BIOMATH
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Biomath Forum
ORIGINAL ARTICLE

Possible means of swimming of red algae spores

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Received: March 4, 2023, Accepted: August 4, 2023, Published: October 17, 2023

Abstract: **This article proposes a model for swimming of red algae spores. The model considers a released spore in unbound water as a spherical particle enclosing a liquid incompressible cytosol, in which oscillates a solid spherical organelle. An analysis of the solutions of the Navier-Stokes equations for the cytosol flow caused by the organelle motion within the cell is presented in the limit of small Reynolds number. It is shown that in the case when the cytosol has Newtonian or Maxwell properties, the spore may swim only when the forward and backward trajectories of the organelle are different. In the case of the shear thinning cytosol properties the spore may swim also when the organelle trajectories are the same, but the velocities of forward and backward movements of the organelle should differ. Such a cell may swim in a straight line. The swimming of the model spores completely satisfies experimental data.**

Keywords: **Cytosol, Fluid dynamics, Navier-Stokes equations, Organelle, Red algae spores**

I. Introduction

It is obvious that the movement of living organisms is of high importance for their survival. Many swimming cells from bacteria to protists and further to unicellular stages of more advanced organisms in the plant and animal kingdoms use flagella as an effective locomotory device [1]. Cilia are the other swimming means exclusively for *Ciliate* structurally identical to eukaryotic flagella, but in general shorter and present in larger numbers, with a more difficult undulating pattern than flagella [2]. Another possible way of swimming of unicellular organisms relies on non-reversible cyclic cell shape changes. For example it is characteristic for protists euglenids or mammalian leukocytes [3, 4]. But each life stage of most zygnematalean green algae, red algae, pennate diatoms, higher land plants, ascomycetes and basidiomycetes are devoid of these "transport means" [5, 6]. Thus red algae spores had been generally considered to be non-motile, which was especially surprising for these extremely successful predominantly marine taxa. So Pickett-Heaps et al. [1] taking into account sporadic reports of red algae spores motility tried to record freshly released live spores with time-lapse video microscopy. It was shown that only 7 of 26 investigated taxa belonging to genera *Flintiella*, *Glaucosphaera* and *Rhodospora* had immobile spores. About 15% of *Sahlingia subintegra* (Rosenvinge) Kornmann spores were amoeboid, that is they swam by means of non-reversible cyclic cell shape changes. There was considerable variation in mean swimming speeds of the rest 18 taxa of red algae spores from 10^{-7} to $2.2 \cdot 10^{-6}\,\mathrm{m} \cdot \mathrm{s}^{-1}$. Most of spores of the latter taxa moved directionally, but the spores belonging to taxa *Erythrotrichia carnea* and *Rhodochaete parvula* moved non-directionally. The maximal swimming velocity of red algae spores recorded was $3.24 \cdot 10^{-6}\,\mathrm{m} \cdot \mathrm{s}^{-1}$. The mechanism of such red algae spores motility is still unknown, but it ensures their dissemination moving them away from the quiescent boundary layer of their sporangia into the turbulent flow of the surrounding water [1, 6].

Thus, a question can be raised: how the cells are able to swim without the flagella, cilia and the ability to non-reversible cyclic cell shape changes? We have

Citation: Oleh Pundyak, Possible means of swimming of red algae spores,
Biomath 12 (2023), 2308047, https://doi.org/10.55630/j.biomath.2023.08.047

tried to answer this question taking into account that the releasing spores are already polarized as they are able to swim [1]. As it is known, in polarized cells microtubules are mostly arranged symmetrically to the cell axis like arcs with different radiuses of curvature from the inner cell radius (close to the cell membrane) up to infinity (along the cell axis), while their minus- and plus-ends are clearly orientated relatively to the cell poles [7], this is true also for brown algae zygotes [8, 9] and for the monospores of red alga *Porphyra yezoensis* [10]. Intracellular organelles are able to be actively translocated on long-distances by means of motor proteins, such as dynein and kinesin, which move towards microtubule minus- and plus-ends, respectively, with different velocities [7, 11, 12].

Ca^{2+}-ions may decrease the relation of active kinesin and dynein concentrations determining the direction of a cargo movement in polarized cells [11, 13]. Not only in animal, but also in plant cells including algae there may take place oscillations of Ca^{2+} level and bound with it oscillations of Ca^{2+} gradient [14, 15]. Thus the conditions are created, under which a cell organelle may be translocated in turn towards different cell poles with different velocities and by different ways. In non-Newtonian fluids friction depends non-linearly on a particle velocity [16, 17]. It allows us to predict that during the whole cycle of intracellular organelle oscillations the mean translocation of the cell may be not equal zero. Rheological peculiarities of cytosol may considerably influence such cell motility. Thus the investigation of green alga *Caenorhabiditis elegans* embryo cytoplasm streamings shows that the cytoplasm is a Newtonian fluid [18]. Also it is revealed that cytosol of many organisms including Chara algae has viscoelastic rheological properties [19]. The shear rate of some adherent cells depends by power law on the constant stress quantity expressing shear-thinning properties of their cytosol [20–22]. Thus let us gradually consider the situation when cytosol is: 1) a Newtonian fluid, 2) a viscoelastic Maxwell fluid, 3) a shear thinning fluid.

II. Model Description

Let us consider the movement of a microscopic spherical cell in unbound water. The cell encloses an incompressible liquid homogeneous cytosol by solid homogeneous cell wall. A spherical solid organelle moves within the cytosol due to a locomotion force, which also simultaneously pushes the cell in the opposite direction. The locomotion force pulls the organelle toward in turn the forward and rear poles of the cell. The locomotion toward one cell pole when reached is changed to the locomotion toward the other pole and then the cycle repeats itself identically. Our goal is to find the mean swimming velocity of the cell.

The world of microscopic particles is the world of low 'Reynolds number', a world where inertia can be neglected. It concerns also the centrifugal force as a variety of the inertial force [23]. During intracellular translocations of an organelle the drag force may reach the order of $10^{-12}\,\mathrm{N}$ [12, 24–27], while the particles weights and the fluctuation force have the order not bigger than $10^{-16}\,\mathrm{N}$. Thus we can neglect the latter as is customary to do so in microswimmers investigations [23, 28]. The Young's modulus of red algae spores walls lies within the framework of 10^6 to $10^8\,\mathrm{Pa}$ [29]. Young's modulus of biological lipid bilayers at $20^{\circ}\mathrm{C}$ is not less than $10^6\,\mathrm{Pa}$ [30]. The thickness of yellow algae cell walls is close to red algae ones and is of order $10^{-7}\,\mathrm{m}$ [31], while the total thickness of the double membrane of a red alga rhodoplast (in red algae cells plastids are called rhodoplasts) is of order $10^{-8}\,\mathrm{m}$ [32]. Thus under the loading of order $10^{-12}\,\mathrm{N}$ the deformations of the cell and the plastid don't exceed $10^{-2}\,\%$ of their dimensions. It allows us to neglect mentioned deformations.

