THE MOVEMENT OF THE SPERMATOZOA OF THE BULL

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(The rate at which the spermatozoa of a sea-urchin propel themselves can be expressed, with surprising accuracy, in terms of the form and frequency of the bending waves generated by the tail (Gray, 1955; Gray & Hancock, 1955). The object of this paper is to consider how far this conclusion is applicable to other types of flagellated spermatozoa; those of the bull with their relatively larger heads and thicker tails provide a useful basis of comparison and contrast.

Under continuous dark-ground illumination an active spermatozoon of the bull exhibits a well-defined optical envelope, usually triangular in outline, with an apex either at the posterior or at the anterior end of the middle piece. Attempts to correlate the form of the envelope with the form of the waves passing over the tail by stroboscopic illumination proved to be much less satisfactory than those based on direct photography. The records shown in Pl. 2 were obtained by means of the equipment described by Brown & Popple (1955), so arranged as to give a known number (three to eight) successive electronic exposures on a stationary film at intervals of \( \frac{1}{8} \) sec. In photographs 2–5 and 12–14 the number of flashes was sufficient to cover at least half of a complete contractile cycle, and the outline of these figures gives the general form of the envelope which would have been seen under continuous illumination. Pl. 2 illustrates three types of movements. (i) Those in which transverse movement is restricted to the tail (e.g. photographs 1–5). (ii) Those in which both tail and middle piece show transverse movement, although the head does not (e.g. photograph 6). (iii) Those in which head, middle piece and tail all show lateral displacement (e.g. photographs 8–14). It seems likely that these differences are largely due to differences in the degree to which lateral movements of the head and middle piece were restrained by contact with the slide; in the absence of such restraint photographs 1–7 would approximate to photographs 8–14. This conclusion is supported by the records shown in Pl. 3 which were obtained on a moving film using flashes at \( \frac{1}{8} \) sec. intervals; lateral oscillation of the head is clearly detectable.

Photographs similar to those shown in Pls. 2 and 3 reveal five features which are relevant to an analysis of the propulsive mechanism of the tail.

(i) The maximum extent to which an element of the tail bends during its contractile cycle is not the same for all elements. The nearer the element lies towards
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The tip of the tail the greater is the amount of bending; this is clearly seen by following the dot (●) marked on the left side of the tail in Pl. 3, photographs 2–8.

(ii) The phase difference between successive elements varies along the length of the tail. Pl. 3 shows that the length of tail between two points on the tail (●, +) which differ in their phase by one-half of a complete cycle is greater at the proximal end of the tail than at the distal end; in other words, the length and speed of propagation of the 'wave' decrease as its crest moves backwards along the tail.

(iii) The amplitude of transverse movement—relative to the head—increases progressively along the tail towards the distal end (Pl. 2, photographs 1–5).

(iv) An element lying towards the distal end of the tail executes a figure-of-eight motion relative to the head; at certain phases of its motion such an element moves backwards relative to the head (Text-fig. 1).

Text-fig. 1. Diagram illustrating the figure-of-eight paths, relative to the head, followed by points lying towards the distal end of the tail (see Pl. 2, photographs 1–4). In Text-fig. 1 a–c the point is approximately 10 μ from the tip of the tail; in Text-fig. 1 d it is at the tip of the tail. The numbers indicate successive stages of the bending cycle.

(v) The angle at which the surface of an element crosses the axis of propulsion increases progressively the nearer the element lies towards the distal end of the tail (Text-fig. 2).

All these characteristic features of the movement of the tail indicate departures from the conditions which form the basis of the argument applied to the sea-urchin (Gray and Hancock 1955); their theoretical significance will be discussed later in this paper.

Text-fig. 3 shows the effect of changes in the maximum degree of bending and in the phase difference between adjacent elements upon the wave-length and amplitude of the resultant waves.
Frequency of bending cycles

As determined photographically the average frequency of the bending cycles exhibited by thirty-one cells in the samples was 9.1/sec. at 37°C, but as shown in Table 1 the range of variation was very considerable, not only between the two samples of sperm but also among the individuals of the same suspension.

The order of frequency recorded for these samples of bull's spermatozoa is much less than that found for the sea-urchin (33-40/sec. at 17°C; Gray, 1955) in spite of the fact that the environmental temperature was much greater. The average translatory speeds of the bull's spermatozoa were rather low (see below); other suspensions might have yielded higher frequencies. During each complete
Text-fig. 3. Relationship of the form of a wave to the maximum degree of bending and the phase difference between adjacent segments. The maximum degree of bending is defined by the reciprocal of the minimum radius of curvature ($R_o$) and the phase difference per unit length as a fraction ($\phi$) of one complete cycle.

