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On the Squirming Motion of Nearly Spherical Deformable Bodies through Liquids at Very Small Reynolds Numbers

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Summary

A spherical deformable body can swim, at very small Reynolds numbers, by performing small oscillations of shape. However, the mean velocity of translation is at most of the order of the square of the amplitude of the deformations. Three examples of swimming motions, in each of which the maximum surface strain is 1/3, are illustrated in Figures 1, 2 and 3. Even in the most efficient of the three (Fig. 2), the mean power required to obtain a given mean velocity is twenty times that given by Stokes' formula for the uniform motion of a rigid sphere under an external force. This ratio varies as the inverse square of the maximum surface strain.

With a view to adding to the data on which discussions of the mechanisms of propulsion of minute organisms can be based, we will investigate mathematically the problem of whether (and, if so, to what extent) a spherical deformable body, by performing small oscillations of shape, can progress through a liquid (in the absence of external forces) if all Reynolds numbers, based on the diameter of the body, the density and viscosity of the liquid, and on either the velocities or accelerations of deformation, are so small that all inertial forces are negligible compared with forces due to the distributions of pressure and viscous stress.

Then, if $\mathbf{v}$ is the velocity vector, p the pressure and μ the viscosity, the equations of motion are

$$(1) \qquad \operatorname{div} \mathbf{v} = 0, \qquad \operatorname{grad} p = \mu \nabla^2 \mathbf{v}.$$

These do not involve the time explicitly. This is connected with the fact that any new position and velocity of the boundary are taken up so slowly that they may be considered as re-determining the flow field with negligible lag.

We will discuss only motions with axial symmetry, so that the velocity field depends only on the two spherical polar coordinates (r, θ) and has only two components, say (u, v) in the directions r, θ increasing respectively. The fundamental solutions of (1) with axial symmetry are derived most easily from two immediately resulting equations, namely

$$(2) \qquad \frac{\partial}{\partial r}(r^2 u \sin \theta) + \frac{\partial}{r\,\partial \theta}(r^2 v \sin \theta) = 0, \qquad \nabla^4(ru) = 0.$$

Retaining only solutions which represent motions with a finite total energy, a complete list is easily deduced:

$$
\begin{aligned}
&u = P_0 r^{-2}, && v = 0; && \\
&u = P_1 r^{-3}, && v = \tfrac{1}{2} V_1 r^{-3}; && \\
&u = P_n r^{-n}, && v = (\tfrac{1}{2}n - 1) V_n r^{-n}, && n \geq 2; \\
&u = P_n r^{-n-2}, && v = \tfrac{1}{2}n V_n r^{-n-2}, && n \geq 2.
\end{aligned} \tag{3}
$$

Here P_n (cos θ) is the ordinary Legendre polynomial, and V_n is defined by equation

$$V_n = \frac{2}{\sin\theta}\int_{\cos\theta}^{1} P_n(t)\,dt = \frac{2}{n(n+1)} P_n'(\cos\theta)\sin\theta. \tag{4}$$

For $n \geq 1$, V_n is an odd function of θ vanishing at $\theta = \pi$ as well as at $\theta = 0$. We shall need the following explicit expressions:

$$V_1 = \sin\theta, \qquad V_2 = \sin\theta\cos\theta, \qquad V_3 = \tfrac{1}{4}\sin\theta\,(5\cos^2\theta - 1).$$

In practice it is convenient to use a moving origin for the spherical polar coordinates (r, θ), which remains roughly at the center of the body in any translation it may undergo, moving only along the axis of symmetry. This motion of the origin makes no difference to the equations of motion (1), since the inertial force associated with it is clearly equally negligible with those already neglected. The system of solutions (3) is therefore unchanged, but it is now necessary that, for any combination of them to have finite total energy, the solution

$$u = -U\cos\theta, \qquad v = U\sin\theta \tag{5}$$

be added to it, where U is the velocity of the origin.

