

**Tests on the locomotion of the elongate and limbless reptile
Ophisaurus apodus (Sauria: Anguillidae)**

CARL GANS AND J.-P. GASC

*Department of Biology, The University of Michigan, Ann Arbor, Michigan 48109, USA and
Laboratoire d'Anatomie Comparée, Muséum National d'Histoire Naturelle, Paris 70005, France*

(Accepted 4 April 1989)

(With 12 figures in the text)

A series of *Ophisaurus apodus* was filmed while traversing plane surfaces, fields of nails and pins at different spacings, and channels of different diameter. Small individuals can practise slow lateral undulation on very rough surfaces, but with increased speed, all shift to slide-pushing, using either constrained bends of the body or very wide swings of the tail. In fields of closely-spaced pins, they travel by undulation, often pushing at a limited number of sites and pulling and pushing the trunk among these. Amid pins of wider spacing, the undulation involves some repositioning of curves. In channels, they utilize continuous bend concertina movement with the initial bend formed anteriorly and subsequent ones added, either to the level of the cloaca or on to the tail as well. The cloacal region cannot be established on the basis of locomotor pattern, as the propulsive waves pass smoothly from head to tail. Maximum voluntary velocities (of the centre of gravity) were 13 cm/s for slide-pushing, 55 cm/s for lateral undulation, and 3 cm/s for concertina movement. Propulsion is entirely effected by bending of the trunk; tests gave no evidence that the dorsal and ventral portions of the integumentary armour show significant anteroposterior displacement relative to each other.

Contents

	Page
Introduction	518
Materials and methods	519
Results	520
Plane surfaces	520
Slide-pushing	521
Fields of pegs	524
Parallel-sided channels	527
Curvatures of the body	531
Vertical movements	531
Discussion	532
General	532
The force required	532
Rules of undulation	533
Slide-pushing	533
Concertina patterns	534
Ecological implications	534
The report of Frey	535
References	535

Introduction

Limbless animals can propel themselves by several distinct locomotor methods and field observations suggest that some species utilize all of these at one time or other (Gans, 1985*b*, 1986, see for bibliography of earlier references). However, the mere observation that animals can and sometimes do apply a range of locomotor modes permits only the widest of comparisons; it does not let one establish the relative advantages of these methods or the specializations exhibited by the animals. This is particularly important for the methods used by limbless lizards, as these show various degrees of specialization which is less than that of snakes (Gans, 1962). The question is not the absolute one, whether the organisms can use a particular method, but asks about the variants of a particular locomotor pattern, the frequency of its usage and the behavioural or environmental attributes thereof.

The anatomy of the propulsive system of limbless squamates has been described (Gasc, 1967, 1981). Other studies have reported on cinematography (Daan & Beltermann, 1968), and cinefluoroscopy of locomotion (Gasc, 1982), on the differences between terrestrial and aquatic movement (Tercafs, 1961; Jayne, 1985), and the movement patterns of reduced limbs (Gasc, 1984; Berger-Dell'Mour, 1985). The present report presents another way of attacking such questions, namely by forcing the organism to traverse several sets of substrata each of which is organized so that one of its variables may be modified. The modifications range about the locomotor patterns observed in the field, but differ from this in both directions. For instance, peg spacings range from those less than the diameter of the animals to those so wide that only one peg can be contacted at a time. The locomotor behaviour actually observed will then indicate the range of the possible substrata that can be utilized without major problems, whereas the difficulties encountered at each end of the behaviour-locomotion range will help to characterize the locomotor method. Computer-assisted motion analysis facilitated characterization and comparison.

The present report deals with the Scheltopusik, *Ophisaurus (Pseudopus) apodus*, a large common

TABLE I
Measurements of the specimens of Ophisaurus apodus used in this study

Weight (g)	Body + tail length (mm)	Tail		Digitized ^a	Source ^b
		Total length (%)	Height (mm)		
510	420 + 606	59	—	—	LU, SP R, dealer
420	390 + 592	60	32	30	CO J, Paris Mus
320	345 + 565	62	—	—	CO, LU, SP J, dealer
250	332 + 543	62	25	24.5	LU J, Antwerp
155	271 + 485	64	21	25	LU, SP J, dealer
112	264 + 455	63.3	—	—	J, dealer
93	235 + 429	64.6	19	19	J, dealer
57	215 + 352	62	18	17	LU, SP J, dealer
55	185 + 345	65	—	—	LU ?, Langerwerf

^aSequences which were digitized, rather than visually analysed. CO, concertina movement; LU, lateral undulation; SP, slide-pushing

^bAntwerp, Royal Zoological Society of Antwerp; J, Yugoslavia; Langerwerf, captive-bred specimen, loan of B. Langerwerf; Paris, Jardin des Plantes; R, Russia

Eurasian anguid lizard. It was selected as it represents a seemingly snake-like lizard, in its lack of obvious limbs and slender, sinusoidally curving trunk. Among the obvious differences between *Ophisaurus* and snakes appear to be the stout, elongate and muscular tail, the armouring of the trunk by a stiff cuirass of osteoderms combined with a lateral sulcus permitting change in diameter during breathing and, of course, the retention of a lacertilian head structure. The family, of which *Ophisaurus apodus* is the largest member, represents one type of adaptation to the limbless condition. Finally, this species appeared of interest for study, as a recent paper (Frey, 1982) had proposed that it utilized a novel and to us perplexing method of burrowing.

Materials and methods

The locomotor studies are based upon observations with 8 specimens from Yugoslavia and one from the USSR. All but one were initially obtained from commercial dealers; the exception was born in captivity and raised and kindly loaned by Mr Bert Langerwerf; 2 specimens were loaned from the collections, respectively, of the Royal Zoological Society of Antwerp and the Jardin des Plantes, Paris. Table I lists the dimensions and source of the specimens and the individuals for which locomotor sequences were digitized; however, as the members of the series showed no apparent intraspecific differences they are not otherwise identified in the results. Table II lists coefficients of static and sliding friction determined from the values on Pesola scales with which 2 anaesthetized specimens were pulled head first and tail first across several of the substrata used.

All of the animals were given a standard series of locomotor tasks and were filmed while they were performing them. Cine records (16·5 50 ft reels) were taken with a tripod-mounted Braun Nizo 801 macro camera on Kodachrome S-8 K-40 film utilizing 2 1000W and 2000W photo lights. Initial analyses were by variable speed projection; images were later digitized as noted below. Whereas the initial room temperature was near 20 °C, the temperature of animals under the lights approached 30 °C; this modified their willingness to move, but did not affect either the locomotor patterns utilized or their frequency.

The animals were encouraged to move (and filmed simultaneously from above at angles near 70°) across 3 types of substrata: plane surfaces, fields of pins or nails and parallel-sided channels; motivation was effected both by touching the animals and by producing mild vibrations in the substratum. However, the animals were

TABLE II
Coefficients of friction for two specimens of *Ophisaurus*

Weight of specimen (g)	Type of friction	Substratum	Coefficient direction	
			Forward	Backward
53	Sliding	Plexiglas	0·32	0·38
53	Sliding	Plywood	0·31	0·35
53	Static	Fine sandpaper	—	0·73
53	Sliding		0·31	0·49
53	Sliding	Coarse sandpaper	0·31	0·49
490	Sliding	Plexiglas	0·30	0·35
490	Sliding	Plywood	0·39	0·48
490	Static	Fine sandpaper	—	0·49
490	Sliding		0·32	0·39
490	Sliding	Coarse sandpaper	0·29	—

not frightened to achieve 'maximum' rates of travel. The tasks selected for these horizontal substrata were those for which substantially different responses could be elicited; we also noted burrowing and climbing movements in 3-dimensional space. The sequence of trials was randomized for each animal, so that the records contain equal numbers of cases that started above and below particular optima. Repeated observations, not necessarily filmed, checked for improvement in the performance of particular specimens. In several cases, films were taken horizontally, to note contact zones and orientation within channels as well as to test the relative movement of the dorsal and ventral portions of the integumentary armour as the animal traversed a vertical step.

