

energy would be in thermal equilibrium. Thus in the solar atmosphere we have an ionized gas which is in anything but thermodynamic equilibrium. Many ions have very low energies and absorb energy readily, while some have very high energies that can be passed on by collision and produce abnormal excitation in other atoms. For example, the maximum energy of a calcium ion is as great as it would be if it were in thermal equilibrium at $12,000^{\circ}$ while a barium ion would approximate $20,000^{\circ}$. We note particularly that the energy of an ion changes continuously during its flight and its energy at collision depends on its position and trajectory. The neutral atoms and electrons are not particularly disturbed by the electric fields and except for their collision with ions of excessive energy, they would approach an approximate thermodynamic equilibrium. The problem of working out the detailed equations of equilibrium between excitation and deexcitation of all the different kinds of ions in the solar atmosphere is an imposing one and

will probably not be solved for some time. It does appear, however, that electric fields in the solar atmosphere will account qualitatively for the observed anomalous characteristics of the sun's radiation, because such fields make possible the selective excitation of the more energetic radiations without disturbing in any important manner the mechanisms which are responsible for the general radiation.

Our studies of the relations of electricity and magnetism to the properties of the sun's atmosphere have demonstrated that electric and magnetic effects play, perhaps, a major rôle in determining the observed phenomena. While it can not be said to be proved beyond doubt that electric fields exist in the sun's atmosphere, yet the internal evidence and the interrelation of much data makes the existence of such fields seem probable. Much additional data are needed to completely test our results, and it is sincerely hoped that the solar eclipse of 1932 will be of material aid in this respect.

ON THE LOCOMOTION OF SNAKES¹

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DURING the years 1929-1931 an investigation dealing with ophidian locomotion and its anatomical basis was carried on in the Department of Anatomy, University of Michigan. Since the publication of the voluminous thesis embodying the results of this work has met with considerable delay, it seems advisable to publish a brief abstract at this time.

The anatomical structures involved in locomotion are the skeleton of the trunk and tail, their musculature and integument. All three show special modifications fitting them for their task.

The vertebral column of a snake consists of a very great number of single pieces, sometimes as many as several hundred; each vertebra articulates with a neighboring one at five points. The shape of the articulating surfaces restricts the possible movements to two main planes, *i.e.*, to the frontal plane, permitting of lateral flexion, and to the sagittal plane, permitting of dorsal and ventral flexion. Moreover, movements in both planes can be so combined as to allow the snake the multitude of graceful windings that makes the ophidian vertebral column the most remarkable instance of mobility in this organ, although rotation about the long axis is wholly impossible. X-ray photographs were used to determine the degree of flexibility in the main planes; it was

found in several different species to be about 25° for lateral flexion between successive vertebrae, about 13° for ventral flexion, while the maximum of dorsal flexion varied from 12° to 18° . The ophidian vertebral column, considered as a mechanical unit, is of an admirable perfection. It permits of almost unrestricted movements in the frontal and sagittal plane, avoiding any loss of energy in the production of these movements by the impossibility of rotation. Moreover, it is very resistant to strain and stress in the long axis, thus making for high efficiency in transferring the locomotor forces from one small section of the body to the whole.

Each vertebra from the second to the last trunk vertebra articulates with two ribs that are attached to it by clublike enlarged extremities, while their other ends are free between the muscle sheets. The vertebrocostal articulation, while it was generally considered as a ball and socket joint, actually functions as a hinge joint, a ginglymus, in which movements are possible in one oblique plane only, due to the peculiar shape of the articulating surfaces. Consequently, the free end of a rib when moved forward is also lifted; when moved backward, it is depressed. This seems to be of significance in locomotion.

The myology of the body of snakes is at the same time simple and complicated. It is simple because, due to the loss of the extremities, the appendicular muscles have disappeared, except for a few rudiments.

¹Abstract of a lecture delivered before the Western Society of Naturalists, Berkeley, California, December, 1931.

Thus the musculature of the body is formed by a repetition of segmental muscles throughout its length, not overlapped by extremal muscles. On the other hand, the myology is complicated, because the remaining system is highly specialized.

