

# A Theory for Ciliary Gliding in Freshwater Planarians

Takeshi Sugimoto\*

Kanagawa University, Japan

*Abstract*—Planarians’ locomotion is called ciliary gliding: they secrete mucus on substrata, and glide there by beating ventral cilia in an antiplectically metachronous manner. A mathematical model for this locomotion consists of the continuity of mass and the Brinkman’s equation for the continuity of momentum in the periciliary layer. The reaction of the mucus layer is treated by the Maxwell constituent equation. The boundary layer developed on the back is analysed. The equation of motion, built up by these models, reveals that planarians attain the stable steady-state gliding at 4.7 mm/s by utilising 28 % of the full power of cilia.

*Index Terms*-- creepy flow, muco-ciliary interaction, adhesive locomotion

## I. INTRODUCTION

Freshwater planarians are small free-living creatures but too large invertebrates to swim by beating the 10  $\mu\text{m}$  long cilia. They are known by their high reproductivity: one three-hundredth piece of a full body becomes a perfect body [1]. Their class name is *Turbellaria*. This derives from the Latin *Turbella* meaning ‘bustle’ or *Turba* meaning ‘disturbance.’ Among biologists planarians are believed to swim by stirring nearby water and making vortices. Hence they are sometimes called vortex worm. But our observation of planarians in the laboratory reveals the following facts: they can not swim, because they are heavier than water; there are no vortices at all.

Their locomotion is so called ciliary gliding: they secrete mucus upon substrata, and they beat 10  $\mu\text{m}$  ventral cilia in an antiplectically metachronous manner [2]. In natural environments they span mucus networks, which they glide along [3].

There is no preceding theoretical study in ciliary gliding at all. Therefore the present study is the very first step to a theory for ciliary gliding. In Section II we set up the basic assumptions; in Section III we model and analyse the flow fields of different regimes, interaction between flow and cilia, and mucus dynamics; then in Section IV we integrate these results into the equation of motion for a whole body to account for ciliary gliding. Lastly we summarise our findings.

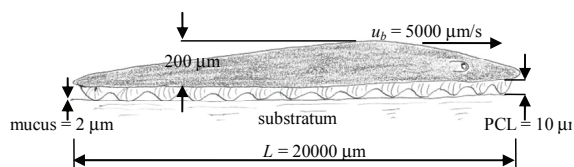


Fig. 1 Dimensions of a planarian G.I.

\* Corresponding author: 3-27-1 Rokkakubashi, Kanagawa Ward, Yokohama 221-8686, Japan, E-mail: take@is.kanagawa-u.ac.jp.

## II. ASSUMPTIONS

### A. Flow fields and planarians

Figure 1 is a rough sketch of our planarians called G.I. and adopted from Prof. Kenji Watanabe, Himeji Institute of Technology. Our observation as well as [2] show that the 20 mm long planarians can glide over substrata at 5 mm/s. They are 2.0 mm wide and 200  $\mu\text{m}$  thick (our measurements and [1]). They are very thin, so they are also called flatworms: they do not have any specific breathing systems, and hence they rely on passive diffusion; therefore they have only three tissue layers and make themselves flat to breathe [1]. Their body structure is called hydrostatic skeleton. Approximating a planarian’s body by a cuboid of water, we estimate its weight to be 8.0 mg.

Next we shall see the features of ciliary gliding through non-dimensional parameters. We use 1000  $\text{kg/m}^3$  as the value for the water density  $\rho$ ; the viscosity of water  $\mu$  is 0.001 Pa·s. The frequency of ciliary beat is at most 30 Hz in case of free motion [4]. But the ATP-cycle experiments show the maximum beat can be of the order of 100 Hz [5]. We assume 90 Hz to account for  $u_b = 5$  mm/s; assuming a cilium sweeps  $\pi/3$  rad in the effective stroke during one fifth of a beating period [4], we obtain the angular velocity  $\Omega$  to be  $150\pi$  rad/s. Let  $u_b$ ,  $L$  and  $h$  be the gliding speed, the body length and the cilium height, respectively. Transience is negligible, because  $\rho\Omega h^2/\mu = 4.7 \times 10^{-2}$ . Reynolds number  $\rho u_b L/\mu$  is as large as 100, whilst  $\rho u_b h/\mu$  is as small as 0.05 in the periciliary layer (in short PCL). Therefore we consider the boundary layer upon the dorsal surface, and we introduce Stokes flow to PCL.

