

## Undulatory Propulsion

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### SUMMARY

1. Typical undulatory progression over a rigid environment depends on three fundamental factors:

- (i) Internal bending couples change the lateral curvature of each region of the body to that previously characteristic of the region lying immediately anterior to itself.
- (ii) The phase of lateral bending varies along the length of the animal's body.
- (iii) The presence of external restraints prevents all regions of the body from moving along any path other than one tangential to their own circumference of curvature.

2. The magnitude of the forward tangential thrust imparted to the body depends on (a) the magnitude of the internally generated bending couples, and (b) the form of the waves. If friction operates on the surfaces of external restraint the thrust also depends on the coefficient of lateral friction and on the position of the restraints.

3. From a mechanical point of view, an undulating organism (irrespective of its size and internal structure) can be regarded either as a series of curved levers or as a series of inclined planes.

4. The general principles of undulatory swimming are the same as for a terrestrial glide, except for the fact that each element of the body must possess a component of motion normal to its surface if it is to contribute towards the propulsion of the animal; this type of motion can only occur when the waves move backwards relative to the ground. The animal cannot move forward as fast as the waves are propagated over the body.

5. The propulsive powers of three-dimensional waves are limited to the extent to which the organism is restrained by external forces from spinning about its own longitudinal axis. Otherwise the principles of progression are the same as for two-dimensional waves: the resultant of all the forces acting normally to the body is equal but opposite to that of all tangential forces.

**D**URING undulatory movement the body of the animal exhibits a train of waves which—with a few interesting exceptions (Gray, 1939)—move, relative to the head, in a direction opposite to that in which the organism moves relative to the ground. This type of motion is found over a wide range of the animal kingdom and over a very wide diversity of bodily size and internal anatomy. In its most intriguing form the movement is displayed by filaments, less than a micron in diameter, whose internal structure must probably be visualized on a molecular level; at the other end of the scale are relatively large animals (e.g. snakes) of known anatomical structure which nevertheless exhibit movements of the same fundamental nature as the [Quarterly Journal of Microscopical Science, Vol. 94, part 4, pp. 551-578, Dec. 1953.]

tail of a spermatozoon. The main object of this paper is to consider the movement of all such systems, in the light of certain general principles common to them all, in the hope that such an inquiry may ultimately throw light on the functional significance of the fibrils and other structures, revealed by the electron-microscope, in a microscopic flagellum.

Irrespective of size and internal structure, all undulatory organisms present two main problems: (i) the nature of the internal mechanism which generates the train of waves passing over the body; (ii) the relationship of the form and frequency of the periodic changes in bodily form to the force driving the animal forward. So long as the undulatory system is relatively large and is exerting its effort against a rigid environment neither of these problems presents any insuperable experimental difficulty (Gray, 1946; Gray and Liissmann, 1950), but when the organism is very small and is exerting its effort against water, a relatively simple exercise in rigid mechanics is transferred to the much more difficult field of hydrodynamics (Taylor, 1951; 1952, *a* and *b*). From a physical standpoint the treatment given in the ensuing paper lacks both elegance and precision, but has, possibly, the advantage of being more readily intelligible to the majority of biologists. The paper should be regarded as a generalized and somewhat over-simplified background against which experimental and observational data will be reviewed in subsequent papers.

# I

## (i) *Two-dimensional undulatory progression under rigid environmental conditions*

In terrestrial animals undulatory progression can be regarded as an adaptation for movement over or through a relatively rigid medium. Four typical examples cover a wide range of size, speed, and internal structure: snakes gliding between stones; arthropod larvae, e.g. *Ceratopogon*, creeping over sand grains; nematode worms creeping between small intestinal villi or through soil; protozoa, such as *Cristaspira*, creeping through the wall of the crystalline style of an oyster. In all these cases, each part of the animal's body moves along a sinuous path and each part follows the same track as that of its neighbours. The essential features of motion can be readily visualized by enclosing a flexible but inextensible cylinder (or the body of a dead snake) within a close-fitting sinuous glass tube (fig. 1); each part of the cylinder is passively bent to fit the tube, and the lateral curvature of each region differs from that of the region next anterior or posterior to itself. If the cylinder is subjected to an external forward tractive force, the degree of lateral curvature of each region is continuously changed to that previously characteristic of the region next anterior to itself, and a bending wave is transmitted posteriorly over the

FIG. 1. Diagram showing the variation in lateral curvature of seventeen elements (*A-Q*) of an undulating body enclosed within a rigid tube. The mean curvature measured towards the left side varies from  $+1$  to  $-1$ . The relative curvature of each element is shown by the numeral on the left side; the centre of curvature of each element is shown by the corresponding small letter (*a-n*). If the cylinder is drawn forward in the direction of the arrow, each element glides forward about its instantaneous centre of curvature, and its radius of lateral curvature changes to that previously possessed by the element next anterior in the series.

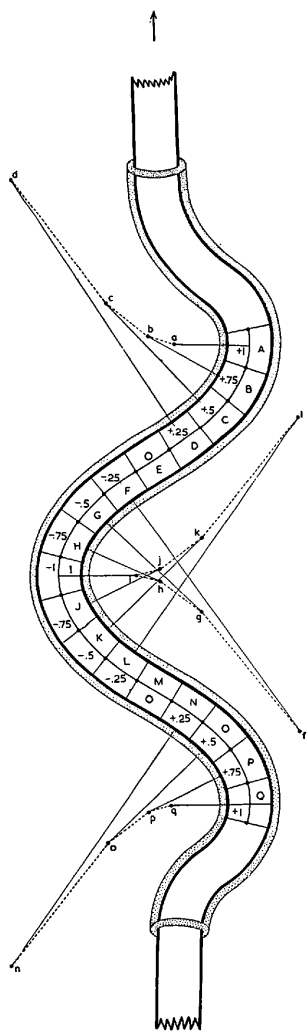


FIG. 1 (see opposite).

cylinder at the same speed as that at which the cylinder is being drawn forward through the tube. The changes in form undergone by the cylinder and its motion relative to the tube are the same as those exhibited by a living animal when gliding actively through a tube of similar shape. In both cases the form of the wave depends on two characteristics of the external environment: (i) the maximum degree to which the tube is bent at its crests (i.e. on the minimum radius of curvature of the tube); (ii) the difference in curvature between adjacent regions of the tube. Physiologically these characteristics of the wave depend on the maximum degree of shortening exhibited by laterally situated tensile elements and on the difference in length of successive such elements along the sides of the body.

The passage of a wave along the body of an organism is an expression of the fact that each element of the body is constantly changing its form towards that previously characteristic of an element adjacent to itself (see fig. 1). If the change is towards that of the element next anterior to itself, the wave travels antero-posteriorly; if the change is towards that of the next posterior element the wave travels postero-anteriorly, i.e. towards the head of the animal. If either the maximum degree of curvature, or the phase interval between adjacent elements, varies in successive elements along the length of the body, the form of the wave changes as it travels along.

In order that each element of the body should undergo these periodic changes in lateral curvature it must be subjected to appropriate bending couples. In vertebrate animals the source of these couples is obvious: the longitudinal axis of the body is rendered incompressible by a chain of rigid vertebrae and, consequently, any muscular tension developed unilaterally about this axis induces compression of the vertebral axis. Equal but opposite bending couples are thereby developed within the element concerned. In arthropods the function of the vertebral column is performed by the exoskeleton; in annelids compression of the axis is resisted by the hydrostatic pressure of the body fluid. Compression elements must also exist within a protozoan flagellum although their nature is, as yet, obscure. In all cases, however, the changes in form undergone by the body of an undulating organism are the result of internally generated bending couples.

#### (ii) *The mechanism of propulsion*

As all parts of an undulating organism move forward with uniform speed along the sinuous path of motion, all tangential forces (e.g. friction) exerted on the body by the external environment retard its motion; they cannot drive the animal forward. The forward propulsive thrust necessary to initiate or maintain progression must be derived from external forces acting normally to the surface of the body. From a mechanical point of view an analysis of undulatory progression is essentially concerned with the mechanism whereby localized internally generated bending couples expose the organism to a pattern of external forces, acting normally to the surface of the body, whose resultant is equal but opposite to the tangential forces of restraint.

