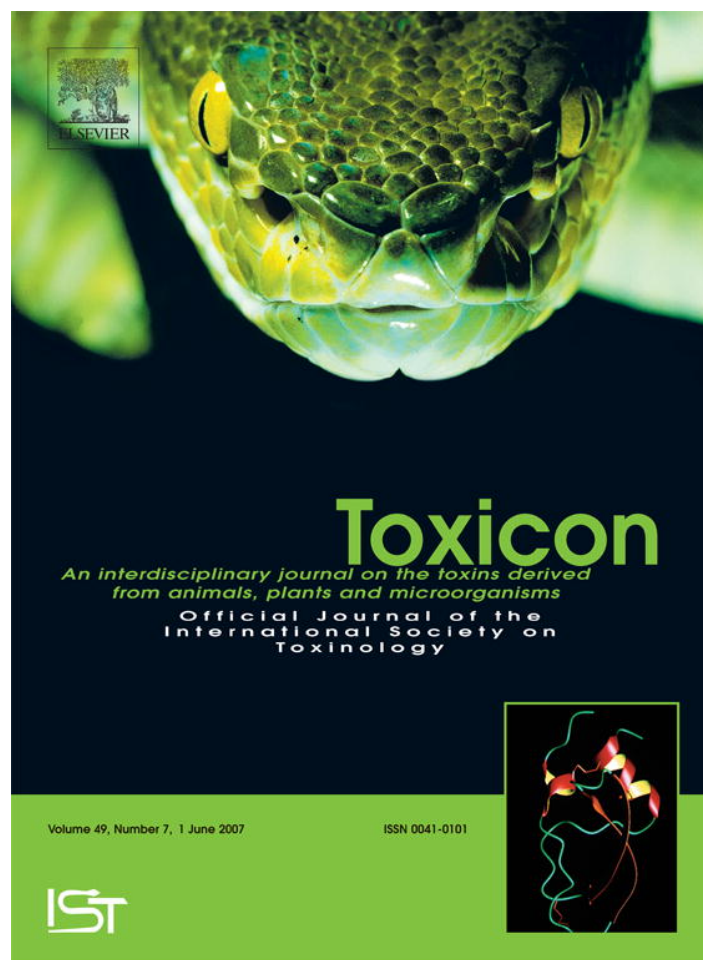


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Toxicon 49 (2007) 975–981

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# The evolution of venom-conducting fangs: Insights from developmental biology

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Received 19 September 2006; received in revised form 30 December 2006; accepted 15 January 2007

Available online 26 January 2007

## Abstract

The present study of the origin of the various types of fang represented among colubroid snakes (i.e., tubular, grooved, and ungrooved) attempts to reconcile the morphology of adult fangs with current phylogenetic hypotheses. Observations of growth series of developing tubular fangs were hypothesised to shed light on the evolutionary origin of fangs in snakes. While molecular phylogenies and evolutionary studies of venom proteins and of other anatomical components of the venom-delivery system reconstruct a consistent evolutionary scenario, the character of a tubular venom-conducting fang does not fit in this scenario. The present review offers a series of possible scenarios to resolve this anomaly. Of these, a new idea argues that a heterochronic mechanism (alteration of the timing of developmental events) may provide the answer that the ungrooved and grooved teeth of colubrid snakes evolved from an ancestral tubular fang by means of attachment of replacement tubular fangs to the maxilla at an earlier developmental stage than usual (precocial ankylosis).

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*Keywords:* Serpentes; Venom; Teeth; Fangs; Morphology; Development; Evolution; Colubroidea

## 1. Introduction

### 1.1. Introduction to the colubroid snakes

A knowledge of the phylogenetic relationships among colubroid snakes is a vital part of any investigation into the evolutionary or developmental origin of the snake venom-delivery system. This is because the large and diverse clade Colubroidea, with some 2400 species (Greene, 1997), includes all 600 species traditionally considered venomous. The past 5 years or so have seen an outpouring of original ideas on the subject of venom-delivery

system evolution. These will be reviewed after a brief synopsis of the state of knowledge that was their starting point.

