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MOTILITY OF MAGNETOTACTIC BACTERIA: MODEL AN THEORY

by

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ABSTRACT

A simple mechanical model for a magnetotactic bacterium is developed. The flagellar torque is explicitly considered and the motion equation is computationally solved. Comparison between theoretical and experimental trajectory shows that the model describes with good accuracy the movement of a magnetotactic bacterium. With this model it is obtained the total flagellar force. The transversal component of the flagellar force is about eight times the longitudinal one for the case treated in this work showing the importance in consider torque effects when is studied motion of bacteria.

Key-words: Magnetotaxy; Bacterial behavior; Magnetism; Motion equation of microorganism.

INTRODUCTION

The study of movement of a bacterium has been made by several authors. In 1951 Sir Geoffrey Taylor, F.R.S. (1951 a,b) analysed the swimming of microorganisms and the action of a rotating tail. Only several years later it was established that flagellum is the organelle responsable for the swimming of several bacteria (Berg and Anderson, 1973). The movement of microorganisms in viscous environments, the action of flagellar bundles and flagellar structures have been treated in several different aspects, (Berg and Brown, 1972, Berg 1975, Läuger 1977, Berg and Purcell, 1977, Oozawa and Hayashi, 1983, Macnab and Aizawa, 1984, Lowe et al.,1987, Carlile et al. 1987). The movement in the dimensions of microorganisms in a liquid medium has a different physics: it is a low Reynolds number problem and this introduces a new approach to treat this problem (Purcell, 1977, Berg and Turner, 1979). Magnetotactic bacteria are very particular organisms to study the movement of microorganisms since they are oriented by an external field in controlled laboratory conditions.

A simplified description of the motion of a magnetotactic microorganism is that these microorganisms swim parallel to the magnetic field lines. Optical microscopy shows that under constant field the microorganisms have a linear trajectory. When the field is suddenly reserved these organisms re-orient in the field, making an U-turn (Esquivel and Lins de Barros, 1986). Electron-microscopy (EM) of several magnetotactic cells shows the presence of flagella. These structures are responsa-

ble for the movement. Typical velocities are of about 100μm/s to 300μm/s under fields of order of 10G, but some species can have lower velocities. The observation of these organisms only in the presence of the geomagnetic field, with no other external field applied, is difficult since induced fields are usually present. At low fields, however, i.e., fields of about 0.5G or less, we observe a complex movement with no strick evidence of magnetic orientation. Low-exposure photographies on dark-field microscopy give the track of trajetory of these microorganisms. These photographies can be made with different homogeneous fields. The trajectory observed is nearly linear but it have particularities. They seems to be the projection (in the plane of the photo) of a cylinder helix trajectory rather than a planar trajectory. In fields of order of 10G the cells have alongated track and in fields less than 2G the track is ondulated. Since the displacement of the cell is produced by the flagellar beat we can associate these characteristics to the action of flagella.

In this work we construct a mechanical model of a magnetotactic microorganism propelled by a flagellum, and we solve the motion differential system equation taking into account randomic contributions. We compare the theoretical trajectory with experimental tracks obtained in a dark-field microscope.

MODEL

To treat the bacterium movement we adopt the usual approach

of rigid body physics. Firstly we describe the translation motion of the Center of Mass (CM) and, secondly we treat the rotation movement in the CM system. We assume a model described as follows: a spherical body with a constant magnetic dipolar moment m, colinear to the average direction of motion and propelled by a flagellum that have a beat. The flagellum produces a constant force F_f that precess around the body simetry axes $\hat{r}$ as shown in figure 1.

This flagellar force, F_f has two components. The longitudinal component F_L, (parallel to $\hat{r}$), is responsable for the translational motion of the body and it is equilibrated by the viscous drag. This component can be considered as constant. The other component is the transversal $\vec{F}_T$, perpendicular to $\hat{r}$, and it is described in our model as a rotating vector with constant intensity and frequency ω. The longitudinal component does not produce any torque on the body with respect to the center of mass system (CM) since it is coincident with the body simetry axis, but the transversal is responsable to a torque that rotates the cell body. With respect to the CM we can write:

$$\vec{F}_f = \vec{F}_L + \vec{F}_T$$

with

$$\vec{F}_L = F_L \hat{r}$$

and

$$\vec{F}_T = F_T \cos\omega t \hat{\theta} + F_T \sin\omega t \hat{\psi}$$

where $(\hat{r}, \hat{\theta}, \hat{\psi})$ are the usual spherical coordinates, and ω is the flagellar frequency, F_f acts on the point A, (figure 1) on

the border of the cell, defined as:

$$\vec{A} = -R\hat{r}$$

where R is the bacterium radius.

