GEOTAXIS IN MOTILE MICRO-ORGANISMS

BY A. M. ROBERTS

Department of Physics, Guy's Hospital Medical School, London S.E.1

INTRODUCTION

Many of the free-swimming protozoa, such as *Paramecium* and *Euglena*, are known to swim preferentially upwards in the absence of other stimuli (i.e. exhibit negative geotaxis) despite the fact that they are more dense than water. Some authors have suggested that contractile vacuoles or other organelles act like statoliths (Lyon, 1905) although there is no real evidence to support this hypothesis. Wager (1911) has suggested that the rear end of *Euglena* is heavier than the front because of density variation within the organism, thus causing it to tilt and move upwards; Dembowski (1931) has outlined a similar mechanism for *Paramecium*. In contrast, other motile organisms are known to exhibit positive geotaxis; rabbit spermatozoa, for example, move preferentially downwards, although there is no significant difference in swimming velocity between upward-moving and downward-moving organisms (Branham, 1969). Jahn & Bovee (1967) have concluded in a recent review that geotaxis is probably mechanical in nature, but point out that no detailed theory has been proposed or investigated.

In this paper it is shown that the variable-density orientation cannot completely account for geotaxis in ciliates such as *Paramecium*, and it is suggested that the principal cause is a hydrodynamic interaction between the organisms and the medium, the magnitude of which is determined by the size and shape of the organism. Many of the motile protozoa, for example, are characteristically wider at the rear than at the front; because larger objects tend to fall more rapidly in a viscous fluid, the rear tends to sink below the front, thus producing an upward orientation. The nature of the hydrodynamic interaction is investigated using small-scale models falling through glycerol, and the results are compared with similar experiments on immobilized paramecia. A general theory is developed for describing the motion of these organisms under gravity, and the predictions of the theory are compared with measurements on suspensions of paramecia in long, vertical columns. The observations that low temperatures (Moore, 1903) and bright sunlight (Fox, 1925) induce positive geotaxis in *Paramecium* are interpreted in the light of the theory. Finally, the possible importance of geotaxis in other motile micro-organisms such as bacteria and spermatozoa is considered.

THEORIES OF GEOTAXIS

(i) *Variable-density orientation*

When a body of uniform density and arbitrary shape is immersed in a liquid the upthrust on the body acts through the centre of gravity, and there is no tendency for buoyancy forces to rotate the body. If there is a variation in density, however, a

torque is experienced, the magnitude of which depends upon the density differences within the body. The orientation produced by a region of volume V and density ρ can readily be estimated. If the region is a distance L from the centre of gravity of the organism the turning moment is $VL(\rho - \bar{\rho})g \sin \theta$, where $\bar{\rho}$ is the mean density of the organism, g is the acceleration due to gravity and θ is the inclination of the long axis of the organism to the vertical (Fig. 1). If the viscous torque per unit angular velocity opposing this rotation is G, the rate of orientation is

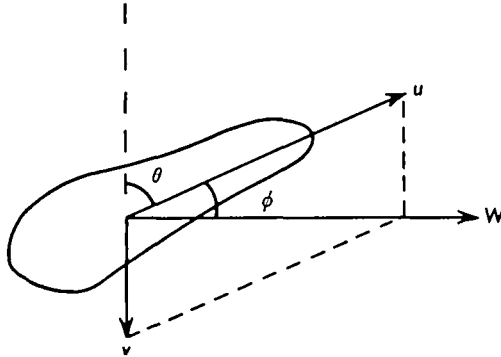$$d\theta/dt = (VL/G)(\rho - \bar{\rho})g \sin \theta. \tag{1}$$

Fig. 1. Diagram showing an organism being propelled at velocity u by its own motile apparatus, and falling under gravity with velocity v. The resultant velocity is W at angle ϕ to the longitudinal axis.
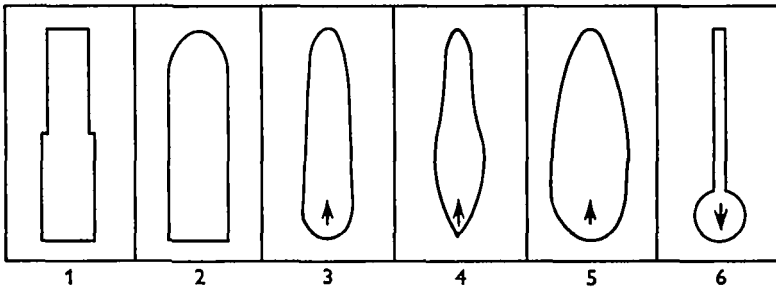

Fig. 2. The figures show the stable orientations assumed by small aluminium scale models (of uniform density) falling under gravity through glycerol at low Reynolds number ($\sim 10^{-3}$). All models rotate until falling wide end first. Models 3–6 represent *Peranema*, *Paramecium*, *Chlamydomonas* and a spermatozoon respectively; the arrows indicate the normal swimming direction of these organisms.