The plane surfaces varied in friction and contour. In decreasing order of magnitude, we tested locomotion across perspex, a tile floor that showed some irregularity at the joints, plywood, fine sandpaper and coarse sandpaper (the latter 2 surfaces prepared artificially by spreading liquid glue on the surface of boards and then applying sand of particular grain diameter). The peg arrays were formed on 1×1 m sheets of moderately smooth plywood with pins placed in rectangular arrays at spacings of 0.5, 1.0 and 2.0 cm and nails at spacings of 4.0 and 8.0 cm. The parallel-sided channels were formed of 3 mm perspex with the walls 4 cm high and bonded to a perspex plate at their base. The width of the free space was 0.5, 1.0, 2.0, 4.0 and 8.0 cm and each animal was tested for its capacity to travel along any channel width into which it could fit, as well as on the outside of the array (only a single resistance wall). A few specimens were tested on arrays of pegs placed into boards covered with high friction coatings.

Sample filmed images were digitized using a Honeywell Hipad digitizing pad coupled to an IBM AT computer with coprocessor, 20 Mb hard disk and turbo switch (12 MHz). Analysis was with a proprietary program utilizing a set of subroutines that generated nested sets of files. These could be displayed graphically, and analysed further or addressed to generate statistics.

Each film image was first corrected to change the length of displayed coordinates to real values. The position of the body was next noted and, using the particular mass distribution for the individual, was used to generate (and sometimes to plot) the position of centre of gravity. Also, the curvature of the trunk was reconstructed using a number of points (50 evenly spaced between snout and caudal tip, for the present analyses). The values corresponding to individual film frames were then combined to plot and calculate the path (as well as velocity and acceleration) of the centre of gravity and of any other points desired. The local curvature of the lizard's trunk and tail (expressed as $1/\text{radius}$ in cm) could be averaged (over any set of sequences) and plotted, thus testing for local differences. The SYSTAT program (version 2.1 c. 1985, Systat, Inc.) was used to generate statistics.

The 3 major locomotor patterns used by *Ophisaurus* are lateral undulation (serpentine of some authors), concertina and slide-pushing, the theoretical basis of which has been noted and illustrated in Gans (1984, 1985*b*). Lateral undulation involves propulsion by sliding push of curves of the trunk laterally against resistance sites. Concertina locomotion involves propulsion by static force transmission against fixed sites of the substratum. Slide-pushing involves propulsion by sliding contact of ventral zones of the body against a flat surface.

Results

Plane surfaces

Whenever *Ophisaurus* is placed on to a smooth surface, it pulls its trunk into an S-shaped set of curves. Slow movement across smooth surfaces may proceed by concertina movement; lizards extend the anterior portion of the trunk away from the posterior portion, which remains in fixed contact with the substratum. Only for coarse (high-friction) sand do the motor methods of the small specimens differ from those of larger ones by using some variant of lateral undulation. Small animals then utilize fixed portions of the rough substratum as force-transmission sites (*points d'appui*). The velocity of propulsion appears critical, as the resistance regions to which forces are

applied are relatively small, so that propulsion appears to require some balancing. As an animal begins to move more rapidly, one observes seeming slippage and repositioning of the sites across which forces are transmitted. This generates some uncertainty and the successive portions of the trunk do not trace out equal paths. Should the locomotion become still more rapid, one notes the transition to an intermittent, but seemingly tortuous, slide-pushing.

Slide-pushing

In more rapid movements across relatively smooth surfaces, for instance on tile floors, the animal uses slide-pushing, in which propulsive forces are generated via zones of sliding friction (Gans, 1984). The head is obviously depressed, the neck is often arched vertically and the snout presses against the substratum. After some such extension, the anterior region becomes almost stationary and the looped middle and posterior portions of the trunk rapidly slide their contact zones posteriorly, whereas the centre of gravity (as calculated from the digitizing program) progresses slowly and sometimes irregularly.

If stressed animals are cool, they tend to essay short slide-pushing sequences across smooth surfaces. In such progression, slow undulant curves pass from neck to caudal tip without eliciting

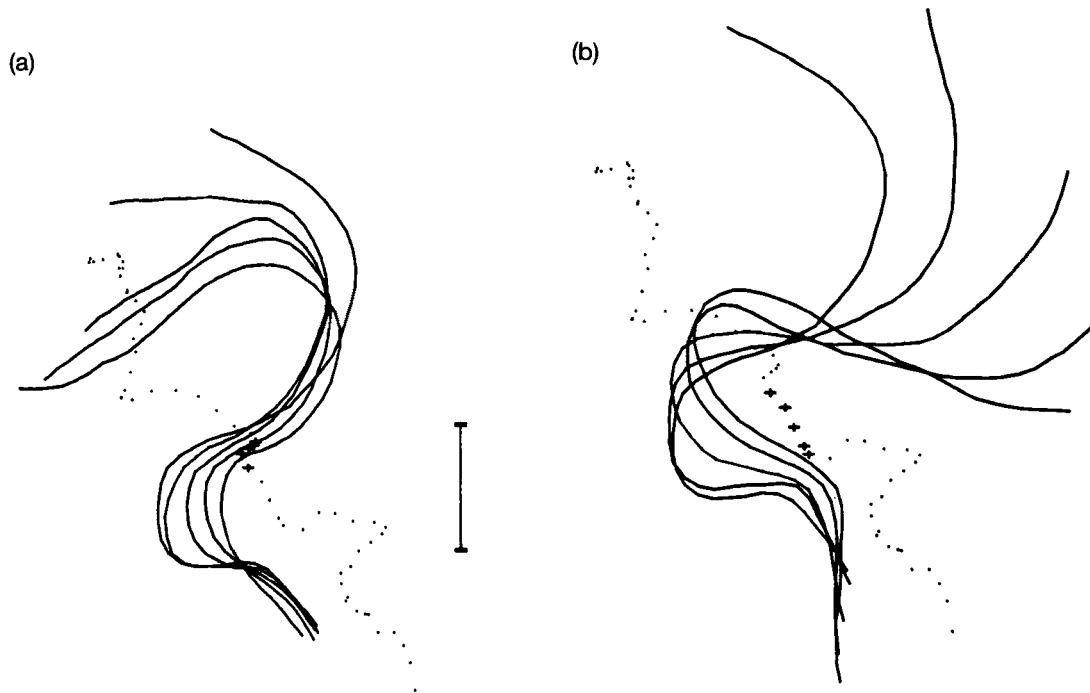


FIG. 1. *Ophisaurus apodus*. (Total length of specimen 756 mm.) Computer corrected sequence showing stages of slide-pushing by wide swings of the tail with the animal travelling slightly diagonally from the top to the bottom of the figure. The sliding friction of the rapidly moving portion generates propulsive contact for intermittent acceleration. The dots show the centre of gravity of the animal for every fifth film frame including the entire sequence and the small crosses show it for the positions traced here. Scale bar equals 100 mm. (a) The tail is thrown away from the centre of gravity. (b) The tail approaches the centre of gravity.

significant progression; the movement of the curve formed in the posterior portion of the animal suddenly accelerates, shifting posteriorly relative to the centre of gravity. This sudden acceleration of the posterior waves jerkily propels the head and anterior trunk for a short distance. As the animals warm up, and whenever they are not fatigued, they tend to fuse such intermittent accelerational waves and achieve continuous propulsion using slide-pushing.

