Jana S, Um SH, Jung S.

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Paramecium swimming in capillary tube

Saikat Jana,[1] Soong Ho Um,[2] and Sunghwan Jung[1]

[1]*Department of Engineering Science and Mechanics, Virginia Tech, Virginia 24061, USA*
[2]*Department of Chemical Engineering, Sungkyunkwan University, Suwon, Gyeonggi-do 440-746, Korea*

Swimming organisms in their natural habitat need to navigate through a wide range of geometries and chemical environments. Interaction with boundaries in such situations is ubiquitous and can significantly modify the swimming characteristics of the organism when compared to ideal laboratory conditions. We study the different patterns of ciliary locomotion in glass capillaries of varying diameter and characterize the effect of the solid boundaries on the velocities of the organism. Experimental observations show that *Paramecium* executes helical trajectories that slowly transition to straight lines as the diameter of the capillary tubes decreases. We predict the swimming velocity in capillaries by modeling the system as a confined cylinder propagating longitudinal metachronal waves that create a finite pressure gradient. Comparing with experiments, we find that such pressure gradient considerations are necessary for modeling finite sized ciliary organisms in restrictive geometries. © *2012 American Institute of Physics*. [http://dx.doi.org/10.1063/1.4704792]

I. INTRODUCTION

Microorganisms use a variety of propulsion mechanisms[1] to swim around in their habitat for predator evasion[2] or to gather food by swimming towards favorable gradients.[3] The locomotory behavior and performance is usually controlled by chemical[4] or hydrodynamic[5] cues arising due to changes in the local environment. Although boundaries are usually neglected, introducing them in the fluidic system have revealed surprising effects in different organisms; for example sperm swimming near surfaces execute circular/curvilinear trajectories[6] and bacteria tend to aggregate near solid surfaces.[7] Boundary effects on bacterial swimming speed/direction, tumbling probability and turn angle in capillaries have been characterized,[8,9] while similar studies in ciliary organisms are rare. Motility of cells and the morphological changes in body shape due to restrictive geometries are active areas of investigation.[10,11] These examples show that organism surface interactions can be critical and cause the organism to exhibit varied swimming characteristics/gaits as compared to swimming in ideal unbounded fluid conditions.

In ciliates propulsion is achieved by coordinated motion of cilia which helps in propagating metachronal waves.[12] Millions of ciliary hairs in mammals help in mucus transport[13] and also function as sensory organelles that help in maintaining balance; signifying the importance of cilia in various systems. The control of ciliary beat in *Paramecium* is an interesting phenomena and has been studied extensively from point of view of Ca^{2+} ion efflux/influx through the ion channels,[14] while the role of hydrodynamic synchronization in beating arrays of cilia is being currently explored.[16] Experiments have been conducted to gain insights into the chemical-physiological[15] effects that cause changes in the ciliary beat[17] and trajectories as well as taxis of ciliates in solutions of varied ionic concentrations have been categorized.[18] The effect of high viscosities on the locomotory traits of *Paramecium* especially with regards to changes in wave velocities, amplitude and wavelength of the metachronal waves have been extensively documented.[19] Experiments on swimming of ciliates in vertically aligned tapered glass tubes[20] have contributed to understanding of drag acting on the bodies.

Theoretically a 2D wavy sheet can be used to describe simplified swimming motion in many micro-swimmers; which provided one of the first theoretical framework for modeling microorganisms, by considering small amplitude expansions of the propagating wave.[21] Further studies extended the 2D sheet model to include effect of planar boundaries and revealed propulsive advantages for specific beat patterns at certain distances from the boundaries.[22] As thousands of cilia in *Paramecium* beat just out of phase to propagate waves in fluid; they have been modeled as infinitely long cylinders[23] or spheres[24] with surface undulations or as a spheroid with slip velocity.[25] These models were also used to validate swimming velocities in variety of ciliates[26] and to develop a boundary layer theory for predicting the near and far field velocities of ciliary micro-organisms in the unbounded fluid.[27]

In most cases, experiments have involved measuring the average velocity; however, various trajectories executed by *Paramecium* have not been studied. While theoretical studies involving swimming *Paramecium* have mostly focused on infinite models without consideration of the boundary effects. We present a unifying experimental and theoretical approach to reveal the locomotive patterns of *Paramecium multimicronucleatum* and rationalize the pressure gradient effects, on the swimming velocities in confined spaces. In Sec. II, we explain the experimental methods of introducing the organisms in confined geometries like the capillary tubes and the techniques used to visualize their motion. A theoretical model incorporating pressure gradient is developed to understand the effect of boundaries in Sec. III. In Sec. IV, we compare the predicted swimming velocity with the experiments, and in Sec. V we discuss other important parameters that might affect locomotion of cilates close to the boundaries.