The skeleton of the trunk is made up of vertebrae and ribs; therefore, we can distinguish principally three main groups of skeletal muscles: (1) Muscles between vertebra and vertebra, (2) between vertebra and rib and (3) between rib and rib. A fourth group of muscles connects the ribs to the integument, and finally there are cutaneous muscles connecting parts of the integument to each other, *i.e.*, scales to scales.

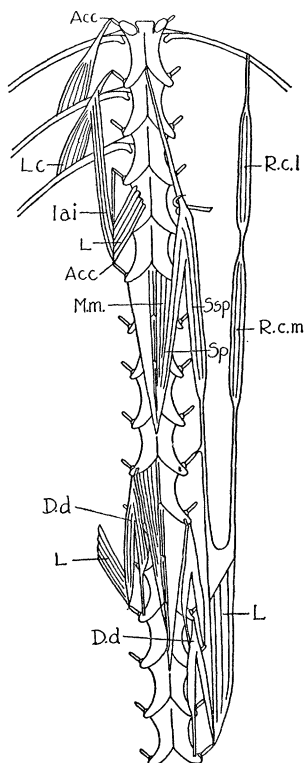


FIG. 1. Diagram of the dorsal trunk musculature of a racer, showing the linking of the long muscles to chains.

All these muscles are strictly segmental, as can be shown by careful dissection, but the individual segments of some of them are very much elongated. This specialization has reached the extreme in the Colubridae, especially in the slender racers; here some of the muscles are linked together so that they extend over more than 30 vertebrae without attachment. The purpose of this is apparently to permit an equal bending over a considerable length of the vertebral column. If the muscles were to stretch over a few segments only, the synchronous and equal flexure would not be as well insured as by very long muscles overlapping each other by one segment only.

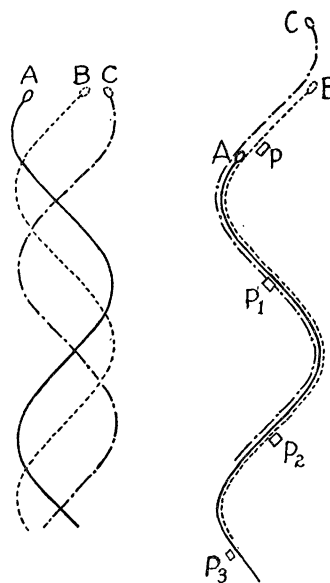


FIG. 2. Diagrams of a snake during horizontal undulatory movement in three phases A, B, C. I. on a glass plate, II. on ground offering circumscribed points of resistance P, P₁, P₂, P₃.

A detailed comparative study of the trunk musculature of over 50 genera showed significant differences between the taxonomic main groups, differences that could well be used for determining relationships and phylogeny of the snakes.²

The specialization of the integument serving locomotion consists in the formation of the broad, imbricating transverse scutes on the ventral surface, replacing the smaller scales of the flanks and the back.

Locomotion of terrestrial snakes is performed by three principal methods: the horizontal undulatory

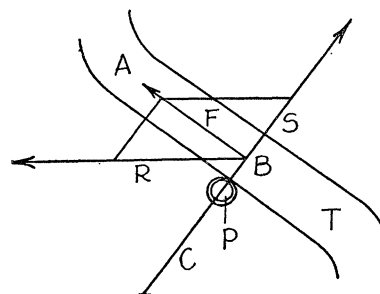


FIG. 3. Diagram of the forces acting on a portion B of a snake's body during horizontal undulatory movement. B is pressed to the left by the force R, S is the reaction of the point of resistance P on the pressing portion, the reaction being normal to the surface as in sliding bodies. F, the resultant of R and S causes the progression along the longitudinal axis AT.

