

Functional plasticity of the venom delivery system in snakes with a focus on the poststrike prey release behavior [☆]

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Abstract

We explored variations in the morphology and function of the envenomation system in the four families of snakes comprising the Colubroidea (Viperidae, Elapidae, Atractaspididae, and Colubridae) using our own prey capture records and those from the literature. We first described the current knowledge of the morphology and function of venom delivery systems and then explored the functional plasticity found in those systems, focusing on how the propensity of snakes to release prey after the strike is influenced by various ecological parameters. Front-fanged families (Viperidae, Elapidae, and Atractaspididae) differ in the morphology and topographical relationships of the maxilla as well as in the lengths of their dorsal constrictor muscles (retractor vomeris; protractor, retractor, and levator pterygoidei; protractor quadrati), which move the bones comprising the upper jaw, giving some viperids relatively greater maxillary mobility compared to that of other colubroids. Rear-fanged colubrids vary in maxillary rotation capabilities, but most have a relatively unmodified palatal morphology compared to non-venomous colubrids. Viperids launch rapid strikes at prey, whereas elapids and colubrids use a variety of behaviors to grab prey. Viperids and elapids envenomate prey by opening their mouth and rotating both maxillae to erect their fangs. Both fangs are embedded in the prey by a bite that often results in some retraction of the maxilla. In contrast, *Atractaspis* (Atractaspididae) envenomates prey by extruding a fang unilaterally from its closed mouth and stabbing it into the prey by a downward-backwards jerk of its head. Rear-fanged colubrids envenomate prey by repeated unilateral or bilateral raking motions of one or both maxillae, some aspects of which are kinematically similar to the envenomation behavior in *Atractaspis*. The envenomation behavior, including the strike and prey release behaviors, varies within families as a function of prey size and habitat preference. Rear-fanged colubrids, arboreal viperids, and elapids tend to hold on to their prey after striking it, whereas atractaspidids and many terrestrial viperids release their prey after striking it. Larger prey are more frequently released than smaller prey by terrestrial front-fanged species. Venom delivery systems demonstrate a range of kinematic patterns that are correlated to sometimes only minor modifications of a common morphology of the jaw

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apparatus. The kinematics of the jaw apparatus are correlated with phylogeny, but also show functional plasticity relating to habitat and prey.

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1. Introduction

Derived snakes (Colubroidea) are characterized by their ability to produce venoms (Greene 1997; Fry et al. 2003a) in special venom-secreting glands that appeared early in colubroid evolution and became associated with structures specialized for the delivery of venom into prey

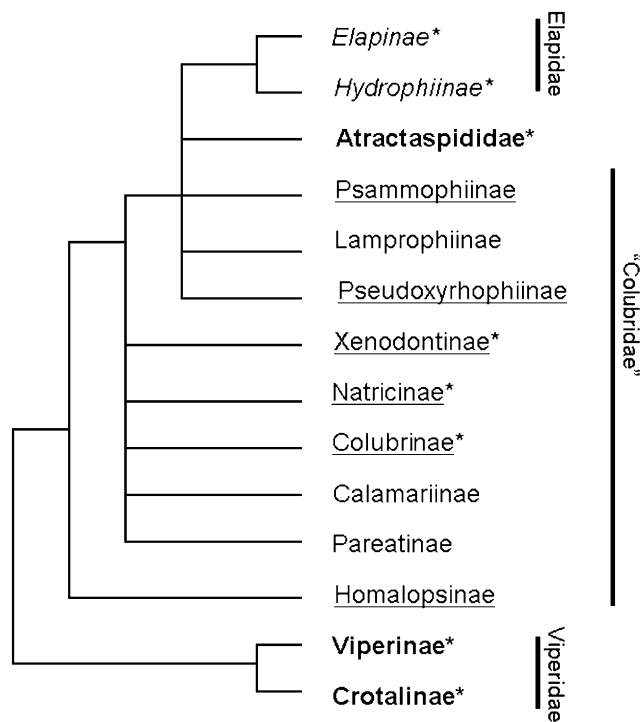


Fig. 1. Simplified phylogeny of colubroid snakes based on Vidal and Hedges (2002). Subfamilies with solenoglyph venom delivery systems are indicated in boldface, those with proteroglyph systems are in italics, and those in which at least some members possess opisthoglyph systems are underlined, proteroglyph systems are in italics, and those in which at least some members possess opisthoglyph systems are underlined. The Elapidae and Viperidae exclusively contain venomous taxa, whereas many colubrid subfamilies contain both venomous as well as non-venomous taxa. Within the Atractaspididae, only the genus *Atractaspis* possesses a solenoglyph venom delivery system, which likely evolved independently from the solenoglyph system of vipers. Subfamilies in regular type do not contain any venomous species. The family Colubridae is paraphyletic and includes all non-venomous colubroids, as well as many rear-fanged taxa. This study includes individuals from taxa that are indicated with an asterisk.

(Vidal 2002). Venom delivery, or envenomation, structures are found in all four families comprising the Colubroidea (Fig. 1). Three of the families, namely the Viperidae, Atractaspididae, and Elapidae, exclusively contain venomous taxa, and there are numerous venomous members in the fourth and largest family, the Colubridae. Furthermore, the venomous nature of some colubrids previously considered non-venomous is being revealed as more taxa are investigated (Greene 1997; Mackessy 2002; Vidal 2002; Fry et al. 2003a). Thus, venom delivery is widespread among snakes, and distinct venom delivery systems are associated with each family.

This study explores aspects of the functional plasticity present in snake venom delivery systems. We begin this paper by briefly introducing the various venom delivery systems that have been described. Next we review in detail the current, often limited, knowledge of morphological and functional variation within the venom delivery systems of colubroid snakes. The review provides the basis for appreciating our study of the predilection of species to release prey after the strike. We then present hypotheses that predict whether prey items will be preferentially released or not released, based on our knowledge of the anatomy and preferred habitat of a snake species, and on the size of the prey items offered.

1.1. Types of venom delivery systems

Traditionally, venom delivery systems have been divided into front-fanged and rear-fanged envenomation systems (e.g. Boulenger 1915, 1896; Kardong 1982a; Vidal 2002; Jackson 2003). Two types of front-fanged systems have been described: (1) the solenoglyph system of the Viperidae and of *Atractaspis* within the Atractaspididae; and (2) the proteroglyph system of the Elapidae. The rear-fanged (i.e., opisthoglyph) system is seen in atractaspidids other than *Atractaspis* and in almost half of the members of the Colubridae, the other half of which are considered non-venomous. These designations, however, are based on superficial similarities of the fangs and maxillae, but probably do not reflect natural groupings. The current consensus is that front-fanged venom delivery systems have evolved independently from one another in the Viperidae, Atractaspididae, and Elapidae, and were possibly lost in some lineages (Fry and Wüster 2004). Furthermore, a number of studies have shown that the family Colubridae is paraphyletic, particularly with respect to

the placement of the Atractaspididae and Elapidae (Slowinski and Lawson 2002; Vidal 2002; Vidal and Hedges 2002), and that the phylogenetic relationships within the Colubridae remain unclear (Cadle 1984, 1985, 1994; Cadle and Greene 1993; Knight and Mindell 1994; Rodríguez-Robles and De Jesús-Escobar 1999; Vidal et al. 2000). Thus, phylogenetic patterns of the evolution of venom delivery systems remain elusive, but within families, morphological and functional patterns have been identified and are discussed below.

All snake venom delivery systems are based on modifications of a common, basic ophidian palato-maxillary morphology that functions in both prey capture and prey transport (Cundall 1983; Deufel and Cundall 2003a). Since the morphology of the jaw adductor muscles and venom gland constrictor muscles has only a minor influence on the kinematics of prey capture, with the possible exception of *Dendroaspis* (Elapidae) and *Xenodon* (Colubridae), in which some jaw adductor muscles are involved in maxillary retraction (Haas 1931; Deufel and Cundall 2003a), we confine our review to the morphology of the palato-maxillary arches and associated muscles.

1.2. Morphology of front-fanged venom delivery systems

Snakes with front-fanged venom delivery systems are superficially similar in possessing a tubular, or canaliculated, fang that is carried rostrally in the mouth on a shortened maxilla.