The cycle of deformation undergone by each element of the body during the passage of a 'two-dimensional' bending wave is illustrated in fig. 2; tensile elements, lying laterally to a more centrally situated axis of compression,

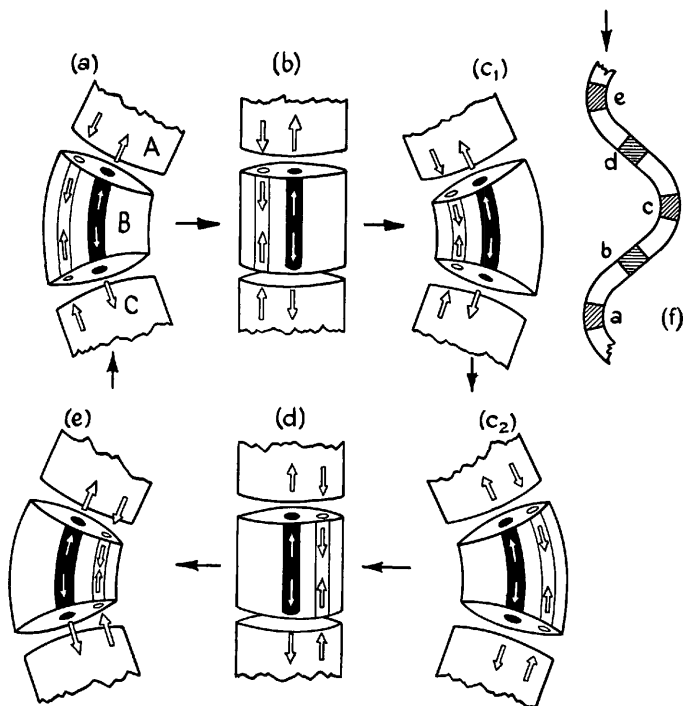


FIG. 2. Diagram illustrating the changes in form and the forces exerted on its neighbours (A and C) by an actively bending element (B). Figs. a-e indicate successive phases of one complete bending cycle. In a the tensile elements of the left side are beginning to shorten and the central axis develops compression; equal and opposite turning couples are exerted on the neighbouring elements A and C. In c<sub>1</sub> the tensile elements of the left side are fully contracted and at this stage those of the right side come into action (c<sub>2</sub>). The position of the phases a-e along the wave is shown in f, where the arrow indicates the direction in which the wave of contraction is passing along the body.

undergo changes in length. Equal but opposite bending couples are thereby generated within the active element, and corresponding turning couples are applied to the elements lying anteriorly and posteriorly to the bending element (fig. 2). As a *prime mover of propulsion* an actively bending element generates a *propulsive thrust*, provided it exerts its effort against neighbouring

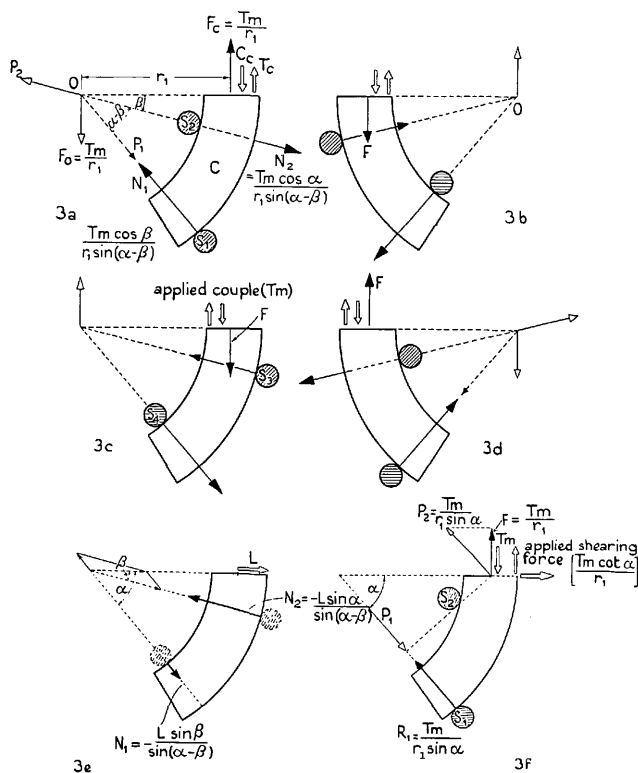


FIG. 3. When a turning couple ( $C_c, T_c$ ) of moment  $T_m$  is applied to a curved element (radius  $r_1$ ) in contact with two rigid restraints ( $S_1, S_2$ ), the resultant is an axial driving force  $\frac{T_m}{r_1}$  exerted at the end of the element. The applied couple is equivalent to a backward force ( $F_0$ ) acting through the centre of curvature  $O$ , and a propulsive force of equal magnitude acting at the end of the rod; the force  $F_0$  elicits, from the restraints, reactions whose resultant is equal but opposite to itself. The rod can be regarded as a lever whose fulcrum  $O$  is fixed by the operation of the restraints. The direction of the propulsive thrust is reversed if the rod is curved towards the opposite side (fig. 3, *b*) or if the sign of the applied couple is reversed (fig. 3, *c*).

A lateral shearing force ( $L$ ) applied to the end of the rod elicits reactions from the restraints (fig. 3, *e*) but does not affect the propulsive thrust derived from an applied couple. For a critical value of shear  $\frac{T_m \cot \alpha}{r_1}$  the reaction from one restraint becomes zero (fig. 3, *f*); alternatively, if a couple is applied to an element which is in contact with one restraint only, the element exerts, at its anterior end, a shearing force as well as a propulsive thrust.

units which conform with three conditions: (i) the units lying anteriorly and posteriorly to the actively bending element must differ from each other in their radius of curvature; (ii) both units must be restrained from moving normally to their own axes by the presence of external restraints; (iii) both units must be sufficiently rigid to resist the shearing stresses imposed on them by external forces. These essential principles are illustrated in figs. 3 and 4.

In fig. 3 the lateral surfaces of a unit  $C$ , of radius of curvature  $r_1$ , are in contact with smooth, rigid external restraints  $S_1, S_2$ . If an external turning couple ( $T_e, C_e$ ) of moment  $Tm$  is applied to the anterior and (by means of an actively bending element comparable with  $B$  in fig. 2) the mechanical effect is expressed in the form of a forward axial thrust  $\left(F_c = \frac{Tm}{r_1}\right)$  and an equal but opposite force ( $F_0$ ) acting through the centre of curvature of  $C$  at  $O$ . The latter force elicits from the restraints ( $S_1, S_2$ ) reactions ( $N_1, N_2$ ) whose resultant is equal but opposite to  $F_0$ . The net effect of the applied couple is therefore the axial thrust  $F \left(= \frac{Tm}{r_1}\right)$ . As shown in fig. 3, *a-d*, the direction of the thrust depends on the sign of the moment of the applied couple about the centre of curvature; hence the direction of the thrust is reversed either by a reversal of the side towards which the element is bent (fig. 3, *b*), or by a reversal of the side of the element on which the tensile elements are active (fig. 3, *c*). Since an actively bending element must apply equal but opposite turning couples to the units lying anteriorly and posteriorly to itself it follows that a net propulsive thrust can only develop when the forward thrust derived from a posterior unit is greater than the backward thrust from the anterior unit or vice versa; in other words, when the radius of curvature of unit  $A$  (figs. 2 and 4) is greater or less than that of  $C$ ; the net propulsive thrust being  $Tm\left(\frac{1}{r_1} - \frac{1}{r_2}\right)$ . This important conclusion is illustrated in fig. 4 where an actively bending element  $B$  (of radius  $r_2$ ) lies posteriorly to an element  $A$  (of radius  $r_3$ ) and anteriorly to an element  $C$  (of radius  $r_1$ )  $r_3 > r_2 > r_1$ ; the system is in contact with six external resistances. If element  $B$  exerts its active effort against its neighbours entirely in the form of turning couples ( $T_a, C_a; T_c, C_c$ ) it elicits from  $A$  and  $C$ , the forces  $F_a$  and  $F_c$  (fig. 4, *b*) whose resultant has a small lateral component (which elicits a reaction from restraint  $S_3$ ) together with a propulsive force  $Tm\left(\frac{1}{r_1} - \frac{1}{r_3}\right)$  turning  $B$  about its centre of curvature at  $p$ ; the reactions from  $S_1, S_2, S_5$ , and  $S_6$  are determined as in fig. 3, *a-d*.

