

RECTILINEAR LOCOMOTION IN A SNAKE
(*BOA OCCIDENTALIS*)

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(With Seven Text-figures)

The mechanics of three common modes of locomotion in snakes has been subjected to a detailed analysis (Gray, 1946; Gray & Lissmann, 1950). These three modes are (i) the serpentine or horizontal undulatory movement; (ii) the concertina movement; (iii) the crotaline or side-winding movement. A fourth, less common mode, described as 'rectilinear movement', has aroused considerable interest since Home (1812) published his 'Observations intended to show that the progressive motion of snakes is partly performed by means of ribs'.

During rectilinear locomotion the whole snake moves forward along a straight line. Lateral bending of the body and lateral resistances from the substrate do not form an essential feature of this movement; it is, therefore, quite unlike the three first-mentioned types. A characteristic of all species in which rectilinear movement has been described (e.g. Boidae, Viperidae, *Ophisaurus*) is a strongly developed ventral cutaneous musculature. Most observers are agreed that waves of muscular contraction followed by relaxation pass over this musculature. Wiedemann's (1932) explanation of the mechanics of this movement can be summed up by his term 'snail principle'; according to this author the waves of muscular contraction travel in a postero-anterior direction. Mosauer's (1932) designation 'caterpillar movement' might imply the same direction of travel, but he states that the movement of the locomotory waves is from head tailward.

Antero-posterior movement of a peristaltic wave would suggest an earthworm's rather than a snail's or a caterpillar's mode of progression. The term 'earthworm principle', however, has been applied by Wiedemann (1932) to the concertina movement. Observations by Wiedemann (1932), Mosauer (1932) and Bogert (1947) suggest that the ribs do not play an active part in rectilinear locomotion.

The differences in kinetics and in neuro-muscular co-ordination between a moving snail and an earthworm are very considerable (see Lissmann, 1945*a, b*; Gray & Lissmann, 1938*a*). Moreover, these invertebrates do not possess a system of rigid levers comparable with the limb bones or vertebrae which play an essential role in most, if not all, vertebrate propulsion. It therefore appeared of interest to obtain additional information about the rectilinear type of progression.

The most strongly developed ventral cutaneous musculature occurs in Boidae. I am indebted to the Zoological Society of London for two young specimens of *Boa occidentalis* (57 and 60 cm. long) which were used for the observations reported below.

MOVEMENT DURING RECTILINEAR PROGRESSION

Rectilinear movement in *B. occidentalis* is a slow method of progression often employed when the snake approaches the living prey. It can also be readily elicited by placing the animal on a smooth surface. To obtain an adequate picture of this

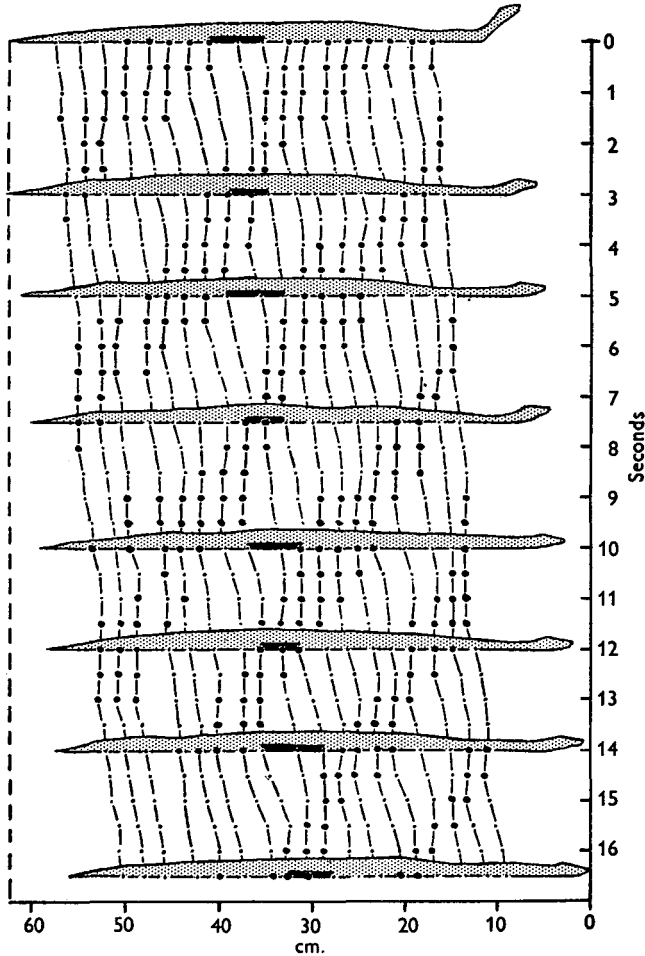


Fig. 1. Rectilinear progression in *Boa occidentalis* (redrawn from film). The vertical lines indicate successive positions of points marked on the ventro-lateral surface. Heavy dots indicate that the points remain stationary relative to the ground or that they exhibit a backward slip; fine dots show the points in forward motion. Note the alternation of shortening and elongation between adjoining points (e.g. the black area in the centre of the body) which passes in form of waves in a posterior direction over the body. At any one time two complete wave-lengths usually extend over the body.

type of movement simultaneous cinematograph pictures were taken of the lateral and ventral aspects of a snake by allowing it to creep over a glass plate and placing an inclined mirror under the glass. In an analysis of the photographs the natural

markings and scales of the *Boa* can be used to advantage; white paint marks were also found useful.