### B. Ciliary Thrust

In this study we consider an entire motion. To do so we need to understand the power output of a cilium, that is the source of thrust. Figure 2 (a) shows the cross-section of a cilium. Nine doublet tubules surround two singlet tubules at the centre. Each doublet has an outer arm with three dyneins and an inner arm with two dyneins reaching a clockwise next doublet. A dynein is a motor protein, which is the source of a ciliary motion. Dyneins cause shearing motion between neighbouring doublets. Here is a scenario brought by [6]. The meaning of +, - and  $\pm$  in Fig. 2 (a) is as follows: the number one doublet pushes down the number two; and then the number two doublet pushes down the number three, and so forth; the number five

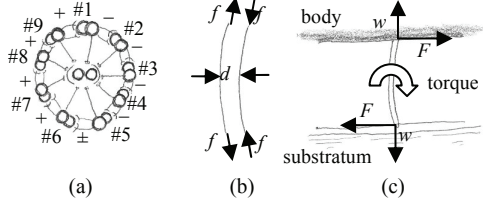


Fig.2 Force exerted by a cilium: (a) Cross-section of a cilium; (b) Bending of a cilium; (c) Thrust due to a cilium.

doublet is permanently linked with the number six; the number six doublet pulls up the number seven; and then the number seven doublet pulls up the number eight, and so forth. This combination produces tension  $f$  in the upper half and compression  $f$  in the lower half, and hence a cilium bends as shown in Fig. 2 (b). Let  $d$  be a diameter of a cilium, and  $fd$  corresponds to bending moment acting on a cilium. As a free end of a cilium reaches the mucus layer, this bending moment, or torque, acts as a source of forces  $F$  and  $w$  as shown in Fig. 2 (c). Since the thickness of PCL is  $h$ ,  $fd \approx Fh$ . Thrust component  $F$  is constrained by the viscoelasticity of the mucus.

A cilium stalled by something solid is known to exert two-digit higher power than a cilium beating a liquid [7]-[9]. Using 5 pN as the optimistic evaluate of dynein output, 198 as the number of dyneins per  $\mu\text{m}$  and  $0.26 \mu\text{m}$  as a diameter of a cilium [2], [6], [9], we obtain 4.4 nN as the value of  $f$ . In this estimate we neglect the contribution of dyneins in the number five doublet, for this is inactive.

### C. Mucus Layer

Mucus behaves as Bingham plastics, which obey Maxwell's constituent law [10].

## III. FLOW FIELDS IN LIQUID LAYERS

### A. Dorsal Boundary Layer

We make use of two-dimensional Rayleigh flow to approximate the boundary layer developed upon the dorsal surface of a planarian, because it is an effectively flat moving plate.

We define the coordinate system fixed to the moving planarian as shown in Fig. 3:  $s$ -axis runs from head to tail, whilst  $z$ -axis points upwards. We interpret  $s/u_b$  as  $t$ , time, and then the basic equation is rewritten in the following form:

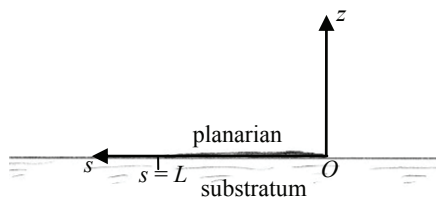


Fig. 3 Coordinate system fixed on a moving planarian

$$u_b \frac{\partial u}{\partial s} = \nu \frac{\partial^2 u}{\partial z^2},$$

subject to the boundary conditions,  $u = u_b$  at  $z = 0$  and  $u \rightarrow 0$  as  $z \rightarrow \infty$ ;  $\nu$  designates the dynamic viscosity,  $\mu/\rho$ . The well-known solution is given by

$$u(z, s) = \frac{2u_b}{\sqrt{\pi}} \int_{\eta}^{\infty} \exp(-\eta^2) d\eta,$$

where

$$\eta = \frac{z}{2} \sqrt{\frac{u_b}{\nu s}}.$$

Using this, we finally obtain the friction acting on the dorsal surface of a planarian with the width  $W$ .

$$\begin{aligned} \mu \int_0^L \left| \frac{\partial u}{\partial z} \right|_{z=0} ds W &= W \sqrt{\frac{\rho \mu}{\pi}} u_b^{3/2} \int_0^L \frac{ds}{\sqrt{s}} \\ &= 2W \sqrt{\frac{\rho \mu L}{\pi}} u_b^{3/2}. \end{aligned}$$