The velocities u and v must, in axisymmetrical flow, be respectively even and odd functions of θ. It follows that their values on a sphere $r = a$ can be expanded in the forms

$$(u)_{r=a} = \sum_0^\infty A_n P_n, \qquad (v)_{r=a} = \sum_0^\infty B_n V_n. \tag{6}$$

(In fact, by (4), B_n is the n-th Legendre coefficient of $\frac{1}{2}\csc\theta\, d[(v)_{r=a}\sin\theta]/d\theta$.) It is easily seen that the only combination of solutions (3) and (5) satisfying the boundary conditions (6) is given by

$$
\begin{aligned}
u &= A_0 \frac{a^2}{r^2} P_0 + \tfrac{2}{3}(A_1 + B_1)\frac{a^3}{r^3} P_1 - U\cos\theta \\
&\qquad + \sum_2^\infty \left(\tfrac{1}{2}n\frac{a^n}{r^n} - \left(\tfrac{1}{2}n - 1\right)\frac{a^{n+2}}{r^{n+2}}\right) A_n P_n, \\
v &= \tfrac{1}{3}(A_1 + B_1)\frac{a^3}{r^3} V_1 + U\sin\theta \\
&\qquad + \sum_2^\infty \left(\tfrac{1}{2}n\frac{a^{n+2}}{r^{n+2}} - \left(\tfrac{1}{2}n - 1\right)\frac{a^n}{r^n}\right) B_n V_n,
\end{aligned} \tag{7}
$$

where the velocity U of the origin is constrained to have the value

$$U = \tfrac{1}{3}(2B_1 - A_1). \tag{8}$$

The reason for this fundamental fact, that the boundary values of u and v on a sphere determine the velocity of translation of the origin, is that the second of the solutions of the type (3) in which u is proportional to P_1 and v to V_1, namely $u = P_1 r^{-1}$, $v = -\frac{1}{2}V_1 r^{-1}$, has infinite energy, and so is absent from (3). This solution arises in the Stokes uniform translation of a *rigid* sphere through a fluid, but this latter motion can be built up only by continued application of an external force. Motions generated simply by squirming must, on the contrary, have a finite total energy.

To describe the motion of a nearly spherical deformable body, we will suppose that the particle on its surface, which in the natural spherical shape has coordinates (a, θ), has the coordinates

$$R = a\left(1 + \sum_0^\infty \alpha_n(t)P_n\right), \qquad \Theta = \theta + \sum_1^\infty \beta_n(t)V_n \tag{9}$$

at time t. The coefficients $\alpha_n(t)$, $\beta_n(t)$ will be taken as oscillatory functions; each is, at any instant, equal in magnitude to the maximum surface strain[1] associated with its particular mode of deformation of the surface. This is easily shown since both $|dV_n/d\theta|$ and $|V_n \cot\theta|$, as well as $|P_n|$, have the maximum value 1 (attained, in all three cases, at $\theta = 0$ and π). Further, the origin will always be taken to move in such a way that $\alpha_1 = 0$, i.e. so that there is no component of translation of the body *relative* to the origin. What is left in (9) is then pure deformation, and the translation arising from it (which is to be determined) has the velocity U of the moving origin.

Now the velocity components at the point (R, Θ) of the surface must be

$$\begin{aligned} u(R, \Theta) &= \dot{R} = a\sum_0^\infty \dot{\alpha}_n P_n, \\ v(R, \Theta) &= R\dot{\Theta} = a\left(1 + \sum_0^\infty \alpha_n P_n\right)\sum_1^\infty \dot{\beta}_n V_n. \end{aligned} \tag{10}$$

If, as a first approximation, the squares of deformations are neglected, the boundary conditions (10) take the simpler form (6), with $A_n = a\dot{\alpha}_n$, $B_n = a\dot{\beta}_n$. The velocity field is therefore (7), with these substitutions made therein, and the velocity U of the origin is constrained to have the value

$$U = \frac{2}{3}a\dot{\beta}_1. \tag{11}$$

Thus the only mode of deformation which, to this first approximation, pro-

[1]Note that the principal surface strains are $(R/a) - 1 + (\partial\Theta/\partial\theta) - 1$ meridionally, and $(R/a) - 1 + (\Theta - \theta)\cot\theta$ azimuthally.

duces translation, is given by $R = a$, $\Theta = \theta + \beta_1 \sin \theta$, which is a purely tangential motion of the boundary without change of shape. The resulting velocity of the sphere is two thirds of the maximum tangential velocity of the boundary.