(ii) *Hydrodynamic orientation*

Since the density of a swimming organism is generally greater than that of the surrounding medium, it tends to sink under gravity, and the body strikes the liquid at an off-axis angle (Fig. 1). If the organism exhibits front–rear asymmetry a hydrodynamic torque may be produced which will tend to align it either vertically upwards or vertically downwards.

The characteristics of the hydrodynamic torque can be demonstrated using small scale models falling through a viscous fluid. Fig. 2 shows the stable orientations assumed by aluminium models of uniform density (some of which represent various

protozoa) falling through glycerol. The gravity-induced torque in the protozoa is invariably in such a direction as to orientate the organism anterior end uppermost. Inspection of the velocity vectors in Fig. 1 shows that in a moving organism the direction of the viscous torque is also in such a direction as to bring the anterior region upwards.

It is difficult to assess the magnitude of the gravity-induced orientation in the protozoa, since in general they possess no axis of symmetry. However, if the orientation rates of immobilized organisms falling under gravity are measured, then, provided Reynold's number is sufficiently small, all forces and torques will be proportional to the first power of the velocity (Happel & Brenner, 1965). It is shown in Appendix A that, provided certain approximations are made, the rate of orientation in a swimming organism is given by

$$\frac{d\theta}{dt} = -\beta \sin \theta, \tag{2}$$

where β is the instantaneous orientation rate for a falling immobilized organism when horizontal. Thus the orientation rate is independent of swimming velocity.

The distribution of organisms under gravity

The resultant motion of an organism under either of the two orientating mechanisms discussed above consists of three components: the swimming velocity (u), the steady downward fall under gravity (v), and the gravity-induced curvature of the trajectories described by equations (1) and (2). In addition, the frequent random changes in swimming direction exhibited by many organisms must be taken into account. It is shown in Appendix B that if a number of simplifying assumptions are made the distribution of organisms with depth is expected to be exponential, with a scale depth (the depth in which the density of organisms has fallen to 37 % of the surface value) given by

$$\delta = \frac{u\tau}{4\left(\dfrac{\beta\tau}{2} - \dfrac{v}{u}\right)}, \tag{3}$$

where τ is the mean time between re-orientations. If the trajectories curve upwards β is taken to be positive, and if $\beta\tau/2 > v/u$ the organisms will exhibit negative geotaxis. If $\beta\tau/2 < v/u$ the organisms will sink to the bottom, and δ is then the scale height measured from the bottom in the upward direction. If

$$\frac{\beta\tau}{2} \gg \frac{v}{u}$$

for a particular organism then equation (3) reduces to

$$\delta = u/(2\beta). \tag{4}$$

RESULTS

1. Observations on immobilized paramecia

Paramecium caudatum was grown in a boiled hay culture medium to which dried milk powder was occasionally added. Specimens were immobilised by adding a few drops of 5 mM-NiCl$_2$ to a few millilitres of culture medium, and were observed with a

travelling microscope as they fell through the medium. Most organisms fell anterior end upwards with velocities in the range 0·01–0·02 cm sec^{-1} at 21 °C. The rate at which organisms re-oriented on falling was very much more variable, however, and some organisms did not fall with their long axes vertical. Such specimens were usually seen to be very deformed due to the action of nickel chloride. The re-orientation rates were determined by measuring the time taken (t) for rotation from $\theta = 45°$ to $\theta = 135°$ (Fig. 1); the relation between β and t is given (integrating equation (2) by $\beta = 1·76/t$. For most organisms β lay in the range 0·01–0·05 rad sec^{-1}. Similar results have been obtained by Kuznicki (1968).
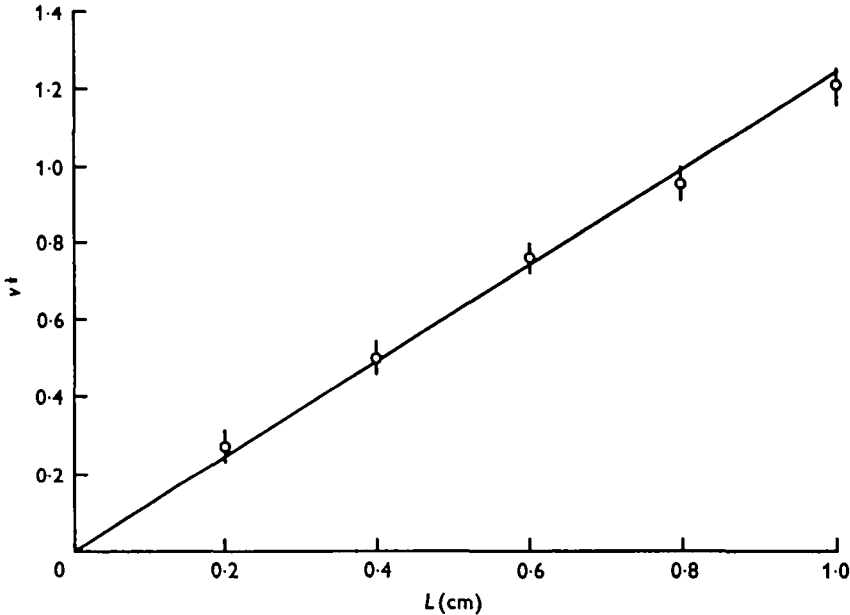

Fig. 3. The square root of the falling velocity for models of various lengths. The shapes are all identical (model 1 of Fig. 2).