III. Cytosol as a Newtonian fluid

Let u_c be the cell swimming velocity, u_o – the velocity of the organelle, u_{oc} – the organelle velocity relative to the cell. Thus we have $u_{oc} = u_o - u_c$. Let u_{oc} be known. Then to determine u_c we need to solve for the flow field $\boldsymbol{\nu}$ and pressure p in the surrounding fluids applying the laws of mass and momentum conservation. As it is known, the Navier-Stokes equations express the mentioned laws for an incompressible fluid [23,33]. At low Reynolds numbers, which characterize cellular and intracellular biological systems the Navier-Stokes equations can be simplified by equations:

$$\nabla\sigma = 0, \quad \nabla\cdot\boldsymbol{\nu} = 0, \quad \sigma \equiv -p\cdot\delta + \tau, \qquad (1)$$

where σ is the Cauchy stress tensor, τ is the viscous stress tensor, δ is the Kronecker delta tensor. For time independent fluids the viscous stress tensor is written as:

$$\tau = \eta\big(\nabla\boldsymbol{\nu} + (\nabla\boldsymbol{\nu})^T\big) = \eta\cdot\gamma', \qquad (2)$$

where η is the fluid viscosity, γ' is the shear rate tensor. When the fluid is Newtonian, equations (1) are simplified to the Stokes equations [23]:

$$\nabla p = \eta\nabla^2\boldsymbol{\nu}, \quad \nabla\cdot\boldsymbol{\nu} = 0. \qquad (3)$$

Remark 1. Let the cytoplasm filling the cell doesn't slip on its inner surface and the organelle outer surface. Analogically, let the same be said for the outside water. The boundary conditions in that case state that the velocities of the fluids at the wall boundaries equal the velocities of such walls. Once ν and p are known, the hydrodynamic force F_s acting on a sphere within a fluid is found by integrating the Cauchy stress tensor over its surface S_i:

$$F_s = \oint_{s_i} \sigma \cdot n \, dS_i, \tag{4}$$

where n is the unit normal to dS_i into the fluid [23].

A. The average speed of the spore swimming

The average speed of the spore swimming can be calculated as:

$$U = \omega \cdot (\Delta x_{cf} + \Delta x_{cb}), \quad \omega \equiv (t_f + t_b\ )^{-1}, \tag{5}$$

where Δx_{cf}, Δx_{cb} are the net motions of the cell during forward and backward movements of the organelle, which have duration times t_f and t_b correspondingly, ω is the frequency of the organelle oscillation. The sum of the net motions of the organelle during the whole oscillation cycle equals 0:

$$\Delta x_{of} + \Delta x_{ob} = 0. \tag{6}$$

For the finding of the net motions of the spore during forward and backward movement of the organelle we should integrate equation:

$$\Xi = -\frac{u_c}{u_{oc}} \tag{7}$$

with respect to the organelle coordinate relatively to the cell center (x_o).Taking into account that $u_{oc}dt = dx_o$ we get:

$$\begin{aligned} \Delta x_{cf} &= -\int_{x_{o_1}}^{x_{o_2}} \Xi(x_o, i_f) dx_o, \\ \Delta x_{cb} &= -\int_{x_{o_2}}^{x_{o_1}} \Xi(x_o, i_b) dx_o, \\ \Delta x_{of} &= -\Delta x_{ob} = x_{o_2} - x_{o_1}, \end{aligned} \tag{8}$$

where i_f and i_b are the forward and backward unitary organelle velocity vectors respectively: $i \equiv u_{oc}/|u_{oc}|$. The velocities ratio Ξ is the function of: 1) the organelle coordinate x_o; 2) the organelle velocity direction i, because in a bounded fluid, spatial homogeneity and isotropy are broken [34]; 3) the spore and the organelle radiuses (R_c and R_o correspondingly). According to (1), (2), (3), σ only change its sign under simultaneous sign changings of the velocities ν in all points of the fluids. Therefore according to (4) we have $\Xi(x_o, i) = \Xi(x_o, -i)$. Thus in the case, when the organelle trajectories are the same for the forward and backward movements, we have $\Xi(x_o, i_f) = \Xi(x_o, i_b)$ and according to (8) we get $\Delta x_{cf} = -\Delta x_{cb}$ so such a cell is non-motile: $U = 0$.

B. The case when the forward and backward trajectories of the organelle are different

That is maximally expressed, when, for example, the forward motion of the organelle is axisymmetric (Fig. 1a), while the backward motion is orbital (Fig. 1b). The organelle velocity direction on the beginning of each stage of its movement is perpendicular to the trajectory on the end of the previous stage. Analogically, it is the same for the spore trajectory.

The average speed of the cell depends on the chain of successive choices of directions of orbital motion of the organelle. The maximal value of U is achieved in the case when the vector of the organelle angular velocity each time in turn changes to the opposite one. In the case of the organelle orbital movement, there appears a torque acting on the spore causing its trajectory to bend.

When both considered fluids are Newtonian, the cell velocity and the rate of the cell velocity orientation changings is proportional to u_{oc}. Thus the radius of curvature of the spore trajectory R_{cur} is a constant during the whole time of the organelle orbital movement regardless of its speed (Fig. 2). According to situation showed on Fig. 2 we have:

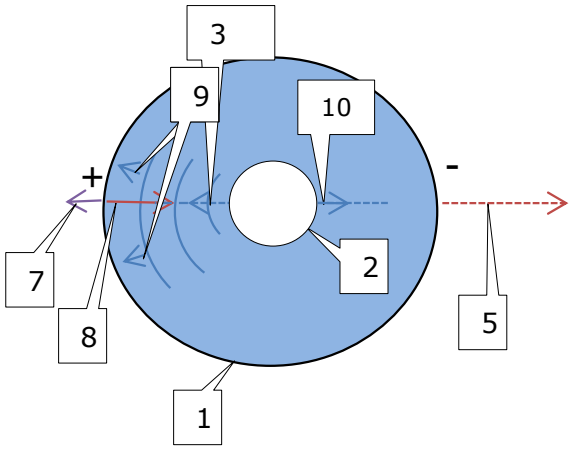
$$U = \frac{1}{2}\omega \cdot (\Delta x_{cf} - 2 i_a R_{cur}) \cdot (1 - \cos\Psi). \tag{9}$$

where i_a is the unitary velocity vector of the organelle axisymmetrical movement.

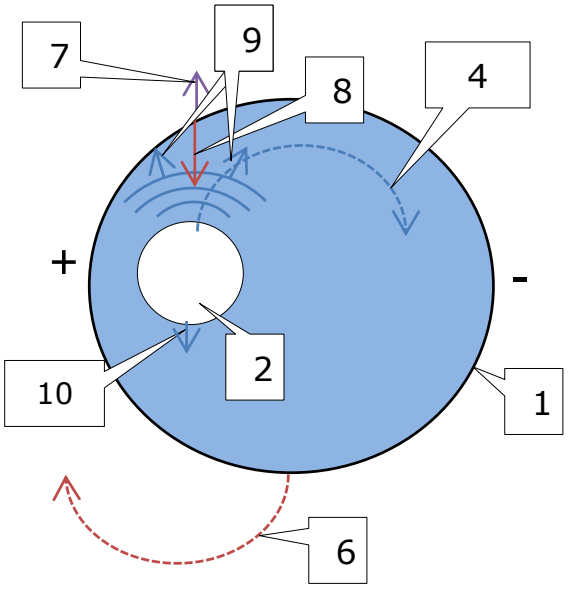
Thus for the finding of the main spore velocity U we should find: 1) the net motion of the cell during forward axisymmetric movement of the organelle Δx_{cf}; 2) the radius of curvature R_{cur} and the angle deviation Ψ of the spore trajectory from the start position during orbital movement of the organelle.

