

THE MECHANISM OF LOCOMOTION IN SNAKES

BY J. GRAY, *Department of Zoology, University of Cambridge*

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(With Plates 4-6 and Twelve Text-figures)

Among snakes four main types of terrestrial progression have been described: (i) serpentine movement which is observable in all, or nearly all, genera; (ii) concertina movement as briefly described by Wiedemann (1932) in *Vipera* and *Coronella*; (iii) crotaline or 'side-winding' as seen in *Crotalus* or *Cerastes* (Mosauer, 1932 *a, b*); and (iv) rectilinear movement as exhibited by boas and other large types (Home, 1812). The observations described in the present paper have all been made on the common grass snake (*Tropidonotus natrix*); the evidence to be presented shows that serpentine, concertina or crotaline movements can all be elicited in this genus by appropriate modification of the external forces operating on the body of the moving animal.

So far as is known, rectilinear movement—in which the animal can progress whilst its body is orientated along a straight line—does not occur in *Tropidonotus*. This type of locomotion depends on active movements on the part of the ribs and ventral scales; such movements have not been seen in *Tropidonotus* whose progression does not depend on active movements of either scales or ribs.

SERPENTINE MOVEMENT

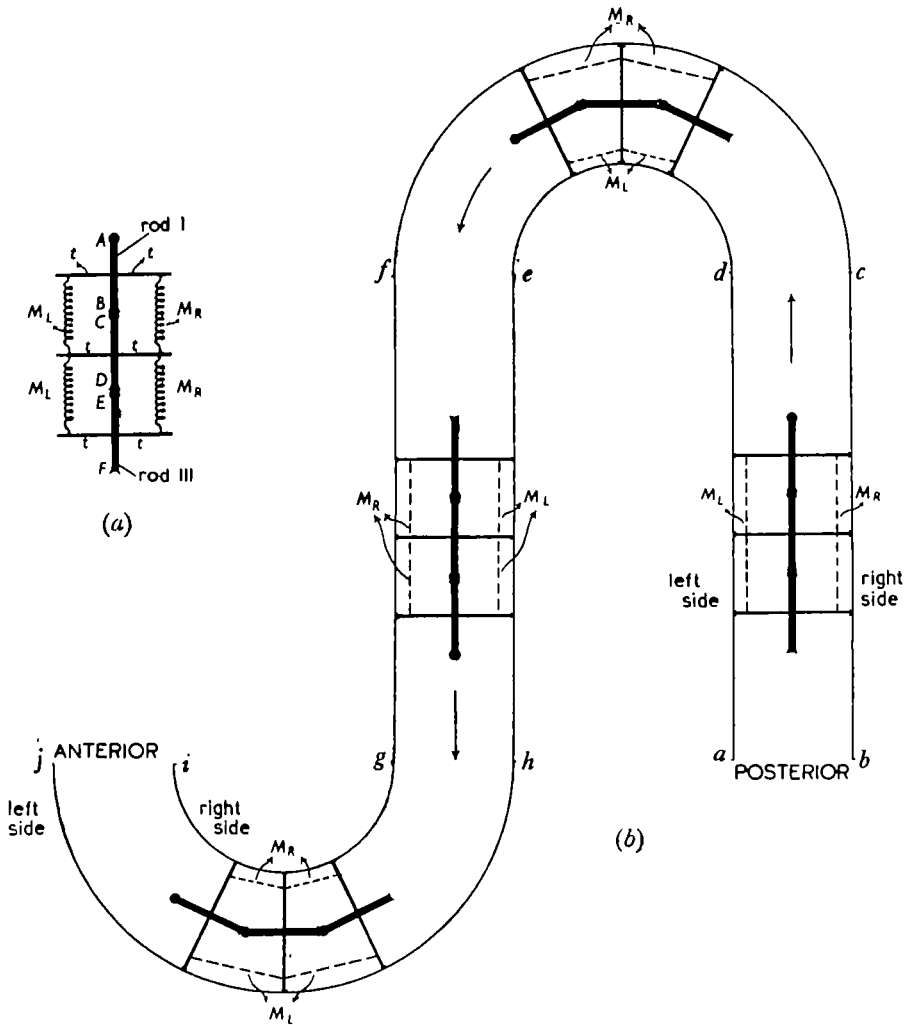
Typical serpentine locomotion is invariably exhibited by *Tropidonotus* when the animal is moving through grass or over a substratum of sufficiently irregular surface. Under such conditions the whole body is thrown into a series of more or less sinusoidal curves, and during movement 'every part of the snake's body and tail faithfully follows the path taken by the head and neck, so that the snake seems to flow gracefully through grass and scrub like a water course in its narrow winding bed' (Mosauer, 1932 *a*, p. 585). When the animal ceases to move, all its segments may stop simultaneously; when movement is resumed, all its segments can be set in motion simultaneously. A typical case of serpentine motion is shown in Pl. 4 in which *Tropidonotus* is gliding over a surface of a smooth metal plate from which project a number of smooth glass pegs free to move about their vertical axes only. In essentially the same way the animal can glide over the surface of sand provided this is made sufficiently irregular by the presence of partially embedded pebbles or glass beads. In no case has any exception been found to the conclusion, clearly enunciated by Mosauer (1932 *a*), that serpentine motion is strictly dependent upon the presence of projections from the ground against which the body of the animal can be engaged. Since every part of the animal's body is gliding forward con-

tinuously, it follows that all frictional forces operating between the body and the ground must tend to retard the animal's motion and consequently—as also clearly stated by Mosauer (1932*b*)—propulsion must be effected by forces acting normally to the surface of the body; these forces can only be due to the activity of the axial muscles of the body. So far as is known there are no observational studies on serpentine movement other than those of Mosauer which are relevant to the present study. Reference may, however, be made to the physical analysis made by Fokker (1927). This work, published in Dutch, is of a somewhat intricate nature and by no means easy to interpret in biological terms; at the same time, there can be little doubt that its fundamental conclusions—as expressed in the very brief English summary—represent a very important contribution to the theory of serpentine mechanics. From a biological standpoint, however, the fundamental problem is to show how propulsive forces, acting normally to the surface of the body, can be generated by tensions set up in the axial musculature of the body.

From a mechanical point of view, the axial skeleton of a snake can be regarded as a series of rigid rods hinged together to form a chain, whilst the axial musculature can be regarded as a series of elastic elements operating, laterally to the hinges, between adjacent rods. If such elastic elements are to provide the energy necessary for propelling the body, conditions must be such that, during movement, the length of the stretched muscles can decrease. If, for example, a series of such rods and associated elements were confined within a rigid closely fitting channel whose walls were either straight or formed the arc of a circle, the length of the elastic elements would be the same whatever be the position of the system within the channel: in other words, no system of axial elastic elements could move the rods along such a channel. A very simple and instructive test of this fact can readily be applied to *Tropidonotus*: as soon as the animal is confined to a straight or circular channel serpentine motion ceases and is replaced by a totally different type of progression (see Pl. 5 and p. 111). In marked contrast is the ability of the animal to glide through a channel of sinusoidal form (Pl. 6(A)).

In order to visualize the fundamental relationship between the sinusoidal form of the body and the ability of the axial muscles to propel the animal in serpentine movement, it is convenient to consider any three adjacent segments of the body as three rigid rods (*AB*, *CD* and *EF*) hinged together as in Text-fig. 1*a*, each rod possessing transverse processes (*tt*) for the attachment of elastic elements (M_L , M_R) operating about the hinges (*BC* and *DE*). All these elastic elements are assumed to be equal in length and exerting equal tensions. If this system be introduced into the straight, closely fitting and smooth channel (*abcd*) shown on the right side of Text-fig. 1*b*, it can be moved from one position to another within this straight channel without altering the length or potential energy of any of the elastic elements. If, however, the system be moved forward by an external force from the straight section (*abcd*) of the channel to the semicircular section (*cdef*), the elements M_L on the left side of the system can shorten with loss of potential energy, whilst those (M_R) on the right side of the system lengthen, thereby involving an increase in their potential energy. The reverse process occurs when the

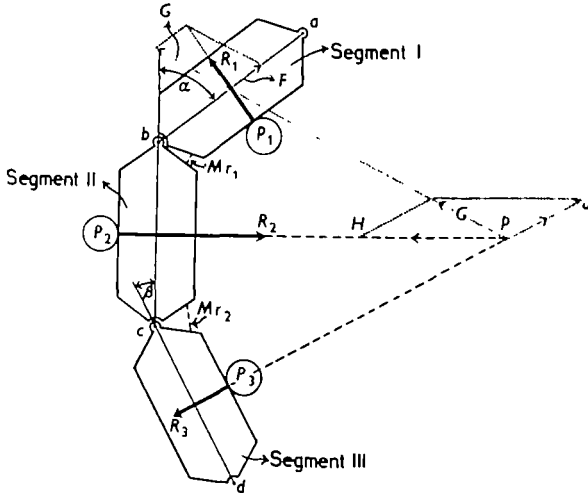
system is moved from the curved section (*cdef*) to the next straight section (*efgh*) of the channel. On moving the system into the second circular section (*ghji*), the elements M_R shorten still further, whilst the elements M_L lengthen, and so on as the system moves through any subsequent sections of the channel. It is clear that each