2. Scale model results

The first aim of the scale-model experiments was to test the validity of the scaling equations derived in Appendix C for bodies of arbitrary shape. Figs. 3 and 4 show the relation between the terminal velocities and orientation rates of a number of models of the same shape (model 1 of Fig. 2) but different sizes, and the model length. Agreement with theory is satisfactory over the measured range. In addition, time-sequence photography of falling models showed that the instantaneous rate of turning depended upon the angle of orientation to the vertical in the manner predicted by equation (2) to within an upper error limit of 10%.

Scale models of slightly different shapes were constructed to represent *Paramecium* (varying between models 3 and 5 in Fig. 2). Such axially symmetrical models are unlike the real organism in that *Paramecium* has a non-symmetrical body; however, since the organism normally spins rapidly about its long axis as it moves the orientational response will depend upon the average shape of the organism about this axis, which will be symmetrical. The terminal velocities and orientation rates of these

models were determined, and the values were scaled to the mean length of *Paramecium* (taken to be 220 μ). The density of *Paramecium* was taken to be 1·05 g cm^{-3} (after Lyon, 1905) and the viscosity of water was taken to be 10^{-2} poise at 20 °C. The scaled terminal velocities of all the models fell within the range 0·01–0·03 cm sec^{-1}, whereas the scaled orientation rates were found to be very susceptible to small changes in shape, varying between 0·04 and 0·30 rad sec^{-1} for the models used. The turning rate for the most reasonable shape (model 4) was 0·04 rad sec^{-1}, which is sufficient to account for the behaviour of the immobilized organisms described in the previous section.
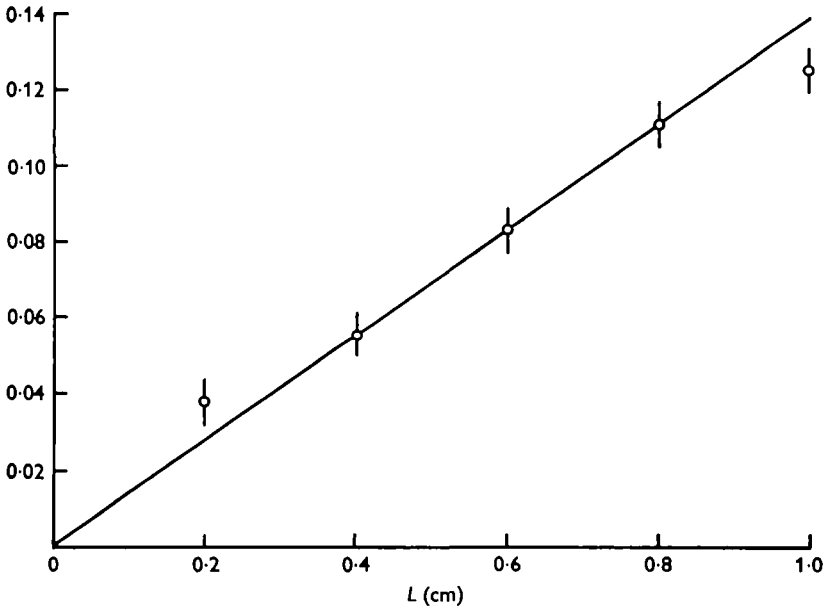

Fig. 4. The reciprocal of the orientation time (t) for models of various lengths. The shapes are all identical (model 1 of Fig. 2).

3. *The distribution of* Paramecium *in long, vertical columns*

Paramecia were taken from the culture medium and washed several times in distilled water containing 4 mM-KCl and 1 mM-CaCl$_2$, and put into long, vertical tubes containing the same medium. It was found necessary to immerse the tubes in a large, stirred water bath to inhibit the formation of convection currents within the tubes. Under these conditions paramecia readily aggregated at the top of a 20 cm water column in about 10–15 min. When conditions were steady, small (10^{-2} ml) samples were drawn from the column at various depths into a capillary tube, and the number of entrained organisms was counted with a low-power microscope. A typical depth distribution is shown in Fig. 5. The distributions were also measured routinely by photographing the column, and counting the density at various positions on the film using a travelling microscope.