Also since, to this first approximation, the velocity of translation is proportional to the rate of deformation in this mode, it follows by integration that at any stage the total distance travelled is proportional to the total deformation in this mode. Hence, to this approximation, the distance travelled is constrained to remain very small.

Therefore, if the body *does* progress through the liquid as a result of suitable small oscillations in shape, its rate of progress must be at most of the order of the *squares* of the deformations. One is encouraged to carry the work on to this further stage, in which only the cubes of deformations are neglected, by Taylor's discovery (private communication) of a similar result for the motion produced by deformation of a progressive wave type to a plane boundary. (In work of this kind there is of course no inconsistency in continuing to use the fully linearised equation of motion, since the Reynolds number is small independently of the size of the disturbances.)

Expressing the values of u and v at the point (R, Θ), by Taylor's theorem, in terms of values on the sphere $r = a$, and ignoring cubes of deformations, we have from (9) and (10)

$$(12)\qquad \begin{aligned} &\left[u + a\left(\sum_0^\infty \alpha_n P_n\right)u_r + \left(\sum_1^\infty \beta_n V_n\right)u_\theta\right]_{r=a} = a \sum_0^\infty \dot{\alpha}_n P_n\,, \\ &\left[v + a\left(\sum_0^\infty \alpha_n P_n\right)v_r + \left(\sum_1^\infty \beta_n V_n\right)v_\theta\right]_{r=a} = a\left(1 + \sum_0^\infty \alpha_n P_n\right) \sum_1^\infty \dot{\beta}_n V_n\,. \end{aligned}$$

Substituting, for the values of u_r, u_θ, v_r, v_θ on the sphere in the quadratic terms on the left, the values of these derivatives for the first approximate solutions (7), with $A_n = a\dot{\alpha}_n$, $B_n = a\dot{\beta}_n$, we obtain for the boundary values of u, v on the sphere to a second approximation

$$(13)\qquad \begin{aligned} (u)_{r=a} &= a\left[\sum_0^\infty \dot{\alpha}_n P_n + \left(\sum_0^\infty \alpha_n P_n\right)\left(2 \sum_0^\infty \dot{\alpha}_n P_n + 2\dot{\beta}_1 P_1\right)\right. \\ &\qquad\left. - \left(\sum_1^\infty \beta_n V_n\right) \sum_0^\infty \dot{\alpha}_n \frac{dP_n}{d\theta}\right], \\ (v)_{r=a} &= a\left[\left(1 + \sum_0^\infty \alpha_n P_n\right)\left(\sum_1^\infty \dot{\beta}_n V_n\right) + \left(\sum_0^\infty \alpha_n P_n\right)\left(\dot{\beta}_1 V_1 + \sum_2^\infty 2n\dot{\beta}_n V_n\right)\right. \\ &\qquad\left. - \left(\sum_1^\infty \beta_n V_n\right) \sum_1^\infty \dot{\beta}_n \frac{dV_n}{d\theta}\right]. \end{aligned}$$

It follows that, if the right hand sides of (13) are expanded in the forms (6), where now A_n and B_n will be correct to a second approximation, the velocity field will be given by (7), and the velocity U of translation of the origin by (8). It is this latter quantity with which we are principally concerned. To calculate it, we need the coefficient of P_1 in $(u)_{r=a}$, and thus in products like $P_m P_n$ and $V_m\, dP_n/d\theta$, and also the coefficient of V_1 in $(v)_{r=a}$, and thus in products like $P_m V_n$ and $V_m\, dV_n/d\theta$. By expressing each of these four required coefficients as an integral, and hence (integrating by parts if necessary) as a Legendre coefficient of order m or n of a polynomial of order $n + 1$ or $m + 1$ respectively, it is easy to verify that each vanishes unless either $m = n + 1$ or $n = m + 1$, and to calculate it in these two cases. From this work the velocity of translation (8) is found to be