### B. Ventral Periciliary Layer

The fluid in PCL is water, which is incompressible. Hence we impose the continuity of mass:

$$\text{div } \mathbf{u} = 0.$$

Next we make use of the active porous medium limit [11] as a basis of our mathematical model for ciliary motion in PCL. To describe the active porous medium we use two-dimensional Brinkman equation [10], [12]. For the description of ciliary-wave propagation we derive a variable  $\xi = x + ct$ , where  $c$  is an antiplectic wave speed. Using  $\xi$  and  $y$  shown in Fig. 4 for one wave length  $\lambda$ , typically  $30 \mu\text{m}$ , we write down the Brinkman equation as follows.

$$\mu \nabla^2 \mathbf{u} = \nabla p + \begin{pmatrix} \mu/k_{\xi} & 0 \\ 0 & \mu/k_y \end{pmatrix} (\mathbf{u} - \mathbf{u}_c),$$

where  $\mathbf{u}$ ,  $p$ ,  $k_{\xi}$ ,  $k_y$  and  $\mathbf{u}_c$  denote the velocity vector, the pressure, the permeability in the  $\xi$  direction, the permeability in the  $y$  direction and the velocity of cilia, respectively;  $k_{\xi}$  and  $k_y$  are the permeability of circular-cylinder alley moving transversely to the centre lines and that moving axially, respectively given by [13] as follows:

$$k_{\xi} = \frac{b^2}{4} \left\{ \ln \frac{b}{a} - \frac{b^4 - a^4}{2(b^4 + a^4)} \right\},$$

and

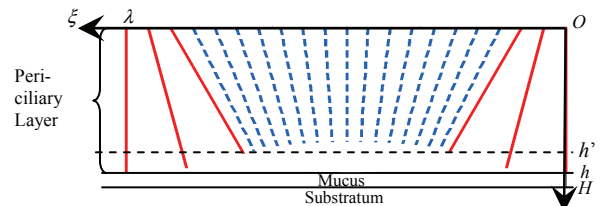


Fig. 4 Coordinate system fixed on a moving planarian: solid lines stand for cilia in effective stroke; dashed cilia are in recovery stroke.

$$k_y = \frac{1}{8b^2} \left( 4a^2b^2 - a^4 - 3b^4 + 4b^4 \ln \frac{b}{a} \right),$$

where  $a$  and  $b$  denote a radius of a cilium and a distance between the centre of the cilium and the surface of the neighbouring cilium, respectively. Using typical values  $0.26 \mu\text{m}$  and  $10 \text{ cilia}/\mu\text{m}^2$  for cilium diameter [2] and cilium density [4], respectively, we obtain the results:  $k_\xi = 2.9 \times 10^{-4} \mu\text{m}^2$  and  $k_y = 4.3 \times 10^{-4} \mu\text{m}^2$ .

We prescribe  $\mathbf{u}_c$  and solve the equations to determine  $\mathbf{u}$  and  $p$ . We split the basic equations into the time-averaged and periodic components. To identify two components we apply subscripts 0 to the time average and 1 to the periodic solution, *i.e.*,  $u_0$  and  $p_0$  for the time-averaged solution and  $\mathbf{u}_1 = (u_1, v_1)$  and  $p_1$  for the periodic solution.

#### Time-Averaged Component

Almost all the theories for muco-ciliary interaction predict such time-averaged flow field that stream is confined only in the very vicinity of the mucus layer. That looks like the step function. The present formalism reduces to the time-averaged form as follows.

$$\mu \frac{d^2 u_0}{dy^2} = \frac{\mu}{k_x} u_0$$

This yields the solution similar to the previous works, *i.e.*, the step function: in such a flow the periciliary water moves with the planarian's body; hence the shearing stress arises at the interface between PCL and mucus; the stress depends on the first derivative of the velocity profile; the first derivative of the step function is Dirac's delta function; hence the stress becomes enormous; the numerical estimates lead us to the conclusion that planarians cannot glide. This is not a plausible scenario.

In this study we split the flow field into the cilium-filled layer and the free flow layer. The locus of the cilium tip approximately assumes a wave shown schematically in Fig. 4; assuming the  $\pi/3$  [rad] sweep angle in the effective stroke, we obtain  $h'$ , the mean line to the locus of the cilium tip, as  $\sqrt{3}h/2$ .

The layer,  $0 \leq y \leq h'$ , is filled with dense cilia as  $10 \text{ cilia}/\text{mm}^2$ ; calculating the drag acting on all the cilia becomes  $35 \text{ N}$ , therefore we treat the cilium-filled layer as dead weight to planarians, *i.e.*, the water moves with the planarian within this layer.

