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REPTATION MOTION OF ANIMALS IN A FLUID

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The plane problem of reptation motion of a biological object in a viscous fluid is solved analytically in a long-wave approximation. The motion if laminar. Computational expressions and asymptotic estimates are obtained for the axial and shear forces, expended energy, and motion trajectory. Results of a numerical analysis of the solution are given.

Key words: *reptation motion, laminar motion, long-wave approximation.*

A model for the eel-like swimming of water animals was proposed by academician Lavrent'ev [1], who was the first to employ the method of plane cross sections to study this problem. The animal's body was treated as a rectangular plate capable of arbitrary bending and remaining cylindrical. The deformations of the plate that ensure its motion in the fluid were found. Lavrent'ev's ideas are further developed in [2, 3].

A theory for the motion of a rod in a viscous fluid flow is presented in [4–6]. The obtained dynamic equations can be used to describe the motion of biological objects (BOs) in a continuous medium.

The problem of the plane reptation motion of animals in a viscous fluid is formulated and solved in a long-wave approximation. The dynamic and kinematic characteristics of the motion are determined. Results of a numerical analysis are given.

1. Formulation of the Problem. We estimate the inertia force for the motion of BOs. For objects of small sizes, we adopt: $d = 10^{-3}$ m, $l \sim 10^{-2}$ m, $v = 10^{-3}$ m/sec, $\rho = 10^3$ kg/m^3, and $\mu = 10^{-3}$ Pa $\cdot$ sec. In this case, the Reynolds number is $\mathrm{Re} = vd\rho/\mu = 1$ (μ and ρ are the viscosity and density of the fluid, d is the body diameter, l is the body length, and v is the velocity). For large objects, $d = 0.05$ m, $v = 1$ m/sec, $l \sim 1$ m, and $\mathrm{Re} = 5 \cdot 10^4$. Consequently, laminar motion is characteristic of small-sized objects moving at a low velocity. Turbulent motion is typical of large objects.

Along with overcoming the viscous friction forces, a moving animal needs to expend energy to overcome the inertia of its own body. Let us estimate the inertia force that acts on the animal's body. According to [7], for $\mathrm{Re}\,\mathrm{Sh} = \rho d^2/(T\mu) \ll 1$ [$\mathrm{Sh} = d/(vT)$ is the Strouchal number and $T \sim l/v$ is the characteristic time] the motion can b e considered quasistationary and the inertia forces due to local acceleration can be ignored. We assume that the average density of the BO body is close to the density of the ambient fluid ($\rho = 10^3$ kg/m^3). We have $\mathrm{Re}\,\mathrm{Sh} = 0.1$ for small-sized objects and $\mathrm{Re}\,\mathrm{Sh} = 2500$ for large-sized objects. Therefore, the inertia forces of the BO body can be ignored.

We limit our consideration to BOs that have a rather prolate body (small-sized fishes such as a water snake in a drying pool, some insect larvae, spermatozoons, micro-organisms), so that the condition $l \gg d$ is satisfied (l is the body length in the prolate state). For directional displacement, the BO performs plane reptation motion, for example, in the horizontal plane. In the case of vertebrate animals, the elastic axis passes along the backbone, which can be treated as a hinged system of rods. We assume that the number of vertebras is infinite and the elastic axis is a monotonic smooth curve. For invertebrate BOs, the elastic axis passes through the centers of cross sections. During the motion, the an elastic axis and the acting forces lie in the plane xOy.

The central nervous system sends command signals to body muscles, so that a nearly sinusoidal traveling wave is formed. The number of the command nerve impulses is finite and corresponds to the number of the working

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muscles, which are located uniformly over the entire length of the body. We assume that the number of the muscles is infinite and that the command signal is a monotonic continuous function.

The Archimedean force is absent since the density of the BO is close to the density of the ambient fluid. The cross section of the body is constant over the entire length of the BO. The fluid flow is laminar.

A fundamental feature that differs the motion of BOs in a fluid from the motion of a suspension of anisometric particles is the distribution of mechanical energy. In the suspension, mechanical energy is supplied from the ambient fluid to a particle, changing the particle configuration or position. In the case of BOs, the power source is the "particle" by itself. If the ambient fluid is conditionally considered stationary, the dispersion of mechanical energy (due to viscous dissipation) is localized in an area commensurable with the dimensions of the BO, i.e., in the region hydrodynamic boundary layer.

