THE PROPULSION OF SEA-URCHIN SPERMATOZOA

By J. GRAY* and G. J. HANCOCK†

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The movement of any short length of the tail of a spermatozoon of *Psammechinus miliaris* and the characteristic changes which it undergoes during each cycle of its displacement through the water can be described in terms of the form and speed of propagation of the bending waves which travel along the tail (Gray, 1953, 1955); the form of the wave depends on the maximum extent of bending reached by each element and on the difference in phase between adjacent elements. The object of this paper is to consider the forces exerted on the tail as it moves relative to the surrounding medium and to relate the propulsive speed of the whole spermatozoon to the form and speed of propagation of the bending waves generated by the tail. The mathematical theory of the propulsive properties of thin undulating filaments has recently been considered by Taylor (1951, 1952) and by Hancock (1953); the present study utilizes and extends their findings but approaches the problem from a somewhat different angle.

I. GENERAL THEORY

As in all self-propelling undulatory systems, the propulsion of a spermatozoon depends on the fact that the retarding effect of all the tangential forces acting along the body is compensated by propulsive components of forces acting normally to the surface of the body (Gray, 1953). Any region of the body eliciting from the water a reaction normal to its surface must have a component of motion normal to this surface, and—if this reaction is to have a forward propulsive component along the axis of translation of the whole cell—the region or element concerned must have an appropriate orientation to this axis (Gray, 1953). To apply this principle to the tail of a spermatozoon it is convenient to consider the forces exerted on a short element (δs) by virtue of the transverse displacement (V_y) impressed on it during the passage of a wave. As explained elsewhere (Gray, 1953), the orientation (θ) of an element to the axis of propulsion (xx_1) depends on the form of the wave and on the element's position on the wave; the element's transverse velocity (V_y) depends on the form of the waves and on their speed of propagation (V_w). An element of this type is shown in Fig. 1A; its velocity along the axis yy' is V_y and its surface is inclined to the axis (xx') of propulsion by an angle θ. The transverse displacement (V_y) has two components: (i) a tangential displacement ($V_y \sin\theta$), and (ii) a displacement ($V_y \cos\theta$) normal to the surface of the element; to both these displacements the water offers

* Department of Zoology, University of Cambridge.
† Department of Aeronautical Engineering, Queen Mary College, University of London.

resistance, and consequently the transverse displacement (V_y) elicits reactions tangential and normal to the surface of the element. The latter force (δN_y) has a component ($\delta N_y \sin\theta$) acting forward along the axis (xx') of propulsion; it is this component which counteracts the retarding effect of all the forces acting tangentially to the surface.