Minor discontinuities of the substratum remain important and affect both the forward slippage of the head and neck and the reaction to the slippage of the posterior portion of the animal. The 'posteriorly' directed undulatory waves proceed asymmetrically; lateral views show the ventral contact occurring alternately on either the left or the right side of the posterior face of the loops, but never on both simultaneously. The portion in posteriorly sliding contact tends to be torsionally rotated (by perhaps 10°) about the long axis of the animal.

The horizontal films document that the animals generate this contact by selectively pushing portions of their trunk against the ground. Only the zone in the extreme posterolateral position of one side is in sliding contact with the ground; the remainder of the trunk is lifted. This concentrates the weight-induced forces to contact zones and keeps the remainder of the posterior portions out of contact. Only if the intermittent, posteriorly directed sliding movements are vigorous do they produce forward slippage and displace the head and anterior portion of the body.

The computer analysis shows the propulsive slide-pushing sequences to be more complex than previously assumed. The animal may slide either the more terminal portions (mainly the tail) or the anterior and middle portion of the body. In the first movement, the anterior portion of the body is

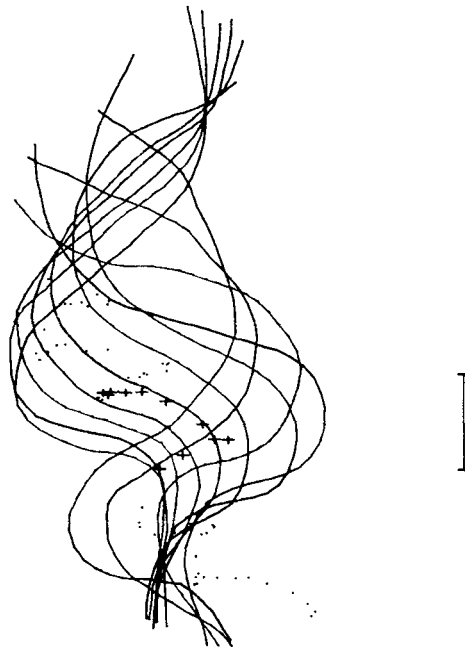


FIG. 2. *Ophisaurus apodus*. (Total length of specimen 910 mm.) Computer corrected sequence showing stages of slide-pushing contact zones on the middle of the body with the animal travelling slightly diagonally from the top to the bottom of the figure. The sliding friction of the rapidly moving portion shifts the centre of gravity first to the left and then to the right of the path. Every fifth frame is plotted. Scale bar equals 100 mm. Other conventions as in Fig. 1.

narrowly curved and slides anteriorly, whereas the posterior portion swings through wide curves, first in one direction and then the reverse. The downward deflection of the trunk generates a zone of contact at ever more posteriorly placed sites on the quickly swinging trunk, so that their sliding friction generates propulsion (Fig. 1). In the second variant, a contact zone begins its posterior travel much further anteriorly, near the 15th percentile of the body, and maximum displacement is achieved near the 40th percentile. By the time the bend has progressed halfway down the lizard, a new contact zone forms on the opposite site of the next curve so that one ordinarily sees posterior travel by two spatially displaced alternating contact zones. In trunk slide-pushing, the curvature extends well on to the tail; it differs from the tail-swing slide-pushing in that the amplitude of curves does not increase caudally (Fig. 2).

The path of the centre of gravity oscillates with an amplitude of approximately 25% the wave length (Fig. 3). This reflects the alternation of phases during which the head advances and those during which various parts of the body are swept posterolaterally.

The quantitative analysis shows major differences in the relative displacement of parts of the body. The maximum velocity of the centre of gravity was 13 cm/s, whereas its mean was only 7 cm/s. Some sites, for instance those between 70 and 100% of the total length, are displaced two to five times as much as the centre of gravity in the tail-swing mode, whereas an excess travel of two and a half times that of the centre of gravity occurred for the middle of an animal travelling by the second mode.

Comparison of the velocity of the centre of gravity with the velocity of the waves of sliding contact (contraction travelling along the body) shows that the latter move 65% faster than the former. Hence, at least 65% of the kinetic energy expended in generating the waves of contraction

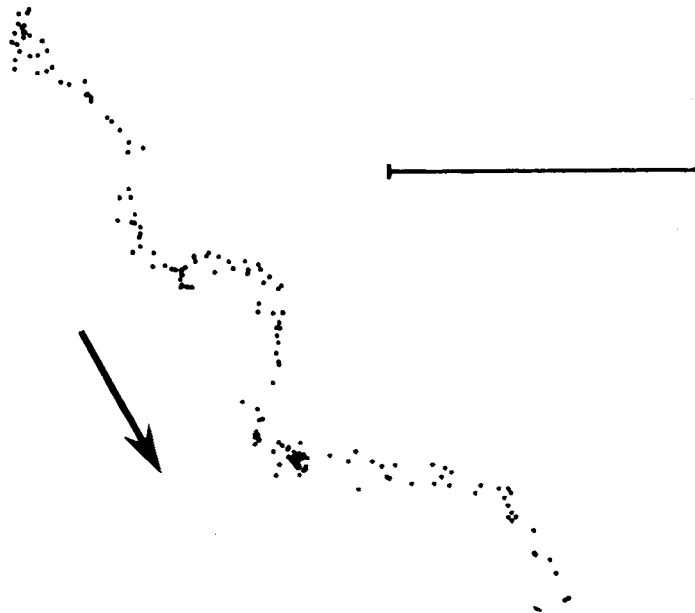


FIG. 3. *Ophisaurus apodus*. (Total length of specimen 567 mm.) Computer mapping of slide-pushing sequence consisting of 3490 frames with every 20th frame plotted. Path of centre of gravity to show three propulsive cycles with the animal travelling slightly diagonally from the left top to the bottom of the figure (see arrow). Scale bar equals 100 mm.

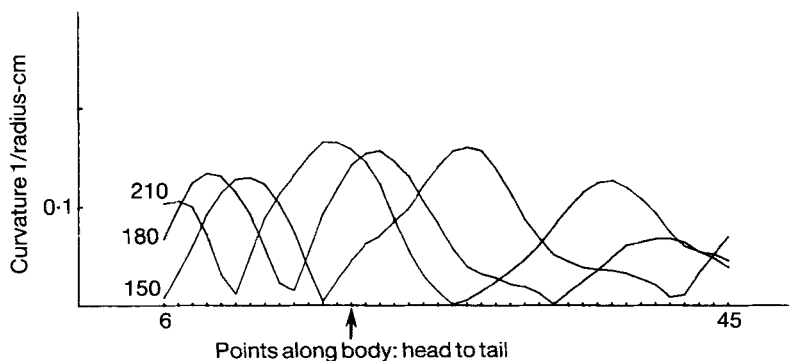


FIG. 4. *Ophisaurus apodus*. (Total length of specimen 910 mm.) Computer mapping of three frames from a slide-pushing sequence showing instantaneous curvature along the trunk averaged during a continuous sequence of slide-pushing with wide swings of the tail. The abscissa shows the total length of the animal subdivided into 50 equidistant points. The vertical arrow shows the level of the cloaca. The ordinate gives the radius of curvature calculated for sets of five points along the animal. The waves passing along the dorsal surface increase in velocity (not amplitude) as they pass the middle of the body. The numbers list plotted frames of the film with the intervals of the curves being 30 frames.

is lost and does not contribute to acceleration of the centre of gravity. Whereas in slide-pushing the lizards form S-curves, which cross the path traced by their centre of gravity, these curves are asymmetrical and not regularly sinusoidal (Fig. 4). The length of the waves varies between 30 and 40% of that of the body.

