THEORY OF ATTACHMENT IN *GIARDIA*

ROGER D. JONES
Applied Theoretical Physics Division, University of California, Los Alamos National Laboratory,
Los Alamos, New Mexico 87545

CHERYL L. LEMANSKI
Department of Microbiology, School of Medicine, University of New Mexico, Albuquerque,
New Mexico 81706

TERESA J. JONES
Espanola Hospital, Espanola, New Mexico 87532

ABSTRACT Using a low Reynold's number hydrodynamic model, the adhesive force in *Giardia* is calculated. It is shown that this force is larger than typical forces that would tend to detach the organism.

INTRODUCTION

Giardia lamblia is an intestinal protozoan parasite. Its range is quite large, extending from the tropics (1) to as far north as Leningrad (2). According to the Center for Disease Control in Atlanta, Georgia, it is the most frequently encountered intestinal parasite in American public-health labs (3). The outstanding anatomical feature of *Giardia* is its large sucking disk that covers almost the entire ventral surface of the organism. The animal uses the disk to attach itself to the intestine wall of its host. This attachment can cause lesions in the intestine mucosa. There have been extensive experimental and electron microscope studies on attachment in *Giardia muris*, a species almost morphologically identical to *Giardia lamblia* (4, 5). In the first of these, Friend (4) introduced an interesting puzzle. He noticed that the cytoskeleton formed such a rigid structure that it was not possible to deform the sucking disk to obtain a vacuum. He suggested that possibly the disk was not responsible for adhesion. Holberton (5) corroborated Friend's findings on the rigid structure of the cytoskeleton. Additionally, using light microscopy, he observed living trophozoites attached to the microscope slide. He noticed that they became detached when the ventral flagella ceased oscillating. Holberton proposed a mechanism for attachment that depended on the ventral flagella for suction in the ventral disk (6).

This paper generalizes the Holberton mechanism to include a number of effects neglected in reference 6. Specifically, pressure type drag, improved mass conservation, wall effects on flagellar motion, and finite length effects will be included in the generalized model. A number of these effects tend to cancel each other. It will be shown that, for a typical set of parameters, the improved model predicts a value for the pressure drop in the ventral disk within a factor of four of the value predicted by Holberton (6). Furthermore, an additional attachment mechanism is proposed. This new mechanism is very similar to the mechanism by which sticky tape attaches itself to a flat surface. In *Giardia*, it affects the speed with which the organism can separate from the intestine wall after the ventrocaudal flagella cease to beat. When the attachment force calculated from the improved model is compared with the forces that would tend to detach the organism, further credence is given to the scheme.

MODEL

Fig. 1 is a schematic of *Giardia*. Running laterally along the ventral disk are two tubes (marginal grooves). These tubes come together at the caudal side of the disk and form a single tube (ventrocaudal groove) that emerges caudally. In the region where the marginal grooves meet the ventrocauadal groove, there is an opening (portal) from the grooves into the ventral disk. Emerging from a position caudal to this opening and lying within the ventrocaudal groove are two flagella that seem to beat coherently. Fig. 2 is a photograph of the ventral surface of the organism.

In the Holberton scheme, the beating flagella draw fluid through the marginal grooves and out through the ventrocaudal groove (the fluid flow is indicated by arrows in Fig. 1). The flow induces a pressure drop along the marginal grooves, which lowers the pressure in the ventral disk. Attachment is due to the pressure differential between the interior of the disk and the exterior of the organism. Additionally, when the organism is moving away from the wall, there is another mechanism that tends to keep the organism attached. For physical dimensions on the order of a few micrometers, fluids, such as water, are very viscous. This viscosity produces a force on the organism that limits

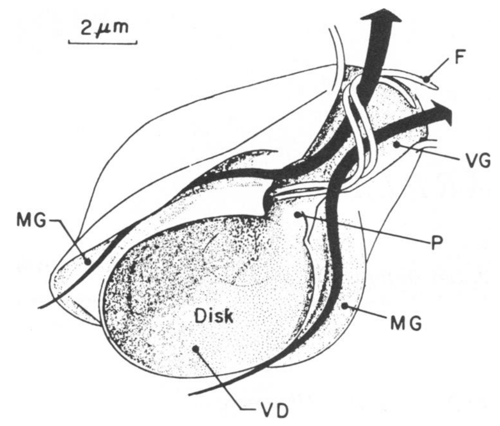

FIGURE 1 Schematic of *Giardia*. Displayed are the ventral disk, *VD*, marginal grooves, *MG*, portal, *P*, ventrocaudal groove, *VG*, and the two flagella, *F*, located in the ventrocaudal groove. The dorsal flagella are not displayed. The fluid flow is indicated by the arrows.

the speed of detachment. If this speed is very small, then the organism can remain in the vicinity of the wall for long periods of time.