The general nature of the forward motion is shown in Fig. 1, in which the relative locations of eighteen individual points on the ventral lateral surface have been marked in thirty-four successive positions. It will be seen that the distance between

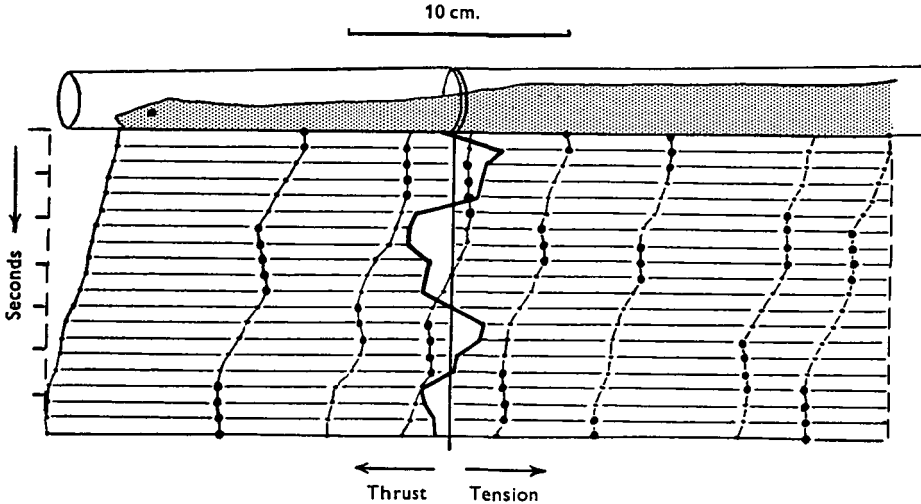


Fig. 2. Recording of external forces set up during rectilinear locomotion. The snake is made to creep through a rigidly fixed glass tube (right) across a narrow gap into a second tube (left) which is suspended by steel springs. The movements of the second tube are magnified by levers and are photographed simultaneously with the movements executed by the snake. Note that the head of the animal moves forward at relatively constant speed, whilst the ventral surface moves forward in 'steps'. Areas of fixation to the ground are indicated by heavy dots. As the areas of fixation move posteriorly over the body and approach the gap, tensions are set up between the two tubes (graph to the right of the vertical line); when the area of fixation has traversed the gap a longitudinal thrust develops (left part of graph).

two points lying close together varies rhythmically in such a manner that waves of alternating longitudinal contraction and elongation appear to pass in a posterior direction over the body. During steady progression two complete waves have been generally observed on the body. As the waves pass along, each point on the ventral surface of the animal is carried forward in rhythmic steps of 2-3 cm. in length. These waves exhibit occasional irregularities and may—as in the earthworm—fail to reach the posterior end of the body.

The similarity between *Boa* and earthworm is emphasized by observations of the external mechanical forces set up during locomotion. The nature of these forces has been recorded by allowing the snake to creep through a rigidly fixed, horizontal glass tube into a second tube which was movably suspended by steel springs. The movement of these springs, indicating tensions and thrusts set up between both tubes, was magnified by levers and was recorded photographically. Fig. 2 shows that a tension is developed as long as an area of fixation of the snake lies anteriorly in the movable tube. When this area of fixation has travelled backwards over the

body and has reached the rigid tube tension changes into a longitudinal thrust—in a manner comparably recorded in the earthworm (Gray & Lissmann, 1938*b*).

There is, however, one significant difference between the two animals: while all parts of the earthworm move forward in 'steps', certain parts of the *Boa*, e.g. the head in Fig. 2, progress at relatively constant speed.

