LOCOMOTION OF SPIRILLA

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ABSTRACT The hydromechanics of spirilla locomotion is analyzed by considering the balance of both rectilinear and angular momenta of the surrounding viscous fluid which is otherwise at rest. The physical model of *Spirillum* adopted for the present analysis consists of a rigid helical body with flagella attached to both ends of the helix. The motion is supposed to be activated first by the polar flagella, both rotating in the same sense, thus causing the helical body to rotate in the opposite sense in angular recoil, which in turn pushes the body forward in response to the balance of linear momentum of the surrounding fluid. The sweeping back of the polar flagella during forward motion is ascribed to a certain bending flexibility of the flagella and of their conjunction with the body. Based on this model some quantitative results for *Spirillum* movement are predicted, and are found to be consistent with existing experimental data.

INTRODUCTION

Phenomenological investigations of the locomotion of *Spirillum* have been well documented. It seems to be generally accepted that *Spirillum* has a rigid, helically shaped body with a number of flagella at each end of the body. During locomotion, both the anterior and posterior groups (or bundles) of flagella rotate in one and the same direction, while the rigid helical body rotates in the opposite direction to that of the flagella, and less rapidly. In the forward propulsion that results from the rotation of a helical body, the anterior and posterior flagella are bent somewhat backwards to appear rotating in two conical surfaces of revolution (Metzner, 1920; Weibull, 1960) with their vertices pointing in the direction of locomotion (see Fig. 1) in a way resembling a set of whirling propeller blades which are free to feather. Sweeping back of these flagella during forward motion may be ascribed to a certain bending flexibility of the flagella and of their conjunction with the body. *Spirillum volutans* was observed by Metzner (1920) to have a flagellar rotational speed of about 40 rps and a helical body rotational speed of between 12 and 14 rps. When both polar flagella change their direction of rotation, the rigid helical body likewise reverses its rotation, and the entire organism accordingly reverses its direction of propulsion. Spirilla are noted for their relatively rapid locomotion in aqueous solutions by means of these helical movements.

The present paper attempts to make a hydromechanical analysis of *Spirillum*

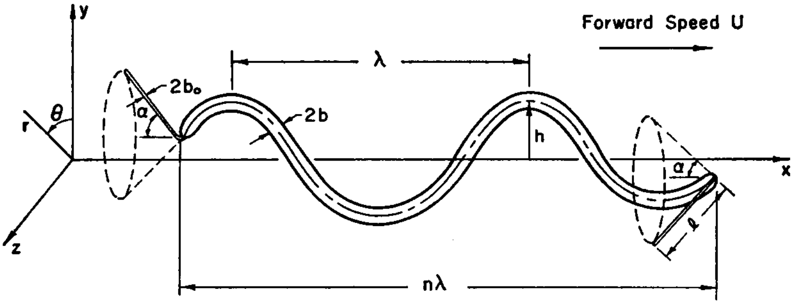

FIGURE 1 Schematic diagram of a self-propelling *Spirillum*.

locomotion on the basis of the following specific model. In this model, the body is assumed to have a helical central axis of a fixed form. We further speak of a "rigid body" when all material points of the body are fixed with respect to one another, and we shall call a body "sheathlike" if its material surface can gyrate with respect to the interior such that the motion of body surface of every cross section (in a plane transverse to the longitudinal x-axis) is specified by a curvilinear translation and an arbitrary rotation. The two polar flagella bundles (at both ends of the helical body) are assumed to be sufficiently stiff to keep rotating on a conical surface, whose vertex angle is related to, or can be estimated by, the moment (in a meridian plane) of the resistive force exerted by the viscous fluid on the advancing flagella. The motion is supposed to be activated first by the polar flagella, both rotating in the same sense, thus causing the helical body to rotate in the opposite sense as a result of an angular recoil, which in turn pushes the body forward in response to the balance of linear momentum of the surrounding fluid.