We will divide the problem into three parts. First, we will calculate the force on the organism given the pressure differential between the inside of the disk and the outside of the organism. Second, we will calculate the pressure differential given the flow speed in the marginal grooves.

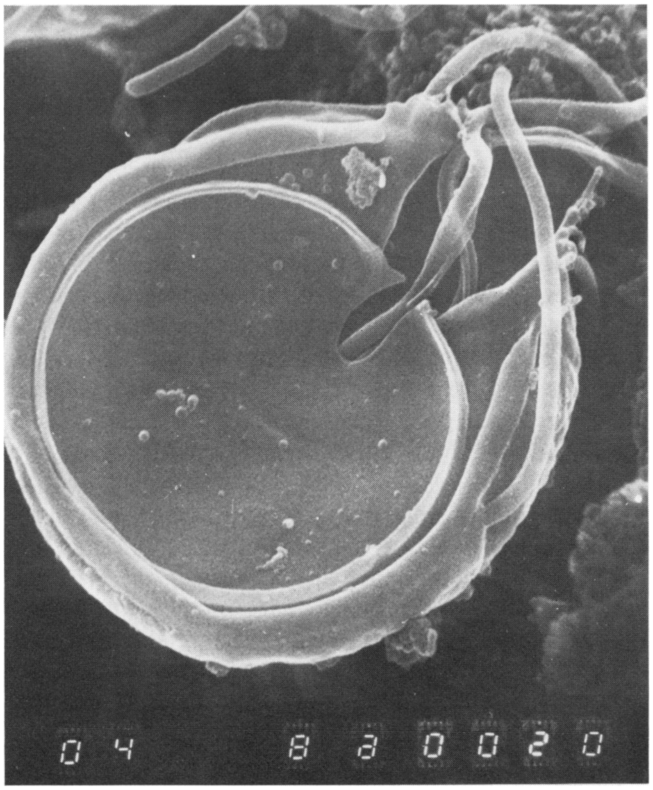

FIGURE 2 Electron scanning microscope picture of the ventral surface of *Giardia muris*. Photograph courtesy of D. V. Holberton.

And finally, we will calculate the flow speed in the marginal grooves, given the frequency of oscillation of the flagella. The frequency is an experimentally observable quantity.

Because viscuous forces dominate over inertial forces (the Reynolds' number is typically 10^{-4} in microbiological applications), the dynamics of the fluid in the neighborhood of the organism is given by Navier-Stokes' equation with the inertial terms dropped,

$$\nabla p = \mu \nabla^2 \mathbf{v}, \tag{1}$$

where p is the local pressure, μ is the viscosity, and $\mathbf{v}$ is the local fluid velocity. This equation is known as the Navier-Stokes' equation in the creeping flow approximation. Eq. 1, along with mass conservation and the assumption of incompressible flow, completely determines the fluid behavior.

A typical set of dimensions, which we will use in this paper, is given in Fig. 3. These dimensions are taken from the text and photographs of references 5 and 6. The radius of the ventral disk, b, is taken to be 4.0 μm. The radii of the marginal groove, r_{MG}, and the ventrocaudal groove, r_{VG}, are 0.1 and 0.2 μm, respectively. The distance, h, from the edge of the ventral disk to the surface of attachment is typically 0.02 μm. The width of the edge of the ventral disk, Δb, is 0.05 μm. The length of the organism is 11 μm. The lengths of the marginal grooves, L_{MG}, and the ventrocaudal groove, L_{VG}, are both 4.0 μm. The diameter of the flagella is 0.03 μm. The viscosity of water is 0.01 poise and we will denote the viscosity of mucous by $\alpha\mu_{\mathrm{W}}$, where μ_{W} is the viscosity of water. We will take the pressure exterior to the organism to be 1.0 atm.