C. Analytical consideration of axisymmetric movement of the organelle

Let us consider translating movement of the organelle in a viscous cytoplasm filling the spore along the line connecting their centers (Fig. 3). A microhydrodynamic model for such kind of movement was carefully considered by Keh and Lee [35]. But they investigated the case when the cavity (in our case it is the spore) was immobile.

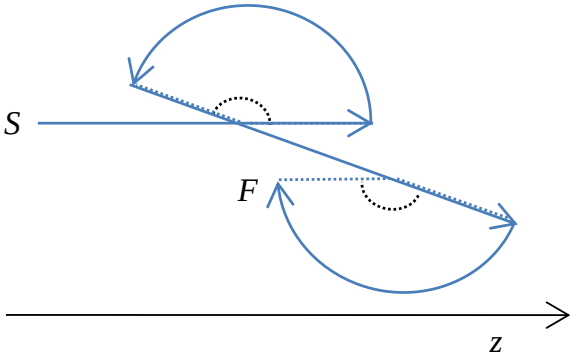


(a) axisymmetric movement

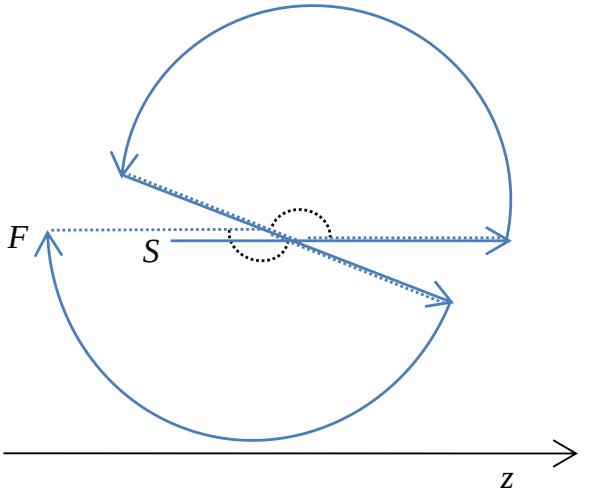


(b) orbital movement

Fig. 1: Geometric sketch of different motions patterns of the organelle and spore movements caused by it: (a) – axisymmetric movement; (b) – orbital movement; $+$ and $-$ are the cell poles, where the $+$ and $-$ microtubule ends are concentrated; 1 is the spore wall; 2 is the organelle; 3, 4 are the organelle axisymmetric and orbital trajectories relative to the cell; 5, 6 are the cell trajectories; 7 is the cell drag force F_{Dc}; 8 is the locomotion force M_c; 9 is the hydrodynamic force acting on the inner walls of the cell caused by the organelle movement F_{Dc}; 10 is the organelle drag force F_{Do}.



(a) the case when $\Delta x_{cf} > 2R_{cur}$



(b) the case when $\Delta x_{cf} < 2R_{cur}$

Fig. 2: Geometric sketch of the trajectory of the spore movement in the case when the forward motion of the organelle is axisymmetric, while the backward motion is orbital (figures show two series of both movements) and the vector of angular velocity of the organelle orbital motion changes in turn to the opposite one. S and F mark the start and finish positions of the cell correspondingly; straight solid arrows mean the cell trajectories during axisymmetric motion of the organelle; curved solid arrows mean the cell trajectories during orbital movement of the organelle; straight dashed lines mean the radius of curvature R_{cur} and dashed arcs mean the angle deviation of the spore trajectory from the start position Ψ during orbital movement of the organelle. (a) – the case when $\Delta x_{cf} > 2R_{cur}$; (b) – the case when $\Delta x_{cf} < 2R_{cur}$.

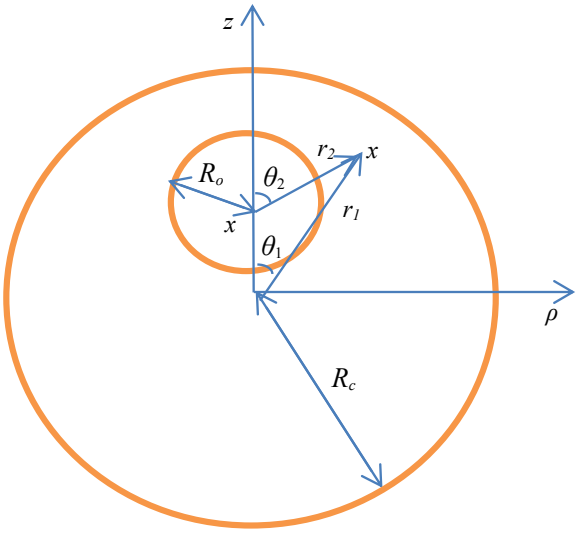


Fig. 3: Geometric sketch of the organelle in the spore: r_1, θ_1, r_2, θ_2 are the spherical coordinates relatively to the centers of the cell and organelle correspondingly; x is a point in liquid cytosol medium; ρ and z are the cylindrical coordinates; x_o is the distance between the particles centers; R_c and R_o are the radiuses of the spore and organelle correspondingly.

As the spore with organelle are spherical and the cytoplasm is homogeneous, we have a system, which is symmetrical relatively to the axis (axisymmetric movement). In such a case for the solving of Stokes equations (3) for the flow field, Keh and Lee [35] proposed to construct a general solution using two spherical coordinate systems based on the centers of both the particle and cavity. Because of their axisymmetric nature such solutions are independent from the angle φ (That is why the angle φ is not presented on the Fig. 3). On the other hand we are interested to obtaining the components of the spatial distribution of the fluid velocities and pressures along the axis and perpendicularly to it. Thus we can express as the solution of equation $\nabla \cdot \mathbf{v} = 0$ from (1) or (3) with the corresponding components of the cytoplasmic fluid velocities in terms of the cylindrical coordinates ρ and z (as it was made by Keh and Lee [35]):

$$\begin{aligned}\mathrm{v}_\rho = \sum_{n=1}^{\infty} & a_n A_n^\rho(r_1,\theta_1) + b_n B_n^\rho(r_1,\theta_1) \\ & + c_n C_n^\rho(r_2,\theta_2) + d_n D_n^\rho(r_2,\theta_2), \end{aligned} \tag{10}$$

$$\begin{aligned}\mathrm{v}_z = \sum_{n=1}^{\infty} & a_n A_n^z(r_1,\theta_1) + b_n B_n^z(r_1,\theta_1) \\ & + c_n C_n^z(r_2,\theta_2) + d_n D_n^z(r_2,\theta_2), \end{aligned} \tag{11}$$

where r_1, θ_1, r_2, θ_2 are the spherical coordinates relative to the centers of the cell and organelle correspondingly; a_n, b_n, c_n, d_n are coefficients independent from the coordinates; we define:

$$A_n^\rho(r,\theta) \equiv -r^{-2-n}(n+2)G_{n+2}^{-1/2}(\cos\theta)\csc\theta, \tag{12a}$$