The traditional interpretation of the Colubroidea was of a group that contained two families of venomous snakes, the Elapidae (cobras and their relatives) and the Viperidae (vipers), and a third, much larger family, the Colubridae, of approximately 2400 species (not to be confused with “Colubroidea” (Boulenger, 1893; Bogert, 1943; Anthony, 1955; Kardong, 1982)). A fourth family of venomous snakes was added with the recognition by Bourgeois (1961) that the Atractaspididae (the back-stabbing snakes), previously included among the Viperidae, represent a separate group. The Colubridae were considered a single group and to

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be the harmless ancestors of elapids and viperids (Boulenger, 1893; Bogert, 1943; Kardong, 1982). These latter two groups have tubular venom-conducting fangs, in contrast to the Colubridae, in which the fang, if present, bears an open groove or is simply an enlarged tooth, which is presumably a less efficient mechanism for the delivery of venom into a bite wound.

### 1.2. *A modern view of the Colubroidea*

The advent of molecular systematics has brought a combination of insight and confusion to the understanding of colubroid phylogeny. Molecular phylogenetic studies by Cadle (1988), Kraus and Brown (1998), Slowinski and Lawson (2002), and Vidal and Hedges (2002) have all arrived at different hypotheses of the phylogenetic relationships among the Colubroidea. However, they all agree that (1) the Colubroidea evolved from a single common ancestor, (2) the family Colubridae is not a single group as previously supposed, but represents many lineages (how many exactly is not agreed upon), and finally (3) the Elapidae, Viperidae, and Atractaspididae do not form a clade, but each represent an independent, monophyletic lineage within the Colubroidea.

While a complete and universally accepted colubroid phylogeny has not yet been proposed, there is currently enough agreement to dismiss the traditional interpretation of colubroid relationships and, most excitingly, to allow studies mapping venom-delivery system characters onto these phylogenies, in an effort to reconstruct the origin of the venom-delivery system. Several studies have mapped venom chemistry and morphological data onto the new phylogenies (e.g., Vidal, 2002; Fry et al., 2003; Jackson, 2003; Fry and Wüster, 2004). All have reached the conclusion (first put forward based purely on morphology by Underwood, 1967) that, in contrast to the traditional understanding of venomous snake evolution, the ancestor of all colubroids possessed at least some components of a venom-delivery system. Thus, many harmless colubrids are now thought to be descended from a venomous ancestor.

### 1.3. *Morphology of the venom-delivery system; evolutionary narrative of components*

I focus in the following on the mapping of morphological components of the venom-delivery system onto recent phylogenetic hypotheses.

#### 1.3.1. *The venom gland*

Elapids, viperids, and atractaspidids possess a large post-orbital gland in which venom is secreted and stored. It is enclosed in a fibrous sheath for the attachment of muscles. Beyond these similarities, however, there is strong evidence for homoplasy in the structure of the venom glands of the three groups (Jackson, 2003). The glands differ in size and shape of their lumen in which venom is stored and in the distribution of the mucous and serous cells that make up the gland. Although these three venom gland morphologies show evidence of being independently derived, there are indications that all venom glands are the homologs of the colubrid Duvernoy's gland, which is found in all but a few colubrids. The similar post-orbital position of both the venom gland and Duvernoy's gland (Kardong, 1982) and the fact that no snake has both a venom gland and a Duvernoy's gland support the homology of Duvernoy's gland and venom glands, suggesting that Duvernoy's gland appeared early in colubroid evolution and subsequently specialized independently into venom glands in the elapids, viperids, and atractaspidids (but see Taub, 1967).

#### 1.3.2. *Compressor glandulae muscle*

Elapids, viperids, and atractaspidids each possess a compressor glandulae muscle, which compresses the venom gland during biting, thereby squeezing venom through the venom duct into their tubular fang. The presence of this venom gland compressor muscle could be considered a synapomorphy of the true venomous snakes. However, a study of the blood supply and innervation of the compressor glandulae muscle in the three true venomous groups revealed that in each case the muscle that compresses the venom gland is derived from a different external adductor muscle, which is present in the temporal region of a snake's skull (Jackson, 2003). The elapid compressor glandulae muscle is derived from the adductor externus superficialis muscle, and the viperid one from the adductor externus profundus muscle. In the Atractaspididae, the adductor externus superficialis muscle is absent, and the venom gland is compressed by the adductor externus medialis muscle. Therefore, there is evidence that the venom gland compressor muscle evolved independently in the three lineages of true venomous snake.