Control experiments were performed with a thin layer of oil on top of the water column to reduce the diffusion of gases into and out of the water, which might affect the response of the organisms. No differences were noted in the distributions of

organisms in these tubes and in tubes without the oil film, even over periods of several days, and the columns were in general left open to the atmosphere during the experiments.

It was noted that the measured density distribution could not be fitted to a single exponential curve (Fig. 5). This probably reflects slight differences in the characteristics (velocity and shape) of the population as a whole, so that a range of scale depths is present. The scale depth of the best-fit curve in the surface region is $1 \cdot 3$ cm,
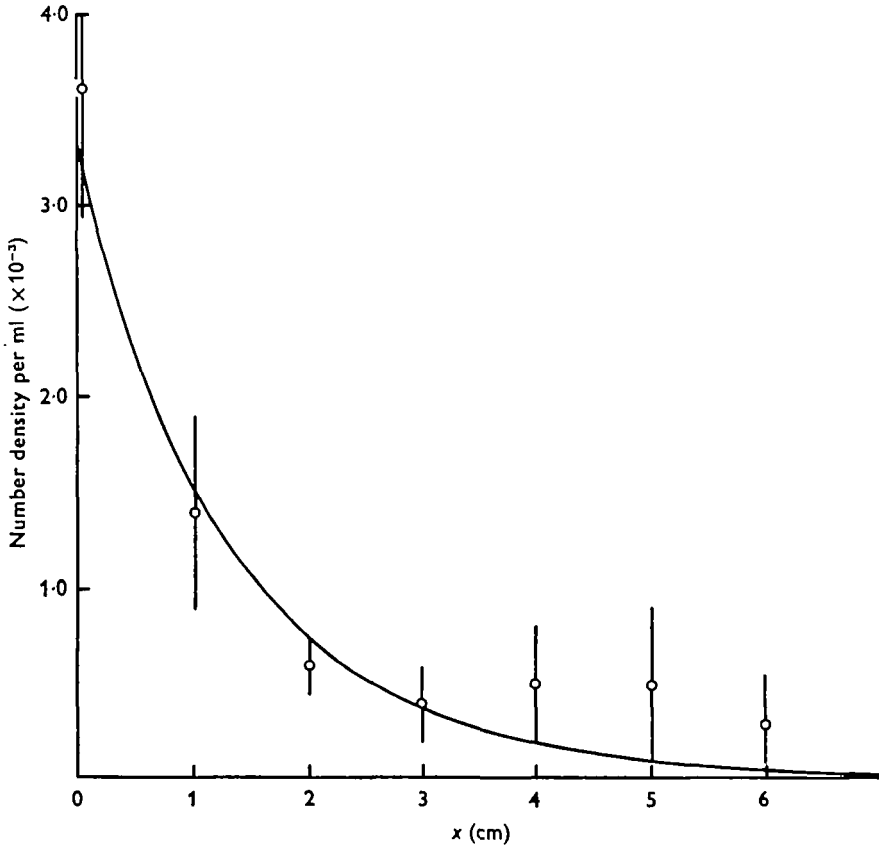

Fig. 5. The measured density distribution of *Paramecium* in a long vertical water column of diameter 3 cm. The solid line is the best-fit exponential curve (scale depth $1 \cdot 3$ cm).

and equation (4) shows that the required value of β to produce this distribution (taking $u = 0 \cdot 1$ cm sec^{-1}, and noting that τ is generally greater than 20 sec) is about $0 \cdot 04$ rad sec^{-1}. This value lies within the range of experimentally determined orientation rates.

It was found that if cultures of paramecia were diluted ($1 : 4$) with distilled water and placed in vertical tubes, the gravitational response varied from one culture to another, ranging from strongly geonegative to strongly geopositive. Although no significant differences in either shape or mean velocity could be detected from one culture to another, the re-orientation time τ was markedly less in the geopositive cultures. On leaving these cultures to stand τ slowly increased, and after 1 or 2 days all the paramecia had risen to the top of the column. This behaviour is predictable from equa-

tion three; the condition for the downward taxis to be replaced by an upward one is that $\beta\tau/2 = v/u$. The measured value of τ at the transition time was about 5 sec (measured by timing the intervals between re-orientations observed by microscope) and $u \sim$ 0·1 cm sec^{-1}, giving $\beta \sim$ 0·04–0·08 rad sec^{-1}, in reasonable agreement with the previous estimates. It is possible that the frequent re-orientations of the geopositive paramecia were related to the high concentration of food particles and bacteria in the medium, and when these paramecia were thoroughly washed in the standard medium the anomalous behaviour disappeared.