We introduce a coordinate system (x, y, z) which is stationary in space (or frozen in the fluid). The coordinates of the points on the elastic line of the BO are denoted by s x, y, and z. Vector parametrization of the curve s is performed by the vector function $\boldsymbol{r}(s,t)$, $0 \leqslant s \leqslant l$ (t is time). The x, y, and z directions correspond to a right-hand oriented trihedron $(\boldsymbol{i}, \boldsymbol{j}, \boldsymbol{k})$. We denote the tangent vector to the elastic line by $\boldsymbol{l}$ ($\boldsymbol{l} = \boldsymbol{r}_s$ and $|\boldsymbol{l}| = 1$), the normal vector by $\boldsymbol{n} = \boldsymbol{b} \times \boldsymbol{l}$, and the binormal vector by $\boldsymbol{b}$.

The equilibrium equations are written as

$$\boldsymbol{F}_s = -\boldsymbol{K}, \qquad \boldsymbol{M}_s = \boldsymbol{F} \times \boldsymbol{l},$$

where $\boldsymbol{M}$ is the moment: $\boldsymbol{F} = (\boldsymbol{F} \cdot \boldsymbol{l})\boldsymbol{l} + (\boldsymbol{F} \cdot \boldsymbol{n})\boldsymbol{n} = N\boldsymbol{l} + Q\boldsymbol{n}$ is the force, and $\boldsymbol{K}$ is the linear density of the external forces. Here and below, the subscript denotes the corresponding derivatives.

For the motion of the BOs considered, the friction force is due to the difference between the velocity of the BO ($\boldsymbol{r}_t$) and the fluid velocity ($\boldsymbol{V}$); therefore, the external friction force $\boldsymbol{K}$ is expressed as

$$\boldsymbol{K} = A\boldsymbol{l}((\boldsymbol{r}_t - \boldsymbol{V}) \cdot \boldsymbol{l}) + B\boldsymbol{n}((\boldsymbol{r}_t - \boldsymbol{V}) \cdot \boldsymbol{n}),$$

where $\boldsymbol{V}$ is the fluid velocity, $A = 2\pi\mu/\ln(0.952/\sqrt{c}\,)$ is a coefficient that characterizes the longitudinal component of the friction forces, c is the volume concentration of the BO in the fluid, $B = 4\pi\mu/\ln(7.4/\mathrm{Re})$ is a coefficient that characterizes the transverse component of the friction force, $\mathrm{Re} = \langle v\rangle\rho d/\mu$ is the Reynolds number, and $\langle v\rangle$ is the characteristic velocity.

We have the following system of equations in scalar form:

$$N_s - Q\varphi_s = -A(\boldsymbol{r}_t - \boldsymbol{V}) \cdot \boldsymbol{l}, \qquad N\varphi_s + Q_s = -B(\boldsymbol{r}_t - \boldsymbol{V}) \cdot \boldsymbol{n}.$$

Performing scalar multiplications in the last equations using the relations $\boldsymbol{r}_t - \boldsymbol{V} = (x_t - v_x)\boldsymbol{i} + (y_t - v_y)\boldsymbol{j}$, $\boldsymbol{l} = \boldsymbol{i}\cos\varphi + \boldsymbol{j}\sin\varphi$, and $\boldsymbol{n} = -\boldsymbol{i}\sin\varphi + \boldsymbol{j}\cos\varphi$, we obtain

$$\begin{gathered} N_s - Q\varphi_s = -A[(x_t - v_x)\cos\varphi + (y_t - v_y)\sin\varphi], \\ N\varphi_s + Q_s = -B[-(x_t - v_x)\sin\varphi + (y_t - v_y)\cos\varphi], \qquad M_s = -Q, \end{gathered} \tag{1.1}$$

where N is the axial force, Q is the shear force, and M is the bending moment.