1.2.1. Viperidae

In vipers, a long fang is carried on a short, highly mobile maxilla (Fig. 2A). The viper fang is long with respect to the size of the snake (Marx and Rabb 1972), recurved, and the external surface of the fang shows little or no evidence of a seam or groove connecting the oval entrance and exit orifices for the venom (Jackson 2002). Two side-by-side fang locations on the maxilla become alternately occupied by functional fangs (Fig. 3A), whose replacement generations develop directly caudal to them. The maxilla is shortened to accommodate only the fang, and there are no other maxillary teeth. The greatest dimension of the maxilla is along the axis extending from the fang attachments to the maxillary–prefrontal joint. The joint between the maxilla and the prefrontal is highly mobile. A concave surface on the dorsal maxilla rotates around a rounded process of the prefrontal. The prefrontal in turn articulates with the braincase in a movable saddle joint. Hyperextension of both joints is checked by ligaments spanning each joint caudally (Kardong 1974). Shortening of the maxilla correlates with an elongation of the ectopterygoid, which articulates with the caudal surface

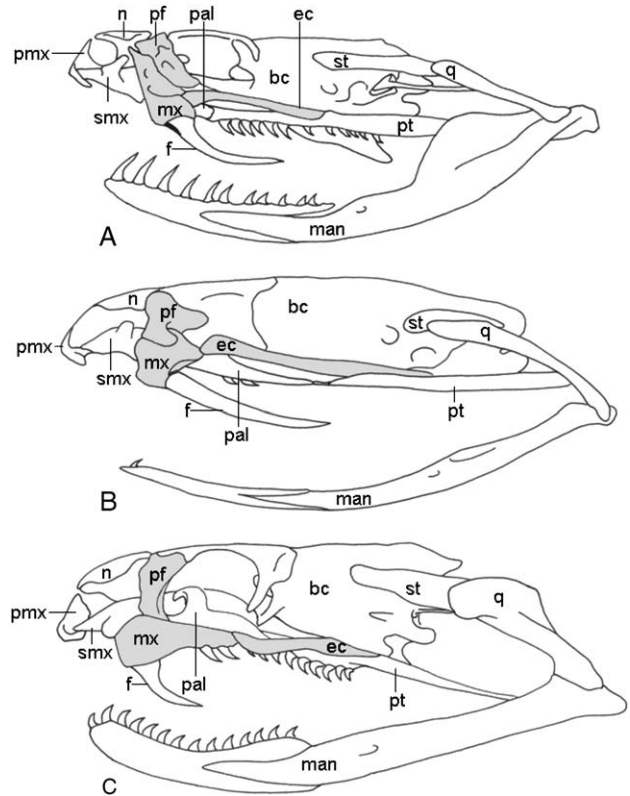


Fig. 2. Diagrammatic left lateral views of the skull of vipers (A), *Atractaspis* (B), and elapids (C). Note the superficial similarity of the venom apparatus of vipers and *Atractaspis*. The maxilla in vipers and *Atractaspis* is shortened to accommodate only the fangs, whereas in elapids the fangs are frequently followed by several short, solid maxillary teeth. bc = braincase; ec = ectopterygoid; f = fang; man = mandible; mx = maxilla; n = nasal; pal = palatine; pf = prefrontal; pmx = premaxilla; pt = pterygoid; q = quadrate; smx = septomaxilla; st = supratemporal. Drawings modified from Bogert (1943), Parker and Grandison (1977), and Gloyd and Conant (1990).

of the maxilla dorsal to the fangs (Fig. 3A). The shortening of the palatine and the mobilizing of its connections to the maxilla and the snout, which includes all bones rostral to the braincase, such as the nasals, vomers, septomaxillae, and premaxilla, facilitates the protraction of the palato-maxillary arches during fang rotation. Furthermore, the snout itself is very mobile and can move around its attachment to the braincase in reaction to palatal movements.

In many vipers, the dorsal constrictor muscles (retractor vomeris; protractor, retractor, and levator pterygoidei; protractor quadrati), which are responsible for movements of the palato-maxillary arches during a strike, are modified. The protractor pterygoidei of many vipers, compared to that of other snakes, originates far rostral on the ventral side of the braincase, directly caudal to the snout (Cundall 2002) (Fig. 3A).

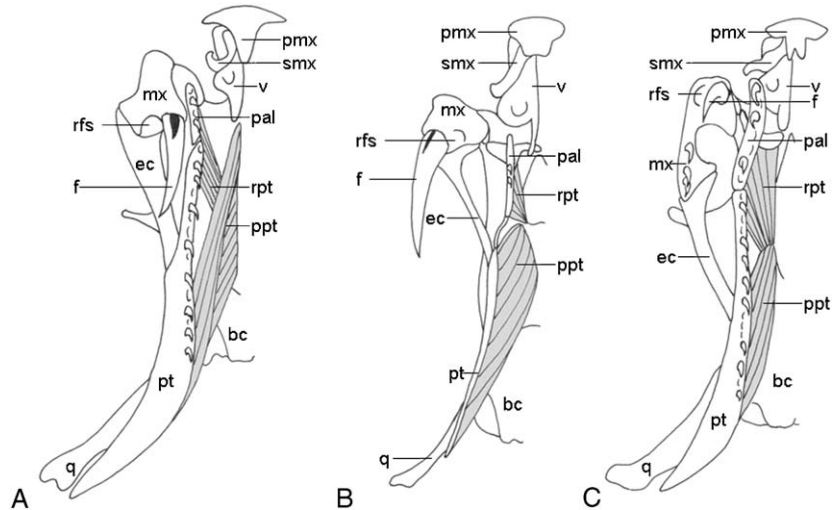


Fig. 3. Diagrammatic ventral views of the right half of the roof of the mouth of vipers (A), *Atractaspis* (B), and elapids (C). The protractor pterygoidei muscle (ppt) is the main muscle responsible for the protraction of the maxilla during a bite. The length of this protractor muscle correlates with the speed of protraction as well as with the maximum distance the maxilla can be protracted. The retractor pterygoidei muscle retracts the palato-ptyergoid bar. Note the replacement of the bony connection between the pterygoid and the palatine by a flexible ligament in *Atractaspis* and the reduction of the palatine as well as the anterior origin of the protractor pterygoidei muscle in vipers. bc = braincase; ec = ectopterygoid; f = fang; mx = maxilla; n = nasal; pal = palatine; pmx = premaxilla; ppt = protractor pterygoidei; pt = pterygoid; q = quadrate; rfs = empty socket for replacement fang; smx = septomaxilla; rpt = retractor pterygoidei; v = vomer.

1.2.2. *Atractaspis*

Within the Atractaspididae, the genus *Atractaspis* has a long, hollow, seamless fang on a very short maxilla, a condition that superficially resembles that of vipers (Fig. 2B). A cutting edge on the caudal side of the fang tip lies on the opposite side from the discharge orifice for the venom (Kochva and Meier 1986). The length of the fang with respect to the length of the skull lies somewhere between the fang length of elapids and that of vipers, but is closer to that of vipers (Visser 1975; Kochva and Meier 1986).

The short maxilla of *Atractaspis* articulates with the prefrontal in a complex, rotatable saddle joint that is stabilized by ligaments running from the prefrontal and the braincase to the maxilla along the posterior aspect of the joints (Deufel and Cundall 2003b). The two ligaments limit maxillary rotation. The prefrontal is tightly attached to the braincase and has only limited mobility. Maxillary shortening, as in vipers, correlates with an elongation of the ectopterygoid (Fig. 3B). In contrast to vipers, in which the palato-ptyergoid bar is mobilized by a reduction in the size of the palatine and its connections, in *Atractaspis*, the palatine remains firmly attached to the snout elements, which are reinforced for burrowing. The protraction of the palato-ptyergoid bar in *Atractaspis* is facilitated by the replacement of the bony joint between the rostral end of the pterygoid and the palatine with a flexible ligament that slackens during pterygoid protraction and does not

transmit the protraction force to the palatine (Deufel and Cundall 2003b) (Fig. 3B).

Because of its fang and maxilla, *Atractaspis* has previously been considered an aberrant member of the Viperidae (Haas 1930a, b; Laurent 1950), which is still reflected in its common names “mole viper” and “burrowing asp”. Although it is no longer considered a viper, the phylogenetic relationships of *Atractaspis* remain unclear (Cadle 1994; Wollberg et al. 1998). It appears, though, to have affinities with some African rear-fanged taxa now included in the Atractaspididae (Vidal and Hedges 2002).

Modifications of the dorsal constrictor muscles involve only the reduction of the retractor pterygoidei and retractor vomeris muscles. Because of the ligamentous connection between the pterygoid and the palatine, there is no protraction of the palatine, and because of the tight connection of the snout to the braincase, there is no movement of the snout. Since there is no protraction of the palatine and no movement of the solidly attached snout, the muscles that usually retract the palatine and snout in other species (retractor pterygoidei and retractor vomeris muscles) are only weakly developed. There is no rostral extension of the origin of the protractor pterygoidei muscle compared to that of some vipers (Cundall 2002; Deufel and Cundall 2003b), correlating with the ligamentous constraints and limited rotation of the maxilla.