The thin layer,  $h' \leq y \leq h$ , is approximately an open space. There is no  $v$ -component in  $\mathbf{u}_0$ , and hence  $p_0$  is known to be constant. Therefore we model the time-averaged form of the momentum equation as follows.

$$\mu \frac{d^2 u_0}{dy^2} = 0$$

subject to  $u_0 = 0$  at  $y = h'$  and  $u_0 = u_b$  at  $y = h$ . This is nothing but Couette flow, but it is free from the apparent setback of the simple-minded time-average; adding that, the stress in Couette flow is apparently

larger than that in the observed flow [10]; this means our estimate becomes pessimistic. The time-averaged velocity is given by

$$u_0(y) = u_b \frac{y - \sqrt{3}h/2}{h(1 - \sqrt{3}/2)}.$$

The total friction due to this flow pattern is given by

$$\mu \left. \frac{du}{dy} \right|_{y=0} LW = \frac{\mu LW}{h(1 - \sqrt{3}/2)} u_b.$$

#### Periodic Component

Introduction of the stream function  $\psi_1$  leads to automatic satisfaction of the continuity of mass. We then rewrite the Brinkman equation as follows.

$$\frac{\partial \omega_1}{\partial \xi} = \frac{1}{\mu} \frac{\partial p_1}{\partial y} - \frac{1}{k_y} \left( \frac{\partial \psi_1}{\partial \xi} + v_c \right),$$

$$\frac{\partial \omega_1}{\partial y} = -\frac{1}{\mu} \frac{\partial p_1}{\partial \xi} - \frac{1}{k_\xi} \left( \frac{\partial \psi_1}{\partial y} - u_c \right),$$

where  $\omega_1$  is the vorticity that satisfies the following relation.

$$\omega_1 = -\nabla^2 \psi_1.$$

We model the velocity profile of cilia by

$$\mathbf{u}_c = \Omega y (m_c(\xi), n_c(\xi)),$$

where  $m_c$  and  $n_c$  are mode functions defined as follows.

$$m_c(\xi) = \begin{cases} +1 & \xi \in [0, \lambda/10], \\ -1/4 & \xi \in [\lambda/10, 9\lambda/10], \\ +1 & \xi \in [9\lambda/10, \lambda], \end{cases}$$

and

$$n_c(\xi) = \begin{cases} -\sin(5\pi\xi/\lambda) & \xi \in [0, \lambda/10], \\ 0 & \xi \in [\lambda/10, 9\lambda/10], \\ +\sin(5\pi\xi/\lambda) & \xi \in [9\lambda/10, \lambda]. \end{cases}$$

The time averages of these mode functions are both naught. Time segments  $[0, \lambda/10]$  and  $[9\lambda/10, \lambda]$  correspond to the effective stroke, whilst a time segment  $[\lambda/10, 9\lambda/10]$  corresponds to the recovery stroke. The ratio of these time segments is 1:4. The tip of a cilium hits the mucus layer at  $\xi = 0$  and  $\lambda$ . The resulting velocity field is shown in Fig. 5.

To solve the Brinkman equation we make use of the double Fourier series. First we introduce the transformation of coordinates defined by

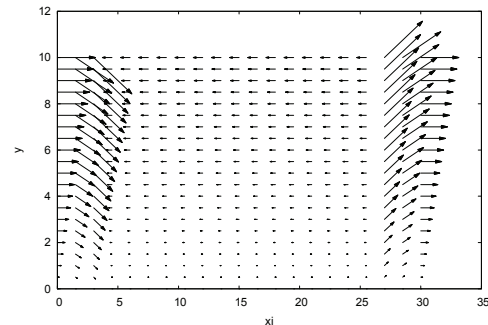


Fig. 5 Velocity field due to motion of cilia: the absolute value of the largest arrows is  $5268 \mu\text{m/s}$ .

$$\theta = 2\pi \frac{\xi}{\lambda},$$

$$\phi = \pi \frac{y}{h}.$$

We expand  $y$ -direction from 0 to  $2h$  as a period and extend  $\mathbf{u}_c$  by using the mirror image  $2h - y$  from  $y = h$  to  $y = 2h$ .