Accordingly, the "improved" equations [4, 5] (obtained by eliminating the functions x and y) for the problem considered are written as

$$\begin{gathered} \varphi_t + B^{-1}(N\varphi_s + Q_s)_s + A^{-1}\varphi_s(N_s - Q\varphi_s) = \frac{\partial v_y}{\partial y}\sin 2\varphi - \frac{\partial v_x}{\partial y}\sin^2\varphi + \frac{\partial v_y}{\partial x}\cos^2\varphi, \\ \varphi_s B^{-1}(N\varphi_s + Q_s) - A^{-1}(N_s - Q\varphi_s)_s = -0.5\Big(\frac{\partial v_x}{\partial y} + \frac{\partial v_y}{\partial x}\Big)\sin 2\varphi - \frac{\partial v_x}{\partial x}\cos 2\varphi. \end{gathered} \tag{1.2}$$

Equations (1.1) and (1.2) need to be supplemented by the geometrical relations

$$x_s = \cos\varphi, \qquad y_s = \sin\varphi, \tag{1.3}$$

and the initial and boundary conditions

$$\begin{gathered} t = 0\colon \quad x = x_0(s), \quad y = y_0(s); \\ t > 0, \qquad s = 0\colon \quad N = Q = 0; \quad s = l\colon \quad N = Q = 0. \end{gathered} \tag{1.4}$$

For convenience of the analysis, we resolve Eqs. (1.1) for the functions x_t and y_t:

$$x_t = -A^{-1}(N_s - Q\varphi_s)\cos\varphi + B^{-1}(N\varphi_s + Q_s)\sin\varphi + v_x,$$
$$y_t = -A^{-1}(N_s - Q\varphi_s)\sin\varphi - B^{-1}(N\varphi_s + Q_s)\cos\varphi + v_y. \tag{1.5}$$

We consider the case of a stationary fluid, i.e., $\boldsymbol{V} = 0$ ($v_x = 0$, $v_y = 0$). Drag is ignored. In the problem considered, the equation that links the moment to the bending angle via flexural rigidity has no physical meaning (as well as the concept of an elastic rod) and is therefore not used.

2. Solution of the Problem. We convert to dimensionless parameters and variables using the largest value of the shear force Q ($Q_0 = |\max Q|$) as the force scale:

$$X = \frac{x}{l}, \quad Y = \frac{y}{l}, \quad S = \frac{s}{l}, \quad e = \frac{A}{B}, \quad n = \frac{N}{Q_0}, \quad q = \frac{Q}{Q_0},$$
$$\tau = \frac{Q_0 t}{Al^2}, \quad \Omega = \frac{\omega A l^2}{Q_0}, \quad K = kl, \quad w = \frac{AlW}{Q_0^2}. \tag{2.1}$$

Here ω is the oscillation frequency.

With allowance for (2.1), the constitutive equations (1.2)–(1.5) become

$$n\varphi_s + q_s = Z; \tag{2.2}$$

$$n_s - q\varphi_s = D; \tag{2.3}$$

$$\varphi_\tau + eZ_s + \varphi_s D = 0; \tag{2.4}$$

$$e\varphi_s Z - D_s = 0; \tag{2.5}$$

$$X_\tau = -D\cos\varphi + eZ\sin\varphi; \tag{2.6}$$

$$Y_\tau = -D\sin\varphi - eZ\cos\varphi; \tag{2.7}$$

$$X_s = \cos\varphi, \qquad Y_s = \sin\varphi; \tag{2.8}$$

$$\tau = 0: \qquad X = X_0(S), \quad Y = Y_0(S); \tag{2.9}$$

$$\tau > 0, \qquad S = 0: \quad n = q = 0; \quad S = 1: \quad n = q = 0. \tag{2.10}$$

For brevity and convenience, we introduced two auxiliary functions $D(S,\tau)$ and $Z(S,\tau)$ defined by Eqs. (2.2) and (2.3). The moment is not used in the solution; therefore, the last equation of (1.1) is omitted.

The nerve impulses transmitted to the body muscles form a traveling wave which ensures translational motion. In Eqs. (2.2)–(2.10), the form of one of the functions n and q or φ needs to be specified *a priori*. We define the plane traveling wave as

$$\varphi = \varepsilon \sin(KS - \Omega\tau), \tag{2.11}$$

where Ω is the dimensionless frequency and ε is the dimensionless parameter ($|\varepsilon| \leqslant 1$); $K = 2\pi i$ ($i = 1, 2, 3, \ldots$). According to the last equality, the length of the BO provides for an even number of half-waves. This significantly simplifies the computational expressions.