Text-fig. 1.

elastic element shortens and thereby liberates potential energy whenever the direction of the track or channel changes towards the side of the system on which that particular elastic element is situated relative to the hinge about which it operates; whenever the channel's direction diverges to the left the elements on the left side of the system can liberate energy by shortening, and whenever the channel diverges to the right the same fact applies to the elements of the right side. It is thus possible to establish on quite general grounds the proposition that if a snake confines itself

to—or is confined to—a closely fitting channel or track, any energy stored in the axial musculature can be liberated for locomotory purposes provided that the channel or track is so shaped that it exhibits increasing curvature towards the side of the animal on which the active axial muscles are situated. If each segment of the snake is to use its left and right muscles alternately, it follows that the direction of motion must be restricted to a path which exhibits alternating changes of curvature first to the left and then to the right.

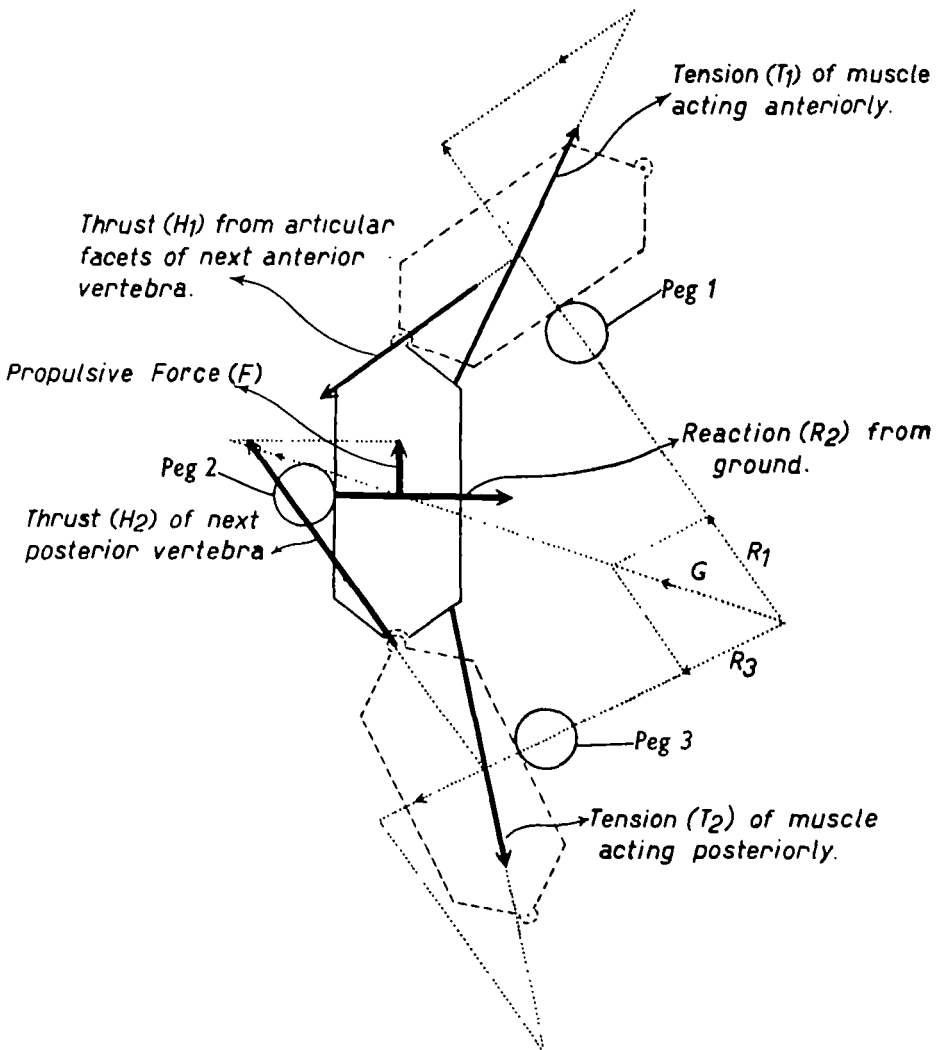


Text-fig. 2. If the posture of three consecutive segments (I, II and III) be such that the angle α (between I and II) is greater than β (between II and III) and each segment is in contact with a rigid resistance (P_1 , P_2 and P_3), forward glide will occur if tension is set up in the elastic elements Mr_1 and Mr_2 acting on the right side of the segments. The reaction of any one peg (e.g. P_1) against the body can be resolved into two components (F and G); the component (F) acting forwards along the axis of segment I is available for the propulsion of the segments past the pegs; the component (G) acting through the point of intersection (p) of the lines of action of the forces acting at P_2 and P_3 can be resolved into forces (H and J) acting along these two lines and is therefore balanced by reactions exerted by pegs P_2 and P_3 .

Before considering the form of a gliding snake from the above point of view, it is convenient to consider the way in which the potential energy of the axial muscles is converted into the kinetic energy necessary for bodily movement. In Text-fig. 2 are shown three successive segments of the body whose posture is such that the longitudinal axis (ab) of segment I forms an angle α on the right of the axis (bc) of segment II, and bc forms an angle β to the right of the axis (cd) of segment III; the angle α being greater than β , the three segments represent a system of increasing curvature towards the right side of the animal. Each segment is in contact at the level of its central transverse axis with a perfectly smooth rigid peg (P_1 , P_2 , P_3), the pegs being arranged as in the figure. Segment I is united to segment II by a rigid element Mr_1 capable of sustaining tension without change in length; segment II is united to segment III by a tensile element Mr_2 which is capable of shortening. So long as Mr_2 is free from tension the rods will exert no pressures against the pegs

and the element Mr_1 will be free from tension. If, however, Mr_2 develops tension, tending thereby to increase the angle β , each segment exerts a pressure against the peg with which it is in contact, but since these points of contact are free from friction, the only forces which the pegs can exert against the segments are reactions which act normally to the surface of the segments. Since the angle α is not equal to β , the reaction which peg 1 exerts on segment I cannot pass through the point of intersection (p) of the forces acting on segments II and III at P_2 and P_3 and, consequently, the system cannot be in equilibrium. Any reaction exerted by peg 1 against segment I can be resolved into two components, both acting at the centre of the long axis of segment I; one (F) of these components acts forwards along the axis of segment I and the other (G) acts through the point p . The latter force can, however, be resolved into components (H and J) acting normally to the surfaces of pegs 2 and 3 and is, consequently, completely balanced by reactions from these pegs. On the other hand, there is no reaction from any of the pegs which can neutralize the tangential force F . Precisely similar arguments apply to any reaction exerted by pegs 2 or 3; in each case the force exerted by any one peg—whatever be its magnitude—can always be resolved into one component which is completely balanced by reactions from the other two pegs, and into a force which acts forwards along the axis of the segment concerned. It is this latter force which provides the driving power for serpentine motion. As soon as this force exceeds the static friction acting between the body and the ground, the former will begin to glide forward; and will continue to move until the angle β has reached the same value as α . It may be noted that the external forces exerted by pegs P_2 and P_3 on segments II and III are transmitted to segment I by a thrust at the hinge b and by the tension of the muscle Mr_1 . The distribution of forces acting on a single segment is illustrated by Text-fig 3.