The velocity field due to motion of cilia is expanded as follows.

$$u_c = \Omega h \sum_{n=1}^{\infty} \frac{5}{2n\pi} \sin \frac{n\pi}{5} \cos n\theta$$

$$\times \left\{ \frac{1}{2} - \frac{4}{\pi^2} \sum_{k=1}^{\infty} \frac{1}{(2k-1)^2} \cos(2k-1)\phi \right\},$$

and

$$v_c = \Omega h \sum_{n=1}^{\infty} \frac{n}{(n^2 - 25/4)\pi} \cos \frac{n\pi}{5} \sin n\theta$$

$$\times \left\{ \frac{1}{2} - \frac{4}{\pi^2} \sum_{k=1}^{\infty} \frac{1}{(2k-1)^2} \cos(2k-1)\phi \right\}.$$

The velocity field above serves as the boundary condition for the Brinkman equation.

Noting the parity of  $u_c$  and  $v_c$ , we expand  $\psi_1$  and  $p_1$  in the following manners:

$$\psi_1 = \sum_{n=1}^{\infty} \left\{ A_{n0} + \sum_{m=1}^{\infty} (A_{nm} \cos m\phi + B_{nm} \sin m\phi) \right\} \cos n\theta,$$

and

$$p_1 = \sum_{n=1}^{\infty} \left\{ C_{n0} + \sum_{m=1}^{\infty} (C_{nm} \cos m\phi + D_{nm} \sin m\phi) \right\} \sin n\theta,$$

where  $A_{nm}$ ,  $B_{nm}$ ,  $C_{nm}$  and  $D_{nm}$  are the Fourier coefficients to be determined.

Substituting all the expansions for the Brinkman equation, we obtain six sets of equations with respect to unknown coefficients.

First we derive the equations with respect to the  $\xi$ -derivative part of the Brinkman equation. Regarding the  $m=0$  and  $\sin n\theta$  terms, we obtain

$$\left\{ -\frac{2n\pi}{\lambda k_y} - \frac{8n^3\pi^3}{\lambda^3} \right\} A_{n0} = -\frac{\Omega h}{2k_y} \frac{n \cos \frac{n\pi}{5}}{(n^2 - 25/4)\pi}.$$

Regarding the  $\sin n\theta \cos m\phi$  terms, we obtain

$$\left\{ -\frac{8n^3\pi^3}{\lambda^3} - \frac{2nm^2\pi^3}{\lambda h^2} - \frac{2n\pi}{\lambda k_y} \right\} A_{nm} - \frac{m\pi}{\mu h} D_{nm}$$

$$= \begin{cases} 0 & \text{for even } m, \\ \frac{4n\Omega h \cos \frac{n\pi}{5}}{m^2(n^2 - 25/4)\pi^3 k_y} & \text{for odd } m. \end{cases}$$

Regarding the  $\sin n\theta \sin m\phi$  terms, we obtain

$$\left\{ -\frac{8n^3\pi^3}{\lambda^3} - \frac{2nm^2\pi^3}{\lambda h^2} - \frac{2n\pi}{\lambda k_y} \right\} B_{nm} + \frac{m\pi}{\mu h} C_{nm} = 0.$$

Next we derive the equations with respect to the  $y$ -derivative part of the Brinkman equation. Regarding the  $m=0$  and  $\cos n\theta$  terms, we obtain

$$-\frac{2n\pi}{\mu\lambda} C_{n0} + \frac{5\Omega h \sin \frac{n\pi}{5}}{4n\pi k_\xi} = 0.$$

Regarding the  $\cos n\theta \cos m\phi$  terms, we obtain

$$-\left\{ \frac{4n^2 m\pi^3}{\lambda^2 h} + \frac{m^3\pi^3}{h^3} + \frac{m\pi}{hk_\xi} \right\} A_{nm} + \frac{2n\pi}{\mu\lambda} D_{nm} = 0.$$

Regarding the  $\cos n\theta \sin m\phi$  terms, we obtain

$$\left\{ \frac{4n^2 m\pi^3}{\lambda^2 h} + \frac{m^3\pi^3}{h^3} + \frac{m\pi}{hk_\xi} \right\} B_{nm} + \frac{2n\pi}{\mu\lambda} C_{nm}$$

$$= \begin{cases} 0 & \text{for even } m, \\ -\frac{10\Omega h \sin \frac{n\pi}{5}}{nm^2\pi^3 k_\xi} & \text{for odd } m. \end{cases}$$