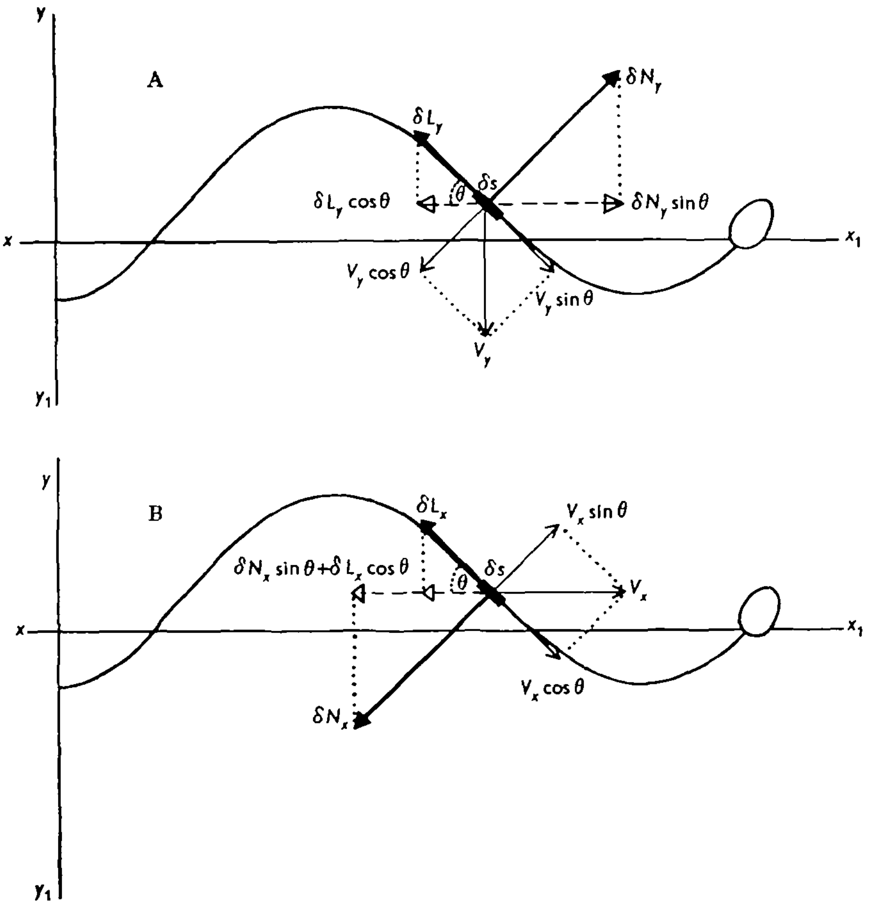

Fig. 1. A. Diagram illustrating the forces impressed on an element δs when moving transversely across the axis of progression (xx_1) at velocity V_y, the resultant propulsive thrust (δF_y) being $\delta N_y \sin\theta - \delta L_y \cos\theta$, where δN_y and δL_y are the reactions from the water acting normally and tangentially to the surface of the element, and θ is the angle of inclination of the element to the axis xx_1. For values of N_y and L_y see text. B. Diagram illustrating the forces impressed on an element when displaced along the xx_1 axis at velocity V_x, the resultant drag (δF_x) being $\delta N_x \sin\theta + \delta L_x \cos\theta$. The net propulsive thrust (δF) due to simultaneous transverse and forward movement is obtained by combining A and B.

As the dimensions of an element are extremely small and the speed of displacement very low, the reactions elicited from the water can (by analogy with those operating on a sphere) be regarded as directly proportional to the velocity of displacement and to the viscosity of the medium. If the velocity of displacement tangential to the body is $V_y \sin\theta$, the tangential drag (δL_y) can be expressed as $C_L V_y \sin\theta\delta s$, and the force ($\delta N_y$) acting normally to the surface as $C_N V_y \cos\theta\delta s$, where C_L and C_N are the coefficients of resistance to the surface of the element for a medium of known viscosity; the resultant forward thrust (δF_y) along the axis (xx') of propulsion is $(C_N - C_L) V_y \sin\theta \cos\theta\delta s$. In other words, the transverse displacement of the element will produce a forward thrust along the axis of propulsion provided the coefficient of resistance to displacement, normal to the surface of the element, is greater than that to displacement along the surface.

In an actively moving spermatozoon, each element is not only moving transversely across the axis of propulsion, it is also moving along the latter axis at a speed (V_x) which depends upon the speed at which the whole spermatozoon is progressing through the water (Fig. 1B). This forward displacement being equivalent to a tangential displacement $V_x \cos\theta$ and a normal displacement $V_x \sin\theta$, the corresponding forces acting tangentially (δL_x) and normally (δN_x) to the surface are $C_L V_x \cos\theta\delta s$ and $C_N V_x \sin\theta\delta s$ respectively. The total forces (δN and δL), acting normally and tangentially to the surface owing to the element's transverse and forward displacements, are

$$\left.\begin{aligned} \delta N &= C_N(V_y \cos\theta - V_x \sin\theta)\,\delta s, \\ \delta L &= C_L(V_y \sin\theta + V_x \cos\theta)\,\delta s. \end{aligned}\right\} \quad \text{(i)}$$

The propulsive components of δN and δL along the axis of propulsion (xx') being $\delta N \sin\theta$ and $\delta L \cos\theta$ respectively, the resultant forward thrust (δF) is

$$\delta N \sin\theta - \delta L \cos\theta:$$

$$\begin{aligned} \delta F &= [(C_N - C_L)\,V_y \sin\theta\,\cos\theta - V_x(C_N \sin^2\theta + C_L \cos^2\theta)]\,\delta s \\ &= \left[\frac{(C_N - C_L)\,V_y \tan\theta - V_x(C_L + C_N \tan^2\theta)}{1 + \tan^2\theta}\right]\delta s. \end{aligned} \quad \text{(ii)}$$

Equation (i) shows the element can only exert a positive forward thrust if

$$V_y > V_x \tan\theta.*$$

Equation (ii) shows that a positive forward thrust only develops if $C_N > C_L$.

During steady motion the resultant thrust (δF) from an element, when integrated over a complete cycle, is zero; it is now possible to express the propulsive speed in terms of the wave speed, if the values of C_N, C_L and θ are known and if the propulsive speed remains constant during the whole cycle of the element's motion.

* If $V_y = V_x \tan\theta$ the element has no component of motion normal to its surface; motion of this type could only ensue if the element were exerting its effort against a rigid medium—and were equivalent to a snake gliding through a rigid close-fitting tube.