(a) In all cases $R_o = 2$; $\phi$ varies from $\frac{1}{6}$ to $\frac{1}{3}$ cyc. Both wave-length and amplitude decrease with increase of $\phi$.

(b) In all cases $\phi = \frac{1}{6}$; $R$ varies from 1.25 to 2.67. An increase of $R_o$ causes an increase of wave-length, but a decrease in amplitude.

(c) If $R_o \phi$ is constant, the general form of the wave remains the same but its absolute size changes.
Table 1

<table>
<thead>
<tr>
<th>Suspension</th>
<th>Frequency of waves per sec.</th>
<th>Total cells</th>
<th>Mean frequency</th>
<th>Mean translatory velocity (μ/sec.)</th>
<th>Mean translatory distance per cycle (μ)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A 3 4 5 6 7 8 9 10</td>
<td>11 12 13 14 15 16</td>
<td>18</td>
<td>7.5</td>
<td>79</td>
<td>10.5</td>
</tr>
<tr>
<td>B — — — — 0 2 3 0 3 1 0 2 2 0</td>
<td>13</td>
<td>11.3</td>
<td>66</td>
<td>6.0</td>
<td></td>
</tr>
<tr>
<td>Total — 1 3 1 4 5 6 3 3 1 0 2 2 —</td>
<td>31</td>
<td>9.1</td>
<td>73</td>
<td>8.0</td>
<td></td>
</tr>
</tbody>
</table>

Contractile cycle a spermatozoon of a sea-urchin moves forward a relatively constant distance of 5.5 μ; those of the bulls used for Table 1 varied, but moved forward an average distance of 8.3 μ. For a wave frequency of 15/sec., the speed of translatory movement would be approximately 120 μ/sec.

Translatory velocity

Correlated with a relatively low frequency of propagated bending cycles, the spermatozoa of the bull exhibit a relatively low speed of progression through the water. As shown in Table 2, the average velocity of 235 cells derived from eleven samples was 94 μ/sec., but as shown in Table 2 and by Text-fig. 4 the spread of variation between different samples and between individuals in a single sample was very considerable.

An average translatory speed of 94 μ/sec. appears to be substantially lower than that (123 μ) observed by Rothschild (1953a). The two figures are, however, not comparable, since the latter records the length of the undulatory track of the head, whereas Table 2 records the displacement along the axis of progression. An examination of Lord Rothschild's films showed that the average ratio of these two measurements is 1:4, and consequently the average speed recorded in this paper represents 131 μ/sec. when measured along the track of the head. As shown in Text-fig. 4 the spread of translatory speed observed in the present work was similar to that recorded by Rothschild. So far as could be determined from a single sample (Text-fig. 4) the absence of the head does not substantially increase the propulsive speed (see Gray & Hancock, 1955).

Movements of the spermatozoon about its median longitudinal axis

The cells figured in Pls. 2 and 3 were moving in close proximity to the surface of the slide and they present one of the flat surfaces of their heads towards the observer during the whole of the contractile cycle. When swimming freely in a relatively deep drop, the head often presents to the observer a broad surface and a narrow surface alternately, thus producing, under dark ground illumination, the well-known 'flashing' effect; the head either 'rocks' or 'rolls' about its median longitudinal axis. During the phases at which the head is seen 'edge on', the optical envelope of the tail approximates to a brightly illuminated line (Pl. 4a,
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Text-fig. 4. Diagram showing variation in propulsive speed. Normal cells, □; headless cells, ⊘.
The curves have the same characteristics as those of Rothschild (1953a) adjusted for the number of cells involved.

