propulsive velocity of the organism.

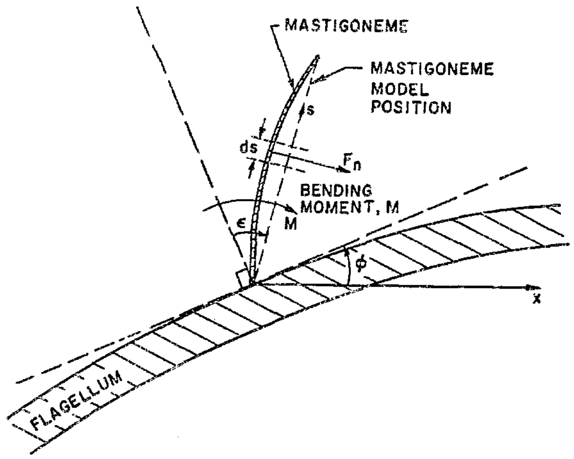

FIGURE 4 A sketch showing the notation used in discussing flexible mastigonemes.

However in order to effect some reduction in the algebraic complexity which such an analysis presents we will assume that the flexibility of both the mastigoneme and the junction can be combined in a "composite junction flexibility". This is at least qualitatively justified since the mastigoneme itself will experience the greatest bending moment and therefore the greatest bending close to the junction. Our model (Figure 4) will then consist of approximating the configuration of the mastigoneme by a straight line whose angle to the flagellar normal, ϵ, is at any instant governed by $\epsilon = M/E^*$ where E^* is the "composite junction stiffness" and M is the bending moment at the base given in the usual manner as

$$M = \int_0^b s\,dF_n \tag{22}$$

where, as before, dF_n is the force normal to an element ds of the mastigoneme.

Consequently the position and velocity components of the mastigoneme element are

$$x_c = x_0 - s\sin(\varphi-\epsilon);\quad y_c = a\sin\theta + s\cos(\varphi-\epsilon);$$

$$u_c = -s\left\{\frac{\partial\varphi}{\partial t}-\frac{\partial\epsilon}{\partial t}\right\}\cos(\varphi-\epsilon);$$

$$v_c = -kac\cos\theta - s\left\{\frac{\partial\varphi}{\partial t}-\frac{\partial\epsilon}{\partial t}\right\}\sin(\varphi-\epsilon)$$

where, φ is still defined by $\tan\varphi = ka\cos\theta$. These equations are generalizations of (3), (5) and (6). Evaluating F_n as before and subsequently the bending moment, M, the resulting differential equation for ϵ becomes

$$\begin{aligned}\frac{2\epsilon E^*}{C_n^m b^2} = &-\frac{(V+c)ka\cos\theta\sin\epsilon}{[1+k^2a^2\cos^2\theta]^{\frac{1}{2}}}\\ &+\frac{(-V+ck^2a^2\cos^2\theta)\cos\epsilon}{[1+k^2a^2\cos^2\theta]^{\frac{1}{2}}}\\ &+\frac{2bk^2ac\sin\theta}{3[1+k^2a^2\cos^2\theta]}-\frac{2b}{3}\frac{\partial\epsilon}{\partial t}\end{aligned} \tag{23}$$

In order to proceed we shall limit the analysis to those cases for which the stiffness E^* is sufficiently large so that ϵ is a relatively small angle. Then defining a dimensionless parameter $T = b^2cC_n^m/E^*$ and taking $T<1$ we may write the following expansion solution for ϵ.

$$\epsilon = T\epsilon_0 + T^2\epsilon_1 + O(T^3) \tag{24}$$

where

$$\epsilon_0 = \frac{\left(-\frac{V}{c}+k^2a^2\cos^2\theta\right)}{2[1+k^2a^2\cos^2\theta]^{\frac{1}{2}}}+\frac{k^2ba\sin\theta}{3[1+k^2a^2\cos^2\theta]} \tag{25}$$

$$\epsilon_1 = \frac{-\epsilon_0\left\{\frac{V}{c}+1\right\}ka\cos\theta}{2[1+k^2a^2\cos^2\theta]^{\frac{1}{2}}}+\frac{kb}{3}\frac{\overset{\partial\epsilon_0}{\cancel{\partial\theta}}}{\partial\theta} \tag{26}$$

In fact it is readily demonstrated that the solution of (23) represented by (24) (25) and (26) is a good approximation even when T if of order unity *provided* the angle ϵ is small. This solution then defines the flexing motion of the mastigoneme as a function of $\theta = k(x_0 - ct)$, that is with the passage of a flagellar wave; however it contains the propulsive velocity, V, which is as yet undetermined. Note that ϵ has both oscillatory parts and a *non-zero* mean.