Brief experiments were conducted on suspensions which were cooled to temperatures just above 0 °C. Although no precise measurements were taken because of the difficulties in maintaining a sufficiently constant temperature to prevent convection currents in the column, it was found that the scale depth first decreased (the animals tending to congregate more noticeably at the top) and then, at a temperature of about 2 °C, increased rapidly, the organisms eventually ending up at the bottom of the tube. In terms of equation (3) this behaviour could be brought about by a decrease in swimming velocity with decrease in temperature, which is a well-known property of cilia (Holwill, 1966) or by a decrease in re-orientation time τ. Since there is no reason to suppose that τ should decrease, the swimming velocity is probably the important parameter in this case.

DISCUSSION

Having obtained a quantitative measure of the gravity-induced orientation in live paramecia, it is possible to assess the importance of the variable-density orientation in this organism. The greatest departure in density from the mean value probably occurs in the contractile vacuoles when filled with water prior to expulsion. Assuming a vacuole diameter of 20 μ (an upper limit), $(\rho - \bar{\rho}) =$ 0·05 g cm^{-3}, $L =$ 50 μ and $G = 2$ 10^{-8} dyne cm rad^{-1} sec (Roberts, 1970) then $\beta =$ 0·05 rad sec^{-1} (equation (1)). Thus the variable-density orientation would be sufficient to explain the results on *Paramecium* provided the anterior vacuole were filled with water while the rear vacuole remained collapsed. In practice, however, the two vacuoles alternately expel water and fill up again in a time very much shorter than that required to establish the gravitational distribution, so that any orientating effects would be very much smaller than this calculated value. The other small differences in density are probably insufficient to produce any noticeable effects, and it is concluded that the variable-density orientation is unlikely to be significant in *Paramecium*.

In contrast, the experimental results on immobilized paramecia and on scale models clearly indicate that the hydrodynamic forces are sufficient to account for the observed geotaxis. Furthermore, since the rotations produced by both the variable-density and hydrodynamic torques are proportional to the length of the organism (equations (1) and (C4): it can be shown by dimensional arguments that G is proportional to L^3)) the hydrodynamic torque will probably always be the greater of the two in ciliates of this type, no matter what the size of the organism.

The form of equation (3) shows that the gravitational response depends on several environmental factors. In particular, any agents which cause changes in swimming velocity will affect the vertical distribution of organisms. Thus the induction of positive geotaxis in *Paramecium* by sunlight is linked by Fox (1925) with the presence of

ultraviolet light, and Saier & Giese (1966) have shown that ultraviolet light produces a steady decrease in swimming velocity. Temperature changes probably affect the distribution by changing the swimming velocity. The presence of obstructions in the medium will also modify the distribution by affecting the mean travelling time τ.

Negative geotaxis may be of considerable survival value to free-swimming organisms which have to move to find food. With no gravity-induced orientation, equation (3) shows (setting $\beta = 0$) that in the absence of convection currents the organisms would be confined to a bottom layer of scale height

$$\delta = u^2\tau/(4v).$$

Assuming $\tau = 5$ sec for *Paramecium* in a typical culture medium, the scale height is about 1 cm. Thus in a deep pond only a very small fraction of the available volume could be sampled. In contrast, organisms exhibiting negative geotaxis can disperse throughout the whole medium, thereby taking maximum advantage of the available food supplies (Carlson, 1962).

Many protozoa move in such a direction that the wider, heavier part of the organism is at the rear. This certainly does not facilitate streamlining, since at these low Reynold's numbers (less than 10^{-1}) the power required to propel the organism along its long axis is the same in either direction. This type of shape may have evolved as a direct result of the advantages conferred on these organisms by the action of the gravity-induced torque. Thus the geotactic response may be more important than has hitherto been considered.

It is of interest to consider the possible occurrence and importance of a geotactic response in smaller swimming animals such as bacteria. The present results on models are not directly applicable to such organisms, since the viscous forces on the flagella have not been considered. The flagella may themselves cause orientation, since in an immobilized organism the viscous drag on them will tend to make the cell rotate about the point of attachment. Although no detailed investigations on gravitational effects in bacteria have been reported (Weibull, 1960), the scaling equations given in Appendix C enable some general conclusions to be drawn. Since β is proportional to the length of the organism for a given shape, the orientation rates in motile bacteria less than $10-20\ \mu$ in length will be very small, and geotaxis is unlikely to be important in bacteria living in extensive media such as ponds, where convection currents would quickly disrupt any gravitational distribution. However, bacteria living and moving in thin liquid films, where disruptive influences will be minimal, may well be influenced by gravity, and further investigation is required in this field.