Table 2

<table>
<thead>
<tr>
<th>Suspension</th>
<th>No. of cells recorded</th>
<th>Mean translatory velocity (μ/sec.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A (c)</td>
<td>31</td>
<td>111</td>
</tr>
<tr>
<td>B (h)</td>
<td>14</td>
<td>118</td>
</tr>
<tr>
<td>C (h)</td>
<td>21</td>
<td>115</td>
</tr>
<tr>
<td>D (h)</td>
<td>18</td>
<td>120</td>
</tr>
<tr>
<td>E (h)</td>
<td>7</td>
<td>129</td>
</tr>
<tr>
<td>F (c)</td>
<td>24</td>
<td>80</td>
</tr>
<tr>
<td>G (c)</td>
<td>56</td>
<td>72</td>
</tr>
<tr>
<td>H (h)</td>
<td>25</td>
<td>94</td>
</tr>
<tr>
<td>I (h)</td>
<td>15</td>
<td>99</td>
</tr>
<tr>
<td>K (c)</td>
<td>14</td>
<td>66</td>
</tr>
<tr>
<td>L (c)</td>
<td>10</td>
<td>65</td>
</tr>
<tr>
<td>Total</td>
<td>235</td>
<td>94</td>
</tr>
</tbody>
</table>

(c) Determined cinematographically, (h) determined by length of head-track per sec.
photograph 3), thus showing that most, if not all, of the elements of the tail execute their transverse movements in a plane coincident with that of the median transverse axis of the head. In thirty-one cells—taken from the same suspension—the frequency of 'flash' varied from 4 to 11/sec. and gave an average value of 8.2/sec.; this is of the same order as that of the average wave frequency.

The tendency to roll about the longitudinal axis does not depend on the presence of the head (see Pl. 4(b)); the 'flashing' of the head must be due to the activity of the tail. An exact correlation between the frequency of flashing and the frequency of the bending waves is shown in Pl. 4(c), where the head 'flashed' when a region of maximum curvature passed over the distal end of the tail. This condition would arise if the passage of a bending wave along the tail were accompanied by a torsional wave, or if the plane of vibration of the distal region of the tail differed from that of the proximal regions; in the first case flashing could occur if the bending wave were suppressed; in the second case, the distal end of the tail would, at the moment of flash, be deflected laterally as in Pl. 4(d). Most, if not all, of the present observations suggest that the tail is slightly twisted when a wave of curvature passes over its distal region.

In some cases the head flashes when its own longitudinal axis lies along the axis of progression, and a dark-ground photograph yields a series of flashes aligned along this axis (see Rothschild, 1953b). In other cases the flashes may be inclined at an angle to this axis to form a series of oblique parallel lines, or a more complex herring-bone pattern. If, as seems probable, a flash depends on the forces exerted against the water by the distal elements of the tail, the onset of a flash would depend on the difference in phase between the lateral displacements of the head and of the end of the tail.

DISCUSSION

The reaction exerted by the water against any short element of a flagellum depends on three main variables. (i) The angle ($\theta$) which its surface subtends with the main axis of forward propulsion. (ii) The velocity ($V_y$) at which the element travels transversely to this axis. (iii) The velocity ($V_x$) at which it travels along this axis. The reaction from the water has two components, one ($dF$) acting along the axis of propulsion and the other ($dT$) acting transversely. The relative magnitude of both these forces can be determined by methods similar to those applied to the propulsive force of a sea-urchin's spermatozoon (Gray & Hancock, 1955).

Initially, it is convenient to consider the distal element of the tail of a bull's spermatozoon whose head is stationary relative to the surrounding waters as in Text-fig. 5; the motion of the element relative to the water is then the same as its motion relative to the head. Such an element has a transverse velocity ($V_y$) and a longitudinal velocity ($V_x$) relative to the head; the latter component alters its sign twice during each complete cycle, and will be regarded as positive when directed away from the head, i.e. in the same direction as that in which the waves of changing curvature pass along the tail. The displacements of the element due to $V_x$ and $V_y$ are equivalent to a tangential displacement $V_t$ and a displacement $V_n$ normal to the element's surface. If the resistance to flow along the surface is $C_L V_t$, whilst that
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normal to the surface is \(2C_L V_n\) (see Hancock, 1953) the total propulsive thrust \((dF)\) and total transverse force \((dT)\) are defined by equations (i) and (ii)

\[
dF = C_L[V_y \sin \theta \cos \theta + V_h (\sin^2 \theta + 1)] ds, \quad (i)
\]

\[
dT = C_L[V_y (\cos^2 \theta + 1) + V_h \sin \theta \cos \theta] ds. \quad (ii)
\]

If \(\sin \theta \cos \theta = a, \quad \sin^2 \theta + 1 = b\) and \(\cos \theta + 1 = c\)

\[
dF = C_L[aV_y + bV_h] ds, \quad (iii)
\]

\[
dT = C_L[cV_y + aV_h] ds. \quad (iv)
\]

As shown in Table 3 the propulsive coefficient of transverse displacement \(a\) is zero at \(0^\circ\), rises to a maximum of \(0.5\) at \(45^\circ\) and then declines to zero again at \(90^\circ\). The corresponding coefficient for longitudinal displacement \(b\) has a minimum value of \(1.0\) at \(0^\circ\) and rises to a maximum of \(2.0\) at \(90^\circ\); \(a\) is always substantially less than \(b\).

