Snake Feeding Strategies and Adaptations—
Conclusion and Prognosis

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Today’s symposium has provided elegant demonstrations that being slender may have advantages to snakes: the advantage of slenderness should be easily recognizable to middle-aged members of the audience and to most of us during the post holiday season. In snakes, slenderness allows traverse of crevices off the ground and below the ground; slender snakes can extend their trunk across unstable branches and bridge discontinuous portions of their environment.

The adaptations of snakes represent the current state of a process that was already underway in the Cretaceous. Clearly, the process of slenderization did not proceed under constant conditions, for not only did the physical environment shift, but their predators and prey evolved possibly at an accelerated rate due to the success of snake specializations. It is obvious also that the adaptive process affected many aspects of snakes; slenderization involved a profound reorganization. Some aspects may have been abandoned or others appear to have been reformed along the way; it is unlikely that such aspects conferred much advantage at the time of loss. The relative advantage of some of these aspects may later have increased under different circumstances. Thus, we observe the reversal of trends, for instance the increased stoutness of some Recent species of vipers (Pough and Groves) and the shift from concentration on large prey to feeding on many small items (Greene). Such cases make it likely that the history of snakes includes multiple reversals of trends and development of analogous substitutes. The sequences we dimly discern are hardly likely to have been orthogenetic.

Slenderization would require solutions to four major problems, namely how to maintain the patency of the trunk, how to maintain salt and water balance, how to control body temperature, and how to acquire adequate amounts of nutrients. Many of the behavioral-structural adaptations seen in snakes would seem to reflect these.

Support and maintenance of the patency of the coelomic cavity represent little problem for fishes, as their density is approximately equivalent to that of water; fishes are thus evenly buoyed and the density of the medium also limits shear stresses. Support in air is more of a problem. Thus, terrestrial, limbless forms that support their trunk by resting on their bellies incur a variety of skeleto-muscular specializations, including well-articulated vertebrae and sometimes laterally extending ribs that maintain the patency of the coelomic cavity. In caecilians, we see such coelomic support by hydrostatic pressure devices involving muscular partitions (personal observations). Also, elongate squamates (amphisbaenians, elongate lizards and snakes) have articulated ribs that extend ventrally and stiffen the trunk, thus avoiding inappropriate pressures on the coelomic contents. Various burrowing lizards show one or more sets of ancillary articulating surfaces among their vertebrae. Snakes always have a double articulation involving zygosphene and zygantrum, as well as the standard lateral zygapophyses. These articulatory stiffenings presumably allow these animals to transmit greater forces along the column and should also facilitate cantilevering of the trunk off the ground.

The maintenance of body fluid concentration and body temperature reflect the
increasing surface-volume ratios induced by progressive elongation. Fishes and most amphibians avoid water stress by remaining in a moist environment, through either complete or partial immersion in water. Other amphibians wait out dry periods by estivation in subterranean cavities. There is no direct information on the use by caecilians of mucus or other retardants of evaporation. Reptiles deal with this problem by developing a variably impervious skin of alpha keratin and entrained lipids. Even in the most elongate forms, the integumentary water loss may be much less than the remaining (pulmonary-ocular) component, although the permeability of the integument is highly species-specific and snakes may utilize special mechanisms for this (P. F. A. Maderson, personal communication). Marine and estuarine species, which may employ integumentary gas exchange, have a more permeable skin than desert forms.