II. EXPERIMENTS

A. Experimental methods

Paramecium multimicronucleatum is a single-celled eukaryote commonly found in warmer regions of the freshwater ponds.[12] Cultures were reared in a double wheat medium and subcultures were placed every 11 days when they reach their peak population. *Paramecium* at the beginning of the their exponential growth curve were used for the experiments. The cultures were centrifuged and washed twice in a Buffer solution consisting 9 mM $CaCl_2$, 3 mM KCl, 5 mM Tris-HCl (pH 7.2) to remove the debris and were allowed to equilibrate for 30 min. The equilibrated cells were then observed under the Leica DMI 3000 microscope at $5\times$, $20\times$, and $40\times$ magnifications with bright field or DIC optics and their motion was recorded using IDT MotionXtra N3 camera.

The ciliary coordination in ciliates is often controlled by a complex collection of external cues that causes the organism to change the frequency or other parameters of wave propagation. However, the difference in directions of the propagating metachronal wave and swimming direction causes the organism to move in helical path. Broadly the locomotory gait can be classified as forward(anterior) or backward(posterior) swimming; with the forward swimming exhibiting different handed helical modes. The anterior swimming direction and wave propagation direction are separated by $135°$ in right handed helix swimmers and by $225°$ in left handed helical swimmers.[18] The ciliary reversal modes of locomotion are characterized by little or no helical motion and lower swimming speed. The helical modes of swimming in contrast to the ciliary reversal modes allows us to better characterize the change in the locomotive pattern and hence will be used to study the effect of boundaries.

To investigate the flow-field around the organism suspensions of Polystyrene microspheres (5 μm diameter, Thermo Scientific) prepared in EDTA(ethyl di-amine tetraacetic acid) solution were introduced into the cultures. Small volume of the cultures 5 μl were then placed on the glass slide which created a very thin film and allowed us to visualize the 2D flow field around the *Paramecium*. Figure 1(a) shows a *Paramecium* swimming in a thin film of liquid. We can see there are two strong swirls forming on the lateral sides of the organism; showing the strong tangential velocity of cilia on the far field of the organism.

The effect of confined geometries on the ciliary dynamics is examined by introducing the organisms in capillary tubes. Tubes required for this purpose are manufactured by attaching a dead weight to the end of the borosilicate glass pipettes and by heating their tips. By controlling the
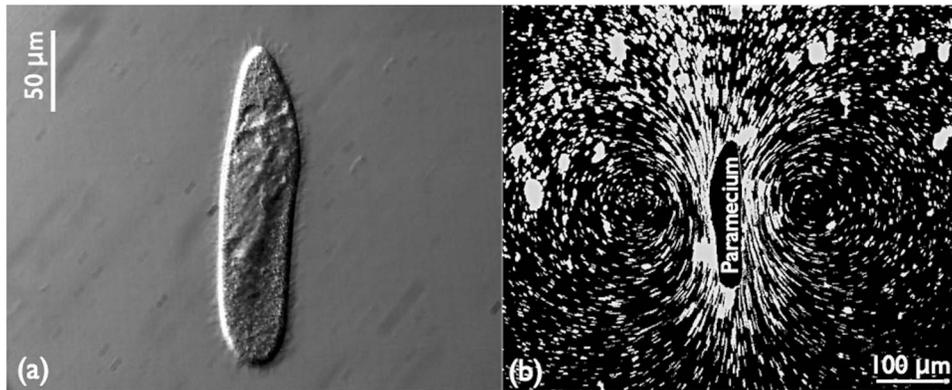
FIG. 1. (a) A *Paramecium* swimming in a thin layer of fluid. (b) Pathlines of particles in flows generated by the cilia.

value of the dead weight and the intensity of the applied heat different diameters of capillary tubes ranging from 90 to 250 μm were manufactured. Some commercially available tubes with specific diameters($d = 100, 150, 200$ μm) made of borosilicate glass were ordered from Vitrotubes. The equilibrated cultures were then transferred to the extruded glass pipettes where they got pulled into the small constant cross section of the tube due to capillary forces.