In equilibrium, both the forward velocity U and angular recoil velocity ω of the helical body are steady, and the motion of every longitudinal element of the body can be expressed in terms of U and ω. To determine the hydromechanical force and torque acting on a body element in a flow of low Reynolds number (of the order 10^{-8}), we shall adopt the formulas of the extended Gray and Hancock method, which was developed first by Gray and Hancock (1955) for planar body waves and later extended to the case of helical movements by Chwang and Wu (1971). If the tangential and normal velocities of a cylindrical body element of length ds are $\mathbf{V}_s$ and $\mathbf{V}_n$ respectively, and its angular velocity about the longitudinal axis is $\mathbf{\Omega}$, then the tangential and normal components of the viscous force acting on this body element are

$$\mathrm{d}\mathbf{F}_s = -C_s\mathbf{V}_s\mathrm{d}s, \quad \mathrm{d}\mathbf{F}_n = -C_n\mathbf{V}_n\mathrm{d}s, \tag{1 a}$$

and the viscous torque about its longitudinal axis is

$$\mathrm{d}\mathbf{M} = -C_m\mathbf{\Omega}\mathrm{d}s, \tag{1 b}$$

where C_s, C_n, and C_m are coefficients of resistance. Gray and Hancock (1955) give C_s and C_n as

$$C_n = 2C_s, \qquad C_s = \frac{2\pi\mu}{\ln(2\lambda/b) - \frac{1}{2}} \tag{2 a}$$

and according to Chwang and Wu (1971),

$$C_m = 4\pi\mu b^2. \tag{2 b}$$

In equation 2, b is the radius of a slender filament, λ the wavelength of a helical body, and μ the viscosity coefficient of the surrounding fluid. The resultant force and torque exerted on a *Spirillum* by the surrounding viscous fluid can be determined by integration of these elementary contributions along the body together with an evaluation of the contribution from the polar flagella.

By assuming that the forces and torques acting on the *Spirillum* in question involve those of hydromechanical origin only, as what has already been discussed above, and none of the other kinds (such as electrostatic or electrodynamic types), then the momentum consideration requires that the total force and torque acting on a *Spirillum* must vanish if the organism is to be self-propelling at a constant velocity U. From the two equations which set the total force and total torque equal to zero (see equation 7), we can determine the ratio U/c of the forward velocity U to the phase velocity $c = \omega/k$ of the helical wave (ω being the angular frequency, k the wave number of the body wave), and the ratio Ω/ω of the angular velocity Ω of a propelling flagellum to the angular recoil velocity ω of the body. Both these two ratios are found to depend on the "pitch angle" kh (h being the radial amplitude of the helical wave), and it is from this result that an optimum range of kh is determined wherein the ratio kU/Ω reaches a maximum. The effects of several geometrical and physical parameters on *Spirillum* locomotion are discussed in some detail in order to gain a deeper insight into the mechanism for the helical propulsion of this bacterium.

GENERAL THEORY FOR A SELF-PROPELLING *SPIRILLUM*

Suppose the helical body of a model *Spirillum* has a cross-sectional radius b, wavelength λ, radial amplitude h, and total length $n\lambda$ in the x direction (see Fig. 1), while each polar flagellum (or a bundle of flagella at one end of the body) has a stretched-straight length l and radius b_0. When both polar flagella rotate in the negative θ direction (with reference to a polar coordinate system (r, θ, x) fixed with respect to the fluid at infinity), a torque is induced that acts to rotate the rigid helical body in the positive θ direction. As a result, the organism experiences a forward thrust and moves in the x direction. This mechanism is therefore analogous to the movement of a corkscrew, the fluid reaction to the rotation of polar flagella here acting in a manner analogous to a "screwdriver." In a steady state, the rigid helical body rotates with a constant angular velocity ω in the θ direction while both polar flagella rotate with a constant angular velocity Ω in the $(-\theta)$ direction, each transversing a conical trajectory whose half-cone angle is designated by α. Meanwhile the whole organism, with a right-handed body helix, moves at a constant mean velocity U in the positive x direction.