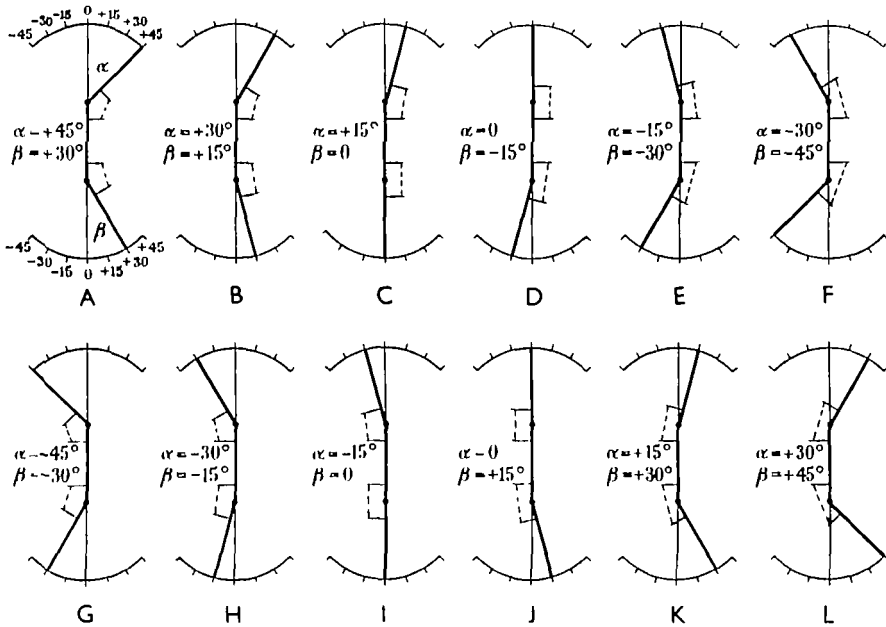
It may be noted that the force available for driving the segments forward varies directly with the difference between the angles α and β (see Appendix I). If α is greater than β , the segments glide forward; if $\alpha = \beta$, the segments remain at rest; if $\alpha < \beta$ the segments glide backwards. On the other hand, if $\alpha < \beta$ the segments will glide forward if the musculature on their left side—instead of the right side—develop tension, for the segments would then represent a system of increasing curvature towards the left. All these conclusions still hold true if the elastic element Mr_1 develops tension and shortens while the element Mr_2 remains of constant length; in other words, forward gliding will occur if both the angles α and β increase—as is the case in a moving snake where each group of muscles shortens and at the same time resists the bending effect exerted on it by its neighbours. The quantitative relationship between the tension of the axial musculature and the force available for propelling the body is considered in Appendix I, but the above facts make it possible to define the essential requirements for active serpentine motion by any short section of the snake's body, namely, (i) the form of the body must be such that the angle which the axis of any segment makes with that of the segment immediately in front of it must be greater than that which it makes with that of the segment immediately posterior to itself, both angles being measured towards the same side of the body; in other words, the posture of the system must be such that the curvature of its anterior



Text-fig. 3. Diagram illustrating the forces, apart from friction or inertia, acting on a single segment of a gliding snake. The tensions (T_1 , T_2) of the axial muscles, together with the thrusts (H_1 , H_2) exerted by the next anterior and posterior segments, exert on the central segment a force (G) identically equal to the resultant of the reactions (R_1 , R_3) from pegs 1 and 3 which act against the anterior and posterior segments. The force G has a component which is compensated by the reaction (R_2) from peg 2 and a forward component F which drives the segment forward. In other words, the driving force represents the resultant component, acting forwards along the median axis of the segment, of all the forces, exerted by the ground against the sides of the snake.

end must be greater than that at its posterior end; (ii) active muscular tension must develop in the axial muscles lying on the side of the body towards which the inclination of the segments or curvature of the body is measured; and (iii) the segments must be subjected to external resistances acting normally to the surfaces of the segments.

Reverting now to the form of a gliding snake it is obvious that the varying curvature of the body is an expression of the fact that the phase of contraction or relaxation exhibited by the muscles varies at different points along the body, the sigmoid or serpentine form being due to the fact that the phase of the muscles operating about any one vertebral joint is slightly further advanced in the cycle of

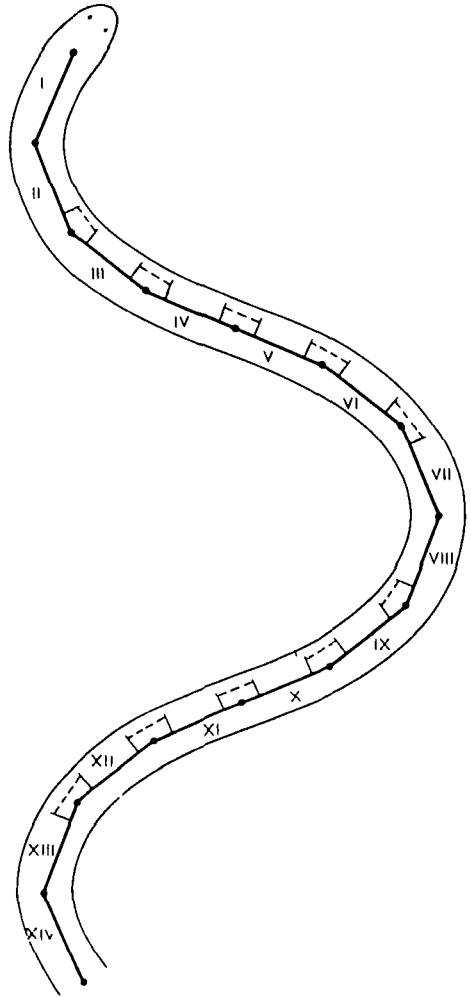


Text-fig. 4. Diagram showing the relative posture of three successive segments each rotating through an arc of 45° to the right and left of its neighbours. The whole cycle is completed in twelve successive phases (A-L); the relative posture of the two anterior rods is always $\frac{1}{2}$ cycle behind that between the two posterior rods. In phases A-F the anterior segment is more inclined to the right of the central segment than is the posterior segment and, consequently, the segments will glide forward if the muscles on the right side of the joints contract. In phases G-L the anterior segment is more inclined to the left of the central segment than is the posterior segment, and consequently the system will glide forward when contraction occurs in the muscles of the left side.

contraction and relaxation than that of those operating about a joint lying slightly anteriorly to itself. Thus if each group of muscles differs in phase from its immediate anterior neighbour by one-twelfth of a complete muscular cycle, any three consecutive segments will exhibit, during one complete cycle of contraction and relaxation, the twelve successive postures shown in Text-fig. 4; between phases A and F (inclusive) the anterior segment is more inclined towards the right of the centre segment than is the posterior segment, and, consequently, all three segments can glide forward provided the muscles on their right sides are active; between phases G and L, on the other hand, the anterior segment is more inclined to the left of the

central segment than is the posterior segment and, consequently, forward glide involves tension and shortening in the muscles on the left side. From the twelve postures shown in Text-fig. 4 it is possible to arrange a series of thirteen successive joints such that the posture of segments I-III is that shown in Text-fig. 4A, that of segments II-IV is that shown in Text-fig. 4B, and so on. In this way the sinusoidal form shown in Text-fig. 5 is obtained. It will be noted that between segments XIV and VII each segment is progressively more and more inclined towards the left of the axis of the segment immediately behind itself, and therefore forward glide can be effected by tension in and shortening of the axial muscles on the left side of the body; between segments VII and I the inclination is progressively towards the right of the next posterior segment, and forward glide is effected by the muscles on the right side of the body. The sigmoidal form of the body of a gliding snake is essentially composed of curves of rhythmically changing curvature first to the left and then to the right, thereby providing the fundamental condition necessary for a rhythmical liberation of useful propulsive energy from each segment by alternating contractions of its right and left musculature.

It is not difficult to construct a dynamic model based on the principles described in this paper, but it is obvious that the form of the animal and its relationship to the environment have been somewhat idealized. It is, therefore, useful to consider in more detail the conditions as they actually exist in a moving animal. (i) In no case is the amplitude of the muscular contraction, or the difference in phase between successive segments, exactly the same for all segments, nor is the duration of the contraction phase of the muscular cycle necessarily the same as that of the relaxation phase. None of these facts, however, affects the main principle. The



Text-fig. 5. A series of fourteen segments so arranged that the posture of segments I-III corresponds to phase A in Text-fig. 4, that of segments II-IV corresponds to phase B in Text-fig. 3, and so on. Between segments VIII and I the body forms, when measured anteriorly, a curve of increasing curvature towards the right and, consequently, the muscles of the right side can propel the body forwards. From segments XIV-VIII the curvature progressively increases towards the left and propulsion is effected by the muscles on the left side of the body.

actual form of the body of a gliding snake is an expression of the precise form of the muscular cycle carried out by each group of segmental muscles and of the phase difference between the muscles of successive segments; in every case, however, gliding motion depends on the same fundamental relationship between the position of the contracting axial musculature in respect to an increase in bodily curvature towards the same side of the body. (ii) It has been assumed that each segment of the body is subjected to external restraint which prevents its movement in a direction normal to its own longitudinal axis. In nature, an approximation to such conditions exists when the animal is moving over a surface such as gravel or small stones, or when the animal is moving through close herbage or grass. Again, when moving over soft dry sand (into which the body tends to sink, or which tends to be heaped up at the sides by the animal's own movements) each segment is subjected to a resistance acting normally to its surface. On the other hand, the distribution of external resistances can be restricted to a limited number of points along the body, as is the case in Pl. 4. Precisely similar arguments apply to such conditions if, instead of regarding each of the rods shown in Text-figs. 2-5 as comparable to one vertebral segment, they are each regarded as composed of several such segments. If the system be composed of curved instead of straight units, it can readily be shown that when the muscles acting across any joint develop tension thereby causing the system to exert reactions against the ground at any three points, the forward thrust exerted on the joint in question is directly proportional to the tension in axial muscles and to the difference in curvature of the regions on the two sides of the hinge (see Appendix II). (iii) In the idealized system represented in Text-figs. 2-5, it is possible to assume that the energy liberated, when the muscles operating across each joint pass from one phase of the contraction cycle to the next, is just sufficient to move the segment concerned from its original position to that previously occupied by the segment immediately anterior to itself. In a living snake this condition is by no means always fulfilled; more frequently, some regions provide some or all of the energy required to move other parts of the body. The fundamental principles are, however, unaffected, although the actual work done by any particular part of the body can only be determined by experimental methods which will be discussed in another paper.