Finally, the general ideas outlined in this paper are applied to spermatozoa, which differ from the protozoa in that the anterior region (the head) is much larger than the tenuous tail. Thus an immobilized spermatozoon should fall head down (Fig. 2). In addition, the head is of greater density than the tail region (Benedict, Schumaker & Davies, 1967) thus providing a reinforcing orientating torque. A lower limit for the orientation rate can be found by noting that if the spermatozoon were the same shape as *Paramecium*, and $50\ \mu$ in length, the orientation rate would be about 0.01 rad sec^{-1} (equation (C4)). With a typical swimming velocity of $50-100\ \mu$ sec^{-1}, which is probably very much greater than the sinking velocity under gravity, most of the sperm in a suspension would be confined to the bottom layer of thickness $2.5-5$ mm (equa-

tion 4). Since the spermatozoon has greater front–rear asymmetry than *Paramecium* the scale depth is likely to be rather smaller than this.

There is no doubt that sperm suspensions in normal concentration do not settle to this extent, and the explanation probably lies in the high sperm concentrations in these suspensions. At a typical concentration of 10^9 cm^{-3} the mean distance between adjacent organisms is about 10 μ. Since mammalian sperm are typically 50 μ long the motion of the organism will be very restricted, and free orientation under gravity will be impossible. The present distribution theory is therefore not applicable in this case.

SUMMARY

1. It is suggested that the principal cause of geotaxis in many motile micro-organisms is a gravity-induced hydrodynamic torque, the size of which depends upon the shape of the organism. The nature of the torque has been investigated using small scale models.

2. An expression for the distribution of organisms in long, vertical columns has been derived.

3. The distribution of *Paramecium* in long, vertical columns has been determined, and it has been shown that the strength of the hydrodynamic interaction is sufficient to account for the negative geotaxis usually exhibited by this organism. The induction of positive geotaxis in certain circumstances has been considered.

4. The survival value of negative geotaxis for free-swimming organisms in search of food may explain the characteristic shape of many protozoa.

REFERENCES

BENEDICT, R. C., SCHUMAKER, V. N. & DAVIES, R. E. (1967). The buoyant density of bovine and rabbit spermatozoa. *J. Reprod. Fert.* **13**, 237–49.

BRANHAM, J. M. (1969). Movements of free-swimming rabbit spermatozoa. *J. Reprod. Fert.* **18**, 97–105.

CARLSON, F. D. (1962). A theory of the survival value of motility. In *Spermatozoan Motility*, pp. 137–46. Ed. D. W. Bishop; Washington: American Association for the Advancement of Science.

DEMBOWSKI, J. (1931). Die Vertikalbewegungen von *Paramecium caudatum. Archiv für Protistenkunde*, **74**, 1, 153–87.

FOX, H. M. (1925). The effect of light on the vertical movement of aquatic organisms. *Proc. Camb. Philos. Soc. Biol. Sci.* **1**, 219–24.

HAPPEL, J. & BRENNER, H. (1965). *Low Reynolds number Hydrodynamics.* Englewood Cliffs, N.J.: Prentice-Hall Inc.

HOLWILL, M. E. J. (1966). Physical aspects of flagellar movement. *Physiol. Rev.* **46**, 696–785.

JAHN, T. L. & BOVEE, E. C. (1967). Motile behaviour of protozoa. In *Research in Protozoology*, vol. 1, 39–198 (editor T. T. Chen). Oxford: Pergamon Press.

LYON, E. P. (1905). On the theory of geotropism in *Paramecium Am. J. Physiol.* **14**, 421–32.

KUZNICKI, L. (1968). Behaviour of *Paramecium* in gravity fields: I. Sinking of immobilised specimens. *Acta Protozool.* **6**, 109–17.

MOORE, A. (1903). Some facts concerning geotropic gatherings of *Paramecium Am. J. Physiol.* **9**, 238–44.

ROBERTS, A. M. (1970). Motion of *Paramecium* in static electric and magnetic fields. *J. theor. Biol.* **27**, 97–106.

SAIER, F. L. & GIESE, A. C. (1966). Action of ultra violet radiation upon ciliary movement in *Paramecium. Expl Cell Res.* **44**, 321–31.

WAGER, H. (1911). On the effect of gravity upon the movements and aggregation of *Euglena viridis* and other microorganisms. *Phil. Trans. R. Soc. Lond.* B **201**, 333–90.
WEIBULL, C. (1960). Movement: in *The Bacteria*, Vol. I., p. 153, ed. I. C. Gunsalus and R. Y. Stanier. New York and London: Academic Press.

APPENDIX A. HYDRODYNAMIC ORIENTATION
IN A SWIMMING ORGANISM

It has been shown that the orientation rate of an immobilized organism can be written in the form

$$d\theta/dt = -\beta \sin \theta,$$

where β (rad sec^{-1}) is a constant. The resultant velocity, W, of a swimming organism moving through the medium is given (by resolving velocity components) as

$$W = (u^2 + v^2 - 2uv \cos \theta)^{\frac{1}{2}} \qquad (A1)$$

and is directed at an angle ϕ to its longitudinal axis, where

$$\tan \phi = v \sin \theta/(u - v \cos \theta) \qquad (A2)$$

and θ is the angle between the longitudinal axis and the vertical (Fig. 1). Assuming that all forces and torques are proportional to velocity, the orientation rate in a swimming organism is given by

$$d\theta/dt = -\beta(W/v) \sin \phi$$

which, using equations A1 and A2, reduces to

$$d\theta/dt = -\beta \sin \theta$$

indicating that in this approximation the rate of orientation is independent of swimming velocity. For simplicity it is assumed that the falling velocity v is independent of orientation, although the paramecium model described in this paper has a 30% velocity variation with orientation.