We are now prepared to carry out the first part of the program, i.e., calculate the force on the organism given that the pressure outside the animal is p_1 and the pressure inside the ventral disk is p_0. In the intestine, the organism is separated from the wall by a thin layer of mucous of thickness, h. On a microscope slide, this layer is water. To calculate the frictional force this layer exerts on the organism, we will assume the animal is separating from the wall with a speed $\dot{h}$. The problem can be solved exactly if we assume h is much smaller than Δb. The spacing, h, is typically less than half of Δb. We will also assume the only contribution to the viscous drag comes from the edge of the ventral disk. Except for the boundary conditions, this problem is similar to a problem in the text by Landau and Lifshitz (7). With the mentioned simplication, Eq. 1 becomes

$$\frac{\partial p}{\partial r} = \mu_{\mathrm{M}} \frac{\partial^2 v_r}{\partial z^2} \tag{2}$$

for the fluid in the layer of thickness, h. The coordinate system is given in Fig. 3. We have denoted the viscosity of the mucous by a subscript M. In Eq. 2, p is a strong function of r and a weak function of z, and v_r, the velocity

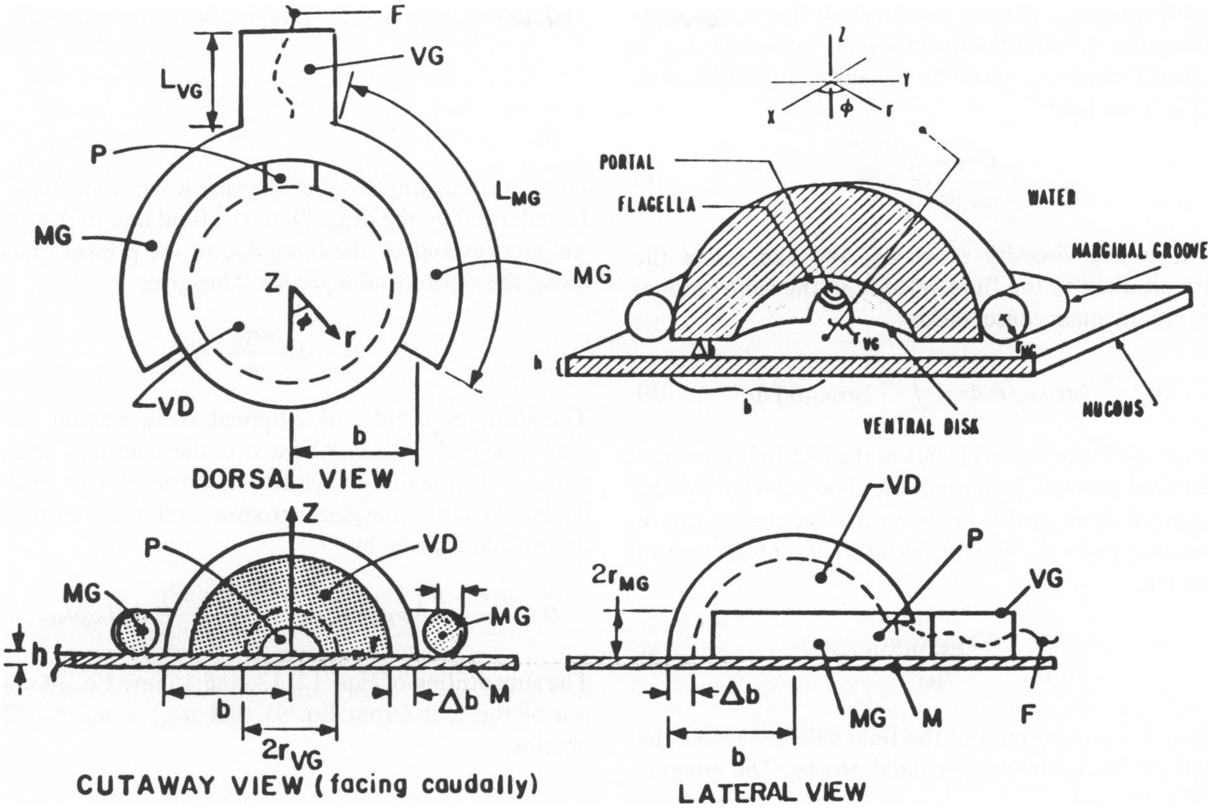

FIGURE 3 Mathematical construct of *Giardia*. The radius of the ventral disk, b, is 4.0 μm; the radii of the marginal grooves, r_{MG}, is 0.1 μm; the radius of the ventrocaudal groove, r_{VG}, is 0.2 μm; the distance, h, of the organism from the surface of attachment is 0.02 μm, the width of the edge of the ventral disk, Δb, is 0.05 μm; the length of the marginal grooves, L_{MG}, and ventrocaudal groove, L_{VG}, are each 4.0 μm. The mucous layer is labeled M. The drawings are not to scale.

in the radial direction, is a strong function of z and a weak function of r. If one assumes the fluid velocity must be zero on the wall and on the organism, then Eq. 2 can be solved for v_r to give

$$v_r = \frac{1}{2\mu_M}\frac{\partial p}{\partial r}(z^2 - zh). \tag{3}$$

Eq. 3 can be used in the equation for mass conservation to obtain an equation for p. Mass conservation gives

$$\int_0^h 2\pi r v_r(z)\mathrm{d}z = \int_{b-\Delta b}^{r} 2\pi r\dot{h}\mathrm{d}r + \int_0^h 2\pi r v_r(z)\mathrm{d}z\,|_{r=b-\Delta b}\,. \tag{4}$$