We ignore, in our model, any flagellar geometry. We consider only the force produced by the flagellum. We restrict our study to the particular case that the flagellar movement is periodic with constant frequency ω. Tumble can be included, later, by the introduction of an intense randomic perturbation.

MOTION EQUATION

The CM translates with respect to the laboratory system (S'). In CM the motion equation is given by:

$$\frac{d\vec{L}}{dt} = \sum \text{Torques} \qquad (1)$$

where $\vec{L}$ is the total angular moment related to the CM origin.

Using spherical coordinates the torque due to the flagellar beatting, $\vec{\tau}_f$, is

$$\vec{\tau}_f = \tau_f(\cos\omega t\hat{\psi} - \sin\omega t\hat{\theta}) \qquad (2)$$

where τ_f is: $\tau_f = F_T R$

The magnetic moment m in CM, is: $\vec{m} = m\hat{r}$.

The magnetic torque $\vec{\tau}_m$ is:

$$\vec{\tau}_m = -mB\sin\theta\,\hat{\psi} \tag{3}$$

where the external field B is parallel to $\hat{z}$ ($\vec{B} = B\hat{z}$).

The viscous torque due to the medium is proportional to the angular velocity and is given by:

$$\vec{\tau}_v = 8\pi\eta R^3\{\dot{\theta}\hat{\psi} + \sin\theta\dot{\psi}\hat{\theta}\} \tag{4}$$

where the term in braquet is the angular velocity expressed in physical coordinates of CM system.

The right-side of eq. (1) includes inertial effects. Since we are interested in the problem of a bacterium moving in a viscous medium, we can ignore all inertial contributions because we are in the regimem of lamellar flow (i.e., low Reynolds numbers). This corresponds to disregard the terms proportional to the second time derivative. The motion equation (1) reduces to:

$$\vec{\tau}_f + \vec{\tau}_m + \vec{\tau}_v = 0 \tag{5}$$

To take into account perturbation terms due to currents flow, non-magnetic interaction between organisms, etc, and thermal disorder we introduce randomic contributions expressed as $C(\hat{\theta},\hat{\psi})$. The total differential equation in its vectorial form is:

$$\frac{d\theta}{dt}\hat{\psi} + \frac{d\psi}{dt}\hat{\theta} = \left(\frac{\tau_f}{8\pi\eta R^3}\cos\omega t + \frac{mB}{8\pi\eta R^3}\sin\theta\right)\hat{\psi} - \frac{\tau_f \sin\omega t}{8\pi\eta R^3 \sin\theta}\hat{\theta} + \vec{C}(\hat{\theta},\hat{\psi}) \tag{6}$$

This is a coupled system of non-linear first order differential equations, as given below:

$$\frac{d\theta}{dt} = \frac{\tau_f}{8\pi\eta R^3}\cos\omega t + \frac{mB}{8\pi\eta R^3}\sin\theta + C_\psi \tag{7}$$

$$\frac{d\psi}{dt} = -\frac{\tau_f \sin\omega t}{8\pi\eta R^3 \sin\theta} + C_\theta \tag{8}$$

where C_ψ, C_θ are the components of $\vec{C}$ with respect to $\hat{\psi}$ and $\hat{\theta}$.

It is interesting to observe that $d\psi/dt$ depends explicitly on θ (or, $\sin\theta$) and there is no explicit dependence on B. This system of coupled equations (eqs. (7) and (8)) was solved numerically using the Gauss method for integration.. We focalize, principally, the behavior of our model under the suddently reversion of the magnetic field, i.e., the U-turn trajectory.