No elongate animal has developed an effective thermal insulation; the weasel’s proportions represent an obvious limiting condition (Brown and Lasiewski, 1973). Because elongation drastically increases the surface to volume ratio, elongate shapes are suitable only for ectotherms. Even whales allow the temperature of their elongate flippers to conform to that of the outside water and maintain their core temperature by countercurrent exchange mechanisms. Similarly, all elongate forms conform to the temperature of the environment. Snakes control their body temperature by judicious placement of their trunk across warmer or cooler portions of the thermal checkerboard of their environment (Regal, 1966); when thermal resources are available, they presumably maintain the temperature of their core (and perhaps their head) by an averaging process. Snakes living in a temperate climate could maintain a body temperature elevated above their environment only by drastically increasing their metabolic rate. Those few snakes that slightly elevate their body temperature when incubating eggs, do so while coiled into a non-elongate mass (Vinegar et al., 1970). Other things being equal, an endothermal snake with the diameter of a mouse, but perhaps twenty times as long, would have about twenty times the heat loss of the mouse, and would have to develop twenty times its absolute food acquisition rate in order to maintain the same temperature. Thus, diameter rather than mass would establish the metabolic rate and nutrient assimilation pattern of such an animal. This would impose severe problems on food acquisition and require levels of other functions demonstrated by no other animal. Consequently, elongation clearly is associated with ectothermy. Similar considerations also underline the problems that must have been encountered by extinct reptiles with long neck and tail. While the absolute size of animals such as brontosaurus may have allowed thermal stability, could Tanystropheus have maintained elevated temperatures?

The final major problem facing elongate animals is the acquisition of nutrients, the theme for the present symposium. It has been stressed by many of the earlier papers that elongation involved the modification of the feeding system to allow ingestion of whole prey and thus the acquisition of more bulk per unit time. For instance, ingestion rates of large rats are 0.00675 g/sec (N = 10, 0.7–3.7 g, 130–483 sec; S = 0.0016), while a boa with a head of equivalent diameter, will gulp approximately ten times the amount of food (0.087 g/sec) within approximately the same time (N = 7, 18.7–56.2 g, 273–633 sec, S = 0.031). These modifications affect not only all aspects of the skull and the soft tissues of the head, but also the vertebrae, ribs and soft tissues of the body wall (involved in elongation and peristaltic movement of prey), the gut, the lung and the circulatory system (Gans, 1975).

Today’s papers have documented examples for multiple workable solutions rather than a single ideal solution for the locomotor and ingestion problems faced by snakes. As noted by Arnold, a good system is one that facilitates survival: to take the argument further, a good system is one that allows the snake to maintain or increase its genotypic contribution to the next generation. This indicates that the relative
effectiveness of feeding systems cannot be derived from inspection of the mechanical or biochemical attributes of the ingestion and the prey-handling systems. Rather the benefit of a modification must reflect the absolute quantity of prey that it may make available in terms of the amounts of calories, amino acids, and trace elements that can be harvested per month, of the seasonal availability and of the habitats that must be occupied to obtain the prey. Finally, the relative quality of the feeding system is also influenced by the size of the prey and the defenses that must be overcome in ingesting it.

The examples, presented during this exciting cycle of studies, have also documented that there is no free lunch. Obviously the specializations for feeding like the specializations involved in elongation, involve both benefits, perhaps by permitting more efficient handling of particular food types, and costs. Certain specializations may preclude or severely restrict the access to alternate food types. This is an area for which we still have too little documentation. One example is the specialization for ingestion of bird eggs in *Dasyptes*. This genus exhibits slenderization of cranial elements and reduction of the dentition which appear to be required for the ingestion of bird eggs, but may preclude or limit the utilization of active prey. These specializations also involved modifications of such “unrelated” aspects as predator deterrence. The utilization of other foods may also be limited by more physiological and indeed behavioral adaptation to food type. Obviously, the cost of an adaptation in any such terms cannot exceed the magnitude of the resource that the adaptation may make available. However, this does not imply an absolute optimization. Mechanical inefficiency that allows the loss of some prey and digestive inefficiency that results in loss of unabsorbed nutrients need not pose an intrinsic problem. A specialization may be adaptive as long as it provides access to a large enough resource, so that the harvest may be “inefficient” as long as it allows the predator to maintain its population in the absence of other limitations.

Four major groups of tetrapods have developed limbless radiations, each with rather different strategies for locomotion and feeding (Table 1). Snakes, including the very aberrant worm snakes, show a single, major suite of characteristics involving many aspects of their body and, of course, their skull. Even though some Recent lizards (e.g. varanids with their loosely attached mandibles) have some similarity to Recent snakes, these groups remain separated by many morphological and physiological differences. This gap may be least for animals, such as *Pygopus* and perhaps *Liias*, among the pygopodids; however it remains substantial. This suggests that once the precursors of snakes developed the initial changes involved in a shift to a highly flexible body and the capacity for dealing with bulky prey, the transition continued rapidly and the intermediate forms, whatever their pattern, were rapidly replaced.

