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OBSERVATIONS ON THE LOCOMOTION OF THE SOUTH WEST AFRICAN ADDER, *BITIS PERINGUEYI* (BOULENGER), WITH SPECULATIONS ON THE ORIGIN OF SIDEWINDING

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(With 2 Text-figures and 2 Plates)

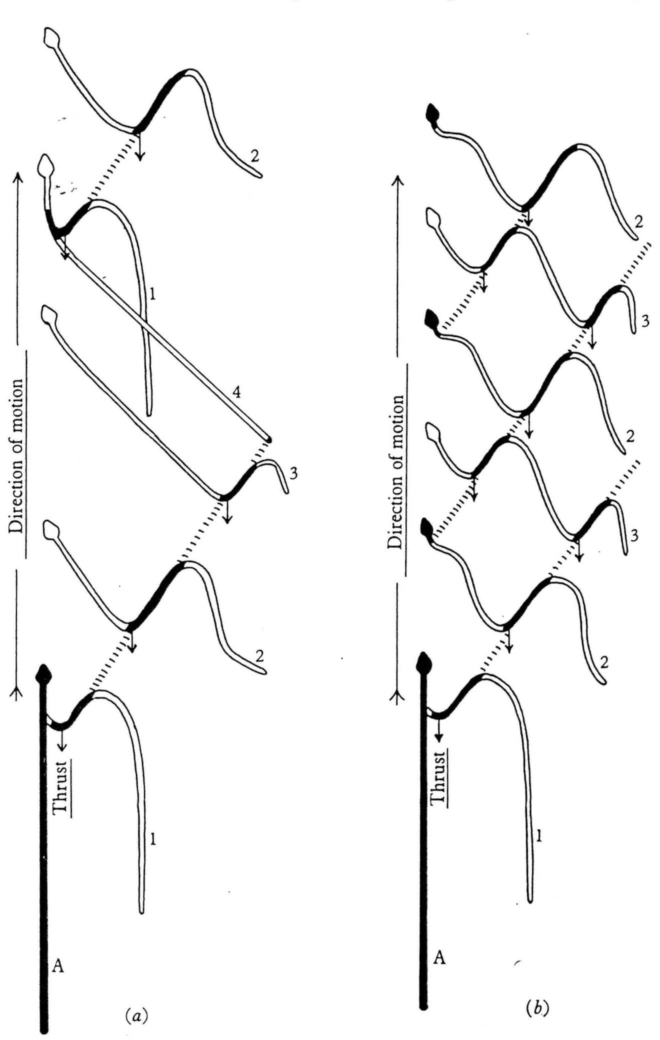
INTRODUCTION

PERINGUEY'S adder is a snake closely confined to the sand areas of the coastal Namib Desert, where it attains a length of about 1 foot. In certain restricted localities it is by no means uncommon, although it is a snake poorly represented in most museum collections. During the course of a single night, for instance, nine specimens were seen by Dr C. Koch at Gobabeb, a waterhole in the Kuisib River course of South West Africa. There can be little doubt that the snake is ordinarily nocturnal, although it may be found abroad on the overcast misty days so characteristic of the coastal Namib at certain times of the year. Normally specimens can most readily be obtained by digging at the bases of small bushes where the snakes lie concealed in the sand of the shaded areas. One specimen was collected as it lay among the branches of a small shrub, showing that these adders are capable of climbing.

LOCOMOTION

The form of locomotion greatly favoured by *Bitis peringueyi* is sidewinding, irrespective of the hardness of the surface over which it moves. In certain circumstances, as when the snake is climing among branches, serpentine glide (horizontal undulatory locomotion) is used, but none of the specimens studied was seen to make use of rectilinear locomotion. When sidewinding, the snake produces tracks similar to those of the better-known American sidewinder, *Crotalus cerastes*: the roughly parallel lines each have a hook at one end made by the head and neck as it is placed down, prior to the making of the track proper. As may be seen in Pl. I A, which shows the snake moving over a sheet of sooted cardboard, a considerable amount of drag takes place between individual parallels. It has been stated (van Riper, 1955) that the parallel tracks of *C. cerastes* are quite separate and unconnected. In order to make a direct comparison between the tracks of this snake and those of *Bitis peringueyi*, some specimens of the horned rattlesnake were kindly supplied by Dr C. E. Shaw of the San Diego Zoological Gardens. Specimens equivalent in size to *B. peringueyi* (about 1 foot total length) were selected and were induced to sidewind over sheets of sooted cardboard as before. The tracks were found to be very similar to those of *B. peringueyi* so far as drag marks were concerned (Pl. I B), but a slight difference in track angle was observed. This will be dealt with shortly. The drag marks of both the rattlesnake and the adder are visible only when records are made on sooted cardboard; they are not apparent when the snake moves over sand.