II. PROPULSIVE EFFECT OF WAVES OF SMALL AMPLITUDE

The possibility of applying the above principles to an undulating flagellum was first pointed out to one of us (J. G.) in 1933 by the late Dr R. C. Howland. If the transverse velocity of an element be dy/dt and the tangent of its angle of inclination be dy/dx, equation (ii) becomes

$$dF=\left\{\frac{(C_N-C_L)\dfrac{dy}{dt}\dfrac{dy}{dx}-V_x\left[C_L+C_N\left(\dfrac{dy}{dx}\right)^2\right]}{1+\left(\dfrac{dy}{dx}\right)^2}\right\}ds, \tag{iii}$$

the total thrust (F) exerted by the flagellum over one wave-length $0 \leqslant x \leqslant \lambda$ is

$$F=\int_0^\lambda dF. \tag{iv}$$

To proceed further Howland restricted attention to cases in which the angle of inclination of an element was sufficiently small to eliminate terms containing $(dy/dx)^2$ and to regard the length of the flagellum constituting one wave-length as approximately equal to the wave-length. Equation (iii) then reduces to

$$\frac{dF}{dx}=(C_N-C_L)\frac{dy}{dt}\frac{dy}{dx}-C_L V_x. \tag{v}$$

If the form of the waves generated by the tail conforms to that of a sine curve

$$y=b\sin\frac{2\pi}{\lambda}(x+V_w t),$$

where b = amplitude, λ = wave-length, V_w = velocity of wave relatively to the head. The transverse velocity (dy/dt) of the element is $\frac{2\pi b V_w}{\lambda}\cos\frac{2\pi}{\lambda}(x+V_w t)$ and the tangent of the angle of inclination (dy/dx) of the element is $\frac{2\pi b}{\lambda}\cos\frac{2\pi}{\lambda}(x+V_w t)$

$$\frac{dF}{ds}\approx\frac{dF}{dx}=(C_N-C_L)\frac{4\pi^2 b^2 V_w}{\lambda^2}\cos^2\frac{2\pi}{\lambda}(x+V_w t)-C_L V_x,$$

$$F=\int_0^\lambda dF=\frac{2\pi^2 b^2 V_w(C_N-C_L)}{\lambda}-C_L\lambda V_x. \tag{vi}$$

Equation (vi) gives the forward thrust exerted by each complete wave.

When an undulating organism (without a head) is propelling itself forward at a steady speed (V_x), $F=0$

$$\frac{V_x}{V_w}=\frac{2\pi^2 b^2}{\lambda^2}\left(\frac{C_N-C_L}{C_L}\right), \tag{vii}$$

or since $V_w=f\lambda$ (where f is the frequency of the waves)

$$V_x=\frac{2f\pi^2 b^2}{\lambda}\left(\frac{C_N-C_L}{C_L}\right). \tag{viii}$$

The active tail of a spermatozoon exerts its effort against the drag of an inert head, and consequently

$$nF = D, \tag{ix}$$

where n is the number of waves exhibited simultaneously by the tail and D is the drag of the head. The drag of the head can be denoted by $hC_L aV_x$, where hC_L is the drag coefficient and a is a linear dimension of the head. From equations (vi) and (ix)

$$\frac{2n\pi^2 b^2 V_w}{\lambda}(C_N - C_L) - C_L V_x(n\lambda + ha) = 0,$$

$$\frac{V_x}{V_w} = \frac{2\pi^2 b^2}{\lambda^2}\left(\frac{C_N - C_L}{C_L}\right)\left(\frac{1}{1 + \frac{ha}{n\lambda}}\right), \tag{x}$$

or

$$V_x = \frac{2f\pi^2 b^2}{\lambda}\left(\frac{C_N - C_L}{C_L}\right)\left(\frac{1}{1 + \frac{ha}{n\lambda}}\right). \tag{xi}$$

Howland thus reached the conclusion that an organism comparable with a spermatozoon should propel itself through the water at a speed which depended on six factors: (1) the frequency of the waves; (2) the square of the amplitude of the waves and (3) their wave-length; (4) the difference between the coefficients of normal and tangential resistance; (5) the drag coefficient and size of the head; (6) the length of the tail.

Until recently, Howland's results appeared to have only limited significance from an experimental point of view, for, apart from the limitation to waves of small amplitude, there seemed no means of determining the values of C_N, C_L and h and no observational data on the amplitude, wave-length and frequency of the waves. It is now known, however (Hancock, 1953), that for very thin filaments (such as the tail of a spermatozoon) C_N is effectively twice C_L. It is also known that the waves passing down the tail of a spermatozoon of *Psammechinus* sometimes conform closely to sine waves of amplitude 4μ and wave-length 24μ, and that their frequency is about 30–40 per sec. (Gray, 1955).