Fields of pegs

Animals that traverse fields of pegs contact relatively few of these; the number and kind of these sites of contact are affected by the peg spacing, the mass and velocity of the animal and the roughness of the surface into which the pegs have been placed. During lateral undulation the centre of gravity essentially traces a straight line (Fig. 5).

Peg spacing appears to impose two kinds of constraints. At the wide end (> 8 cm), most of our specimens contact an insufficient number of *points d'appui* to let them maintain the major requirement of undulant locomotion, namely that each portion of the trunk should retrace the path of more anterior portions. In rapid movements, the waves instead sweep backward and achieve propulsion due to reaction from whatever pins they happen to contact. For much slower travel, specimens tend to traverse grids of wider spacing by slight modification of the path of the body every time the head reaches out to a new contact site; instead of providing a single linear track, successive positions show deformation of this path (and shift in the direction of force vectors) along the peaks of the waves.

Even during traverse of 4 cm grids (which represented seemingly the best for all but the largest size specimen here tested), the animals have little need to apply forces continuously along their trunk; instead, forces are often applied at a single contact loop, and the animals slide their body through this position. Apparently, the low friction surface reduces the force required to propel the trunk (Table II). As the first loop reaches the tail, a new one forms near the head. The lizards then drag the posterior portion of the body and stem the anterior one. The path of the body is not regularly sinusoidal, but meets the criteria of regular lateral undulation. Whereas we did not complete quantification of the effect, we gained the impression that lizards moving from a peg array on smooth plywood to one set on sandpaper utilized more *points d'appui*.

More contact points are utilized to start than to maintain motion. This is particularly obvious at

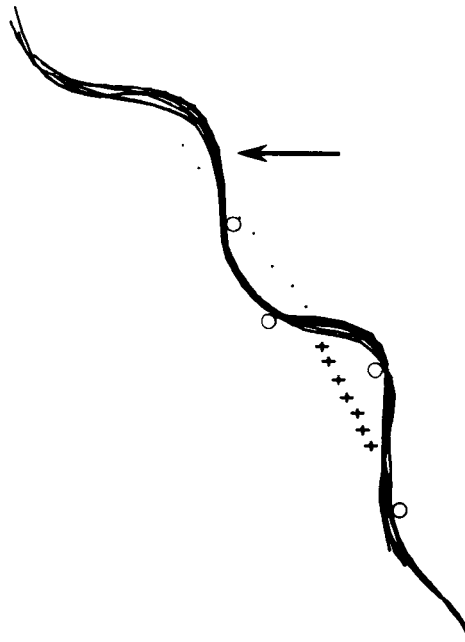


FIG. 5. *Ophisaurus apodus*. (Total length of specimen 567 mm.) Computer mapping of sequence with animal travelling diagonally by lateral undulation in a grid of nails from bottom to top of figure. The arrow indicates the position of the change between an 8 cm nail spacing (top) and a 4 cm spacing (bottom). The circles show nails against which the animal was obviously pushing during the sequence. The slight displacements of the path indicate minor repositioning of the contact sites.

transition sites among pin spacings and whenever the field of pegs ends and a smooth surface begins. The caudal end may then be seen to push by itself, and one transition of movement becomes obvious just at the moment at which the caudal tip of an *Ophisaurus* loses contact with the final peg of an array. The caudal tip often overshoots, suggesting that it was transmitting forces until contact was lost (Fig. 6).

Whenever the head of the animal reaches a new contact site, the centre of gravity accelerates (Fig. 7). For narrower peg spacing, the curves of the body are established initially by the path of the head; the fixed pins keep the track from being modified significantly thereafter. For very narrow peg spacing, the diameter of the animal tends to be limiting. Indeed, *Ophisaurus* tends to lift the snout whenever it is traversing extremely narrow spacings (see remarks below on burrowing). The lifting of the head reduces its turning radius. The skull and head joint must be able to shift among the pegs and their composite length and anatomical flexibility represent limiting conditions for turning. The array further constrains the direction of motion as the animal must travel parallel or diagonally to the rows of pins.

Velocity values recorded for points on the body were 15 to 70 cm/s for lizards in regular undulation. The velocity shows a good correlation with the frequency of propulsive waves (Fig. 8); that with the frequency times body length is slightly better, although body lengths (or mass) themselves show no obvious correlation with velocity. The velocities documented by us are voluntary and clearly non-maximum. Comparison of the displacements (or velocities) of the centre of gravity with those of the body along the track shows that the latter exceed the value of the former by 20%. This suggests a ratio of kinetic energy conversion three times better than achieved in slide-pushing.



FIG. 6. *Ophisaurus apodus*. (Total length of specimens: (a) 567 mm; (b) 756 mm.) Computer mapping of lateral undulation sequence with animal travelling diagonally from right top to bottom of figure. The arrow indicates the position of the change between an 8 cm nail spacing (top) and a 4 cm spacing (bottom). The circles show nails against which the animal was obviously pushing during the sequence. Note the displacements of the path which indicate repositioning of the contact sites (a). In each sequence, the tail accelerated briefly as it lost contact with one of the pins on 8 cm spacing, thus indicating that it was exerting forces. All frames are shown.

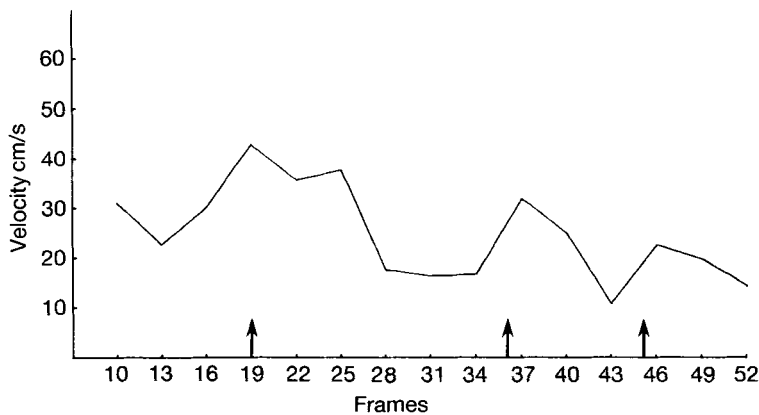


FIG. 7. *Ophisaurus apodus*. (Total length of specimen 567 mm.) Computer mapping of velocity of the centre of gravity throughout a sequence during which the animal was undulating through a 4 cm grid. The velocity peaks (arrows) correspond to instances at which the head of the animal had just contacted and was beginning to push against a new peg in the array.

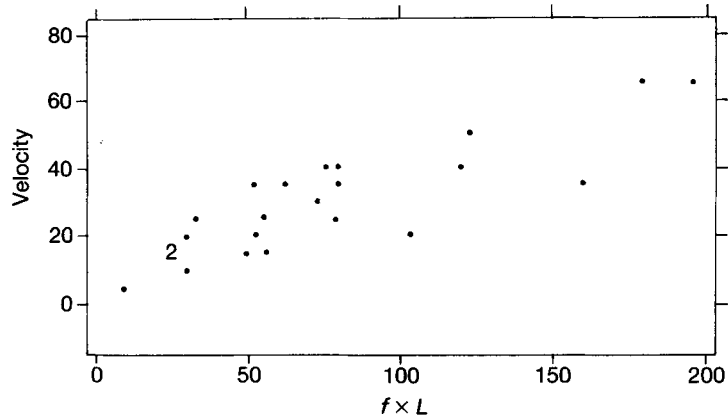


FIG. 8. *Ophisaurus apodus*. Computer-generated plot of velocity (v) versus frequency of propulsive waves (f) times the total length of specimens (L) for all digitized sequences of lateral undulation at a steady rate. The statistics for the relation are $N: 23$, $v = 7.4 + 0.28 f \bullet L$, standard error for y intercept = 3.2, standard error for slope = 0.036.