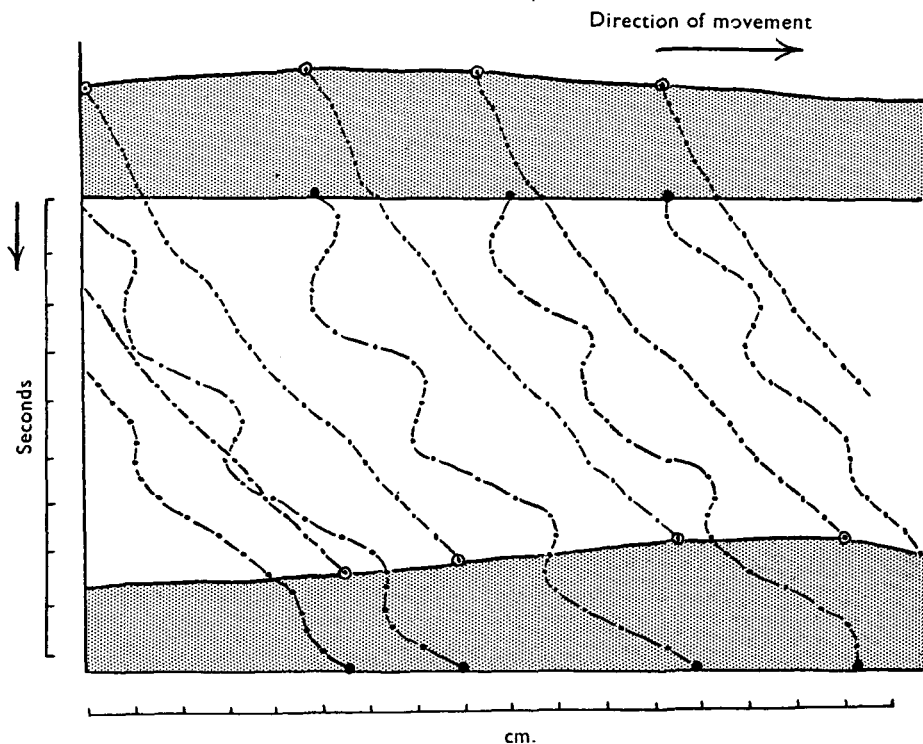


Fig. 3. Forward movement of dorsal and ventral points on the body of a *Boa* in rectilinear progression. The shaded areas represent the lateral view of the middle region of the body. Note that the dorsal points move at relatively constant speed, whilst the ventral points move forward in 'steps' each 2-3 cm. long.

This is shown in greater detail in Fig. 3, which also shows that whereas progression of any point on the ventral side is characterized by periods of forward movement alternating with periods of rest, any point located on the dorsal side moves forward at relatively constant speed and, therefore, all points on the dorsal side retain an equal distance from one another throughout the locomotory cycle. If the muscular waves are regular, this is also true for any two points on the ventral side as long as the distance between them is one complete wave-length or the multiple of one complete wave-length.

Maximal changes in length occur between two points on the ventral surface which lie half a wave-length apart, e.g. point *g* and *o* in Fig. 4*B*. Provided there is no backward slip, the length of a step is determined by the difference of maximal elongation and maximal shortening between these two points; the speed of the whole animal is the length of a step multiplied by the frequency of waves which

pass over the body. The telescoping of the ventral scales provides a useful measure of the degree of contraction of the ventral musculature. In Fig. 4A the forward movement, relative to the ground, of every fifth ventral scale of the central portion of the body is shown. A clearer picture of the shortening and elongation is obtained for the same region by plotting the movement of the scales relative to a fixed point

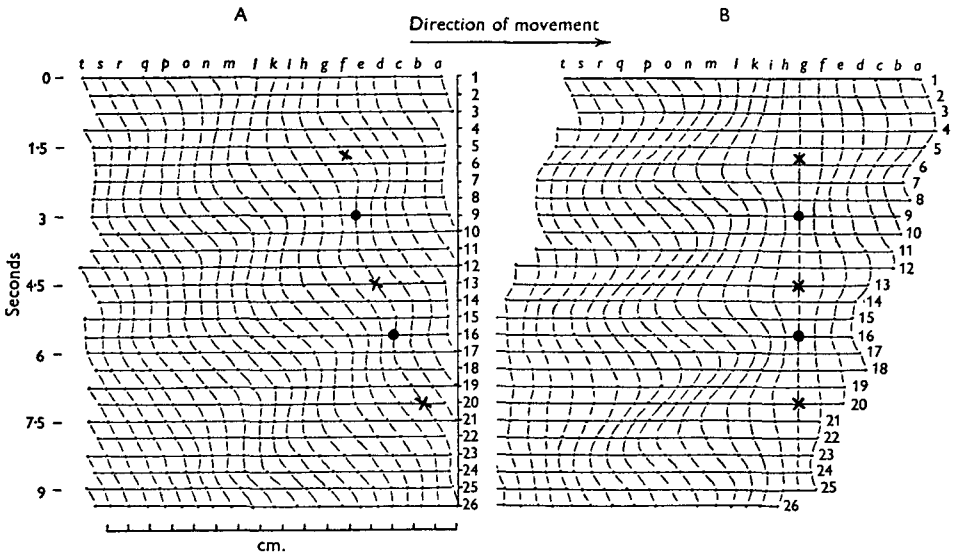


Fig. 4. The points *a*, *b*, *c*, etc., on the horizontal lines indicate the distances between five ventral scales. (A) shows the forward motion relative to the ground of these points; (B) shows the changes in shape on the body during the same period; the distances between the points are plotted relative to point *g*. Note that conditions of maximal extension of the regions adjoining *g* (marked \times) occur at positions 5-6, 13 and 20. In this state the scales glide forward relative to the ground with maximal velocity (\times in A). Maximal contraction near point *g* occurs at positions 9 and 16 (marked \bullet). These positions coincide with the stationary phase in Fig. 4A. Point *o* (in B) is about half a wave-length posterior to point *g*; the difference between its maximal elongation from *g* (positions 7, 14 and 22) and its maximal contraction towards *g* (positions 11 and 18) equals the length of one 'step'.

on the body (point *g* in Fig. 4B). Comparison of Fig. 4A and B shows that as long as a region of the body is maximally contracted it remains stationary relative to the ground, and on a very smooth surface may even slip backwards. This region begins to glide forward with increasing velocity as soon as relaxation sets in and slows down with the onset of the next wave of longitudinal contraction until it comes to rest again in a state of maximal contraction.

