ENVENOMATION STRATEGIES, HEAD FORM, AND FEEDING ECOLOGY IN VIPERS

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ABSTRACT: Kinematic analyses of field and laboratory strikes in several species of rattlesnakes (*Crotalus*) closely match selected features of previous descriptions of strikes in other species of *Crotalus* and in the viperines *Bitis* and *Vipera*. Vipers strike at prey using moderate, not maximum gapes. The bite phase of a strike is usually as long as the time interval taken to reach the prey. Release of the prey is rapid and involves gape angles and maxillary protractions nearly double those used in reaching the prey. These features of viperid strikes suggest that one of the critical kinematic phases of strikes generating selection pressures on head form and kinematic range is prey release, not prey envenomation. Measures of anterior trunk form show a reduction of anterior body mass in viperids, and these features may correlate with average strike distances and peak strike velocities. In many species, increased posterior body mass, possibly aided by fecal retention, may serve in increasing the inertia and reducing reaction distances moved by the caudal trunk when the cranial trunk is accelerated rapidly at prey. Vipers represent structural/functional compromises to achieving rapid strikes while retaining the capacity to transport prey of relatively large diameter.

INTRODUCTION

The envenomating apparatus that defines vipers (Underwood, 1967; McDowell, 1987) includes the head with a rotating maxilla and a trunk modified for rapidly accelerating the head (Gasc, 1981; Janoo and Gasc, 1992; Kardong and Bels, 1998). Thus, how the head moves is determined not only by particular features of the head, but also by features of the trunk. If the potential range of head movements defines the predatory strategy of a viper, then we should be able to gain some measure of the kinds of selection pressures influencing the evolution of vipers by analyzing how the various parts of the body influence the behavior of the head. Body form variables might add to the suite of measurable morphological correlates to both behavior and ecology, as suggested by Pough and Groves (1983). In combination with features of the head critical to striking, aspects of body form broaden our views on feeding constraints from those primarily influencing gape and events occurring *after* prey capture (Arnold, 1983; Greene, 1983) to include those events *preceding* and *including* prey capture.

Vipers and constrictors share an ability to capture and immobilize prey larger than they are capable of eating. But because snakes are rarely observed in the act of subduing prey, efforts to test relationships among gape size, head size, and prey size or type have been keyed largely to what snakes have swallowed (e.g., Camilleri and Shine, 1990; Forsman, 1991; Forsman and Lindell, 1993; Arnold, 1993; Shine et al., 1998). In this paper I explore how the prey came to be in a swallowable condition, taking the perspective that because snakes cannot eat what they cannot catch,

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selection for successful prey catching strategies in vipers may have had priority over selection acting on all subsequent prey handling processes.

Prey Capture and Striking Mechanics

The abilities of vipers to envenomate us have colored many interpretations of how viper heads function (e.g., Mitchell, 1861; Rubio, 1998). Studies of viper head anatomy (e.g., Kathariner, 1900; Phisalix, 1914, 1922; Haas, 1929, 1931, 1952; Radovanovic, 1935, 1937; Dullemeijer, 1956, 1959; Boltt and Ewer, 1964; Brattstrom, 1964; Kardong, 1973) have been periodically illuminated by empirical data on function. Early photographic studies of strike kinematics (e.g., Van Riper, 1954, 1955; Lester, 1955) apparently began with the view that the head of a viper is best understood as a defensive apparatus. Most subsequent studies have concentrated on predatory strikes (Kardong, 1974, 1986, 1992; Kardong et al., 1986; Janoo and Gasc, 1992; Kardong and Bels, 1998).

Recent data on viperid strikes (Janoo and Gasc, 1992; Kardong and Bels, 1998; LaDuc, this volume) have high temporal resolution and provide a base for understanding the time course of events and changing velocities and accelerations of different parts of the snake's head and body. Of the five species of vipers examined to date (*Bitis gabonica*, *B. nasicornis*, *Crotalus atrox*, *C. viridis*, *Vipera ammodytes*), all share similar timing of movements during the extension phase of the strike, and all usually hit the prey first with the mandible. *Crotalus viridis* slows just before contact with the prey (Kardong and Bels, 1998), but *C. atrox* reaches peak velocity at or just after prey contact (LaDuc, this volume). All species bite the prey after contact, and this phase usually lasts longer than the extension phase. In terrestrial vipers, the bite often ends in a rapid release of the prey,
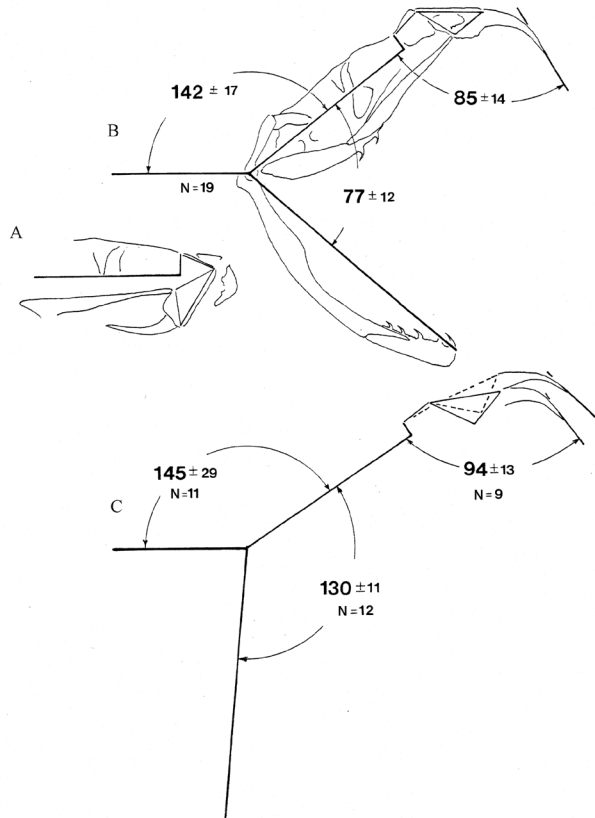
Fig. 1. Diagrammatic summary of maximum angles reached from rest (A) between the braincase and fang tip, braincase and neck, and braincase and mandible (gape) during extension (B) and during release and withdrawal (C) in adult *Crotalus horridus*.