#### 1.4. The fang problem

While the phylogenetic distribution of other components of the venom-delivery system, such as the venom glands and compressor muscles as described above and the venom proteins (Fry et al., 2003), can be accounted for by scenarios consistent with contemporary views of colubroid phylogeny, the presence of tubular fangs in elapids, viperids, and atractaspidids is more difficult to explain. Although the tubular fangs of the three groups are similar in appearance, all evidence indicates that the elapids, viperids, and atractaspidids do not represent a monophyletic group and that, therefore, tubular fangs may have evolved independently in the three taxa, in spite of their marked morphological similarity.

The present study examines in detail the morphology of tubular fangs in both adult and replacement series, as well grooved and ungrooved fangs of non-tubular-fanged colubroids. The objective is to identify morphological evidence to determine whether the morphological similarity of the tubular venom-conducting fangs of the elapids, viperids, and atractaspidids represents homology or homoplasy (convergence). If tubular fangs have evolved independently in several groups, for example, they might all resemble one another in being tubular in shape for the conduction of venom into a bite wound, but differ from one another in the nature of the developmental pathway leading to the tubular shape, and in morphological details which are not related to function but rather vestiges of the morphology of the ancestral tooth from which the fang is derived.

#### 1.5. The application of an evo-devo approach to colubroid fangs

“Descent with modification” was the central tenet of Darwin’s theory. A more contemporary addition might be to say that morphological “modification” results from changes in the genes that guide development. Studies integrating developmental biology with evolution have the potential to reveal morphology that is hidden in studies of only the adult organism, but which may provide the missing piece of the pattern that leads to an interpretation of the evolutionary history of a structure. The present study uses data obtained from the study of growth series of venom-conducting fangs to construct a hypothesis that offers a solution to the intransigent

problem of how to account for the distribution of character states of fangs among the living Colubroidea.

## 2. Materials and methods

### 2.1. The nature of the present study

With the exception of some new SEM observations of *Atractaspis* fangs, this study was a thought experiment, or Gedanken experiment, rather than a lab-based experiment. It should be considered an integrative sequel to the studies by Jackson (2002, 2003). A career’s worth of SEMs, notes, and personal observations of colubroid teeth were re-examined and, for the first time, considered in the context of reconciling them with recent research findings about the relationships among colubroid snakes (Jackson and Fritts, 1995, 1996, 2004; Jackson et al., 1999; Jackson, 2002; Jackson, pers. obs.). Maxillary fangs (grooved, ungrooved, and tubular ones) and growth series of adult replacement fangs from elapid, viperid, and atractaspidid species were examined. In addition, the very first fang formed in an embryonic elapid tubular-fanged snake, *Naja kaouthia*, was studied (Jackson, 2002). For details of preparation and specific specimens examined, the reader is referred to the above publications.

## 3. Results

### 3.1. Background information about snake teeth

The details of structure, function, and development of snake teeth are described extensively in the publications referred to in Section 2. The presence of fangs is a colubroid synapomorphy (shared derived character). These fangs may be ungrooved and resembling enlarged teeth with some slight morphological differences (Jackson and Fritts, 1995) (Fig. 1C); grooved and possessing an open channel along the lateral or anterolateral surface, presumably facilitating the introduction of venom into a bite wound (Fig. 1D); or tubular, in which a closed channel runs through the shaft of the fang for the conduction of venom into a bite wound (Fig. 1B). All these states are represented among the Colubroidea in a range of degrees from shallow grooves to deep grooves, etc. Of the tooth-bearing bones in colubroid snakes (i.e., the maxillary, palatine, pterygoid, and dentary), fangs are always situated on the maxilla. They range in position