PARTICULAR CASES

If $\tau_f = 0$ (or, there is no flagellar torque), and C = 0 (or, we ignore thermal disorder and randomic perturbations) eqs. (8) gives:

$$\psi = \underline{cte} \quad .$$

That is, the azimuthal angle is constant and the trajectory of the microorganism is planar. In this case, eq. (7) reduces to the familiar differential equation of the C. Bean model, (Esquivel and Lins de Barros, 1986), and we have an analytical solution for the problem:

$$\int \frac{d\theta}{\sin\theta} = \frac{mB}{8\pi\eta R^3}(t - t_o) \tag{9}$$

$$\psi = cte \tag{10}$$

If B = 0 (or m = 0) and the randomic terms are zero, we obtain equations of motion for a model of one microorganism propelled by a flagellum. This equation is:

$$8\pi\eta R^3 \frac{d\theta}{dt} = \tau_f \cos\omega t \tag{11a}$$

and

$$8\pi\eta R^3 \frac{d\psi}{dt} = -\frac{\tau_f \sin\omega t}{\sin\theta} \tag{11b}$$

Integrating the θ equation:

$$\theta = -\frac{\tau_f/\omega}{8\pi\eta R^3} \sin\omega t + \theta_o \tag{11c}$$

Where θ_o is the constant of integration related to initial conditions. Eqs. (11) show that for a non-magnetotactic microorganism (or a magnetotactic microorganism in the absence of magnetic field) θ varies between:

$$\theta_o - \theta_f \leq \theta \leq \theta_o + \theta_f$$

where

$$\theta_f = \frac{\tau_f/\omega}{8\pi\eta R^3} \tag{12}$$

and θ is the angle between the tangent to the trajectory and the z-axis and gives informations about the turn of the trajectory. It is important to note that knowing θ as a function of t we can obtain the ratio between τ_f and ω. The angular frequency, w, can be obtained directly from the experimental data and τ_f cannot be measured directly. Eq. (12) gives a method to estimate the torque intensity of the flagellum with respect to the CM.

Note that τ_f depends on F_T (not on F_L). Usually it is assumed that flagellum is a very long rigid organelle (about 10μm for cells with 1μm radius) with a string configuration (i.e., rigid organelle with an helix shape with several turns). If the flagellum have an integer number of turns there is no transversal force, or $\tau_f = 0$. Actually several bacteria has long flagella with about an integer number of turns. In this case we have

$$\tau_f \sim 0 \quad \text{and} \quad \theta \sim \theta_o \ , \tag{13a}$$

where θ_o is the initial angle. In this case (i.e., $\tau_f \to 0$) the movement is produced by F_L and a good approximation is $\theta_o = 0$. (Since there is no inertial effects $\vec{v} // \vec{F}_f$). Using the θ expression, eq. (11c), and making the usual approximation, $\sin\theta \sim \theta$ for $\theta \to 0$, eq. (11b) is written as:

$$\frac{d\psi}{dt} = -\frac{\tau_f \sin\omega t}{8\pi\eta R^3\theta} = \frac{\tau_f \sin\omega t}{8\pi\eta R^3\left\{\frac{\tau_f/\omega}{8\pi\eta R^3}\sin\omega t + \theta_o\right\}}$$

Since we assume $\theta_o \sim 0$ we can integrate the above equation and then:

$$\psi = \omega t + \psi_o \qquad (13b)$$

Equations (13a and b) are the parametric equations of a cylindrical helix and represents the trajectory of a bacterium with long flagellum with approximately an integer number of turns.

To compare our results with laboratory observations it is necessary to write eqs. (7) and (8) in the laboratory system (lab). Since the bacterium swims in a typical low Reynolds number regimen there is no inertial effects and the velocity, $\vec{v}$, is parallel to the flagellar force, $\vec{F}_f$. The equations can be written in the lab system as:

$$x = x_o + dr.\sin\theta.\cos\psi$$

$$y = y_o + dr.\sin\theta.\sin\psi$$

$$z = z_o + dr.\cos\theta$$

where dr = v dt, dt is the time interval, and v is the instantaneous velocity, $v = |\vec{v}|$. (x,y,z) are the usual laboratory cartesian coordinates and x_o, y_o and z_o their values at $t = 0$. We take the z-axis in the laboratory system parallel to the z-axis of the CM system.

APPLICATION OF THE MODEL TO A PARTICULAR EXPERIMENTAL CASE

Figure 2 shows a typical trajectory of a bacterium swimming under a magnetic field. This figure was obtained with a dark field illumination in optical microscopy and represents the trace of the body of the bacterium over the film emulsion. In $t = 0$ (point P, in figure 2 and 4) the applied field was suddenly reversed and the bacterium re-orients to the field line and makes an U-turn. The trajectory seems to be the projection of a cylindrical helix and we note that during the re-orientation the bacterium describes the same spinning around 3-axis as observed when the cell swims parallel to the field line. This complex movement is due to the flagellar action.