1.2.3. Elapidae

The second front-fanged venom delivery system, the proteroglyph system, is seen in elapids. In elapids, the fang is generally shorter than in similar-sized vipers (Marx and Rabb 1972), with the possible exception of the genus *Acanthophis*, which resembles vipers in both body form and some behavioral aspects (Shine 1980). The fang of elapids is tubular with a seam connecting the entrance and exit orifices for the venom. This seam has been mentioned in support of the hypothesis that smooth tubular fangs evolved by a gradual change from a grooved fang, whose groove deepened until its edges came together to close off a central canal (Tomes 1875; re-examined by Jackson 2002, 2003). In some elapids (e.g., some *Naja* species), the exit orifice for the venom is modified (round instead of oval) to facilitate the defensive behavior of spitting venom at an attacker (Bogert 1943; Wüster and Thorpe 1992; Rasmussen et al. 1995). Two fang sockets are situated side-by-side on the rostral end of the maxilla, which become alternately occupied by functional fangs (Fig. 3C). The maxilla is shortened to a lesser degree than that of vipers (Fig. 2C). The maxilla of most elapids is C-shaped in a ventral view, with both ends curving medially. In a lateral view, the maxilla is generally taller rostrally, with the fang lying directly below, or slightly rostral to the maxillary–prefrontal joint. The genus *Dendroaspis* is unusual in that its maxilla articulates with the prefrontal halfway along its length, placing the fang far rostral to the maxillary–prefrontal joint and allowing large fang rotations (Deufel and Cundall 2003a). Frequently, the fang is followed caudally by a number of solid maxillary teeth separated from the fang by a diastema (Bogert 1943). The maxilla of elapids has a simple, broad attachment to the prefrontal that allows a rocking-sliding motion during fang erection (Deufel and Cundall 2003a). The prefrontal is also movably connected to the frontal. There are no strap-like ligaments that limit the maxillary and prefrontal rotations as seen in vipers and *Atractaspis*, but fang rotation is limited by the short ligament fibers that span the broad joint between the maxilla and the prefrontal. The palatine has loosened its attachments to the maxilla and snout only in one of the two subfamilies of elapids, namely the Australasian Hydrophiinae. In contrast to the dorsal constrictor muscles of vipers, those of elapids are unmodified. There is generally no rostral extension of the origin of the protractor pterygoidei muscle to approach the snout (Deufel and Cundall 2003a) (Fig. 3C).

1.3. Morphology of rear-fanged venom delivery systems

Rear-fanged, or opisthoglyph venom delivery systems are found in the families Atractaspididae (with the

exception of *Atractaspis*) and Colubridae. The Colubridae are a speciose, paraphyletic family that does not contain any front-fanged species (Fig. 1). The phylogenetic relationships of colubrid subfamilies remain unresolved (Vidal and Hedges 2002), but venom delivery systems appear to have evolved independently in several lineages (Kraus and Brown 1998; Gravlund 2001; Kelly et al. 2003). Thus, rear-fanged snakes, like front-fanged taxa, do not form a natural group and are united only by superficial similarities of the palato-maxillary arches.

In rear-fanged species, the fang is carried on the caudal end, or rarely in the middle, of the maxilla and is preceded, or sometimes followed, by a variable number of solid maxillary teeth. Often, there is a diastema between the fangs and the solid maxillary teeth (Anthony 1955). Placement of the fang with respect to the maxillary–prefrontal joint varies, with the fang placed directly below the prefrontal in some species (Bourgeois 1968), or caudal to the prefrontal in some other species (Boulenger 1915; Anthony 1955). The fang of rear-fanged species, which varies in relative size, but is usually larger than the more rostral maxillary teeth, bears either a cutting edge or a groove of variable depth (Jackson and Fritts 1995; Jackson 2003) and points caudally at rest. Maxillary shape, length, and topographical relationships vary widely in rear-fanged snakes, and the maxilla's attachment to the prefrontal is usually somewhere along the middle of the bone (e.g., Anthony 1955; Bourgeois 1968) (Fig. 4). Muscles associated with the venom delivery system in those rear-fanged snakes that have been examined so far show a slightly more rostral origin of the protractor pterygoidei muscles than those in non-venomous colubrids (Haas 1931; Anthony and Serra 1951; Kroll 1976).

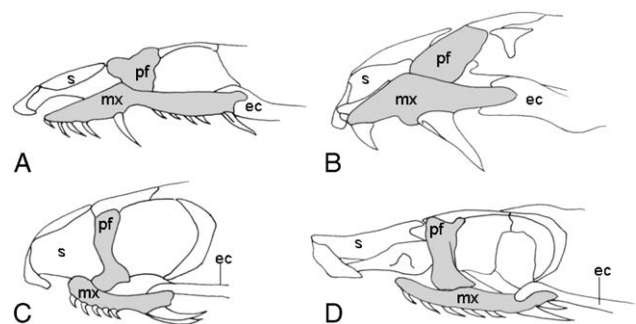


Fig. 4. Diagrammatic left lateral views of the rostral portions of the skull of some ophioglyph snakes, showing some of the variation in maxillary shape and fang placement. (A) *Dryophis*, in which only the caudal enlarged tooth is grooved and functions as a fang; (B) *Polemon*, in which the enlarged rear fang is placed directly ventral to the maxillary–prefrontal joint; (C) *Xenodon*, in which the maxilla rostral to the prefrontal is shortened; (D) *Heterodon*. ec = ectopterygoid; mx = maxilla; pf = prefrontal; s = snout. Drawings modified from Boulenger (1915), Anthony (1955), and Bourgeois (1968).

1.4. Function of the venom delivery systems

1.4.1. Viperidae

The behavior of the venom delivery system has been studied by far most widely in vipers, particularly crotalines. This may be due to geographical bias, because much of this work is done by North American workers on readily available rattlesnakes, or because of the relative ease with which vipers can be handled in the lab compared to most elapids, *Atractaspis*, and many venomous colubrids.

Many vipers are ambush predators that launch rapid strikes at their prey (Greene 1997). Their body form reflects this behavior. Many terrestrial vipers concentrate their mass in the caudal two-thirds of their body to serve as an anchor point from which strikes are launched. The cranial region that is accelerated toward the prey frequently is reduced in mass (Cundall 2002). During acceleration of the head toward the prey during a strike, the mandibles are depressed and the prefrontal and snout become elevated. As the gape increases, the prefrontal is elevated to such a degree that it pulls up a fold of skin that partially or completely obscures the snake's eye. The movement of the prefrontal carries the maxilla rostrally and dorsally. As the strike progresses, maxillary rotation on the prefrontal carries the fang tip rostrally. Angles of about 80° are formed between the tip of the fang and the braincase as the snake reaches the prey (Young et al. 2001; Cundall 2002). In most strikes, the braincase of a snake passes over the prey and contact with the prey is made first by the mandibles. Deceleration of the mandibles as they hit the prey causes the braincase to be carried around the prey, and the fangs often enter the prey on the side opposite from the origin of the strike as the mouth closes in a bite. Whereas maxillary rotation alone would depress the fang from the level of the roof of the mouth, rotation of the prefrontal elevates the fang tip and, thus, reduces the chance that the fang catches on the surface of the prey during the strike. However, maximal maxillary and prefrontal rotations are not reached during the extension and bite phases of the strike during which the snake approaches and reaches the prey. Maximal rotations of those elements, ranging from 90° to 120°, are only seen during release of and withdrawal from the prey after the strike (Cundall 2002).

The astounding palato-maxillary mobility seen in vipers is correlated with a number of morphological features. Both the maxillary–prefrontal as well as the prefrontal–braincase joints are reduced in size and are extremely mobile. Furthermore, the palatine lacks a maxillary process in all vipers examined so far, and the choanal process is absent in viperines and reduced in crotalines. The choanal process forms part of the roof of the nasal passage and anchors the palatine dorsally in other snakes (Underwood 1999). Reduced palatine

connections to the maxilla and nasal passage and a mobile snout that can be deflected by the palatine and the maxilla allow enhanced protraction of the palato-maxillary arches by contraction of the protractor pterygoidei muscle (Cundall 1983). In many viper taxa, the origin of the protractor pterygoidei muscle has migrated far rostrally, thereby elongating the muscle and, thus, greatly increasing the distance and velocity it is able to protract the palato-maxillary arches (Cundall 2002) (Fig. 3A).

1.4.2. Atractaspis

Although the superficial similarity of the venom delivery system of *Atractaspis* to that of vipers may suggest viper-like maxillary kinetics, the venom delivery system in *Atractaspis* functions very differently from that of vipers. *Atractaspis* envenomates prey with a downward-backwards stab with a single, long, caudally directed fang that is extruded from the closed mouth while the snake crawls alongside its prey. It does not launch strikes from a distance as do vipers (Corkill et al. 1959; Visser 1975; Golani and Kochva 1988; Deufel and Cundall 2003b). Only one fang is extruded from the closed mouth until the fang reaches an angle of about 50° with the braincase. Maxillary rotation beyond that point is limited by two ligaments that span the maxillary–prefrontal joint caudally. The fang is jabbed into the prey by a caudoventral jerk of the head toward the prey. The fang remains embedded in the prey for a variable amount of time and is extracted by rostradorsal movements of the snake's head (Deufel and Cundall 2003b). Fang extraction is facilitated by a cutting edge on the caudal surface of the fang tip (Kochva and Meier 1986). Frequently, prey items are envenomated multiple times and if several prey items are available at the same time, such as a litter of rodent pups, all the prey items are envenomated sequentially before any are consumed (Deufel and Cundall 2003b).