$$\begin{aligned} U = a\Big[&\frac{2}{3}\dot{\beta}_1 + \frac{2}{3}\alpha_0\dot{\beta}_1 - \frac{8}{15}\alpha_2\dot{\beta}_1 - \frac{2}{5}\dot{\alpha}_2\beta_1 \\ &- \sum_2^\infty (\alpha_n\dot{\alpha}_{n+1} + \dot{\alpha}_n\alpha_{n+1})\frac{2(n+1)}{(2n+1)(2n+3)} \\ &+ \sum_2^\infty \frac{-2n\dot{\alpha}_n\beta_{n+1} + (4n+6)\alpha_n\dot{\beta}_{n+1}}{(2n+1)(2n+3)} - \sum_2^\infty \frac{(4n+2)\alpha_{n+1}\dot{\beta}_n + (2n+4)\dot{\alpha}_{n+1}\beta_n}{(2n+1)(2n+3)} \\ &+ \sum_1^\infty \frac{4(n+2)\beta_n\dot{\beta}_{n+1} - 4n\dot{\beta}_n\beta_{n+1}}{(n+1)(2n+1)(2n+3)}\Big]. \end{aligned} \tag{14}$$

Thus, to this second order in the deformations, U is *not* the exact time-derivative of an oscillatory function. Therefore, by suitable combinations of the various possible modes of deformation, the body may make gradual progress, on balance, as time goes on. In fact, if the α_n and β_n are periodic functions with the same period T, then, using the symbol $\oint$ to indicate integration over a single period, the distance travelled during one period may be written as

$$\begin{aligned} \oint U\, dt = a\oint\Big[&\frac{2}{3}\alpha_0\, d\beta_1 - \frac{2}{15}\alpha_2\, d\beta_1 + \sum_2^\infty \frac{6(n+1)}{(2n+1)(2n+3)}\alpha_n\, d\beta_{n+1} \\ &- \sum_2^\infty \frac{2(n-1)}{(2n+1)(2n+3)}\alpha_{n+1}\, d\beta_n + \sum_1^\infty \frac{8}{(2n+1)(2n+3)}\beta_n\, d\beta_{n+1}\Big]. \end{aligned} \tag{15}$$

Note that, if α and β are periodic, integrals like $\oint \alpha d\beta$ may be made positive if on the whole α is larger when β is increasing than when β is decreasing. If α and β execute simple harmonic oscillations with amplitudes λ_1, λ_2 then the integral is maximized by taking the phase of α 90° degrees ahead of that of β, in which case $\oint \alpha d\beta = \pi\lambda_1\lambda_2$.

To assess which combination of modes is likely to produce translation most efficiently, it is now necessary to consider the work done by the body in the squirming motion. To a first approximation (which will be sufficient for our purposes) the rate at which the body does work, against the radial stress $p - 2\mu\partial u/\partial r$ and transverse stress $\mu(-\partial v/\partial r + v/r - \partial u/r\partial\theta)$ at the surface, is

$$P = \int_0^\pi \left[u\left(p - 2\mu\frac{\partial u}{\partial r}\right) + v\mu\left(-\frac{\partial v}{\partial r} + \frac{v}{r} - \frac{\partial u}{r\partial\theta}\right)\right]a^2 \sin\theta\, d\theta, \tag{16}$$

where u and v are given by (7) with $A_n = a\dot{\alpha}_n$, $B_n = a\dot{\beta}_n$, while the pressure p is deduced from the second of equations (1) in the form

$$p = \mu \sum_2^\infty \frac{n(2n-1)}{n+1} \dot{\alpha}_n \frac{a^{n+1}}{r^{n+1}} P_n . \tag{17}$$