Figure 2 was taken at field of 4.1 G and exposure time was 0.6 sec. This bacterium was found in muds of a sample collected in Itaipu lagoon, a coast lagoon from Rio de Janeiro region. The sample was collected as describe elsewhere. (Lins de Barros and Esquivel, 1985, Esquivel and Lins de Barros, 1986). We have also used slow-motion video coupled to the optical microscope to monitorate all of our observations as well as to measure velocities, characteristic times and other parameters.

We made measurements of the bacterium velocity as a function of the applied magnetic field and of its reversal time and diameter of U-turn. We made, also, transmission electron microscopy micrographs of several bacteria of the same samples (figure 3). The samples for E.M. was prepared as usually (described in literature (Lins de Barros and Esquivel, 1985; Wajnberg et al. 1986). Some important characteristics of the bacteria ana-

lysed are presented in table 1.

We note that figure 2 shows a deflection of the trajectory due to a transversal residual magnetic field induced in the microscope apparatus and, eventually, due to the geomagnetic field. Using the C. Bean model, the data presented in table 1 and the radius obtained by E.M. we can estimate the total magnetic moment of one cell. This value is 0.48×10^{-12} emu.

Figure 4 is other figure of the bacterium track in the same conditions of figure 2 with a larger amplification. This photo shows the complex trajectory of the cell. θ is the angle between the tangent to the track and the z-axis at the middle amplitude point (point M in figure 4) we obtain $\theta_f = 57^0 \pm 3^0$. Using this value to θ and assuming that this trajectory is a roughly approximation for a zero field trajectory, and using eq.(12) we obtain:

$$\tau_f = 0.25\omega R^3 = 1.6fR^3$$

where f is the frequency and can be estimated directly from the dark-field photo, measuring the number of cycles and dividing by the exposure time. Table 2 shows the parameters m,f, v, τ_f. Using these values in eqs. (7) and (8), and integrating numerically, we obtain, after transforming to the laboratory coordinate system, the bacterium trajectory presented in figure 5. Comparison between figure 4 and figure 5 shows that this model describes very well the bacterium motion.

Parameters in table 2 allow us to obtain the total flagellar force, F_f:

$$F_L = 6\pi\eta Rv = 1.9 \times 10^{-7} \text{dyn}$$

$$F_T = \tau_f / R = 3.3 \times 10^{-7} \text{dyn}$$

and

$$F_f = \sqrt{F_L^2 + F_T^2} = 3.8 \times 10^{-7} \text{dyn}$$

Note that $F_T/F_L \sim 1.7$. In this case the flagellar transversal component of F_f is greater than the longitudinal one. This suggests a bacterium with a single small assimetric flagellar body. This is confirmed by transmission electron microscopy (figure 6).

The magnetic torque is: $\tau_m = m.B = 2 \times 10^{-12}$ cgs, at B = 4.1G. This value is about 8 times smaller than the flagellar torque. The magnetic torque acts as an orientation mechanism of the envoltory shape of the trajectory. The flagellar periodic beat produces local variations of the trajectory. The mean trajectory is described by the magnetic interaction while the specific characteristics of the trajectory is described by the flagellar action.

For fields higher than 40 G, when $\tau_m > \tau_f$, it is probable that there will be a strong change in the trajectory shape. The field will extend the trajectory.

CONCLUSIONS

The application of this model to some other particular cases

gives a good agreement with experimental trajectory as presented in the previous section 5. Although it is a simple model, in the sense that only a precessing flagellar force is considered, this model describes with good accuracy the movement of magnetotactic microorganisms and permits us the calculation of the total flagelar force. The basic limitation of this model is the fact that we are describing microorganisms propelled by only one flagellum or by flagellar bundle bound to the cellular body by only one basal body. Several bacteria has bundles not described by this model.

The model permits to obtain informations on the movement and the motility of magnetotactic microorganisms in very low fields. It is difficult to obtain these fields in the laboratory and our model can contribute to understand some questions about efficiency of magnetic orientation in microorganisms (Lins de Barros and Esquivel, 1987).

Perturbation can be easily introduced. The randomic term can describe environmental perturbations (currents, water flow) or flagellar tumble.

We adopt a spherical body for the bacterium. To generalize for another body shape it is only necessary to change the analytical expression of the viscous force (Berg, 1983).

Finally this model can be generalized to describe a magnetotactic bacterium with a magnetic moment non-colinear to the longitudinal component of the flagellar force. This introduces several analytical difficulties but it is a more realistic description to a magnetotactic microorganism.