The total force acting on a rigid helical body in the x direction has been evaluated by Chwang and Wu (1971, their equations 4, 6, 11, and 12, now with the velocity in the θ direction given by $V_\theta = h\omega$), and the result for the present case is

$$F_x = n\lambda C_s(1 + \kappa^2)^{-1/2}[-U(1 + 2\kappa^2) + \kappa h\omega], \tag{3}$$

where $\kappa = kh$ and C_s is given by equation 2 *a*. By resolving the velocity of each revolving flagellum into a tangential and normal component in the meridian plane containing the flagellum, and by employing the same method for the helical body, we obtain the total resistance on the polar flagella in the x direction as

$$\begin{aligned} F_x^0 &= -m\int_0^l (C_s'U\cos^2\alpha + C_n'U\sin^2\alpha)\,\mathrm{d}s \\ &= -mlUC_s'(1 + \sin^2\alpha), \end{aligned} \tag{4}$$

where m denotes the number of polar flagella (or number of bundles of flagella; $m = 2$ for the model *Spirillum* shown in Fig. 1). C_s' may be approximated again by equation 2 *a*, and $2\lambda/b$ replaced by the ratio $2l/b_0$, the latter being thought of as proper to the polar flagella problem.

Before calculating the torque, we recall the difference between a rigid helical body and a soft sheathlike one. As illustrated in Fig. 2, the motion of a rigid helical body is the sum of sheathlike body motion and pure spin of the sheath. With an appropriate modification of the body surface spin which was considered earlier for a different case by Chwang and Wu (1971), a relationship applicable to the present

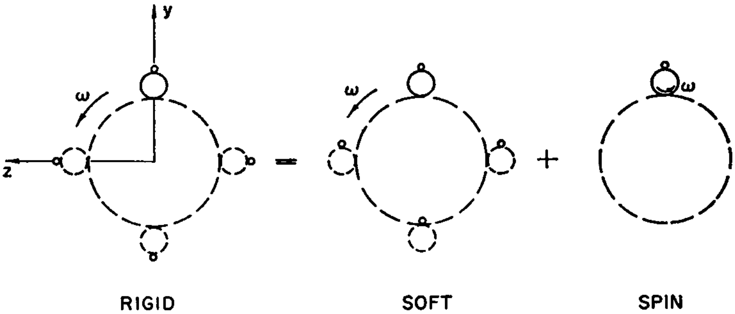

FIGURE 2 The motion of a cross section of a tagged helical body.

case may be obtained for the resultant torque (about the x-axis) on the entire rigid helical body as

$$M_x = n\lambda h C_s(1+\kappa^2)^{-1/2}[\kappa U - (2+\kappa^2+B)h\omega], \tag{5 a}$$

where

$$B = \frac{4\pi\mu}{C_s}\left(\frac{b}{h}\right)^2. \tag{5 b}$$

Similarly, the torque about the x-axis exerted on m polar flagella by the surrounding fluid is given by the moment of the azimuthal component of force integrated along the flagella, which is

$$\begin{aligned} M_x^0 &= m\int_0^l C'_n\Omega s^2 \sin^2\alpha ds \\ &= \frac{2}{3} m\Omega l^3 C'_s \sin^2\alpha. \end{aligned} \tag{6}$$

For a *Spirillum* propelling at a constant mean speed in a viscous fluid, the equilibrium condition requires that both the net force and net torque acting on it must vanish; that is,

$$F_x + F_x^0 = 0 \quad \text{and} \quad M_x + M_x^0 = 0. \tag{7}$$

Hence, by equations 3–7, we have

$$(1 + 2\kappa^2 + mA)U - \kappa h\omega = 0, \tag{8}$$

and

$$\kappa U - (2+\kappa^2+B)h\omega = -(2/3)mDh\Omega, \tag{9}$$

where

$$A = (1+\sin^2\alpha)(1+\kappa^2)^{1/2}(l/n\lambda)(C'_s/C_s), \tag{10 a}$$

$$D = \sin^2\alpha(1+\kappa^2)^{1/2}(l/h)^2(l/n\lambda)(C'_s/C_s). \tag{10 b}$$

The ratio of the forward propulsion velocity U to the phase velocity $c(c = \omega/k)$ and the ratio of the angular velocity of flagella Ω to that of the rigid helical body ω are readily obtained from equations 8 and 9 as

$$\frac{U}{c} = \frac{\kappa^2}{1+2\kappa^2+mA}, \tag{11}$$

$$\frac{\Omega}{\omega} = \frac{3}{2mD}\left[B + \frac{2(1+\kappa^2)^2 + m(2+\kappa^2)A}{1+2\kappa^2+mA}\right]. \tag{12}$$

In the special case wherein the body has no polar flagella at all, i.e. $m = 0$, the above solution reduces to

$$U = \omega = 0. \tag{13}$$

A physical interpretation of this result is clear. A *rigid* helical body cannot propel itself when it is deprived of the sole motive power provided by active polar flagella.