It will be noted that if $C_N = 2C_L$ equation (vii) becomes

$$\frac{V_x}{V_w} = \frac{2\pi b^2}{\lambda^2}. \tag{xii}$$

Equation (vii) is thus identical with that derived by Taylor (1952) and by Hancock (1953) for waves of small amplitude. Howland's argument has been set out in some detail in view of the fact that its underlying physical principles can readily be visualized from a biological point of view.

III. PROPULSIVE THRUST FROM WAVES OF RELATIVELY LARGE AMPLITUDE

If a filament is deformed into a single complete sine curve of relatively large amplitude, the length (s) of the filament is considerably greater than the wave-length (λ), and the length (δs) of the filament intercepted by a short distance (δx) along the axis of propulsion varies with the phase of transverse motion. Consequently each point on a non-extensible filament executes a figure of eight movement relative to the head of the filament. The motion of each element relative to fixed axes is therefore a figure of eight superimposed upon a forward propulsive velocity ($\overline{V}_x$) defined by the velocity of forward propulsion when averaged over a complete cycle of activity.

The length of filament (δs) intercepted by a small fraction (δx) of a wave-length is given by equation (xiii)

$$(\delta s)^2 = (\delta x)^2 + (\delta y)^2,$$

$$\delta s = \left[1 + \left(\frac{dy}{dx}\right)^2\right]^{\frac{1}{2}} \delta x. \tag{xiii}$$

Equation (iii) now becomes equation (xiv)

$$dF = \frac{\left\{(C_N - C_L)\dfrac{dy}{dt}\dfrac{dy}{dx} - \overline{V}_x\left[C_L + C_N\left(\dfrac{dy}{dx}\right)^2\right]\right\}}{\left[1 + \left(\dfrac{dy}{dx}\right)^2\right]^{\frac{1}{2}}} dx. \tag{xiv}$$

If $C_N = 2C_L$

$$dF = \frac{C_L\left\{\dfrac{dy}{dt}\dfrac{dy}{dx} - \overline{V}_x\left[1 + 2\left(\dfrac{dy}{dx}\right)^2\right]\right\}}{\left[1 + \left(\dfrac{dy}{dt}\right)^2\right]^{\frac{1}{2}}} dx \tag{xv}$$

For a sine wave

$$\frac{dy}{dx} = \frac{2\pi b}{\lambda} \cos \frac{2\pi}{\lambda}(x + V_w t),$$

$$\frac{dy}{dt} = \frac{2\pi b V_w}{\lambda} \cos \frac{2\pi}{\lambda}(x + V_w t).$$

Substituting in equation (xv) and denoting dy/dx as A

$$dF = \frac{C_L[V_w A^2 - \overline{V}_x(1 + 2A^2)]}{(1 + A^2)^{\frac{1}{2}}} dx. \tag{xvi}$$

The forward thrust (F) from one complete wave is $\displaystyle\int_{x=0}^{x=\lambda} dF$,

$$F = C_L\left[V_w \int_0^\lambda \frac{A^2}{(1 + A^2)^{\frac{1}{2}}} dx - \overline{V}_x \int_0^\lambda \frac{1 + 2A^2}{(1 + A^2)^{\frac{1}{2}}} dx\right]. \tag{xvii}$$

Putting

$$\int_0^\lambda \frac{A^2}{(1 + A^2)^{\frac{1}{2}}} dx = I \quad \text{and} \quad \int_0^\lambda \frac{1 + 2A^2}{(1 + A^2)^{\frac{1}{2}}} dx = J,$$

$$F = V_w I - \overline{V}_x J. \tag{xviii}$$

If $F=0$

$$\frac{\overline{V}_x}{V_w}=\frac{I}{J}, \tag{xix}$$

where

$$I=\int_0^\lambda \left\{ \frac{\frac{4\pi^2b^2}{\lambda^2}\cos^2\frac{2\pi}{\lambda}(x+V_wt)}{\left[1+\frac{4\pi^2b^2}{\lambda^2}\cos^2\frac{2\pi}{\lambda}(x+V_wt)\right]^{\frac{1}{2}}} \right\} dx$$

and

$$J=\int_0^\lambda \left\{ \frac{1+\frac{8\pi^2b^2}{\lambda^2}\cos^2\frac{2\pi}{\lambda}(x+V_wt)}{\left[1+\frac{4\pi^2b^2}{\lambda^2}\cos^2\frac{2\pi}{\lambda}(x+V_wt)\right]^{\frac{1}{2}}} \right\} dx.$$