In the following discussion, on the movements involved during the locomotion of Peringuey's adder, reference should be made to the diagrams in Text-fig. 1. Parts of the snake shaded black represent those parts of the body in contact with the ground; all unshaded length is raised above the surface. Clearly, Text-fig. 1*a* represents a completely hypothetical case and one which could not work in practice, since the snake is not able to support practically its whole length while pivoted near its head or tail. Nevertheless, this simplification is of value



Text-fig. 1. Body movements involved during sidewinding: (*a*) a hypothetical case in which one track only might be produced during a complete muscular cycle; (*b*) the normal condition where two parallel tracks are made simultaneously.

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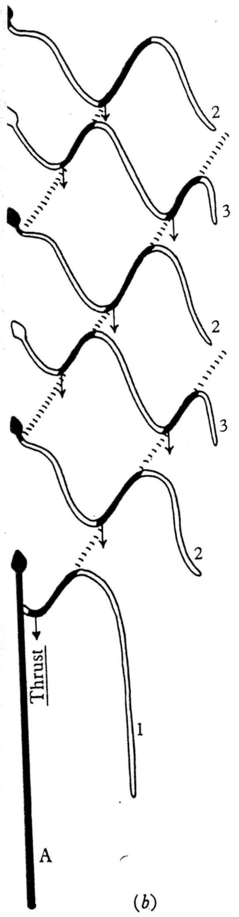

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as it shows how one track only might be made during a complete cycle of movement. The normal condition in which two tracks are produced simultaneously is less easy to visualize. In position A the snake lies upon the surface with its head pointing in the direction of intended movement. A loop is then formed in the body, while the head and tail sections are raised. As the loop passes tailwards, the snake moves forwards along the track as shown since propulsive force is generated at the positions of the arrows. By stage 4 the cycle is complete and can be recommended.

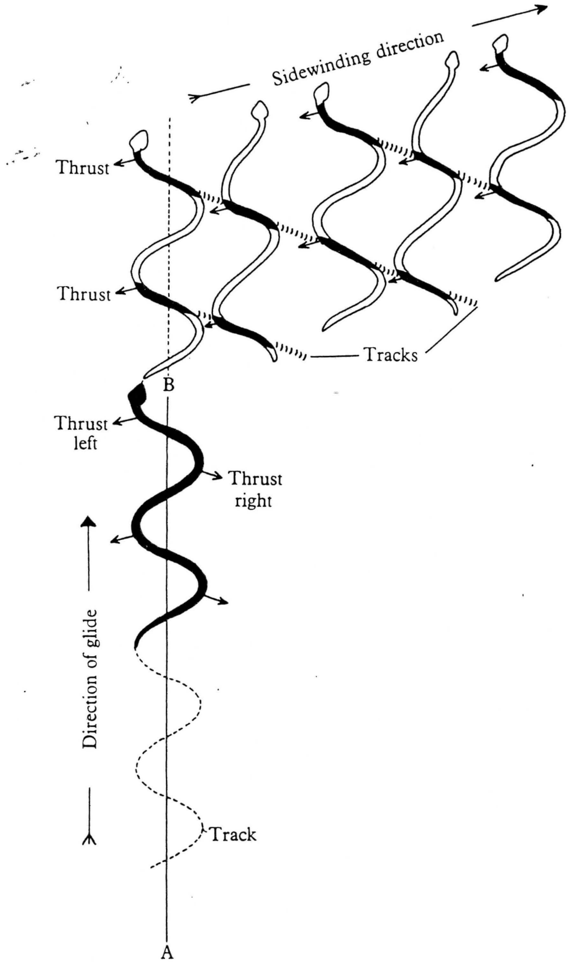
In practice, the sidewinder moves in precisely this manner except that two loops, not one, are formed in the body and two tracks are made simultaneously (Text-fig. 1*b*). When this happens, the snake's body fluctuates between two primary positions, numbered 2 and 3. In position 2 the head is just commencing a new track; in 3, two parallels are in the process of being made.