When only one polar flagellum is missing, however, whether anterior or posterior, a *Spirillum* can still propel itself without significant difference from a normal *Spirillum*. In this case we simply put $m = 1$ in equations 11 and 12. It is quite clear that the difference in the values of U/c, when m is reduced from 2 to 1, is rather small when κ is of the order $O(1)$ and $A \ll 1$, as found in practice. Some experimental observations pertinent to this point have been reported by Weibull (1960), who noted that "the propulsive effect of the two kinds of flagella were, however, the same. This was shown by the movement of spirilla that were flagellated at only one end. Such spirilla, which were only occasionally found, swam at approximately the same speed irrespective of whether the flagella were at the front or the rear end of the bacterium, i.e., irrespective of whether the flagella formed a tail behind or an envelope around the cell."

The power required to propel the rigid helical body through a fluid is given by

$$P_{\text{body}} = -UF_x - \omega M_x . \tag{14}$$

The negative signs in equation 14 signify that the force or torque are exerted by the rigid body on the surrounding fluid. The power expended in moving the polar flagella alone is

$$\begin{aligned} P_{\text{flag}} &= -UF_x^0 + \Omega M_x^0 \\ &= UF_x - \Omega M_x , \end{aligned} \tag{15}$$

where equation 7 has been applied in the second step.

Hydromechanical efficiency η may be defined a number of ways depending upon the propulsion quality one wishes to evaluate. We shall define the hydromechanical efficiency η as the ratio of the power required for propelling the rigid helical body alone to the total power expended in moving the entire organism; then, by equations 14 and 15, we have

$$\begin{aligned} \eta &= P_{\text{body}}/(P_{\text{body}} + P_{\text{flag}}) \\ &= \frac{UF_x + \omega M_x}{(\omega + \Omega)M_x} . \end{aligned} \tag{16 a}$$

Upon substitution of equations 3, 5, and 8–10 into equation 16 a, η becomes

$$\eta = \frac{1 - \frac{3}{2}\left(\frac{U}{c}\right)^2\left(\frac{\omega}{\Omega}\right)\left(\frac{A}{\kappa^2 D}\right)}{1 + \frac{\Omega}{\omega}} , \tag{16 b}$$

where A and D are given by equation 10.

THE INFLUENCE OF VARIOUS PHYSICAL PARAMETERS, OPTIMUM PERFORMANCE

The dependence of the angular velocity ratio Ω/ω, given by equation 12, on kh for several fixed values of kb is shown in Fig. 3. In this figure, n is taken to be 2, $\alpha = 45°$, $b_o = 0.1b$, and $l = 0.5\lambda$, this set of values being typical for common *S. volutans*. From Fig. 3 we note that the angular velocity ratio Ω/ω increases more rapidly with increasing kh (for fixed kb) than with increasing kb when kh is held fixed. For *S. volutans*, experimental observations indicate that the value of kb is usually between 0.4 and 0.6 while kh is near 1. At $kh = 1$, Ω/ω varies from 2.4 for $kb = 0.4$ to 3.2 for $kb = 0.6$, as shown in Fig. 3. This theoretically predicted range of Ω/ω (between 2.4 and 3.2) agrees with the observations made by Metzner (1920). As mentioned earlier in the Introduction, Metzner found Ω to be about 40 rps and ω between 12 and 14 rps, and the corresponding angular velocity ratio Ω/ω between 2.85 and 3.33.