From a biological point of view, the rate of progression of a snake depends on the rate at which the animal moves along its own axis of symmetry—in other words, on the wave-length of its sinusoidal track rather than on the rate at which a segment glides along the track itself. For rapid progression, the curvature of the body should be such as to provide curves of long wave-length and low amplitude. For this purpose, the amplitude of the muscular contractions and the phase differences between adjacent segments should both be small; curves of this form would, however, yield relatively small propulsive components, and would therefore require greater muscular effort. It would be of considerable interest to consider the relationship of the forms of the body in different genera in relationship to their speed of locomotion.

Before leaving serpentine movement it may be noted that the propulsive mechanisms of a gliding snake and of an eel moving through grass are essentially

the same; the smooth surface of the eel with its associated mucus reduces friction to a minimum and is therefore ideally adapted for serpentine movement. The analysis of serpentine movement given above can readily be modified to cover conditions under which friction acts against the sides of the snake whenever these are pressing against the ground; the greater the coefficient of friction, the greater is the tension of the muscles necessary to propel the animal.

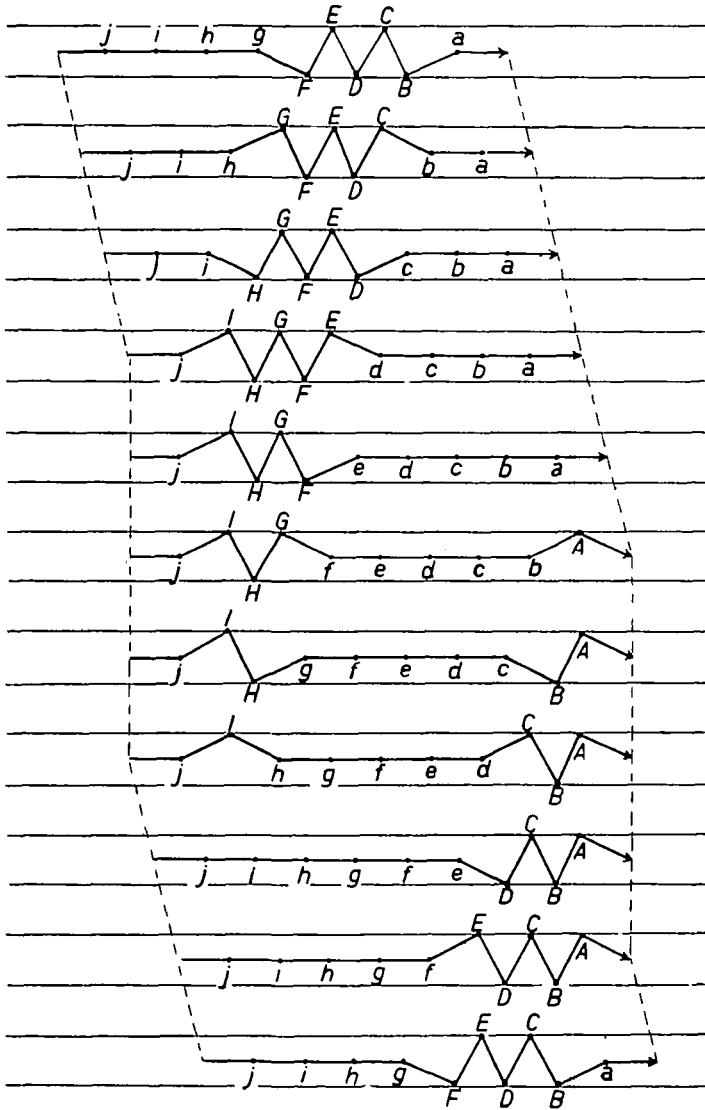
CONCERTINA MOVEMENT

As already mentioned, the type of movement exhibited by a snake when confined within a channel whose walls are either straight or form the arc of a circle differs strikingly from that exhibited within a channel of varying curvature. In a straight or circular channel, locomotion is effected by highly characteristic concertina movements illustrated by Pl. 5, from which it can be seen that the body is thrown into a number of curves, of comparatively short wave-length, which are in contact at their crests with the walls of the channel; as the cross-section of the channel is decreased so the number of curves exhibited by the body increases, whilst, at the same time, their wave-length decreases. Reference to Pl. 5 shows that the segments of the body which constitute a fully developed wave constitute regions which are at rest relative to the walls of the channel, whereas segments are in motion when they lie on regions where the curvature is being increased or decreased. Each fully formed wave represents a rigid structure firmly pressed against the wall of the channel, thus forming a *point d'appui* towards which (or away from which) the moving regions can be drawn against the sliding friction of the floor of the channel.

The kinematics of motion are shown in Text-fig. 6 in which capital letters denote points on the body which are in firm contact with the walls of the channel whilst regions in motion are shown by smaller letters. As motion proceeds, fresh *points d'appui* are established behind existing ones, whilst the segments which constitute the most anterior of the wave series are drawn away from the walls of the channel and begin to move forward. It will be noted that each segment, in turn, comes to rest and then moves forward, thus executing definite and discrete steps.

The pattern of muscular effort and the distribution of external forces acting on the body during concertina movement are shown in Text-fig. 7a, in which the sections of the body *cd* and *de* are locked to the sides of the channel at *c*, *d* and *e* by virtue of the tension in the muscle *Md* operating between *cd* and *de*. The forward movement of the anterior end of the body is due to (i) an unlocking action at *c* due to contraction of the muscles (*Mc*) operating on the right side of hinge at *c*, and (ii) contraction of the muscles *Ma* and *Mb* operating to the right and left of their respective hinges *a* and *b*. Similarly, the forward movement of the region of the body posterior to *e* is due to the shortening of the muscles *Me*, *Mf* and *Mg*. In order that the animal should propel itself through the tube, the static friction (Text-fig. 7b, *Fc*, *Fd* and *Fe*) operating between the body and the tube at *c*, *d* and *e* must be equal to the total sliding friction (*Fh* and *Ft*) of all parts of the body which are in motion, so that the pressures (*Pc*, *Pd* and *Pe*) exerted on the animal

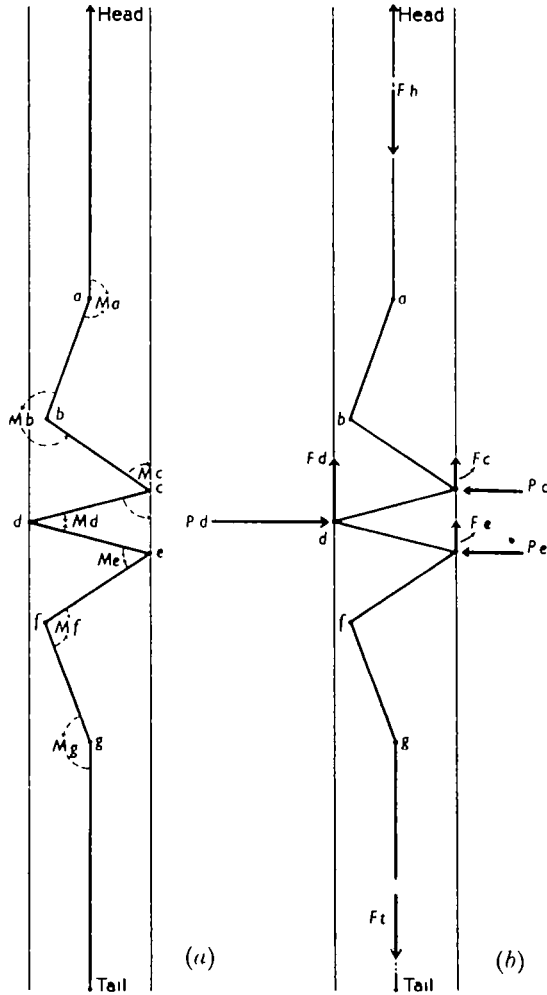
normally to the sides of the channel must be such that at none of the points *c*, *d* or *e* is the ratio of friction to pressure in excess of the coefficient of friction.