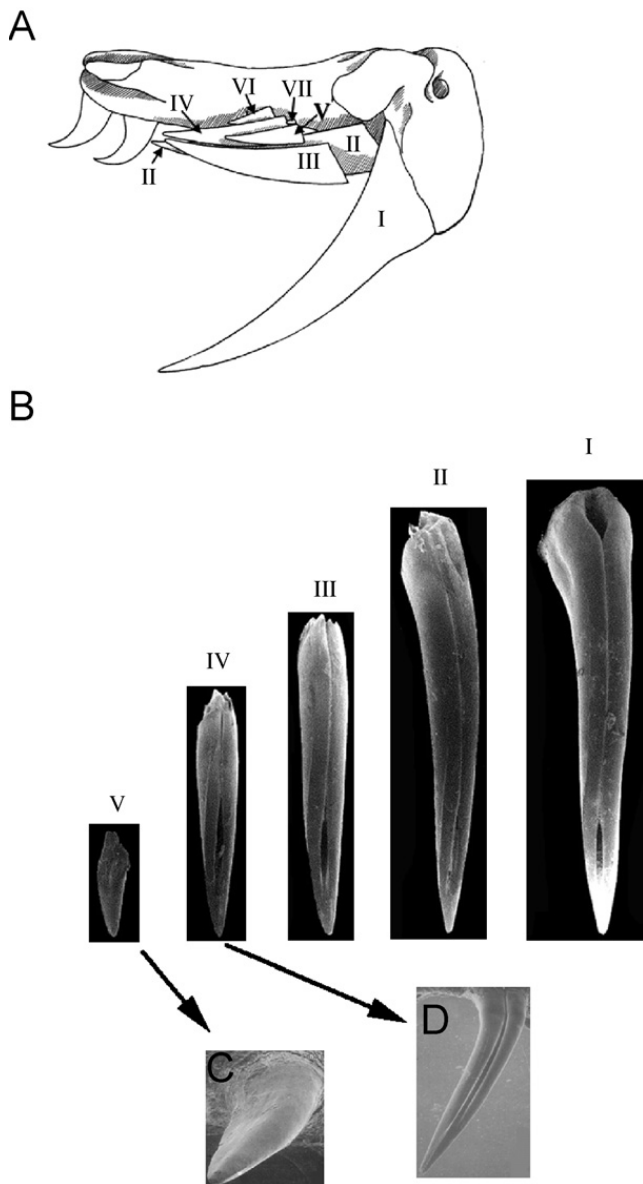


Fig. 1. The development of tubular fangs as a model for their evolution: (A) lingual view of the left maxilla of an elapid, *Naja melanoleuca*, showing the positioning of replacement fangs relative to the functioning fang (Bogert, 1943), (B) SEM pictures of a functioning fang and a replacement fang series from *Naja melanoleuca* (reprinted and modified with permission from J. Morph. (Jackson, 2002)), (C) ungrooved fang from *Stegonotus diehli* (reprinted and modified with permission from Amphibia–Reptilia (Jackson and Fritts, 1995)), and (D) grooved fang from *Boiga irregularis* (reprinted and modified with permission from Amphibia–Reptilia (Jackson and Fritts, 1995)). Arrows from early-stage developing tubular fangs indicate how a very early-stage fang could have become an ungrooved fang, and how a somewhat more developed fang could have become a grooved fang. The roman numerals on the fangs in (A) and (B) identify corresponding teeth.

along the maxilla from the caudal to the rostral end, with the tubular fangs generally situated at the rostral end. The length of the maxilla is also

variable, being represented in viperids and atractaspidids, for example, as a mere stub serving as a base for the fang.

Fangs, like all snake teeth, are replaced continuously throughout life. At any given time one, or occasionally more than one, fang is ankylosed to the maxilla. This is the functioning fang. Caudal to it, and not attached to any dentigerous bone, is a series of replacement fangs (Fig. 1A). When the functioning fang is shed, the next fang in the series will ankylose to the maxilla in its place, and so on.

In a fully formed, functioning fang (Fig. 1B), the channel that runs through it does not extend all the way to the distal tip of the fang, but rather ends somewhat more proximally to the tip, thereby forming a beveled tip like that of a hypodermic needle. The fangs in the replacement series (Fig. 1B) form by starting with what will be the distal tip of the functioning fang, and grow by a gradual accretion of material to the proximal end.

### 3.2. Evidence for tubular fang homology

Once again I will try to present my results briefly here, referring the reader to the publications listed in Section 2, in which the morphology of colubroid teeth and fangs is exhaustively described. Within a clade of about 2400 species, considerable variation exists. In spite of this variation, a remarkable number of constants can nonetheless be found in colubroid dentition (Jackson, 2003). Tubular fangs, for example, while variable in length within and among the three tubular-fanged groups, the Elapidae, Viperidae, and Atractaspididae, are remarkably uniform in all other features. Each fang is a tooth with a closed channel running through its shaft. Venom enters the channel via an entrance opening at the base of the fang and exits the channel into the bite wound through a discharge orifice at the tip of the fang. Joining the entrance opening and discharge orifice is a line resembling a suture running along the rostral surface of the fang although the middle portion of this line may be obscured in especially elongated fangs.