1.4.3. Elapidae

Elapids are mostly slender snakes in which the head is not much wider than the cranial trunk (Greene 1997). They are generally considered active foragers that chase and capture active prey (Shine 1977, 1979; Shea et al. 1993). There are few data in the literature on how elapids capture prey, but Kardong (1982b) described prey capture in *Naja* as much less “deliberate” than in vipers. Cobras in his study did not set up an ambush posture, but struck at the prey from above as they were crawling toward it. Most elapids appear to simply crawl up to a prey and grasp it in their mouth (Greene 1997; Deufel, personal observation). Australian elapids in the genus *Acanthophis* may be an exception, being similar to vipers in body form and behavior. They are stocky snakes with large, triangular

heads that launch rapid strikes from an ambush position (Shine 1980).

Prey capture kinematics of elapids remains poorly explored and awaits detailed functional morphological study based on empirical data. Published accounts of elapid striking focus on measuring readiness to strike, strike speed, and accuracy of defensive strikes without morphological analysis or with an analysis of the movements of cranial elements, such as the degree of fang rotation, gape, etc. (Whitaker et al. 2000). Other aspects of elapid strikes, such as the nature of visual stimuli that are needed for prey capture (Kardong et al. 1997) or the influence of prey size or presentation of multiple prey items on prey capture behavior (Kardong 1982b), have been studied, but did not involve a morphological analysis. Morphological studies of the elapid venom delivery system, in turn, have not included empirical analyses of predatory strikes. Based on morphology alone, the mechanism of fang erection has been described for several Australian elapids (McKay 1889; Fairley 1929), as well as for some African and Asian taxa (Phisalix 1922; Radovanovic 1928; Haas 1930a; McDowell 1970). All authors agree that in elapids maxillary rotation is limited to a slight rocking motion of the maxilla on the prefrontal when the caudal end of the maxilla is depressed by the protracting ectopterygoid. Exceptions are found in *Dendroaspis*, in which the length of the maxillary–prefrontal joint is reduced and lies in the middle of the maxilla, allowing more rotation than in other elapids (McDowell 1970; Deufel and Cundall 2003a), and in *Acanthophis*, in which fang erection is due mostly to rotation of the prefrontal on the frontal, which carries the maxilla rostradorsally (McKay 1889; Fairley 1929). Deufel and Cundall (2003a) measured maxillary rotation in several African elapids during prey transport and found mean maximum maxillary–braincase angles to vary between 20° (*Dendroaspis*) and 9° (*Ophiophagus*). However, they did not explore how much of the maxillary rotation is due to rotation of the prefrontal on the frontal or whether maxillary rotation is greater during prey capture than during prey transport.

1.4.4. Rear-fanged snakes

As in elapids, descriptions of prey capture by rear-fanged snakes rarely include kinematic analyses of the behaviors. Prey capture in *Heterodon* simply involves crawling up to the prey and grabbing it (Kroll 1976), and the same may be true for many other rear-fanged snakes. Envenomation of prey by enlarged rear teeth, which bear only open grooves or cutting edges to introduce the venom into the prey at low pressure, appears to require that the snake holds on to the prey after first contact and repeatedly slashes the prey with its fang (Smith and Bellairs 1947; Kardong 1979, 1980; Cundall 1983). Similar unilateral slashing motions have

been observed in *Oligodon*, which uses its enlarged rear maxillary teeth to open reptile eggs to swallow their contents (Coleman et al. 1993). Some rear-fanged snakes are able to achieve remarkable degrees of maxillary rotation that brings the rear fangs, which point caudally at rest, to a fully erect position. Boulenger (1915) described maxillary rotation from horizontal to almost vertical in a specimen of *Xenodon* that attempted to bite him as he grasped it behind the neck. Descriptions of *Xenodon* morphology suggest that the placement of the maxillary–prefrontal joint near the rostral end of the maxilla, together with a reduction in the size of the joint, facilitates maxillary rotation. There appear to be no obvious modifications in the dorsal constrictor muscles to facilitate large palato-maxillary protractions (Haas 1931; Anthony and Serra 1951).

1.5. Functional plasticity of venom delivery systems

Vipers generally are thought to capture prey by rapidly striking from an ambush position, releasing the prey after envenomation, and following the scent trail of the prey to the location where it succumbed to the venom. Elapids and rear-fanged snakes, in contrast, are generally believed to forage actively for prey and grab it, without a strike, upon encountering it. In vipers, the most extreme fang rotation is seen during defensive bites and during the release and early withdrawal phases of prey capture, not during the head and trunk extension and bite phases as they approach the prey (Cundall 2002). During prey release, the maxillae and prefrontals are rotated through a large arc to pull the embedded fangs out of the prey. The extreme rostral origin of the protractor pterygoidei muscle in many vipers and the reduction of the palatine and its connections allow the large protraction of the palato-ptyergoid bar. The reduction and increased mobility of the maxillary–prefrontal joint, as well as the increased mobility of the prefrontal on the braincase, account for this kinematic potential in vipers. Thus, snakes without an elongated protractor pterygoidei muscle and with less mobile maxillary–prefrontal and prefrontal–braincase joints, such as elapids and venomous colubrids, are expected to hang on to prey at the end of their strike, whereas most vipers are expected to release prey after the strike.

Because the palatine is more loosely connected to surrounding bony elements in hydrophiine elapids (i.e., Australasian terrestrial taxa and most sea snakes) than in elapine elapids (i.e., African, American, and Asian taxa) (McDowell 1970), hydrophiines may have greater palato-maxillary mobility, and they are expected to be more likely to release prey after striking than elapine elapids with their more tightly attached palatine. Because the fangs of rear-fanged snakes usually are caudally located in the mouth and do not possess an

enclosed venom duct, envenomation requires prolonged laceration of the prey with the fang. Thus, we expect that rear-fanged snakes are likely to hang on to their prey to introduce sufficient venom to incapacitate the prey.

Release of the prey after a strike has the advantage of removing the snake from any retaliation by the prey before it succumbs to the venom. The snake can trail the prey at a safe distance and consume it after it is no longer dangerous. However, there are several ecological factors that may influence the likelihood and advantage of releasing prey. First, releasing prey only makes sense for terrestrial or fossorial species. In an arboreal environment, most released prey would drop to the ground without leaving a scent trail and then die. The likelihood of recovering such a prey item is relatively low and would require the snake to descend from the tree, expending energy, and potentially exposing itself for a prolonged period of time to predators and scavengers attracted to the prey item as it attempts to locate the dead prey. Thus, we expect that terrestrial vipers will usually release their prey, whereas arboreal species will be more likely to hang on to their prey after the strike. Similar reasoning applies to aquatic snakes. In an aquatic environment, envenomated prey would likely be washed away and be difficult to trail, resulting in similar disadvantages as those experienced in an arboreal environment. Second, a larger prey item potentially poses a greater risk to a snake than a small one through retaliating bites and scratches. We can, thus, expect that larger prey items are released more frequently than smaller ones. In non-venomous species, however, we expect that the snakes hold on to prey of most sizes since released prey, without envenomation, will likely be lost to the snakes.

In summary, we hypothesize that terrestrial vipers and hydrophiine elapids release prey after the strike, particularly if the prey is relatively large, and that arboreal and aquatic vipers, elapine elapids, rear-fanged taxa and non-venomous snakes hold on to prey after striking it.

Besides functional plasticity in prey release behavior that is correlated with preferred habitat and prey size, functional plasticity may be seen in the Australasian *Acanthophis*, an hydrophiine elapid that is purported to be similar to vipers in both body form and prey capture behavior (Shine 1980). As a member of the Hydrophiinae, *Acanthophis* has relatively loose connections of the palato-pterygoid bar to the maxilla, nasal passage, and snout and is purported to have greater maxillary rotation capabilities compared to that of other elapids (McKay 1889; Fairley 1929). We examined the prey capture kinematics of *Acanthophis* to determine whether *Acanthophis* shows functional plasticity in its venom delivery system and is able to use its elapid morphology to strike like a viper.

2. Material and methods

For our investigation of the influence of preferred habitat and prey size on the propensity to release prey, we analyzed video and film records of prey capture in representative colubroids (Table 1). Most records of prey capture were taken over a number of years in the context of other studies and were recorded in a variety of settings, including a number of zoos. The selection of species for our study was dependent on their availability in the collections of colleagues, friends, zoos, and on whether they could be purchased locally. This situation resulted in a large number of vipers in our sample. Furthermore, most snakes were long-term captives, and, because snakes feed very infrequently, many feeding records were single replicates of single individuals. We also frequently traveled a long distance to a location, only to have the snake we intended to videotape not eat in front of the camera, because it was disturbed by the bright lights required to achieve video images that are in focus and not blurry. Additionally, not all successful strikes could be used for our analysis because the direction of the strikes was oriented obliquely to the picture plane, introducing problems with parallax, or because a strike was captured only partially or not at all. Unfortunately, these problems precluded us from following a balanced statistical test design.