### Table 3

<table>
<thead>
<tr>
<th></th>
<th>0°</th>
<th>15°</th>
<th>30°</th>
<th>45°</th>
<th>60°</th>
<th>75°</th>
<th>90°</th>
<th>120°</th>
<th>135°</th>
<th>180°</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a)</td>
<td>0</td>
<td>0.25</td>
<td>0.43</td>
<td>0.5</td>
<td>0.25</td>
<td>0</td>
<td>0.43</td>
<td>0.25</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>(b)</td>
<td>1.0</td>
<td>1.07</td>
<td>1.35</td>
<td>1.5</td>
<td>1.75</td>
<td>1.93</td>
<td>2.0</td>
<td>1.75</td>
<td>1.5</td>
<td>1.0</td>
</tr>
<tr>
<td>(c)</td>
<td>1.0</td>
<td>1.04</td>
<td>1.35</td>
<td>1.5</td>
<td>1.25</td>
<td>1.07</td>
<td>1.0</td>
<td>1.25</td>
<td>1.5</td>
<td>1.0</td>
</tr>
</tbody>
</table>

Recovery or preparatory phase

Effective phase

Recovery or preparatory phase

Text-fig. 5. Diagram illustrating the orientation and displacement (relative to the head) of a distal element during the recovery and effective phases of its cycle. In the former \(V_h\) is negative, \(\theta\) is small and \(V_t\) is low; during the effective phase \(V_h\) is positive, \(\theta\) is large and \(V_t\) is high.

Propulsive forces

When the element is travelling along its figure-of-eight path near its position of maximum transverse displacement it is inclined at a small angle to the axis of propulsion, its transverse velocity is low and it is travelling forward relative to the head (i.e. \(V_h\) is negative) (see Text-fig. 5). All these characteristics indicate that during these phases of its motion the propulsive force exerted must be negligibly small if not negative. On the other hand, when the element carries out its main transverse sweep its angle of inclination is relatively large, its transverse velocity is high, and it is travelling away from the head (i.e. \(V_h\) is positive), Text-fig. 5. All these characteristics indicate that it is during these latter phases that the element exerts its main propulsive effort; the whole cycle can be divided into two effective
phases and two preparatory or recovery phases. During each complete cycle the values of $\theta$, $V_h$ and $V_y$ are varying, but a rough comparison between the two phases can be obtained by substituting in equation (iii) average values derived from observational data.

<table>
<thead>
<tr>
<th>Effective phase</th>
<th>Preparatory phase</th>
</tr>
</thead>
<tbody>
<tr>
<td>$V_x = 5 \times 10^{-4}$ cm/sec.</td>
<td>$V_x = 1 \times 10^{-4}$ cm/sec.</td>
</tr>
<tr>
<td>$V_y = 1 \times 10^{-4}$ cm/sec.</td>
<td>$V_y = -1 \times 10^{-4}$ cm/sec.</td>
</tr>
<tr>
<td>$\theta = 60^\circ$</td>
<td>$\theta = 10^\circ$</td>
</tr>
<tr>
<td>$dF = 4 \times 10^{-4} C_d ds$</td>
<td>$dF = -2 \times 10^{-4} C_d ds$</td>
</tr>
</tbody>
</table>

From a similar line of argument, it follows that elements lying towards the front end of the tail can exert little or no propulsive thrust; their angles of inclination and their transverse speeds are low, and they do not exhibit longitudinal movement relative to the head. It may, therefore, be concluded that the propulsive properties of an element of the tail of a bull's spermatozoon increase progressively the nearer the element lies towards the distal end of the tail. The function of the proximal elements is discussed later.