Ungrooved fangs are distinguished from simply being enlarged teeth by the presence of ridges along the distal rostral and caudal surfaces as opposed to the lateral and lingual surfaces as is found in unspecialised colubroid teeth. A pair of presumably homologous ridges are often visible on the surfaces of grooved and tubular fangs in positions that give the appearance of the ungrooved fang having been

stretched by the deepening of a groove along its lateral surface (Jackson and Fritts, 1995).

A study of developmental series of replacement fangs in elapids, viperids, and atractaspidids shows no difference between the taxa, and in all cases takes place as described in Section 3.1 and as illustrated in Fig. 1B., that is, replacement tubular fangs in adult viperid, elapid, and atractaspidid snakes form beginning with the distal tip of the fang, and proceed basally, through the gradual accretion of material to the basal end of the fang, until finally a fully formed fang ankyloses to the maxilla. The discharge orifice forms basal to the tip of the fang, on its anterior surface. Distally, the orifice is an open groove. As it extends basally the sides of the groove come into contact, creating a closed canal.

## 4. Discussion

### 4.1. Morphological evidence supporting the homology of tubular fangs

In contrast to venom glands, which specialized in different ways in the three groups of true venomous snakes, and to the venom gland compressor muscle, whose morphological differences clearly indicate that it is not homologous in the three taxa, the tubular fangs of the true venomous snakes present a puzzle. There is nothing in the morphology or development of the tubular fangs of the three groups of true venomous snakes to give any indication of homoplasy. To argue for homology on the grounds of similar structure alone may not be considered compelling. But consider the distribution and nature of venom-conducting fangs across vertebrate taxa. Helodermatid lizards have mildly venom-conducting grooves in the dentary teeth (the venom gland is in the lower jaw), and some mammals (e.g., shrews, solenodons) possess lightly grooved teeth and mildly toxic salivary secretions. A single example of a tubular fang has been found in a Triassic “reptile” of uncertain taxonomic affiliation (Sues, 1991), but the interpretation of this tooth as a venom-conducting fang is open to question. In any case, it is morphologically entirely different from the tubular fangs of colubroid snakes. Faced with the evidence of (1) great morphological similarity, (2) the absence of any comparable structure ever evolved among vertebrates, (3) similarities that bear no relation to function across all three tubular-fanged groups, e.g., suture line and discharge orifice always present and always on the anterior surface,

fangs are always on the maxilla, never on other dentigerous bones, and (4) such differences as exist, between taxa, are attributable to the functional morphology of the fang in the context of the structure of the rest of the skull, e.g., viperid and atractaspidid fangs are more elongated than elapid fangs, consistent with having a shortened maxilla that rotates the long fangs against the roof of the mouth when not in use, it is difficult to doubt the homology of venom-conducting fangs. How can this be explained in the context of other components of the venom-delivery system? Here I offer four possible scenarios, of which I favour the fourth.

### 4.2. Possible explanation for discrepancy: the phylogenies are wrong

If we go back to the days of Bogert (1943), the problem of tubular fang evolution is solved. Using only the maxillary dentition to reconstruct the evolution of venomous snakes, leads to the conclusion that viperids (which in those days included the atractaspidids) and elapids represent a clade, because of the great morphological similarity of the fangs. Thus, tubular fangs evolved only once among the Colubridae, and that tubular-fanged ancestor has given rise to all tubular-fanged colubroids and no other snakes. This explanation can be summarily dismissed based on the very strong current evidence against monophyly of the three tubular-fanged groups.

### 4.3. Possible explanation: tubular fangs have evolved independently three times

In the absence of a detailed knowledge of the morphology of colubroid tubular fangs, and the nature and distribution of other types of venom-conducting tooth existing in vertebrates, one might consider the notion of homoplasy of the viperid, elapid, and atractaspidid tubular fangs a convincing evolutionary scenario. However, I refer the reader back to Section 4.1 for a description of the evidence for homology of the structures in question.

### 4.4. Possible explanation: the tubular fang is a latent homolog

Here, the scenario presented is that the colubroid tubular fang represents an “underlying synapomorphy” (sensu Saether, 1979). This concept has more recently been dubbed a “latent homolog” by Wake

(1999). Applied to colubroid fangs, this would mean that the genetic instructions for building a tubular fang were present in the common ancestor of all colubroids. However, these instructions were only “switched on” in three lineages of snakes. The structural and developmental similarity of the fangs is, thus, explained by their homologous genetic underpinnings. The implication would be that these genetic instructions are present but not expressed in all non-tubular-fanged colubroid groups. This possibility is difficult either to prove or to disprove, and raises all sorts of questions, such as what the nature of the sudden origin of the original tubular-fang-making instructions were, and why these instructions were suppressed and not expressed immediately. What induced their expression much later in three lineages and why?