Two equations among the six above are two independent equations with respect to the single coefficients,  $A_{n0}$  and  $C_{n0}$ ; another four are divided into two sets of the simultaneous equations with respect to the two coefficients,  $\{A_{nm}, D_{nm}\}$  and  $\{B_{nm}, C_{nm}\}$ . Solving these analytically, we obtain the following solution set:

$$A_{n0} = \frac{\Omega h \lambda^3 \cos \frac{n\pi}{5}}{4\pi^2(n^2 - 25/4)(\lambda^2 + 4n^2\pi^2 k_y)},$$

$$A_{nm} = \frac{-8n^2\Omega h \cos \frac{n\pi}{5}}{\pi^2(n^2 - 25/4)m^2\lambda k_y}$$

$$\times \left\{ \frac{4n^2\pi^2}{\lambda^2 k_y} + \frac{m^2\pi^2}{h^2 k_\xi} + \left( \frac{4n^2\pi^2}{\lambda^2} + \frac{m^2\pi^2}{h^2} \right)^2 \right\}^{-1},$$

$$B_{nm} = \frac{-10n^2\Omega h \sin \frac{n\pi}{5}}{\pi^2 n m k_\xi}$$

$$\times \left\{ \frac{4n^2\pi^2}{\lambda^2 k_y} + \frac{m^2\pi^2}{h^2 k_\xi} + \left( \frac{4n^2\pi^2}{\lambda^2} + \frac{m^2\pi^2}{h^2} \right)^2 \right\}^{-1},$$

$$C_{n0} = \frac{5\Omega h \mu \lambda \sin \frac{n\pi}{5}}{8n^2\pi^2 k_\xi},$$

$$C_{nm} = \frac{2n\mu h}{m\lambda} \left( \frac{4n^2\pi^2}{\lambda^2} + \frac{m^2\pi^2}{h^2} + \frac{1}{k_y} \right) B_{nm},$$

and

$$D_{nm} = \frac{m\mu\lambda}{2nh} \left( \frac{4n^2\pi^2}{\lambda^2} + \frac{m^2\pi^2}{h^2} + \frac{1}{k_\xi} \right) A_{nm}.$$

If  $m$  is none-zero and even, all the coefficients are naught. The coefficients have physical dimensions: the

dimension of  $A_{nm}$  and  $B_{nm}$  is  $\mu\text{m}^2/\text{s}$ , whilst the dimension of  $C_{nm}$  and  $D_{nm}$  is Pa.

The Brinkman equation is an empirical model [12] and hence it does not satisfy the no-slip condition. But the result is not at all far from usual fluid phenomena. Since motion of cilia is periodic, the result satisfies the periodic boundary conditions at  $\xi = 0$  and  $\lambda$ .

Let us see and annotate the solution set by using the numerical representation. We use  $100 \times 101$  coefficients: from  $n = 1$  to 100 and from  $m = 0$  to 199. To avoid the loss of information we take summation starting from the least down to the largest terms.

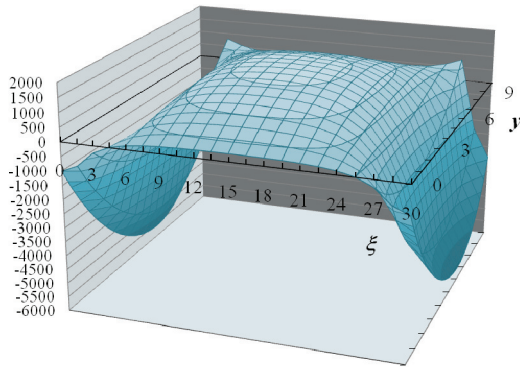


Fig. 6 Stream function for the periodic solution in PCL:  $\xi$ -axis runs from left to right in  $\mu\text{m}$ ;  $y$ -axis runs inward in  $\mu\text{m}$ ;  $\psi_1$  is graduated vertically by the  $\mu\text{m}^2/\text{s}$ .

Figure 6 shows the distribution of the stream function  $\psi_1$ . Negative  $\psi_1$  region corresponds to the effective stroke, whilst positive region corresponds to the recovery stroke. Note that there are circulatory flows in both regions. Circulations do not necessarily mean the existence of vortices. The circulatory flow in the effective-stroke region is almost three times stronger than that in the recovery-stroke region.