It may be noticed that the axial propulsive force elicited from the system is independent of any shearing effect which element  $B$  may exert on its neighbours or vice versa; but, as shown in fig. 3, *e, f*, these forces influence the reactions which develop from the individual restraints and thereby alter the bending moments of these forces about each cross-section of the elements  $A$  and  $C$ . In fig. 4, *c*, the shearing forces operating across the surfaces of contact of the three elements have the limiting value defined by fig. 3, *f* and only three restraints ( $S_1, S_3, S_5$ ) are operative. In the

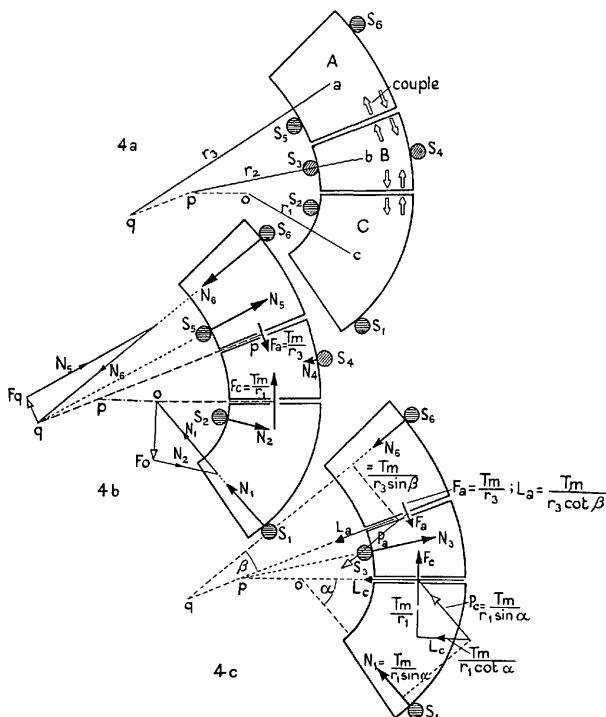


FIG. 4. *a*, an element *B* of average radius  $r_2$  (*bp*) lies posteriorly to an element *A* of radius  $r_3$  (*aq*) and anteriorly to an element *C* of radius  $r_1$  (*co*). It is in contact with six smooth rigid restraints ( $S_1$ – $S_6$ ).

FIG. 4. *b*, if element *B* develops internal bending couples on its right side without exerting any shearing forces across its surfaces of contact with *A* and *C*, element *B* is subjected to a forward axial thrust ( $F_c = \frac{Tm}{r_1}$ ) from *A* and a backward thrust ( $F_a = \frac{Tm}{r_3}$ ) from *C*; these forces exert a small outward force against  $S_4$ , and a forward axial thrust ( $\frac{Tm}{r_1} - \frac{Tm}{r_3}$ ) rotating element *B* about its centre of curvature  $p$ . The reactions from  $S_1, S_2, S_3$  and  $S_6$  are determined as in fig. 3.

FIG. 4. *c*, if element *B* develops its bending couples when the system is restrained by  $S_1, S_3$  and  $S_6$  only, the surfaces of contact between *B* and its adjacent elements must resist shearing forces ( $L_a; L_c$ ); the axial thrust applied to *B* is however unaltered.

(In this figure the reactions from the restraints are shown on half-scale.)



inanimate system the lateral bending stresses operating on *A* and *C* are determined by the positions of the external restraints; but, in a living system free to operate against more than three restraints, the reaction from each restraint is determined by the relative tension of adjacent series of tensile elements and not vice versa.

In fig. 4 the whole of the propulsive energy is derived from element *B*, for only this element undergoes an active change in shape. Element *B* is the prime mover. The elements *A* and *C* can be regarded as rigid propellers; their lateral tensile elements responding passively and exerting sufficient force to enable *A* and *C* to resist bending under the forces exerted on them by element *B* and by the external restraints with which they are themselves

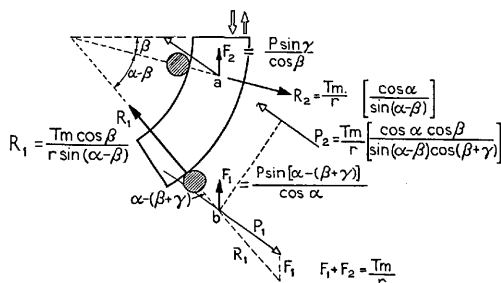


FIG. 5. Diagram illustrating the action of surfaces of contact as inclined planes. The applied couple is equivalent to forces ( $P_1$ ,  $P_2$ ) acting at the points (*a*, *b*) of intersection of the reactions from  $S_1$  and  $S_2$  with the line of the propulsive thrust. The forces  $P_1$  and  $P_2$  act obliquely to the line of the reactions from  $S_1$  and  $S_2$ ; the sum of their propulsive components ( $F_1$  and  $F_2$ ) is  $\frac{Tm}{r}$  and the values of  $R_1$  and  $R_2$  are the same as in fig. 3, *a*, where the rod can be regarded as a lever pivoted at its centre of curvature.

in contact. In a living organism there is no such division between prime mover and propeller; all elements of the body change their shape and all transmit, to each other, forces which enable the whole system to exert its effort against the outside world.

Although the energy required to maintain a forward propulsive thrust is derived from internally generated bending couples, it is usually more convenient to define the propulsive thrust as the resultant of the external forces acting normally to the surface of the organism. Each element of the body can be regarded as a curved lever; in fig. 3 the centre of curvature *O* can be regarded as a rigid fulcrum fixed by means of the external restraints  $S_1$  and  $S_2$ . Alternatively, the surfaces of restraint can be regarded as inclined planes (see fig. 5) and the system regarded as a 'two-dimensional screw'.

During steady motion the propulsive thrust which is the resultant of all the forces acting normally to the body must be equal but opposite to the total tangential drag. A snake gliding through a rigid glass tube or *Cristaspira* creeping through the wall of the crystalline style of an oyster can be regarded as a two-dimensional screw of variable pitch driven through a rigid nut by

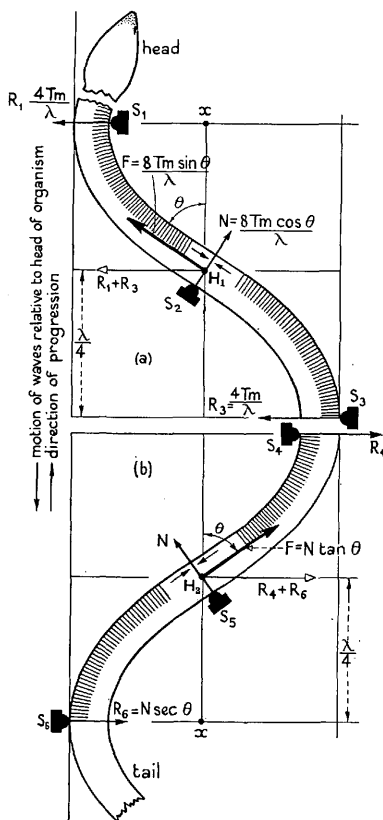


FIG. 6. Two half waves of wavelength  $\lambda$ , and cutting the axis (xx) of progression at an angle  $\theta$ , are each restrained by three restraints ( $S_1$ - $S_3$  and  $S_4$ - $S_6$ ).

Fig. 6, a, shows the value of the tangential driving force ( $F$ ) and the reactions ( $N$ ,  $R_1$ - $R_6$ ) from each restraint in terms of the maximum couple developed about  $H_1$  and  $H_2$  (opposite  $S_2$  and  $S_3$ ) by the lateral tensile units; the shaded areas show the side of the body on which the tensile units are active. If  $Tm$  is the moment of the couple operating opposite  $S_2$  or  $S_3$ , the tangential propulsive thrust is  $\frac{8Tm \sin \theta}{\lambda}$  and the reaction ( $N$ ) from  $S_2$  is  $\frac{8Tm \cos \theta}{\lambda}$ .

Fig. 6, b, shows the value of the propulsive force and reactions from  $S_4$  and  $S_6$  in terms of the reaction ( $N$ ) from  $S_5$ ;  $F = N \tan \theta$ . The driving force is the resultant of the three external reactions ( $R_4$ ,  $N$ , and  $R_6$ ). If the two half-waves operate as a unit, the reactions from  $S_3$  and  $S_4$  become zero, and equivalent shearing forces operate between the two half-waves.

an internal source of energy. A simple model is provided by a short length of flat spiral spring in contact with three smooth nails driven into a board; if the spring is drawn backward against the restraint of the nails, the curvature is altered between the points of restraint; the spring glides forward as soon as it is released.