$$\begin{aligned} B_n^\rho(r,\theta) \equiv -r^{-n}(n+2)\Big(& G_{n+2}^{-1/2}(\cos\theta)\csc\theta \\ & -2G_{n+1}^{-1/2}(\cos\theta)\cot\theta\Big), \end{aligned} \tag{12b}$$

$$\begin{aligned} C_n^\rho(r,\theta) \equiv -r^{n-1}\Big(& (n+2)G_{n+2}^{-1/2}(\cos\theta)\csc\theta \\ & -(2n+1)G_{n+1}^{-1/2}(\cos\theta)\cot\theta\Big), \end{aligned} \tag{12c}$$

$$\begin{aligned} D_n^\rho(r,\theta) \equiv -r^{n+1}\Big(& (n+2)G_{n+2}^{-1/2}(\cos\theta)\csc\theta \\ & -(2n+3)G_{n+1}^{-1/2}(\cos\theta)\cot\theta\Big), \end{aligned} \tag{12d}$$

and

$$A_n^z(r,\theta) \equiv -r^{-2-n}P_{n+1}(\cos\theta), \tag{13a}$$

$$\begin{aligned} B_n^z(r,\theta) \equiv -r^{-n}\Big(& P_{n+1}(\cos\theta) \\ & +2G_{n+1}^{-1/2}(\cos\theta)\Big), \end{aligned} \tag{13b}$$

$$\begin{aligned} C_n^z(r,\theta) \equiv -r^{n-1}\Big(& P_{n+1}(\cos\theta) \\ & +(2n+1)G_{n+1}^{-1/2}(\cos\theta)\Big), \end{aligned} \tag{13c}$$

$$\begin{aligned} D_n^z(r,\theta) \equiv -r^{n+1}\Big(& P_{n+1}(\cos\theta) \\ & +(2n+3)G_{n+1}^{-1/2}(\cos\theta)\Big), \end{aligned} \tag{13d}$$

where $G_n^{-1/2}$ and P_n are the Gegenbauer and Legendre polynomials of order n respectively. As the particles are homogeneous further we will consider their velocities and the forces acting on them as scalars, which all are the projections on the axis z (Fig. 3) or on other axes bounded with it.

Let us consider the case, when the centers of the particles coincide ($x_o = 0$). Thus we have $r_1 = r_2 = r$ and $\theta_1 = \theta_2 = \theta$ in formulas (10) and (11). According to Remark 1 and considering for sake of simplicity that the inner and outer radiuses of the cell equal one another, our margin conditions are:

$$\begin{aligned} & \mathrm{v}_\rho(R_c,\theta) = \mathrm{v}_\rho(R_o,\theta) = 0, \\ & \mathrm{v}_z(R_c,\theta) = u_c, \quad \mathrm{v}_z(R_o,\theta) = u_{oc}, \end{aligned} \tag{14}$$

for any possible θ. To solve this system, it is enough to set only the four coefficients with $n = 1$. The other

ones equal zero. Thus according to (10)–(14) we get:

$$a_1 = \frac{(1-\lambda^3)R_o^3}{2G}\,u_{oc}, \tag{15a}$$

$$b_1 = -\frac{3(1-\lambda^5)R_o}{2G}\,u_{oc}, \tag{15b}$$

$$c_1 = -\frac{(4\lambda^5+5\lambda^2-9)\lambda}{4G}\,u_{oc} - u_c, \tag{15c}$$

$$d_1 = -\frac{3(1-\lambda^2\,)\lambda R_c^{-2}}{4G}\,u_{oc}, \tag{15d}$$

where we define:

$$G \equiv 1 - \frac{9}{4}\lambda + \frac{5}{2}\lambda^3 - \frac{9}{4}\lambda^5 + \lambda^6, \quad \lambda \equiv \frac{R_o}{R_c}. \tag{15e}$$

According to Newton's 3rd law the locomotion force acting on the cell M_c is opposite to the locomotion force acting on the organelle M_o and equals the organelle drag force F_{Do}:

$$M_c = -M_o = F_{Do}. \tag{16}$$

The difference between the locomotion force and the hydrodynamic force acting on the inner walls of the cell caused by the organelle movement F_{Dh} should be equilibrated by the cell drag force F_{Dc} (Fig. 1a):

$$F_{Dc} = M_c - F_{Dh} = F_{Do} - F_{Dh}. \tag{17}$$

In the case when the viscosity of the outer fluid equals zero ($\eta_w = 0$) the cell drag force F_{Dc} equals inner friction force, which according to the Stokes equations (3) is proportional to cytosol viscosity η_c, the cell radius R_c and the cell velocity u_c. In the case $\eta_c = 0$ according to Stokes law, we have $F_{Dc} = -6\pi u_c R_c \eta_w$. Thus we get:

$$F_{Dc} = -6\pi u_c R_c(\eta_w + \vartheta\eta_c),\ 0 < \vartheta = const. \tag{18}$$

Therefore taking into account (17) we have:

$$6\pi u_c R_c(\eta_w + \vartheta\eta_c) = F_{Do} - F_{Dh}. \tag{19}$$

In the general case when the particles centers don't coincide, the summary hydrodynamic force acting on a sphere in the cytosol depending on its radius $F(r)$ is determined by the formulas (3), (4), (10)–(14) can be expressed by the polynomial with infinite array of the coefficients $a_1, \dots a_n,\ b_1, \dots b_n,\ c_1, \dots c_n,\ d_1, \dots d_n$. In the case when the particles centers coincide, according to these equations, $F(r)$ can be expressed analytically by the polynomial with only the four coefficients $a_1,\ b_1,\ c_1,\ d_1$ determined by formulas (15a)–(15d):

$$F(r) = -6\pi\eta_c\Big(R_o u_{oc} + 2a_1 r^{-2} + \frac{3}{2}b_1 + c_1 r + \frac{1}{3}d_1 r^3\Big). \tag{20a}$$

For $r = R_o$ it equals the drag force F_{Do} and we have:

$$F(R_o) = F_{Do} = -6\pi\eta_c R_o\Big(\frac{1-\lambda^5}{G}u_{oc} - u_c\Big). \tag{20b}$$

When $r = R_c$ it equals F_{Dh} and we get:

$$F(R_c) = F_{Dh} = -6\pi\eta_c\Big(R_o u_{oc} + \frac{1-\lambda^5}{G}R_o u_{oc} - R_c u_c\Big). \tag{20c}$$

Therefore in the case when the cell and organelle centers coincide according to (7), (19), (20b) and (20c) we have:

$$\Xi_0(\lambda,\xi) = \frac{\lambda}{\xi + 1 + \vartheta - \lambda}, \quad \xi \equiv \frac{\eta_w}{\eta_c}. \tag{21a}$$

In the case when $\xi \to 0$ and $\lambda \to 1$ according to the laws of mass and momentum conservation we have $\Xi_0 \to 1$. Taking it into account and according to (21a), we determine that $\vartheta = 1$ and thus we have:

$$\Xi_0(\lambda,\xi) = \frac{\lambda}{\xi + 2 - \lambda}. \tag{21b}$$

Since $0 \le \xi \le 1$ and $0 < \lambda < 1$, the function $\Xi_0(\lambda,\xi)$ weakly increases with the decreasing of $\xi \to 0$, but strongly decreases with the decreasing of $\lambda \to 0$.