Text-fig. 6. Diagram illustrating the movement, relative to the ground, of a snake during concertina movement through a straight tube. Capital letters indicate regions of the body at rest; smaller letters indicate regions of motion. Each segment of the body moves forward in a series of distinct steps.

Although concertina movement is highly characteristic of snakes moving in channels of straight or circular form, it nevertheless sometimes occurs in a somewhat modified form when a snake is moving over open ground of fairly uniform surface. An example of this is given in Text-fig. 8. This type of movement depends on the fact that movement of a series of segments backwards along their own

longitudinal axis causes the posterior edges of the ventral scales to engage passively with the surface of the ground and so enables such segments to act as a *point d'appui*. The force required to tow an inert *Tropidonotus* linearly backwards is four

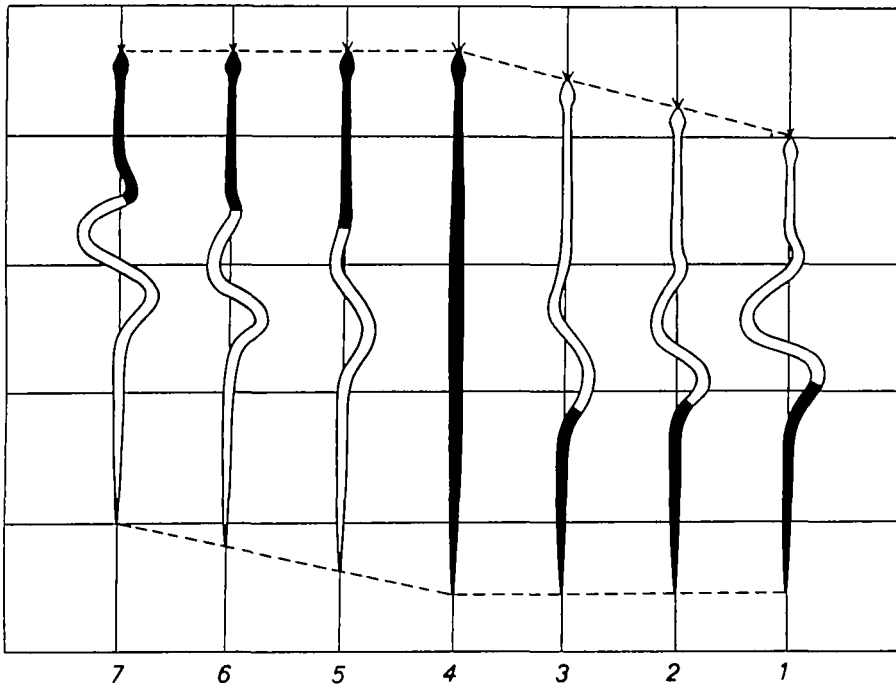


Text-fig. 7. *a*. Diagram illustrating the mechanism of concertina movement in a straight tube. The sections of the body cd and de are locked against the walls of the tube by contraction of the muscles M_d ; the region of the body anterior to c is being extended forwards by contraction of the muscles M_a and M_c , operating about the right side of joints a and c , and of M_b about the left side of joint b . The region of the body posterior to e is being drawn forward by contraction of the muscles M_f and M_g . *b*. Diagram illustrating the external forces acting on the body during concertina movement. P_c , P_d and P_e are the forces exerted by the walls of the tube normally to its surface at c , d and e ; F_c , F_d and F_e are the frictions acting anteriorly to c , d and e ; F_h and F_t are the sliding frictions between the floor of the channel and the anterior and posterior ends of the body respectively.

or five times greater than that required to tow it forward even if the substratum is relatively smooth; if active concertina movements are restricted to the central half of the body, the regions in front of and behind the active region can act alternately as efficient fixed *points d'appui* as in Text-fig. 8.

CROTALINE OR SIDE-WINDING MOVEMENT

When a grass snake moves over a relatively smooth and uniform surface its mode of progression tends to be irregular, and serpentine movement is replaced either by side-winding, or by concertina movement, or a combination of the two. The precise mechanical conditions of the substratum necessary for the elicitation of side-winding in its most characteristic form cannot be defined at present, but an instance is shown in Pl. 6 (C), in which the animal is moving over a painted metal plate; Text-fig. 9a shows the movement, relative to the ground, of the animal seen in



Text-fig. 8. Successive phases (1-7) in the concertina movement of a snake not subjected to any lateral restraint, but in which curvature of the body is restricted to the central region of the body. Regions of the body at rest are shown in black. Progression is due to the passive action of the ventral scales whose free posterior edges cause the static resistance to a backward displacement of the body to be four or five times greater than that to forward displacement.

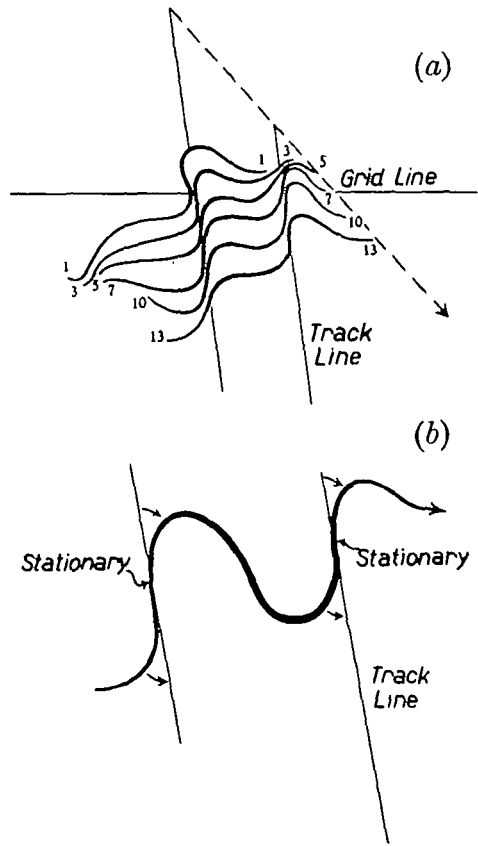
Pl. 6 (C). During this type of progression two sections of the snake's body remain at rest relative to the ground, whereas the remainder is in motion (Text-fig. 9b); consequently, the whole body moves sideways in essentially the same way as was described by Mosauer (1932 a, b) as the normal method of progression in the 'side-winder' (*Crotalus cerastes*) or for the sand-vipers (*Cerastes cornuta* and *C. vipera*).

Although a good description of crotaline movement has been given by Mosauer, it is perhaps convenient to recall its essential features before considering the kinetics of this type of movement. A side-winding snake leaves on the ground a series of more or less parallel straight tracks inclined at an angle to the path of motion of the animal's head. These tracks represent lines along which each segment

of the body is placed, in turn, and from which it is, in due course, lifted in order to be moved to the next track in the series. Segments of the body actually lying on the track are at rest relative to the ground, segments lying immediately anteriorly to those at rest are being lifted off the track, whilst segments lying immediately posteriorly to those at rest on the track are being placed down (Text-fig. 9*b*)—the terms anterior and posterior being used relative to the head of the animal. The whole cycle is essentially similar to that of the treads of a caterpillar drive of a tank or tractor. During crotaline movement, contact between the body and the ground is, to a very large extent, restricted to segments of the body which are lying at rest on the rectilinear tracks but the inability of *Tropidonotus* to side-wind over sand-paper shows that at least some of the moving segments must, in this form, be in contact with the ground.