If $\cos^2\frac{2\pi}{\lambda}(x+V_wt)$ is replaced by the equivalent expression $\frac{1}{2}\left[1+\cos\frac{4\pi}{\lambda}(x+V_wt)\right]$, the contribution to the integrals I and J of the term $\cos\frac{4\pi}{\lambda}(x+V_wt)$ will be smaller than the remaining terms; if this term is neglected I/J approximates (over all the range of values of $2\pi b/\lambda$) to

$$\frac{2\pi^2b^2}{\lambda^2}\left(\frac{1}{1+\frac{4\pi^2b^2}{\lambda^2}}\right);$$

hence

$$\frac{\overline{V}_x}{V_w}=\frac{2\pi^2b^2}{\lambda^2}\left(\frac{1}{1+\frac{4\pi^2b^2}{\lambda^2}}\right), \tag{xx}$$

or

$$\overline{V}_x=\frac{2f\pi^2b^2}{\lambda}\left(\frac{1}{1+\frac{4\pi^2b^2}{\lambda^2}}\right). \tag{xxi}$$

It will be noted that equation (xx) is identical with that already obtained from a different line of approach (Hancock, 1952, p. 106) and yields the same result as equation (xii) for waves of small amplitude.

IV. UNDULATING FILAMENT PROPELLING AN INERT HEAD

In the case of a filament propelling an inert head

$$n\int_0^\lambda dF-C_H\overline{V}_x=0, \tag{xxii}$$

where n = number of waves exhibited by the whole tail and C_H = drag coefficient of the head. Assuming the head to be spherical $C_H=6\pi a\mu$, where a is the radius of the head and μ the viscosity of the medium.

From equations (xvii) and (xxii)

$$nV_wC_L\int_0^\lambda \frac{A^2}{(1+A^2)^{\frac{1}{2}}}dx=\overline{V}_x\left[nC_L\int_0^\lambda \frac{1+\frac{C_N}{C_L}A^2}{(1+A^2)^{\frac{1}{2}}}dx+6\pi a\mu\right].$$

If $C_N = 2C_L$

$$nV_w C_L \int_0^\lambda \frac{A^2}{(1+A^2)^{\frac{1}{2}}} dx = \overline{V}_x \left[nC_L \int_0^\lambda \frac{1+2A^2}{(1+A^2)^{\frac{1}{2}}} dx + 6\pi a\mu \right], \qquad \text{(xxiii)}$$

where

$$A = \frac{2\pi b}{\lambda} \cos \frac{2\pi}{\lambda}(x + V_w t).$$

To utilize equation (xxiii) it is necessary to know the absolute value of C_L. This can be derived from equation (7) of a previous paper (Hancock, 1953, p. 102), which gives the fluid velocity V in the vicinity of an element of length δs moving with a velocity V_t tangentially to itself in a fluid which is at rest:

$$V = V_t \frac{\left(\log \frac{r}{2\lambda}\right) + \frac{1}{2}}{\left(\log \frac{d}{2\lambda}\right) + \frac{1}{2}},$$

where V is the velocity of the fluid parallel to the element surface, d = the radius of the filament, r = the distance from the filament surface, $2\pi/k = \lambda$ = the wave-length.

The tangential drag force dF on the element is therefore

$$dF = \frac{2\pi\mu V_t . ds}{\left(\log \frac{d}{2\lambda}\right) + \frac{1}{2}},$$

$$C_L = -\frac{2\pi\mu}{\left(\log \frac{d}{2\lambda}\right) + \frac{1}{2}}. \qquad \text{(xxiv)}$$

Substituting this value for C_L in (xxiii) and using the integrals already defined

$$\frac{\overline{V}_x}{V_w} = \frac{I}{J - \frac{3a}{n\lambda}\left[\left(\log \frac{d}{2\lambda}\right) + \frac{1}{2}\right]},$$

reducing approximately, by a similar argument as before, to

$$\frac{\overline{V}_x}{V_w} = \frac{2\pi^2 b^2}{\lambda^2} \left\{ \frac{1}{1 + \frac{4\pi^2 b^2}{\lambda^2} - \left(1 + \frac{2\pi^2 b^2}{\lambda^2}\right)^{\frac{1}{2}} \frac{3a}{n\lambda}\left[\left(\log \frac{d}{2\lambda}\right) + \frac{1}{2}\right]} \right\}, \qquad \text{(xxv)}$$

or

$$\overline{V}_x = \frac{2f\pi^2 b^2}{\lambda} \left\{ \frac{1}{1 + \frac{4\pi^2 b^2}{\lambda^2} - \left(1 + \frac{2\pi^2 b^2}{\lambda^2}\right)^{\frac{1}{2}} \frac{3a}{n\lambda}\left[\left(\log \frac{d}{2\lambda}\right) + 1\right]} \right\}. \qquad \text{(xxvi)}$$