APPENDIX B. THE DISTRIBUTION OF RANDOMLY MOVING
ORGANISMS IN LONG, VERTICAL COLUMNS

The distribution is derived subject to the following assumptions:

1. That the organisms normally travel in straight lines with a velocity u, and that they re-orient very rapidly in new directions, chosen at random, every τ seconds.

2. That the effect of gravity is to produce a steady downward sinking of velocity v, and to curve the paths of the organisms with an orientation rate given by

$$d\theta/dt = -\beta \sin \theta \qquad (B1)$$

where β is positive for trajectories which curve upwards.

3. That hydrodynamic interactions between organisms can be neglected.

If an organism starts moving at an angle θ to the vertical, the distance travel led vertically upwards in time τ can be found by solution of equation (B1). Since the organism has also fallen a distance $v\tau$ downwards, the net upward distance travelled is

$$y = (u/\beta) \log_e[\sin \theta \cosh (\log_e \tan \tfrac{1}{2}\theta - \tau\beta)] - v\tau. \qquad (B2)$$

It is possible to define a mean free path λ and a mean time τ for a given population, where $\lambda = u\tau$. If β is positive the probability of its moving upwards (p_u) during the next mean free path is greater than that of its moving down (p_d). If x is the vertical

depth in the medium, and $n(x)\, dx$ is the differential density distribution with depth, in the steady state as many will move up as move down, so that

$$n(x)\, p_d = n(x+\lambda')\, p_u = [n(x)+dn/dx.\lambda']\, p_u,$$

where λ' is the component of the mean free path in the x-direction. It can readily be shown by integration that $\lambda' = \frac{1}{2}\lambda$. Thus

$$\frac{dn}{n} = -2(p_u-p_d)\, dx/(\lambda p_u)$$

and

$$n(x)\, dx = n_0 \exp\left(-2\Delta p x/(p_u\lambda)\right)\, dx,$$

where $\Delta p = p_u-p_d$. Then the density distribution should be exponential with a scale depth δ given by

$$\delta = p_u\lambda/(2\Delta p).$$

Equation (B2) can now be used to derive the values of p_d and p_u. If $y = 0$ in this equation the resulting value of θ represents the direction which separates the upward from the downward moving organisms. If re-orientation occurs in all directions at random, the probabilities of moving up or down are defined by the solid angle ω subtended by the two regions. Since the solid angle subtended by a cone of half-angle θ is

$$\omega = 2\pi(1-\cos\theta),$$

then

$$p_u = \frac{1+\cos\theta}{2}; \quad p_d = \frac{1-\cos\theta}{2}; \quad \Delta p = \cos\theta.$$

Since θ cannot readily be found from equation (B2) it is noted that in general the curvature of the paths is small, and θ does not vary greatly from $90°$. With this simplification, and setting $y = 0$, equation (B2) can be written in the form

$$\theta = \frac{\pi}{2}+\frac{\beta\tau}{2}-\frac{v}{u}.$$

Then

$$p_d \sim p_u = 0.5$$

and

$$\Delta p = \frac{\beta\tau}{2}-\frac{v}{u}$$

and the scale depth of the distribution is

$$\delta = \frac{u\tau}{4\left(\dfrac{\beta\tau}{2}-\dfrac{v}{u}\right)}. \tag{B3}$$

This results shows that as the mean free time gets longer the orienting effect of gravity becomes more important than the direct sinking effect.

In a clean medium the mean free path of *Paramecium* becomes comparable with the scale depth of the distribution, and the use of the present diffusion treatment is no longer valid. In this case a more appropriate approximation is one in which the mean free path is assumed to be infinitely large, and the organisms are considered to be moving in a semi-infinite medium bounded only at the upper or lower surface (depending on whether β is positive or negative, respectively), where all the re-

orientations occur. Neglecting the downward fall under gravity, the trajectories are described by equation (B1), and the problem is to find the number of organisms at any instant in a layer of thickness dx at depth x in the medium.