(iii) *The relationship of propulsive thrust to wave-form*

As each half-wave of an undulating organism is characterized by progressive change in curvature along its length, it can operate as a single propulsive unit when actuated by the tensile structures lying on the side towards which the curvature is increasing anteriorly, successive half-waves being actuated by tensile structures on opposite sides of the body. As the animal glides along, all the elements constituting a half-wave change their shape and can thereby contribute towards the propulsive thrust. The relative contribution of each of the elements concerned could be determined either from a knowledge of the tension developed at various stages in the shortening of the tensile units, or from a precise knowledge of the distributions and magnitude of the forces acting normally to the body. Neither of these requirements can, as a rule, be satisfied experimentally and further analysis involves two assumptions: (i) that a fully stretched or fully shortened tensile unit has zero tension; (ii) that the tension developed by each unit rises until half of the shortening process has occurred and then falls again to zero, the rise and fall of tension being symmetrical. So long as the system conforms to these requirements the propulsive thrust  $F$ , acting tangentially to  $S_2$  (fig. 6, *a*), can be expressed in terms of the maximum tensile couple ( $Tm$ ) exerted by any one element, the wave-length ( $\lambda$ ) of the wave, and the angle ( $\theta$ ) at which the wave cuts the axis of progression ( $xx$ ); the tangential thrust ( $F$ ) is  $\frac{8Tm \sin \theta}{\lambda}$  where  $Tm$  is the moment of the bending couples operating about the mid-point ( $H_1$ ) of the system. Alternatively, the tangential thrust can be expressed in terms of the forces acting normally to the body (fig. 6, *b*).

A series of half-waves, similar in form and tensile effort, is shown in fig. 7. External resistances operate at the two ends of the system and against the posterior face of each half-wave. The strain on the tensile units (indicated in the figure by shading lines) is greatest at points situated on the main axis ( $xx$ ) of progression and falls to zero at the troughs and crests of the waves where the shearing forces reach their maximum value. Each of the external forces ( $N$ ) operating against the posterior surface of a half-wave (see fig. 7, *b*) has two components (fig. 7, *b*) (i) a driving force ( $N \sin \theta$ ) acting along the axis ( $xx$ ), (ii) a transverse ( $yy$ ) component ( $N \cos \theta$ ). During steady movements  $\sum N \sin \theta$  is equal but opposite to the backward components ( $\sum L \cos \theta$ ) of the tangential drag ( $L$ ) acting against the ventral surface of each segment of the body; the resultant of all the transverse forces

$$(\sum N \cos \theta + \sum L \sin \theta + R_1 + R_2)$$

is zero.

As seen in fig. 8 the value of  $\theta$  increases with the amplitude and decreases with the length of the waves; consequently, the tangential thrust ( $F$ ) to be derived from any particular level of maximum bending effort ( $T_m$ ) will vary

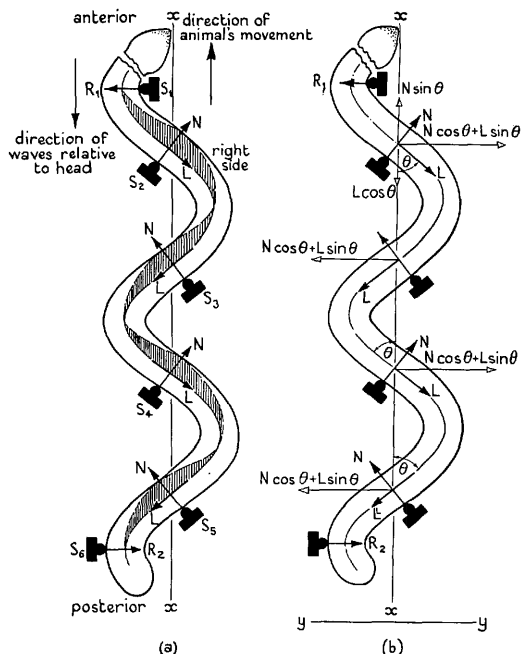


FIG. 7. Diagram showing the general equilibrium between the normal and tangential forces acting on an undulatory organism.

In fig. 7, *a*, the resultant of all the forces ( $R_1$ ;  $N_1-N_6$ ;  $R_2$ ) acting normally to the surface of the animal is equal but opposite to that of all the tangential forces ( $L$ ); the latter forces being equal but opposite to the propulsive thrusts shown in fig. 6. The shaded areas show the distribution of active tensile units; the width of the area shows the relative degree of tension of the tensile units.

Fig. 7, *b*, the forces ( $N$ ) acting against the reverse faces of the waves have components ( $N \sin \theta$ ) acting forwards along the axis ( $xx$ ) of movement and transverse components ( $N \cos \theta$ ); the drag forces have backward components ( $L \cos \theta$ ) acting along the axis  $xx$ , and transverse components ( $L \sin \theta$ ); during steady motion  $N \sin \theta = L \cos \theta$ , and the resultant of all the transverse forces is zero.

accordingly. Waves of large amplitude and short length may be regarded as adaptations for overcoming high frictional resistance between the ventral surface of the body and the environment. Similarly, if the surfaces of contact between the sides of the body and the external resistances are not perfectly

smooth the forward tangential thrust ( $F$ ) becomes  $\frac{8Tm \sin \theta}{\lambda} (1 - \mu \cot \theta)$

where  $\mu$  is the coefficient of lateral friction; if  $\mu = \tan \theta$  no driving thrust is available—in other words, the organism would have to increase the pitch of the waves in order to propel itself forwards. On the analogy of vertebrate muscles in general, maximum undulatory efficiency may be expected to occur when the extent and rate of shortening of the tensile units (i.e. the form of the waves) bears a particular relationship to the tangential resistance to be overcome.

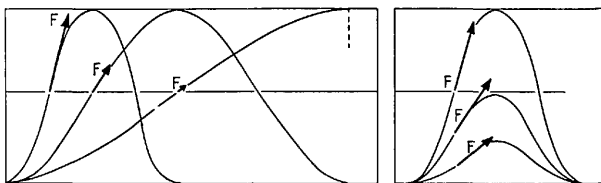


FIG. 8. Diagram illustrating the relationship between the tangential axial thrust (developed by couples of equal maximum strength) to the wavelength and amplitude of the bending wave. The thrust decreases with wavelength and increases with amplitude.

## II

### (i) *Two-dimensional undulatory movement in water*

Just as an undulatory organism gliding through a close-fitting and rigidly fixed sinuous tube can be compared with a screw moving in a rigid nut, so the motion of the animal in water can be compared with the same screw when operating against a fluid resistance. Alternatively, the swimming organism can be regarded as gliding through a glass tube which slips backwards relative to the ground as the organism moves forward. Neither in the case of a swimming organism nor a screw propeller is it possible to provide a comprehensive picture of the whole system.

Under terrestrial conditions each element of the animal's body is constrained to move along its own circumference of curvature. The external resistances, being rigidly fixed to the ground, are able to exert forces normal to the surface of the body without allowing any part of the body to move normally to its own longitudinal axis: the animal moves forward, relative to the ground, at the same speed as the waves travel backwards along the body. When swimming in water, on the other hand, forces acting normally to the body can only develop against an element of the body when the latter possesses a component of motion normal to its own longitudinal axis—in other words, when the element is moving with its surface inclined by an appropriate angle ( $i$ ) to its path of motion. As shown in fig. 9, this fundamental requirement implies that the waves move backward relative to the ground; this backward movement or 'slip' of the waves (as measured along the axis ( $xx$ ) of progression) is the most distinctive feature of all undulatory swimming organisms irrespective of size and internal structure; it is, in fact, a measure of the

extent to which each element of the wave has a component of motion normal to its own longitudinal axis and thereby is able to elicit a normal reaction from the surrounding water. The greater the normal component of motion (relative to the tangential component) the greater is the 'slip' of the waves and vice versa. Since the rate of the animal's forward progression is equal to the difference between the speed of propagation of the waves over the body and the velocity of the 'slip', it follows that the maximum speed of forward progression for any aquatic undulating organism must be less than that at which the waves are travelling backwards relative to the head of the animal.