#### 4.5. *Explanation favoured here: tubular fangs represent the ancestral condition for the Colubroidea*

The simplest explanation for the homology of tubular fangs in elapids, viperids, and atractaspidids is that they are derived from a common ancestor, which possessed a tubular fang. This idea was proposed in Section 4.2, and I hasten to make it clear here that I am working within the context of modern phylogenetic hypotheses of the relationships among colubroid taxa. To support this hypothesis, two major evolutionary steps must be explained, and I will present proposed explanations here: (1) how did the initial tubular fang of the colubroid ancestor originate? and (2) how and why was this ancestral tubular fang lost in so many grooved-fanged and ungrooved-fanged colubroid lineages?

##### 4.5.1. *Origin of the ancestral tubular fang*

Upon examining colubroid fangs that are ungrooved, slightly grooved, deeply grooved almost to the point of creating a closed canal, or tubular with a suture line suggesting evolutionary formation by the closing of two sides of a deep groove, what evolutionary morphologist can resist the explanatory scenario of a tubular fang being formed by natural selection for a gradually deepening groove? This scenario was illustrated by Jackson and Fritts (1995) and implicit in the evolutionary scenarios put forward by earlier morphologists (Boulenger, 1893; Bogert, 1943; Kardong, 1982). Here I propose that this is the evolutionary mechanism by which the first tubular fang was derived. I maintain that natural

selection for such an obviously advantageous adaptation would have been very strong, increasing the efficiency of delivery of venom into a bite wound, and the tubular state of a fang would have been reached very rapidly—prior to the branching off of basal colubroid lineages represented today. So to all intents and purposes we start the base of the colubroid bush with a tubular-fanged snake. Kuch et al. (2006) report fossil fangs from the lower Miocene, which are morphologically indistinguishable from modern Elapid and Viperid fangs. This discovery, if the lower Miocene is long enough ago to be the time of the major radiation of colubroid lineages, may be evidence in support of a tubular-fanged ancestral colubroid. Otherwise, it is simply another observation of the remarkable morphological similarity of the tubular fangs of already-diverged elapid and viperid lineages.

##### 4.5.2. *Origin of grooved and ungrooved fangs*

Examination of a growth series of developing replacement fangs in elapid, viperid, and atractaspidid snakes, reveals that the earliest teeth in the series have already the shape of the tip of a developing tubular fang. Since the channel through the tubular fang does not extend to the very tip of the fang, this early fang is neither grooved nor tubular. Similarly, a slightly more developed replacement fang in the series is not yet tubular, because it forms the grooved discharge orifice of the future tubular fang. Thus, at this stage, the fang bears a groove in which the sides of the groove do not yet form a completely closed channel. Now, let us suppose that through some mutation, resulting perhaps in an acceleration of the fang-replacement process, one of these early-stage replacement fangs were to ankylose precociously to the maxilla, that is, a temporal shift in ankylosing of teeth before the tubular fang is completely developed. The result would be a maxilla bearing an ungrooved or grooved, but no longer tubular, fang (Fig. 1C and D). This is the developmental mechanism I propose to explain the evolution of ungrooved and grooved-fanged snakes from a tubular-fanged one.

What selective pressures would support the loss of an enclosed channel in a fang? There is an intuitive tendency among biologists to suppose that the morphologically most specialised form represents the most derived condition. It is easy to imagine the advantage to a snake of possessing tubular fangs as part of a venom-delivery system for introducing venom into a bite wound. What

possible advantage could there be to the simpler morphology of ungrooved fangs to a snake? It is a question open to speculation. Perhaps, there is some advantage to a less specialised feeding system. Perhaps, there is some gain from being able to form ungrooved fangs more rapidly (and perhaps cheaply) than tubular ones? Whatever the answer, the best evidence that a specialised tubular-fanged venom-delivery system does not represent the pinnacle of adaptive perfection is perhaps the rarity of such systems. They represent a relatively small minority even within colubroid snakes, and among vertebrates as a group they are unique.

### Acknowledgements

I thank the Smithsonian Institution's National Museum of Natural History, Harvard's Museum of Comparative Zoology, and the Royal Ontario Museum for the specimens used in this study. This work was funded by an NSERC Postdoctoral Fellowship to KJ.

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