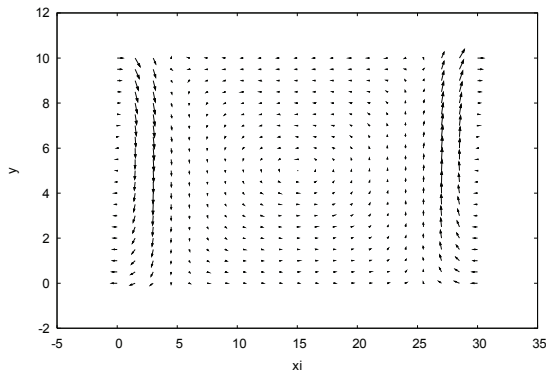


Fig. 7 Flow field in PCL stirred by cilia: the absolute value of the largest arrows on top of the second left and second right columns is  $1968 \mu\text{m}/\text{s}$ .

Figure 7 shows the vector presentation of flow field generated by motion of cilia. The strong circulatory flow is visualised. Note that there is flow reversal in the vicinity of the body. Near the body motion of cilia is

very small, but stirred water moves away from cilia in this region. The flow in the recovery-stroke region is very creepy.

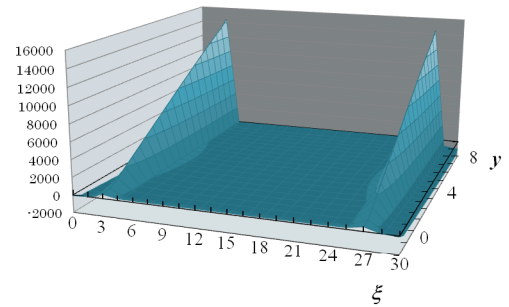


Fig. 8 Vorticity distribution in PCL:  $\xi$ -axis runs from left to right in  $\mu\text{m}$ ;  $y$ -axis runs inward in  $\mu\text{m}$ ;  $\omega_1$  is graduated vertically by the  $\text{s}^{-1}$ .

Figure 8 shows the vorticity distribution in PCL. As already mentioned, this figure shows that circulatory flows are not vortices. Strong vorticity exists in the quite limited portions of the flow field that correspond the start and end of the effective stroke. Otherwise there are almost no vorticity, because the very high frequency vorticity decays very quickly. Therefore the name “vortex worm” stems on an implausible legend.

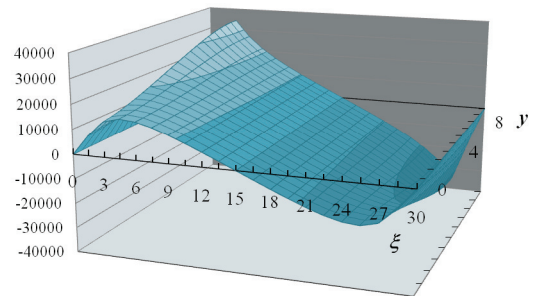


Fig. 9 Perturbed pressure distribution in PCL:  $\xi$ -axis runs from left to right in  $\mu\text{m}$ ;  $y$ -axis runs inward in  $\mu\text{m}$ ;  $p_1$  is graduated vertically by the Pa.

Figure 9 shows perturbed pressure distribution in PCL. Although there is negative pressure, in the water  $p_0$  is more than atmospheric pressure, typically  $1.013 \times 10^5$  Pa. Therefore the magnitude of periodic perturbation in pressure is one digit smaller than the time average. The approaching cilia push the water toward the mucus layer, and hence the pressure goes up; and *vice versa* in the recovery stroke. This is the nature described by the Brinkman equation that is in between Darcy’s law and Stokes flow.

### C. Mucus Layer

Suppose the frequency of cilium beat is 90 Hz, then the speed of the cilium tip attains 4.71 mm/s. This is

comparable to the observation, *i.e.*,  $t u_b = 5$  mm/s. As the cilium tip reaches mucus layer, the cilium is stalled by mucus. A stalled cilium is known to exert two digits larger force than a cilium in free motion, as already mentioned in the introduction. We concern if the thrust is large enough to propel the body forward at  $u_b = 5$  mm/s.

Let us consider the reaction of mucus layer when the cilium tip reaches there. We make use of the Maxwell constituent equation for the Bingham plastics for mucus dynamics. It is given by

$$\mu_m \frac{d\varepsilon}{dt} = \kappa_m \frac{d\tau}{dt} + \tau,$$

where  $\mu_m$ ,  $\varepsilon$ ,  $\kappa_m$  and  $\tau$  denote the viscosity of mucus, the strain, the settling time and the shearing stress, respectively. The strain velocity for fluids is given by

$$\frac{d\varepsilon}{dt} = \frac{\partial u}{\partial y} + \frac{\partial v}{\partial x}.$$