Parallel-sided channels

Parallel-sided channels are traversed only by variants of concertina movement. Gray's rule (1946) that lateral undulation cannot generate progression in such a setting still applies. *Ophisaurus* is relatively ineffective in its generation of concertina propulsion and seems limited by the kinds of waves it generates.

The most important generalization of bend formation in this species is that the bend always starts with fixation of the head. The head is bent laterally relative to the anterior axis of the trunk; indeed it is as if the animal starts by attempting to burrow laterally into the side of the channel. If the channel is sufficiently narrow for the bent head joint to contact the opposite side of the channel, the trunk recurves sharply and bends through more than 90° , with the next posterior contact being on the side against which the snout is pushing. The formation of tight alternating concertina coils continues posteriorly along the trunk, sometimes until even the caudal tip has been laid into bends. Slight pushing movements (by the experimenters) indicate that the observed curves are pressed outward, generating frictional interaction and fixing the trunk in place. The net effect is an anterior shift of the centre of gravity of the animal along the length of the channel. If the animal is entering the channel from a smooth surface, one sees the transition, with concertina bends anteriorly and posterior slide-pushing swings that intermittently drive the trunk into the channel (Fig. 9).

Next, the trunk is straightened, which tends to start in the region of the head. As long as the posterior portion of the trunk remains fixed in tight curves, the centre of gravity of the animal gradually shifts along the channel (Fig. 10). Whenever the animal attempts to move very rapidly, one sees that the straightening affects more than the anteriormost portion; the 'extension' of the head actually propels the more posterior (and still curved) portion posteriorly and the overall centre of gravity shifts little if at all. Clearly, more is involved than curve formation; in the latter case, relaxation of the posterior curves has preceded the anterior straightening. They are no longer pressed against the walls of the channel; consequently, repeated cycles show little progression.

Concertina progression is strongly dependent on channel width. Although the trunk is stiffly

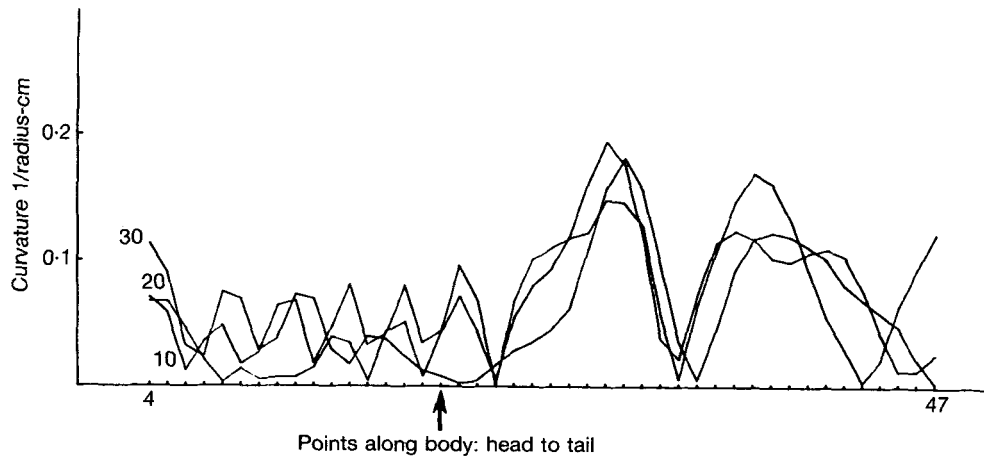


FIG. 9. *Ophisaurus apodus*. (Total length of specimen 982 mm.) Computer mapping of rectified curvatures during penetration of a 4 cm-wide channel. The abscissa shows the total length of the animal subdivided into 50 equidistant points. The vertical arrow shows the level of the cloaca. The ordinate gives the radius of curvature calculated for sets of three points along the animal. The anterior portion is progressing by concertina, the posterior by slide-pushing on the smooth perspex surface. The intervals of the curves are 10 frames. For frame 10 the anterior part is wedged into place, whereas the tail is sweeping broadly. In frame 20, the anterior part of the trunk has been extended. In frame 30, the anterior part of the trunk forms a new set of curves.

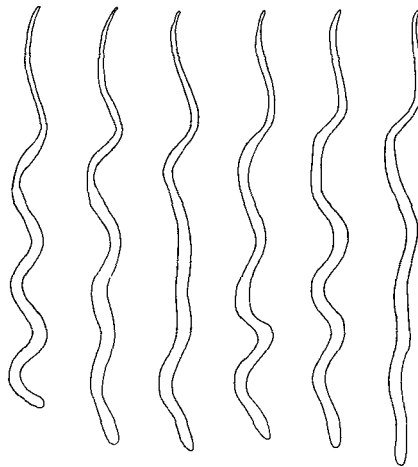


FIG. 10. *Ophisaurus apodus*. Reconstruction of a concertina-movement sequence during which the animal slowly shifted down a 4 cm-wide (approx. $2.5 \times$ body diameter) tunnel. The intervals are 12 frames, indicating a velocity of 2.8 cm/s.

armoured, *Ophisaurus* effectively traverse the narrowest channels, those that barely exceed their diameter. There seems to be no lower limit for the radius of bends; instead, the lower limit is due to bends that must be too shallow to exert effective lateral forces against the walls of a wide channel. Most specimens (in the size range of our experiments) do best for channel widths near 4 cm; in