Half a wave-length of muscular activity extends over a region in which some 20-30 ribs can be counted on either side. If the average step is about 2 cm. long a change of distance less than 1 mm. between two adjacent tips of the ribs could account for the changes in length observed on the surface during one locomotory cycle. On the other hand, if the movements of the ribs are similar to those of vertical lines drawn on the skin of the animal then any rib should swing through a considerable angle round its base when the adjoining musculature passes from a condition

of extreme contraction to one of extreme elongation. These movements might be expected to be parallel to the movements of vertical lines drawn on the body of a creeping animal as shown in Fig. 5.

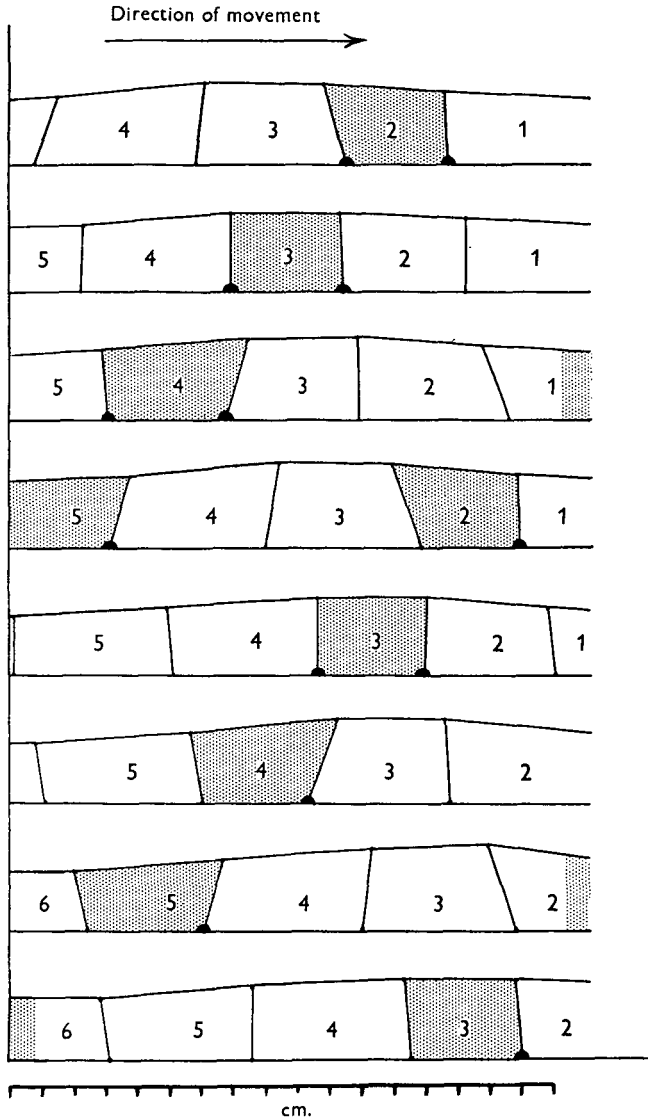


Fig. 5. Forward movement of vertical lines drawn on the surface of the snake during 6 sec. of rectilinear progression. The state of maximal contraction of a region between two lines is indicated by shading; the region posterior to it undergoes contraction whilst the anterior section elongates. Comparison of a region during maximal contraction and maximal elongation shows that the angle which the vertical lines form with the horizontal (vertebral column) varies considerably. Areas of fixation to the ground are marked by heavy ventral dots.

In order to determine whether the tips of the ribs execute any appreciable movement relative to the vertebral column during movements exhibited by the skin,

small lead disks were attached to the ventral lateral surface of a snake and successive X-ray photographs were taken of the various phases of the locomotory cycle.* The movement of the disks relative to the ribs and the vertebral column is given in Fig. 6 for three positions. It will be seen in Fig. 6 (i) and (iii) that the centre of maximal elongation is between the 11th and 26th vertebrae; Fig. 6 (i) also shows the succeeding posterior centre of contraction between the 67th and 77th vertebrae. In Fig. 6 (ii) the states of contraction and elongation are reversed at the same levels. In all figures the tips of the ribs retain accurately the same positions relative to the vertebral column, whereas the lead disks glide past the tips of the ribs; the same surface region, when elongated, extends over six more ribs than it does in a contracted state. This result is in agreement with the observations of Wiedemann (1932), Mosauer (1932) and Bogert (1947) and in contradiction to the 'rib-walking theory'.

DISCUSSION

The picture of the mechanics of rectilinear progression can be elucidated to a certain extent by taking into account the following facts: (1) the ventral surface of the *Boa* moves forward in rhythmic steps, while waves of muscular contraction and relaxation pass in a posterior direction over the ventral cutaneous musculature; (2) the vertebral column moves forward at relatively constant speed; (3) the ribs do not perform any appreciable movement relative to the vertebral column; (4) the vertebral column and the ventral cutaneous musculature are mechanically connected through the ribs and two distinct sets of muscles.