involving gape angles greater than those used during extension, and then withdrawal of the head. Rapid reversal of head movements in some terrestrial vipers differs from the behavior of some (possibly most) arboreal vipers and from booids. The former hold onto prey until immobilization from envenomation (D. Cundall, unpublished data for various arboreal viperid taxa), and the latter usually retain their grasp on the prey during constriction (Cundall and Deufel, 1999; Deufel and Cundall, 1999). Here I re-examine three events during extension, release, and withdrawal phases of the strike from the perspective of recent data for strikes in *C. horridus* recorded in the field and in the lab. I then consider how momentum may influence strike kinematics, body form, and foraging behavior.

Methods of Analyzing Strike Kinematics

Strikes were recorded with a Panasonic AG-486 SVHS video camera at 60 fields/sec and analyzed with a Panasonic AG-1970 VCR. These low temporal resolution records prevent detailed analysis of movement changes possible with faster framing rates but

still provide clues to the behavioral potential of the snakes. Filming conditions varied for the different snakes studied. Twenty-four strikes by one adult *C. horridus* to live mice and rats of various sizes were made in a filming chamber with a mirror mounted vertically at the left side at 45° to the focal plane. Fifty-nine strikes to small live mice were recorded for eight neonate and juvenile *C. horridus* in their home cages. Finally, five strikes by two free-ranging, radio-tagged *C. horridus* to live *Rattus norvegicus* (~ 150 g body mass) were analyzed (Cundall and Beaupre, 2001). These strikes test the equivalence of kinematics in the laboratory and in the field despite potential increases in kinematic variance arising from differences in prey size, prey type, and the age and size of the snakes (Hayes, 1991, 1995).

Analysis of the strikes concentrated on detecting maximum angles of the braincase to the anterior trunk, braincase to mandible (gape, as measured in Cundall and Deufel, 1999, not as in Kardong and Bels, 1998), and braincase to fang tip (Fig. 1). Distance to the prey when the strike began was measured in snake head-lengths. Fate of the strike was coded as: 1, a successful strike with no corrections; 2, a successful strike but prey bit snake; 3, a miss; 4, a miss followed by correction and envenomation, 5, contact with prey but no bite phase and no fang penetration.

Movements of the Prefrontal

As the mouth opens during the extension phase of the strike, the prefronto-maxillary joint and snout are elevated in some crotalines (e.g., *C. horridus*) but presumably not in all vipers (e.g., Liem et al., 1971). Rotation of the prefrontal around its attachment to the frontal carries the fang base dorsally relative to the snake's braincase (Fig. 2.1–2.4). As the extension phase progresses and gape increases, the maxillae appear to be rotated from 70–90° (Fig. 3a), occasionally to 110°, but nearly half the apparent rotation of the maxilla may be accounted for by rotation of the prefrontal. In the frame prior to that in Figure 3a (see Cundall and Beaupre, 2001), the snout is flexed dorsally, moving both the nostril and pit upward relative to the axis of the braincase. That such movements of the prefrontal and maxilla are possible is shown in many photographs of striking or yawning (e.g., *C. ruber*, Phelps, 1981; *C. atrox*, Halliday and Adler, 1986) or venom extraction (e.g., *B. arietans*, Patterson, 1987; *C. adamanteus*, Rubio, 1998).

The snake's braincase usually passes over the dorsal surface of the prey as the mandibles hit the prey
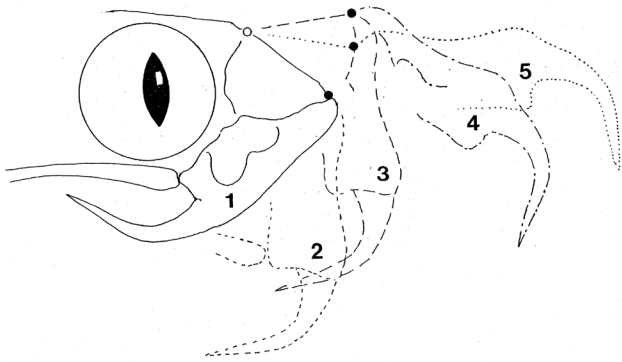
Fig. 2. Proposed prefrontal and maxillary excursions during predatory strikes in crotalines. In most crotalines, the ectopterygo-maxillary joint lies at the ventral edge of the pit emargination of the maxilla, not at the edge of the dentigerous surface as shown. 1 = resting position, 2 = maxillary position in mid-protraction with no prefrontal rotation (all rotation occurred at the maxillo-prefrontal joint), 3 = maxillary position in mid-protraction following pre-frontal rotation with essentially no rotation at the maxillo-prefrontal joint (the usual behavior), 4 = maxillary position near contact with the prey, with fang tip angle still not vertical to the braincase axis, and 5 = full maxillary protraction, seen during release of the prey. Position of the maxillo-prefrontal joint at (5) remains unknown. The ectopterygo-pterygoid joint at (4) and (5) lies near or under the prefrontal-frontal joint, leaving the anterior end of the pterygoid under the snout. Palatine movements appear to vary among viperid taxa.

Fig. 3. Video frames from a tape recorded at 60 fps of a strike by *Crotalus horridus* in the Ozark Mountains of Arkansas showing head form (A) immediately prior to prey contact and (B) 16.5 msec after contact.

