APPROACHES TO THE EVOLUTION OF LIMBLESS LOCOMOTION

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Limblessness is a condition common among reptiles, but rare among endotherms. It provides an excellent working surface for evolutionary studies, as organismic diversity provides us with many intermediate stages. These are hardly the arrested stages on an ongoing process; however, the structural and behavioral diversity they display provide us with models of past evolutionary stages. This essay provides a summary of past and possibly ongoing studies in analyzing this system.

Introduction

This is a progress report of various studies of the locomotion of elongate squamates, amphisbaenians, snakes and lizards. However, it is not a detailed analysis of species sampled and experiments performed. Instead, the report includes a bit of random speculation about things that might be interesting to me and hopefully to this audience. It lets me ask some questions about issues that appear to deserve test by new techniques. Specifically it allows me to utilize a sequence of combined approaches, namely the use of experiments and the generation of scenarios. Help and cooperation in these studies were provided by Pieter Aerts, Eric S. Allen, W. Vanden Berge, Dave Carrier, Ann Creager, Jean-Pierre Gasc, Allen Greer, Christina Hinman, Hyung Kim, Jason Lazlo, Cecil Leonard, D. Meirte, Brad Moon, William K. Morgan, Henry Mushinsky, and Bradley Wylie; whereas many others donated animals.

Limblessness

There are more than a dozen independent situations in which members of a squamate lineage seem to have elongated their trunk and started to reduce their limbs. Such elongate and limb-reduced beasts are ubiquitous among the Lepidosauria. Fewer occur among the Amphibia and none in Aves. Among the mammals, elongation only occurs in aquatic groups, and a few small elongate insectivores, such as weasels. This scarcity of elongation in other groups leads to the question of why elongation has occurred so commonly among the Lepidosauria. Analysis has suggested that elongation occurs because it is

possible without major cost!

In lizards, limblessness is always preceded by elongation. Such elongation poses potential surface-volume problems for the transfer of heat, water and solutes. However, ectothermy permits elongation as a low cost option, as ectotherms can conform to their thermal environment. Their body temperatures may track those of the environment and they need not compensate for heat flow. The squamate integument, furthermore, is unlike that of amphibians in that it provides a barrier to water loss and allows solute maintenance. Elongation is hence an available option.

Granted that elongation was possible, one needs to establish its costs and advantages for the earliest elongate and limb-reduced beasts. Elongation allows animals to pass narrow crevices, either narrowly spaced surface vegetation or subterranean tunnels. Tunnel occupation is clearly advantageous, as the underground buffers flow of heat and moisture and tunnels furthermore limit predation. Indeed, stresses from heat and moisture only become critical whenever tunnel-adapted animals re-emerge onto the surface.

The Problems of Successful Emergence

Successful re-emergence, the transition from the underground to the surface, and the reverse may have occurred repeatedly in evolutionary time, and may have limited the specialization for the subterranean biotope. It posed various problems, mainly in overcoming the difficulties posed by slenderization. How could such organisms develop new systems, for instance, for feeding and locomotion after return to the surface?

The success of re-emergent animals would have to be measured in terms of further adaptive

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radiation after re-emergence. It demanded the use of a key adaptation, whatever it was. Likely, locomotion on the surface and in the soil is one of the key factors in the story of limblessness. Naturally the re-emergence was easiest whenever the limbless niche on the surface proved to be unoccupied.

Limbs generally lack advantage in crevices and in tunnels, whether self-made or invaded. Similarly, they are useless in clusters of tightly spaced vegetation. If they are swung, they widen the path that is required for the transit of the animal. Hence, limbs tend to be reduced and sometime lost in such environments. However, it may be that there is an advantage to the retention of reduced limbs, as long as a species does not become permanently associated with the crevice biotope!