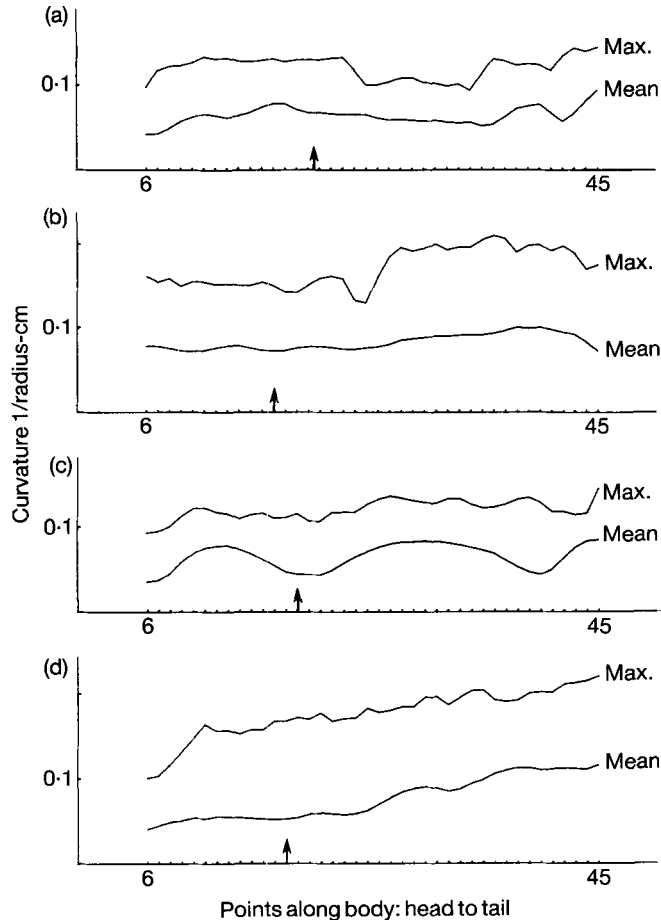


FIG. 11. *Ophisaurus apodus*. Summary of the mean and maximum rectified curvatures (bottom line, mean; top line, maximum value) achieved by portions of the body as specimens move by lateral undulation in various patterns. The vertical arrow shows the level of the cloaca. (a) A specimen of 1025 mm body length moving through a field of pins on 40 mm spacing at a velocity (of its centre of gravity) of 2.5 cm/s. Summary for 330 frames. Note that the curvature is relatively steady along the trunk, only the last 30% of the tail showing increased amplitude. (b) A specimen of 756 mm body length moving through a field of pins on 80 to 40 mm spacing at a velocity (of its centre of gravity) of 60 cm/s. Summary for 26 frames. Note the steady curvature along the trunk. (c) A specimen of 910 mm body length moving through a field of pins on 80, then 40 mm spacing at a velocity (of its centre of gravity) of 20 cm/s. Summary for 70 frames. Locomotion involved very pronounced repositioning, which does not seem to have affected all parts of the trunk equally. (d) A specimen of 530 mm body length moving through a field of pins on 40 mm spacing at a velocity (of its centre of gravity) of 22 cm/s. Summary for 60 frames. Note that the waves pass regularly down the trunk and tail but that the amplitude increases, mainly on the caudal region. The modification of the path involves some caudal repositioning.

order to contact the walls of the 8 cm channels, the animals seemingly must form curves with radii greater than those ordinarily formed (or alternate curved and straight sections). Thus, one sees fixation of the anterior portion of the trunk with its posterior portion forming S-curves matched to the 4 cm width and hence not touching the walls of the channel. (The latter phenomenon does not reflect previous 'experience' with narrow channels; it was also noted in those tests which proceeded in descending order of channel width.)

In wide channels, the animals initially address (interact with) a single wall and then move their neck and anterior trunk until it (accidentally) contacts the opposite wall. The animals next bring the trunk about to contact the first surface; this tripod of support then is used to pull up the posterior portion, although (as noted above), this concertina movement proceeds ineffectively and

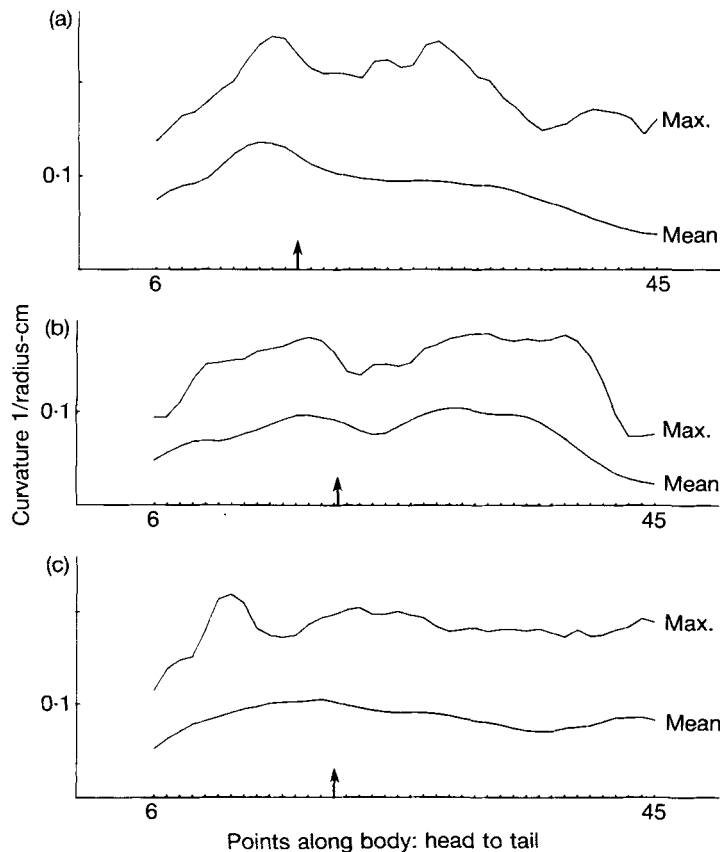


FIG. 12. *Ophisaurus apodus*. Summary of the mean and maximum rectified curvatures (bottom line, mean; top line, maximum value) achieved by portions of the body as specimens move by slide-pushing. The vertical arrow shows the level of the cloaca. (a) Plot of a specimen of 756 mm body length moving over a smooth surface by tail-swing slide-pushing at a velocity (of its centre of gravity) of 7 cm/s. Summary for 300 frames. (b) A specimen of 1025 mm body length moving over a smooth surface by body-swing slide-pushing at a velocity (of its centre of gravity) of 2.5 cm/s. Summary for 275 frames. (c) A specimen of 910 mm body length moving over a smooth surface by body-swing slide-pushing at a velocity (of its centre of gravity) of 5 cm/s. Summary for 580 frames. Note the absence of any change of curvature near the cloacal region.

contact here is irregular. At least two (better three) portions of the body must contact the wall in order to allow the anterior portion to be extended and the centre of gravity shifted anteriorly. Only medium to large-sized animals can propel themselves through 8 cm channels. It should be emphasized that the newly fixed anterior end can also pull up the posterior portion by forming continuous curves. This is an alternative to maintenance of the general shape of the anterior and posterior regions, alternately relaxing and fixing their contact zones and propelling the animal by alternately extending and curving the intermediate trunk (as seen in *Typhlops*).

Concertina progression is very slow, with velocities of near 2–3 cm/s. We have too few recordings of the entire animal (rather than only part of it) occupying a channel to compare the velocity of the centre of gravity with the summed velocity of all parts of the body. However, the available values suggest that the effectiveness is better than for slide-pushing, but worse than for lateral undulation.

Curvatures of the body

Locomoting *Ophisaurus apodus* do not display a simple distinction between the bends formed by trunk and tail. Curves pass from one to the other without change in amplitude, nor does one see either moving independently. Hence, it is impossible to predict the position of the cloaca from any of the graphs (Fig. 11).

The passage of curves along the trunk is constant for steady traverse of peg arrangements by lateral undulation. However, repositioning of particular resistance points and readjustment of the curves here introduces irregularities (Fig. 11). Nodes seem to form, suggesting that the animals have a tendency to limit the curvature of particular portions of the trunk.

The wide swings seen in slide-pushing show a markedly different pattern in that displacement of the head region is very much less than that of the posterior trunk. Also, specific sites of the trunk show concentrated bends, whereas other zones have very regular curvature (Fig. 12). In specimens travelling by tail-swing slide-pushing, one sees a sharply concentrated zone of anterior bending (Fig. 12a); those with midbody bending show much more regular curves without local peaks.

Vertical movements

When observed in the open (and the field: Ribeyrol & Gasc, 1971), *Ophisaurus* commonly lift the head and neck and look about rather than gliding along with the mandible close to the surface. They also climb bushes. Whenever they engage in slide-pushing and similar movements, they tend to press the head against the substratum; indeed, they seem actively to push the anterior region against the ground. Laterally directed films show that short sections of the ventral surface are then depressed and thereafter lifted rapidly out of contact with the ground, independent of the more dorsal armour which acts like a cantilevered support element. However, lateral films of specimens bearing vertical paint stripes showed no evidence of significant antero-posterior displacement of the dorsal versus the ventral armour.

The lizards apparently can lift and depress local portions of the ventral surface. This lets them determine the sites of transmission of forces in slide-pushing; the vertebral column itself does not have to curve vertically. Anatomical studies (Gasc, 1981) suggest that contraction of successive bundles of the *M. obliquus externus subcutaneous* might lift the ventral surface. These bundles originate from the ribs and insert on the edges of the rictal boss; they can provide local elevation, but not pro- or retraction, hence the mechanism of depression remains to be studied.