Substituting Eq. 3 into Eq. 4 and integrating $\partial p/\partial r$ over r gives

$$p(r) - p_0 = \frac{-6\mu\dot{h}}{h^3}(r - b + \Delta b)^2 \quad \text{for} \quad b - \Delta b \le r < b \tag{5}$$

and $p(r) = p_0$ for $0 \le r < b - \Delta b$.[1]

We have dropped terms of order $\Delta p = p_1 - p_0$ in obtaining Eq. 5. When we calculate the total force, these terms will be of order $\Delta p \Delta b/b$, and thus negligible when compared with terms of order Δp. Also, we have only kept terms to lowest order in $(r - b + \Delta b)$. The net force holding the organism to the wall is $F = \pi b^2 p_1 - \pi(b - \Delta b)^2 p_0 - 2\pi \int_{b-\Delta b}^{b} p(r) r\mathrm{d}r$. This force is directed into the wall. If we perform the integration and retain terms to lowest order in Δb and Δp, we obtain

$$F = \pi b^2 \Delta p + G 6\pi b \mu_M \dot{h}, \tag{6}$$

where

$$G \equiv \frac{2}{3}\left(\frac{\Delta b}{h}\right)^3. \tag{7}$$

The expression multiplying G in Eq. 6 will be recognized as Stokes' law for a sphere of radius b. For the typical parameters given earlier, G is equal to 10. If the organism is very close to the wall, the Stokes' drag on the animal is enhanced by an order of magnitude, thus justifying our assumption that the viscous drag is due primarily to the region of contact with the wall.

We are now prepared to carry out the second stage of the program, i.e., calculate p_0/p_1, given the flow speed in the ventrocaudal groove. Consider a marginal groove of radius

---

[1] Our Eq. 5 differs by a factor of two from the corresponding result in reference 7. This results from the fact that fluid is flowing under the disk from both inside and outside in our calculation, and in reference 7 the fluid flows only from the outside.

r_{MG} and length L_{MG}. Choose the z axis so that it measures distance along the length of the groove. If we assume L_{MG} is much larger than r_{MG}, then, by the same arguments that led to Eq. 3, we have

$$v_{MG} = \frac{1}{4\,\mu_W}\frac{\partial p}{\partial z}(r^2 - r_{MG}^2). \tag{8}$$

Here, μ_w is the viscosity of water. We can relate the pressure gradient to the fluid velocity in the ventrocaudal groove, v_{VG}, by mass conservation

$$2\int_0^{r_{MG}} 2\pi r v_{MG}(r)\,\mathrm{d}r = \int_0^{r_{VG}} 2\pi r v_{VG}(r)\,\mathrm{d}r. \tag{9}$$