Now the incremental force dF_x on the same element of mastigoneme in the positive x direction is given by

$$dF_x = C_n^m \Big[V\{-1 + \tfrac{1}{2}\sin^2(\varphi - \epsilon)\} + s\left\{\frac{\partial\varphi}{\partial t} - \frac{\partial\epsilon}{\partial t}\right\}\cos(\varphi - \epsilon) + \tfrac{1}{2}kac\cos\theta\cos(\varphi-\epsilon)\sin(\varphi-\epsilon)\Big] \tag{27}$$

Our solution (24) for ϵ must then be substituted into this and the force dF_x integrated from $s = 0$ to $s = b$ to obtain the total force F_x on a mastigoneme in the positive x direction. Subsequently this force is integrated over one cycle in time to obtain the mean value, F_m, of F_x. Though this procedure is algebraically complicated the basic idea is simple. The final result is a power series in T. The zeroth order term is identical to the F_m defined by Eq. (13). The terms which are first order in T yield no contribution to F_m. Hence the need for the second order in the expansion (24); up to this second order the result for F_m is

$$\begin{aligned}\frac{2F_m}{bcC_n^m} = {} & -\frac{V}{c} + 1 - \frac{\left(\frac{V}{c}+1\right)}{(1+k^2a^2)^{\frac{1}{2}}} \\ & + \frac{T^2}{8}\Bigg[\frac{4\left(\frac{V}{c}+1\right)^3}{(1+k^2a^2)^{\frac{3}{2}}} - \frac{2\left(\frac{V}{c}+1\right)^2\left(\frac{V}{c}+9\right)}{(1+k^2a^2)^{\frac{1}{2}}} \\ & + 10\left(\frac{V}{c}\right)^2 + 26\frac{V}{c} + 14 - k^2a^2\left(2\frac{V}{c}+3\right) \\ & + \frac{2k^2b^2}{9}\Bigg\{\frac{\left(\frac{V}{c}+1\right)}{(1+k^2a^2)^{\frac{3}{2}}} + \frac{2}{(1+k^2a^2)^{\frac{1}{2}}} \\ & - \left(\frac{V}{c}-1\right)(1+k^2a^2)^{\frac{1}{2}} - 4\Bigg\}\Bigg]\end{aligned} \tag{28}$$

The forces on the head and flagellum must be added to NF_m and the sum equated to zero. Using the same definitions as before these other forces are respectively given by

$$\frac{2F_h}{NbC_n^m c} = -\frac{1}{\beta}\frac{V}{c} \tag{29}$$

and

$$\frac{2F_f}{NbC_n^m c} = \frac{2\alpha}{\beta}\left[-\frac{V}{c} - \frac{1}{2} + \frac{\left(\frac{V}{c}+1\right)}{2[1+k^2a^2]^{\frac{1}{2}}}\right] \tag{30}$$

Finally we obtain the following equation which must be solved for V/c:

$$\begin{aligned}\frac{V}{c}\left[\frac{(\beta+2\alpha+1)}{(\beta-\alpha)} + (1-k^2a^2)^{-\frac{1}{2}}\right] & \\ = [1-(1+k^2a^2)^{-\frac{1}{2}}] + \frac{\beta T^2}{8(\beta-\alpha)} & \\ \Bigg[\frac{4\left(\frac{V}{c}+1\right)^2}{(1+k^2a^2)^{\frac{3}{2}}} - \frac{2\left(\frac{V}{c}+1\right)^2\left(\frac{V}{c}+9\right)}{(1+k^2a^2)^{\frac{1}{2}}} & \\ + 10\left(\frac{V}{c}\right)^2 + 26\frac{V}{c} + 14 - k^2a^2\left(3+2\frac{V}{c}\right) & \\ + \frac{2k^2b^2}{9}\Bigg\{\frac{\left(\frac{V}{c}+1\right)}{(1+k^2a^2)^{\frac{3}{2}}} + \frac{2}{(1+k^2a^2)^{\frac{1}{2}}} & \\ - \left(\frac{V}{c}-1\right)(1+k^2a^2)^{\frac{1}{2}} - 4\Bigg\}\Bigg] &\end{aligned} \tag{31}$$