D. Some important approximations

As mentioned, in confined systems friction of a spherical particle is anisotropic [34], excluding the center of a symmetric spherical cavity. Generally, the drag force for axisymmetrical movement in immobile cavity cannot be expressed analytically, as consequence of the infinite array of the coefficients $a_1, \dots a_n,\ b_1, \dots b_n,\ c_1, \dots c_n,\ d_1, \dots d_n$. According to [35] the drag force can be approximated as:

$$F_{Do}(u_{oc}, x_o) \sim F_{Do}(u_{oc}, 0) \tag{22a}$$

within wide diapason of λ under the condition:

$$\frac{|x_o|}{R_c - R_o} < \frac{1}{2}. \tag{22b}$$

As shown by Villa et al. [34], the viscous drag of the spherical particle moving parallel to infinite non-slip plane is always lower than of the corresponding particle moving perpendicular, taken at the same distance from the plane. It allows us to state that within the same interval (22b) an approximation (22a) is also valid for the organelle movement in different directions (for example the axisymmetrical Fig. 1a and orbital Fig. 1b movements). All these cases we can interpret as the

organelle movement parallel to the axis z in Fig. 3, but on certain distance from the axis z. Analogically, let the same be valid not only for immobile cavity, but also for a free cell in unbound water. Similarly, we can assume that under the condition (22b), the following approximations are valid for our model spore:

$$F_{Do}(u_{oc}, x_o, L) \sim F_{Do}(u_{oc}, 0, 0), \tag{22c}$$

$$F_{Dh}(u_o, x_o, L) \sim F_{Dh}(u_o, 0, 0), \tag{22d}$$

$$F_{Dc}(u_c, x_o, L) \sim F_{Dc}(u_c, 0, 0), \tag{22e}$$

where L is the distance between the axis z and the axis along which the organelle moves, so that (22b) becomes:

$$\frac{\sqrt{x_o^2 + L^2}}{R_c - R_o} < \frac{1}{2}. \tag{22f}$$

Now let us consider the case when the organelle is outside the region (22f).

Let us define $\chi(x_o, L) \equiv \frac{F_{Do}(0,0)}{F_{Do}(x_o,L)}$. As the hydrodynamic force F_{Dh} is the cause of the organelle drag force dissipation throughout the cell, we can generally assume that $\chi(x_o, L) \sim \frac{F_{Dh}(0,0)}{F_{Dh}(x_o,L)}$. Let us use formulas (20b) and (20c) as an approximation, right hand sides of which are multiplied by χ^{-1} and also formula (19).

Now let us determine according to the laws of mass and momentum conservation as after (21a) that $\chi\vartheta = 1$. Thus we can approximate the velocity relation in such way:

$$\Xi(x_o, L) \sim \frac{\lambda}{\chi(x_o, L)\xi + 2 - \lambda}. \tag{23a}$$

Let an approximation (23a) be valid for the axisymmetrical movement $\Xi_a = \Xi(x_o, 0)$, $\chi_a = \chi(x_o, 0)$, as well as for the orbital one $\Xi_{or} = \Xi(0, L)$, $\chi_{or} = \chi(0, L)$. The aim of our study is only to evaluate the order of the cell swimming velocity. According to formulas (8), (23a), and also to the numerical data shown in [35], the net motion of the cell during axisymmetrical movement of the organelle with the margin points equaling $x_{o_1} = -x_{o_2} = -\frac{1}{2}\Delta x_o$ can be approximated as:

$$\Delta x_c \approx -\frac{\lambda}{\chi_{ai}\xi + 2 - \lambda}\,\Delta x_o,$$
$$\chi_{ai} \equiv 1 - \frac{1}{3}\left(\frac{|\Delta x_o|}{R_c - R_o}\right)^5. \tag{23b}$$

For the sake of simplicity, sometimes further we will consider the organelle movement satisfying condition (22f), so that according to (23b) and [34] the velocity relation Ξ remains constant and is independent from the movement direction. Therefore, in that case according to (8) the net motion of the spore cell Δx_c during the net motion of the organelle Δx_o approaches:

$$\Delta x_c \approx -\Xi_0 \cdot \Delta x_o. \tag{23c}$$

E. The case of the organelle orbital movement

In the absence of rotational motion of the particle according to (5), (8) and (23c), under the condition (22f) the average speed of the spore swimming always equals zero. Now let us consider the organelle orbital movement. It causes the spore rotational motion and thus the bias of the inertial coordinate system for the organelle, so that equations (8) are invalid. Therefore, in the case when the forward motion of the organelle is axisymmetric, while the backward motion is orbital, the average speed of the spore swimming should be calculated only according to formula (9).

We already found Δx_c from (23b) and (23c). Now we are interested in finding the radius of curvature R_{cur} and the angle deviation Ψ of the spore trajectory from the start position. The radius of curvature of the cell trajectory during the organelle orbital movement R_{cur} can be written as:

$$R_{cur} = \left|\frac{u_c}{\Omega_{oc} + \Omega_c}\right|, \tag{24a}$$

where Ω_{oc} is the angle velocity of the organelle orbital movement relative to the spore cell, Ω_c is the angle velocity of the cell. The angle deviation Ψ of the spore trajectory from the start position can be found as:

$$\Psi = \int_0^{t_b} (\Omega_{oc} + \Omega_c)dt. \tag{24b}$$

Also, Ω_{oc} is determined as:

$$\Omega_{oc} = \frac{2u_{oc}}{\Delta x_o} \approx -\frac{2u_c}{\Xi_{or}\Delta x_o}. \tag{25a}$$

If $\Omega_c = 0$ and taking into account that during the orbital movement χ_{or} and Ξ_{or} are constant, then according to (23a), (24a), (25a), we have $2R_{cur} = \Xi_{or}|\Delta x_o|$ and $\Psi = \pi$. But in real systems, due to the organelle orbital movement, there appears viscous torque T_{Dc} causing rotation movement of the cell, so that we always have:

$$\Xi_{or}|\Delta x_o| < 2R_{cur}, \quad -1 < \frac{\Omega_c}{\Omega_{oc}} < 0. \tag{25b}$$

This fits Fig. 2b. Let us try to find Ω_c. Using analogical arguments as for formula (19) (see Fig. 1b) we can express the cell viscous torque as:

$$T_{Dc} = -8\pi(\eta_w + \widetilde{\vartheta}\eta_c)\Omega_c R_c^3,$$

where $\widetilde{\vartheta} > 0$ is analogical to ϑ for formula (19); the organelle drag torque:

$$T_{Do} \equiv \frac{1}{2} F_{Do} \Delta x_o,$$

which appears due to the organelle binding with cytoskeletal structures; and the hydrodynamic force torque:

$$T_{Dh} \equiv \int_{S_1} r_1 \times (\sigma \cdot n) dS_1, \tag{25c}$$

where integrating is done with respect to the cell inner surface. Thus Ω_c can be written as:

$$\Omega_c = \frac{\frac{1}{2} F_{Do} \Delta x_o - T_{Dh}}{8\pi(\eta_w + \widetilde{\vartheta}\eta_c) R_c^3}. \tag{25d}$$

According to formulas (10)–(14) it is not possible to express analytically T_{Dh} by using equations $\nabla p = \eta \nabla^2 \nu$ from (3), $\sigma \equiv -p \cdot \delta + \tau$ from (1) and formula (25c). Numerical data of computer calculation of the hydrodynamic torque appearing during the orbital movement of the particle in a cavity is also absent.