(Fig. 3b). In adult *C. atrox* and *C. horridus* the snake's head is usually travelling near peak velocity when the mandibles contact the prey (Young et al., 2001; LaDuc, this volume). In four of 20 predatory strikes by one adult and in 24 of 54 strikes by eight neonate and juvenile *C. horridus* in which direction of fang entry could be seen, the fangs appeared to be dropped onto or stabbed into the prey. In the remaining strikes, the fangs entered the prey during the contact or bite phase of the strike.

Elevation of the prefrontal reduces the distance of the fang tip from the roof of the mouth. Given the geometry of the prefrontal and maxilla in many cro-talines, simple rotation of the maxilla without prefrontal elevation would carry the fang base and fang ventrally if the maxillary-prefrontal joint remained in its resting position (Fig. 2.2; see Klauber,1972; Savitzky, 1992; Rubio, 1998). The benefits of prefrontal elevation may seem counterintuitive. However, in many predatory strikes of larger *Crotalus*, the fangs usually are not stabbed into the prey but are carried over the dorsal surface of the prey. Maxillary positions near 4 (Fig. 2), which appear to be the most common at the end of extension, may reduce the possibility of the fangs
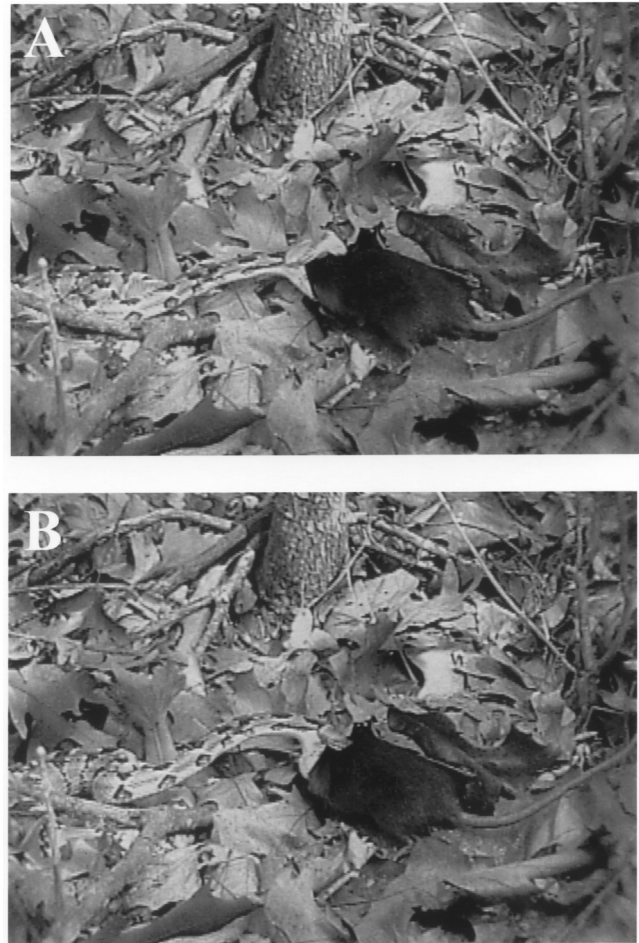
catching on the prey surface before the relative velocity of the upper jaw to the prey surface falls to near zero.

During extension, crotalines usually rotate the braincase upward on the neck. But, in many strikes, maximum dorsal rotation of the braincase relative to the anterior trunk (Fig. 1b) occurs in mid extension (Kardong and Bels, 1998), and the braincase begins to rotate ventrally on the neck before the snake reaches the prey. Hence, the position of the head shown in Figure 1b is not the position of the head at prey contact but simply maximum angles achieved at some point during extension (Table 1). As in booids (Deufel and Cundall, 1999), the actual kinematic patterns of both the braincase and the fangs appear designed to increase the probability that the fangs tips are directed posteroventrally, not anteroventrally at prey contact (Fig. 2). Given this orientation, as the snake's mandibles contact the prey, accelerating the prey in

Table 1. Maximum angles (means ± SD), distances (in head lengths) to prey for predatory strikes by one adult and eight neonate and juvenile *Crotalus horridus*.

	Adult	N	Neonate/Juvenile	N
Extension				
Fang to braincase	85 ± 14	19	80 ± 9	39
Trunk to braincase	142 ± 17	19	160 ± 16	41
Gape	77 ± 12	19	66 ± 13	26
Withdrawal				
Fang to braincase	94 ± 13	9	90 ± 10	25
Trunk to braincase	146 ± 29	11	129 ± 22	25
Gape	130 ± 11	12	126 ± 12	26
Distance to prey	1.9 ± 0.9	20	1.4 ± 0.9	46

the direction of the strike, the fangs are brought down on the prey's surface (e.g., Rubio, 1998:83). What this means is that the fangs often penetrate the prey on the side opposite that from which the strike began, and fang entry occurs as a function of the bite or contact phase, not the extension phase. Hence, at the critical moments of prey contact and envenomation both upper and lower jaws lie well below maximum displaced positions.

Timing of Maximum Gape and Fang Positions

Although my records lack the temporal resolution of those of Janoo and Gasc (1992) and Kardong and Bels (1998), our combined observations show that gape during the initial stages of withdrawal reaches angles greater than achieved during extension (Fig. 1c). Maximum fang angles have a different timing. As noted above, angle of the fang tips to the braincase at contact are usually slightly less than 90°. The fangs are presumably partially retracted during the bite phase, although how much is impossible to see because the fangs are embedded in the prey. Release and early withdrawal are accompanied by the appearance of astonishing fang angles, which may be arrived at only if the maxillae are extended nearly horizontally in front of the braincase (Fig. 2.5). Achieving such angles requires extraordinary mobility of the maxilla and may have favored loss of bony palatine associations with the snout in most vipers (Underwood, 1999), and extraordinary loosening of snout associations with both the braincase and the upper jaw. Full protraction is typically maintained for only a short time after contact with the prey surface is lost (probably less than 15 msec; my records lack the resolution to give more precise estimates), and usually the fangs are retracting as peak gapes are reached in withdrawal. In

other words, mandibular abduction continues as the palatomaxillary arches are brought caudally, a feat that must involve complex modulation of pterygoideus, mandibular depressor, and possibly palatine retractor activities.