Discussion

General

Each of the tasks given these animals proves to be artificial in that it tests the capacity for dealing with one restricted aspect taken out of the context of the overall environment in which it is unlikely to appear in this form. However, the artificiality represents an advantage in that it presumably transcends differential experience within the population and permits us to establish their capacity for dealing with a physically defined task. As the physics of the system determined the tasks, it seemed appropriate to modify each of them by changing their dimensions through a range that likely included those most effectively traversed by the animals.

Effectiveness of traverse may, of course, be estimated in several ways. We here define it by minimum standards, namely by the capacity of a lizard to move at a more or less uniform rate along a selected path. This study tests mechanism and co-ordination; it sets aside for future study the velocity attainable, the capacity to change velocity (and sometimes direction) and the energetic cost of the travel. The idea of using minimum standards reflects a first level of mechanical effectiveness and directly relates to degree of morphological specialization. Most important is that the 'optimal' conditions being established differ among species (Gasc & Gans, In prep.). This difference permits comparison of the conditions observed in each, and their correlation with structural and ecological differences.

The force required

Standardized diagrams generally illustrate the forces exerted by each curve of a regularly undulating animal as being equal. Departures from this regularity, such as those seen in the illustrations of Gray (1946), tend to be interpreted as noise and ignored. The observations in the present experiment (and others of this series) indicate that this generalization may be inappropriate. Repeatedly we saw animals that formed a single loop (in a field of pegs) and then passed the entire trunk through this, pushing only here and not establishing other *points d'appui*. Also, animals that were leaving a field of pegs to enter a smooth surface would push the distal tip of their tail against resisting sites, exerting forces as long as the surfaces remained in contact. Clearly, the forces exerted at a single contact site were sufficient to overcome the sliding friction incurred by the entire animal. (The possibility of this is, of course, also indicated in the figure by Gray & Lissmann, 1950, which shows a moving snake bending against a single peg, in what is clearly not lateral undulation. See also Gasc *et al.*, 1989.)

These observations confirm that *Ophisaurus* has independent options for undulatory curve formation. The anterior portion of the body does have to be stiffened, either by use of its internal musculature or by using the pin array to keep it from deflecting laterally (i.e. to keep it from long column deflection). A reduced number of propulsion sites has the benefit of reducing the laterally directed force vectors, the magnitude of which rises with the number of *points d'appui* which the animal utilizes; it would be interesting to see how this translates into energetics. As lizards pass very narrowly spaced arrays of pegs by travelling for long distances in a straight line and only then turning, it may be that multiple turns may impose other costs, such as requirements for more complex co-ordination.

Rules of undulation

The computer analysis of lateral undulatory sequences shows that the path of the centre of gravity traces an almost straight line; this line shows minimal deviations, even during traverse of wider-than-optimum spacings in which the body shows lateral adjustments whenever the head and neck reach for new contact sites. For steady travel, the velocity of points on the animals should be constant from head to tail; however, the overall rate of travel often shows some variable irregularity. This variability becomes obvious, for instance in curves of the acceleration with time of any point on the lizard.

Even more obvious irregularities are produced whenever the animal starts to move, as the path travelled by the body then changes, and only reaches a constant curvature once the animal moves at a steady velocity. Whereas, in steady travel, the velocity of the centre of gravity will be the same as that of the waves in the body, the centre may temporarily travel at a slightly lower (70–90%) velocity during acceleration bouts (and also whenever the curved path is being adjusted).

Lateral undulation differs, for instance from undulant swimming, in that each point of the animal almost exactly retraces the path of the preceding one (Gray, 1946; Daan & Beltermann, 1968). As the bends of the body are independent of site, the graphs of mean (and maximum) curvature along the trunk show more or less steady values (Fig 11a, b).

Whereas specimens of *Ophisaurus* do traverse a wide range of peg spacings, their traverse of the more widely spaced arrays significantly departs from the above generalization. The curves change locally by repositioning as new points are contacted by the neck and the tail loses contact with posterior ones. The changes in the curvature during repositioning of contact sites may occur preferentially at particular sites of the trunk, in which case the passage of waves along the trunk is not constant but shows nodes (Fig. 11c, d).

The phenomenon described is clearly length-dependent. As the animal enters wider spacings, the number of pegs that it may contact decreases. Theoretically, the path may be maintained for as few as four contact sites; actually, transitions are then associated with significant shifts in the shape of the coils and, in particular, of the angle at which the body contacts the pegs. Most important is that the undulant movement appears opportunistic and slight rearrangements of body position are common. That more is involved than mere curving of the trunk to a standard pattern is seen in cases in which the animal starts to back up along the path; all force transmission sites shift in anticipation of the reversal.

The observations on undulation also support the concept that in this species the trunk and tail act as a single unit. Waves pass smoothly past the cloacal region and the tail participates in the application of forces. This is of obvious importance in the transit of wide spacings and wide channels.

Slide-pushing

Slide-pushing was first described as a distinct motor entity only five years ago and appeared to pertain to the movement of some snakes on special substrata (Gans, 1984). The present observations indicate that it is a common locomotor pattern for *Ophisaurus* which resort to it routinely. Also, the capacity to depress the ventral surface in order to generate sliding contact suggests that slide-pushing is more than an incidental propulsive device. As the most rapid movement in this motor pattern occurs in the tail, it may also be advantageous in view of the well-known proclivity of predators for concentrating on fast-moving parts of their prey (Arnold, 1987).

As interesting is the result of the kinematic analysis, which documents that slide-pushing is a specific, well definable and regular motor sequence. Whereas the path of the centre of gravity is cusped rather than rectilinear, the propulsive phases succeed each other in a regular sequence and the occurrence of two variants of the pattern (Fig. 12) suggests it should be searched for in other species as well.

The pattern is clearly less effective and possibly less efficient than lateral undulation, and probably concertina movement. However, it allows these lizards easily and fairly rapidly to traverse plane surfaces that might otherwise impose barriers to their distribution. It would be interesting to test for the extent to which such locomotor patterns are actually used by freely ranging animals. In the absence of such time budgets it remains possible to speculate that in this case the energetic efficiency of a rare behaviour may be less significant than the general capacity of rapidly crossing open areas on which predation might represent a major risk.

Concertina patterns

Ophisaurus can traverse parallel-sided tunnels and does so relatively effectively. However, the method used is quite simple. The head tends to wedge in order to start the tight coils. Also the entire trunk is curved each time, being pulled up and curved up to and beyond the level at which the bends make lateral contact. There seems to be little local control and we never saw three-site contact zones formed by the front and rear of the animal to be alternately slid anteriorly, as can be seen in many snakes and reported for *Anguis* (Gasc & Gans, 1988).

Ecological implications

The general impression is that *Ophisaurus* is an active forager, able rapidly to traverse open areas, to climb moderately well and to burrow in litter and possibly in poorly compacted soils. Personal observations (in Bulgaria during 1970 by JPG) indicate that the animals there occur in open rocky pasture and escape across the surface and by climbing into bushes. It would seem worthwhile to establish their activity rhythm and to compare this with that of such species as *Anguis*.

Incidental observations indicate that *Ophisaurus* climbs effectively in bushes and branches, although the spacing of possible contact regions (relative to the size of the animal) is important. Also, we noted repeated occasions in which the animals climbed out of channels, utilized shelter boxes to climb out of cages and balanced themselves across the tops of nails in tight spacing. This agrees with reports from the literature about climbing behaviour possibly associated with escape and predation (Ribeyrol & Gasc, 1971).