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FIGURE CAPTION

Figure 1 - CM System of spherical bacterium. $\vec{m}$-magnetic moment. $\vec{F}_f$ - flagellar force. (r,θ,ψ) are the spherical coordinates. $\vec{B}$-external magnetic field.

Figure 2 - U-turn trajectory of bacteria at 4.1 G. Bar = 10 μm. This photo was taken at dark-field optical microscopy illumination with exposure time of 0.6 sec. The sample was collected in brackish waters of Itaipu lagoon (Rio de Janeiro, Brazil).

Figure 3 - Scanning electron micrograph of several magnetotactic bacteria collected in Itaipu lagoon. Bar = 10μm.

Figure 4 - (a) Same as figure 2, with bar = 10 μm. (b) U-turn trajectory with no contribution of external constant field induced. Bar = 10 μm.

Figure 5 - Computer solution of motion equation a magnetotactic bacterium. Magnetic moment = 0.48×10^{-12} e.m.u., flagellar frequency, ω=84 Hz, instantaneous velocity, v = 200 μm/sec and flagellar torque = 16.5×10^{-12} cgs. Bar = 10 μm.

Figure 6 - (a)-Electron micrograph of a magnetotactic bacterium from Itaipu showing one flagellar bundles coupled to the bacterium body by one basal bodies. Note that this bacterium has short flagella. This is in agreement with our computer solution for the motion equation. Bar = 2μm. (b)-Electron micrograph of the same bacterium showing two internal chains of magnetic material. Bar = 2μm.