We assume that the functions D and Z depend on φ. Thus, Eq. (2.4) can be written as

$$\varphi_\tau + eZ_\varphi \varphi_s + D\varphi_s = 0,$$

where $Z_\varphi = \partial Z/\partial\varphi$. In view of expression. (2.11), the last equation becomes

$$-\Omega + eKZ_\varphi + KD = 0. \tag{2.12}$$

Accordingly, Eq. (2.5) is written as

$$D_\varphi = eZ. \tag{2.13}$$

Differentiating Eq. (2.13) with respect to φ and substituting the result into (2.12), we obtain the second-order inhomogeneous linear differential equation

$$D_{\varphi\varphi} + D = \Omega/K.$$

Its solution has the form

$$D = C_1 \sin\varphi + C_2 \cos\varphi + \Omega/K, \tag{2.14}$$

where C_1 and C_2 are unknown functions of time.

Substitution of expression (2.14) into (2.13) yields the function Z:

$$Z = e^{-1}(C_1 \cos\varphi - C_2 \sin\varphi). \tag{2.15}$$

From Eqs. (2.2) and (2.3), we find the functions n and q, which are also assumed to depend on φ. Using (2.14) and (2.15), we have

$$n + q_\varphi = Z\varphi_s^{-1}; \tag{2.16}$$

$$n_\varphi - q = D\varphi_s^{-1}. \tag{2.17}$$

Differentiating both sides of Eq. (2.17) with respect to φ and adding the result to (2.16), we obtain the following second-order inhomogeneous differential equation for the function n:

$$n_{\varphi\varphi} + n = Z\varphi_s^{-1} + (D\varphi_s^{-1})_\varphi.$$

Its solution has the form

$$n = C_3 \sin\varphi + C_4 \cos\varphi - \cos\varphi \int [Z\varphi_s^{-1} + (D\varphi_s^{-1})_\varphi] \sin\varphi \, d\varphi$$
$$+ \sin\varphi \int [Z\varphi_s^{-1} + (D\varphi_s^{-1})_\varphi] \cos\varphi \, d\varphi$$

or, after integration by parts and simple transformations,

$$n = C_3 \sin\varphi + C_4 \cos\varphi - \cos\varphi \Big[\int_0^S e^{-1}(C_1 \cos\varphi - C_2 \sin\varphi) \sin\varphi \, dS - \int_0^S (C_1 \sin\varphi + C_2 \cos\varphi + \Omega/K) \cos\varphi \, dS \Big]$$
$$+ \sin\varphi \Big[\int_0^S e^{-1}(C_1 \cos\varphi - C_2 \sin\varphi) \cos\varphi \, dS + \int_0^S (C_1 \sin\varphi + C_2 \cos\varphi + \Omega/K) \sin\varphi \, dS \Big]. \tag{2.18}$$

Substitution of expression (2.18) into Eq. (2.17) yields the shear force:

$$q = C_3 \cos\varphi - C_4 \sin\varphi$$
$$+ \sin\varphi \Big[\int_0^S e^{-1}(C_1 \cos\varphi - C_2 \sin\varphi) \sin\varphi \, dS - \int_0^S (C_1 \sin\varphi + C_2 \cos\varphi + \Omega/K) \cos\varphi \, dS \Big]$$
$$+ \cos\varphi \Big[\int_0^S e^{-1}(C_1 \cos\varphi - C_2 \sin\varphi) \cos\varphi \, dS + \int_0^S (C_1 \sin\varphi + C_2 \cos\varphi + \Omega/K) \sin\varphi \, dS \Big]. \tag{2.19}$$

The unknowns coefficients C_3 and C_4 are found using the condition from (2.10): $n = q = 0$ for $\tau > 0$ and $S = 0$; for (2.18) and (2.19) it leads to the system of equations

$$C_3 \sin\varphi_0 + C_4 \cos\varphi_0 = 0, \qquad C_3 \cos\varphi_0 - C_4 \sin\varphi_0 = 0,$$

where $\varphi_0 = \varphi\Big|_{s=0}$. The solution of this system has the form $C_3 = 0$, $C_4 = 0$.