The numerical solution of this equation yielded V/c as a function of the parameters ka, kb, α, β and T. Since, typically, $\alpha \ll \beta$ we shall for simplicity present solutions only for $\alpha = 0$. Figure 5 presents

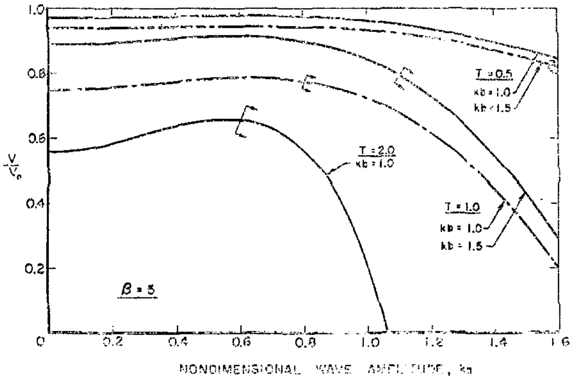

FIGURE 5 The ratio of the propulsive velocity due to flexible mastigonemes, V, to that for rigid mastigonemes, V_0, plotted against the non-dimensional wave amplitude, ka, for $\beta = 5$, $\alpha = 0$ and various values of kb and the mastigoneme flexibility, T. The small angular deflection theory is only numerically accurate for points to the left of a position indicated by ⊏.

values of the ratio of the propulsive velocity, V, to that for rigid mastigonemes, V_0, plotted against ka for various kb and T when β takes the value of 5.0 relevant to *Ochromonas malhamensis*. Within the relevant ranges of values for ka and kb it is clear that the propulsive effect of the mastigonemes is significantly impaired when they are flexible enough for T to be about unity or greater. Further results are presented in Figure 6 where V/V_0 is plotted against T for various kb and β when ka takes a value of 0.9. This primarily shows that the results are virtually independent of β provided this is greater than about unity. In particular from the point of view of *Ochromonas* for which $kb \approx 1$, $ka \approx 0.9$ the propulsive velocity is reduced by 3%, 12% and 30% for values of T of 0.5, 1.0 and 1.5.

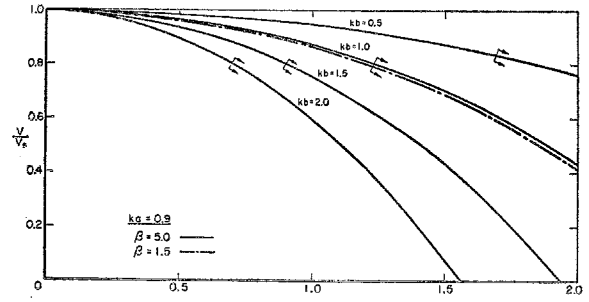

FIGURE 6 The ratio of the propulsive velocity due to flexible mastigonemes, V, to that for rigid mastigonemes, V_0, plotted against the mastigoneme flexibility, T, for $ka = 0.9$ and various values of kb and B. The small angular deflection theory is only numerically accurate for points to the left of a position indicated by ⇨.

Since the observed velocity of *Ochromonas* (55–60 μm/sec) is within 10% of that predicted for rigid mastigonemes (60 μm/sec) one can conclude that there is little such degradation of performance for this organism. Hence it would appear that the relevant value of T for *Ochromonas* is less than unity.

Having obtained values for V/c, the corresponding angular deflections, ϵ, of the mastigonemes can be computed from Eqs. (24), (25) and (26) as functions of the position/time variable $\theta = k(x_0 - ct)$. Typical deflection patterns are shown in Figure 7 for $ka = 0.95$, $kb = 1.0$, $\beta = 5$ and $\alpha = 0$ (values relevant to *Ochromonas malhamensis*) and for two values of mastigoneme flexibility, T. For a particular mastigoneme (i.e. fixed x_0) the instants when a peak, a trough and nodes of the flagellar wave are passing this mastigoneme are also identified for convenience of interpretation. Values of the deflection at these instants are then plotted in Figure 8 as functions of the non-dimensional wave amplitude, ka, for $kb = 1$, $\beta = 5$, $\alpha = 0$ and a variety of mastigoneme flexibilities, Γ.