However, only snakes and pygopodids show successful emergence, as defined by an adaptive radiation. Some anguids emerged, but without further radiation. Amphisbaenians remained below the surface. It is interesting that only the snakes, among once subterranean squamates, show the reorganization of the eye and optic cortex, which has been claimed to document past passage of a subterranean niche. Snakes also are unique in showing a complex radiation after emergence. Which subterranean specializations might explain the differential success after emergence of squamates to the surface?

Successful re-emergence may have been constrained by such specializations for subterranean survival as elongation, limb loss and associated characteristics. Alternatively, the limitation may have been due to aspects or mechanisms that have been required for surface survival? Answers to such questions requires a survey of burrowers, involving analysis of morphological specializations, of environmental patterns occupied and of behaviors associated therewith.

In evaluating adaptations, it is important to consider not just the beasts "best" from an engineering standpoint, but the many species showing much simpler, morphologically "intermediate" conditions. After all, such "intermediate" animals also survive and make a living. In general, adaptation is for sufficiency, not for perfection.

Adaptations for Burrowing

The fates of the major burrowing specialists are easiest to explain. These forms concentrated on tunnel widening and elongation, the former first. Furthermore, the true burrowers can generate tunnels by penetrating hard soils. The cost of tunnel formation increases with the tunnel diameter. Almost all such species have reshaped their skulls to form a penetrating wedge. Greatest modification is seen in three kinds of amphisbaenians and in the Indian shield-tailed snakes - the uropeltids.

Reformation of the head and skull for burrowing involves compromises. The semicircular canals must be spread to an extreme lateral width in order to achieve enhanced signal detection. Development of an anterior digging spade limits muscle packing and force application to the mandible. Two compensations are possible. Bite force enhancement requires shortening of the snout, which limits width of the gape. Alternatively, the burrower may concentrate on soft prey.

In amphisbaenians, the snout has become so modified that there appears to have been no effective return to the surface. Indeed, conflicts for methods of propulsion within some of the radiation blocked invasion of different types of soils. The emerging snakes and some pygopodids shifted to the flexible ingestion mechanisms that facilitated the swallowing of entire prey.

Elongation has other costs and requires other compromises beyond those restricted to the head. In South African skinks, the percentage of the midbody cross section devoted to the coelom decreases with increasing elongation and reduction of limbs, whereas section of muscle mass and vertebral column increases. However, the coelomic space must hold the food-filled gut as well as the oviduct and its embryos. Burrowing uropeltid snakes show modifications of head-and-neck for digging and further changes in the trunk muscles. Modern snakes show modified vertebrae, unique intervertebral joints and a reworking of the axial musculature into more complex networks and more elongate slips.

Limbless Locomotion

For the moment, let us look at the patterns of locomotion and their influence on mechanical design. Thirty years ago I encountered need to deal with the various kinds of limbless locomotion. Observation suggested that the four kinds of movement then proposed, namely lateral undulation, sidewinding, rectilinear movement and concertina, differed primarily in the use of friction by the animal (Gans, 1974). Undulation (and the later described "slide pushing", Gans, 1984) involved continuous slippage of the body past environmental contact sites. For progression by rectilinear locomotion, concertina movement, and sidewinding the animal established fixed, static

sites. Sidewinding (or less appropriately, crotaline movement; Gray 1968) was first described by Mosauer (1930) and discussed by Cowles (1956). Brain (1960) later proposed that sidewinding was a modified form of lateral undulation; however, Gans (1962) suggested the origin from concertina.

Various observations gradually suggested that snakes might not be useful models for early stages of limbless locomotion. The patterns observed were too derived, specialized and complex; they suggested that the animals clearly had encountered multiple changes. Thus, snakes show several ways of swimming, of climbing trees, of traversing branches of bushes and of crossing flat areas. These methods involve changes in the length-diameter ratio of the trunk, in its scale pattern, in trunk muscle arrangement and in muscular coordination.