B. Experimental observations

Paramecia were found to have a long and slender structure with axial length around 212 ± 14 μm and diameter around 57 ± 5 μm (shown in Fig. 1(a)). The velocity of these micro-swimmers in semi-infinite fluid domain (a drop of fluid on a glass slide) was found to be 1534 ± 278 μm/s. We then performed experiments with capillary tubes of different diameters. *Paramecium* swimming in buffer (isotonic solution) was put into the capillary tubes which caused them to be confined in small circular geometry. A generic code written in MATLAB was used to track the motion of these organisms and their velocities were calculated.

In order to measure the vital parameters for swimming; we captured the cilia motion in semi-infinite fluid domain with the high speed camera at 300 fps, which allowed us to visualize the metachronal wave propagation over the organism. Each cilium was found to be 10–12 μm in length and 0.2 μm in diameter and beats slightly out of phase compared to the nearby cilium, thereby causing a traveling wave to pass over the surface of the organism. The typical wavelengths of the metachronal waves measured from five different videos of *Paramecium* in semi-infinite fluid medium were found 27 ± 3 μm, half of peak to peak amplitude measured around 4.2 ± 0.2 μm and the frequency of the beat being around 30 Hz.[12] These vital parameters for swimming are assumed to be constant for the swimming *Paramecium* in variety of constrained geometries. Using the mean swimming speed in unbounded fluid we calculate the *Re* $\sim$0.36 which further decreases to *Re* $\sim$0.024 for the smallest diameter tubes that we use in our experiments.

Imaging of round capillaries under microscope caused optical distortions which leads to recording of altered amplitudes and velocities. We directly took the cross sectional images of various capillaries to get a relation between the true and the observed inner diameters of the tubes, which was further used to correct the observed amplitude and velocities of the organisms.

In tubes of extremely small diameter the swimming velocity of the organism was very low with almost a straight line motion and variable rotation rates. Whereas in tubes of larger diameter the organism was seen to move in a helical path instead of straight line motion as shown in Fig. 3. We applied a correction factor for the path of the swimming organisms, as the image analysis only revealed the 2D projection of the helix.

It is observed that the *Paramecium* swims slowly as the tube diameter is decreased. This can be attributed to the increased drag felt by the organism due to the proximity of the boundaries. For the

capillary tubes whose diameter were very close to the diameter of the *Paramecium*, the swimming velocity was close to zero.

In tubes of smaller diameter ($R/c \sim 1.5$) we observed that a backward (posterior) swimming *Paramecium* executed a helical swimming trajectory with small amplitude wavelengths (shown in Fig. 3(b)). Such swimming gait have not been reported before in the literature.[18,28] In this range of tube diameters and for the forward swimming *Paramecium*, very few cases of anterior helical motion of the organism is observed.

III. THEORETICAL MODEL

The governing equations for very low Reynolds number flows ($Re \ll 1$) are the Stokes equations: $\nabla p = \mu \nabla^2 \mathbf{u}$, $\nabla \cdot \mathbf{u} = 0$. Since these organisms have a large length to diameter ratio; they can be effectively modeled as cylinders. As seen in Fig. 2 the cilia create synchronized motion to produce metachronal waves; to an observer this seems like a material wave propagating on the surface of the organism. Under the assumption that no fluid penetrates the wave of cilia tips since they are densely packed all over the surface of the organism, the concept of envelop model can be applied to the physical system. The boundary in this case is the circular capillary tube; thus the problem reduces to modeling a cylinder with a wavy surface swimming inside a cylindrical geometry.