The factor of two on the left is due to the fact that there are two marginal grooves. Assuming the fluid velocity has the same type parabolic profile in the ventrocaudal groove as in the marginal grooves, we can perform the integration in Eq. 9 giving

$$\frac{\partial p}{\partial z} = \frac{-2\,\mu_W r_{VG}^2 u_{VG}}{r_{MG}^4}. \tag{10}$$

Here, u_{VG} is the maximum of the fluid velocity across the parabolic profile in the ventrocaudal groove. The integration of Eq. 10 gives

$$\Delta p = 2\mu_W \frac{r_{VG}^2}{r_{MG}^2} L_{MG} u_{VG}, \tag{11}$$

where Δp is $p_1 - p_0$. We have assumed that the pressure at the portal is p_0. In *Giardia* the cross sections of the marginal and ventrocaudal grooves tend to be elliptical rather than circular. For elliptical cross sections, Eq. 11 becomes

$$\Delta p = (1 + n^2)\,\mu_W \frac{r_{VG}^2}{r_{MG}^2} L_{MG} u_{VG}, \tag{12}$$

where r_{MG} and r_{VG} are now the semiminor axes of the marginal and ventrocaudal grooves, respectively. The semimajor axes are given by r_{MG}/n and r_{VG}/n. Here, n is typically 0.5. We have assumed that the marginal and ventrocaudal grooves have the same eccentricity. This result differs by a factor of two from a similar result obtained by Holberton (Eq. 1 of reference 6, $r_{VG}/r_{MG} = 2.0$). The difference arises because Holberton took u_{VG} to be half the maximum fluid velocity in the marginal grooves rather than relating the two through Eq. 9.

We can now use the well established theory of flagellar motion (8) to relate u_{VG} to the frequency of oscillation of the ventrocaudal flagella. The net force on the fluid in the groove due to a sine wave propagating along the flagellum is (8) $P = K_T L_{VG}\,[(\nu\lambda - u_{VG})\beta - \nu\lambda] + K_N L_{VG}\,(\nu\lambda - u_{VG})\,(1 - \beta)$. Here, ν and λ are, respectively, the frequency and wavelength of the sine wave, K_T and K_N are the tangential and normal resistances, and β is given approximately by

$$\beta = \frac{1}{1 + \dfrac{2\pi^2\eta^2}{\lambda^2}}. \tag{13}$$

Here, η is the amplitude of the sine wave. This force must be balanced by the drag, D, of the fluid due to the walls of the grooves and by the force due to the pressure increase along the ventrocaudal groove. This gives

$$D + \Delta p\frac{\pi r_{VG}^2}{n} = P. \tag{14}$$

The drag in a tube of elliptical cross section is $D = [2(1 + n^2)/n]\ \pi\mu_w L u$, where L is the length of the tube, and u is the maximum velocity in the tube. The total drag is due to both marginal grooves and the ventrocaudal groove and is given by

$$D = \frac{4(1 + n^2)}{n}\pi\mu_w L_{MG} u_{MG} + \frac{2(1 + n^2)}{n}\pi\mu_w L_{VG} u_{VG}. \tag{15}$$

The substitution of Eqs. 12, 13, and 15 into Eq. 14 and the use of the fact (from Eq. 9) that $u_{MG} = u_{VG} r_{VG}^2/(2r_{MG}^2)$ obtains

$$\frac{u_{VG}}{\nu\lambda} = \frac{(1 - \rho_K)(1 - \beta)}{1 - \beta + \rho_K\beta + \delta_D + \delta_P}. \tag{16}$$

Here, ρ_K is the ratio of the normal to the tangential resistance, $\rho_K = K_T/K_N$, δ_D and δ_P are the ratios, respectively, of the drag and pressure forces to $K_N L_{VG} u_{VG}$,

$$\delta_D = \frac{2\pi\mu_w}{K_N}\frac{1 + n^2}{n}\left(1 + \frac{L_{MG}}{L_{VG}}\frac{r_{VG}^2}{r_{MG}^2}\right) \tag{17}$$

and

$$\delta_P = \frac{2\pi\mu_w}{K_N}\frac{(1 + n^2)}{n}\frac{1}{2}\frac{L_{MG}}{L_{VG}}\frac{r_{VG}^4}{r_{MG}^4}. \tag{18}$$