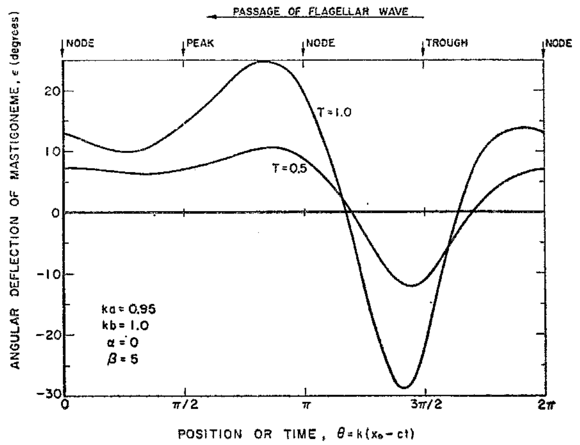

FIGURE 7 The angular deflection of the mastigonemes, ϵ (in degrees from the flagellar normal), as a function of θ, i.e. with x_0 position at fixed time *or* with the passage of a flagellar wave past a particular mastigoneme. Deflection for $ka = 0.95$, $kb = 1$, $\beta = 5$, $\alpha = 0$ and two values of mastigoneme flexibility, T, of 0.5 and 1.0.

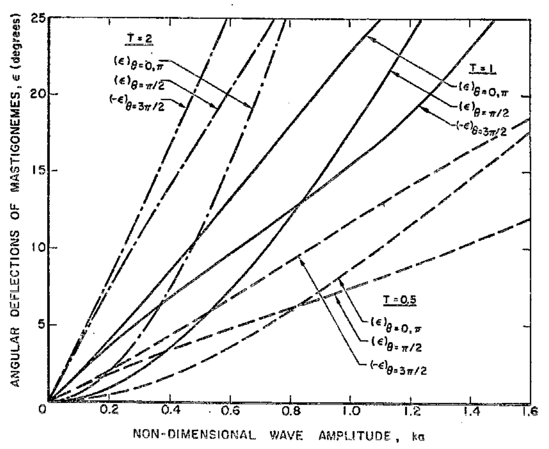

FIGURE 8 The angular deflections of the mastigonemes, ϵ (in degrees from the flagellar normal), at the passage of a peak in the flagellar wave ($\theta = \pi/2$), at the passage of a trough ($\theta = 3\pi/2$) and at the passage of the node points ($\theta = 0, \pi$) as a function of the non-dimensional wave amplitude, ka, for $\beta = 5$, $\alpha = 0$, $kb = 1$ and various values of the mastigoneme flexibility, T; $T = 0.5$, - - - - - -; T = 1.0, ———; $T = 2.0$, —— · ——.

Finally we should recall that the numerical accuracy of the small deflection theory used here is restricted to fairly small values of ϵ. In order to record this limit in the figures, a nominal maximum value of $|\epsilon|$ of 25° was selected and the corresponding regions of doubtful numerical accuracy recorded in Figures 5 and 6.

Despite this restriction all the numerical results indicate that for values of T greater than about 2 the propulsive effect of the mastigonemes has virtually vanished. In this limit it would seem eminently reasonable therefore to conclude that the propulsion system has reverted to an effectively smooth flagellum.