In parallel, it became clear that the many species of elongate and reduced-limbed lizards differed in their locomotor capacities. They didn't just wriggle! I started to look at this situation in Australia where the local skinks showed multiple radiations. Each radiation included animals that lacked limbs; however, in some radiations, most species showed forelimb reduction, and in others the species showed hindlimb reduction. Some radiations included animals without any limbs.

Analysis of Limbless Locomotion

The key to the analysis was the recording of the locomotion of multiple species on similar substrates, and the correlation of the results with the detailed biotopes on which the animals were being captured. Initially I filmed species on boards with different coefficients of friction, then added arrays of nails at different spacings and channels with different widths and frictional coatings of the walls. We always furnished the animals with a range of tasks, i.e. channels with a width of 0.5 mm, 1.0 cm, 2.0 cm and 4.0 cm.

Although film was expensive, I soon generated too many movies to allow effective analysis. This suggested the merit of computerizing analysis. I began with the development of computer programs that allowed correction for the parallax obtained when filming at a non-normal angle. From these records I could calculate the center of gravity and curvature of the moving animal, as well as the path of any of its parts. Also, I could plot the various velocities, of points along the trunk, and from this calculate the kinetic energy involved in locomotion. The ratio of the sum of the kinetic energy of all particles of the swinging trunk to the kinetic energy calculated from the movement of the center of gravity offered a value that estimates the effectiveness of locomotion.

The analysis soon showed that the films that I had recorded represented an inadequate database. The analytical system demanded that the animals had to move through three to four continuous sequences before a repeatable sequence was obtained. Commonly the animals changed their direction during a propulsion sequence, often in reaction to events proceeding outside the field being filmed. This made the filming cost exorbitant. Happily, my current system lets me record and analyze sequences taken with home video cameras, which reduced the cost of recording to one twenty-fifth that of film.

Experimental Results

Problems.

The observations initially produced some clear examples of misleading effects due to preconceived notions. I had expected all lizards to be able to engage in lateral undulation and tunnel concertina. Consequently, I refused to accept that reduced-limbed skinks could do neither, indeed that the lizards seemed unable to use any of the four initially described types of snake locomotion, although some lizards did use a variant of slide-pushing. These observations made the interpretation of the results very frustrating.

There clearly was a need for less biased observations. I had to record the actual movements performed by the animals and to ask whether these permitted any generalizations. Several conclusions derived from the initial analyses.

Elongate skinks show two functional patterns. Each occurs multiple times. First are animals inhabiting a subterranean substrate that is irregular, mainly soils filled with rocks and roots. Secondly are animals inhabiting a subterranean substrate that is homogeneous, mainly consisting of loose sands. The lines representing these characteristic patterns differ in limb reduction, functional morphology and control.

The Irregular/Continuous Conflict

The issue of limb reduction is complicated by the potential differential reduction of the body diameter, limb size and the two girdle pairs. Animals in continuous substrates always reduce the forelimbs before the hindlimbs and might even increase the length of the hindlimbs; however, the limbs commonly are slender. In contrast, the animals occupying irregular substrates always reduce their hindlimbs before the forelimbs. Also, they display less of a tendency to slenderize the limb rather than to shorten them.

Animals burrowing in continuous substrates tend

to produce tunnels of regular diameter that swing in wide amplitude. During underground travel both pairs of limbs are adpressed to the body, and propulsion is from the wide curves of the trunk acting against the sand. During entry into the soil, the spread limbs provide a wide base that allows the head and anterior trunk to penetrate the sand.

Animals burrowing in irregular substrates tend to produce irregularly curved tunnels, often of varying amplitude. During underground travel, the hindlimbs are adpressed to the body; however, the forelimbs may aid in positioning the penetrating head, keeping it from lateral deflection. They similarly direct the aspect of the head in initial penetration.

Functional morphology of animals in continuous substrates indicates synchronization of head direction with hindfoot placement and consequently resistance to posterior slippage. The head needs first to be driven horizontally and then shifted or oscillated at a right angle to this, thus widening the tunnel. Animals in irregular substrates use their forelimbs to position the head in order to avoid sites that cannot be penetrated.