The balance of forces required to maintain the steady forward propulsion of an undulatory organism in water is of the same fundamental nature as that in a terrestrial animal, namely, the retarding effect of all tangential forces must be balanced by the propulsive effect of all the forces acting normally to the body. Determination of these forces is beyond the range of direct observation and further analysis is largely restricted to an attempt to express the rate at which an organism can propel itself through the water in terms of the frequency and form of the waves which it propagates along its body. An inquiry of this type encounters very formidable difficulties but a useful qualitative picture of the propulsive properties of a wave can be obtained by visualizing the forces which operate on a single element of the body at a particular phase of its movement, and considering later the extent to which it is possible to deduce the propulsive properties of the whole organism as the integrated effect of all its constituent elements.

The force exerted on an element as it moves through the water depends on the size and form of the element and on the speed and direction of its movement relative to the surrounding water. So long as the surface of the element is inclined to its path of motion, the resultant force has two components, one ( $N$ ) normal to the surface of the element and the other tangential ( $L$ ) to this surface. If the element is moving with velocity  $Q$  with its surface inclined to the path of motion by an angle  $i$ ,

$$N = C_D(Q), \quad L = C_L(Q),$$

where  $C_D$  and  $C_L$  are coefficients which vary with the size and form of the element, its absolute speed, and with the angle  $i$ ; if  $i$  is zero,  $C_D$  is zero and there is then no propulsive force.

The propulsive or retarding action of both normal and tangential forces on the movement of the element along the main axis ( $xx$ ) of propulsion can be visualized by expressing the velocity and direction of the element's motion through the water in terms of its displacement in respect of the main axes ( $xx$ ,  $yy$ ) of propulsion and of the angle at which the element is inclined to the axis (fig. 10). If the element is inclined to the  $xx$ -axis at an angle  $\theta$  and is moving in respect to this axis at velocity  $V_x$  and along the  $yy$ -axis at velocity  $V_y$ , the angle of incidence ( $i$ ) of the surface to the path of motion is such that

$$\tan i = \frac{V_y - V_x \tan \theta}{V_x + V_y \tan \theta}.$$

The angle of incidence has a maximum value ( $90^\circ = \theta$ ) when the element has no component of forward motion ( $V_x = 0$ ) and approaches zero as  $V_x$  approaches  $V_y \cot \theta$ .

The coefficient ( $C_D$ ) of normal resistance increases with the value of  $i$ , hence the force acting normally to the element has a maximum value when  $V_x$  is

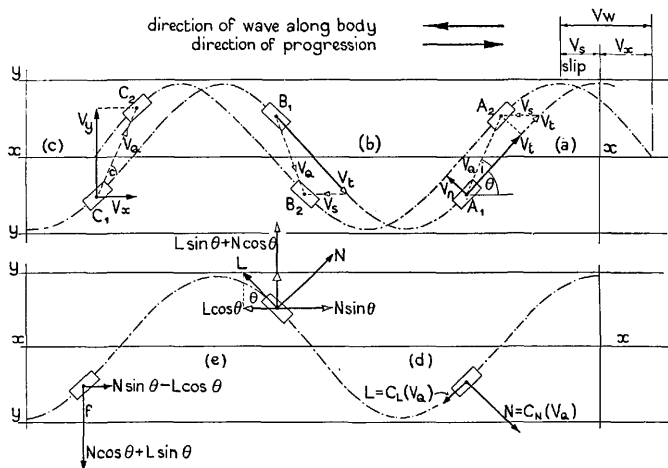


FIG. 9. To exert a forward propulsive thrust an element must possess a component of motion normal to its surface and, consequently, the waves must move backward relative to the ground.

Fig. 9, *a*, the resultant displacement ( $V_0$ ) of an element moving with normal velocity  $V_n$  and a tangential velocity  $V_t$  is the same as for an element moving with a tangential velocity  $V_t$  and a backward velocity ( $V_n$ ) in respect to the  $xx$ -axis.  $V_s$  is the velocity of 'slip' of the waves; if  $V_n$  is zero,  $V_s$  is zero. If  $V_w$  is the speed of conduction of the waves, the forward speed of the animal ( $V_x$ ) in respect of the  $xx$ -axis is  $V_w - V_s$ .

Fig. 9, *c*, the motion of an element moving at a velocity  $V_0$  (inclined at an angle  $i$  to its path of motion) expressed in terms of transverse ( $V_y$ ) and forward ( $V_x$ ) components.

Fig. 9, *d* and *e*, the element elicits a reaction ( $N = C_N(V_0)$ ) from the water normal to the surface and a reaction [ $L = C_L(V_0)$ ] tangential to its surface. The propulsive thrust in respect of the  $xx$ -axis is  $N \sin \theta - L \cos \theta$ , whilst the transverse force is  $N \cos \theta + L \sin \theta$ .

zero and falls to zero as  $V_x$  approaches  $V_y \cot \theta$ . In order to yield a resultant propulsive force along the axis of progression, the propulsive component of  $N$  must be greater than the retarding component of  $L$ ; in other words,  $N \sin \theta > L \cos \theta$ ; and, during forward motion at a steady speed,  $L = N \tan \theta$  whilst the resultant of all the transverse ( $yy$ ) forces is zero. The conditions are thus fundamentally the same as under terrestrial conditions (see figs. 7, 9).

An application of these principles to a whole cycle of an element's transverse movement and to the propulsive properties of the organism as a whole involves known values of  $C_L$ ,  $C_D$ ,  $\theta$ ,  $V_w$ , and  $V_y$  for all phases of the cycle and pre-supposes that  $V_y$  can be expressed in terms of the velocity ( $V_w$ ) at which the waves pass along

the body. In a recent paper Taylor (1952) has considered the case of an organism projecting sine waves of known speed, amplitude, and wavelength, and applied values of  $C_D$  and  $C_L$  derived from wires set at an angle to a wind; he has shown that the expected ratio of the forward propulsive speed  $V_x$  to the speed of the waves  $V_w$  increases with the amplitude of the waves, and decreases with their wavelength. At the same time, this ratio increases with the absolute size and speed of the organism concerned. An application of the theory to a snake, leech, and ceratopogonid larva shows a very fair measure of agreement between observed and calculated values (see Taylor, 1952 *b*, fig. 4).

Although the above treatment may yield a useful general picture of the mechanical principles involved during undulatory swimming, its application to living organisms must be carried out with extreme caution. At least three limitations must be borne in mind. (i) In few, if any, swimming organisms do the propagated bending waves maintain constant amplitude and wavelength as they pass along the body. Two serious complications thus arise: (*a*) the rate of propagation ( $V_w$ ) of the waves is not constant, (*b*) the transverse velocity ( $V_y$ ) and the angle of inclination ( $\theta$ ) of an element at any given phase of the cycle is not the same for all elements. (ii) The theoretical analysis assumes that the water in contact with each element of the body can be regarded as at rest relative to the ground and not affected by the activity of neighbouring elements. (iii) The theory neglects the special conditions which exist at the two ends of the system.

Further consideration of some of the difficulties referred to above will be given elsewhere. For the moment it is possible to draw only four main conclusions. (i) The mechanical principles involved during two-dimensional undulatory swimming are fundamentally the same as those used during a terrestrial glide except for the fact that any element which contributes towards the propulsion of the body must possess a component of motion normal to its own longitudinal axis and thus move with a positive angle of attack between its own surface and its path of motion. Each element functions as an inclined blade or hydrofoil—eliciting from the water a reaction normal to its surface. The propulsive component of this reaction along the axis of progression overcomes the retarding component of the tangential forces acting on the body. (ii) As an undulating organism swims forward the waves passing down the body must move backwards relative to the ground and the maximum rate of the animal's progression must be less than the rate at which the waves are propagated backwards over the body. (iii) The propulsive power of a wave may be expected to increase with an increase of amplitude and decrease with an increase of wavelength (Taylor, 1952 *a*). (iv) The ratio of speed of progression to speed of conduction of waves may be expected to be greater in large animals than in small ones (Taylor, 1952 *b*).

#### (ii) *Three-dimensional undulatory movement*

Whereas the bending movements exhibited by relatively large animals (snakes, eels, polychaete worms) can be regarded as restricted to a single



plane, those of some small aquatic organisms—notably certain Protozoa—are more complex. Accurate observation of such movements is by no means easy; it is important not to underestimate their complexity or overlook the considerable degree of versatility displayed by a single individual organism under different environmental conditions.