V. APPLICATION OF THEORETICAL ANALYSIS TO OBSERVATIONAL DATA

The calculated propulsive speed of the spermatozoa of *P. miliaris* can be derived from equation (xxvi) by utilizing the data provided in a previous paper (Gray, 1955), bearing in mind the uncertainty of some of the values involved.

As a general test of agreement between the calculated and observed speeds, the following values will be used:

Amplitude of waves	(b)	$4\,\mu$
Length of waves	(λ)	$24\,\mu$
No. of simultaneous waves	(n)	1·3
Frequency of waves	(f)	35 per sec.
Radius of head	(a)	$0{\cdot}5\,\mu$
Radius of tail	(d)	$0{\cdot}2\,\mu$

From equation (xxvi) $$\bar{V}_x = 462\,\frac{1}{1+1{\cdot}1+0{\cdot}3}$$

$$= \frac{462}{2{\cdot}4} = 191\,\mu \text{ per sec.}$$

The average observed speed (as derived from 89 cells) was $191{\cdot}4\,\mu$ per sec. for an average frequency of 34·5 per sec. For thirty-three of these cells the speed of propulsion was determined photographically, whilst the frequency was measured stroboscopically; for 56 cells both speed and frequency were measured photographically. The significance of the very remarkable agreement between the calculated and observed results must not be over-emphasized. Quite apart from the theoretical considerations referred to below, it must be borne in mind that the values used for the effective radius of the head and tail are necessarily approximate,

Table 1

No. of cells	Average freq. per sec (f)	Speed of wave (μ per sec) $(V_w = 24f)$	Speed of propulsion (μ per sec.)		Ratio $(\bar{V}_x/V_w)$	
			Calc.	Obs.	Calc.	Obs.
33	36·9	886	201	208	0·23	0·20–0·25
56	33	792	180	181	0·23	0·20–0·25

and that most of the other values represent the arithmetic mean of populations showing considerable variation between individuals; thus in a population of 29 cells the frequency of the waves varies between 25 and 46 per sec., and in the population of 89 cells referred to above, the propulsive speed varied from 100 to $290\,\mu$ per sec. Probably the safest estimate of agreement between observed and calculated values is provided by the ratio $\bar{V}_x/V_w$, since this eliminates any error in an estimate of wave frequency; the calculated value of 0·23 indicates that the passage of each wave of $24\,\mu$ wave-length over the tail should propel the spermatozoon through a distance of $5{\cdot}52\,\mu$; a very large number of records show that the observed distance lies between 5 and $6\,\mu$.

VI. DISCUSSION

The theoretical analysis involves at least three assumptions which differ from the observed facts:

(i) The form of the wave—both in amplitude and wave-length—only conforms to a sine curve during part of its propagation along the tail; the movements executed by elements of the tail at the two ends are different from those situated more centrally. The values given for amplitude and wave-length are, therefore, average values not only for a number of cells but also averages over one complete cycle. As shown in the Appendix, however, this limitation is not likely to be serious as far as variations in amplitude are concerned.

(ii) In order that the form of the tail should conform to that of a sine wave the changes in curvature and rate of transverse displacement about the axis of progression must be symmetrical. In many instances this is not the case (Gray, 1955).

(iii) The formula assumes that the head travels along the axis of progression without oscillating from side to side. In fact, the head always oscillates during each cycle for a distance comparable with its forward displacement. It may be noted, however, that on theoretical grounds the effect of the head on the rate of forward propulsion is likely to be small. Equation (xxvi) indicates that the presence of the head of the sperm of *P. miliaris* only reduces the speed of propulsion by about 15 %. In the absence of the head, the last term in the denominator becomes zero, and the calculated speed of progression at 35 waves per sec. rises to about 220 μ per sec. In other words, the propulsive component of the forces acting normally to the surface of the tail largely operates against the tangential drag of the tail—and only to a minor extent against the drag of the head.

Finally, it must be remembered that all the data on speeds of translation are derived from spermatozoa which are moving in close proximity to a glass or air surface, and the assumption is made that these figures also apply to spermatozoa moving freely in a bulk of fluid.