Animals entering continuous substrates likely retain the original locomotor coordination or control sequence. For animals in irregular substrates, there tends to be a new search strategy that samples and responds to subsoil resistance. Also, coordination must have been modified with bodily elongation and reduction of limbs. In both cases, there is the need for steering the underground path. The evolutionary source of the two strategies remains to be determined.

Passage of Parallel-sided Tunnels

A surprising observation was that none of the Australian skinks could employ tunnel concertina; thus, they could not traverse parallel-sided tunnels. This is in spite of the fact that this method is used by all snakes, amphisbaenians, caecilians, and some pygopodid lizards.

The absence of concertina clearly represents an issue of control and coordination rather than mechanical capacity. The various skinks can and do bend their trunk into curves that are adequate for concertina movement down the parallel-sided tunnels. However, the curvature involves bending of the trunk toward the center of gravity of the mass. The skinks next relax these curves symmetrically. This generates movement, but not progression. The animals commonly note that they are not travelling and may tend to propel themselves vertically, out of the channels; indeed, such animals tend to jump.

Some species of lizards change approach upon repeated exposure to parallel sided channels; they wedge their head and neck at the start of curve formation and gradually relax asymmetrically. This leads to a learning of methods for poor concertina progression; other species do not learn. Also there is further diversity within the Scincidae. Thus, the Indian skink *Barkudia* does use a fairly effective concertina; whereas, the South African species of *Scelotes* and *Acontias* do not do so.

Undulatory Propulsion

The lateral undulation seen in snakes is seemingly the most generalized locomotor method of limbless vertebrates; yet it did not seem to be used by slowly moving lizards! Why was it absent from the repertoire of many squamates? Years ago, I had assumed it to be the most primitive locomotor method of squamates. After all, fishes undulate their trunk. Many lizards adpress their limbs to the trunk and then swim with purely undulant movements. Similarly, large crocodilians can descend steep slopes by undulating down to the water. This made the hypothesis likely that lateral undulation is retained from the ancestral condition, that it is based on a plesiomorphic phenotype. However, observation on Recent animals suggests that this view was incorrect.

Observation of elongate skinks moving through arrays of pegs indicated that the spacings were critical. In fairly narrow spacings, the skinks did locomote by establishing one or more narrow curves in their trunks and passing these posteriorly. However, they seemed to bend the body into a propulsive curve and then use the narrow spacings as guidance. The anterior portions of the body were seemingly stiffened as the animals pushed forward. This portion of the trunk could be modelled as elements in long column compression, that was kept from buckling by incidental lateral bracing. Posterior portions of the trunk were dragged up.

Elongate animals would use the head to enter between pegs lateral to the track; there they formed additional single or paired propulsion sites. The greater the friction of the substrate, the larger the number of propulsion sites developed by the animal. This kind of progression seemingly involves limited control demands. A wave of curvature passes the trunk from front to rear; the spacing of propulsion sites reflects the local resistance of the substrate.

In more open spacings, the skinks locomote by establishing wide curves in their neck and passing these posteriorly. The shape of the regular "sinusoidal" waves that pass down the trunk is established by internal constraints and the center

of gravity generally passes along a straight line. Whenever resistance sites are contacted, they may accelerate the animal, but this does not change the local curvature of the trunk. Consequently, if the spacing is very wide, the body slips irregularly past the contacted pegs. The path of the center of gravity is then jagged. If the spacing is too narrow, the curves are constrained. Hence, there seems to be an "optimum" spacing for each snake length and curvature pattern.

In these skinks, propulsion by sinusoidal waves is suitable only for rapid transit in which the momentum of the trunk is maintained. This does not require novel control patterns, but rather generates a locomotion tolerable for quick transit, independent of substrate. Reorientation of head and neck, will change the direction of travel of the animal.