Substitution of Eq. 16 into Eq. 12 obtains

$$\Delta p = \left(\frac{r_{VG}}{r_{MG}}\right)^2 \frac{(1 + n^2)\mu_w L_{MG}\lambda}{r_{MG}^2}\frac{(1 - \rho_k)(1 - \beta)\nu}{1 - \beta + \rho_k\beta + \delta_D + \delta_P}. \tag{19}$$

This expression gives the pressure drop in the ventral disk in terms of the known or measurable properties of the organism and surrounding fluid, if K_T or K_N are known from theory or measurement. Gray and Hancock (9) find the value of ½ for the ratio, ρ_K, of the two resistances is consistent with the observation of sea-urchin spermatazoa. Lighthill (8) argues that this value results from the flagella being in close proximity to a stationary wall. This is similar to the situation in *Giardia*, where the ventrocaudal flagella beat inside a stationary tube. The value of ½ is also the value used by Holberton (6). The resistance, K_N, also appears in the expressions for δ_D and δ_P. Lighthill (8) gives the expression

$$K_N = \frac{8\pi\mu_w}{1 + 2\ln\left(\frac{2\lambda}{d}\right)} \tag{20}$$

for flagella beating far from a stationary wall and the expression

$$K_N = \frac{8\pi\mu_w}{2\ln(2r/d)} \tag{21}$$

for the flagella beating a distance *r* from a stationary wall, where *r* is much smaller than a wavelength of the sine wave propagating down the flagella. Here, *d* is the diameter of the flagellum. Since this latter condition is satisfied by the ventrocaudal flagella, Eq. 21 is more appropriate for *Giardia* with *r* taken to be r_{VG}.

Holberton (6) obtains an expression similar to Eq. 19 for Δp,

$$\Delta p_H = \frac{2(1 + n^2)\,\mu_w L_{MG}\lambda}{r_{MG}^2}\,\frac{(1 - 1/2)(1 - \beta)\nu}{1 - \beta + \beta/2 + \delta_H}, \tag{22}$$

where

$$\delta_H = \left[\ln\left(\frac{2\lambda}{d}\right) - \frac{1}{2}\right]\frac{(1 + n^2)}{n}\,\frac{(L_{MG} + L_{VG})}{m\lambda}. \tag{23}$$

Here, *m* is the number of wavelengths of the sine wave along the flagella. Eq. 22 is simply Eqs. 2 and 5 of reference 6 written in our notation. In Eq. 22, the ratio, r_{VG}/r_{MG}, has already been taken equal to 2.0, and ρ_K has been set equal to $1/2$.

Eq. 22 is improved by Eq. 19 in a number of ways. A more careful treatment of mass conservation increases the numerical coefficient in front of Eq. 22 by a factor of two, for $r_{VG}/r_{MG} = 2.0$. The effects of the pressure drop along the ventrocaudal groove are represented by δ_P in Eq. 19. These effects have been neglected in Eq. 22. It will be demonstrated that these effects are significant. The drag term, δ_H in Eq. 22 and δ_D in Eq. 19, has been improved in three ways. In the derivation of Eq. 23 an expression for K_N has been used that is appropriate for flagella beating far from the wall. If Eq. 21 is used in Eq. 17, then δ_D in Eq. 19 includes the wall effects. Improved mass conservation considerations alter Eq. 23. And finally, it has been assumed in Eq. 23 that the entire length, $m\lambda$, of the ventrocaudal flagella contributes to the pressure drop, Δp. More appropriately, only that portion of the flagella located in the ventrocaudal groove contributes. Therefore, $m\lambda$ is replaced with L_{VG}.

To judge the importance of these effects, we can substitute a typical set of parameters into Eqs. 17, 18, and 23. Using the numbers given earlier, one obtains the values of 16 and 23 for δ_D and δ_P, respectively. Thus we see that pressure effects are larger than drag effects and should not be neglected. If the wavelength is taken to be 4.5 μm, and *m* is taken to be 5, then Eq. 23 gives for δ_H a value of 4.6. Therefore, δ_H is nearly an order of magnitude smaller than $\delta_D + \delta_P$. These terms dominate the denominator in Eqs. 19 and 22. For $2\pi\eta/\lambda$ equal to 1.4, $1 - \beta/2$, which represents flagellar drag, is equal to 0.75. Using these parameters, Eqs. 19 and 22 become $\Delta p = (0.52 \text{ dyne} - \text{s/cm}^2)\,\nu$ from Eq. 19, and $\Delta p_H = (2.1 \text{ dyne} - \text{s/cm}^2)\,\nu$ from Eq. 21. Thus, the improved model agrees with the Holberton model to within a factor of four, with the improved model giving the smaller result.