Let the number of organisms striking the upper surface be N cm^{-2} sec^{-1} (taking β to be positive). If all re-orientations occur at random, the number emitted per unit solid angle in any direction is $N/2\pi$ ster^{-1} cm^{-2} sec^{-1}. The number of organisms lying in dx at any instant depends upon the number of paths which cross the plane and the angle at which they cross it. Thus.

$$\frac{dn}{dx} = \frac{N}{2\pi} \frac{1}{u} \frac{d\omega}{\cos\theta},$$

where $d\omega$ is the solid angle subtended at the surface. Equation (B1) can be manipulated to show that

$$\sin\theta = \sin\phi \, \exp(x\beta/u),$$

where ϕ is the value of θ at $x = 0$. The total number of organisms at depth x is found by integrating over all values of ϕ: thus

$$\frac{dn}{dx} = \frac{N}{u} \int_0^{\phi_0} \frac{\sin\phi \, d\phi}{\sqrt{(1 - a^2 \sin^2\phi)}},$$

where

$$d\omega = 2\pi \sin\phi \, d\phi, \quad a = \exp(x\beta/u)$$

and

$$\phi_0 = \sin^{-1}(a^{-1}).$$

On integrating this gives

$$\frac{dn}{dx} = \frac{N}{ua} \log_e\left(\frac{1 + a^{-1}}{\cos\phi_0}\right)$$

which, for $x \gtrsim u/2\beta$, further reduces to

$$\frac{dn}{dx} = \frac{N}{ua^2} = \frac{N}{u} \exp(-2x\beta/u)$$

which is an exponential distribution of scale depth $\delta = u/2\beta$.

In addition to the curvature of the paths, gravity produces a steady downward velocity v which increases the scale depth. Most organisms found at a given depth will be describing trajectories for which $\theta \sim \frac{1}{2}\pi$ at that depth. The distance, d, fallen under gravity in the time taken for the organism to reach $\theta = \frac{1}{2}\pi$ is

$$d = (v/\beta) \log_e \tan(\frac{1}{2}\phi).$$

For $x \gtrsim u/\beta$ equation (B4) reduces to

$$\phi = \exp(-x\beta/u)$$

and

$$d = (v/\beta) \log_e [\frac{1}{2} \exp(-x\beta/u)].$$

Thus equation (B5) is more appropriately written

$$\frac{dn}{dx} = \frac{N}{u} \exp[-(2\beta/u)(x - d)]$$

which is an exponential distribution of scale depth

$$\delta = \frac{u}{2\beta(1 - v/u)}.$$

To summarize, the scale depth of organisms moving with a short mean free path is given by equation (B3). As the mean free path increases this result remains valid provided $(v/u) \ll 1$, although the form of the distribution then becomes more dependent on the precise way in which the organisms re-orient on striking the boundary.

APPENDIX C. SCALE MODELS AND SCALING EQUATIONS

The origin and characteristics of the hydrodynamic torque can be demonstrated by considering the motion of an asymmetric dumb-bell falling under gravity. Two spheres of the same density (ρ) but unequal radii $(a_1$ and $a_2)$ are connected by a light rigid rod of length L. The terminal velocity v of one sphere alone is found by equating the viscous force (given by Stokes's law) with the net downward gravitational force. Thus

$$6\pi\eta a v = \frac{4}{3}\pi a^3(\rho - \rho_0)g$$

and

$$v = \frac{2}{9}\frac{\rho - \rho_0}{\eta}g\, a^2, \tag{C1}$$

where η and ρ_0 are the viscosity and density of the medium respectively. Clearly the larger sphere falls faster, dragging the smaller one down with it, and the dumb-bell rotates to its stable falling position with the larger sphere beneath the smaller. Assuming that there are no hydrodynamical interactions between the spheres, and that Reynold's number $(\rho v L/\eta)$ is less than unity, Stokes's law can be applied to each sphere in turn, and it is readily shown that the terminal velocity in the stable position is

$$v = \frac{2}{9}\frac{\rho - \rho_0}{\eta}g\left(\frac{a_1^3 + a_2^3}{a_1 + a_2}\right) \tag{C2}$$

and that the orientation rate is given by

$$\frac{d\theta}{dt} = \frac{2}{9}\frac{\rho - \rho_0}{\eta}\frac{g}{L}(a_1^2 - a_2^2)\sin\theta. \tag{C3}$$

The orientation rate is clearly very much more dependent upon the shape of the model than is the falling velocity.

For more complex bodies, in which hydrodynamic interactions between various regions of the body are not negligible, equations similar to equations (C2) and (C3) will probably describe the falling motion. Thus scale models of these bodies should obey scaling equations of the form

$$\left.\begin{array}{l} \dfrac{v}{v_m} = \dfrac{\rho - \rho_0}{(\rho - \rho_0)_m}\dfrac{\eta_m}{\eta}\dfrac{L^2}{L_m^2}, \\[3mm] \dfrac{(d\theta/dt)}{(d\theta/dt)_m} = \dfrac{\rho - \rho_0}{(\rho - \rho_0)_m}\dfrac{\eta_m}{\eta}\dfrac{L}{L_m}, \end{array}\right\} \tag{C4}$$

where the subscript m refers to the model system, and L is a characteristic length of the model.