Because of the peculiar, specialized envenomation mechanism of *Atractaspis* (see above), no prey captures of that genus were analyzed for prey release (for a detailed account of prey capture in *Atractaspis*, see Deufel and Cundall 2003a). Unfortunately, we had no access to live individuals of any of the other species in the Atractaspididae and could not analyze their prey capture behavior.

Prey offered to the snakes consisted mainly of live rodents, but occasionally included other live animals if those were the preferred prey of a species (Table 1). With the exception of the feeding records of *Heterodon platirhinos*, prey capture was recorded with a Panasonic AG-456 S-VHS video camera or a Sony DCR-TRV740 digital video camera. *Heterodon platirhinos* was filmed on Super-8 film with a Canon XLS-1014 camera. Records were analyzed by playback on a video monitor or screen-projected Super-8 film.

For successful strikes, we recorded whether prey items were released after the strike or not. We also measured the head length of the snakes in lateral views from the tip of the snout to the caudal end of the bulge formed around the quadrato-articular joint. The recording of prey captures at zoos, unfortunately, precluded us from weighing the snakes that we fed and we were thus unable to obtain snake to prey weight ratios to estimate relative prey size. Therefore, to estimate relative prey size, we measured the height of the prey in lateral views when both the snake and prey were visible in the same plane

Table 1. Species investigated, typical habitat of the species, numbers of individuals studied within each species, number of analyzable prey capture events of each individual, and type of prey captured

Species	Common name	Habitat	Individuals	# of Captures	Prey items
Non-venomous colubrids					
<i>Elaphe guttata</i>	Corn snake	T	1	1	Mouse
			2	5	Mouse
			3	8	Mouse
<i>Elaphe obsoleta</i>	Rat snake	T	1	2	Mouse, rat
<i>Farancia abacura</i>	Mud snake	W	1	8	Amphiuma
			2	2	Amphiuma, Siren
			3	1	Amphiuma
<i>Nerodia fasciata</i>	Banded water snake	W	1	2	Fish
			2	3	Fish
<i>Nerodia rhombifer</i>	Diamondback water snake	W	1	1	Fish
			2	2	Fish
			3	1	Fish
<i>Thamnophis sirtalis</i>	Eastern garter snake	T	1	1	Fish
<i>Thamnophis proximus</i>	Western ribbon snake	T	1	2	Fish
Rear-fanged colubrids					
<i>Diadophis punctatus</i>	Ringneck snake	T	1	2	Salamander
<i>Helicops angulatus</i>	Mountain keelback	W	1	1	Fish
			2	1	Fish
			3	1	Fish
<i>Heterodon platirhinos</i>	Hognose snake	T	1	1	Frog
			2	2	Toad
Viperidae: Viperinae					
True vipers					
<i>Atheris chlorechis</i>	Western bush viper	A	1	1	Mouse
<i>Atheris squamiger</i>	Green bush viper	A	1	1	Mouse
			2	1	Mouse
			3	3	Mouse
<i>Bitis arietans</i>	Puff adder	T	1	1	Mouse
			2	1	Mouse
			3	1	Mouse
<i>Bitis nasicornis</i>	Rhinoceros viper	T	1	3	Mouse
<i>Causus defilippi</i>	Snouted night adder	T	1	3	Tadpole, newborn mouse
			2	6	Tadpole, newborn mouse
<i>Cerastes cerastes</i>	Sahara horned viper	T	1	2	Mouse
<i>Daboia palaestinae</i>	Palaestian viper	T	1	1	Rat
<i>Daboia russellii</i>	Russell's viper	T	1	1	Mouse
<i>Macrovipera mauritanica</i>	Moorish viper	T	1	1	Mouse
<i>Vipera bornmuelleri</i>	Lebanese mountain viper	T	1	1	Mouse
<i>Vipera raddei</i>	Armenian mountain viper	T	1	1	Mouse
<i>Vipera transcaucasiana</i>	Transcaucasian sand viper	T	1	2	Mouse
<i>Vipera wagneri</i>	Wagner's viper	T	1	2	Mouse
<i>Vipera xanthina</i>	Turkish viper	T	1	1	Mouse
			2	1	Mouse
			3	1	Mouse
Viperidae: Crotalinae					
Pit vipers					
<i>Agkistrodon contortrix</i>	Copperhead	T	1	1	Mouse
			2	1	Mouse
<i>Agkistrodon piscivorus</i>	Cottonmouth	W	1	1	Mouse
			2	1	Mouse
<i>Agkistrodon taylori</i>	Taylor's cantil	T	1	1	Mouse
<i>Atropoides mexicanus</i>	Mexican jumping viper	T	1	4	Mouse
			2	4	Mouse
<i>Bothriechis nigroviridis</i>	Black-speckled palm pitviper	A	1	1	Mouse
<i>Bothriechis schlegelii</i>	Eyelash viper	A	1	1	Mouse

Table 1. (continued)

Species	Common name	Habitat	Individuals	# of Captures	Prey items
			2	1	Mouse
<i>Bothrops alternatus</i>	Urutu	T	1	1	Mouse
			2	1	Mouse
<i>Bothrops caribbaeus</i>	St. Lucia pitviper	T	1	1	Mouse
<i>Bothrops venezuelensis</i>	Venezuelan lancehead	T	1	1	Mouse
<i>Crotalus abyssus</i>	Grand canyon rattlesnake	T	1	1	Mouse
<i>Crotalus atrox</i>	Western diamondback rattlesnake	T	1	4	Mouse, rat
			2	3	Mouse, rat
			3	3	Mouse, rat
<i>Crotalus cerastes</i>	Mojave sidewinder	T	1	1	Mouse
			2	1	Mouse
<i>Crotalus horridus</i>	Timber rattlesnake	T	1	2	Mouse, rat
			2	1	Mouse
			3	1	Rat
<i>Crotalus molossus</i>	Black-tailed rattlesnake	T	1	1	Mouse
<i>Crotalus polystictus</i>	Lance-headed rattlesnake	T	1	1	Mouse
			2	2	Mouse
			3	1	Mouse
<i>Crotalus tigris</i>	Tiger rattlesnake	T	1	1	Mouse
			2	2	Mouse
<i>Gloydius blomhoffi siniticus</i>	Yangtze mamushi	T	1	1	Mouse
<i>Gloydius saxatilis</i>	Rock mamushi	T	1	1	Mouse
<i>Lachesis muta</i>	Amazonian bushmaster	T	1	1	Mouse
			2	1	Mouse
			3	1	Rat
<i>Lachesis stenophrys</i>	Central American bushmaster	T	1	1	Mouse
<i>Ovophis monticola</i>	Mountain pitviper	T	1	1	Rat
<i>Porthidium ophyomega</i>	Slender hognose viper	T	1	1	Mouse
			2	1	Mouse
<i>Protobothrops jerdoni</i>	Jerdon's pitviper	T	1	1	Mouse
<i>Sistrurus catenatus</i>	Eastern massasauga	T	1	1	Mouse
<i>Sistrurus miliarius</i>	Pigmy rattlesnake	T	1	1	Mouse
<i>Trimeresurus borneensis</i>	Bornean pitviper	A	1	1	Mouse
<i>Trimeresurus fasciatus</i>	Banded pitviper	A	1	1	Mouse
<i>Trimeresurus flavomaculatus</i>	Philippine pitviper	A	1	1	Mouse
			2	1	Mouse
<i>Trimeresurus stejnegeri</i>	Chinese bamboo viper	A	1	4	Mouse
<i>Trimeresurus trigonocephalus</i>	Sri-Lankan bamboo viper	A	1	2	Mouse
Elapidae: Elapinae					
<i>Aspidelaps lubricus</i>	Coral cobra	T	1	8	Mouse
			2	5	Mouse
<i>Aspidelaps scutatus</i>	Shield-nosed cobra	T	1	3	Mouse
<i>Naja pallida</i>	Red spitting cobra	T	1	2	Mouse
			2	2	Mouse, frog
			3	1	Mouse
			4	3	Mouse, frog
			5	1	Mouse
Elapidae: Hydrophiidae					
<i>Acanthophis antarcticus</i>	Death adder	T	1	10	Mouse
			2	1	Mouse
<i>Oxyuranus scutellatus</i>	Taipan	T	1	1	Rat
<i>Pseudechis australis</i>	King brown snake	T	1	1	Rat

Species are grouped by their type of venom delivery system. Abbreviations for typical habitat are as follows: T = terrestrial; A = arboreal; W = aquatic.

on the video image. Because of the pliable nature of rodents, prey height likely underestimates the true size of the prey, but because rodents are all of similar shape, it still gives a reasonable estimate of size. To calculate snake to prey size ratios, we divided prey height by the head length of the snake, since head size determines gape size, which is the limiting factor for ingestion. Snakes were grouped into the habitat categories terrestrial, aquatic, and arboreal, based on information in the literature.