Geometrically, most if not all the complex movements observed in protozoan flagella by Uehlela (1911) and other authors, can be described in terms of a system wherein the plane of bending changes as the contraction wave passes from one element to another. If the change in the plane of bending followed an appropriate pattern, the system would acquire the form of a regular helix, and the form of the waves would resemble those which pass along a rope when one end is rotated in a circle. How far the movements of any living organism conform with this regular pattern is open to serious doubt, but the mechanical principles involved have an interesting bearing on the mechanism of movement of such organisms as spirochaets and spirilla, and, possibly, some bacteria.

A static helical form could be impressed on an elongated structure in two ways: (i) by *uniform* bending in one morphological plane, accompanied by an appropriate angle of torsional displacement between adjacent elements; (ii) by simultaneous sinusoidal bending in two planes normal to each other; i.e. by combining 'lateral' bending with 'dorso-ventral' bending and maintaining a constant phase difference of one-quarter of a complete cycle between the two. These two systems are illustrated by fig. 10 where the resultant helical 'organisms' are shown circumscribing imaginary cylinders. The external form of the two systems is identical, but the type of internal deformation of the original filaments is different. From a dynamical point of view only the potentialities for changes in *external* form need be considered.

There appear to be only two methods by which a helical system could propel itself. (i) By acting as a passive rigid screw rotated by an external couple; according to Metzner (1920) this type of motion is exhibited by *Spirillum volutans*, where the requisite couple is provided by terminal flagella. No change in form is exhibited by the elements of the body itself. (ii) Each element of the body should undergo cyclical changes in form. It is the latter possibility which is of immediate interest.

If each element of a helical system is regarded as a short cylinder, its contribution towards the propulsion of the body depends on its ability to change, by internal effort, the radius of curvature of each of its main morphological surfaces; the radius of curvature of its 'dorsal', 'ventral', and 'lateral' surfaces must be constantly changing. If, as in fig. 10, the organism is visualized as in contact with a circumscribed cylinder, it must—if it is to be capable of self-propulsion—be able to bring each of its morphological surfaces in turn into contact with the surface of the cylinder. No animal could progress if it kept the same surface in contact with the cylinder, for under such conditions there would be no change in the form of its constituent elements and, consequently, no source of propulsive energy.

In their simplest form the changes in shape undergone by each element of a self-propelling helical system are illustrated by fig. 11, *a*, where the

element possesses four tensile elements (*Dorsal, Left, Ventral, Right*) arranged round a central axis of compression. In fig. 11, *b* an element (*B*) of this type lies between two rigid rods (*A, C*); if one of these (e.g. *C*) is rigidly fixed, the other (*A*) sweeps over the surface of a cone when the tensile units of *B* shorten either in the order *Dorsal, Right, Ventral, Left* (or *Dorsal, Left, Ventral, Right*).

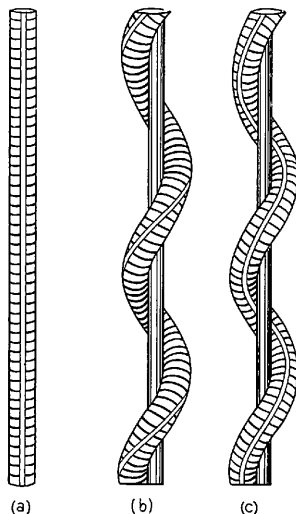


FIG. 10. A uniform cylinder (fig. 10, *a*) can be converted into a helical form either (i) by uniform bending in one plane accompanied by torsion (fig. 10, *b*) or (ii) by simultaneous sinusoidal bending in two planes normal to each other (fig. 10, *c*). The external form of the two systems is the same but the pattern of internal deformation differs. Note that in fig. 10, *b*, the original dorsal surface of the undeformed cylinder (marked by the white line) is of uniform curvature and passes spirally round the central axis of the body; in fig. 10, *c*, the dorsal line is of varying curvature and does not pass round the body.

A series of active elements differing from each other by a constant difference in the phase of its contractile cycle would assume the form of a regular helix circumscribable round a cylinder; as a contractile cycle passes round each individual element, the element would (since it is restrained from spinning about its own central axis) move round the cylinder in a direction opposite to that in which the process of shortening sweeps round the element's tensile units (see fig. 12). The changes in form undergone by each element are essentially those exhibited by each short length of a flexible rope when drawn, *without torsion*, through a rigid helical tube; as an element moves forward through the tube each of its 'morphological' surfaces (*Dorsal, Right, Ventral, Left*) is in turn bent to fit the 'inner' surface of the tube and during each

complete bending cycle the element moves in a circle round the surface of the cylinder about which the helical tube can be circumscribed.

It is essential to note that a rotary displacement of each element about a circumscribed cylinder (or about the axis of symmetry of the helix) only

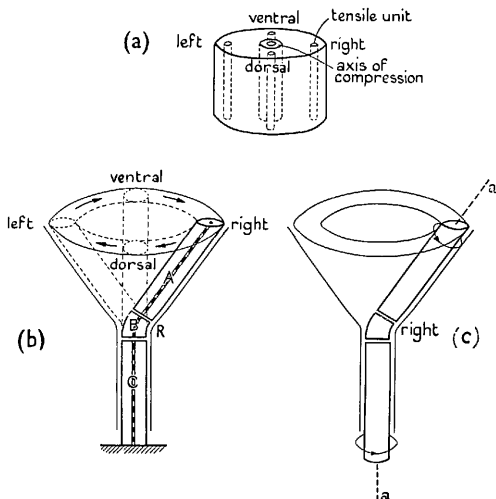


FIG. 11, *a*, a contractile element possessing four tensile units (Dorsal, Left, Ventral, Right) arranged round a central axis of compression; the tensile units being able to shorten in the order Dorsal, Left, Ventral, Right (or *L, V, R, D*). In fig. 11, *b*, an element (*B*) of this type operates against two other rigid elements *A* and *C*, the element *C* being restrained from rotation about its own central axis.

As shown in the figure, the right tensile unit is shortened and the three elements are viewed from the dorsal surface.

If the tensile elements shorten in the order Dorsal, Left, Ventral, Right, element *A* sweeps over the surface of a cone in the direction shown by the arrows in fig. 11, *b*. If, as in fig. 11, *c*, the same contractile cycle occurs when element *A* is not restrained from rotation, the three elements spin about their central axes *aa* without displacement of *A* or *C* relative to the circumference of the cone. Note that the direction of spin is opposite to that in which element *A* moves round the cone in fig. 11, *b*. In fig. 11, *b*, the dorsal surface (shown as a dotted band) of the elements would remain uppermost during the whole contractile cycle; in fig. 11, *c*, the dorsal surface would only be visible during one-quarter of a cycle.

occurs if the element—and therefore the body as a whole—is prevented from spinning freely about its own median axis. In the absence of such restraint each element can undergo its cycle of bending movements without moving its position relative to the surface of a circumscribed cylinder or the walls of a rigid helical container. Thus in fig. 11, *c*, the same bending cycle is occurring as in fig. 11, *b*, but the anterior end of the element does not sweep round the surface of a cone; it remains in the same position spinning about the axis

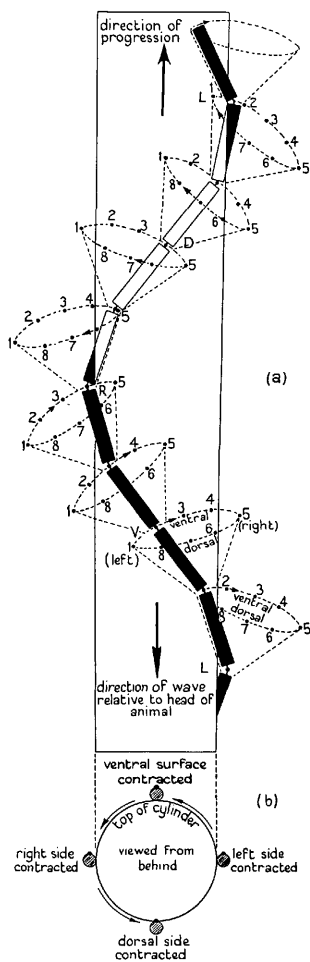


FIG. 12 (see opposite).