The unknown coefficients C_1 and C_2 are found using the condition from (2.10): $n = q = 0$ for $\tau > 0$ and $S = 1$. In this case, expressions (2.18) and (2.19) lead to the system of equations

$$-\cos\varphi_0\Big[\int_0^1 e^{-1}(C_1\cos\varphi - C_2\sin\varphi)\sin\varphi\,dS - \int_0^1 (C_1\sin\varphi + C_2\cos\varphi + \Omega/K)\cos\varphi\,dS\Big]$$

$$+\sin\varphi_0\Big[\int_0^1 e^{-1}(C_1\cos\varphi - C_2\sin\varphi)\cos\varphi\,dS + \int_0^1 (C_1\sin\varphi + C_2\cos\varphi + \Omega/K)\sin\varphi\,dS\Big] = 0,$$

$$\sin\varphi_0\Big[\int_0^1 e^{-1}(C_1\cos\varphi - C_2\sin\varphi)\sin\varphi\,dS - \int_0^1 (C_1\sin\varphi + C_2\cos\varphi + \Omega/K)\cos\varphi\,dS\Big]$$

$$+\cos\varphi_0\Big[\int_0^1 e^{-1}(C_1\cos\varphi - C_2\sin\varphi)\cos\varphi\,dS + \int_0^1 (C_1\sin\varphi + C_2\cos\varphi + \Omega/K)\sin\varphi\,dS\Big] = 0.$$

Here we took into account the equality $\varphi_0 = \varphi\Big|_{s=0} = \varphi\Big|_{s=1}$, which follows from the condition $K = 2\pi i$ $(i = 1, 2, \ldots)$.

Simple transformations yield the system of equations

$$C_1(e^{-1} - 1)\int_0^1 \cos\varphi\sin\varphi\,dS + C_2\Big[(1 - e^{-1})\int_0^1 \sin^2\varphi\,dS - 1\Big] = \frac{\Omega}{K}\int_0^1 \cos\varphi\,dS,$$

$$C_1\Big[e^{-1} + (1 - e^{-1})\int_0^1 \sin^2\varphi\,dS\Big] + C_2(1 - e^{-1})\int_0^1 \cos\varphi\sin\varphi\,dS = -\frac{\Omega}{K}\int_0^1 \sin\varphi\,dS.$$

Using the equalities

$$\int_0^1 \cos\varphi\sin\varphi\,dS = 0, \qquad \int_0^1 \sin\varphi\,dS = 0,$$

we obtain

$$C_1 = 0, \qquad C_2 = \frac{\Omega}{K}\int_0^1 \cos\varphi\,dS \Big/ \Big[(1 - e^{-1})\int_0^1 \sin^2\varphi\,dS - 1\Big].$$

In (2.11), setting $|\varepsilon| \ll 1$, expanding the integrands of the last expression in a series, and integrating, we have

$$C_2 = \frac{\Omega}{K}\,\frac{1 - \varepsilon^2/4 + \varepsilon^4/64 + \ldots}{(1 - 1/e)(\varepsilon^2/2 - \varepsilon^4/8 + \ldots) - 1}. \tag{2.20}$$

Let us determine the trajectory of motion of the BO. With allowance for expressions (2.14), (2.15), and (2.20), Eqs. (2.6) and (2.7) become

$$X_\tau = -(\Omega/K)\cos\varphi - C_2, \qquad Y_\tau = -(\Omega/K)\sin\varphi.$$

Integration yields

$$X = -\frac{\Omega}{K}\int_0^\tau \cos\varphi\,d\tau - C_2\tau + X_0(S), \qquad Y = -\frac{\Omega}{K}\int_0^\tau \sin\varphi\,d\tau + Y_0(S), \tag{2.21}$$

where $X_0(S)$ and $Y_0(S)$ are unknown functions.