Thus the body does work at a rate

$$\begin{aligned} P = \mu a^3 \int_{-1}^{1} \Bigg[& \left(\sum_0^\infty \dot{\alpha}_n P_n\right)\left(\sum_2^\infty \frac{n(2n-1)}{n+1} \dot{\alpha}_n P_n + 4 \sum_0^\infty \dot{\alpha}_n P_n + 4\dot{\beta}_1 P_1\right) \\ & + \left(\sum_1^\infty \dot{\beta}_n V_n\right)\left(2\dot{\beta}_1 V_1 + \sum_2^\infty (2n+1)\dot{\beta}_n V_n\right. \\ & \left.\left. + \sum_2^\infty \frac{1}{2} n(n+1)\dot{\alpha}_n V_n\right)\right] d(\cos\theta) \qquad (18) \\ = \mu a^3 \Bigg[& 8\dot{\alpha}_0^2 + \frac{8}{3}\dot{\beta}_1^2 + \sum_2^\infty \left\{ \frac{4n^2+6n+8}{(n+1)(2n+1)} \dot{\alpha}_n^2 \right. \\ & \left. + \frac{4}{2n+1}\dot{\alpha}_n\dot{\beta}_n + \frac{8}{n(n+1)}\dot{\beta}_n^2 \right\} \Bigg]. \end{aligned}$$

To get an idea of the efficiency of the squirming process it is reasonable to take the mean value $\bar{P}$ of P over a single period, and compare this mean power exerted by the body, which produces a mean velocity $\bar{U}$ given by expression (15) divided by the period T, with the Stokes value $6\pi\mu a(\bar{U})^2$ for the power which has to be applied externally to maintain a *rigid* sphere in *uniform* motion with velocity $\bar{U}$. Thus the efficiency is

$$\eta = 6\pi\mu a(\bar{U})^2/\bar{P}. \tag{19}$$

It is clear from (15) and (18) that this is of the order of the square of the deformations, and so we will consider the problem of maximizing η/ϵ^2, where ϵ is the maximum surface strain.

From the remarks made after (15) it is reasonable, at any rate at first, to seek to do this under the restriction that the displacement (10) consists of only two modes, simple harmonic and 90° out of phase. Now if the α_n and β_n corresponding to the two modes are $\lambda_1 \cos(2\pi t/T)$ and $\lambda_2 \sin(2\pi t/T)$, respectively, then the maximum strain is $\epsilon = (\lambda_1^2 + \lambda_2^2)^{1/2}$ since any $|P_n|$, $|dV_n/d\theta|$ or $|V_n \cot\theta|$ has the maximum 1 and achieves it at the same places $\theta = 0$ and π. Further, if the coefficient of

$$a \oint \lambda_1 \cos(2\pi t/T)\, d[\lambda_2 \sin(2\pi t/T)]$$

in (15) is C, and if the coefficients of the two non-vanishing $\dot{\alpha}_n^2$ and $\dot{\beta}_n^2$ in (18) are D_1 and D_2 respectively, then the efficiency η is, by (19),

$$\eta = \frac{6\pi\mu a[aC\lambda_1\lambda_2\pi/T]^2}{\mu a^3(2\pi^2/T^2)(D_1\lambda_1^2 + D_2\lambda_2^2)}. \tag{20}$$

The maximum of the ratio of this expression to the square $\lambda_1^2 + \lambda_2^2$ of the maximum surface strain ϵ, is reached when $(\lambda_1/\lambda_2)^4 = D_2/D_1$. For this case

$$\frac{\eta}{\epsilon^2} = 3\pi\left(\frac{C}{\sqrt{D_1} + \sqrt{D_2}}\right)^2. \tag{21}$$

The ratio η/ϵ^2 derived from (21) is tabulated in Table 1 for a large selection of the pairs of modes for which it is non-zero, indicating each by writing down the two coefficients from (10) which do not vanish therein, with the mode whose phase has to be *ahead* by 90° written first. It is seen that the most efficient combination is $\alpha_2\beta_3$, with $\eta/\epsilon^2 = 0.44$.

TABLE 1.