Perhaps the most critical difference between snakes and other elongate squamates is that the latter include relatively few food specialists while food specialization is the key for snakes. The studies of Pianka (1967) suggest that most lizards eat non-noxious prey that fit a particular size range. Voris, Savitzky and Greene have shown that many snakes eat a more restricted range of prey taxa. Indeed, the studies of Burghardt on tongue-flick mechanisms (1979) have long indicated the substantial genetic component to prey “choice.” We have seen forms specializing on the eggs of fish and birds, adult earthworms, slugs, snails, centipedes, crabs and vertebrates. We know from the studies of D. G. Broadley (1971a, b, 1977) of the very restrictive matching of particular snakes to specific prey species. This high level of food specialization suggests that there remains a fruitful field in determining the generality of the types of prey recognition and locomotor structure adduced in the papers of De Cock-Buning and Ruben. It seems likely that many species may show as yet uncharacterized approaches to such problems.

The feeding specializations of snakes reflect their occupation and adaptations to the physical aspects of different habitats;
### Table 1. Characteristics of the major groups of elongate and "limbless" tetrapods

<table>
<thead>
<tr>
<th>Aspect</th>
<th>Skinks</th>
<th>Landals</th>
<th>Amphibians</th>
<th>Carapods</th>
</tr>
</thead>
<tbody>
<tr>
<td>Environment</td>
<td>Everywhere</td>
<td>Covered sites on surface, few</td>
<td>Only underground, true burrowers</td>
<td>Underground, also in streams</td>
</tr>
<tr>
<td>Limb remnants</td>
<td>Only in some species, hedonic function</td>
<td>All degrees of reduction and use</td>
<td>Good forelimbs in one family; no external remnants elsewhere</td>
<td>Entirely lost</td>
</tr>
<tr>
<td>Elongation effects</td>
<td>Trunk, sometimes tail also</td>
<td>Trunk, or tail</td>
<td>Trunk</td>
<td>Trunk</td>
</tr>
<tr>
<td>Basic feeding strategy</td>
<td>Distend around prey, retract with body undulations</td>
<td>Cut, rip or distend to some extent</td>
<td>Cut, set interlocking dentition, spin</td>
<td>Rip, use tunnel walls when spinning, retract</td>
</tr>
<tr>
<td>Cranial Kinesis</td>
<td>Present</td>
<td>Absent, sometimes present</td>
<td>Absent</td>
<td>Absent</td>
</tr>
<tr>
<td>Food types (all carnivores)</td>
<td>Specialists, prey by groups or species; ontogenetic preference change</td>
<td>Generalists, take all prey of right size, not noxious</td>
<td>Generalists, take all prey of right size, not noxious</td>
<td>Generalists, take all prey of right size, not noxious</td>
</tr>
<tr>
<td>Body size*</td>
<td>Large</td>
<td>Very small (119 species)</td>
<td>Small</td>
<td>Small</td>
</tr>
<tr>
<td>- 10 g</td>
<td>16.5%</td>
<td>81.5%</td>
<td>67.4%</td>
<td>50.6%</td>
</tr>
<tr>
<td>- 100 g</td>
<td>4.6%</td>
<td>3.4%</td>
<td>4.5%</td>
<td>6.9%</td>
</tr>
</tbody>
</table>

*From Pough (1980 and personal communication).*
they also reflect the achievement of different sizes and proportions. Each such set of conditions allows snakes to encounter and perhaps to utilize distinct categories of prey. All of this occurs within the constraint of being a snake which, with few exceptions, means the ingestion of large food items without preliminary reduction (cf. Greene).

The sensory modalities and the cues used by snakes have long been known to differ innately and to change with ontogeny. So do their prey preferences, and such non-obvious aspects as the composition of the venom produced by some poisonous forms (Minton, 1967). One important and very poorly studied correlate of ontogeny is learning. How much is learned and how soon? How does learning affect the choice of food items and the mechanisms of subduing and ingesting prey? This behavioral component may be emphasized here in terms of the demonstration by Cundall of the marked complexity and of the functional division of cranial elements into capture and ingestion units. There is also the role of the motor program during ingestion; movement of the axial column shifts the prey-ingesting forces and reduces the need for a direct pull by the palatopterygoid arch and mandibles.