We used χ^2 tests to analyze whether rear-fanged snakes, arboreal vipers, and elapine elapids have a propensity to hang on to their prey after they strike it. We also explored whether terrestrial vipers and hydrophiine elapids preferentially release prey. To find out whether the size of the prey influences the propensity of front-fanged species to release it, we performed a one-way analysis of variance or the Kolmogorov–Smirnov test in those cases where variances were not homogeneous. All statistical analyses were performed using SPSS 13 for Windows.

For our investigation of the strike kinematics of *Acanthophis*, we recorded three specimens striking at live mice. One specimen was also recorded striking live lizards (*Eublepharus* spp., *Sceloporus* spp.) on three occasions. Records were taken and analyzed with the same equipment as described above. Unfortunately, only the strikes by the largest *Acanthophis* were parallel to the focal plane of the camera and could be analyzed. To compare the strike kinematics of *Acanthophis* to published records of strikes in vipers (Cundall 2002), we measured the following variables on video images: (1)

The distance between the tip of the snout of the snake and the prey at strike initiation in terms of head lengths; (2) the angle between the long axis of the fang and the braincase of the snake at maximum fang extension just before the fang becomes obscured when hitting the prey; (3) the angle between the long axis of the braincase and the anterior trunk of the snake at prey contact; and (4) the gape of the snake as the maximum observed angle between the braincase and the long axis of the mandible. Ranges, means, and standard deviations were calculated for those values using SPSS 13 for Windows.

3. Results

The influence of the habitat on the propensity of snakes to release prey is summarized in Table 2. Both non-venomous colubrids and most rear-fanged colubrids (except one individual of *Diadophis punctatus*) hang on to their prey as predicted (for reasons for our predictions see Section 1.5). Terrestrial vipers do not preferentially release prey as we had expected, but hang on to prey almost as often as they release it. Their propensity to release prey is actually not significantly different from random ($\chi^2 = 0.2$, $p = 0.655$). Arboreal snakes on the other hand, as expected, are much less likely to release prey than terrestrial snakes (16 out of 18 analyzed strikes resulted in the snakes not releasing their prey). In the two recorded strikes by semi-aquatic vipers (*Agkistrodon piscivorus*), the prey was released after the strike. Among all elapids analyzed, all of which are

Table 2. Summary of the results of χ^2 tests on the preponderance of releasing a prey item after a strike

Group	Post-strike behavior	Observed frequency	Expected frequency	χ^2	p																																																			
Non-venomous colubrids (39 strikes by 14 individuals)	Released	2	1	1.026	0.311																																																			
	Not released	37	38			Rear-fanged colubrids (8 strikes by 6 individuals)	Released	1	1	0.000	1.000	Not released	7	7	Terrestrial vipers ^a (52 strikes by 36 individuals)	Released	42	79	1386.329	0.000	Not released	38	1	Arboreal vipers (13 strikes by 9 individuals)	Released	2	1	1.059	0.303	Not released	16	17	All Elapids ^a (38 strikes by 12 individuals)	Released	7	1	36.973	0.000	Not released	31	37	Elapinae ^a (25 strikes by 8 individuals)	Released	4	1	9.375	0.002	Not released	21	24	Hydrophiinae ^a (13 strikes by 4 individuals)	Released	3	12	87.750	0.000
Rear-fanged colubrids (8 strikes by 6 individuals)	Released	1	1	0.000	1.000																																																			
	Not released	7	7			Terrestrial vipers ^a (52 strikes by 36 individuals)	Released	42	79	1386.329	0.000	Not released	38	1	Arboreal vipers (13 strikes by 9 individuals)	Released	2	1	1.059	0.303	Not released	16	17	All Elapids ^a (38 strikes by 12 individuals)	Released	7	1	36.973	0.000	Not released	31	37	Elapinae ^a (25 strikes by 8 individuals)	Released	4	1	9.375	0.002	Not released	21	24	Hydrophiinae ^a (13 strikes by 4 individuals)	Released	3	12	87.750	0.000	Not released	10	1						
Terrestrial vipers ^a (52 strikes by 36 individuals)	Released	42	79	1386.329	0.000																																																			
	Not released	38	1			Arboreal vipers (13 strikes by 9 individuals)	Released	2	1	1.059	0.303	Not released	16	17	All Elapids ^a (38 strikes by 12 individuals)	Released	7	1	36.973	0.000	Not released	31	37	Elapinae ^a (25 strikes by 8 individuals)	Released	4	1	9.375	0.002	Not released	21	24	Hydrophiinae ^a (13 strikes by 4 individuals)	Released	3	12	87.750	0.000	Not released	10	1															
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	Not released	21	24			Hydrophiinae ^a (13 strikes by 4 individuals)	Released	3	12	87.750	0.000	Not released	10	1																																										
Hydrophiinae ^a (13 strikes by 4 individuals)	Released	3	12	87.750	0.000																																																			
	Not released	10	1																																																					

^aTaxonomic groups that show a result that differs significantly from what we expected. See text for more detail.

Table 3. Mean maximum angles (mean \pm SD) and distances to prey (in head lengths) for strikes by one adult *Acanthophis antarcticus* and for *Crotalus horridus* from Cundall (2002)

Measure	Species		N
Fang to braincase angle	<i>Acanthophis antarcticus</i>	54 \pm 11	15
	<i>Crotalus horridus</i>	85 \pm 14	19
Trunk to braincase angle	<i>Acanthophis antarcticus</i>	166 \pm 7	17
	<i>Crotalus horridus</i>	142 \pm 17	19
Gape angle	<i>Acanthophis antarcticus</i>	67 \pm 13	15
	<i>Crotalus horridus</i>	77 \pm 12	19
Distance to prey in head lengths	<i>Acanthophis antarcticus</i>	0.75 \pm 0.6	20
	<i>Crotalus horridus</i>	1.9 \pm 0.9	16

All angles were measured during the extension phase of the strike during which the snakes accelerated toward the prey.

terrestrial, many more hang on to their prey than release it (31 out of 38 analyzed strikes resulted in the snakes not releasing their prey), which still is significantly more prey releases than expected. The same is true when only elapine elapids are analyzed (21 out of 25 analyzed strikes resulted in the snakes not releasing their prey). Hydrophiine elapids, in contrast to what we expected, also preferentially hang on to their prey (10 out of 13 analyzed strikes resulted in the snakes not releasing prey).

The analysis of the influence of prey size on the prey release behavior of snakes revealed that in terrestrial vipers the mean prey size relative to the size of the snake was significantly greater in those capture events in which prey was released (mean = 0.698) than in capture events in which the snakes did not release their prey (mean = 0.645) (Kolmogorov–Smirnov $Z = 1.366$, $p = 0.048$). In elapids, which released their prey less frequently in general, mean relative prey size was larger for those capture events in which the snakes released their prey (mean = 0.979) than in those capture events in which the snakes did not release their prey (mean = 0.758), but the differences in mean prey sizes were not significant ($F = 4.1$, $df = 37$, $p = 0.051$). When only elapine elapids were considered, there was a significant effect of prey size on their propensity to release their prey. The relative size of prey that were released was significantly larger (mean = 1.046) than the relative size of prey that were not released (mean = 0.681) ($F = 32.72$, $df = 24$, $p = 0.000$). For hydrophiine elapids, there was no significant difference in size between the released and not released prey ($F = .015$, $df = 12$, $p = 0.904$). In fact, mean size for released prey was smaller (mean = 0.889) than for prey that was not released (mean = 0.920).

To solve the question about the possible convergence of the strike behavior of *Acanthophis* with that of vipers, only 19 strikes could be analyzed, all by the same

individual. Our results, as well as comparators from the literature (Cundall 2002), are summarized in Table 3. *Acanthophis* specimens initiate strikes when they are closer to their prey, have smaller gapes and smaller fang angles to the braincases during a strike, and raise their heads relative to their trunks more steeply compared to *Crotalus*.