![Text-fig. 6. Graph showing the effect of forward displacement and change in angle $\theta$ of inclination on the longitudinal force developed by element. A resultant forward thrust only develops if the speed of forward displacement ($V_x$) is less than about one-quarter to one-third of its transverse speed.](image)

When a spermatozoon is propelling itself freely through the water, the thrust developed by a distal element during its effective phase will be less than that of a cell whose head is fixed to the slide, whilst the drag during the recovery phase will be increased. Since the two phases are of approximately the same duration and the forces proportional to the element's velocity, the limit of propulsive speed is reached when the average thrust during the effective phase is equal to the average drag during the recovery phase. The effect of superimposing a longitudinal displacement on an element's transverse displacement is shown in Text-fig. 6. If the head of a spermatozoon is moving forward with velocity $V_h$, whilst an element is
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executing its figure-of-eight movement relative to the head, the element’s forward longitudinal velocity will be \( V_h + V_p \) during the recovery phase and \( V_h - V_p \) during the effective phase. The resultant propulsive thrust will be zero when

\[
aV_y + b(V_h - V_p) = b_1(V_h + V_p).
\]

If the average value of \( \theta = 45^\circ \) during the effective phase and \( 10^\circ \) during the recovery phase, whilst \( V_h = 0.25 V_y \), the resultant thrust will be zero when \( V_p = 0.25V_y \); in other words, an element of this type cannot propel itself at a velocity greater than one-quarter of its transverse speed. The average value of the transverse velocity of a distal element of a bull’s spermatozoon is of the order of 500 \( \mu \) sec, thus giving a maximum propulsive speed of about 125 \( \mu \) sec. As calculated in this way no regard is paid to the fact that the distal elements have to overcome the drag of the proximal elements and of the head. In the case of a sea-urchin, where the duration of the recovery phase is extremely short and \( V_h \) is zero, the resultant thrust becomes zero when \( V_p = aV_y/b \). If \( a/b \) is given its maximum value of 0.33 and \( V_y \) is 600/sec., the calculated speed of propulsion (200/sec.) is very close to the observed value (Gray & Hancock, 1955).

Transverse forces

An element of the tail cannot elicit a propulsive thrust from the water without encountering transverse resistance; the development of both forces implies that equal but opposite forces are operating against other parts of the cell. In Text-fig. 7 a distal element (C) is moving towards the right side of the axis of propulsion (xx\_\_\_), and eliciting a reaction (R\_\_\_) which has a propulsive component (F\_\_\_) and a transverse component (T\_\_\_); under such conditions the movements of the rest of the cell relative to the water must be such as to produce a drag force equal, and opposite to \( F \), and a transverse force equal, but opposite to \( T \). These conditions can be satisfied if there are two other elements, or groups of elements situated anteriorly to C, one of which (A) is moving towards the right side and the other (B), towards the left side of the propulsive axis; the whole length of the tail must therefore form more than one complete ‘wave-length’; at some phases of the cycle there may be four centres of transverse pressure instead of three (see Text-fig. 8).

As already indicated, the transverse force exerted by an element depends on its speed of transverse and longitudinal displacement and on its angle of inclination. The quantitative relationship between these three factors is shown in Text-fig. 9. High transverse forces are elicited by elements with low angles of inclination and by movement of the element forwards along the axis of propulsion; these conditions exist in the proximal regions of the tail; on the other hand, relatively low transverse forces are developed by the distal elements where the angle of inclination is relatively high. The main dynamic function of the elements lying towards the anterior end of the tail (together with the head and middle piece) is to provide a stable fulcrum against which the distal elements can exert their propulsive effort. As a propulsive system the spermatozoon of a bull is comparable with a fish, such as a trout, where the front end of the body provides the fulcrum against which the tail
Text-fig. 7. Diagrammatic representation of the forces exerted by the water against three groups of elements of the tail. If a distal group of elements (C) is moving to the right and eliciting a reaction \( R_e \), the motion of the rest of the spermatozoon relative to the water must be such as to elicit a reaction equal but opposite to \( R_e \). This condition is satisfied if (as in the figure) there is an anterior group of elements (A) together with the head) moving to the right and eliciting a reaction \( T_a \) and an intermediate group of elements (B) moving to the left and eliciting a reaction \( R_b \). The resultant of the forward components (\( F_e \) and \( F_b \)) of \( R_e \) and \( R_b \) is equal to the total backward drag of the whole cell, whilst the resultant of the transverse forces (\( T_a, T_b, T_c \)) is zero. The small arrows show the direction of lateral movement of the three groups of elements.

Text-fig. 8. Diagram showing the general distribution of transverse forces as a bending wave passes along the tail. Regions of maximum curvature are shown at \( C_1, C_2, C_3 \) and \( C_4 \). The directions of the movement of the various regions of the tail are shown by the small arrows.