Bearing in mind the above limitations it seems, nevertheless, remarkable that the forward speed of propulsion of a spermatozoon can be calculated (well within the limits of experimental error) in terms of the form and frequency of the bending waves generated by the tail, on the basis that the coefficient of resistance of displacement of the tail normal to its surface is twice that of its displacement tangential to this surface and that all regions of the tail contribute equally towards the necessary propulsive thrust.

APPENDIX

Effect of variation in amplitude of waves

In many undulatory organisms the amplitude of the waves tends to increase as the waves pass posteriorly along the body (Gray, 1953). This feature can be incorporated into the theoretical analysis by assuming that the wave form is described by

$$y = b(x) \sin k(x + V_w t),$$

where the amplitude function $b(x)$ depends on x, and $k = 2\pi/\lambda$.

The increment of force dF acting in the x direction may be defined by a similar argument as before:

$$\frac{dF}{dx} = \frac{V_w(C_N - C_L)\,[b^2k^2 \cos^2 k(x+V_w t) + \tfrac{1}{2} bb'k \sin 2k(x+V_w t)]}{\{1 + [bk \cos k(x+V_w t) + b' \sin k(x+V_w t)]^2\}^{\frac{1}{2}}} - \frac{V_x\{C_N[bk \cos k(x+V_w t) + b' \sin k(x+V_w t)]^2 + C_L\}}{\{1 + [bk \cos k(x+V_w t) + b' \sin k(x+V_w t)]^2\}^{\frac{1}{2}}}, \qquad (\mathrm{i}\,a)$$

where the dash denotes differentiation with respect to x. The velocity of propulsion $\overline{V}_x$ can be obtained from equation (i a) by taking the integral $\int dF = 0$ as before. A number of applications are now developed:

(i) Consider a semi-infinite filament ($0 \leqslant x \leqslant \infty$) with steadily decreasing amplitude as x increases, assuming that

$$b(x) = b\, e^{-kx/a},$$

then

$$b^1 = \frac{-bk}{a} e^{-kx/a},$$

where a is the parameter defining the rate at which the amplitude changes and in particular the ratio of any two amplitudes distance one wave-length apart is $e^{-2\pi/a}$; $a = \infty$ gives the case of constant wave-length. This wave form is shown below in Fig. 2. Hence from equation (i a), using the fact that for extremely thin filaments $C_N = 2C_L$,

$$\frac{\overline{V}_x}{V_w} = \frac{I}{J},$$

where

$$I = \int_0^\infty \frac{\left[b^2k^2 \cos^2 k(x+V_w t) - \frac{b^2k^2}{2a^2} \sin 2k(x+V_w t)\right] e^{-2kx/a}}{\left\{1 + b^2k^2 e^{-2kx/a} \left[\cos k(x+V_w t) + \frac{1}{a} \sin k(x+V_w t)\right]^2\right\}^{\frac{1}{2}}}\, dx, \qquad (\mathrm{ii}\,a)$$

and

$$J = \int_0^\infty \frac{1 + 2e^{-2kx/a} b^2k^2 \left[\cos k(x+V_w t) + \frac{1}{a} \sin k(x+V_w t)\right]^2}{\left\{1 + b^2k^2 e^{-2kx/a} \left[\cos k(x+V_w t) + \frac{1}{a} \sin k(x+V_w t)\right]^2\right\}^{\frac{1}{2}}}\, dx.$$

Hence

$$\overline{V}_x = 0, \qquad (\mathrm{iii}\,a)$$

since I is finite and J is infinite. This result is to be expected in this hypothetical case since the propulsive elements at the rear of the filament (in the neighbourhood of finite x) cannot propel the non-propulsive elements of filament at $x=$ infinity.

(ii) Consider a finite filament of n wave-lengths ($0 \leqslant x \leqslant 2\pi n/k$), the upper limit of the integrals I and J is $2\pi n/k$ instead of infinity. This formula is complicated for all values of bk, but if the assumption is made that bk is small (so that b^3k^3 can be neglected), then a formula is given which can be compared with that given by the theory of constant amplitude which is valid over the same set of values of bk.