The velocity ratio U/c, given by equation 11, is plotted in Fig. 4 vs. kh for several fixed values of kb, other physical and geometrical parameters being the same as in

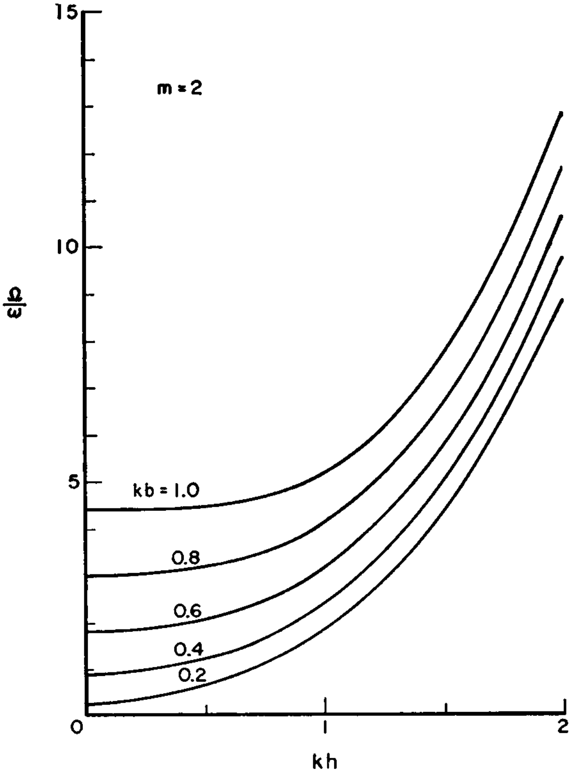

FIGURE 3 Dependence of the angular velocity ratio Ω/ω on the pitch angle kh.

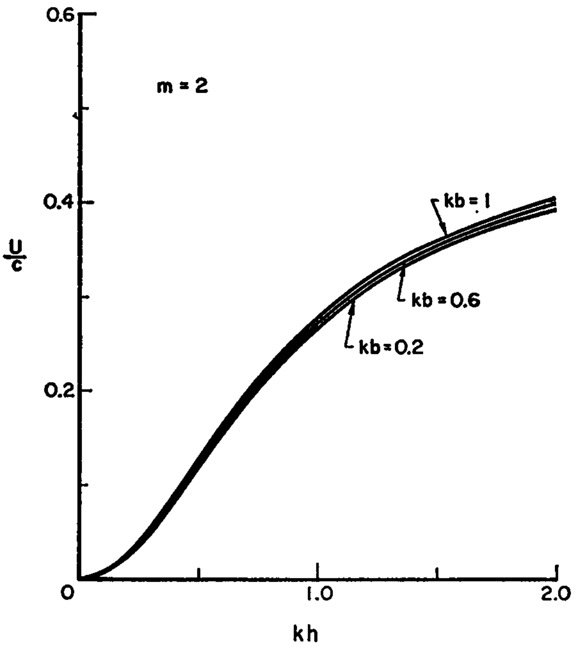

FIGURE 4 Dependence of the velocity ratio U/c on the pitch angle kh.

Fig. 3. It is of interest to note that the velocity ratio U/c depends primarily on kh since Fig. 4 shows U/c to be almost insensitive to change of kb when kh is fixed. At $kh = 1$, the velocity ratio U/c is about 0.275, which is somewhat lower than the typical values of U/c experimentally observed thus far (authors' unpublished data), albeit such low values of U/c (of the order 0.2) are rather typical of the flagellated movements of microorganisms at low Reynolds numbers (of the order 10^{-3}), as has been noted by Gray and Hancock (1955) and by Lighthill (1969).

It should be noted that the relationship $C_n = 2C_s$ in equation 2 *a* is only valid for very thin filaments, or for values of $kb \ll 1$. For arbitrary values of kb, the ratio C_n/C_s may have a value somewhat lower than 2 (Brokaw, 1970). In the case of *S. volutans*, although the polar flagella are thin enough to justify the use of equation 2 *a*, the helical body may not be. If we assume for the helical body that

$$C_n = \sigma C_s, \tag{17}$$

where σ is a positive parameter having a value less than or equal to 2, equations 11 and 12 will become

$$\frac{U}{c} = \frac{(\sigma - 1)\kappa^2}{1 + \sigma\kappa^2 + mA}, \tag{18}$$

$$\frac{\Omega}{\omega} = \frac{3}{2mD}\left[B + \frac{\sigma(1+\kappa^2)^2 + m(\sigma+\kappa^2)A}{1+\sigma\kappa^2+mA}\right]. \tag{19}$$

There is no effect of equation 17 on the expression for hydromechanical efficiency η (equation 16 *b*). The effect of σ on the velocity ratio U/c and angular velocity ratio Ω/ω are shown in Figs. 6 and 5 respectively with other parameters being the same as in Fig. 3. From these two figures, we notice that the ratio Ω/ω is almost insensitive to the change of σ; however, the velocity ratio U/c decreases from 0.27 to 0.13 as σ decreases from 2 to 1.4 at $kh = 1$ and $kb = 0.4$.