² Presented under the title, "The Trunk Muscles of Snakes and Their Bearing on Phylogeny and Taxonomy," before the American Society of Zoologists, Cleveland, Ohio, December 1930.

movement, the sidewinding or rolling movement and the caterpillar movement. The first one is the typical serpentine wriggling, the method used by most snakes for rapid locomotion. It is produced by the progression of transverse waves over the body of the snake from the head to the tail, principally like the movements of many aquatic animals in water. These transverse waves result in the displacement of each point of the snake's length in a direction approximately normal to the direction of locomotion, if there is no lateral resistance, as on a glass plate, where because of the side slippage, the snake's wriggling is futile, not resulting in progression. Under natural conditions the ground always furnishes points of resistance in the form of rocks or pebbles, the stems of plants or simply small unevennesses. The snake uses

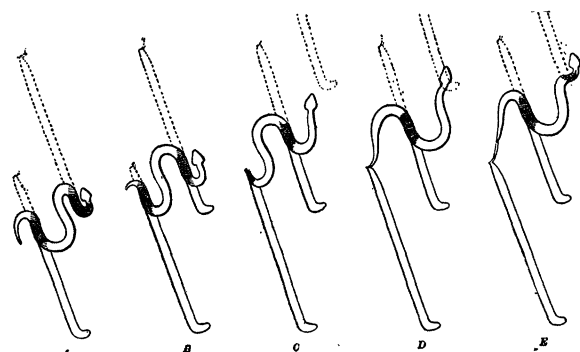


FIG. 4. Diagram of a snake in sidewinding locomotion, representing 5 phases. Only the shaded parts of the snake touch the ground. The formation of parallel, oblique, disconnected tracks is shown.

these points of resistance by applying its curves to them, whereby mainly the body portions midway between two successive vertices are pressed against the projections of the ground. Then any side slippage is avoided by the half cylindrical shape of the body and especially by the sharp keels present in many snakes along the flanks. Every point 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 shrubs like a water course in its narrow, winding bed. The diagram Fig. 3 shows how the forces brought about by the horizontal undulations are transformed into progress in the longitudinal axis.

The main work is done at the points midway between two vertices of the sinuous curve; here the forces are greatest, gradually decreasing towards the vertices, where they may be zero. The ventral scales are of no use in the horizontal undulatory movement.

The sidewinding or rolling movement is applied by viperide snakes inhabiting sand deserts, namely, the members of the genus *Cerastes* in the Sahara and the "Sidewinder" (*Crotalus cerastes*) in the southwestern deserts of the United States. This progress is principally like the sidewise rolling of a circular helix or screw—the tracks left by a wire helix being, like those of a sidewinding snake, a series of disconnected equidistant and parallel bands, set at an angle to the direction of motion, each as long as the helix (or snake, respectively). The advantage of this type for the sandy habitat consists in its not requiring any resistance or reactions of the substratum, except that the latter has to carry the weight of the snake.

The caterpillar movement is the one method in which the ventral scales play that important rôle which was formerly attributed to them for snake locomotion in general. It consists of an alternate movement of the skin on the body and of the latter within its tube of skin. First the skin is pulled forward, then it is anchored on the ground, whereby the ventral scales catch points of resistance, and the body is pulled forward until the corresponding portions of integument and body are in touch again. The ribs are not employed in the sense of the "rib walking" theory maintained by former authors. The movement described proceeds rhythmically from the head tailward. By this method a snake can glide slowly forward, stretched out fully or slightly undulating. The caterpillar movement is applied mostly by thick-bodied snakes like Boidae and Viperidae, e.g., rattlesnakes. Finally, snakes can move by alternately bending and straightening portions of their bodies. Speed-testing experiments with the famed "Blue Racer" have shown that the apparent rapidity of many snakes is a psychological delusion rather than actual speed in meters per second. However, more extensive tests along this line are desirable.

The author is at present engaged in an investigation dealing with the locomotion and the locomotor adaptations of sand reptiles.

OBITUARY

JUNE ETTA DOWNEY

THE University of Wyoming lost its most distinguished scientist when Dr. June Etta Downey, professor of philosophy and psychology, died on October 11, 1932. Dr. Downey was born in Laramie, Wyo-

ming, on July 13, 1875, and resided there throughout life. Her researches in the fields of handwriting, imagery, "will-temperament" testing, handedness and esthetics earned for her international recognition.

Dr. Downey was graduated from the University of