The limited functional morphological literature on viper strikes is dominated by the view that the fangs move directly anteroposteriorly in a parasagittal plane (Dullemeijer, 1956; Dullemeijer and Povel, 1972; Boltt and Ewer, 1964; Kardong, 1974; Kardong et al., 1986). Anterior views of the strike show that the entire palatomaxillary apparatus moves markedly laterally as well as rostrally such that the distance between fang tips when they penetrate the prey is approximately double ($\bar{x} = 2.3$ times the resting distance for five adult strikes, 2.2 for three neonate strikes) the resting distance between the fangs. Fang puncture marks for defensive strikes compared to resting fang tip distances in *C. atrox* show equivalent lateral spread of the fang tips (Zamudio et al., 2000). The approximate direction of fang travel is therefore anterolaterally and posteromedially, and appears to occur over a surprisingly long path (Fig. 4). This departure from past interpretations means 1) that both fang tips are unlikely to penetrate the same anatomical region of smaller prey, 2) the probability that one fang will hit the prey increases, and 3) the probability that one fang tip will penetrate soft tissues (and not hit bone) increases.

Maximum Bone Displacements and Viperid Head Design

The important point in the timing of fang and gape angles is that maximum displacements of both the mandibles and the fangs are usually achieved *after* envenomation, rarely before or during (Janoo and Gasc, 1992; Kardong and Bels, 1998). Anteroposterior
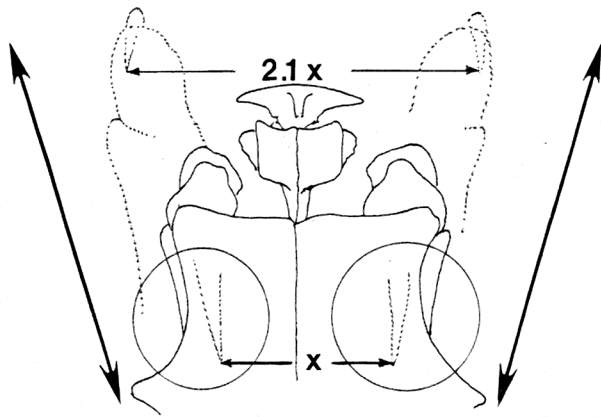
Fig. 4. Dorsal view of the anterior end of a typical crotaline skull showing fang tip positions at rest (x) and following protraction during a strike (2.1x). The precise relationship between fang tip spread and protraction remains to be determined.

palatomaxillary movements in vipers exceed those so far recorded for any other major clade of living snakes. Increased palatomaxillary excursion correlates with restructuring of the floor of the braincase and its associated dorsal constrictor muscles. In most non-viperid colubroids examined, the pterygoid protractor arises from the basisphenoid at or well caudal to the caudal edge of the orbit, and also caudal to the origin of the palatopterygoid and vomerine retractors (e.g., Albright and Nelson, 1959; Weaver, 1965; Haas, 1973; Varkey, 1979; Cundall, 1986). Also, these taxa are characterized by a narrow interorbital parasphenoid. In many vipers, conversely, the origin of the pterygoid protractor has migrated to the extreme anterior end of the parasphenoid at the anterior edge of the orbit whereas the retractor origin still lies caudal to the orbit (e.g., Boltt and Ewer, 1964; Kardong, 1973). The parasphenoid is broad in many taxa (e.g., Jan and Sordelli, 1881; Boulenger, 1896; Radovanovic, 1937; Dullemeijer, 1959; El-Toubi and Magid, 1961; Zhang and Zhao, 1990; Zerova and Chikin, 1992; Zhang, 1993). In many vipers, the net effect of these structural reorganizations is to increase the length of the two muscles that protract and retract the palatopteryoid bar relative to the length of the palatopterygoid bar itself (Fig. 5). Whereas the palatomaxillary arches of most non-viperid snakes appear to move at most 10–15% of the total length of the arch, the upper jaws of some *Crotalus* may move between 20 and 30% of total arch length, and similar abilities will presumably be demonstrated eventually in other vipers, but probably not all. Typical colubrid relationships for the pterygoid protractor and retractor are seen in some viperines, like *V. berus* (Dullemeijer, 1956) and *V. aspis*
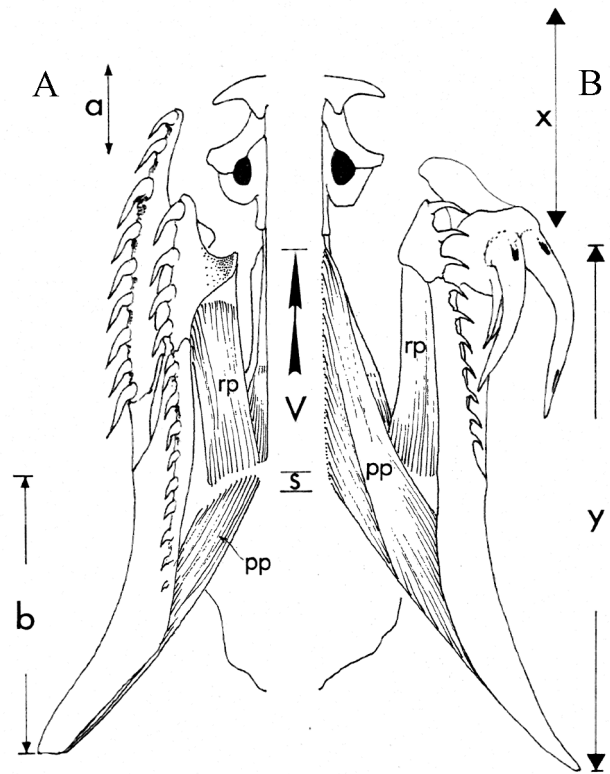