*aa* in the opposite direction in which it would, if prevented from spinning, sweep round the cone (or round a circumscribed cylinder). From purely geometrical considerations it follows that an organism could, by developing appropriate trains of dorso-ventral and lateral bending waves, propel itself forward along a rigid helical container provided the walls of the container can prevent the body spinning on its own helical axis.

From a dynamical standpoint the basic principles of helical motion are fundamentally the same as those of a two-dimensional system; during steady motion the forward components of forces acting normally to the body must equal the retarding components of all tangential forces. The difference in the two systems lies in the fact that whereas the lateral components of all normal and tangential forces of a two-dimensional wave summate to zero, those of a helical wave yield couples tending to rotate the body in the opposite direction to that in which the elements are moving round the median axis of motion (fig. 13). As shown in fig. 14 any such rotation reduces the speed at which the elements move relative to the environment; if the organism spins through  $360^\circ$  during the passage of each complete wave of bending, the wave would remain stationary relative to the ground and possess no propulsive power. From a functional standpoint helical waves would possess their maximum propulsive power when one end of the system is rigidly fixed—as in the case of a flagellated cell forming part of an epithelium. In such a case the rotating couple set up by the flagellum would be neutralized by forces exerted by the fixed environment. In freely swimming systems, however, some amount of 'spin' is inevitable. Its effect is to reduce the effective speed at which the waves travel relative to the environment, and since the latter factor determines the magnitude of the propulsive thrust, the speed of progression must inevitably be less than when all spin is eliminated. If the frequency of spin were equal to the frequency of propagation of the waves down the body, the waves would remain stationary relative to the medium and no forward thrust would develop; on the other hand, if there is no 'spin' the rate of travel of the waves relative to the medium would be equal to the rate at which they are travelling relative to the head of the organism minus the speed at which the latter is moving forward through the water. Again, the propulsive thrust would be greatest in the case of a flagellum attached to a fixed cell and less in the case of a free-swimming organism; in the latter case the thrust would be increased if the flagellum were propelling a flat ellipsoidal cell or (possibly)

FIG. 12. A series of elements similar to that shown in fig. 11 differing from each other by one-eighth of a contractile cycle form a helix circumscribable about a cylinder. If each element changes its form to that characteristic of the element next anterior to itself whilst the whole body is restrained from spinning on its own axis, each element passes round the circumscribing cylinder once during each contractile cycle.

The motion of the body relative to the circumference of the cylinder is identical to that of a rope drawn forward (in the direction of the top arrow) *without torsion* through a close-fitting helical tube of similar form to the series of elements shown in the figure. The large letters *L*, *V*, *R*, *D*, *L* indicate the location of the fully shortened tensile elements.

In fig. 12, *b*, the dorsal side of the body is marked by a black dot; the shortened elements are located at the surface of body in contact with the cylinder.

if the flagellum itself were elliptical in cross-section. If the frequency of generation of the waves were  $x$  per second and the body is spinning about the axis of motion  $x - n$  per second, the frequency of the waves relative to a fixed point in

the environment would be  $n$  per second and the organism would, owing to 'slip', advance about a helical path whose pitch is less than that of the waves and it would complete  $n$  turns of this helix per second. As noted by Reichert (1909), the existence of spin is highly characteristic of many flagellated Protozoa, and the above discussion confirms that author's conclusion concerning its mechanical origin.

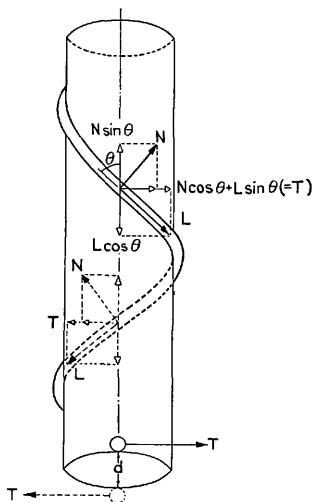


FIG. 13. In a regular helical system all the forces (normal and tangential) exerted on a wave act tangentially to the surface of a cylinder. For any one element the normal force ( $N$ ) has a forward component  $N \sin \theta$  and a transverse component  $N \cos \theta$ ; the tangential drag ( $L$ ) has a backward component  $L \cos \theta$  and a transverse component  $L \sin \theta$ . For an element situated one half of a wavelength from the first, the total transverse force will, with that of the first element, yield a couple turning the elements and the body as a whole about the axis of the cylinder in a direction opposite to that in which the elements are moving round the cylinder. During steady motion  $N \sin \theta = L \cos \theta$ , whilst the 'spinning' couple is  $d \cdot L \csc \theta$ , where  $d$  is the diameter of the helix.

The motion of a *regular* helical system, relative to the surrounding medium, would (if the system be prevented from spinning as a whole about its long axis) be identical with that of a rigid screw of the same helical form when rotated, by an external couple, at a frequency equal to that at which the bending waves are being propagated along the length of the actively undulating organisms. The two systems could only be distinguished from each other by observation of a point marked on the surface of the body. If the body were opaque, a point visible at any phase of motion of the active flagellum would be visible at all others, whereas a similar point on a rigid screw would only be visible for half of each cycle. The essential difference between the two systems lies in the fact that each element of the active organism is constantly changing its shape, whereas no change occurs in a passively rotated rigid screw. The motion of the organism through the water depends on its ability to execute these changes in shape against the resistance of the surrounding medium.

Further consideration of so-called 'helical' organisms will be given elsewhere but two general points may be mentioned here. First, an examination of the behaviour of grass snakes in the light of the above analysis has revealed a somewhat striking fact. These animals can glide through sinuous tubes lying in a vertical plane with the same facility as that displayed through horizontal tubes. During a 'vertical' glide the animal uses its dorso-ventral

musculature and uses its lateral muscles when gliding horizontally. There is, therefore, no anatomical reason why it should not negotiate a helical tube of equivalent pitch and diameter. All attempts to elicit a helical glide have however failed; one is tempted to wonder whether the animal has failed to evolve a type of muscular co-ordination which, in the absence of any 'anti-rotation' device, would be of no functional value! It would be interesting to know whether a snake with an elliptical cross-section could, on the other hand, negotiate a regular helix of similar cross-section. Second, it should be borne in mind that the existence of a 'self-propelling' organism of regular helical form is by no means too well established: most three-dimensional waves are probably elliptical in cross-section and not circular, and in such forms the spinning couple imparted to the body is correspondingly reduced.

A mathematical derivation of the magnitude of the spinning couple operating on a self-propelled helical system has recently been given by Taylor (1952 *a*).

### III

#### *Notes on observational data*

So long as an animal is gliding against rigid restraints the application of the principles described above does not encounter any obvious difficulties. In large animals the equilibrium between the forces acting normally and tangentially to the body has been established experimentally (Gray and Lissmann, 1950) and there is no reason to suppose that smaller forms, less amenable to experimental analysis, should behave differently. On the other hand, the observation of organisms swimming in water reveals data which indicate the limitations of any existing theoretical analysis. For the sake of convenience, attention will be restricted for the moment to relatively large organisms (eels, snakes, and ceratopogonid larvae); nematodes and unicellular systems will be dealt with in separate communications.

The form of the waves passing down the body of an anguilliform fish has been described elsewhere (Gray, 1933). The animal exhibits rather more than one complete wavelength and the amplitude of transverse displacements increases as the wave passes posteriorly. The changing form of the moving wave is conveniently expressed in terms of the body's displacements relative to fixed axes through the head of the animal; the area which includes the body during one complete muscular cycle being regarded as its characteristic envelope. In an anguilliform fish this envelope is approximately an isosceles triangle with its apex at or near the anterior end of the body. The same general characteristics are revealed by a snake (*Natrix natrix*) swimming in water. Photographic records reveal two features of the snake's movements which are not covered by the theoretical analysis. (i) Both amplitude and wavelength are approximately doubled as a wave crest moves between a point situated about one-quarter of the body length from the head to a point one quarter of the body length from the tip of the tail; the rate of propagation ( $V_w$ ) of the wave therefore increases as the wave travels backward. (ii) The