$\alpha_0\beta_1$	$\alpha_2\beta_3$	$\alpha_3\beta_4$	$\alpha_4\beta_5$	$\beta_1\alpha_2$	$\beta_2\alpha_3$	$\beta_3\alpha_4$	$\beta_1\beta_2$	$\beta_2\beta_3$	$\beta_3\beta_4$
.21	.44	.31	.22	.02	.005	.007	.35	.13	.07

It does not appear to be possible to obtain significantly higher ratios of the efficiency to the square of maximum surface strain by using more than two modes. For example one might seek to increase the amplitudes of the optimum modes α_2 and β_3, without increasing the maximum surface strain, by adding small multiples of other modes, 180° out of phase, to each. This would be most effective if the latter were modes requiring only small power to maintain them, but it appears that such modes are extremely ineffective in increasing the amplitude of the optimum modes without a corresponding increase in ϵ. Even when for example the additional mode β_4 is used (180° out of phase with α_2) which has the special advantage that the combinations $\alpha_2\beta_3$ and $\beta_3\beta_4$ both make positive contributions to the mean velocity, there is so little increase in the amplitude of α_2 for given ϵ, that what with the slight additional power required the ratio η/ϵ^2 cannot, apparently, be increased above 0.52. One may, alternatively, while retaining only two modes, seek increased efficiency by not taking them in simple harmonic motion. Actually the optimum shape of an oscillation curve has sharp peaks, but its adoption increases the efficiency of the $\alpha_2\beta_3$ mode only to 0.49.

Hence, as representative examples to be discussed in detail of the more efficient kinds of squirming motion, we may choose three from Table 1, namely $\alpha_0\beta_1$, $\alpha_2\beta_3$ and $\beta_1\beta_2$. These are illustrated in Figures 1, 2 and 3 respectively, for the case when the maximum surface strain is 1/3. In each case the meridian section of the body is shown at successive intervals of one eighth of the period T. The tangential motion of the surface can be followed in these figures by means of the eighteen marked particles, which in the unstrained spherical state (not shown) are distributed uniformly round the circumference. In each position the resulting instantaneous velocity of translation of the centre (the origin) is indicated; under each figure is noted the mean velocity $\bar{U}$, the mean power exerted $\bar{P}$, and the efficiency η. It may be remarked at once that the motion illustrated in Figure 3 is probably closest to a motion of which a small organism could be capable. (As throughout, μ denotes the viscosity.)

In Figure 1, the basic translation-producing motion $\dot{\Theta} = \dot{\beta}_1 \sin \theta$ is performed in the positive sense when the sphere is largest and in the negative sense when it is smallest; because, by (11), the velocity produced at any instant is

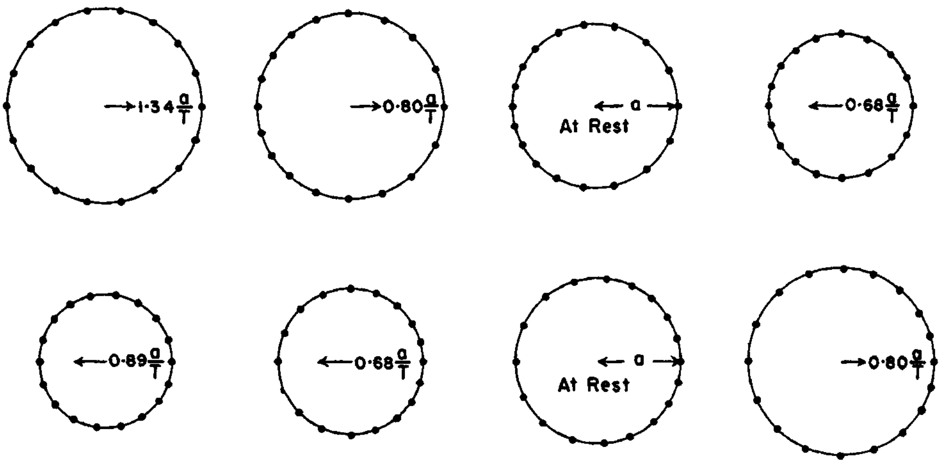

FIG. 1. Mode $\alpha_0\beta_1$ with maximum surface strain 1/3. Mean velocity of translation = 0.11 (a/T). Mean power exerted = 10 $(\mu a^3/T^2)$. Efficiency = 2.3 percent. Formula of deformation: $R = a[1 + 0.202 \cos (2\pi t/T)]$, $\Theta = \theta + 0.265 \sin \theta \sin (2\pi t/T)$.

proportional to the radius, progress results. In fact the inflated sphere pushes more effectively than the deflated sphere pulls, even though the sphere suffers no net strain after a complete cycle. However the energy required is rather large, because of the heavy dissipation of energy (indicated by the coefficient 8 of $\dot{\alpha}_0^2$ in (18)) associated with the "source" motion consequent on the volume changes. Figure 1 shows that the motion is essentially achieved by a constriction at the rear during the first quarter-period, a constriction at the front (completing the reduction in volume) during the second, an expansion at the rear during the third, and an expansion at the front during the last.