Fig. 5. Ventral views of the floor of the braincase, palatomaxillary arches, and pterygoid protractor and retractor of (A) a typical colubrid and (B) crotalines and derived viperines. Labeled arrows show approximate range of anteroposterior motion of the palatomaxillary arch (a,x) and approximate lengths of the pterygoid protractor (b,y). Abbreviations: pp, protractor pterygoidei; pt, pterygoid; rp, retractor pterygoidei; s, shared region of origin of protractor pterygoidei; V, viperid extension of protractor origin—varies among viperids as suggested by double arrow.

(Kramer, 1977), as well as in *Azemiops feae* (Liem et al., 1971) and in *Causus* sp. (Sülter, 1962). Although the relationship between muscle length and fang excursion remains to be analyzed quantitatively in any viperid, *V. berus* (Dullemeijer, 1956), like *B. arietans* (Boltt and Ewer, 1964) and possibly most terrestrial viperids, releases larger prey after envenomation.

Full palatomaxillary protraction is rarely seen during prey transport in crotalines (Kardong, 1977; Cundall, 1983; Kardong et al., 1986; Cundall and Greene, 2000). Hence, it seems unlikely that prey transport drove the evolution of this movement capability. Although vipers have the most efficient transport capabilities measured for snakes (Pough and Groves, 1983), it appears that, for crotalines at least, this efficiency is achieved using only part of palatomaxillary excursion potential. Hundreds of recorded transport cycles for *Agkistrodon piscivorus* and *C. horridus* have yet to show fang protractions beyond position 3
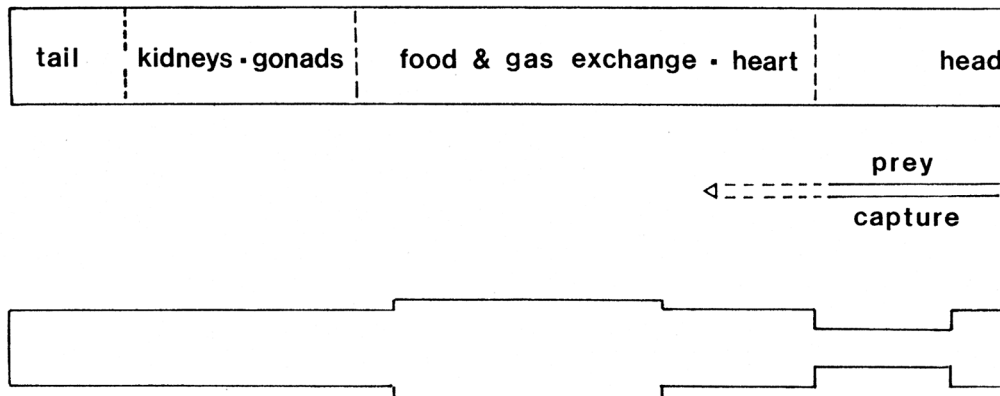
Fig. 6. Simplified views of snake trunks. In the top diagram, which fits the general design of basal alethinophidian snakes, the body is a simple cylinder with longitudinal partitioning of major functions and their associated structures. Viperids and other rapidly striking snakes conform more closely to the distribution of mass shown in the lower figure. The shift in mass conforms to evolutionary changes in primary functions of the anterior trunk from locomotion to prey capture.

in Figure 2. Viperine transport and strike kinematics have been studied in less detail (Cundall and Greene, 2000). Although other explanations for rearrangements of the dorsal constrictors are possible (e.g., increased kinesis of the palatomaxillary arch allows shock absorbing movements at prey contact), the most likely explanation relates to one of the behaviors that uses maximum excursions, release of living prey after envenomation. Hence, the kinematic potential of the envenomating apparatus of many viperids appears to be an evolutionary response to selection pressures arising from the mechanical demands of prey release, not to the mechanics of envenomation of prey. If defensive strike kinematics also use the full excursion potential of the palatomaxillary arch (Young et al., 2001; LaDuc, this volume), the question then arises as to which function is actually driving selection or whether both have contributed. A partial answer to this question may lie in the variance of the two kinematic patterns.

Body Design, Mass, and Momentum

Although vipers vary in body shape, most have distinct heads and relatively narrow "necks." Assuming that snakes really are extended thoraxes (Cohn and Tickle, 1999), the anterior trunk of vipers is noticeably smaller in circumference than midtrunk regions. Comparing 17 colubrid species to 30 viperid species based on the relationship between maximum circumference of the body to snout-vent length showed that viperid bodies are relatively more stout (Pough and Groves, 1983). Further, vipers have relatively longer skulls and mandibles and their skulls are wider with greater circumference at the quadrates than are those of non-vipers (Pough and Groves, 1983).

These morphological features correlate with the ability of vipers to eat prey that is relatively large in both mass and circumference. As noted above, behavioral assays based on numbers of palatomaxillary cycles to complete oral transport showed that vipers use fewer jaw movement cycles than colubrids when handling prey of equivalent relative mass, interpreted as increased efficiency (Pough and Groves, 1983). Stoutness of the trunk correlates with the tendencies of many vipers to use rectilinear locomotion and sit-and-wait ambush predation (Pough and Groves, 1983; Greene and Santana, 1983; Reinert et al., 1984; Greene, 1992, 1997).