The net force of attachment is given by Eq. 7 with *p* given by Eq. 19.

$$\begin{aligned} F &= \pi b^2\left(\frac{r_{VG}}{r_{MG}}\right)^2 \frac{(1 + n^2)\mu_w L_{MG}\lambda}{r_{MG}^2}\,\frac{(1 - \rho_k)(1 - \beta)\nu}{1 - \beta + \rho_k\beta + \delta_D + \delta_P} \\ &\quad + G6\,\pi b\mu_M \dot{h} \\ &= (2.6 \times 10^{-7}\,\text{dyne} - \text{s})\nu \\ &\quad + \left(7.5 \times 10^{-9}\,\frac{\text{dyne} - \text{s}}{\mu\text{m}}\right) G\alpha\dot{h}. \end{aligned} \tag{24}$$

We have used the parameters given in Fig. 3 and the text to evaluate Eq. 24. The first term on the right side is the force due to the beating flagella. Holberton (5) noticed that detachment occurred when $\nu < 1$ beat/s. Therefore, for this theory to be viable, typical external forces must be smaller than $\sim 3 \times 10^{-7}$ dynes. The second term on the right of Eq. 24 determines how fast the organism separates from the wall. If the organism experiences an external force, F_{ext} and the flagella are not beating, the animal will separate from the wall at a speed

$$\dot{h} = \frac{F_{ext}}{\left(7.5 \times 10^{-9}\,\frac{\text{dyne} - \text{s}}{\mu\text{m}}\right) G\alpha}. \tag{25}$$

For the given parameters, *G* is ~10. If the organism is situated totally in water, as in the Holberton experiment (5), then an external force of 10^{-7} dynes would cause the animal to separate from the wall with a speed on the order of micrometers per second. With mucous present, this speed is much smaller.

COMPARISON WITH EXTERNAL FORCES

There are three external forces, immediately evident, that would act to detach the organism from the intestine wall. They are (*a*) the viscous drag of the fluid flowing over the

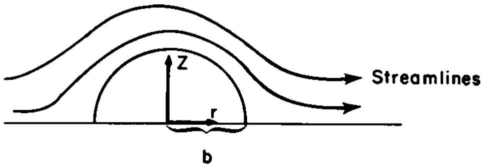

FIGURE 4 Schematic of fluid flowing over *Giardia*.

top of the organism, (*b*) the gravitational/bouyant force, and (*c*) the force of the six flagella other than the ventrocaudal flagella. If these forces are larger than Eq. 24, then the mechanisms that led to Eq. 24 become suspect.

It is quite easy to estimate the viscous force. The situation is illustrated in Fig. 4. From mass conservation we have the condition $v_r \simeq v_z \equiv v$ on the surface of the organism. From the Navier-Stokes' equation we have

$$\frac{\mu v}{b^2} \simeq \frac{\Delta p}{b}, \tag{26}$$

where Δp is the pressure difference between the top and the bottom of the animal. The net lift on the organism is

$$F_s = \Delta p \pi b^2 \simeq \pi \mu b v. \tag{27}$$

This is approximately Stokes' law. The velocity, v, is given, assuming Poiseuille flow in the intestine, by

$$v = v_{\text{int}}\left(1 - \frac{r^2}{r_{\text{int}}^2}\right).$$

Here, v_{int} is the flow speed in the center of the intestine, and r_{int} is the radius of the intestine. Taking r equal to $r_{\text{int}} - b$ gives for Eq. 27

$$F_s \simeq \frac{b}{r_{\text{int}}} 2\pi \mu b v_{\text{int}}. \tag{28}$$

Taking r_{int} to be 2 cm and v_{int} to be 1 cm/s gives

$$F_s \simeq 5 \times 10^{-9}\text{dynes}, \tag{29}$$

which is much smaller than Eq. 24.