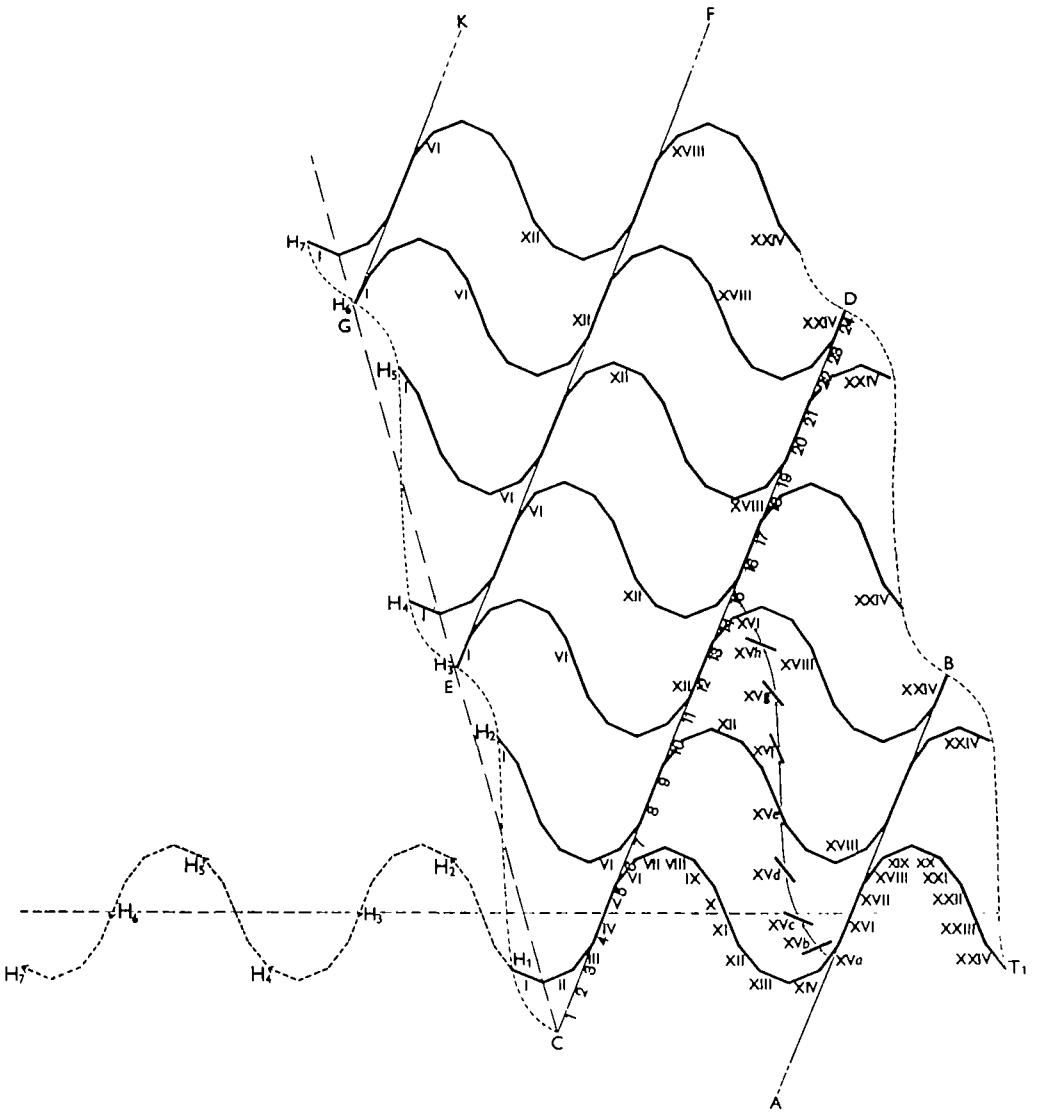
The mechanical relationship of side-winding to serpentine motion is simple; it depends, primarily, on a difference in the external forces which oppose the contraction of the axial muscles. At the lower right side of Text-fig. 10 is shown a series of twenty-four segments whose positions relative to each other are exactly comparable to those of the fourteen segments shown in Text-fig. 5. If adequate lateral resistances and muscular effort are available, the whole series of segments would, during two complete muscular cycles, glide by serpentine movement along the sigmoidal track (H_1-H_7) which traverses the horizontal line at the base of the figure. On the other hand, if the external

resistances are such as to allow unrestrained movement to each segment except at the end of each complete cycle of movement (as defined by the phase at which the segment subtends no angle with the axis of either the segment in front of or behind itself) the displacement of the animal relative to the ground, during two complete muscular cycles, is shown in Text-fig. 10 by the six postures seen above the original position of the animal. When movement starts, segment V remains at rest whilst segment IV is deflected towards the morphologically right



Text-fig. 9*a*. Diagram showing successive positions of the animal shown in Pl. 6 (C), relative to a fixed grid line; the numbers correspond with those in the Plate.

Text-fig. 9*b*. Diagram showing the motion of various regions of the body relative to the track lines during crotaline movement.



Text-fig. 10. Diagram illustrating the relationship of side-winding to serpentine motion. If adequate external resistances act normally to the surface of the twenty-four segments shown at the lower right side of the diagram, the animal will glide to the left from its initial position ($H_1 T_1$) along the sinusoidal track (H_1-H_7) traversing the horizontal dotted line shown at the lower left side of the figure. If, on the other hand, all segments are unrestrained by any external forces except when they are in the phase shown by segments V and XVII in the animal's initial position at $H_1 T_1$, then the animal will side-wind towards its right side; the head of the animal moves along a curve whose axis is CEG . Each segment in turn comes to rest on one of the track lines (AB, CD, EF, GK) and is subsequently moved to the next track line in the series. The movement of an individual segment, during one complete muscular cycle, is shown in the case of segment XV when moving from track line AB to track line CD .

side of segment V; simultaneously, the angle between segments V and VI is reduced until segment VI comes to rest with its axis in line with that (*CD*) of segment V. Similarly, segment XVII remains at rest whilst segment XVI moves to the right of the axis (*AB*) of segment XVII, whilst segment XVIII moves to its position of rest on this axis. As the muscular cycle proceeds, segments VII, VIII, IX, ... are laid down along the line *CD* and segments XIX–XXIV are laid down along the line *AB*; simultaneously, segments which have previously been at rest along these lines are lifted and moved forward towards the next track line of the series; the movement, relative to the ground, of one such segment is shown in the case of segment XV from its position *XVa* on the track line *AB* to *XVi* just before taking its place on track line *CD*. It will be noticed that the total length of each track line is the same as the length of the animal; the track lines will only be parallel to each other throughout the whole of their course if the amplitude of the muscular movements and the phase difference between adjacent segments are the same along the whole body. A good illustration of actual track lines is given by Mosauer (1928).

The ability to side-wind depends on the ability of the snake to transfer some or all of its weight to the segments which are to remain at rest, thus increasing static friction at these points and reducing or abolishing the sliding friction of the regions of the body which are in motion; this is effected by rhythmical changes in tension in the dorso-ventral axial musculature.

According to Mosauer (1932*a*) the substratum of a true side-winder does not provide a propulsive force necessary for progression. This can only be true under theoretical conditions where movement is occurring at a perfectly uniform speed and when all the moving parts are out of contact with the ground. Unless static friction operates posteriorly between the ground and the stationary segments, the animal could not start from rest—for the whole body would slip freely over the ground as is the case when the animal is on an extremely smooth plate; further, if any external restraining force acts on the moving segment, a corresponding amount of friction must act posteriorly on the segments lying at rest on the ground.

APPENDIX I

The propulsive effect of reactions acting normally to the surface of the body can be visualized quantitatively from Text-fig. 11 in which *ac* is a rigid angular bar in contact with two smooth pegs P_1 and P_2 and hinged at *c* to a straight rod *cd* which is in contact with the peg P_3 ; an elastic element *Mr* acts on the right side of the hinge at *c*.

If the tension of the element *Mr* be *T* and its moment about the hinge be *Tz*, the two rods will be exposed to equal and opposite turning couples of moment *Tz*; the reaction (R_3) of peg 3 against *cd* will be Tz/x .

If *F* is the external friction, forward glide at constant speed can occur when the resultant of R_1 , R_2 and R_3 is equal but opposite to *F*; in other words when

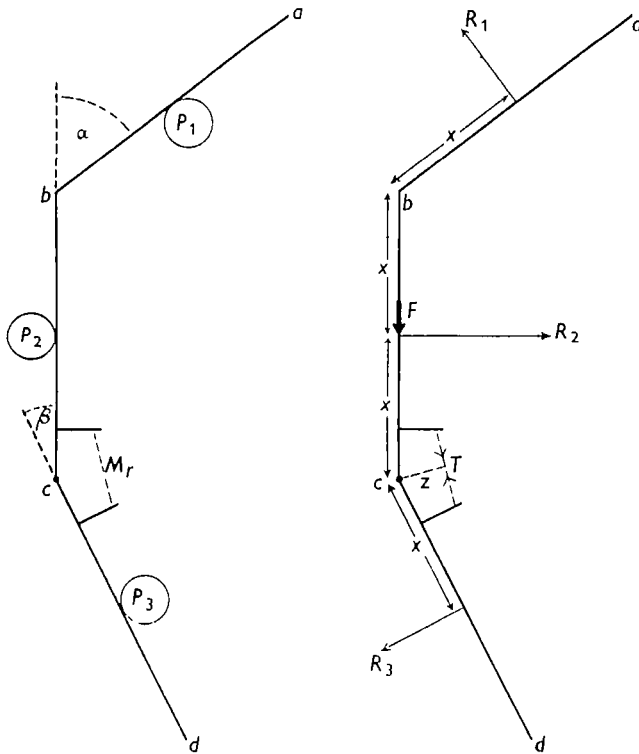
$$\begin{aligned} F &= R_1 \sin \alpha - R_3 \sin \beta, \\ R_2 &= R_1 \cos \alpha + R_3 \cos \beta, \\ R_2 &= R_3 (1 + 2 \cos \beta) - R_1. \end{aligned}$$

Under such conditions the force tending to drive the animal forward is equal but opposite to F and has the following value:

$$\frac{Tz}{x} \left[\frac{\sin \alpha - \sin \beta + \sin (\alpha - \beta)}{1 + \cos \alpha} \right]$$

If $\alpha = \beta$, F becomes zero—as when a snake's body is in the form of the arc of a circle or lying along a straight line.