Correlations based on relative stoutness of the trunk hide a number of other correlations to particular design features of viperid trunks. Vipers do not simply have stout trunks, they have trunks in which mass is partitioned along the length (Fig. 6). Although it is obvious that the anterior trunk is relatively slender compared to the posterior trunk in many vipers, quantifying the nature of the form in some biologically meaningful fashion is more difficult.

Methods of Body Design Analysis

The basic design of Pough and Groves' experimental approach to examining body form was extended to consider how body shape relates to prey capture. Using fluid displacement, the masses of the anterior fifth, fourth and third of the trunks of 115 snakes from four major groups (1, basal alethinophidians; 2, booids; 3, viperids; and 4, acrochordids + nonviperid colubroids) were measured (D. Cundall et. al., unpublished). The method assumes that the outer shape of the body is an accurate reflection of the rela-

Table 2. Paired comparisons of skull dimensions in viperids and booids. N = number of pairs (one booid and one viperid value). * = $P < 0.05$. ** = $P < 0.01$.

Ordering variable	Viperids	Booids	
Related variables	$\overline{x} \pm$ SD	$\overline{x} \pm$ SD	N
Braincase length (mm)	24.4 ± 5.4	24.5 ± 5.6	20
Total length (mm)	34.2 ± 8.8	37.9 ± 9.9	17
Total mass (g)	4.78 ± 4.79	2.98 ± 2.43	20
Right mandible length (mm)	55.8 ± 18.2*	42.6 ± 12.0*	19
Left mandible length (mm)	55.3 ± 17.7*	42.0 ± 12.0*	20
Right mandible mass (g)	0.68 ± 0.67	0.56 ± 0.43	15
Left mandible mass (g)	0.67 ± 0.57	0.61 ± 0.43	15
Right mandible length (mm)	48.5 ± 14.6	48.6 ± 15.0	20
Braincase length (mm)	22.4 ± 4.8**	28.2 ± 7.0**	20
Total length (mm)	31.4 ± 7.1**	43.1 ± 12.1**	18
Total mass (g)	3.15 ± 3.64**	5.20 ± 6.16**	20
Right mandible mass (g)	0.52 ± 0.53*	0.99 ± 1.19*	16
Left mandible mass (g)	0.52 ± 0.53*	0.97 ± 1.17*	16

tive mass of the region. This is undoubtedly not the case but the assumption is a useful starting point for future analyses of trunk organization in snakes that will need to use analyses of cross sections like those of Moon and Candy (1997).

To gain some preliminary measure of the limitations on head design, skulls of 46 pythonids and boids (booids) and 37 viperids were measured and weighed to estimate differences in skull mass. Variables measured included total skull weight, total skull length, straight-line lengths of the left mandible, and weights for each mandible. The behavior of these variables was analyzed using paired t tests on 28 booid and 26 viperid skulls (Appendix I). Skulls of each major clade were paired on the basis of similar values (difference ≤ 0.05 times the smaller of the two values) for each of two variables. The first ordering variable was braincase length (from anterior edge of frontal on the dorsal surface to the caudal edge of the atlantal crest in the midline), the second, straight-line length of the right mandible. The number of pairs analyzed for each variable is given in Table 2.

Body Mass and Design

One-way ANOVA and post hoc Bonferroni comparisons of anterior trunk masses showed that booids and viperids are similar. In both clades, the first fifth of the trunk averaged 0.58 of the value for a cylinder, but progressively longer regions (quarter, third) were relatively more massive (~ 0.64 for first quarter, 0.75 for first third). Hence, the reduction in mass is concen-

trated in the region of the trunk immediately behind the head in both clades, as simple observation suggests. Further, because the first fifth included the head, the trunk region is significantly reduced in relative mass compared to basal alethinophidian taxa in which the same region of the trunk (including head) was 0.97 of the value for a cylinder.

Skull Design and Skull Mass

For a given braincase length, viperid skulls differ significantly from those of booids only in having longer mandibles (Table 2). The reciprocal comparison, looking at the relationships of the variables when pairs are arranged by length of the right mandible, gives a more revealing picture of how viperid skulls differ from those of booids (Table 2). For a given mandible length vipers have skulls that are two-thirds the length of booid skulls and just over half the weight. Importantly, viperid mandibles are only slightly more than half the weight of booid mandibles of the same length. Despite high variances, which probably reflect the phylogenetic diversity of the samples used and are similar in extent to those obtained by Pough and Groves (1983), all of these differences are significant. Vipers have either experienced selection for reduced skull length and mass for a given gape size, or increased gape size for skulls of a given length. In the absence of data on length and mass of the bodies associated with the skulls, these relationships are impossible to explore further.
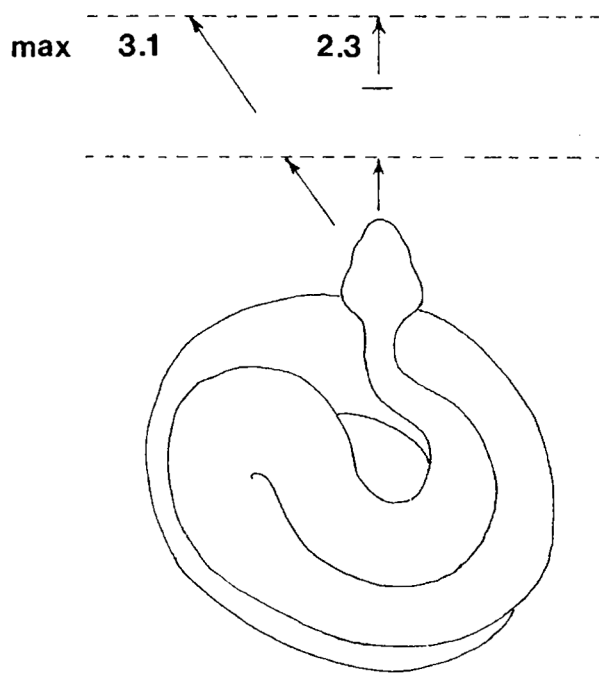
Fig. 7. Drawing taken from a photograph by G. MacGregor of a foraging *Crotalus horridus* in the Pine Barrens of New Jersey. The snake's head rested on a log that represented a runway for *Peromyscus leucopus*. The snake struck a running *P. leucopus* at the approximate position shown by the dash mark directly in front of the snake's head, (estimated to be 3 cm in front of the head of a snake 77 cm in total length) a strike length of less than 2 headlengths. If the snake's head extended to the opposite edge of the log, it would have traveled 2.3 head lengths. If the snake struck at the mouse on an angle, before the mouse reached or after the mouse had passed the resting position of the snake's head, the snake would have struck a possible maximum (max) strike distance from this foraging position, just over three times its head length.