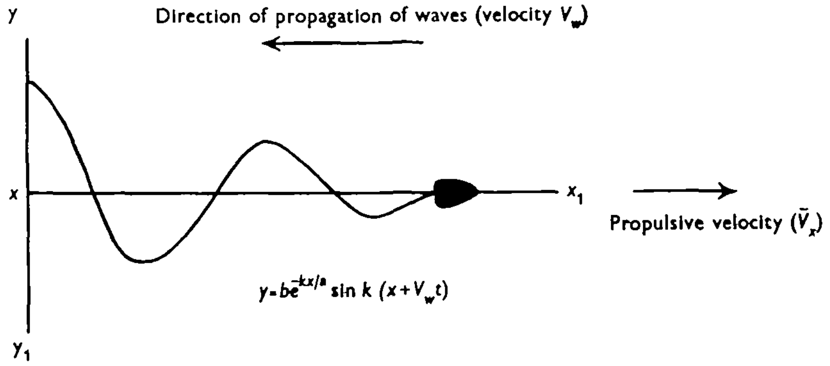

Fig. 2.

Equation (ii a), on the basis of this assumption, reduces to

$$\frac{\bar{V}_x}{V_w} = \tfrac{1}{2}b^2k^2(1-e^{-4\pi n/a})\left(\frac{a}{4\pi n} - \sin\frac{2kV_w t}{4\pi n}\right). \qquad \text{(iv } a\text{)}$$

This equation becomes
$$\frac{\bar{V}_x}{V_w} = \frac{b^2k^2}{2}$$

for no variation of amplitude (this follows by expanding the function $e^{-4\pi n/a}$ and letting $a \to \infty$) which is the standard formula for this case. Equation (iv a) also tends to zero as n, the number of wave-lengths, tend to infinity, which agrees with equation (iii a).

(iii) Taking the special case $a = 4\pi$ then a table of the mean values of $\bar{V}_x/V_w$ depending on n the number of wave-lengths can be determined. Note that in this case the ratio of successive amplitudes between each wave-length is 0·6. For $a=4\pi$

n	$\bar{V}_x/V_w$,
1	$0{\cdot}32b^2k^2$,
2	$0{\cdot}22b^2k^2$,
3	$0{\cdot}16b^2k^2$.

It is interesting to note how the above values compare with the formula

$$\frac{\bar{V}_x}{V_w} = \tfrac{1}{2}\bar{b}^2k^2,$$

where $\bar{b}$ is the mean amplitude of the motion, defined by

$$\bar{b}=\frac{1}{1+n}\sum_{a=0}^{a=n} b_a,$$

where b_a are the successive amplitudes after each wave-length, then

$$\bar{b}=\frac{b}{1+n}\left[\frac{1-0\cdot6^{n+1}}{0\cdot4}\right]$$

in the special case considered here. This approximation is equivalent to regarding the motion with varying amplitude as equivalent to that with the constant amplitude equal to the mean amplitude of the original motion. For $a=4\pi$

n	$\bar{V}_x/V_w=\frac{1}{2}\bar{b}^2k^2$,
1	$0\cdot32b^2k^2$,
2	$0\cdot22b^2k^2$
3	$0\cdot15b^2k^2$
∞	0.

It is seen that the correspondence between these two sets of results is very good, and gives an easy approximate method for obtaining the velocity of propulsion. This agreement is only valid for small values of bk, but it will be assumed that the same approximation of taking the mean amplitude will give reasonable results for all the larger values of bk.

SUMMARY

1. The general theory of flagellar propulsion is discussed and an expression obtained whereby the propulsive speed of a spermatozoon can be expressed in terms of the amplitude, wave-length and frequency of the waves passing down the tail of a spermatozoon of *Psammechinus miliaris*.

2. The expression obtained is applicable to waves of relatively large amplitude, and allowance is made for the presence of an inert head.

3. The calculated propulsive speed is almost identical with that derived from observational data. Unless the head of a spermatozoon is very much larger than that of *Psammechinus*, its presence makes relatively little difference to the propulsive speed. Most of the energy of the cell is used up in overcoming the tangential drag of the tail.

4. Although the amplitude may change as a wave passes along the tail, the propulsive properties of the latter may be expected to be closely similar to those of a tail generating waves of the same average amplitude.

REFERENCES

Gray, J. (1953). Undulatory movement. *Quart. J. Micr. Sci.*, N.S., **94**, 551–78.

Gray, J. (1955). The movement of sea-urchin spermatozoa. *J. Exp. Biol.* **32**, 775–801.

Hancock, G. J. (1953). The self-propulsion of microscopic organisms through liquids. *Proc. Roy. Soc.* A, **217**, 96–121.

Taylor, Sir Geoffrey (1951). Analysis of the swimming of microscopic organisms. *Proc. Roy. Soc.* A, **209**, 447–61.

Taylor, Sir Geoffrey (1952). The action of waving cylindrical tails in propelling microscopic organisms. *Proc. Roy. Soc.* A, **211**, 225–39.