Figure 4 shows the schematic of the organism swimming inside the tube with a velocity U_{swim}. In previous studies *Paramecium* has been modeled as an infinitely long cylinder so that there is no pressure gradient at the front and the back while swimming in the unbounded fluid. Similar infinite models can be developed for a *Paramecium* swimming inside a tube.[23] However, due to the presence of the confined spaces the finite sized *Paramecium* experiences a pressure gradient at its ends that influences its locomotion within tubes. We consider the propagating wave on the surface of the organism to be of frequency ω, wavelength λ, radial amplitude b, transverse amplitude a, and wave number $k = \frac{2\pi}{\lambda}$; so that any material point S on the undulating surface can be written as

$$r_s = c + b\sin(kz - \omega t), \; z_s = z + a\cos(kz - \omega t + \phi), \tag{1}$$

where ϕ is the phase difference.

We choose the frame of reference as one in which the organism is swimming with a velocity U_{swim}. In the small amplitude limit, the boundary conditions of the surface of the organism at $r = c$ and on the solid walls at $r = R$ can be written as

$$u_r|_{r=c} = -b\omega\cos(kz - \omega t), \; u_z|_{r=c} = a\omega\sin(kz - \omega t + \phi),$$

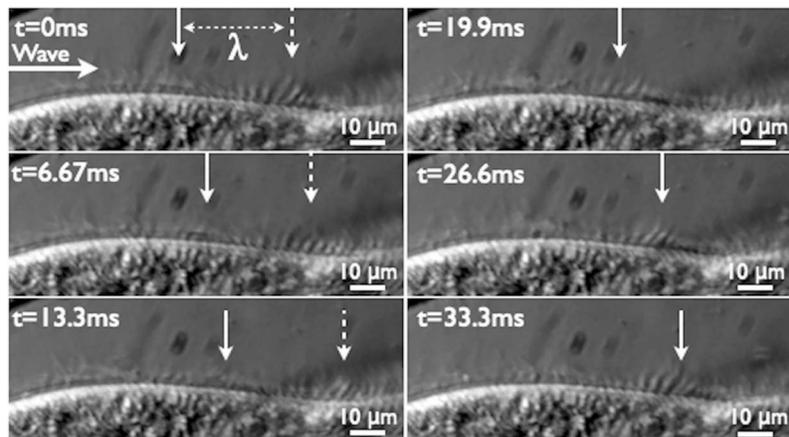$$u_r|_{r=R} = 0, \; u_z|_{r=R} = U_{swim}. \tag{2}$$

FIG. 2. The metachronal waves propagated by the cilia of the *Paramecium* over a period of 33.3 ms. The sweep of the cilia and the direction of propagation of the wave can be visualized. Arrows follow the peak amplitude of the waves (enhanced online) [URL: http://dx.doi.org/10.1063/1.4704792.1].
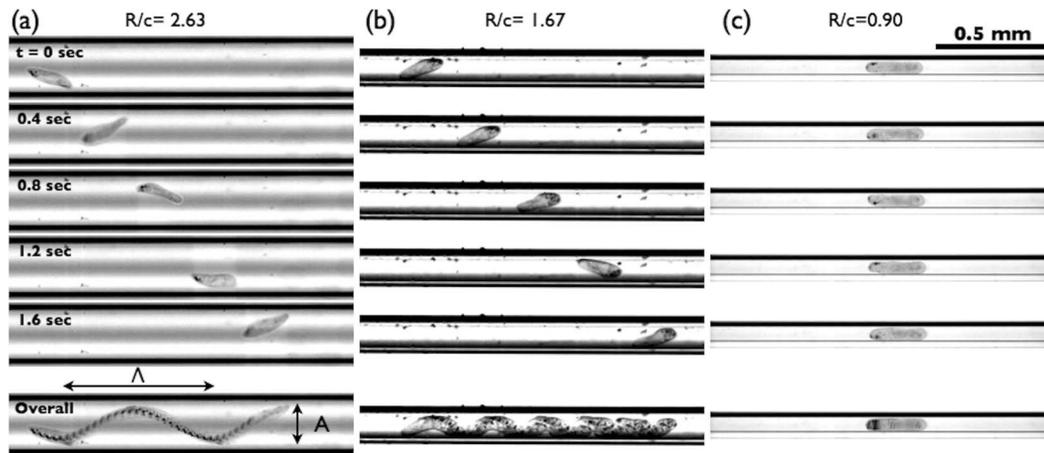
FIG. 3. Swimming of *Paramecium* in tubes of different diameters. Λ denotes the wavelength and A the amplitude of the helical trajectory traced by the organism in tubes of different diameter. (a) shows swimming in large tube ($R/c = 2.63$) where the trajectory of the motion is helical. In swimming inside tubes of intermediate diameters ($R/c = 1.67$) small wavelength helices are seen. In very small tubes($R/c = 0.9$) as shown in (c) *Paramecium* swims in a straight line.