When interpreting a set of completed tracks it is sometimes difficult to decide on the direction in which the snake has moved. In such a case, a line should be drawn linking the head-hooks at the end of each parallel track. This line then represents the path taken by the head, while the open ends of the hooks point in the direction of motion. It should be noted that the head-hooks can be at the right- or left-hand ends of the parallels. During eight consecutive runs over sheets of sooted cardboard, a Peringuey's adder moved four times with its head to the left and four with it to the right, suggesting that the snake has no preference for either position. During eight different runs, angles between the 'parallel' tracks and the line linking the head-hooks varied from 21 to 47 degrees, the average being 35 degrees. The equivalent angles for tracks of *Crotalus cerastes* varied from 17 to 40 degrees, with an average of 26 degrees, suggesting that the rattlesnake flexes its body more acutely during sidewinding than does the adder. In the case of *Bitis peringueyi*, the lengths of the tracks, inclusive of the head-hooks amount, on average to 90% of the total length of the snake, thus it is possible to deduce the approximate length of a specimen from a measurement of the tracks which it produces.

SPECULATIONS ON THE ORIGIN OF SIDEWINDING

In the following discussion a suggestion is made on how sidewinding locomotion may have been derived from the more normal serpentine glide. Reference should be made to the diagram in Text-fig. 2, where shaded areas of the snake again represent parts of the body in contact with the ground. The lower part of the figure shows the snake gliding along a sinusoidal track. As has been pointed out by Gray (1946, 1953), propulsive thrust is generated in those parts of the body which show *increasing* curvature to the right or the left, when reading from the tail to the head of the snake. Forces exerted by the snake against projections in the ground act at right angles to the body of the snake as shown by the arrows in the diagram. During even motion, the resultant of all these normal forces 'produces a forward thrust equal but opposite to the frictional or tangential forces opposing the snake's motion' (Gray, 1953). For the snake to be able to progress in the direction indicated by the line A–B, however, it is essential that the forces exerted to the left of the line should balance those exerted to the right. If the magnitude of the left-hand forces exceeds that of the right-hand ones, it is obvious that the path followed by the snake will be deflected to the right-hand side.

Quite the most important feature of sidewinding is that alternate curves of the snake's body are raised above the ground and are thus incapable of exerting any force against small surface projections except at those points where contact is still maintained. The upper part of Text-fig. 2 shows the sidewinding condition in which forces are only exerted towards the left, since those parts of the body capable of exerting right-hand forces are no longer in contact with the ground. The result is that the snake moves laterally as well as forwards. Sidewinding can thus be regarded as an inevitable consequence of the snake raising alternate sections of its body while progressing in a normal serpentine glide.



Text-fig. 2 Diagram showing the relationship between horizontal undulatory locomotion (lower) and sidewinding (upper). The snake is able to glide in the direction A–B since left-hand thrusts balance those to the right. When sidewinding, body-raising causes all propulsive thrust to be exerted on one side only (left in this case), with the result that the snake moves laterally as well as forward.

Various writers have maintained that sidewinders do not press back or sideways against the substratum during locomotion and that the force is applied vertically to the surface over which the snake moves. Mosauer (1932) states that the advantage of sidewinding 'for the sandy habitat consists in it not requiring any resistance or reactions of the substratum, except that the latter has to carry

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the weight of the snake'. Van Riper (1955) writes, concerning *Crotalus cerastes*: 'the tracks were made by pressure only from above'. This is certainly not the case in Peringuey's adder which produces quite a considerable ridge behind its parallel tracks when traversing very loose sand (Pl. II A). It is clear that the higher the snake raises its body between contact points, the more steeply inclined will be the direction of its propulsive thrust. Nevertheless, it is essential that a horizontal component should exist, as a snake which applies its locomotory force vertically to a surface will be capable of lifting itself upwards but not of propelling itself forwards.