Lateral Undulation

Propulsion by undulant waves differs from the lateral undulation displayed by snakes, the latter can be used independent of speed. Whereas the snake method retains the capacity for local adjustment of the track, each part of such an undulating animal traces the same path, like a railroad train moving along a track. The waves of the undulating body travel at the same velocity as the center of gravity of the whole. Also, the animal can practice lateral undulation independent of the placement and spacing of the resistance sites. Pygopodids and snakes can also select their rate of travel. A 50 cm-long member of the former group has been recorded during travel as slow as 1.2 m/hr.

Cues for the mechanism of lateral undulation were given long ago by James Gray (1953). The key to this is the push against a single peg. Gray offered the model of an irregularly curved strip being contacted by a snake at three contact sites; the model would then travel along the strip. As in the design of a cam follower, the model travelled along the strip in the direction of the wider curvature. Hence, understanding of limbless locomotion requires more than a map of curvature and the "contact" sites between snake and substrate. Information is needed about the sites at which forces exerted. Furthermore, local curvatures have to be matched to each contact site. This need for flexibility may be the basis for the increase in the number of trunk vertebrae. Not only this, but the fixed set of local curves, must travel down the trunk at a rate equivalent to the speed of the center of gravity. The experiment suggests that the capacity to curve the trunk is phylogenetically old. However, the capacity for locally directed

force exertion is new.

How does the snake establish the curves, monitor them, and transmit the sequence down the trunk? These questions are now being tested by electromyography of individual trunk muscles of snakes. Some of the snakes are made to travel over surfaces of differential friction and past peg arrays instrumented to record the pressures exerted against individual pegs. Other snakes are allowed to swim; indeed, they are made to pull paravanes, inducing varied drags.

The spacing of the pegs, their stiffness and resistance to the forces by the snakes are clearly critical to lateral undulation. Where does the animal monitor such information? Dorsal root transection suggests that it does not occur peripherally. We must remember that snakes also climb which substantially complicates their locomotion.

Evolution of the Limbless Locomotion System

What bearing do these observations have on the evolution of the limbless locomotion system? Indeed, do they allow one to derive the current conditions via a reasonable sequence of minor changes or need we to assume macroevolutionary saltations?

The earliest stages of these animals were obviously tetrapodal. Presumably, this was followed by their slenderization for crevice passage, by their elongation and increase in the number of trunk vertebrae, and the reduction of limb length and diameter, ultimately leading to limbless concertina. Evolution led to loss of coordination among the crossed extensors and between trunk bending and movement of limbs. Also, whenever limbs shorten in proportion to body diameter, while this diameter is retained, they will have less muscle available for propulsion.

The sequence proposes a departure from walk/ trot, to walking concertina. In this, the forelimbs are fixed and the trunk curved, followed by walking up of the hindlimbs to a more anterior position. The hindlimbs are next fixed and the trunk extended, followed by walking up of the forelimbs. Whereas force transmission to the substrate remains a function of the limbs, feet and claws, propulsion gradually shifts from being a function of the axial to on of the appendicular musculature. The need for force transmission, explains the retention of claws, even as the digits are reduced!

Next, further slenderization and elongation continues until static forces are transmitted by curves of the trunk resting on the ground. Once such surface concertina is possible, the limbs can be lost. It is important that transmission of any

lateral forces requires control over the site in static frictional contact. Lateral loading must be less than that which will cause slippage. Control or coordination probably allowed fairly controlled slow movement, it becomes the key to the sequence of evolutionary changes.

Hence, we can see that rapid passage of undulant curves is facile. However, the longer the trunk, the greater will be the number of vertebrae and the more facile the formation of curves. Improvement of local control allows the animals to lift portions of the trunk or apply local forces. The complications here involved direct the questions: How are the curves established initially? how are they monitored? and how is the control sequence transmitted down the trunk?

For finely controlled, slow locomotion transmission of the central sequence must not only be of a curvature pattern, but also of local resistances against contact sites. Such contact sites are individually adjusted, because only some of the curves serve the transmission of forces. The activation regime of multiple muscles should be changed from segment to segment.