4. Discussion

4.1. Releasing prey

One aspect of functional plasticity we investigated was the predilection of species to release their prey after striking at it. We hypothesized that this predilection should be influenced by preferred habitat and by the size of the prey item. The vast majority of non-venomous colubrids we observed did not release prey after they grabbed it. This was expected, because without immobilization of the prey by venom or constriction any prey released by a non-venomous species is likely to sustain only minor injuries and be able to escape. In our records, prey items were released in only two instances out of 36 prey capture events. Both involved the same individual *Farancia abacura* feeding on *Amphiuma tridactylum*. *Amphiuma* specimens are large, slippery, eel-like aquatic salamanders that are difficult to subdue. An attack by *Farancia* usually results in a violent struggle between predator and victim, during which the snake attempts to constrict the *Amphiuma* while at the same time maneuvering its head to one end of the prey to swallow it. If the snake loses its grip, the *Amphiuma* is very likely to be able to escape. In two of eight prey capture events involving *Farancia* and *Amphiuma*, the *Amphiuma* won the struggle. A ninth capture event by *Farancia* involving *Siren*, a smaller eel-like salamander, resulted in a successful capture.

Rear-fanged colubrids also behaved as we expected. Only one out of ten prey captures resulted in the prey being released after the initial capture (Table 2). A *Diadophis punctatus* released a *Plethodon cinereus* on one occasion. In rear-fanged species, in which the passageway for the venom is not fully enclosed within the fang, as it is in vipers and elapids, the venom cannot be pressurized when it is being injected into the prey as it is in vipers (Young et al. 2000, 2003; Young and Zahn 2001) and probably also in elapids. Instead, it is introduced into the prey at low pressures, which is a slow method of envenomation, resulting in many rear-fanged snakes holding on to their prey after grabbing it and repeatedly slashing it with their fang (Smith and Bellairs 1947; Kardong 1979, 1980; Cundall 1983). Thus, releasing prey soon after first grabbing it would likely result in insufficient envenomation of the prey. This means that the prey would be lost to the snake, even if it ended up dying after a period of time.

Vipers are generally considered to strike at the prey from an ambush position and to release their prey after envenomation to trail it at a safe distance until it succumbs to the venom. This strategy removes the snake from any danger of retaliation by the prey, but is disadvantageous in an arboreal environment, because dropped prey items that fall to the ground do not leave a scent trail, and the snake would potentially be exposed to predation while spending considerable time trying to locate a scent trail and retrieve the envenomated prey. By hanging on to struck prey, arboreal snakes usually are able to avoid such predation risks on the ground where their camouflage may often be less effective. Our observations confirm that arboreal snakes do not release prey after they capture it. Only two prey captures out of 18 recorded for arboreal vipers, one by *Atheris squamiger*, another by *Trimeresurus flavomaculatus*, resulted in prey being released after the strike (Table 2). During a strike by an individual of *Trimeresurus*, the prey was struck on its dorsum and did not retaliate. However, the prey was relatively large, and this may explain why the prey was released (see also below). In a strike by an individual of *Atheris*, the relative size of the prey was not particularly large, but this prey capture event was unusual in that the snake had descended from its perch to the bottom of the cage and had grabbed the prey by the abdomen, which then initiated several vigorous defensive bites by the mouse to the snake's head until the snake finally let go.

Aquatic vipers were expected to hold on to prey for similar reasons as arboreal snakes, namely that released prey would be difficult to track in water. Only two strikes by aquatic vipers were observed; both were by *Agkistrodon piscivorus* feeding on terrestrial prey (i.e., mice) in a terrestrial setting (i.e., a filming box). Both animals released their prey after striking them. In the wild, *A. piscivorus* are often associated with the banks of

bodies of water or streams and are known to take a large variety of prey, from fishes and rodents to carrion (Savitzky 1992). Even when feeding on live fishes, however, the mode of attack of *A. piscivorus* is essentially terrestrial. *Agkistrodon piscivorus* grab a fish when it is trapped near the banks of a body of water and pull it ashore for consumption; they are not capable of pursuing fishes in water in contrast to, for example, *Nerodia* (Savitzky 1992). In light of this, *A. piscivorus* should be classified as a terrestrial feeder. Thus, their release of prey is not all that surprising. In fact, no vipers are considered to be fully aquatic (Pough et al. 2001), which suggests that there might be some constraints operating on this family entering aquatic habitats. These constraints may possibly relate to their prey capture behavior, but this remains to be explored.

In terrestrial vipers, we expected snakes preferentially to release prey because this behavior removes them from potential retaliation by their prey. However, terrestrial vipers released prey only slightly more often than holding them after striking them (42 releases Versus 38 holds). One aspect we hypothesized to influence the prey release behavior of snakes was the size of the prey. Prey usually does not die instantaneously when it is struck by a snake but succumbs gradually to the venom. The larger the prey is relative to the size of a snake, the less venom per unit of body mass it is likely to receive and the longer it will take to die. Thus, relatively larger prey items will be able to struggle for a longer period of time before dying. This struggle frequently involves violent hopping of the prey, which may result in equally violent movements of the snake's head. It may be advantageous to release such violently struggling prey and trail it at a safe distance. Indeed, we found that the prey was significantly larger in strikes that ended in prey release than in strikes, in which snakes retained their grasp of the prey.

Besides prey size, morphological factors may also influence the propensity to release prey by a snake. In many vipers, the dorsal constrictor muscles, which are responsible for the movements of the palato-maxillary arches during the strike, are long, allowing great maxillary and prefrontal rotations during prey capture. The protractor pterygoidei muscle of many vipers, in contrast to that of other snakes, originates far rostral on the ventral braincase, directly caudal to the snout and can, thus, protract the palato-maxillary arches further and faster (Fig. 3A). This capacity to protract the jaw apparatus is not exhausted during the extension and bite phases of the strike, as one might expect, but reaches its maximum during the quick release of and withdrawal from the prey when the snakes pull their long fangs from the prey (Cundall 2002). The snake can then quickly remove itself from the still alive and potentially dangerous prey. Since long protractor pterygoidei muscles allow the withdrawal of long, curved fangs from a

prey, variation within vipers in the rostral extension of the protractor pterygoidei muscle may influence their propensity to release prey. Vipers with short protractor pterygoidei muscles may hold on to prey after striking it, wait until the prey is dead and no longer dangerous, and then remove their fangs. Removal of the fangs from the prey under those conditions should be possible with short protractor pterygoidei muscles, particularly in species with shorter fangs. Vipers with long protractor pterygoidei muscles may have a greater propensity to release prey after striking it. Unfortunately, the length of the muscle is not known for many viperids. It would be interesting to determine whether the morphology of their protractor pterygoidei muscle correlates with the length of the fangs and with the propensity to release a prey after striking it.

In elapids, the protractor pterygoidei muscle is similar in its rostral extension to that of most non-venomous colubrids and does not extend as far rostrally as in many vipers. Thus, we expected that elapids may not release their prey after striking it. Indeed, elapids were less likely to release their prey, even though a few more individuals released prey than we predicted (seven releases out of 38 prey captures). This was the case for both subfamilies of elapids, even though the palato-maxillary arches of hydrophiines appear to have greater kinetic potential than those of elapines, because the connections of the palatine to the snout (nasals, premaxilla, vomers, and septomaxillae) and maxilla are reduced in that subfamily (McDowell 1970). The fact that elapids hold on to their prey has been mentioned in the literature. Lambiris (1967) observed *Naja haje* “retaining the grip and chewing until the toad died.” The same has been observed in the same species by Kardong (1982b), who used mice as prey items, as well as in *Micrurus fulvius* (Greene 1984). In contrast, Greene (1997) reports that *Dendroaspis* and *Oxyuranus* frequently bite and release prey. Our single analyzable strike by *Oxyuranus scutellatus* showed the snake holding on to its prey after the strike.

Whether elapids hold on to their prey because of reduced palato-maxillary mobility compared to that of most vipers, remains unclear. Other factors that may influence the frequency of prey release include the length of the fangs and the effectiveness of the venom. The fangs of elapids are shorter than those of vipers (Marx and Rabb 1972) and should, thus, be easier to extract from a prey, not requiring a viper-like palato-maxillary mobility. So why do most elapids not release their prey? Another factor potentially influencing the prey release behavior of snakes may be the efficacy of the venom. A snake with venom that immobilizes prey rapidly is in less danger of being harmed by its prey than a snake with slower-acting venom. This may mean that snakes with a fast-acting neurotoxic venom, such as elapids, may face less risk from retaliating prey and have a higher propensity for

holding a prey they have struck than snakes with a slower-acting hemolytic venom, such as most vipers. This statement is, of course, a simplification of a complex situation. The problem with such a simplified statement is that the dichotomy of neurotoxic venom *versus* hemolytic venom is not at all clear cut and that venom action and toxicity is difficult to assess, being influenced by the amount of venom injected, the site of venom injection, and the type of prey the venom is injected into (e.g., Hodgson and Wickramaratna 2002; Mackessy 2002; Fry et al. 2003b). For example, we have observed viper strikes, in which mice were struck in mid-air as they were dropped into the filming arena and died, or became immobile, before or as they hit the ground. In contrast, we have also observed strikes by elapids, in which the prey took minutes to die and hopped around, while the snake held on to the prey.