A knowledge of the geometrical arrangement of the different muscles makes it possible to determine their changes in length throughout a locomotory cycle as long as the length of any one of them is known.

Ventral cutaneous musculature. On anatomical grounds this massive muscle can be expected to represent the main source of energy for rectilinear progression. Its changes in length have been described in the previous section, but the mechanism of these changes remains controversial. During movement, each complete locomotory wave can be subdivided diagrammatically into four regions (*A* to *D*, Fig. 7, 1†) according to the state of muscular activity.

(i) An anterior group of ventral cutaneous muscle fibres is in a state of maximal contraction (Fig. 7, 1, *A*) and cannot provide any propulsive energy to the rest of the system, although this region can form a *point d'appui* against which muscles lying posteriorly can exert a tractive force. The fixation to the ground on a smooth surface such as glass can only be due to static friction. On rough ground the free posterior margins of the scales assist in anchoring this area to the substrate.

(ii) Immediately posterior to the region of maximal contraction is a region undergoing contraction (Fig. 7, 1, *B*). This is the only group of ventral cutaneous muscle fibres which are active in a locomotory sense, for when they shorten actively they develop tensions against frictional resistance of the ground. Any point of this contracting region moves forward with decreasing velocity.

* My thanks are due to Mr J. A. Fozzard for his assistance in taking these photographs.

† For Fig. 7 see Folder V.

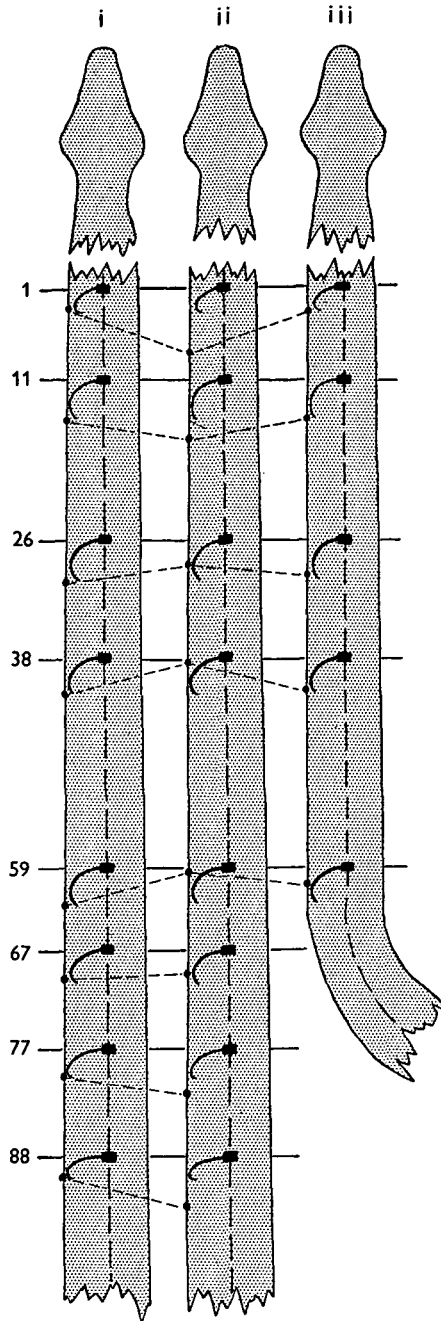


Fig. 6. Analysis of three successive X-ray photographs of a *Boa* during rectilinear progression. The points on the outline of the animal indicate the positions of lead disks attached to the surface. Other lead disks along the median dorsal line mark the vertebrae. The centre of maximal elongation for (i) and (iii) lies between the 11th and 26th vertebrae, for (ii) between the 67th and 77th. Centres of contraction are between the 11th and 26th vertebrae in the case of (ii), and between the 67th and 77th in the case of (i). Note that the lead disks on the ventro-lateral surface are displaced relative to the vertebral column, while the position of the tips of the ribs does not change.

(iii) The next posterior region (Fig. 7, 1, *C*) comprises muscle fibres of maximal elongation moving forward relative to the ground with maximal velocity. The velocity of this region is greater than that of the vertebral column; it does not, however, contribute any energy for its own forward motion or for that of any adjoining part.

(iv) Fig. 7, 1, *D* represents a region in which the muscle fibres elongate, each point moving forward with increasing velocity. As long as this region lies posterior to a *point d'appui* the elongation of its fibres offers no theoretical difficulty, for elongation could be achieved by passive stretch from an anterior contracting region (*B*) acting against friction. However, if within the cycle of activity the phase of maximal contraction is reached at the most anterior part of the body (e.g. Fig. 7, 1 and 5) there would be no anterior cutaneous muscle fibres which could contribute to an elongation by pulling against an anterior point which is fixed to the ground.