Suppose the mass density of the organism differed from the density of water. Then the animal would experience a gravitational or a bouyant force depending on whether the density was greater or less than that of water. Take an extreme case. Suppose the mass density in the interior of the animal is zero. Then the animal would feel a bouyant force of

$$F_g = \rho V g, \tag{30}$$

where ρ is the mass density of water and is $\rho = 1.0\ \text{g/cm}^3$, V is the volume of the animal and will be taken to be $V = (4.0\ \mu\text{m})^2(11.0\ \mu\text{m}) = 176\ \mu\text{m}^3$, and $g = 980\ \text{cm/s}^2$ is the acceleration due to gravity. This gives a force of $\sim 2 \times 10^{-7}$ dynes, roughly the same order of magnitude as Eq. 24. Since the organism is composed primarily of water, it is unlikely the mass density would take this extreme value. Eq. 30 would thus tend to be smaller than Eq. 24.

Finally, we can calculate the force due to the six flagella other than the ventrocaudal flagella. An upper bound on the force exerted by one flagellum is (8)

$$P < K_N L \nu \lambda (1 - \beta). \tag{31}$$

Here, L is the length of the flagella. If we let r equal b in Eq. 21 and evaluate Eq. 31 using the typical parameters, we find $P < (1 \times 10^{-8}\ \text{dyne-s})\nu$. If we assume that all six flagella are beating in a direction such that the force is directed away from the wall, then we obtain a maximum possible force of detachment that is a factor of five smaller than Eq. 24. Since the flagella are separated from the wall by a distance of ~4 micrometers and the length of the flagella is ~20 micrometers, this configuration is physically impossible. We are thus led to the conclusion that none of the three mentioned detachment mechanisms is strong enough to overcome the adhesive force given in Eq. 24.

CONCLUSION

We calculated the force of adhesion in *Giardia* using a low Reynolds' number hydrodynamic model. We improved on earlier models in a number of ways. Specifically, we included the effects of the pressure drop in the ventrocaudal groove, treated mass conservation more carefully throughout, and have taken into account the fact that only a fraction of the length of the ventrocaudal flagella contributes to the pressure drop in the ventral disk. The adhesive force on *Giardia* was a few tenths of a microdyne. Our result differs by a factor of four from earlier results. In addition, we proposed another adhesion mechanism that relies on the stickiness of mucous or water at low Reynolds' number. This mechanism limits the speed with which the organism can separate from the intestine wall. Finally, we compared the adhesive force with typical forces that would tend to detach the organism. We found that the detachment forces are not strong enough to overcome the force of adhesion.

This work was partially supported by the U. S. Department of Energy.

Received for publication 24 June 1981 and in final form 15 April 1983.

REFERENCES

1. Babb, R. R., O. C. Peck, and F. G. Vescia. 1971. Giardiasis, a cause of traveler's diarrhea. *J. Am. Med. Assoc.* 217:1359–1361.
2. Brodsky, R. E., H. C. Spencer, and M. G. Schultz. 1974. Giardiasis in American travelers in the Soviet Union. *J. Infect. Dis.* 130:319–323.
3. 1979. Intestinal parasite surveillance. *In* Annual Summary, 1978, Center for Disease Control.
4. Friend, D. S. 1966. The fine structure of *Giardia muris. J. Cell Biol.* 29:317–332.
5. Holberton, D. V. 1973. Fine structure of the ventral disk apparatus and the mechanism of attachment in the flagellate *Giardia muris. J Cell Sci.* 13:11–14.
6. Holberton, D. V. 1974. Attachment of *Giardia*—a hydrodynamic model based on flagellar activity. *J. Exp. Biol.* 60:207–221.
7. Landau, L. D., and E. M. Lifshitz. 1979. Fluid Mechanics. Pergamon Press, Ltd., Oxford. 70–71.
8. Lighthill, J. 1975. Mathematical Biofluiddynamics. *Soc. Indust. Appl. Math. (Phila).* 45–62.
9. Gray, J., and G. J. Hancock. 1955. The propulsion of sea-urchin spermatazoa. *J. Exp. Biol.* 32:802–814.