It is likely that the propensity to release prey is influenced to some degree by all the factors that have been mentioned so far. There is evidence that some snakes modify their release behavior as a function of prey size or with the number of prey items they have envenomated, as reported for *Agkistrodon piscivorus* and *Naja haje* by Kardong (1982b). When *Agkistrodon piscivorus* were presented with several prey items in rapid succession, they released the prey they captured early on, but held on to prey they captured later (Kardong 1982b), presumably adjusting their behavior to the depletion of venom. *Naja haje*, in contrast, had a tendency to hang on to its prey and generally only released it when the prey retaliated. Both species, though, tended to release larger prey (Kardong 1982b). Another factor that may relate to prey release is the amount of venom that can be injected in a bite. Hayes et al. (2002), in a review of the factors that influence venom expenditure in venomous snakes, found that vipers are often able to inject more venom into a prey during a bite than are colubrids and elapids, with the exception of *Acanthophis*. They proposed that the need to inject sufficient venom into a prey results in the inclination to maintain a hold on the prey item in elapids and venomous colubrids. Hayes et al. (2002) also found that the duration of fang contact with the prey did not influence the amount of venom delivered by vipers that release prey, suggesting that those snakes are able to inject sufficient amounts of venom very quickly and then retreat from the prey to avoid retaliation.

4.2. An elapid species striking prey like a viper

Acanthophis sp. are unusual elapids that resemble vipers in body shape and some behavioral aspects, such as sit-and-wait predation (Shine 1980). Morphological and behavioral similarity extends even to retinal anatomy (Walls 1942) and caudal luring (Carpenter

et al., 1978). In fact, *Acanthophis* is so similar in appearance to vipers that it once was classified as the only Australian viper (McCoy 1878–1890). Whereas most terrestrial elapids have slender bodies with heads not much wider than their anterior trunk (Spawls and Branch 1995), *Acanthophis* is a short, stout snake with a large, triangular head (Cogger 2000). Unlike most terrestrial elapids that forage actively for prey (Shine 1977, 1979), *Acanthophis* is a sit-and-wait forager that strikes a prey from an ambush position (Shine 1980). Compared to other elapids, *Acanthophis* also has relatively large fangs, a shorter maxilla (Marx and Rabb 1972; Cogger 2000), and, like other hydrophiine elapids, lacks close connections between the palatine, maxilla, and snout (nasals, premaxilla, vomers, septomaxillae) (McKay 1889; Deufel and Cundall 2003a). It has been suggested that *Acanthophis* has the most extensive maxillary rotation of any elapid and that most of this rotation is due to a rotation of the prefrontal on the frontal, carrying the maxilla rostrally (McKay 1889; Fairley 1929).

Our analysis of numerous strikes to live mice and some lizards by *Acanthophis antarcticus* revealed that it does indeed launch very rapid strikes from an ambush position. The ambush position of *Acanthophis* differs, however, from that of vipers. Whereas terrestrial vipers frequently form multiple coils with their bodies from which they launch their head on a slender anterior trunk (Cundall and Beaupre 2001; Cundall 2002), *Acanthophis* usually forms only one loop with its short body, placing its tail tip with the caudal lure directly in front of its snout (Fig. 5). *Acanthophis* also differs from *Crotalus* in the timing of the strike initiation. Whereas *Crotalus* usually struck a prey that was almost two head lengths away from its snout, *Acanthophis* waited to strike until a prey had approached closely, usually to within a distance of less than one head length. Strikes by *Acanthophis* were so forceful that two thirds of the snake's body frequently left the ground. The potential for palato-maxillary

movement of *Acanthophis* also does not reach the extent of that of *Crotalus horridus* (Table 3). *Acanthophis* does not elevate its head, rotate its fangs, or opens its mouth to the same degree as *Crotalus*. In *Acanthophis* the origin of the protractor pterygoidei muscle appears to be more rostrally located than in other elapids, although probably not to the same extent as in most vipers (McKay 1889; Fairley 1929). The palatine of *Acanthophis* does not show the reduction in length that is seen in vipers. Thus, the palatine may limit the excursion of the palato-maxillary arches by abutting against the ventral snout elements (vomers, septomaxillae), even though the palatine is not as tightly connected to the snout as it is in elapine elapids. The admittedly limited morphological and kinematic evidence we have currently suggests that the palato-maxillary kinematics of *Acanthophis* might be intermediate between that of most elapids and that of vipers.

4.3. Summary and conclusions

Colubroid snakes have evolved a range of behavioral and morphological solutions to deliver venom into prey. The Viperidae, the most basal branch of the colubroid tree, arguably has the most modified venom apparatus with the greatest palato-maxillary mobility. Once evolved, the viperid feeding apparatus was so successful that it has not changed greatly. In fact, viperids are arguably the most successful clade of venomous snakes. Anatomical modifications allowing the kind of maxillary mobility seen in vipers are the mobilization of the palato-ptyergoid bar from the snout in combination with a reduction in the size of the palatine, the elongation of the protractor pterygoidei muscle, and the conversion of the maxillary–prefrontal joint from a broad sliding articulation to a mobile hinge joint that is constrained to move around a defined axis, causing the fangs to rotate antero-laterally during protraction.



Fig. 5. *Crotalus horridus* (A) and *Acanthophis antarcticus* (B) in ambush position. *C. horridus* rests with its body in several coils, whereas *A. antarcticus* forms only one coil with its body. Note the viper-like body proportions and caudal lure placed in front of the head of *A. antarcticus*. The *Crotalus* was photographed in the field, whereas the *Acanthophis* was photographed in captivity.

The kinetic potential of the viper venom delivery system is most fully realized in those species that release prey immediately after the envenomating strike.

Atractaspis has evolved the solenoglyph condition independently from that of vipers and the anatomical similarity between its venom delivery system and that of vipers is only superficial. In *Atractaspis*, the constraints of a fossorial lifestyle have resulted in palato-maxillary arches in which the pterygoid has been freed from a palatine that is firmly attached to the vomers and premaxilla of a robust snout. Although the palato-maxillary arches of *Atractaspis* may appear very mobile upon casual inspection, maxillary rotation is actually limited to facilitate prey envenomation by a downward-backwards stab of a fang. *Atractaspis* crawls up next to its prey in an underground tunnel or rodent burrow, projects the tip of the fang that lies closer to the prey from its closed mouth, and embeds this fang, which is pointing caudo-laterally, by jerking its head toward the prey (Deufel and Cundall 2003b).

The proteroglyph venom delivery system of elapids is less profoundly modified from the generalized colubrid condition as compared to the solenoglyph venom delivery system of vipers and *Atractaspis*. The maxilla is shortened to a lesser degree, and its joint with the prefrontal is a broad sliding articulation with less rotational mobility in the sagittal plane. The palatopterygoid bar is freed from its connections to the snout only in hydrophiine elapids, and the protractor pterygoidei muscle is not elongated. Elapids are active foragers that lunge at prey, which they generally do not release after striking it. This behavior is possibly a reflection of their comparatively immobile palato-maxillary arches and fast-acting venom. Effectiveness of the proteroglyph venom delivery system on prey under natural conditions is unclear and largely untested, but innumerable fatal human envenomations by many different elapids are testament to its potential (e.g., Shine and Covacevich 1983; Shea et al. 1993; Spawls and Branch 1995; Fry et al. 2002, 2003b). Elapids have achieved their greatest diversity in Australasia, and in some parts of that region (i.e., Australia, New Guinea), they have no competition from vipers. One Australasian elapid, *Acanthophis*, has evolved a prey capture strategy and apparatus that begins to converge on that of vipers. However, elapid diversity throughout much of the range of the family may also reflect an adaptation to exploit diverse, but mostly ectothermic prey.

Very little is known about the prey capture kinematics of most opisthoglyph snakes. The wide range of morphologies found in rear-fanged snakes may be correlated with very varied prey capture behaviors, although all the species that have been examined perform unilateral maxillary movements during prey capture. This behavior has been observed in snakes feeding on diverse prey, such as *Heterodon* capturing

toads (Cundall 1983) or *Oligodon* feeding on reptile eggs (Coleman et al. 1993). Exploration of the feeding kinematics in opisthoglyph snakes would be a valuable contribution that may help elucidate not only the evolution of venom delivery systems but may also shed some light on the many unresolved questions of colubrid relationships.

All snake venom delivery systems are based on the same set of palato-maxillary structures and operate within the constraints imposed by the fact that there is much overlap in the structures used for prey capture and prey transport (Cundall 1983). Remarkably, increased palato-maxillary mobility associated with prey capture does not appear to increase prey transport performance in most cases (see Cundall & Deufel, in this issue). Only in *Atractaspis* have modifications for prey envenomation resulted in a decreased prey transport performance, which is possibly not detrimental only because of the relatively protected fossorial lifestyle of this genus (Deufel and Cundall 2003b). Hence, we conclude that venom delivery systems in most ophidian clades are functionally remarkably flexible, enabling behavioral modifications to evolve to suit various types of prey or habitat.

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