Momentum-Reaction Model of Predatory Striking

Small vipers in the act of striking can react rapidly to prey proximity and often simply bite the prey as they contact it. Their heads and anterior trunks have little mass, and the muscle, skeletal, and connective tissues apparently operate well within biomechanical limits. This model may apply not only to juveniles of large species, but also to adults of many of the smaller species, like some species of *Cerrophidion* which may use a variety of foraging strategies and select a wide variety of prey (e.g., Campbell and Solorzano, 1992). Limits on accelerating and decelerating the head may be defined by contraction times for the head and trunk muscles, most of which probably have reaction times less than 15 msec, possibly half that duration.

Larger vipers incur increasing constraints due to scale because momentum increases as the product of both mass and velocity. The heads of larger snakes travel the same number of head lengths in the same time as those of smaller snakes (Table 1) but now both mass and velocity have increased. The larger a viper becomes, the more its strike behavior becomes captive to the effects of momentum. Potential solutions to the problems of increasing momentum are many. Evolutionary solutions may have involved restructuring the body to reduce mass in the regions that attain the highest velocity, and restructuring the head to increase shock-absorbing ability. Thus, the reduced mass of the anterior trunk, and the longer, generally lighter mandibles with muscle attachments reduced and limited to their caudalmost region, may be part of a suite of evolutionary responses to the mechanical effects of momentum.

Momentum effects will also likely influence kinematic properties of the strike. Larger vipers are likely to accelerate their heads maximally during extension but then be unable to stop exactly when they reach the prey, not because their reaction times have changed but simply because momentum at contact will carry the head past the prey. For smaller prey with limited inertia, contact by the mandibles of the snake may still suffice to accelerate the prey in the direction of the strike. For larger prey with greater inertia, the snake's mandibles will decelerate rapidly as the rest of the head and anterior trunk continue on, rotating around whatever point on the mandible becomes immovably connected to the prey surface. The behavior is similar to that seen in MAN strikes of booids (Cundall and Deufel, 1999) and for essentially the same reasons.

To generate high momentum on the head and anterior trunk requires that the rest of the trunk is either anchored in some way or has sufficient inertia to prevent reactive movements away from the prey. This simple expedient may underlie the tendency for arboreal vipers to have relatively slender bodies with little regional differentiation and for vipers frequenting unstable substrates (e.g., sand, dry leaves) to have more pronounced regional differentiation of body mass. In many complex environments, anchoring against irregularities in the environment probably suffices, but there are few field records describing anchoring of ambushing snakes. In more homogeneous environments or on relatively smooth substrates, vipers may depend primarily on the inertia of the posterior trunk provided simply by its mass. Given that most predatory strikes of terrestrial species will be made horizontal to the substrate, increased mass raises frictional resistance to movement. Fecal retention

(Lillywhite et al, 1998; this volume) in some vipers might substantially improve strike performance by increasing the mass of the posterior trunk. Tests of these possibilities will be extremely difficult given the number of variables involved in a typical predatory strike.

Kinematics in the Laboratory vs the Field

Laboratory kinematic studies suggest that most successful strikes are short (one to two head lengths). Predatory strikes longer than three head lengths are rare. Hence, captive vipers prefer to strike at prey only when they are relatively close. Is this a reasonable model for the behavior of vipers in the field and, if so, what does such a kinematic model tell us about the evolution of foraging in vipers?

How vipers strike at prey in the field is largely unknown. Video records of field strikes show properties similar to those recorded in the laboratory for the same species—distance to the prey was 1.3 head lengths for the first strikes by each snake recorded in the field (Cundall and Beaupre, 2001). Although there may be numerous photographic records in the hands of professional photographers, none have yet been kinematically analyzed. The only record I know of for a natural foraging viperid seen to strike a natural prey item comes from field observations by G. MacGregor (pers. comm.). Foraging position was photographed and the site at which the prey (*Peromyscus leucopus*) was struck was seen and recorded (Fig. 7) but not photographed or videotaped. MacGregor's observations match published records of foraging posture (e.g., Reinert et al., 1984) and selective use of specific runways by potential prey (Douglass and Reinert, 1982), suggesting that successful field strikes may also be relatively short.

In the field, viperid strikes may be pre-arranged in terms of direction, nature of prey, and approximate distance. In other words, the snake selects a foraging (ambushing) site, presumably by chemosensory cues left by a potential prey on the substrate, and then arranges itself within striking distance of the substrate trail (Reinert et al., 1984). Snakes may identify the nature of the prey likely to appear in addition to differentiating envenomated from non-envenomated prey (Duvall et al., 1978; Chiszar et al., 1992; 1999). It is probably equally important that snakes be able to distinguish the trails of envenomated prey from trails left by non-envenomated prey (Chiszar et al., 1999; Kardong and Smith, this volume). On the other hand, chemosensory cues play little role in eliciting or directing the strike (Hayes and Duvall, 1991; Kardong, 1992).