If $\alpha > \beta$ the animal must glide forward if the axial muscles develop tension on the right side of the body towards which side α and β were measured. If these muscles became active when $\alpha < \beta$ the animal would glide backwards.



Text-fig. 11.

If $\alpha < \beta$ and the muscles on the left side develop tension the animal would glide forward.

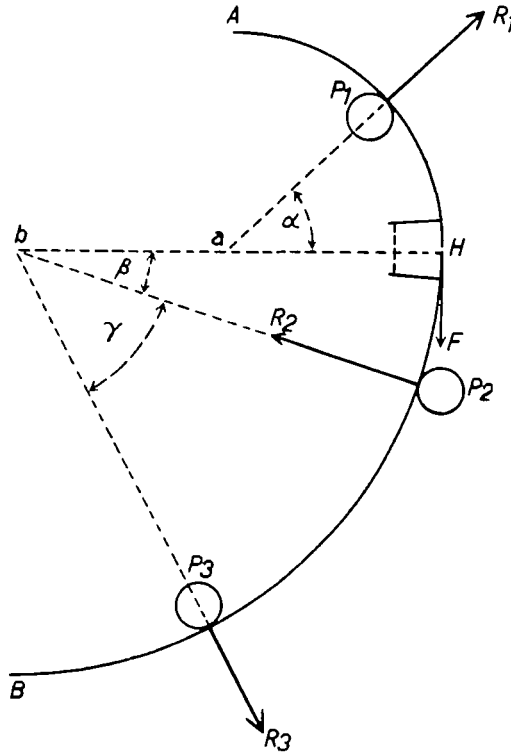
If a muscle (Mr) acting about a joint at c shortens, the muscles acting about b (on the same side of the body) must resist the bending moment of Mr and vice versa. In life both groups of muscles shorten and each contracts against the bending forces induced by the other.

It may be noted that the propulsive force represents the sum of those components of the reactions from all three pegs which acts along the axis of the central segment in Text-fig. 3.

APPENDIX II

Let AB be a region of the snake's body such that the radius of curvature between B and H is r_2 , whilst that between A and H is r_1 , r_2 being greater than r_1 (Text-fig. 12). At H , the

point at which the radius of curvature changes, is a hinge on the left of which the axial musculature is under tension whilst the body is in contact with smooth external resistances at P_1 , P_2 and P_3 whose positions relative to the hinge are defined by the values of r_1 and r_2 and by the angles α , β and γ . If the tension of the axial muscles be T and their moment about the hinge be Tx , the reaction (R_1) exerted on the body by peg 1 is $\frac{Tx}{r_1 \sin \alpha}$; if the body is not to rotate about the centre of curvature (b) of the region BH , the system must



Text-fig. 12.

be exposed to a force which restrains the turning moment of R_1 about b . If this restraining force (F) is applied as a force at H acting tangentially to the body

$$Fr_2 = R_1(r_2 - r_1) \sin \alpha.$$

Since
$$R_1 = \frac{Tx}{r_1 \sin \alpha}, \quad F = Tx \left(\frac{1}{r_1} - \frac{1}{r_2} \right)$$

In other words the resultant of the reactions from the pegs represents a force, tending to accelerate the hinge forwards, which is proportional to the tension developed by the muscles and to the difference in the curvature on the two sides of the hinge. It should be noted that the positions of the pegs do not affect the tangential gliding force; they do, however, affect the values of the reactions exerted by the pegs and therefore influence the

bending moments which must be resisted by the muscles of those segments of the body not in contact with the pegs:

$$R_1 = \frac{Tz}{r_2 \sin \alpha},$$

$$R_2 = \frac{Tz[r_2 \cot \alpha + r_1 \cot \gamma]}{r_1 r_2 [\cos \beta - \sin \beta \cot \gamma]},$$

$$R_3 = \frac{Tz[r_1 \cos \beta + r_2 \cot \alpha \sin \beta]}{r_1 r_2 \sin \gamma [\cos \beta - \sin \beta \cot \gamma]}.$$

SUMMARY

1. Of the four main types of locomotion observed in snakes, three (serpentine, concertina and crotaline) can be elicited from the common grass snake (*Tropidonotus natrix*) by appropriate modification of the animal's environment.

2. Serpentine motion depends on three factors. (i) The body must be thrown into one or more curves each of which exhibits an increase of curvature when measured towards the head of the animal. (ii) Active muscular tension must develop in the axial muscles which lie on the same side of the body as that in which the curvature is increasing. (iii) The body must be subjected to at least three external resistances acting normally to the surface of the body. The propulsive force is the resultant of the reactions exercised by all these external resistances.

3. A snake cannot propel itself by serpentine movement along a straight or circular path. Under such conditions *Tropidonotus* progresses by concertina movements, the nature of which are described.

4. The muscular cycle of a snake exhibiting 'crotaline', or side-winding, movements is essentially the same as that during serpentine motion; the difference in the type of movement relative to the ground is due to a difference in the nature of the external resistances offered by the animal's environment. The mechanical principle of crotaline movement is, fundamentally, that of a caterpillar tractor.

5. Serpentine, concertina, and crotaline movements do not depend on active movements on the part of the ribs or scales. Rectilinear movement involving these structures has not been observed in *Tropidonotus*.

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EXPLANATION OF PLATES

PLATE 4

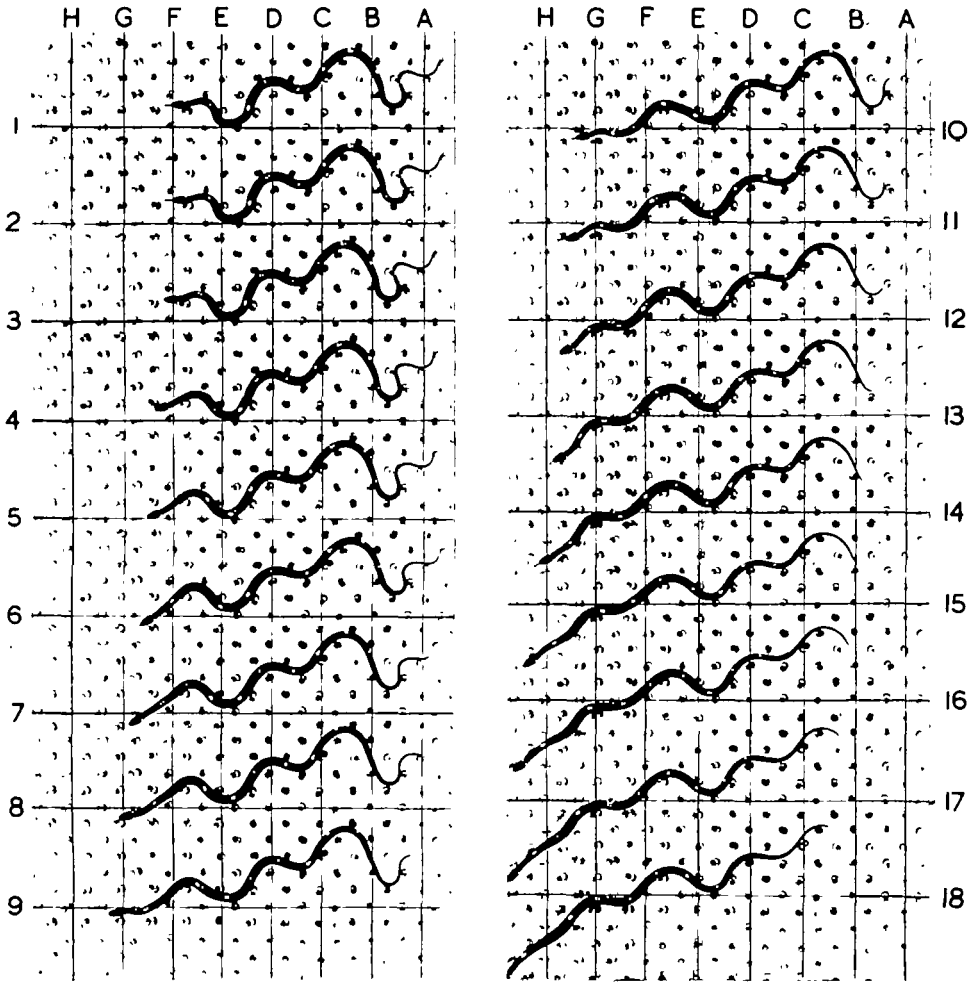
Eighteen successive photographs of a snake (*Tropidonotus natrix*) gliding over a smooth plate from which project a series of rigid pegs. The vertical lines *A-H* and the horizontal lines 1-18 are drawn through the same pegs in all the photographs. The progress of the animal can be followed by noting the successive position of any one of the white spots, painted on the back of the animal, relative to the grid lines. For example, the spot which, in photograph 1, lies about midway between grid lines *B* and *C*, has, in photograph 18, passed beyond grid line *E* by following a path which is defined by the form of the body as seen between lines *B* and *E* in photograph 1. Note that the animal starts to move soon after photograph 2. Interval between successive photographs 0.25 sec.; distance between vertical grid lines, approx. 3 in.