Since body-raising is a pre-requisite for sidewinding, it is interesting to speculate on the reason for a snake raising its body during locomotion in the first place. Several writers have presumed that sidewinding represents a specific adaptation allowing the snake to move over a loose unstable surface of sand (e.g. Cowles, 1920; Van Denburgh, 1922; Mosauer, 1932; Pope, 1937). However, Cowles (1956) has pointed out that *C. cerastes* lives in a desert area having perhaps less than 1% of its area covered by loose sand. By far the greatest part of the surface is hard and smooth, attaining a periodic temperature of more than 60° C. In view of this, Cowles has suggested that sidewinding in the horned rattlesnake is not a specific adaptation to life on loose sand, but rather assists the snake by reducing heat uptake by conduction while moving over the hot surface. Cowles also points out that among pit-vipers, sidewinding allows more rapid locomotion than does the conventional serpentine glide. On the extensive open plains this may be of particular importance since the snake often has to travel far to find food and a mate. Body-raising as a means of minimizing contact with a hot surface certainly seems to be a sound possibility, although nocturnal sidewinders would presumably have to contend with high surface temperatures only during times of enforced diurnal activity or when unexpectedly expelled from their hideouts by a predator.

Perhaps some information on the origin of sidewinding may be derived from a study of those snakes which do not usually sidewind but which, when placed on a sufficiently smooth surface, can be induced to do so. One such animal is the common South African house snake, *Boaedon fuliginosus*. Under normal conditions this aglyphous snake moves by means of serpentine glide but when released on a smooth surface, devoid of adequate superficial projections, resorts to sidewinding which allows fairly rapid locomotion. The movement is, however, seldom regular and is punctuated by frequent stops. This fact makes it difficult to obtain a satisfactory track on sooted cardboard since after producing two or three parallel lines, the snake is inclined to rest and then on starting again, to erase the existing tracks with its tail. Fortunately, some undamaged records have been obtained and these do not differ substantially from the ones made by Peringuey's adder. Pl. II B shows how loops of the house snake's body are raised above the surface during sidewinding. The function of this body-raising is almost certainly to ensure that the propulsive thrust is no longer exerted horizontally, but rather at an angle, obliquely into the surface (Pl. II C). This inclined thrust then compensates for the absence of the larger surface irregularities, required for horizontal undulatory locomotion, while the fact that the weight of the snake is now applied over a relatively restricted length of body means that the bearing pressure per unit area is increased. These two factors would undoubtedly serve to improve traction.

In the desertic areas of Southern Africa there occur three different sidewinding snakes: *Bitis peringueyi*, *B. caudalis* and *B. cornuta*. Of these, *B. peringueyi* is restricted to sandy areas, but the other two are very commonly found on hard arid surfaces. Were *B. peringueyi* the only sidewinder, one might be tempted to conclude that its form of locomotion had been developed specially for life on loose sand. The other two species however indicate that sidewinding is useful on hard surfaces as well.

Boaedon fuliginosus is one of the many snakes capable of sidewinding when the surface characteristics demand it. If the surface is smooth enough, such snakes will sidewind, irrespective of whether the substrate is hot or cold. It seems likely therefore that Cowles's concept of sidewinding as a response to a heated surface may not be applicable in all cases. In the case of Peringuey's adder, which is nocturnal and capable of burrowing, this explanation seems less likely than it does in other diurnal snakes. Where nocturnal sidewinders are concerned, it is suggested that sidewinding may have arisen from the necessity of moving over a very smooth surface either of loose sand or of hard-baked earth. Once the pattern had been established, body-raising associated with this form of locomotion would doubtless have assisted the snake greatly in its occasional daytime excursions over an uncomfortably hot surface.

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Tadpoles	35 mm. long; light br underside of body di with a lighter area un mouth; head flat; m apex; eyes on sides; colourless
Mouth	Slender horny jaws, s lower side only; no nor below; double r below (Text-fig. 1)
Young tailless frog	12 mm. from snout t