(8a). All elements posterior to \( C_4 \) are moving towards the right side of the axis (xx) of progression; elements between \( C_1 \) and \( C_2 \) are moving to the left, whilst the head and elements anterior to \( C_1 \) are moving to the right. The centres of transverse pressure against these three regions are at \( a, b \) and \( c \), respectively, and the forces acting are \( T_a, T_b \) and \( T_c \), their resultant being zero.

(8b). The phase of movement has advanced by one-quarter cycle, the regions of maximum contraction (\( C_1 \) and \( C_4 \)) lie nearer to the tip of the tail. A new region of maximum contraction is developing at \( C_5 \), and all elements anterior to \( C_5 \) are moving to the left of the axis and elicit the reaction \( T_d \). The resultant of \( T_a, T_b, T_c \) and \( T_d \) is zero.

(8c). One-quarter cycle ahead of Text-fig. 8b. The form of the tail and the distribution of transverse forces are the mirror images of those in Fig. 8a.

(8d). One-quarter cycle ahead of Text-fig. 8c: the figure is the mirror image of Text-fig. 8b.

(8e). The tail has completed one whole cycle.
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and caudal fin exert their propulsive effort; the spermatozoon of a sea-urchin is equivalent to an eel or snake where the motion relative to the water, is more nearly the same for all elements. In all cases the form of the movements is probably closely related to the length and inherent flexibility of the body.

![Graph showing the effect of longitudinal displacement on the total transverse force elicited by an element. This force increases as the rate of forward movement increases. At low angles of inclination the relative value of the transverse force approximates to twice that characteristic of high angles.]

SUMMARY

1. The maximum extent to which an element of the tail of a bull’s spermatozoon bends during its contractile cycle is not the same for all elements; the nearer the element lies towards the tip of the tail the greater is the amount of bending.

2. The phase difference between successive elements varies along the length of the tail; and consequently the speed of propagation of the bending wave decreases as the latter moves backwards.

3. The amplitude of transverse movement relative to the head increases progressively along the tail towards the distal end.

4. Distal elements execute figure-of-eight movements relative to the head.

5. The frequency of the bending cycles and the propulsive velocity of the whole cell vary considerably. The average frequency for thirty-one cells was 9.1/sec., and the average propulsive speed for 235 cells was 94 μsec.

6. Cells moving freely in water ‘flashed’ with a frequency similar to that of the bending waves. The rotation of the head about its longitudinal axis appears to be...
due to the fact that all elements of the tail are not executing their transverse move-
ments in exactly the same plane during the whole of their contractile cycles.
7. The rate at which an element can propel itself forward cannot be greater than
about one-third to one-quarter of its average transverse velocity.
8. The distal elements of the tail exert their propulsive effort against the fulcrum
provided by the proximal elements.
9. It is impracticable to relate the speed of propulsion to the form and speed of
propagation of the waves passing along the tail.

The photographs for this paper were taken by Mr K. C. Williamson to whom
the author wishes to express his very sincere thanks.

REFERENCES
802-14.
30, 178-99.

EXPLANATION OF PLATES 2-4

PLATE 2
Dark-ground photographs taken on stationary film. Interval between flashes 1/30 sec. Note transverse
displacement of middle piece in photograph 6; transverse movement of head and middle piece
in photographs 8-14.

PLATE 3
Dark-ground photographs taken on moving film. Interval between exposures 1/15 sec. Note increase
in maximum curvature and change of shape as a wave (6, +) passes posteriorly along the tail
(photographs 2-10). Also note asymmetry of bending on two sides of tail (photographs 6, 10).
[In order to reproduce the original photographs it proved necessary to retouch the distal end
of the tail].

PLATE 4
(a) Successive dark-ground photographs of the optical envelope of a flashing cell. Exposure 1/15 sec.,
interval between exposures 1/15 sec.
(b) Successive dark-ground photographs (exposure 1/15 sec., interval 1/15 sec.) of a headless cell when
rolling about its main longitudinal axis.
(c) Successive photographs (phase contrast—exposure 1/15 sec., interval 1/15 sec.) of a cell which
‘flashed’ each time a region of maximum curvature passed over the distal region of the tail.
(d) Dark-ground photograph (three electronic flashes) of a ‘flashing’ cell: note that the plane of
beat of the distal end of the tail is not the same as that of the rest of the tail.
(e) Photograph of four cells exhibiting co-ordinated movement.
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(Facing p. 108)
GRAY—THE MOVEMENT OF THE SPERMATOZOA OF THE BULL.
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