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Feeding in *Atractaspis* (Serpentes: Atractaspididae): a study in conflicting functional constraints

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Summary

African fossorial colubroid snakes of the genus *Atractaspis* have relatively long fangs on short maxillae, a gap separating the pterygoid and palatine bones, a toothless pterygoid, and a snout tightly attached to the rest of the skull. They envenomate prey with a unilateral backward stab of one fang projected from a closed mouth**.** We combined structural reanalysis of the feeding apparatus, video records of prey envenomation and transport, and manipulations of live and dead *Atractaspis* to determine how structure relates to function in this unusual genus of snakes. Unilateral fang use in *Atractaspis* is similar to unilateral slashing envenomation by some rear-fanged snakes, but *Atractaspis* show no maxillary movement during prey transport. Loss of pterygoid teeth and maxillary movement during transport resulted in the inability to perform‘pterygoid walk’ prey transport. *Atractaspis* transport prey through the oral cavity using movement cycles in which mandibular adduction, anterior trunk compression, and ventral flexion of the head alternate with mandibular abduction and extension of head and anterior trunk over the prey. Inefficiencies in manipulation and early transport of prey are offset by adaptability of the envenomating system to various prey types in both enclosed and open spaces and by selection of prey that occupy burrows or tunnels in soil. *Atractaspis* appears to represent the evolutionary endpoint of a functional conflict between envenomation and transport in which a rear-fanged envenomating system has been optimized at the expense of most, if not all, palatomaxillary transport function.

Key words: Colubroidea, envenomation, evolution, fossoriality, functional integration, morphology, prey transport, tradeoff

Introduction

The genus *Atractaspis* includes 15 to 18 species of small, fossorial African and Middle Eastern snakes (Golay et al., 1993; Spawls and Branch, 1995; David and Ineich, 1999) known for their ability to envenomate prey with a backwards stab of a single fang (Corkill et al., 1959; Visser, 1975; Golani and Kochva, 1988). Their curious envenomation behavior is associated with unusual features of cephalic anatomy (Kochva, 1987; Underwood and Kochva, 1993), including a viper-like maxilla, a palatopterygoid bar with a gap between the pterygoid and the palatine, as well as few teeth on the palatine and none on the pterygoid. The rest of the skull is modified for burrowing, and the lower jaw is fragile with only two or three small teeth (Bourgeois, 1968; Underwood and Kochva, 1993). The structure of the head suggests that *Atractaspis* might use its fangs for envenomating, manipulating, and transporting prey (moving prey through the oral cavity to the esophagus), although Haas (1931a) found it difficult to explain how the fang could be used in prey transport. Remarkably, since Haas' questions about prey transport in *Atractaspis,* all discussions have centered on the use of the fang and there remain no descriptions of, or even questions about, how *Atractaspis* transports prey with a toothless pterygoid. Here we describe both fang use and prey transport in two species of *Atractaspis*. We suggest an evolutionary hypothesis favoring a mechanis for envenomating prey in tunnels that entailed the loss of the

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'pterygoid walk' mode of prey transport (Boltt and Ewer, 1964) and the use of a transport mechanism that converges on features seen in basal alethinophidians.

The evolutionary problems presented by *Atractaspis* are reflected in its systematic history. Of the species currently assigned to *Atractaspis*, the first was described by Reinhardt (1843) as *Elaps irregularis*. The genus *Atractaspis* was erected by Smith (1848) for South African *A. bibronii*. As its common names 'mole viper' and 'burrowing asp' suggest, *Atractaspis* was long considered an aberrant member of Viperidae (Haas, 1931a, b; Laurent, 1950), based on its possession of a long, hollow fang attached to a very short, rotatable maxilla. Bourgeois (1961, 1968) was first to suggest an affinity of *Atractaspis* with aparallactine snakes, many of which share the peculiar gap between the pterygoid and palatine bones. Since then, *Atractaspis* has variously been considered a member of Atractaspidinae as a sister taxon to Aparallactinae (Heymans, 1975), or both groups have been united to form one clade, Atractaspinae or Aparallactinae, within Colubridae (Underwood and Kochva, 1993). McDowell (1986, 1987) also proposed a single group, basal to vipers and colubrids, but with possible, though remote, elapid affinities. Relationships of *Atractaspis* remain unclear (Cadle, 1994; Wollberg et al., 1998) but its affinities appear to lie with a number of African genera now included in Atractaspididae (e.g., Zaher, 1999; Pough et al., 2001; Vidal and Hedges, 2002; Fig. 1).