Wiedemann (1932) assumed that elongation of the contracted longitudinal fibres is accomplished by passive relaxation of the elastic connective tissue. This would mean that during longitudinal contraction energy is being stored in the connective tissue and becomes effective as soon as tension in the ventral musculature ceases. Wiedemann observed an elongation of the body of a decapitated snake after release from longitudinal compression. In the absence of more precise data it is impossible to decide how far such an elastic recoil is sufficient in extent, speed and power to elongate, against friction, the ventral cutaneous musculature; further, this explanation does not cover the fact that part at least of the extension may be due to the passive stretch exerted by the vertebral column which is moving forward continuously.

An alternative and more active mechanism of elongation of the ventral cutaneous musculature is suggested by the distribution of the muscles uniting the ventral surface of the body to the ribs. These muscles form two groups (Buffa, 1905): (i) *M. costo-cutanei superiores* running from each rib to a more posterior region of the ventral skin; (ii) *M. costo-cutanei inferiores* running from the ribs to more anterior regions of the ventral skin (Fig. 7). If these muscles maintain constant length during the whole locomotory cycle they must act as a rigid system whereby the forces exerted by the ventral musculature are transmitted to the dorsal regions of the body and vice versa. If the elongation of anteriorly contracted fibres of the ventral cutaneous musculature is to be effected at the required rate by means of a rigid connexion with the vertebral column, there can be only one point at which the movement of the cutaneous musculature can be transmitted to the vertebral column by a non-extensile element. This point must be located exactly one wave-length behind the anterior end of the ventral cutaneous musculature. Such a rigid attachment would, however, mean that the vertebral column would have to move forward in the same rhythmic manner as its point of attachment at the ventral surface and not at constant speed. Since the vertebral column does move forward at constant speed, and since it has muscular attachments with the ventral skin at many points along the entire locomotory wave, the muscles forming this connexion must undergo cyclic changes in length as is diagrammatically shown in Fig. 7, 1-7.

M. costo-cutanei superiores. The changes in length of these muscles in co-ordination

with the activity of the ventral cutaneous musculature can be followed from Fig. 7, 1-7. The anterior end of the ventral surface presents the clearest mechanical conditions. In Fig. 7, 1 the anterior region *A* of the ventral cutaneous musculature is maximally contracted and is fixed to the ground while the vertebral column and ribs are travelling forward at constant speed. During the transition from Fig. 7, 1 to 2 the posterior margin of region *A* remains stationary while the anterior margin begins to move forward with increasing velocity and must, therefore, overcome longitudinal ventral friction. The force required to overcome this friction and to stretch the muscles can be derived from the longitudinal thrust of the vertebral column which is propelled forward through the activity of more posteriorly situated sections of the musculature. This forward thrust (recorded in Fig. 2) is transmitted to the anterior margin of region *A* of the ventral cutaneous musculature via anterior ribs and *M. costo-cutanei superiores*. Since the anterior margin of the ventral cutaneous musculature begins to accelerate from rest while the vertebral column travels forward at constant speed, the *M. costo-cutanei superiores* must at first be stretched passively while developing sufficient tension to overcome ventral friction. The rate of stretch decreases, presumably with increasing tension, until the anterior margin of region *A* of the ventral cutaneous musculature has attained a speed equal to that of the vertebral column; at that point the length of the *M. costo-cutanei superiores* remains constant.

However, throughout each complete locomotory cycle the average speed of the vertebral column and of the ventral surface must be the same. Since the ventral surface remains stationary during part of the cycle its speed must, at times, exceed that of the vertebral column. The acceleration of the ventral surface beyond the speed of the vertebral column can only be achieved through an active shortening of the *M. costo-cutanei superiores* (Fig. 7, 2-3). Since these muscles shorten at the same time as developing tension against the frictional resistance of the anterior region they must contribute propulsive energy to the whole system. The phase of active contraction sets in shortly after the point of cutaneous attachment of this muscle has begun to glide forward (i.e. between positions 1 and 2 in Fig. 7); it extends until this point has passed its maximal velocity and begins to slow down (i.e. between positions 3 and 4 in Fig. 7).

Conversely, as soon as the point of the ventral surface to which the *M. costo-cutanei superiores* are connected has slowed down to a speed below that of the vertebral column, these muscles will be passively elongated through the forward movement of the vertebral column; this occurs before the point of the ventral surface becomes stationary relative to the ground, e.g. at the anterior end between positions 3 and 4 in Fig. 7. This elongation will continue throughout the period of fixation to the ground (positions 4 and 5, Fig. 7). During this period tension in the *M. costo-cutanei superiores* could only have the effect of resisting the forward motion of the vertebral column, and it seems likely that the muscles remain inactive in this phase. Elongation ceases between positions 5 and 6 in Fig. 7, as soon as the velocity on the ventral attachment again equals that of the vertebral column.

This scheme of rhythmic changes in length and tension has been arrived at by

considering the anterior end of the animal. If the regularity of movement is to be maintained and if the muscles are not to slacken between their points of attachment, similar changes in length must occur throughout the whole length of the animal. It is not equally certain that comparable tensional changes also occur, because additional forces for elongation and propulsion may become available from the contracting regions of the ventral cutaneous musculature as long as they are situated posterior to a *point d'appui*.