Because the hydrodynamic force F_{Dh} is a consequence of the drag force dissipation throughout the cell, the relation $\frac{\frac{1}{2} F_{Dh} \Delta x_o}{T_{Dh}}$ may be considerably bigger than 1. If $\lambda \geq \frac{1}{2}$ according to the definition of G and λ from formula (15e) we have $\frac{1-\lambda^5}{G} \gg 1$. According to it and to formulas (20b), (20c), (25a), (25c) and to the written after formula (22f), in the case when $\xi < 1$, the relation $\left| \frac{\Omega_c}{\Omega_{oc}} \right|$ may be not very small, and $\Xi_{or} |\Delta x_o|$ considerably differs from R_{cur}.

Let us try to make an analytical approximation of R_{cur} at once without using the expression for Ω_c. When the spore is in vacuum $\eta_w = 0$, Newton's 3rd law guarantees that $U = 0$. If $\lambda \to 0$, then we have $R_{cur} = 0$. When $\xi \to 0$ and $\lambda \to 1$ according to the laws of mass and momentum conservation we get $R_{cur} \to \frac{1}{2} |\Delta x_o|$ and $\Psi \to \pi$. Taking these conditions into account and also (9), (23b), we find approximations for R_{cur} and Ψ as:

$$R_{cur} \sim \frac{1}{2} \Xi_{orb} |\Delta x_o|, \tag{26a}$$

$$\Psi \sim \frac{\Xi_{or}}{\Xi_{orb}} \pi \sim \frac{\kappa \chi_{or} \xi + 2 - \lambda}{\chi_{or} \xi + 2 - \lambda} \pi, \tag{26b}$$

where we define Ξ_{orb} analogically to (23a):

$$\Xi_{orb} \equiv \frac{\lambda}{\kappa \chi_{or} \xi + 2 - \lambda} \tag{26c}$$

and $0 < \kappa \leq 1$ is a decreasing function of $|\Delta x_o|$.

Let us consider the organelle orbital movement close to the cell wall, when $\frac{|\Delta x_o|}{R_c - R_o} \sim 1$. According to the numerical data shown in [34], and taking into account (26a), (26c), and also that the value of the organelle orbital movement drag force is more higher than of the free particle near plane wall, formula (26a) can be rewritten as:

$$R_{cur} \approx \frac{1}{2} \frac{\lambda}{2 - \lambda} |\Delta x_o|. \tag{27}$$

For its axisymmetrical movement under analogical conditions according to (23b) we get:

$$\Delta x_c \approx -\frac{\lambda}{\frac{2}{3}\xi + 2 - \lambda} \Delta x_o. \tag{28}$$

Applying (26b), (27), (28) to (9) we obtain:

$$U \approx \omega \lambda \Delta x_{of} \left((2 - \lambda)^{-1} - \left(\frac{2}{3} \xi + 2 - \lambda \right)^{-1} \right). \tag{29a}$$

In the case when the average modules of the organelle velocities $u_{avm} = \omega \Delta x_o$ on both stages of the oscillation cycle equal each other, formula (29a) can be rewritten:

$$U \approx Y \cdot u_{avm}, \tag{29b}$$

$$Y \equiv \lambda \left((2 - \lambda)^{-1} - \left(\frac{1}{2} \xi + 2 - \lambda \right)^{-1} \right) \left(\frac{1}{2} \pi + 1 \right)^{-1},$$

The size relation between red algae rhodoplasts and the cells λ is relatively high and may exceed 0.5 [36]. Let us have $0.4 \leq \lambda \leq 0.7$ for our model spore. It was also established that viscosity ratio between water and the cytosol of green alga *Chara coralline* was about 0.8 [37], while for red blood cells such a ratio didn't exceed 0.2 [38]: let $0.2 \leq \xi \leq 0.8$.

Like $\Xi_o(\lambda, \xi)$, the function $Y(\lambda, \xi)$ on the mentioned interval, $0.4 \leq \lambda \leq 0.7$, $0.2 \leq \xi \leq 0.8$, strongly decreases with the decreasing of λ, but weakly decreases with the decreasing of ξ: $0.01 \leq Y \leq 0.1$. It means that the advantage in swimming speed first of all have the cells with bigger organelles under fixed cell size.

The cells with lower cytosol viscosity also have some advantage. Intracellular velocities of organelles investigated reached $10^{-5}\,\mathrm{m} \cdot \mathrm{s}^{-1}$ [12, 25]. Thus, in the case when the cytoplasm has Newtonian properties, the model may satisfy experimental data. Amplitude of such organelles oscillations $|\Delta x_o|$ plays the key role: our data for Y were calculated in the case of maximal possible amplitude $\frac{|\Delta x_o|}{R_c - R_o} \sim 1$. In the case of smaller amplitude, according to formula (26a) and taking into account the data shown in [34], [35], Y may be lower.

From this section also follows that the spores with Newtonian cytosol don't swim in a straight line.

IV. Cytosol as a viscoelastic Maxwell fluid

The simplest way of describing a viscoelastic fluid is with the Maxwell model, which can be written as:

$$\tau + l \cdot \frac{\partial}{\partial t}\tau = \eta\big(\nabla\mathbf{v} + (\nabla\mathbf{v})^T\big) = \eta \cdot \gamma', \qquad (30)$$

where l is the relaxation time, η is the constant zero viscosity [17]. Substituting equation (30) for the viscous stress tensor into the general momentum conservation equation for an incompressible fluid at low Reynolds numbers (1) we obtain:

$$\nabla p = \eta\nabla^2\mathbf{v} - l \cdot \frac{\partial}{\partial t}\tau, \quad \nabla \cdot \mathbf{v} = 0. \qquad (31)$$

According to (4), (30) and (31), the expressions for $F_{Dcm}(u_c)$, $F_{Dom}(u_c, u_{oc})$, $F_{Dhm}(u_c, u_{oc})$, $T_{Dcm}(u_c)$ for the Maxwell cytosol can be written by the expressions (18), (20b), (20c), (24a) for corresponding quantities for the Newtonian cytosol:

$$F_{Dcm}(u_c) = F_{Dc}(u_c) - l \cdot F_{Dc}(\dot{u}_c), \qquad (32a)$$

$$F_{Dom}(u_c, u_{oc}) = F_{Do}(u_c, u_{oc}) - l \cdot F_{Do}(\dot{u}_c, \dot{u}_{oc}), \qquad (32b)$$

$$F_{Dhm}(u_c, u_{oc}) = F_{Dh}(u_c, u_{oc}) - l \cdot F_{Dh}(\dot{u}_c, \dot{u}_{oc}), \qquad (32c)$$

$$T_{Dcm}(u_c) = T_{Dc}(u_c) - l \cdot T_{Dc}(\dot{u}_c), \qquad (32d)$$

$$T_{Dhm}(u_c, u_{oc}) = T_{Dh}(u_c, u_{oc}) - l \cdot T_{Dh}(\dot{u}_c, \dot{u}_{oc}), \qquad (32e)$$

where $\dot{u}_c \equiv \frac{du_c}{dt}$, $\dot{u}_{oc} \equiv \frac{du_{oc}}{dt}$ and we set $\eta_w = 0$ for the expressions of the functions $F_{Dc}(\dot{u}_c)$ and $T_{Dc}(\dot{u}_c)$.