The motion of Figure 2, while more than twice as efficient, might be harder for a small organism to achieve than that of Figure 1. In it the maximum velocity is kept down to within 60% of the mean (thus reducing the power required) by eschewing the crude large scale motions associated with the mode β_1 in favor of the mode β_3, which involves backward tangential motion of the boundary ahead and behind, but forward motion in a central ring. Such motion produces forward velocity when the sphere is deformed into a prolate spheroid, but the contrary motion produces forward velocity when the sphere is deformed into an oblate spheroid. This is perhaps due to the fact that in the former shape the *area* of surface (before and behind) in which V_3 is positive exceeds that of the central ring in which it is negative, while in the latter shape this state of affairs is reversed. Hence at all stages of the motion the mean tangential movement of the boundary (weighted according to surface area) is backward—although again no net strain occurs in a complete cycle. Inspection of Figure 2 indicates that the motion may be regarded as produced by a constriction in a

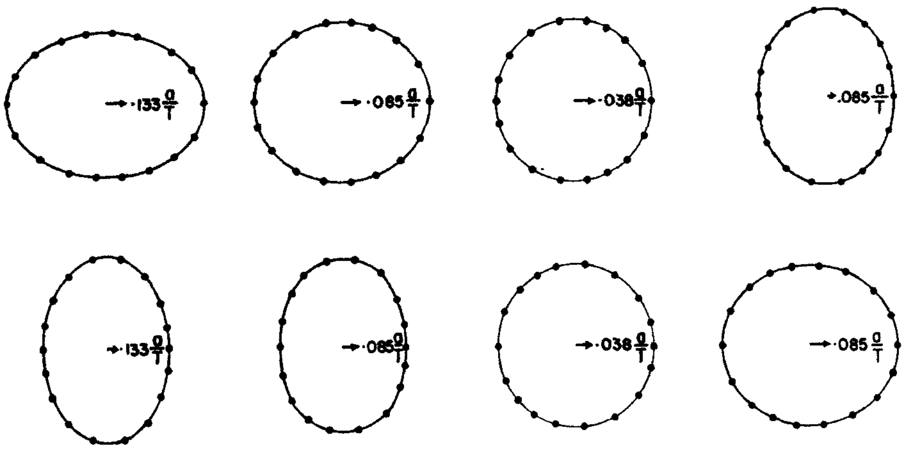

FIG. 2. Mode $\alpha_2\beta_3$ with maximum surface strain 1/3. Mean velocity of translation = 0.085 (a/T). Mean power exerted = 2.8 $(\mu a^3/T^2)$. Efficiency = 4.9 percent. Formula of deformation: $R = a[1 + (0.294 \cos^2 \theta - 0.098) \cos (2\pi t/T)]$, $\Theta = \theta + \sin \theta (0.337 \cos^2 \theta - 0.067) \sin (2\pi t/T)$.

disc at the rear, and in an annulus a little behind the front, during the first quarter period, followed by a constriction in the other parts of the surface (a disc at the front and an annulus a little ahead of the rear) in the second. In each case a slight expansion is found in the more central parts which are not being constricted, and the whole is followed by the reverse process in the same order.

The motion illustrated in Figure 3, on the other hand, involves no change of shape at all, but only tangential movements. Broadly speaking, the rear part of the surface is moved forward, followed by the front part; then the rear part is retracted, again followed by the front part. This is strongly reminiscent of the motion of worms, and it might be expected that if the efficiency could be calculated for a similar motion of a highly eccentric prolate spheroid it would prove much larger. It is to be observed from the figure that in such a motion the area of backward tangential movement at a typical instant (e.g. in the first position) is less than that of forward tangential movement half a period later, again although no net strain occurs in a cycle. It is this which makes progress possible.