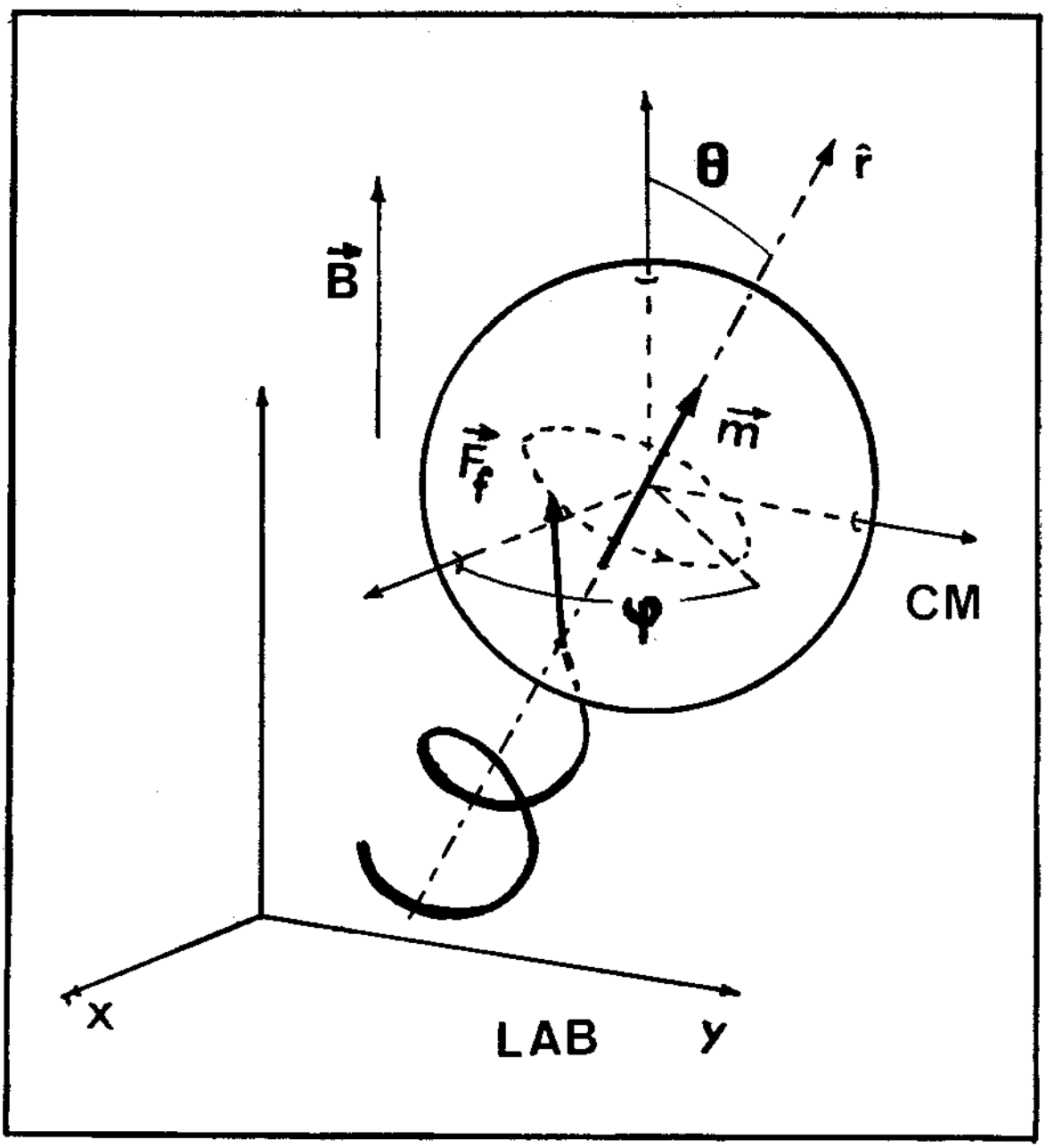


Figura 1

Figure 2

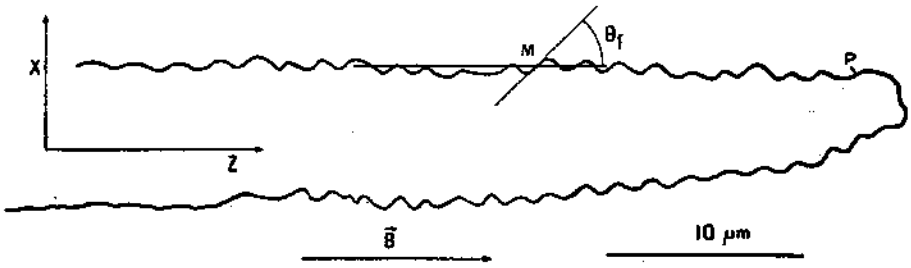
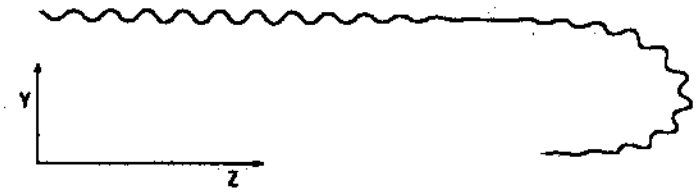