Integration of the geometrical relations (2.8) yields

$$X = C_5(\tau) + \int\limits_0^S \cos\varphi\, dS, \qquad Y = C_6(\tau) + \int\limits_0^S \sin\varphi\, dS. \tag{2.22}$$

Any point on the elastic axis of the BO describes the same trajectory. The value $S = 0$ corresponds to the trajectory of the head of the BO. Equating expressions (2.21) and (2.22) for $S = 0$, we obtain the equalities

$$\begin{gathered} X\Big|_{S=0} = -\frac{\Omega}{K}\int\limits_0^\tau \cos\varphi_0\, d\tau - C_2\tau + X_0\Big|_{S=0} = C_5(\tau), \\ Y\Big|_{S=0} = -\frac{\Omega}{K}\int\limits_0^\tau \sin\varphi_0\, d\tau + Y_0\Big|_{S=0} = C_6(\tau). \end{gathered} \tag{2.23}$$

The initial condition (2.9) reduces the first equality to the relation $X = X_0\Big|_{S=0} = C_5(\tau) = 0$ for $\tau = 0$. In addition, comparing the expressions for X in (2.21) and (2.22) for $\tau = 0$, we write the equality

$$X\Big|_{S=0} = X_0\Big|_{S=0} = \int\limits_0^S \cos\varphi\Big|_{\tau=0} dS.$$

Therefore, expression (2.21) for X becomes

$$X = -\frac{\Omega}{K}\int\limits_0^\tau \cos\varphi\, d\tau - C_2\tau + \int\limits_0^S \cos\varphi\Big|_{\tau=0} dS. \tag{2.24}$$

The second equality in (2.23) for the initial time gives the relation $Y\Big|_{S=0,\tau=0} = Y_0\Big|_{S=0} = C_6\Big|_{\tau=0}$. In addition, the second expressions in (2.21) and (2.22) imply the equality

$$Y\Big|_{\tau=0} = Y_0(S) = C_6\Big|_{\tau=0} + \int\limits_0^S \sin\varphi\Big|_{\tau=0} dS.$$

In view of the last relations, formula (2.21) for Y becomes

$$Y = Y_0\Big|_{S=0} + \int\limits_0^S \sin\varphi\Big|_{\tau=0} dS - \frac{\Omega}{K}\int\limits_0^\tau \sin\varphi\, d\tau. \tag{2.25}$$

The constant $Y_0\Big|_{S=0}$ is found from the condition of symmetric deviation of the BO from the X axis:

$$\int\limits_0^1 Y\Big|_{\tau=0} dS = 0.$$

We have

$$Y_0\Big|_{S=0} = -\int\limits_0^1 \int\limits_0^S \sin\varphi\Big|_{\tau=0} ds\, ds.$$

Taking into account that $\varphi\Big|_{\tau=0} = \varepsilon \sin KS$, as a first approximation, we obtain $Y_0\Big|_{S=0} \simeq -\varepsilon/K$. The expression for Y in (2.25) with accuracy to terms of order ε^3, is written as

$$Y = -(\varepsilon/K)\cos(KS - \Omega\tau) + O(\varepsilon^3). \tag{2.26}$$

Expanding the integrands in series and integrating (2.24), we obtain the following approximate expression for the function X:

$$X = (1 - e^{-1})\frac{\varepsilon^2\Omega\tau}{2K} + S\Big(1 - \frac{\varepsilon^2}{4}\Big) + \frac{\varepsilon^2}{8K}\,\sin(2KS - 2\Omega\tau) + O(\varepsilon^4). \tag{2.27}$$

The mechanical energy of the body muscles finally becomes heat because of dissipation of mechanical energy by the ambient fluid. Let us find the energy expended by the BO in motion.

According to the results of [4] the energy W expended by a particle to move in a viscous fluid is defined by the integral

$$W = \int_0^l (\boldsymbol{r}_t - \boldsymbol{V})\boldsymbol{K}\,ds.$$

The relations of Sec. 1 imply the equalities $\boldsymbol{r}_t - \boldsymbol{V} = -B^{-1}(N\varphi_s + Q_s)\boldsymbol{n} - A^{-1}(N_s - Q\varphi_s)\boldsymbol{l}$ and $\boldsymbol{K} = -[(N\varphi_s + Q_s)\boldsymbol{n} + (N_s - Q\varphi_s)\boldsymbol{l}]$. Thus, the computational formula becomes

$$W = \int_0^l [B^{-1}(N\varphi_s + Q_s)^2 + A^{-1}(N_s - Q\varphi_s)^2]\,ds.$$

Using (2.1)–(2.3), we write this expression in dimensionless form

$$w = \int_0^1 (eZ^2 + D^2)\,dS.$$

Taking into account (2.14), (2.15), and (2.20), we have

$$w = C_2^2(e^{-1} - 1)\int_0^1 \sin^2\varphi\,dS + C_2^2 + \frac{\Omega^2}{K^2} + 2C_2\,\frac{\Omega}{K}\int_0^1 \cos\varphi\,dS. \tag{2.28}$$