Apart from the horizontal forwardly directed force of the *M. costo-cutanei superiores*, it may be assumed that, by virtue of their more dorsal attachment on the ribs, contraction in these muscles may tend to elevate or to reduce the pressure on the ground of those parts which are gliding forward (Fig. 7), thus reducing their friction. This would inevitably increase the pressure and efficiency of the areas of fixation.

M. costo-cutanei inferiores. The picture of rectilinear movement derived so far is based on the assumption that the vertebral column is travelling forward at constant speed, without considering the forces which propel it forward. The position of the *M. costo-cutanei inferiores* suggests (Fig. 7) that these muscles transmit to the vertebral column the propulsive force exerted by the ventral cutaneous muscles. It seems reasonable to suppose that the length of these muscles changes rhythmically in a manner similar to that of the *M. costo-cutanei superiores*, except that the *M. costo-cutanei inferiores* must shorten wherever their point of attachment to the skin travels forward more slowly than the vertebral column (e.g. at the anterior end in Fig. 7 this period must start between positions 3 and 4, and it must end between positions 5 and 6). Only in this phase can the *M. costo-cutanei inferiores* directly contribute a propulsive thrust to the vertebral column. It is interesting to note that this contraction begins as a *point d'appui* approaches from the anterior end the cutaneous attachment of this muscle; it persists throughout the period of fixation to the ground and includes the early stages of acceleration.

Elongation of the *M. costo-cutanei inferiores* takes place whenever the point of cutaneous attachment travels faster than the vertebral column, i.e. at the anterior end beginning between positions 1 and 2 and ending between positions 3 and 4 in Fig. 7. If these muscles develop tension during the phase of elongation they would act directly against the propulsive phase of the *M. costo-cutanei superiores* and resist the forward motion of the anterior end of the ventral cutaneous musculature. There is clearly an antagonistic effect of all *M. costo-cutanei inferiores* and *M. costo-cutanei superiores* which have their cutaneous attachments at the same level of the body, and their phases of activity are likely to be linked by a mechanism of reciprocal excitation-inhibition. This may apply not only to the anterior end of the animal but to the entire length of the body. On the other hand, it is conceivable that the *M. costo-cutanei inferiores* should maintain continuous tension throughout all phases of the locomotory cycle wherever contracting regions of the ventral cutaneous musculature develop sufficient tension to elongate and advance posterior regions. Throughout all phases of elongation, however, tension in the *M. costo-cutanei inferiores* could assist only indirectly the propulsion of the vertebral column by transmitting the tractive force of more anteriorly situated ventral cutaneous musculature.