8. PRACTICAL ESTIMATES OF THE FLEXIBILITY PARAMETER *T* AND IMPLICATIONS OF THE ANALYSIS

In order to obtain some estimates of a practical value of T we note that according to its definition E^* would be given by $\lambda EI/b$ for a loaded cantilever of length b, stiffness EI, second moment of inertia I and modulus of elasticity, E. For a uniformly distributed load, λ [redacted] IS 4; FOR A POINT LOAD λ IS 3. Hence E^* is rather insensitive to the distribution of the loading and we shall choose $\lambda = 4$ as a representative value. Thus an estimate of the value of the flexibility parameter T can be obtained from

$$T = \pi\mu cb^3/EI\{ln(2b/r)+\tfrac{1}{2}\} \qquad (32)$$

where for a homogeneous cylindrical rod~~e~~ we would set $I = \pi r^4/4$, r being the radius of the cross-section. Choosing values of c, b or r relevant to the propulsion of *Ochromonas malhamensis* and an aqueous viscosity, μ, of 10^{-10} dyne sec/μm^2 it follows that $T = 3.45\times 10^{-16}/EI$ where EI is in units of dynes cm^2. Stiffnesses, EI, of biological fibres are often used in preference to the moduli of elasticity, E, since one is approaching the level of single molecular bonds. Nevertheless it is worth noting that the above value corresponds to $T = 4.39/E$ where E is in units of dynes/μm^2 if we take a value of $I = 8\times 10^{-9}$ μm^4 calculated from $I = \pi r^4/4$. Note that this would be close to the values of I of 13×10^{-9} μm^2 calculated by Holwill (1965) for a micro-tuble in the flagella of *Strigomonas oncopelti*. Since we concluded in the last section that the value of T for *Ochromonas* mastigonemes must be less than unity this places lower bounds of about 4×10^{-16} dyne cm^2 and 5 dynes/μm^2 on EI and E respectively.

To put these values in perspective it is instructive to compare them with estimates of the structural properties of single muscle fibres for which Bozler (1957) quotes a value of $E = 0.6$ dynes/μm^2 and of single fibrils or micro-tubules in cilia and flagella. Rikmenspoel (1966) and Brokaw (1972) both estimate the *overall* stiffness of the flagella of sea urchin spermatozoa at about 10^{-13} dyne cm^2 which, if one neglects the possibly significant strength of the structural links between the microtubules, leads to a value of E of about 0.8 dyne/μm^2. Similarly Rikmenspoel and Sleigh (1970) estimate E for the fibrils of the gill cilia of *Sabellaria* and *Modiolus* at about 0.4 dynes/μm^2. Somewhat larger values for the overall stiffness of cilia in the neighbourhood of 5×10^{-12} dyne cm^2 are suggested by Harris (1961) and by Brokaw (1966) and would lead to elastic moduli of the microtubules of the order of 10 dynes/μm^2. Recently, however, Baba (1972) inferred very much larger values for cilia stiffness from his experimental data; Brokaw (1972) has questioned the degree to which the active elements in the cilia contribute to Baba's measurements. Finally, a comparison with prokaryote flagella seems even more relevant since a typical bacterial flagellum has a diameter (order 0.02 μm) comparable with that of the mastigonemes. Fujime, Maruyama and Asakura (1972) recently obtained a stiffness, EI, of 20×10^{-16} dyne/cm^2 for bacterial flagellum by quasielastic scattering of laser light; this corresponds to a value of about 40 dynes/μm^2 for E.

Thus the lower bounds on the stiffness, EI, and elastic modulus, E, of 4×10^{-16} dyne cm^2 and 5 dynes/μm^2 for the mastigonemes of *Ochromonas* indicated in the present paper are consistent with the structural properties of similar organelles. The closest analogy is with bacterial flagellum and if mastigonemes do indeed have a similar rigidity then they will be just stiff enough to provide the observed propulsive effect. It should also be noted that significant changes in T can be accomplished by variation in the viscosity of the medium in which the organism is moving. Thus it is quite possible that an experimental study of an organism such as *Ochromonas* in mediums of various viscosities would yield considerably more information on the structural properties of mastigonemes.

Finally we should also observe that T is most sensitive to the thickness of the mastigonemes, r, being inversely proportional to its fourth power. Thus reducing this thickness by about a half can increase T by a factor of ten and could result in a complete crossover from the region of effectively rigid mastigonemes to the region in which the latter are totally ineffective. Holwill and Sleigh (1967) note that the hairs on the flagellum of *Euglena* are much thinner than those of *Ochro-*

monas. Assuming roughly the same structural properties we can conclude from the results of the present study that these hairs would be very flexible and hence have little or no propulsive effect. Indeed no reversal in swimming direction of *Euglena* is observed and the flagellum is effectively "smooth".

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