The physical quantity kU/Ω (or equivalently $[U/c]/[\Omega/\omega]$) which may be regarded as another definition of η is of some practical importance. The higher the value of kU/Ω, the greater the forward propulsion velocity will be, as compared with the rotational speed of polar flagella. In other words, a large value of kU/Ω signifies that the organism can achieve a high forward speed while spending relatively little effort in rotating the polar flagella. Accordingly, a maximum kU/Ω, if it exists, would be desirable from the operational point of view. In Fig. 7, kU/Ω is plotted vs. the wave pitch angle kh for several values of kb. It is of interest to note that for fixed kb, kU/Ω reaches a maximum at a particular value of kh; for example, with $kb = 0.6$, kU/Ω reaches a maximum at $kh = 0.9$. In general, the optimum range of kh is between 0.8 and 1.1 when kb lies between 0.4 and 1.0. If this argument has sufficient biophysical basis in suggesting that this type of movement is preferential

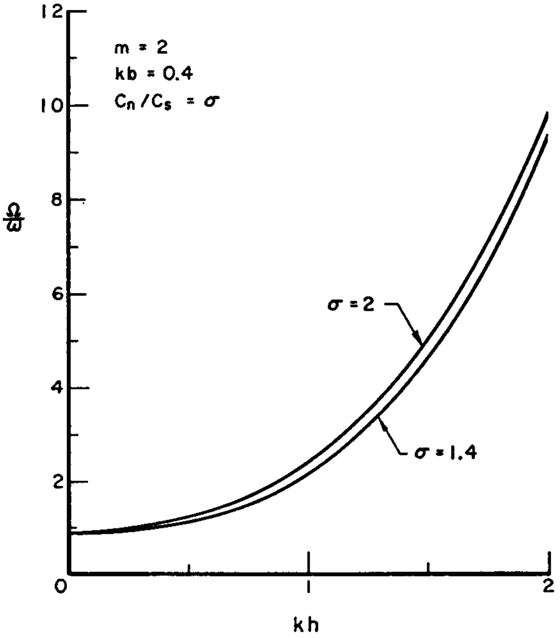

FIGURE 5 The effect of σ on the angular velocity ratio Ω/ω.

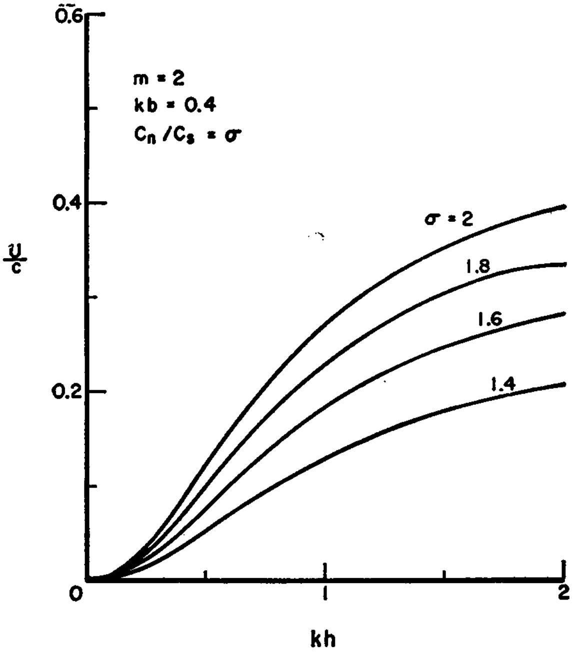

FIGURE 6 The effect of σ on the velocity ratio U/c.