Integrating the first terms of the expansion of the integrands, we obtain the asymptotic estimate

$$w = \Omega^2\varepsilon^2/(2eK^2) + O(\varepsilon^4).$$

Using relations (2.1) for $A = 2\pi\mu/\ln(0.952/\sqrt{c})$ and $y_m/l = \varepsilon/K$, we write the computational formula for the energy in dimensional form

$$W = 2\pi\mu l\omega^2 y_m^2/\ln(7.4/\mathrm{Re}) + O(\varepsilon^4), \tag{2.29}$$

where y_m is the maximum deviation of the elastic axis from the x axis.

With allowance for the results (2.20), the expression for the dimensionless axial load (2.18) becomes

$$n = C_2\Big\{\cos\varphi\Big[(e^{-1} - 1)\int_0^S \sin^2\varphi\,dS + S\Big] + \frac{1}{2}\,(1 - e^{-1})\sin\varphi\int_0^S \sin 2\varphi\,dS\Big\}$$
$$+ \frac{\Omega}{K}\Big[\sin\varphi\int_0^S \sin\varphi\,dS + \cos\varphi\int_0^S \cos\varphi\,dS\Big]. \tag{2.30}$$

Accordingly, formula (2.19) can be written as

$$q = C_2\Big\{\frac{1}{2}\,\cos\varphi\,(1 - e^{-1})\int_0^S \sin 2\varphi\,dS - \sin\varphi\Big[(e^{-1} - 1)\int_0^S \sin^2\varphi\,dS + S\Big]\Big\}$$
$$+ \frac{\Omega}{K}\Big[\cos\varphi\int_0^S \sin\varphi\,dS - \sin\varphi\int_0^S \cos\varphi\,dS\Big]. \tag{2.31}$$

Formulas (2.30) and (2.31) are not suitable for analysis; therefore, using expansions of trigonometric functions, we write the following asymptotic estimates for the functions n and q:

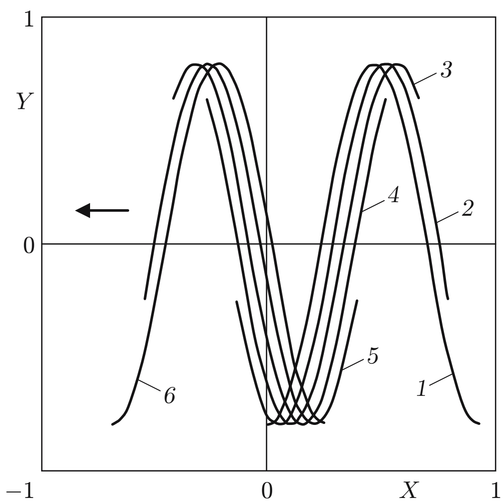

Fig. 1

$$n = (\Omega\varepsilon^2/(4K^2))\{(1/e - 1/2)[\sin(2KS - 2\Omega\tau) + \sin 2\Omega\tau]$$

$$- (4/e)\sin(KS - \Omega\tau)[\cos(KS - \Omega\tau) - \cos\Omega\tau]\} + O(\varepsilon^4); \qquad (2.32)$$

$$q = -(\Omega\varepsilon/(K^2 e))[\cos(KS - \Omega\tau) + \cos\Omega\tau] + O(\varepsilon^3). \qquad (2.33)$$

Thus, an exact analytical solution of the problem is obtained. The main parameters of the motion of the BO are determined: the axial force is described by expression (2.29) and is estimated asymptotically by (2.32); the shear force is described by expression (2.30) and is estimated asymptotically by (2.33); the expended energy is described by (2.28) and (2.29); the motion trajectory is expressed in parametric form by the accurate relations (2.24) and (2.25) and by approximate relations (2.26) and (2.27). To determine the element, one can use the last equation in (1.1) $M_s = -Q$.