According to (3), (4) and (31) all functions in (32a)–(32e) are linear relatively to u_c and u_{oc} on the whole interval of $\frac{|\Delta x_o|}{R_c - R_o}$ and i. Thus according to (17), (18), (32c) equation (7) transforms into:

$$u_c = -\Xi\, u_{oc} + f_u(\dot{u}_c, \dot{u}_{oc}), \qquad (33)$$

where $f_u(\dot{u}_c, \dot{u}_{oc})$ is a linear unambiguous function of $\dot{u}_c$, $\dot{u}_{oc}$ with $f_u(0,0) = 0$. Integrating (33) according to (7) we get:

$$\Delta x_{cfm} + \Delta x_{cbm} = \Delta x_{cf} + \Delta x_{cb} + f_u\big(u_c|_0^{t_f+t_b}, u_{oc}|_0^{t_f+t_b}\big), \qquad (34a)$$

$$\Delta x_{cfm} = \Delta x_{cf} + f_u\big(u_c|_0^{t_f}, u_{oc}|_0^{t_f}\big), \qquad (34b)$$

where Δx_{cfm}, Δx_{cbm} are the net motions of the cell during direct and reversal movements of the organelle in viscoelastic cytoplasm, while Δx_{cf}, Δx_{cb} are the net motions in analogical conditions, but in Newtonian cytoplasm.[1] As the organelle movement in our model is periodical, then we always have $u_c|_{t_f+t_b} = u_c|_0$ and $u_{oc}|_{t_f+t_b} = u_{oc}|_0$.[2] Thus the third term on the right hand side of (34a) equals zero. It means that in the case of the organelle axisymmetrical oscillations in viscoelastic cytoplasm the cell is immotile.

According to (25a), (25d), (32a)–(32e) and taking into account the written before formula (32e), we can write:

$$\Omega_{ocm} + \Omega_{cm} = \Omega_{oc} + \Omega_c + f_\Omega(\dot{u}_c, \dot{u}_{oc}), \qquad (35a)$$

where $f_\Omega(\dot{u}_c, \dot{u}_{oc})$, analogically to f_u, is a linear unambiguous function of $\dot{u}_c$, $\dot{u}_{oc}$ with $f_\Omega(0,0) = 0$. According to (35a) formula (24a) for the radius of curvature of the cell trajectory with the Maxwell cytosol R_{curm} can be rewritten as:

$$R_{curm} = \left|\frac{u_c}{\Omega_c + \Omega_{oc} + f_\Omega(\dot{u}_c, \dot{u}_{oc})}\right|, \qquad (35b)$$

where $\Phi > 0$ is a constant. Therefore in the case when the forward motion of the organelle is axisymmetric, while the backward motion is orbital, the trajectory of the cell will be similar with that showed on Fig. 2b with an only difference – the arcs of the cell trajectories during the organelle orbital motion will be more flattered or convex depending on the stage of the motion. Thus for the main swimming velocity U_m in the Maxwell fluid, formula (9) can be written as:

$$U_m = \frac{1}{2}\omega \cdot (\Delta x_{cfm} - R_{curm}^{end} - R_{curm}^{beg})(1 - \cos\Psi_{\mathrm{m}}), \qquad (36a)$$

where Ψ_m is the angle deviation of the spore trajectory with the Maxwell cytosol from the start position during orbital movement of the organelle, R_{curm}^{beg} and R_{curm}^{end} are the beginning and the end radiuses of curvature of the cell trajectory, correspondingly. According to (35a) and analogically with (34b) we can write:

$$\Psi_m = \Psi + f_\Omega(u_c|_{t_f} - u_c|_0, u_{oc}|_{t_f} - u_{oc}|_0). \qquad (36b)$$

It is natural to consider that at the beginning and the end of each motion stage $u_{oc} = \dot{u}_{oc} = 0$ and thus $u_c = \dot{u}_c = 0$. According to (34b), (35b) and (36b), we have $\Delta x_{cfm} \approx \Delta x_{cf}$, $R_{curm}^{end} = R_{curm}^{beg} = R_{cur}$ and $\Psi_m = \Psi$. According to (36a) the average swimming speed of the model spores with the Maxwell cytosol is close to that of the Newtonian one $U_m \sim U$ and can be evaluated according to formulas (29a) and (29b).

[1] Notation $u_c|_0^{t_f+t_b}$ means that the vector u_c is evaluated at $t_f + t_b$ and from that value is subtracted the same vector evaluated at zero.

[2] Notation $u_c|_{t_f+t_b}$ means that the vector is evaluated at $t_f + t_b$.

So as for the Newtonian cytoplasm, for the Maxwell one the model cell swimming velocities may satisfy experimental data.

V. Cytosol as a shear thinning fluid

The shear thinning fluid differs from Newtonian one in the way that its apparent viscosity decreases with increasing of the shear rate. The most of the time-independent, non-Newtonian biological fluids reported including cytoplasm of certain cells have shear thinning properties. Most of them demonstrate power law dependence with the power law index $n < 1$ [16,17,20,39]:

$$\tau = k \cdot \dot{\gamma}^n, \tag{37}$$

where $\dot{\gamma}$ is shear rate, k is the consistency index, which equals the fluid viscosity when its shear rate is $1\,\mathrm{s}^{-1}$. According to (2) and (37):

$$\eta = k \cdot \dot{\gamma}^{n-1}. \tag{38}$$

Taking into account that the particles radiuses are of the same order, for such a fluid we can assume that shear rate is independent from coordinates and in each point equals the mean shear rate:

$$\widetilde{\gamma} \equiv \frac{|u_{oc}|}{R_c - R_o}. \tag{39}$$

Then the cytosol viscosity η_c according to (38) and (39) has such a form:

$$\eta_c = k \cdot \widetilde{\gamma}^{n-1}. \tag{40}$$

According to (40) η_c is independent from coordinates. Therefore, for our model shear thinning cytosol formulas (1)–(23c) are also valid.

When $n \neq 1$, then according to (21a), (21b), (40) the velocities ratio Ξ depends on u_{oc}. If the time dependence of the forward and backward velocities of the organelle differ with one another according to (5), (8), (21a), (21b), (39) and (40) the cell has an opportunity to swim: it may be the case when $U_s \neq 0$.