Figure 4



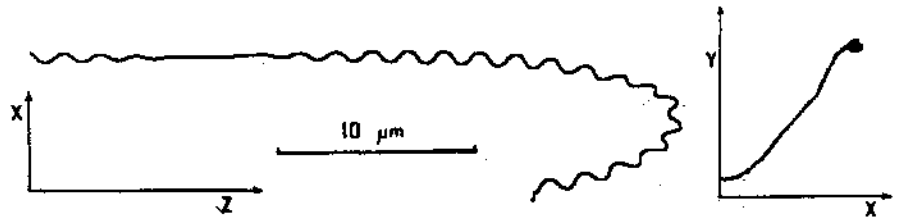


Figure 5

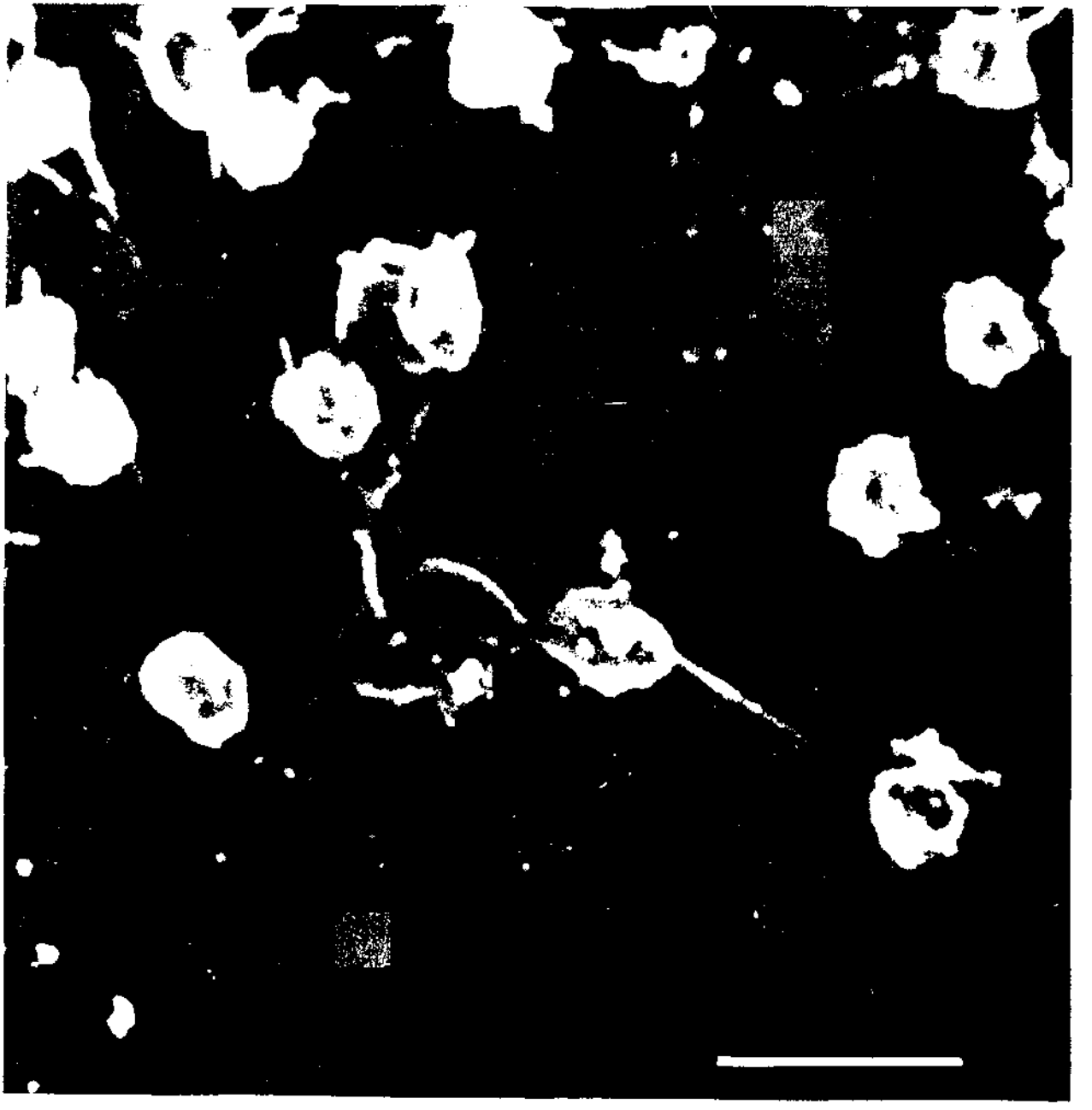


Figure 3

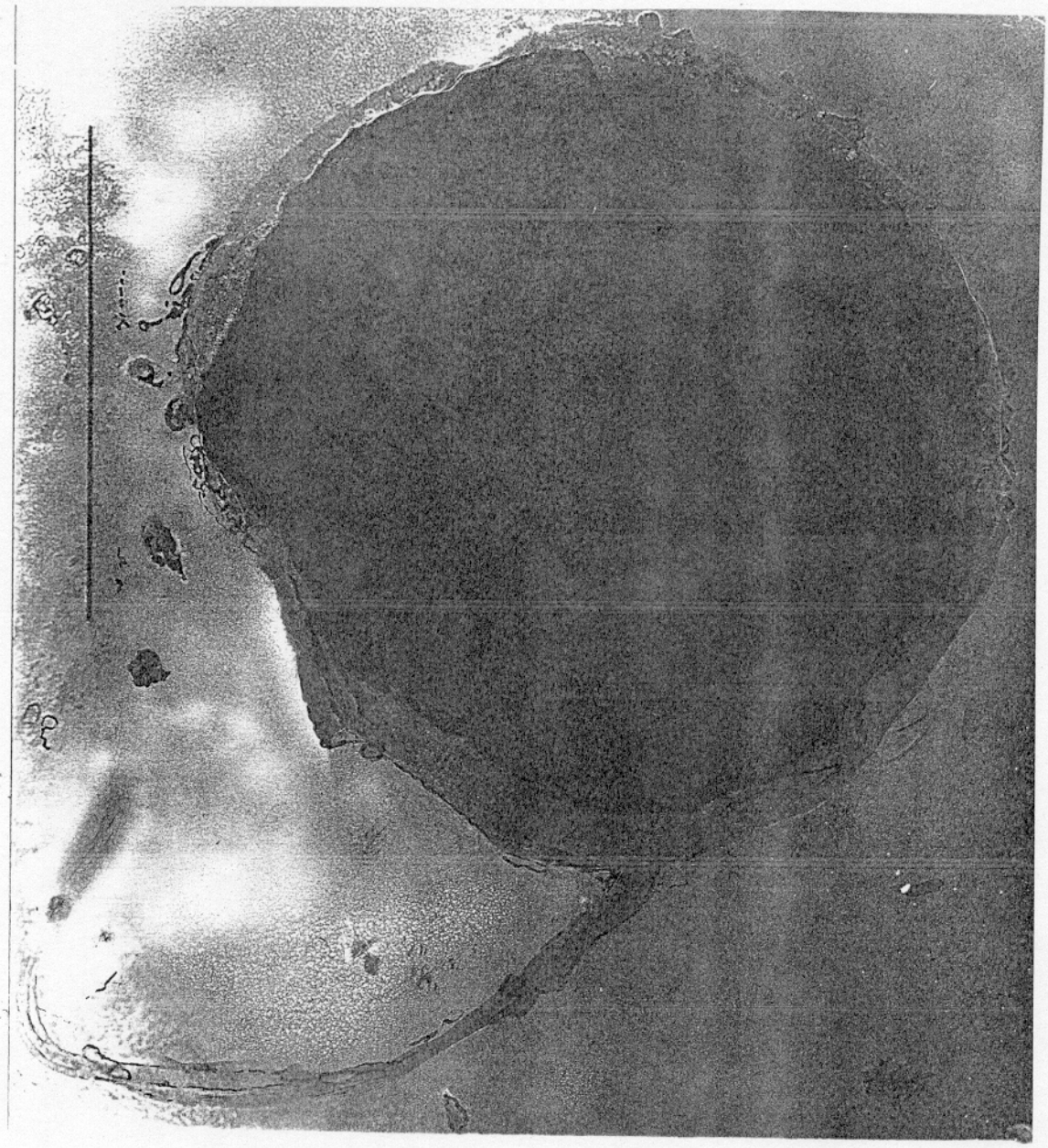


Figure 6a

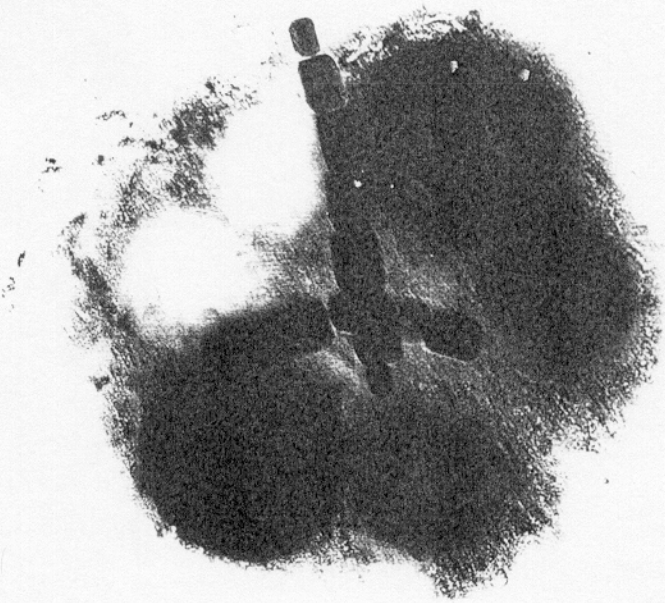


Figure 6b

TABLE CAPTIONS

Table 1 - Experimental parameters of bacteria collected in Itaipu lagoon. All measurements were made with B = 4.1 G. U-turn time was calculated using C. Bean model. The radius was measured by scanning electron microscopy.

Table 2 - Parameters experimentally obtained for the bacterium treated in this work. m - magnetic moment (obtained from U-turn analysis), f- flagellar frequency (obtained from dark-field photography), v-instantaneous velocity (obtained from dark-field analysis and video record), τ_f flagellar torque (obtained from eq. (12)).

TABLE 1

MEAN VELOCITY AT 4.1 G	U-TURN DIAMETER AT 4.1 G	U-TURN TIME AT 4.1 G		RADIUS (EM)
		Exp.	Theo.	
160 μm/s	8 μm	0.113 seg	0.073 seg	0.5 μm

TABLE 2

B = 4.1 G			
m (emu)	f (Hz)	v (μm/s)	τ_f (Ags)
0.48×10^{-12}	84	200	16.5×10^{-12}

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