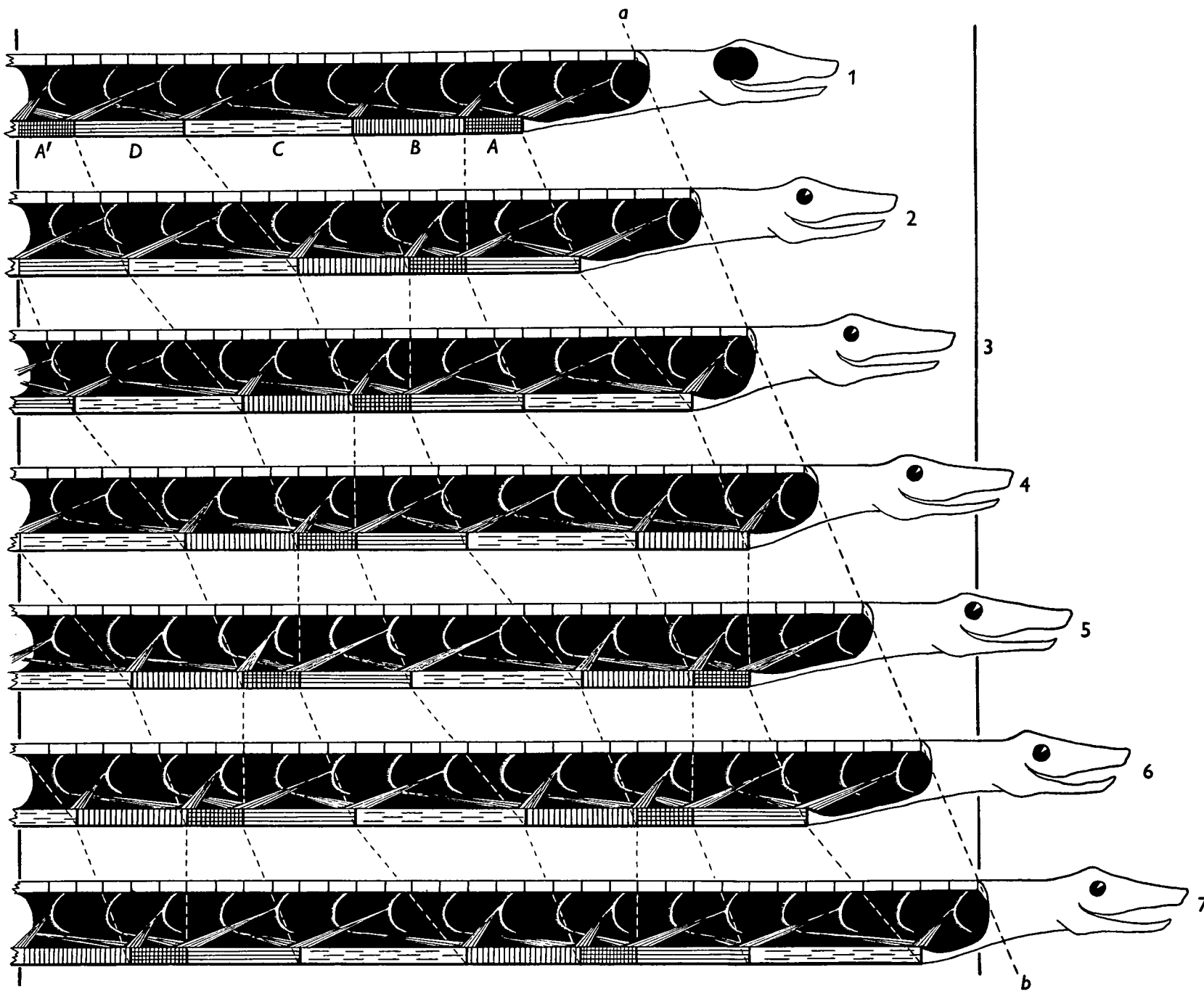


Fig. 7. Diagram illustrating in seven successive positions (1-7) the mechanism of rectilinear progression and the arrangement of muscles involved. On the ventral side the cutaneous musculature is represented in different states of activity. Position 1 shows the anterior region *A* of this musculature in a state of maximal contraction and stationary relative to the ground; region *B* is composed of fibres undergoing contraction; region *C* is in a state of maximal elongation; region *D* is in the process of elongating. In each succeeding position (2-7) these states of activity are shifted in a posterior direction over this muscle, the posterior margin of the maximally contracted region (*A*) remaining fixed to the ground.

The ventral cutaneous musculature and the vertebral column are united by the ribs and two sets of muscles: (i) *M. costo-cutanei inferiores* extending between the tips of the ribs and an anterior region of the ventral skin; these muscles move the vertebral column forward at constant speed (line *ab*); (ii) *M. costo-cutanei superiores* which are attached higher up on the ribs and run to a ventro-lateral region of the skin. These muscles are capable of producing tensions between the vertebral column and the ventral skin and thus to propel the ventral surface forward against frictional resistance. Contractions and extensions of both sets of muscles are related to the stationary activity of the ventral cutaneous musculature near which they are attached to the skin. Muscle slips of the two sets with cutaneous attachments at the same level of the body work in strict antagonism; e.g. at the anterior end the *M. costo-cutanei superiores* begin to contract between positions 1 and 2; contraction ceases between 3 and 4. From that moment until midway between positions 5 and 6 these muscles are being passively extended through the forward movement of the vertebral column. In the corresponding anterior *M. costo-cutanei inferiores* contraction and extension are reversed during the same periods.

Although it seems reasonable to suppose that all three groups of muscles contribute propulsive energy to the animal by fulfilling the fundamental requirement of shortening while under tension, it is not easy to demonstrate this conclusively with the present methods. Theoretically, the system could operate without tensions in the ventral cutaneous musculature, if the *M. costo-cutanei inferiores* were able to exert a sufficient force against the posterior edges of the areas of fixation, propelling the vertebral column forward and thus enabling the *M. costo-cutanei superiores* to detach and elongate the anterior margins of the ventrally fixed regions.

In view of the anatomical arrangement, however, it seems more plausible if the vertebral column and all parts rigidly connected with it are considered as a cylinder gliding at constant speed in a tube, or half tube, formed by the skin and the ventral cutaneous musculature which moves forward at varying speeds. The main force required is that for overcoming the external ventral friction and for the successive acceleration of the various regions of the tube. The horizontal, longitudinal arrangement of the ventral cutaneous muscle fibres seems to be best suited for this purpose. This forwardly directed force is balanced by an equal and opposite static reaction under the areas of fixation to the ground. Whatever forward force is imparted to the dorsal cylinder by the *M. costo-cutanei inferiores* must originally be derived from the substrate. The effects of this force are returned to the substrate via the *M. costo-cutanei superiores*.

SUMMARY

1. The rectilinear mode of progression in *Boa occidentalis* is described. It is fundamentally similar to that of an earthworm. The terms 'snail' and 'caterpillar' principles of other authors are inappropriate.
2. During movement, waves of muscular contraction and relaxation pass in a posterior direction over the ventral cutaneous musculature.
3. The ventral surface moves forward in 'steps' while the vertebral column and all parts rigidly connected with it move forward at relatively constant speed. The ribs do not execute any appreciable movement relative to the vertebral column.
4. The probable interaction of the musculature, as deduced from the mechanics and the geometrical arrangements, is discussed.
5. Rectilinear progression is probably a unique type of vertebrate locomotion in so far as it does not involve any lever actions of skeletal structures.

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