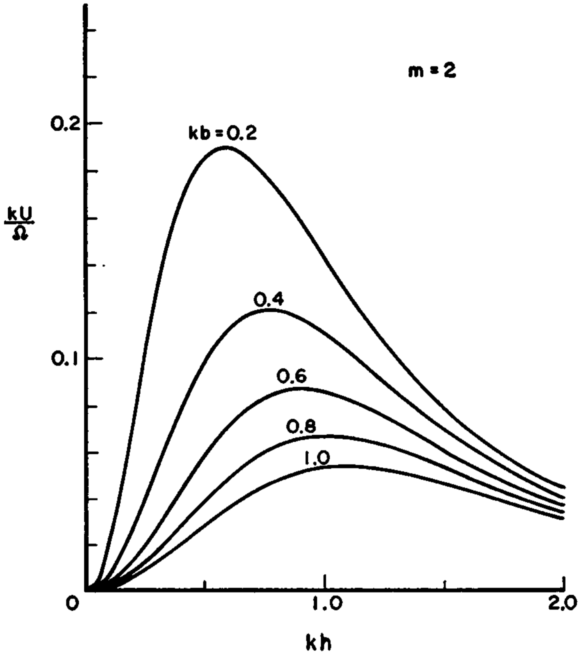

FIGURE 7 Variation of kU/Ω with kh and kb.

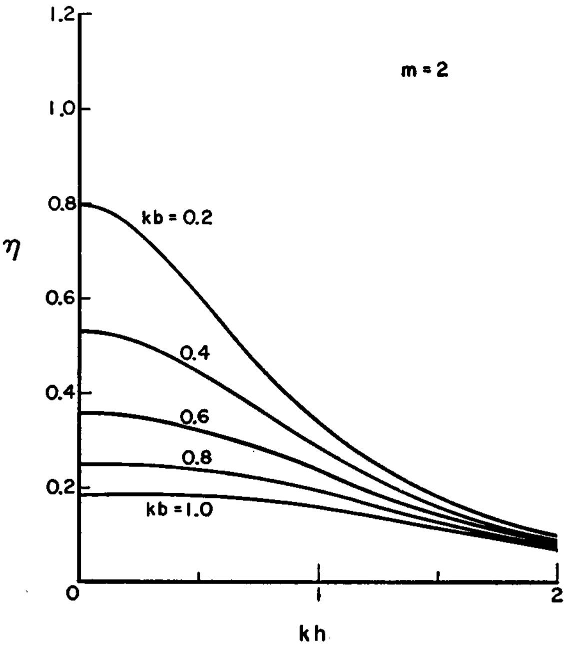

FIGURE 8 The hydromechanical efficiency η as a function of kh and kb.

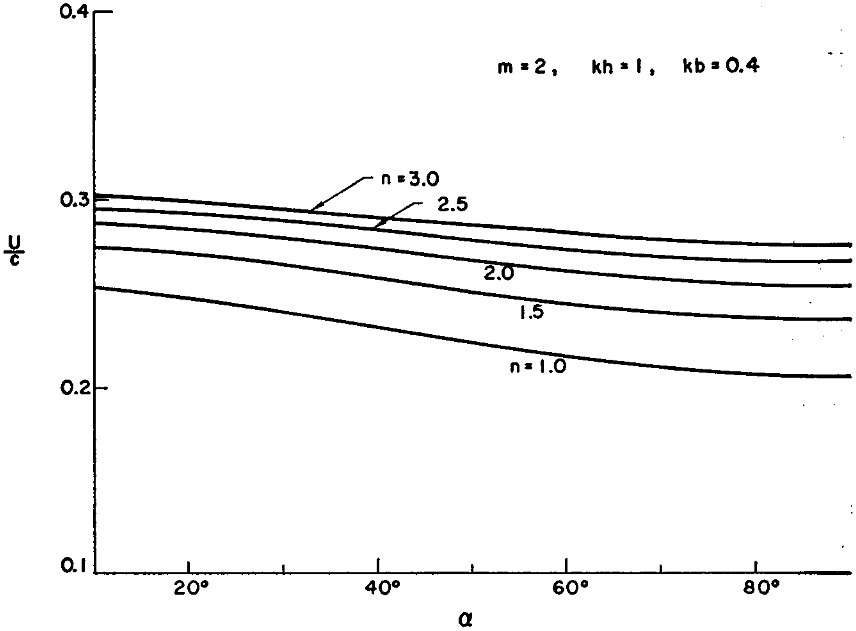

FIGURE 9 The influence of the half-cone angle α upon the velocity ratio U/c.