As the *Paramecium* swims inside the capillary, effects of pressure gradient caused due to translation of a body within finite spaces as well as shearing motion (due to ciliary motion) need to be taken into account. The boundary conditions employed for our case are analogous to the case of peristaltic pumping; where the velocity boundary conditions are enforced in a similar fashion and pressure is assumed to drop along the length for which the wave travels.[29,30] Thus the swimming problem can be envisioned as sum of pressure driven flow and shear flow in the narrow annulus that surrounds the *Paramecium*. We seek a solution in terms of the axisymmetric streamfunction ψ such that $\psi = \psi^{(p)} + \psi^{(s)}$ where $\psi^{(p)}$is the streamfunction corresponding to pressure driven flow and $\psi^{(s)}$due to the shear flow. Using cylindrical co-ordinates and axisymmetric stream function we can write the velocity components to be $u_r = -\frac{\partial \psi}{r \partial z}$, $u_z = \frac{\partial \psi}{r \partial r}$. Solving for the pressure driven flow with
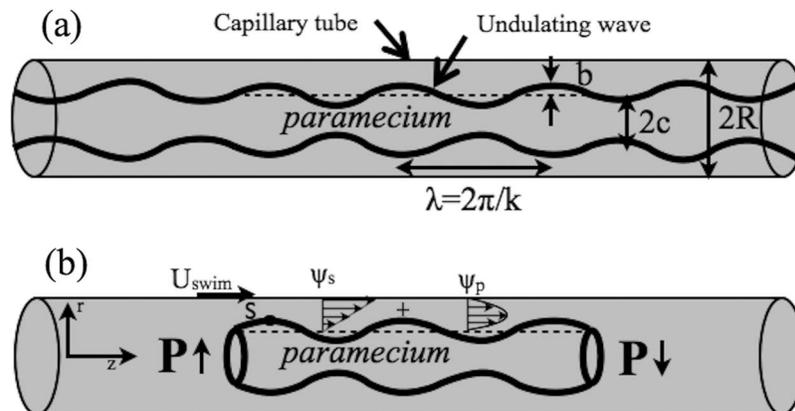

FIG. 4. Schematic of a wavy (a) infinite cylinder or (b) finite cylinder swimming inside the cylindrical tube. It is assumed that the organism is swimming in the negative z direction with a velocity U_{swim}. By transforming the coordinate system to one, where the organism is swimming with velocity U_{swim} we get the current schematic with the descriptions of the velocities on the walls of capillary.

stationary boundaries we can get the streamfunction for the pressure driven flow to be

$$\psi^{(p)} = \frac{1}{4\mu}\frac{\partial p}{\partial z}\left[\frac{R^2 - c^2}{\ln\frac{R}{c}}\left(\frac{r^2}{4} - \frac{r^2}{2}\ln\frac{r}{c}\right) + \left(\frac{r^4}{4} - \frac{c^2 r^2}{2}\right)\right]. \tag{3}$$

For the shear flow case we can substitute the velocity components in the Stokes equation and by taking curl we end up with an equation of the form $\left(\frac{\partial^2}{\partial r^2} - \frac{1}{r}\frac{\partial}{\partial r} + \frac{\partial^2}{\partial z^2}\right)^2\psi^{(s)} = 0$.

Rewriting coordinate systems as $\eta = kr$ and $\zeta = kz - \omega t$ and using separation of variables in η and ζ we can obtain a streamfunction solution of the form:

$$\psi^{(s)} = \frac{U_{swim}\eta^2}{2k^2} + \sum_{i=0}^{m} F_n \sin(\zeta) + \sum_{i=0}^{m} G_n \cos(\zeta), \tag{4}$$

where

$$F_n = \eta\left[A_n K_1(n\eta) + B_n \eta K_2(n\eta) + C_n I_1(n\eta) + D_n \eta I_2(n\eta)\right],$$

$$G_n = \eta\left[\alpha_n K_1(n\eta) + \beta_n \eta K_2(n\eta) + \gamma_n I_1(n\eta) + \delta_n \eta I_2(n\eta)\right],$$

and $A_n, B_n, C_n, D_n, \alpha_n, \beta_n, \gamma_n, \delta_n$ are the constants to be determined from the boundary conditions and I and K are modified Bessel functions of the first and second kind.