The complex interaction of morphological and behavioral factors in feeding can perhaps be demonstrated by an anecdote. Decades ago, I started to analyze the snail-eating mechanisms of dipsadine snakes, the specialized (obligate) members of which differ from most other snakes in having a free mandibular apparatus that permits them to extract snails from their shell. However, a number of related forms, such as *Sibon nebulosus* lack the obvious snail extraction mechanism. One day I noted that one of my *Sibon* had managed to get its mandibles "stuck" in the shell of a snail and was "desperately" crawling backwards through the cage, scraping its prey against the walls and bottom, apparently trying to dislodge it. Naturally, I "freed" the valuable specimen from its predicament. It was not until 15 years later that I discovered my error. Many dipsadines show a level of specialization in which they sink their relatively unmodified mandibles into the prey and allow these elements to be pulled into the shell, while the maxillae and palatopterygoid arches remain outside. The snake then crawls backwards through crevices until it wedges the shell and can pull the soft tissues of the mollusc out of the shell by contraction of the body muscles, rather than the cephalic ones. The condition seen in *Sibon* may parallel an early stage in the development of a mechanically more advanced snail extraction mechanism. Presumably, *Sibon* and some other slightly modified species of facultative snail eaters benefit from retention of a seemingly clumsy snail extraction pattern by their capacity of feeding on other invertebrates that they capture and ingest by use of the dentition of both the upper and lower jaws. Such observations suggest that the utilization of a new food is often likely to start with a behavioral, rather than a structural change (Gans, 1979). They also document the need for analysis of both living and preserved material.

The analysis of behavioral, physiological and morphological aspects of snake diversity here reported represents a welcome trend that deserves further emphasis. However, in analyzing feeding patterns in a multiplicity of snakes, it remains useful to avoid over-emphasis on specializations. An old German proverb reads "In der Not frisst der Teufel Fliegen" (during famine, the devil sups on flies). To understand the kinds of adaptation here analyzed, we need to know more about what represents "famine" for different snakes and how often such "famines" occur in the life of specimens or species. In short, modern functional anatomy must incorporate a field, as well as a laboratory, component. Furthermore, while the ways in which the structures of a particular snake are matched to the environment may be studied, using the techniques of ethology, physiology and functional morphology, the association of functional change, for instance with limblessness, may only be characterized by comparisons both of limbed and limbless species.

The day has shown us examples of specializations and conflicts. It is quite clear that many uncertainties remain. Also
remaining are the inevitable errors reflecting an as yet inadequate database for many current interpretations. We have, for example, heard many references to multiple and perhaps conflicting biological roles and to changes in adaptive patterns. However, nothing in the reports suggests that limb loss and elongation were accidental phenomena, that snakes became spontaneously specialized due to some genetic-developmental accident and even less due to a supernatural event. Nothing suggests that adaptation later refined the spontaneous result to a currently occupied environment or that specialized snakes search for a situation in which they might appear adapted. The animals we see today certainly show more than minimal current adaptation, often to very special circumstances. The analyses here reported repeatedly documented their non-obvious but significant matching of structure, physiology and behavior to the physical circumstances, and to the predators and prey of those environments currently occupied by these snakes. This makes it unlikely that their history involved periods of profound non-adaptive circumstances, after which the snakes became secondarily refined to their environment. Given current observations, this would hardly be the simplest possible or even a particularly plausible argument. In current parlance it would not be parsimonious.

I would like to conclude by thanking Dr. F. H. Pough for his efforts in organizing this successful symposium and by expressing my pleasure at the vigor, diversity and inventiveness of approaches currently demonstrated by this interesting field. Preparation supported by NSF DEB 80-803678. Ms. M. Stein and R. Thomas obtained the feeding data. I appreciate the comments of D. Cundall, H. F. Greene, F. H. Pough and P. Regal.

REFERENCES