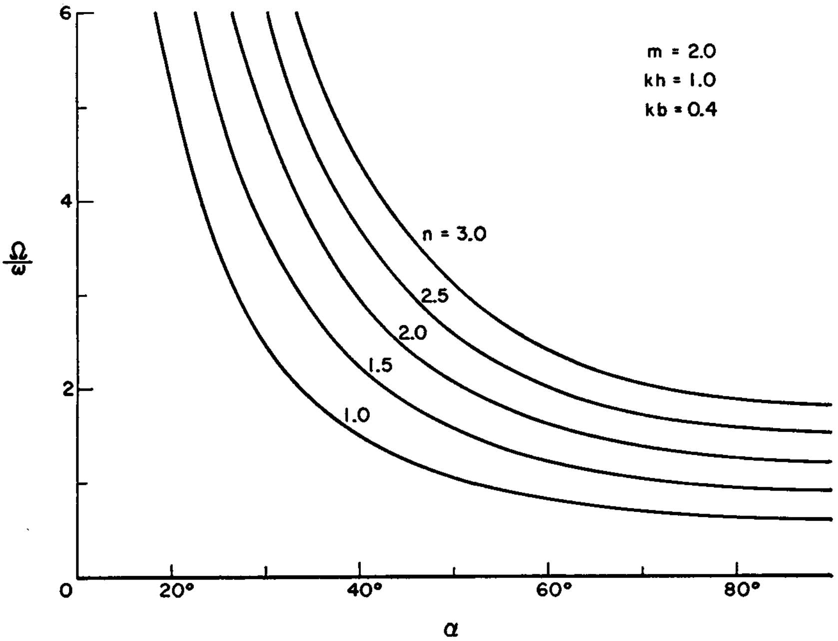

FIGURE 10 The influence of the half-cone angle α upon the angular velocity ratio Ω/ω.

and advantageous, then spirilla would be expected to swim, more often than not, within this optimum range of kh. To this end, it is noteworthy that spirilla have been observed to operate generally in this optimum range.

Variations of the hydromechanical efficiency η, as defined for the spirilla motions by equation 16, with the wave pitch angle kh and kb (other physical quantities being the same as in Fig. 3) are shown in Fig. 8. We note that the η so defined is relatively low in general; it decreases with increasing kh for fixed kb, and increases as kb is decreased, with kh fixed; however, the rate of change in η becomes less appreciable at higher values of kh and kb. At $kh = 1$, η lies somewhere between 15 and 35%, depending on the value of kb. Such low values for η are, of course, not unexpected in the flagellated movements of microorganisms in general (Lighthill 1969); they may also be ascribed partly to a certain degree of arbitrariness in the definition of η.

The influence of other geometrical quantities, such as the half-cone angle α and the number of turns of the rigid helical body n on the forward velocity ratio U/c and the angular velocity ratio Ω/ω are shown in Figs. 9 and 10, respectively. In these two figures, kh is assumed to be 1, $kb = 0.4$, $b_o = 0.1b$, and $l = 0.5\lambda$. These two figures show that an increase in n from 1 to 3 produces no significant changes in U/c and Ω/ω. As the half-cone angle α is increased from 10 to 90°, the velocity ratio U/c decreases slightly, indicating a small gain for a *Spirillum* which keeps its polar flagella rotating at a small half-cone angle. As α becomes too small, however, e.g. less than 40°, the angular velocity ratio Ω/ω then increases markedly as shown by

Fig. 10, indicating that a higher mechanical power is required of the *Spirillum* to rotate its polar flagella. A balanced picture therefore suggests that an efficient movement is for the *Spirillum* to keep the half-cone angle α somewhere between 45 and 65° so that it may attain a high forward speed at a saving of mechanical power in rotating the polar flagella.

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