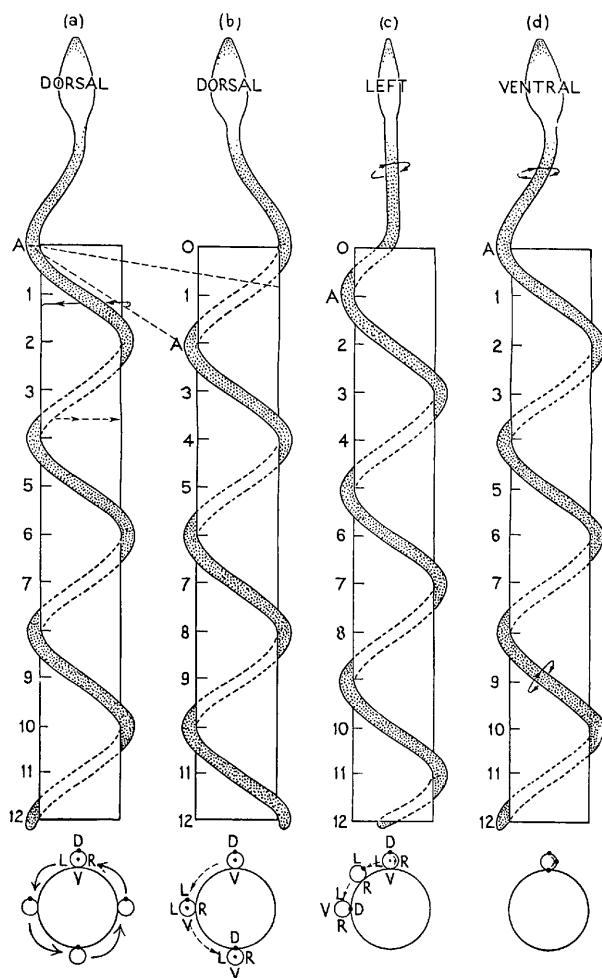


FIG. 14 (see opposite).



forward speed ( $V_x$ ) of the animal's progression is relatively constant. Consequently, the ratio  $\frac{V_x}{V_w}$  varies during the passage of the wave; towards the posterior end of the body the ratio is of the order 0.4–0.5, whereas at the front

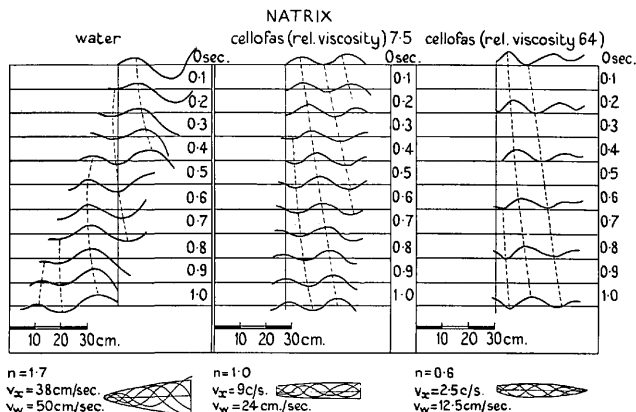


FIG. 15. Diagram illustrating the effect of viscosity on the form and frequency of the swimming movements of a snake (*Natrix natrix*).

end of the body the ratio may be unity or even more; the *average* value being 0.7–0.8 (see Taylor, 1952 *b*).

The extent to which the form of a wave changes as it passes along the body depends on the nature of the external fluid. As shown in fig. 15, these characteristics vary with the viscosity of the medium. In a sufficiently viscous medium the amplitude progressively *decreases* as the wave passes posteriorly, the tip of the tail exhibiting little or no transverse movement. The facts

FIG. 14. Diagram illustrating the effect of axial spin on the movement of helical waves. The movement of the waves is indicated relative to a smooth cylinder which maintains a constant distance behind the head of the animal. The head of the animal is flattened dorso-ventrally. Dotted areas show regions of the body lying over the cylinder. The wavelength is four units.

In fig. 14, *a*, the organism is at rest and presents its dorsal surface to the observer; the most anterior wave crest (*A*) is at zero on the cylinder. If each element of the body executes one half of a complete contractile cycle whilst the body is completely restrained from spinning, each wave crest travels half-wavelength backwards along the cylinder (fig. 14, *b*); if the organism as shown in fig. 14, *a*, spins through 90° whilst undergoing one-half of a contractile cycle, the wave crests only travel one-quarter of a wavelength as in fig. 14, *c*; if the body spins 180° during each half-contractile cycle, the wave crests remain stationary as in fig. 14, *d*.

Note that for any given element the phase of contraction is exactly the same in figs. 14, *b-d*, viz. half-cycle ahead of that in fig. 14, *a*; in fig. 14, *b*, the organism still presents its dorsal surface to the observer at the end of the half-cycle of contraction, whereas it presents its left surface in fig. 14, *c*, and its ventral surface in fig. 14, *d*. In each case the direction of 'spin' is in the direction opposite to that in which each element of the system moves round the circumscribed cylinder.

indicate that the speed and form of the waves are determined by external mechanical forces.

The contrast in form (and frequency of movement) between a creeping and a swimming ceratopogonid larva is even more marked than those of a snake; on transference to water the frequency of the larva's movements is greatly increased, and the extremities of the body exhibit relatively little bending. As shown in fig. 16, the animal moves forward spasmodically as the

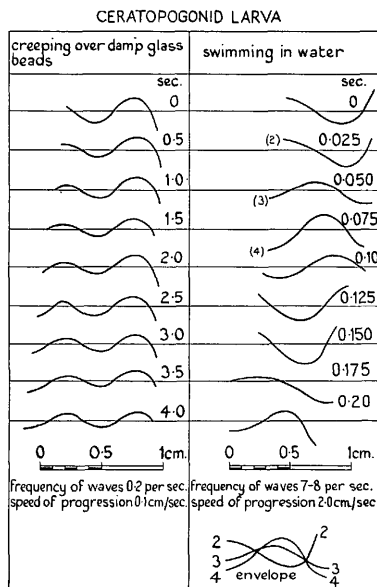


FIG. 16. Diagram illustrating the form of movement of a Ceratopogonid larva when creeping over a solid surface and when swimming freely in water.

posterior end of the body sweeps across the axis of progression and remains relatively stationary whilst the waves pass over the front two-thirds of the body. The ratio of average speed of progression to the speed of propagation of the wave is relatively small, and since the frequency of the movement is of the order of 7-8 per second the form of the 'envelope' is visible to the eye of the observer. This envelope is shown diagrammatically in fig. 16, and exhibits two well-marked 'nodes'. Envelopes of this type clearly differ fundamentally from those of any system propagating a train of waves of constant form, and it is open to doubt how far such living systems can, at present, be subjected to satisfactory theoretical analysis. Well-defined nodal

envelopes are exhibited by certain nematodes, but for the moment it is interesting to note that they can readily be elicited from an eel placed in air on a smooth level table. In the latter case the displacements of the body relative to the table are in conformity with the assumption that the centre of gravity of the body remains fixed. The phenomenon of nodal envelopes will be further discussed elsewhere, but there can be little doubt that they are determined by the nature of the external medium, and confirm the conclusion that the frequency and form of the bending cycles exhibited by each element of the body of an undulating organism are determined by extrinsic mechanical forces.

As indicated earlier in this paper, undulatory movement appears in its most interesting form in structures such as flagella or the tails of many spermatozoa. Many of these forms are only a small fraction of a micron in diameter and it is of interest to consider the types of problems which they raise in the light of the general principles discussed above. These problems are three in number. Firstly, the movements exhibited by the flagellum are an expression of internally generated bending couples, and, consequently, the flagellum must possess both tensile and compression elements. If the fibres observed in 'preserved' specimens are a reliable guide to the structure of the living flagellum, are some of these tensile and others compression elements, and if so, how are they arranged in the living system? Secondly, what is the mechanism which controls the extent of the contraction of the tensile elements and the difference in phase between adjacent elements? Is it necessary to postulate some form of 'neuroid' transmission from element to element, or is the form of the wave entirely determined by elements which contract as soon as they are exposed to a particular pattern or intensity of external mechanical forces? Thirdly, each element of the flagellum must be fed with sufficient potential energy to maintain its own rhythmical motion. The nature of this essential part of the mechanism, like the others already alluded to, must be sought by methods comparable with those used for a physiological analysis of undulatory motion in larger organisms; they are unlikely to be revealed by static observation of dead cells by means of microscopes—electronic or otherwise.

Thanks are due to a number of colleagues—to Dr. T. Gold, Dr. H. W. Lissmann, and Lord Rothschild in particular—for their interest in this problem and for the many valuable suggestions made by them during the progress of the work.

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