Let the organelle velocities of the forward and backward movements u_{of}, u_{ob} and thus the mean shear rates $\widetilde{\gamma}_f$, $\widetilde{\gamma}_b$ be as unambiguous functions of coordinates x_o of the organelle. Let also the amplitude of the organelle oscillations satisfy the condition (22b). Then to avoid complicated integration of equation (7) and taking into account (23a)–(23c), the net displacement of the cell can be written in a simplified form:

$$\begin{aligned} \Delta x_{cfs} &= -\frac{\lambda}{\langle \xi_f \rangle + 2 - \lambda} \Delta x_{of}, \\ \Delta x_{cbs} &= -\frac{\lambda}{\langle \xi_b \rangle + 2 - \lambda} \Delta x_{ob}, \end{aligned} \tag{41}$$

where

$$\langle \xi_f \rangle \equiv \frac{\eta_w}{k \langle \widetilde{\gamma}_f \rangle^{n-1}}, \quad \langle \xi_b \rangle \equiv \frac{\eta_w}{k \langle \widetilde{\gamma}_b \rangle^{n-1}},$$

and $\langle \widetilde{\gamma}_f \rangle$, $\langle \widetilde{\gamma}_b \rangle$ are averaged mean shear rates of cytosol during the forward and backward movements of the organelle. We can assert that:

$$\begin{aligned} \langle \widetilde{\gamma}_f \rangle &= \widetilde{\gamma}(\widetilde{x}_{of_1}) = \widetilde{\gamma}(\widetilde{x}_{of_2}), \\ \langle \widetilde{\gamma}_b \rangle &= \widetilde{\gamma}(\widetilde{x}_{ob_1}) = \widetilde{\gamma}(\widetilde{x}_{ob_2}), \end{aligned} \tag{42}$$

where $\widetilde{x}_{of_1}$, $\widetilde{x}_{of_2}$, $\widetilde{x}_{ob_1}$, $\widetilde{x}_{ob_2}$ are coordinates of the organelle satisfying conditions:

$$\begin{aligned} R_2 - R_1 < \widetilde{x}_{of_1} < 0 < \widetilde{x}_{of_2} < R_1 - R_2, \\ R_2 - R_1 < \widetilde{x}_{ob_1} < 0 < \widetilde{x}_{ob_2} < R_1 - R_2. \end{aligned}$$

Let us assume that:

$$\widetilde{x}_{of_1} \approx \widetilde{x}_{ob_1}, \quad \widetilde{x}_{of_2} \approx \widetilde{x}_{ob_2}. \tag{43}$$

Let $\zeta \equiv \frac{u_{of}}{u_{ob}}$ be a constant for all possible x_o. Thus taking it into account, and also (42), (43), we can write:

$$\zeta \approx \frac{\langle \widetilde{\gamma}_f \rangle}{\langle \widetilde{\gamma}_b \rangle}. \tag{44}$$

Therefore, according to (5), (41), (44), and the approximation $U_s \approx Y_s \cdot u_{esv}$ in (29b), where u_{esv} plays the role of an experimentally stated organelle velocity in one direction (in contrary to the assuming of the equality of the forward and backward organelle velocities for formula (29b)):

$$Y_s \approx \lambda \cdot \left((\widetilde{\xi} + 2 - \lambda)^{-1} - (\widetilde{\xi} \zeta^{n-1} + 2 - \lambda)^{-1} \right), \tag{45}$$

where $\widetilde{\xi}$ is an experimentally stated value of ξ. Like for the Newtonian or Maxwell cytosol, the average swimming speed of the model spore with shear rate cytosol U_s strongly increases with the increasing of λ (it means that the advantage in the swimming have the cells with bigger organelles). As the Newtonian U or Maxwell U_m cytosol, the shear rate cytosol U_s weakly increases with the increasing of $\widetilde{\xi}$ on the interval $0.2 \leq \widetilde{\xi} \leq 0.8$, $0.4 \leq \lambda \leq 0.7$ (the advantage in the swimming have the cells with lesser viscous cytosol with lower consistency index k). It also weakly increases with the decreasing of n (for $n < 1$) and ζ.

Therefore, the advantage have the cells with lower power-law index n (higher expressed cytosol shear thinning properties) and higher expressed organelle oscillation asymmetry ζ. The relation of stall forces (which are close to maximal forces created by both motor proteins, that is ζ) of dynein and kinesin in different investigations falls between 0.14 – 0.38 [40]: $0.14 \leq \zeta \leq 0.38$.

Let our model cytosol exhibit shear-thinning properties with n within the range from 0.35, as it was shown for cytoplasm of *Entamoeba histolytica* [39], to 0.5, as was shown for human neutrophils [20]: $0.35 \leq n \leq 0.5$. In such a situation $0.023 \leq Y_s \leq 0.164$. These results also satisfy experimental data.

VI. Discussion

The three variants of considered hydrodynamic peculiarities of the cytosol – Newtonian, Maxwell, shear thinning – completely satisfy the framework of investigated swimming speeds of red algae spores from 10^{-7} to $10^{-6}\,\mathrm{m}\cdot\mathrm{s}^{-1}$ [1]. The possible swimming speed diapason of the model spores with shear thinning cytoplasm is slightly shifted up compared to Newtonian or Maxwell cytosol, as seen from the comparison of the corresponding sections. As was shown by the mentioned authors, such red algae taxa as *Erythrotrichia carnea* and *Rhodochaete parvula* move non-directionally. It completely satisfies our model spores with Newtonian or Maxwell cytosol, which trajectory is not a straight line. As it was shown, the fast spores move directionally [1]. In the framework of our model, it means that they have shear thinning cytosol and their organelles move axisymmetrically with different velocities forward and backward. In that case, the red algae species with the fast spores should have values of the relation between the organelle and cell sizes λ no less than 0.5 and the main cytoplasm viscosity close to water viscosity $\widetilde{\xi} \sim 0.8$, or a low ratio of the forward and backward velocities of the organelles $\zeta < 0.2$. While the cells, which swim slower, may have smaller organelles, they have higher main cytoplasm viscosity or higher ζ.

Contrary to the Newtonian and Maxwell cytosol, swimming velocity of the cells with shear thinning cytosol does not depend on the amplitude of the organelle oscillations. It means that in the latter case the organelles may move on small distances, while in both previous ones to reach the appropriate cell speed the organelles should move throughout the whole cell.

In order for our model cells to swim, the momentum of the organelle (generated by the molecular motors) needs to be asymmetrically transmitted to the external viscous fluid. Thus, when the spore is in vacuum, Newton's 3rd law guarantees that movement of the organelle around inside the cell can not produce propulsion, no matter what the rheological properties of the cytosol are. Formulas (29b) and (45) confirm the already mentioned above: we have $\xi = \widetilde{\xi} = 0$, $Y = Y_m = Y_s = 0$, $U = U_m = U_s = 0$.

So, we can conclude that, though do not studied yet, the organelle asymmetrical oscillations may serve as a possible means for red algae cell swimming. This model may inspire new researches in this field.

VII. Conclusions

1) Red algae spores may swim thanks to oscillations of their organelles.
2) The spores with Newtonian or Maxwell cytosol may swim only if the forward and backward organelle movements have different trajectories. The spores with shear thinning cytosol may swim also in the case when the organelles oscillate axisymmetrically, but with different velocities forward and backward. Such spores may swim in a straight line.
3) The swimming of the model spores completely satisfy experimental data.

Acknowledgements

I would like to express my gratitude to an anonymous reviewer for the persistent stimulation to advance my article, and to the journal manager Nikolay Ikonomov for great patience in editing and friendly atmosphere.

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