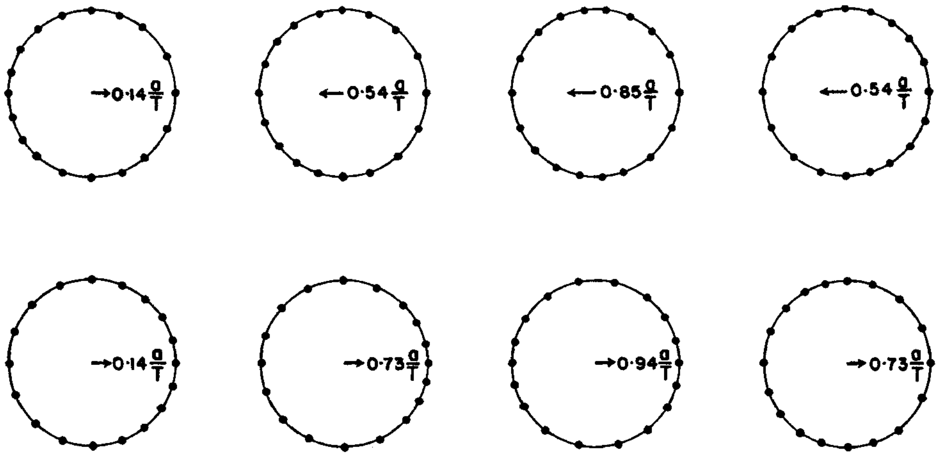

FIG. 3. Mode $\beta_1\beta_2$ with maximum surface strain 1/3. Mean velocity of translation = 0.09 (a/T). Mean power exerted = 4.1 $(\mu a^3/T^2)$. Efficiency = 2.3 percent. Formula of deformation: $R = a$, $\Theta = \theta + 0.214 \sin\theta \cos(2\pi t/T) + 0.127 \sin 2\theta \sin(2\pi t/T)$. (Of the three squirming motions illustrated this is the one which a small organism is likely to be able to reproduce most closely.)

It must be reiterated that it is essential for the accuracy of the theory that the Reynolds number, which can be written $\rho a^2/\mu T$, be small. It is probably sufficient in practice that this Reynolds number be less than 1, since difficulties such as those noted by Oseen in connection with the Stokes solution will not arise in motions like those considered here with finite total energy. In the motion illustrated in Figure 2 the Reynolds number could probably be somewhat higher, since the maximum velocity is considerably less than a/T.

It is worth remarking in conclusion that all the flows considered in this paper have negligible total axial momentum. For, first, the momentum outside the sphere $r = a$ is zero, because for any motion of an incompressible fluid the axial momentum between two concentric spheres is equal to the difference between the coefficients of P_1 in the values of $r^3 u$ on each sphere, and actually the coefficient of P_1 in the solutions (3) for u is proportional to r^{-3}. Hence the momentum of the fluid arises only from the regions lying between the true body surface and the exact sphere $r = a$, whence it is easily calculated to a first approximation as

$$(22) \qquad \rho a^4 \sum_1^\infty \frac{2(n+1)(\alpha_n\dot{\alpha}_{n+1} + \dot{\alpha}_n\alpha_{n+1}) + 4(\dot{\beta}_n\alpha_{n+1} - \alpha_n\dot{\beta}_{n+1})}{(2_n+1)(2_n+3)}.$$

Forces associated with the rate of change of this momentum (which, like all inertial forces, have been neglected in the above) are of order $\rho a^4 \epsilon^2/T^2$; the rate at which work is done by them is therefore of order $\rho a^5 \epsilon^3/T^3$. This bears to the power P (see (18)) required, at any instant, to counteract viscous forces, a small ratio of order $\rho a^2 \epsilon/\mu T = R\epsilon$. In the particular motions illustrated in Figures 1, 2 and 3 the actual maximum value of the said ratio is 0, 0.007R and 0 respectively.