We seek perturbation expansions of the velocities $u_r = -k^2\frac{\partial\psi}{\eta\partial\zeta}$ and $u_z = k^2\frac{\partial\psi}{\eta\partial\eta}$ derived from the stream function to the zeroth $O^0(bk)$ and first order $O^1(bk)$ and compare the velocities with Eq. (2). For calculations of the zeroth and first order the constants $\alpha_n, \beta_n, \gamma_n, \delta_n$ do not have any contribution and hence we are left to determine four unknowns for the problem.

Coupled with the pressure driven flow this gives us a set of five equations and six unknowns $A_1, B_1, C_1, D_1, U_{swim}, \frac{\partial p}{\partial z}$. We note that in the stationary frame the swimming *Paramecium* squeezes out a volume of fluid through the annulus which is given by $Q = U_{swim}\pi c^2$ where c is the radius of organism. Also in the translating frame we can calculate flux which can be given by $Q' = \iint u_z r d\theta dz$. Both the fluxes thorough the annulus should be the same which gives us a relation between U_{swim} and $\frac{\partial p}{\partial z}$. Thus we get a set of five equations and five unknowns which can be solved to find out the constants and the swimming velocity U_{swim} of the organism. After solving we get the swimming velocity of the *Paramecium* to be

$$U_{swim} = \frac{k^3 b}{2}F_n(\eta_c) + \frac{a^2 k\omega}{2} + \frac{abk\eta_c\cos\phi}{8\mu}\frac{\partial p}{\partial\zeta} - \frac{abk\cos\phi}{8\mu\eta_c}\frac{\partial p}{\partial\zeta}\frac{\eta_R^2 - \eta_c^2}{\ln\frac{\eta_R}{\eta_c}}, \tag{5}$$

where $\eta_R = kR$ and $\eta_c = kc$.

The above expression shows that the swimming velocity is directly dependent on $(ak)^2$ and also on the pressure gradient terms. For the infinite boundaries case with no pressure gradient the above equation reduces to the following expression:

$$U_{blake} = \frac{\omega k}{2}\left[\frac{(K_0^2 - K_1^2)b^2}{K_1^2 - K_0 K_2} - \frac{2K_1^2 ab\cos\phi}{\eta_c(K_1^2 - K_0 K_2)} - a^2\right], \tag{6}$$

which is same as in Ref. 23.

IV. RESULTS

The motivation of the study was to rationalize the behavior of the organisms in close proximity to the boundaries. As the *Paramecium* swims inside the tube it traces out a helical path with the body being aligned in the swimming direction. Figure 5 shows the variation of the amplitude of the helical path of organism as it swims in capillary tube of different diameters. As the radius of the capillary increases the *Paramecium* also increases the diameter of the helix in which it swims. However, in case of semi-infinite fluid the amplitude of the swimming trajectories are much smaller as compared to those in the largest tube.
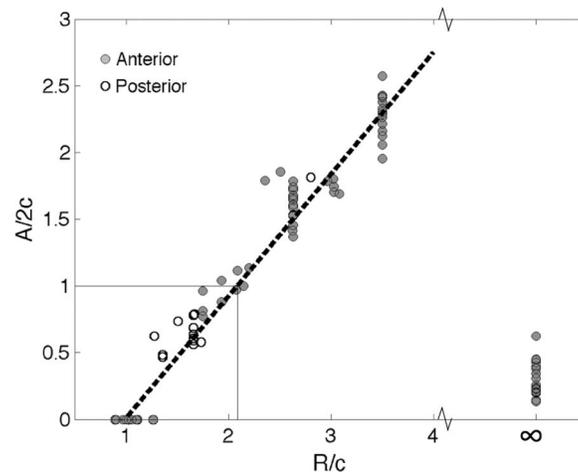
FIG. 5. Plot of the non-dimensional amplitude of the helical path vs. the non-dimensional radius of the tube. The plot shows a linear variation which increases with the radius of the tube.