Development of Further Specialization

Why did snakes evolve so many discrete locomotor patterns? The answer does not appear to lie in the reduction of energy expenditure! Thus, our analyses suggest that lateral undulation, surface concertina and sidewinding require the expenditure of equivalent kinetic energy, suggesting that the cost of transport is more or less equivalent. (Slide pushing and tunnel concertina are obviously more costly.) Naturally, the resting metabolism of lepidosaurians is likely lower for travel across horizontal than for climbing movements.

However, the common denominator is not energy. The locomotor methods of snakes permit the animals to cross different substrates. Also they differ in the velocities at which the snakes may travel over these surfaces. Finally they differ in the exposure they provide to the gaze of predators and of prey.

Perhaps the most important recognition is that most snakes can practice most methods. Too many past studies have concentrated on, and derived generalizations from, a single species or a single locomotor method. A fruitful approach might ask which cues trigger the shift among propulsive methods by particular species of snakes. Also whether there is a standard hierarchy for the recruitment of such cues. Most important remains the question of how these patterns differ among the multiple lepidosaurian species?

One may conclude by noting that, to me, the fundamental questions now concern the coordination of parts and their control. The approaches here illustrated, are founded on detailed analyses of mechanisms, designed to gain an idea of the evolutionary diversity of organisms. Study of the surviving squamates, the products of millennia of natural selection, while these can still be sampled, seems most likely to yield productive tests of present hypotheses.

Sample References

(also see bibliographies therein)

Brain, C. K. 1960. Observations on the locomotion of the South West African adder *Bitis peringueyi* (Boulenger), with speculations on the origin of sidewinding. *Ann. Transvaal Mus.* 24(1):19-24.

Cowles, R. B. 1956. Sidewinding locomotion in snakes. *Copeia* 1956 (4):211-214.

Gans, C. 1980. Biomechanics. Approach to Vertebrate Biology. [Reissue.] *The University of Michigan Press, Ann Arbor.*

Gans, C. 1984. Slide-pushing - A transitional locomotor method of elongate squamates. In (M. W. J. Ferguson, ed.). The Structure, Development and Evolution of Reptiles. *Symp. Zool. Soc. London,* (52):13-26.

Gans, C. 1985. Limbless Locomotion - A Current Overview. In (H. R. Duncker and G. Fleischer, eds.). Functional Morphology of Vertebrates. *Fortschritte der Zoologie,* 30:13-22.

Gans, C. 1986. Locomotion of limbless vertebrates: Pattern and Evolution. *Herpetologica,* 42(10):31-46.

Gans, C. & J.P. Gasc 1990. Tests on the locomotion of the elongate and limbless reptile *Ophisaurus apodus* (Sauria: Anguidae). J. Zool. Lond., 220(2):517-536.

Gasc, J.P. & C. Gans 1990. Tests on the locomotion of the elongate and limbless reptile *Anguis fragilis.* *Copeia,* 1990(4):1055-1067.

Gans, C., W. K. Morgan & E. S. Allen 1991. Surface locomotion of the elongate and limbless reptile *Anniella pulchra.* *Herpetologica,* 48(2):242-258.

Gans, C. & S. Kim 1992. Kinematic description of the sidewinding locomotion of four vipers. Israel J. Zoology, 38(1):9-23.

Gray, J. (1953). "How Animals Move." *Cambridge Univ. Press,* Cambridge.

Gray, J. (1968). "Animal Locomotion." Weidenfeld and Nicolson, London. *W. W. Norton,* New York.

Mosauer, W. 1930. A note on the sidewinding locomotion of snakes. *Am. Nat.* 64:179-183.

Mushinski, H. & C. Gans 1992. The role of the tail in tunnel passage by *Neoseps reynoldsi. Amphibia-Reptilia,* 13(4):393-404.