The experiments described in this paper document the capacity of *Ophisaurus* to move effectively over smooth surfaces and through fields of pegs. *Ophisaurus* are less effective in traversing straight-sided tunnels; however, their capacity of moving through tight grids of pins suggests that irregular tunnels can be passed with little difficulty.

The present report represents a continuation of earlier observations on Australian skinks and pygopodids (thus far published only in abstract: Gans & Greer, 1982; Gans, 1985a), as well as on some Indian scincid species (Gans, unpublished). *Ophisaurus* shows major differences from all Australian skinks thus far tested. For instance, it effectively traverses parallel-sided channels, which is impossible for the skinks. The significant differences thus documented in the locomotor patterns of limbless lizards suggest the utility of surveying the yet untested groups.

The report of Frey

Frey (1982; also Seilacher, 1982) published a surprising report about *Ophisaurus*, noting incorrectly that they burrow by sliding their dorsal and ventral armour relative to each other. The paper contains numerous misquotations, misstatements and errors. (The items in quotation marks on p. 217, by implication ascribed to Gans (1974), are not used by this author. The head of *Ophisaurus* is remarkably similar to that of other lizards and not 'either blunt or conical' (p. 217). The skull of *Ophisaurus* is hardly 'convergent to the amphisbaenids' (p. 221); indeed the head appears like that of any large lizard and the large eyes correctly suggest a diurnal habit.) Also, the functional interpretations in Frey appear based only on observations, unsupported by cinematography. Most critical for us is our inability to duplicate the putative burrowing habits and the relative shift of dorsal and ventral armour.

The report states (p. 220) that the animal can move the dorsal and ventral parts of the armour independently. This appears based upon the slight relative shift of the armour whenever the animal bends the head or rotates the body out of the horizontal plane. This is seen whenever the head is depressed into the soil and an animal uses the dorsal sweep to excavate a cavity. This excavation method (not a 'drilling' but a scraping which is also seen in many tetrapod teiids and lacertids) obviously requires some relative sliding of the portions of the armour. However, such displacement is imposed by the bending trunk rather than causing the trunk to bend. It also occurs whenever the animal crawls off the edge of a table (or rock). None of our manipulative experiments with anaesthetized lizards showed a significant capacity (< 1 mm) for relative shift of dorsal and ventral armour. It proved impossible to slide one versus the other in unanaesthetized animals. Hence, the described phenomenon does not appear to be real and the report had best be set aside.

This report is based upon studies carried out while CG was Professeur Associé au Laboratoire d'Anatomie Comparée du Muséum d'Histoire Naturelle, Paris, and was completed while JPG was Visiting Professor at The University of Michigan. The Menagerie du Jardin loaned one of the animals for the experiments. Grant NSF-G-BSR-850940 provided support for some of the analyses. We thank Dr Sabine Renous for assistance with the experiments and the manufacture of some test apparatus and are particularly grateful to Ms Jeannine de Vree for her help in transporting a series of animals from Antwerp. The initial analytical programs were written by Danny Meirte, Peter Aerts and W. van den Bergh in Belgium and modified by Bill Morgan in Ann Arbor, who also aided most significantly in the process of analysis while participating in the NSF program of Research Experience for Undergraduates.

REFERENCES

- Arnold, E. N. (1987). Caudal autotomy as a defense. In *Biology of the Reptilia* 16: 235–273. Gans, C. & Huey, R. B. (Eds). New York: A. R. Liss, Inc.
- Berger-Dell'Mour, H. A. E. (1985). The lizard genus *Tetradactylus*: a model case of an evolutionary process. In *Proceedings of the international symposium on African vertebrates: systematics, phylogeny and evolutionary ecology*: 495–510. Schuchmann, K. L. (Ed.). Bonn: Museum Alexander Koenig.
- Daan, S. & Beltermann, T. (1968). Lateral bending in locomotion of some lower tetrapods I and II. *Proc. K. ned. Akad. Wet. (C)* 71: 245–266.
- Frey, E. (1982). *Ophisaurus apodus* (Lacertilia. Anguidae)—a stemming digger? *Neues Jb. Geol. Paläont. Abh.* 164: 217–221.
- Gans, C. (1962). Terrestrial locomotion without limbs. *Am. Zool.* 2: 167–182.
- Gans, C. (1974). *Biomechanics: an approach to vertebrate biology*. Philadelphia: J. B. Lippincott. (Reprint. Univ. Michigan Press, 1980.)

- Gans, C. (1984). Slide-pushing—A transitional locomotor method of elongate squamates. *Symp. zool. Soc. Lond.* No. 52: 13–26.
- Gans, C. (1985a). Motor coordination factors in the transition from tetrapody to limblessness in lower vertebrates. *Semin. Ser. Soc. exp. Biol.* No. 24: 183–200.
- Gans, C. (1985b). Limbless locomotion—a current overview. *Fortschr. Zool.* **30**: 13–22.
- Gans, C. (1986). Locomotion of limbless vertebrates: pattern and evolution. *Herpetologica* **42**: 31–46.
- Gans, C. & Greer, A. (1982). Locomotor patterns in some crepuscular skinks of Australia. *Abstr. Meet. Soc. Stud. Amph. Rept.* **1982**: 72.
- Gasc, J.-P. (1967). Retentissement de l'adaptation à la locomotion apode sur le squelette des squamates. *Colloques Cent. natn. Rech. scient.* No. 163: 373–394.
- Gasc, J.-P. (1981). Axial musculature. In *Biology of the Reptilia* **11**: 355–435. Gans, C. & Parsons, T. S. (Eds). London: Academic Press.
- Gasc, J.-P. (1982). Le mécanisme du fouissage chez *Amphisbaena alba* (Amphisbaenidae, Squamata). *Vertebr. hung.* **21**: 147–155. [In French with English summary.]
- Gasc, J.-P. (1984). Analyse expérimentale du déplacement du saurien *Bachia cophias* (Schneider), microtéide à membres réduits. Un modèle simplifié de reptation par ondulations. *Amphibia Reptilia* **5**: 356–365.
- Gasc, J.-P., Cattaert, D., Chasserat, C. & Clarac, F. (1989). Propulsive action of a snake pushing against a single site: combined analysis. *J. Morph.* **201**: 315–329.
- Gasc, J.-P. & Gans, C. (1988). Comparison of the locomotor patterns of two anguid lizards. *Am. Zool.* **28**: 15A.
- Gasc, J.-P. & Gans, C. (In prep.). *Tests on the locomotion of the elongate and limbless reptile Anguis fragilis.*
- Gray, J. (1946). The mechanism of locomotion in snakes. *J. exp. Biol.* **23**: 101–120.
- Gray, J. E. & Lissmann, H. W. (1950). The kinetics of locomotion of the grass-snake (*Tropidonotus natrix*). *J. exp. Biol.* **26**: 354–367.
- Jayne, B. (1985). Swimming in constricting (*Elaphe g. guttata*) and nonconstricting (*Nerodia fasciata pictiventris*) colubrid snakes. *Copeia* **1985**: 195–208.
- Ribeyrol, M. & Gasc, J.-P. (1971). Le serpent en Bulgarie: connaissance populaire et connaissance scientifique. *Objets Mondes* **11**: 371–390.
- Seilacher, A. (1982). Introduction: burrowing strategies. *Neues Jb. Geol. Paläont. Abh.* **164**: 205–206.
- Tercafs, R. R. (1961). Observations sur la natation chez les reptiles. *Bull. Soc. r. Zool. Anvers* No. 20: 3–19.