Theoretically we considered the small amplitude expansions for the waves and hence the expression derived for the swimming velocity would only be valid for smaller capillary tubes in which there is very less off axis movement. From the plot above and the constraints on the amplitude of swimming of *Paramecium* we can conclude that for $A/(2c) < 1$, our experimental and theoretical results would remain valid. This gives us corresponding value of the non-dimensional radius of the capillary tube $R/c < 2.1$.

Figure 6 shows the variation of velocity with the radius of the capillary tube. The dotted line shows the swimming velocity when no pressure gradient effects are considered and the solution converges very quickly to the case for which the boundaries are at infinity. In the experiments we observe a slowly increasing trend of velocity. For a finite size *Paramecium* swimming inside a restrictive geometry there exists a finite pressure gradient between its ends. The plot of the swimming velocity considering finite pressure gradient is shown by the solid line. It shows a slowly increasing trend and finally converges to the case of infinite boundary and no pressure gradient for very large R/c values. It can be seen that for $R/c < 2.1$ both the experiments and theory show an increasing trend and predictions match quite well. For the semi-infinite case we see that the velocities are a little larger as when compared to the values predicted by our theoretical model.

Figure 7 shows the variation of wavelengths of the helical path while they are swimming in the tube. The wavelengths also show a linearly increasing trend for the limit $R/c < 2.1$. In this limit the helices of the swimming are well defined and periodic wavelengths are observed. While swimming in tubes of larger diameter($R/c > 2.1$) it was observed many times that the organism did not execute a full helix.

In order to compare the swimming efficiency (η) of *Paramecium* in different diameter tubes (in which they might swim in a helix or a straight line); we estimate an efficiency parameter $\eta = U_{swim}T/P$ where T denotes the thrust force per unit area generated by the organism $T = \mu U_{swim}/\lambda$, U_{swim} is the swimming velocity obtained experimentally, λ is the wavelength of the metachronal wave.[23] P denotes the power generated per unit area by the undulating wavy *Paramecium* when it is swimming in the unbounded fluid; which has already been derived by Blake for an infinite model.[23] This is a good reference for comparison because we are calculating the efficiency in different level of boundedness; from extremely confined to infinite fluid case. As observed from Fig. 8 for the infinite fluid cases the efficiency is close to 3%, however, in confinements where $R/c < 2.1$ the efficiency is lower than 0.5%. It suggests that the swimming efficiency of *Paramecium* in smaller tubes is lower as *Paramecium* experiences more drag from confinements.
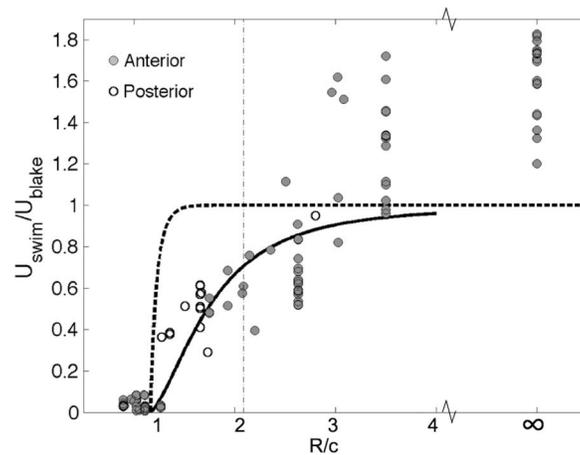
FIG. 6. Plot of normalized swimming velocity vs. the non-dimensional radius of the tube. Two different cases are compared, one with the dotted line shows the model of an infinite ciliate swimming in capillary tube. The solid line shows the velocity variation of the finite sized *Paramecium* inside confined geometries. Dots represent the experimental result and compares well with the finite pressure gradient model in the restrictive environment.