3. Analysis of the Solution. In (2.27), the coefficient at τ in the first term $(1-e^{-1})\varepsilon^2\Omega/(2K)$ characterizes the average dimensionless velocity of translational motion of the BO along the X axis. With allowance for (2.1), this velocity can be written in dimensional form $y_m^2 k\omega$, where $y_m = \varepsilon/k$ is the oscillation frequency [see (2.26)]. Therefore, the velocity of translational motion of the BO is proportional to the squared oscillation frequency, the tortuosity of the body k, and the frequency of muscle contraction ω of the BO.

According to expression (2.32), the axial load exerted on the backbone has a cyclic nature. The amplitude of the load $N/Q_0 \simeq \omega A y_m^2/Q_0$ is proportional to the frequency of muscle contraction ω, the squared deviation y_m^2, and the axial friction force A. The drag force is ignored.

The shear force (2.33) exerted on the intervertebral disks also has a cyclic nature. The amplitude of the force $Q/Q_0 \simeq \omega B y_m/(Q_0 k)$ is proportional to the frequency of muscle contraction ω, the deviation y_m, and the shear friction force B and is inversely proportional to the bending frequency of the body k.

According to expression (2.29), the energy expended in motion W is proportional to the body length l, the squared frequency of muscle contraction ω^2, and the squared deviation y_m^2.

Figure 1 shows the configurations of the elastic axis of the BO at various times. The calculations were performed using formulas (2.26) and (2.27) for the following conditions: $\varepsilon = 0.5$, $\Omega = 2\pi$, $K = 2\pi$, and $e = 2/3$. The step in time τ is 2.2. Curve 1 corresponds to the time $\tau = 0$ and curve 6 to $\tau = 2.2 \cdot 5 = 11$. The object moves to the left along the X axis. The arrow shows the motion direction.

A numerical analysis of (2.26) and (2.27) shows that to ensure the correct direction of motion (agreement between the motion of the body and the direction of its motion along the X axis) the condition $e < 1$ should be satisfied. The parameter e characterizes the ratio of the longitudinal and transverse friction forces and is defined by the formula

$$e = \ln(7.4/\mathrm{Re})/(2\ln(0.952/\sqrt{c})).$$

Therefore, the Reynolds number should be in the range $8.167c < \text{Re} < 7.4$. The obtained mathematical model is adequate for describing the motion of small-sized BOs at a low velocity.

It should be noted that the body surface of some BOs releases a secretion that imparts non-Newtonian properties to the hydrodynamic boundary layer. The longitudinal friction is lowered because the parameter e decreases. In this case, determining the parameter e exactly is rather problematic.

According to (2.26), the parameters ε characterizes the dimensionless amplitude (span) of oscillations of BOs. According to (2.27), the velocity of the axial motion is proportional to the squared span of the oscillations ε^2. The parameter K characterizes the tortuosity of a BO, namely, the number of half-waves of the bent body. Thus, the body has two half-waves for $K = 2\pi$, four half-waves for $K = 4\pi$, etc. A BO moving without friction in a glass tube of the sinusoidal shape $Y = \varepsilon \sin KS$ would have the maximum possible velocity equal to the velocity of the traveling wave Ω/K [3]. However, since BOs have to overcome viscous friction forces, they has lower velocities, i.e., lag behind the indicated traveling wave (see Fig. 1). Therefore, the parameters ε and e should satisfy the condition $0.5(e^{-1} - 1)\varepsilon^2 \leqslant 1$.

The function φ [see expression (2.11)], which is the argument of trigonometric functions, should satisfy the condition $\varphi < \pi/2$, which implies the relation $\varepsilon < \pi/2$. The violation of the last condition leads to a distortion of the shape of the elastic axis by high-frequency harmonics.

The law of motion of the BO was specified *a priori*. It is possible that the governing equation (2.11) is not optimal, i.e., it does not ensures the minimum energy consumption in motion. This issue, however, requires a separate consideration.

As can be seen from Fig. 1, the orientation of the head of the BO changes periodically, which is due to by the adopted form of the governing equations (2.11). Some BOs retain the axial (along the X axis) orientation of the head during motion. In this case, it is necessary to adopt a different governing equation, which should satisfy the boundary condition $t > 0$, $s = 0$, $\varphi = 0$. In addition, adding an auxiliary term (a constant or a function of time) to the right side of Eqs. (2.11), it is possible to change the direction of motion of the BO: to the right, to the left, on a circle, on a spiral, etc.

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