PLATE 5

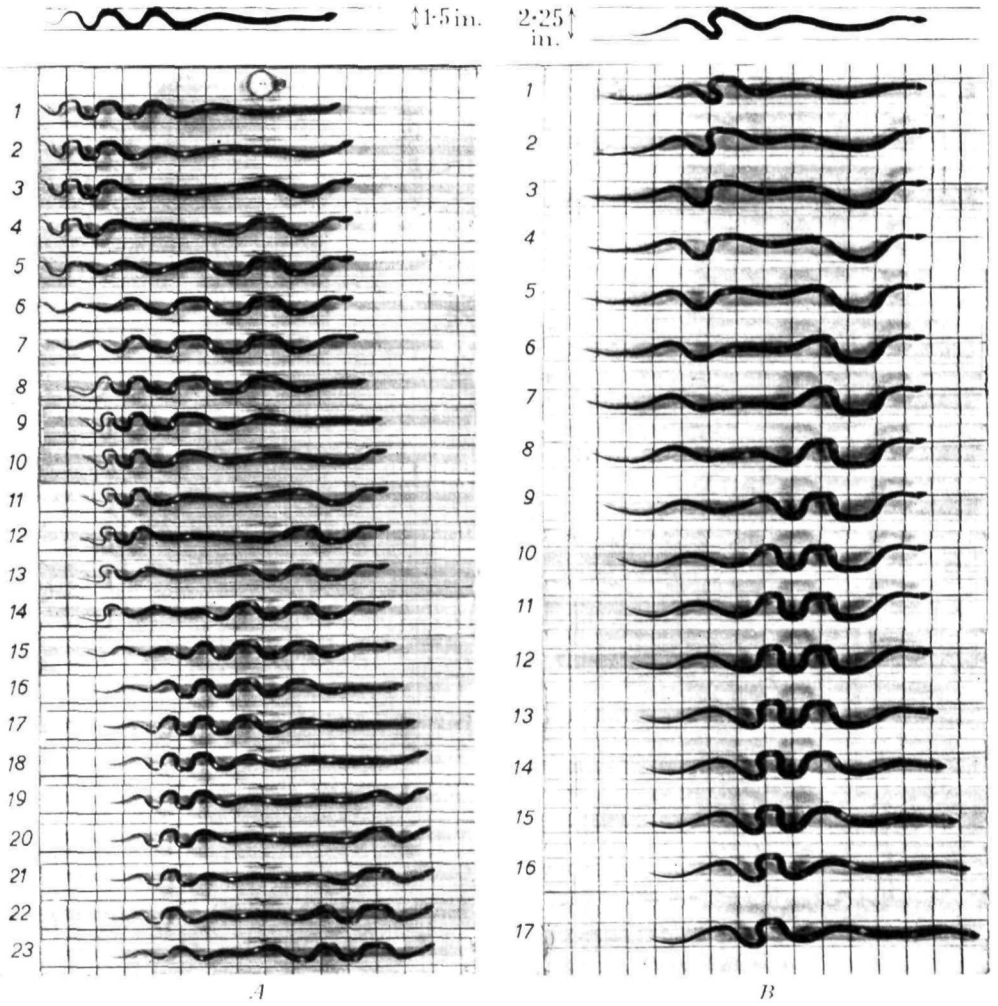
'Concertina' pattern of movement displayed by *Tropidonotus natrix* when confined within a straight glass tube. The diameter of the tube is shown by the drawing at the top of each series of photographs. Interval between successive photographs, in series A, 0.25 sec.; in series B, 0.5 sec. Distance between vertical grid lines 2 in.

PLATE 6

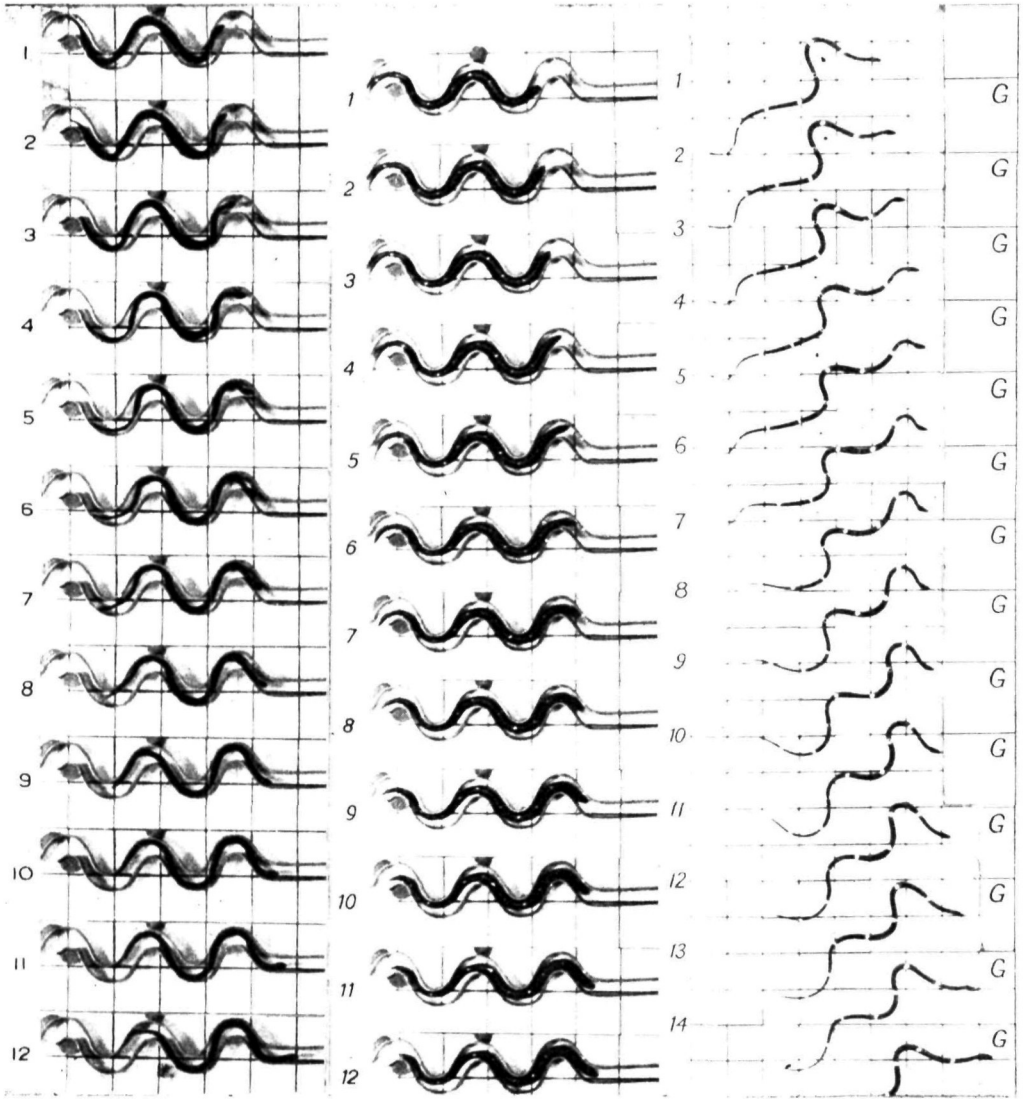
A. Serpentine movement of *Tropidonotus natrix* through a channel of varying curvature. Interval between successive photographs 0.25 sec. Distance between vertical grid lines 2 in. B. Serpentine movement of a slow-worm (*Anguis fragilis*) through a channel of varying curvature. Interval between successive photographs 1.5 sec. Distance between vertical grid lines 2 in. C. Side-winding movement of *Tropidonotus natrix* when moving over a metal plate. Interval between successive photographs 0.2 sec. Distance between vertical grid lines 2 in. For displacement of the body relative to the ground see Text-fig. 9a.



Tropidonotus natrix



Tropidonotus natrix



(A) *Tropidonotus natrix*

(B) *Anguis fragilis*

(C) *Tropidonotus natrix*

G = identical grid line