V. DISCUSSION

We investigated the locomotion of ciliary organisms in confined geometries. As the boundaries close on the organism, more viscous effects are felt by the cilia. The swimming velocity of *Paramecium* decreases due to the effect of close boundaries. Also in such confined spaces a finite sized organism feels a pressure gradient across the ends. This pressure gradient affects the swimming velocity and needs to be considered while modeling similar self propelling objects in restrictive geometries. By taking into account the effects of pressure gradient we were able to capture the increasing trend of velocities. One might point out that swimming velocities in the semi-infinite domain are under-predicted by theoretical model, which might be due to the simplifying assumption in which we consider the beat pattern as a simple 2D sinusoidal whereas the ciliary beat in *Paramecium multimicronucleatum* is 3D diexoplectic. It is also observed that there are very few cases in which *Paramecia* tend to swim in straight lines with the velocity values being in the lower range of the swimming values obtained for the case of helical swimming. Comparing the straight line
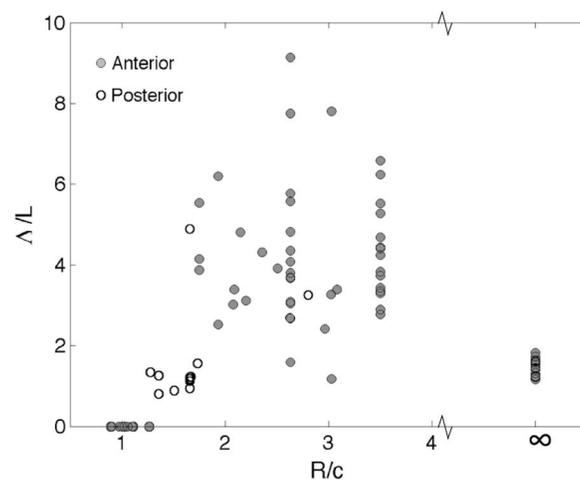

FIG. 7. Plot of the non-dimensional wavelength vs. non-dimensional radius of the tube. No apparent trend is seen for larger radius of the tube. In contrast while swimming in the semi-inifnite domain the *Paramecium* has well defined wavelengths of the helical path.
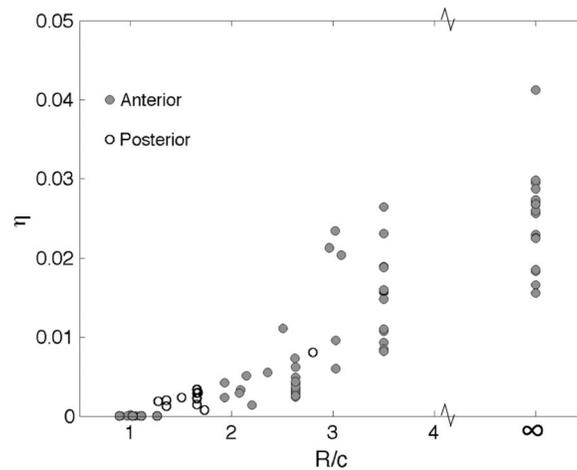
FIG. 8. Plot of the efficiency of the various trajectories inside the tube as well as semi-infinite domain from experiments as compared to a *Paramecium* swimming in semi-infinite fluid domain.

motion with helical motion, it can be concluded from these data that amplitude of the trajectory of the *Paramecium* has very less bearing on the velocity in the tubes when $R/c < 2.1$. Our current investigations focused on the gap thicknesses which are mostly outside the lubrication limit and predicts a slowly increasing trend of velocities for increasing gap widths. However, in the case of extremely small gap thickness when $R/c < 1.16$, one might need to consider the lubrication approximation (rather than the small perturbation expansion).

Many interesting questions arise from this study especially about the amplitude of the waves propagated by the *Paramecium*. In a restrictive channel the beat of the waves is limited by the dimensions of channel and the size of organism. The helical path traced out by the *Paramecium* with the anterior portion of the body aligned towards the local swimming direction is also an interesting locomotory trait. It was also observed that as the radii of the capillary tube increased the radius of the swimming helix also increased. This is in contrast to the freely swimming *Paramecium* in unbounded fluid which has very small radii of helical trajectories and at times the trajectories seem to be straight with no lateral undulations.

The study revealed the interesting locomotory patterns of ciliates in presence of solid wall. Future work would involve investigating the hydrodynamic effects of different textured boundaries on the swimming characteristics of the organism. We plan to examine the effects of boundaries of various wavelengths on the metachronal wave of the *Paramecium* and understand the effects on swimming velocities. Different waves will cause different distribution of stresses over the body of the organism, which might cause different swimming speed of the organism. The study with solid walls was a precursor to understanding the behavior of these organisms and will provide a basis for comparison with textured boundaries.

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