In captivity, on the other hand, the appropriate pre-strike cues are unlikely to exist. Filming boxes used by functional morphologists tend to be used repeatedly for all kinds of filming. If snakes are given the opportunity to settle in the box for some time prior to filming, no indication that foraging posture was adopted is ever given in kinematic descriptions. In the field, the snake may "know" what it will strike at and approximately where the prey is likely to appear. In captivity, the appearance of the prey may mimic some events in the field, but the vomolfactory environment of the snake is rarely controlled or manipulated. Although use of laboratory mice instead of prey species taken in the field appears not to affect strike events (Kardong, 1993), the absence of tests on the effects of different vomolfactory environments on pre-strike behavior and striking kinematics characterizes all past functional-morphological work. Methods for making the laboratory environment more realistic at olfactory and vomolfactory levels during studies of striking kinematics may be worth investigating.

Ambush strategies depend on prolonged immobility, crypticity, the ability to react rapidly, the ability to detect approaching prey, and the ability to accelerate the head rapidly at the prey without prior, revealing movements. Greene and Santana (1983), Reinert et al. (1984) and G. MacGregor (pers. comm.) have shown that ambushing pitvipers may remain at the same location for several days. Continuous behavioral observation over 24-h periods by H. Reinert and L. Bushar (pers. comm.) showed *C. horridus* occasionally to be immobile for periods of 6–7 hrs. How snakes acquire sufficient alertness and muscle tone to perform a typical strike after prolonged inactivity remains unknown.

Timing, Distance, and Strike Success

Janoo and Gasc (1992) and Kardong and Bels (1998) both documented flawed strikes in which the snakes' head traveled to the prey but fang penetration did not occur during the initial bite. Among the strikes recorded by me, 19/88 (22%) were flawed in some respect and 9/19 (47%) resulted in no fang penetration at all. Four strikes with no fang penetration and two of five strikes ending in corrective movements appeared to have been directed at the mirror image of the prey (the cage used for filming had a mirror at one end at 45º to the focal plane of the camera).

Predatory strikes are often assumed to cover considerable distance. In captivity, as relative strike distance increases, the probability of missed fang contact and prey retaliation rises. Hence, the sequence of events at

the end of the extension phase of the strike is critical both to successful envenomation and, for larger prey, release of the prey before it can retaliate. Kardong and Bels (1998), using average velocity changes from 21 strike records, showed that *C. viridis* slows just prior to prey contact. Longer strikes may result in the head slowing and the mouth closing before the snake's head reaches the prey (Janoo and Gasc, 1993), and one such strike was recorded in the field (Cundall and Beaupre, 2001). For viper species that use ambush postures near definable prey trails, field measures of distances between a viper's head and the trail (along with measures of the snake) might provide another set of values to establish typical strike regimes.

Functional Morphology and Viperid Evolution

Studies of striking and feeding mechanics are now possible in the field. Digital cameras will make the problems of recording and analyzing rapid events in the field a thing of the past. It is now time to start exploring the vast range of viperid behaviors not displayed by *Bitis*, *Crotalus*, or *Vipera* species. Linking the kinematics of feeding in opportunistic predators like *C. godmani* (Campbell and Solorzano, 1992) or highly specialized feeders like *Lachesis muta* (Greene, 1992) to their morphology and phylogeny will begin to add necessary details to the sketchy outline of viperid head and body evolution given above. Examinations of skulls for phylogenetic studies should consider how the skull is used. Critical suites of functionally relevant characters, such as the height of the maxilla, exact position of the ectopterygoid-maxillary joint, length of the prearticular crest on the compound bone, curvature of the fangs, position of the last pterygoid and dentary teeth, and others will all influence how the head behaves. Much insight can be gained from even a few visual records of feeding, and good records of striking may be even more illuminating. Viperid evolution has been particularly influenced by the subtle mechanics of a venom apparatus that has had global effects on anatomy and behavior.

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APPENDIX I

Booid Taxa: *Boa constrictor*, AMNH 62561, 75267, 75478, 95941, LU 2215, P. Gritis uncatalogued specimen; *Candoia carinata*, P. Gritis uncatalogued specimen; *Corallus caninus*, AMNH 57788, 73347, J. D. Groves uncatalogued specimens (2); *C. cookii*, P. Gritis uncatalogued specimen; *C. hortulanus*, AMNH 74832; *Eunectes murinus*, AMNH 62560; *Aspidites melanocephalus*, AMNH 7620; *Morelia spilota*, AMNH 79043; *Morelia viridis* AMNH 110148; *Python curtus*, AMNH 57802; *P. molurus*, AMNH 7184, 71036, LU 2266, P. Gritis uncatalogued specimen; *P. regius*, AMNH 31921, 73157, 75263, LU 1290, P. Gritis uncatalogued specimen; *P. sebae*, AMNH 73615.

Viperid Taxa: *Agkistrodon contortrix*, AMNH 73800, 75268; *A. piscivorus*, AMNH 57801, 65543, 67014, 69181, LU 2156; *A. taylori*, AMNH 140853; *Crotalus adamanteus*, AMNH 69123, 69726; *C. atrox*, AMNH 74830, 74863, 81546, 82420; *C. horridus*, AMNH 73850, 75173; *Bitis arietans*, AMNH 80061, 88612; *B. gabonica*, AMNH 11818, 57799, 64518, 102249; *B. nasicornis,* AMNH 75742, 77644*; Cerastes vipera*, AMNH 75088; *Daboia russelii*, AMNH 75739.