Since there is no mass transfer in  $y$ -direction,  $v_1 = 0$  in the mucus layer. Therefore the second term on the right-hand side of the identity is naught. Since  $u_b = u_c$  at the time of cilium-impact, the first term on the right-hand side of the identity above is equal to  $\Omega$ . Approximating this sudden generation of strain by a step function, we obtain the solution as follows.

$$\tau(t) = \mu_m \Omega \{1 - \exp(-t / \kappa_m)\} + \tau(0) \exp(-t / \kappa_m),$$

where  $\tau(0)$  is the initial stress. Suppose  $\tau(0)$  is a residue of the stress generated by one former impact at  $t = -p$ . Then  $\tau(0)$  is found to be equal to  $\mu_m \Omega$ , and hence  $\tau(t) = \mu_m \Omega$ . This also regulates the order of thrust exerted by a cilium. We shall use  $\mu_m \Omega$  itself as the measure of thrust. The total thrust is calculated by considering the cross-section of cilium and the number of cilia touching the mucus layer.

#### IV. OVERALL LOCOMOTION

Building up everything into one, we obtain the equation of overall motion as follows.

$$m \frac{du}{dt} = \frac{\mu_m \Omega \pi a^2 WL}{b\lambda} - 2W \sqrt{\frac{\rho \mu L}{\pi}} u^{3/2} - \frac{\mu WL}{h(1 - \sqrt{3}/2)} u,$$

where the first term is the thrust that mucus layer can sustain; we model that  $\Omega$  depends on  $u$  linearly:

$$\Omega(u) = \Omega(0) + \{\Omega(u_b) - \Omega(0)\} u / u_b,$$

where  $\Omega(0)$  and  $\Omega(u_b)$  are assumed to be 30 Hz, the maximum free beat, and 90 Hz, respectively.

Figure 10 shows the phase portrait in case the steady state is located at  $u_b = 4.7$  mm/s. The second term on the right-hand side of the equation hardly contributes at the ratio 1:12.5 to the third term. To attain the required steady-state the value of  $\mu_m$  is found to be 1.3 Pa·s, which is well within the known range of measured values 0.1-10 Pa·s [14]. The corresponding force exerted by a cilium is 32.5 pN, which is 28 % of the optimistic maximum estimate [9]. Therefore ciliary gliding is efficient locomotion for planarians.

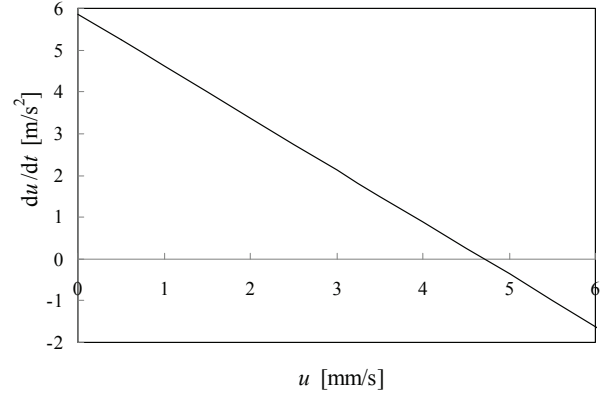


Fig. 10 Phase portrait of ciliary gliding

This steady state is stable: the slower-speed region is in the acceleration phase, whilst the faster-speed region is in the deceleration phase.

#### V. CONCLUSION

There is no preceding theoretical study in ciliary gliding at all. Therefore the present study is the very novel proposal of the theoretical framework to understand ciliary gliding in freshwater planarians. We summarise our findings:

- (1) A dorsal boundary layer is described as Rayleigh flow by replacing  $t$  with  $s/u_b$ .
- (2) A ventral periciliary layer is modelled by Stokes flow for the time-averaged component and the Brinkman equation for the periodic component.
- (3) As the time-averaged flow we make use of dead weight model for the inner layer and Couette flow for the outer layer.
- (4) We show the way how to analytically solve the Brinkman equation by use of double Fourier expansions subject to the prescribed motion of cilia.
- (5) The reaction of mucus is modelled by the Maxwell constituent equation that is solved analytically subject to the prescribed motion of cilia.
- (6) Based on the flow analyses above we propose the equation of overall motion of a planarian that predicts the energetics of ciliary gliding and the stability of the steady-state locomotion.

We hope experiments will be conducted to measure the relevant parameter values of ciliary gliding in the freshwater planarians.

Yet another challenge is to investigate the ciliary gliding on the free surface. Planarians and their mucus are wet and heavier than water. Why can they cling to the water surface and move around?

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