The fossorial habits and relatively small size of *Atractaspis* have limited studies of its behavior and feeding mechanics. Existing published observations of the mechanics and behavior of the envenomating apparatus are based on manipulations of dead animals (Corkill et al., 1959; Visser, 1975) and film analysis of living *Atractaspis* stabbing a rubber membrane (Golani and Kochva, 1988). All three studies agree that maxillary rotation is limited in extent and occurs in a ventrolateral direction on one side only with the mouth closed.

Within the genus *Atractaspis* two groups of species may be recognized based on the morphology of the venom gland: one group has a short venom gland restricted to the head, the other an elongate gland extending into the trunk (Kochva et al., 1967; Kochva, 1987; Underwood and Kochva, 1993). We examined the short-glanded species *Atractaspis bibronii* and the long-glanded *A. microlepidota*. Species of the genus also differ in their possession of a rictal gland (Underwood and Kochva, 1993; Wollberg et al., 1998). These differences, and the homologies of other anatomical features to conditions in elapids and viperids, have been the primary focus of most anatomical treatments (Phisalix, 1912, 1914; Haas, 1931a, b; Bourgeois, 1961, 1968; Kochva, 1962; Thireau, 1967; Heymans, 1975, 1982; McDowell, 1986; Underwood and Kochva, 1993; Zaher, 1994). Structural studies directed at resolving function have been limited to observations of the maxillary-prefrontal joint (Corkill et al., 1959) and Young's (1998, 1998/99) description of intermandibular connective tissue links and their influence on separation of the two mandibular rami. Some critical anatomical features have been illustrated but their functional relevance unappreciated (e.g., Haas, 1931b, anterior insertion of rectus capitis anterior).

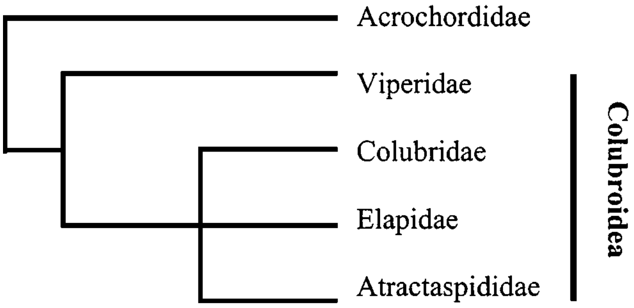

Fig. 1. Phylogenetic hypothesis of relationships of higher snakes. The placement of the Atractaspididae remains unresolved. (Source: Pough et al., 2001).

Evidence existing at the beginning of our study suggested that the jaw apparatus of *Atractaspis* differs from that of most other advanced snakes. The separation of the palatine from the pterygoid, the absence of teeth on the pterygoid, and the short maxilla with a long fang contribute to a critical rearrangement of the colubroid upper jaw functional unit (Wagner and Schwenk, 2000; Schwenk, 2001; Schwenk and Wagner, 2001). However, there were no behavioral data available to relate structural modification to function. We examined the behavior of the system, referred back to the literature to see how much of the existing anatomical detail explained the observed function, and then further explored the anatomy when our questions were not answered by the literature. Our correlation of function and anatomy is grounded in concepts of form-function relationship recently explored under the rubric of functional units (Schwenk, 2001). We regard the functional unit concept as a powerful analytical approach to investigate the evolution of complex systems, and we invoke it here to model the jaw apparatus of *Atractaspis* and to relate the function of the jaw apparatus to known ecological attributes.

Materials and methods

Behavior

Feeding

Seven adult *Atractaspis bibronii* and four adult *A. microlepidota*, all wild-caught and purchased from a commercial supplier, were individually housed at a temperature of 23–28 °C with free access to water. Feeding trials were conducted approximately every two weeks in a quiet room with minimal disturbance. At each trial, individual animals were transferred to a small filming arena with a tunnel extending from one side. The arena and tunnel were mounted on a rolling table (Fig. 2). This allowed us to gently move the filming arena to keep a moving snake in view of the camera without continuously readjusting camera angle and lighting. Feeding was videotaped with a Panasonic AG-456 S-VHS camera using the macro lens setting. When the snake entered the end of the tunnel, a live neonate mouse (2–4 g, approximately matching the girth of the snake) or snake was introduced at the opposite end and fang use, prey handling, and transport were videotaped. In the case of mice, whenever feeding occurred, additional neonate mice were offered until the snake no longer showed interest. In ten feeding trials, three to five mice were introduced simultaneously to simulate presumed natural conditions when the snakes find a rodent nest. Snake prey offered included hatchling *Lampropeltis alterna* or neonate *Thamnophis sirtalis* and *Nerodia sipedon*. Stomach contents of wild caught *Atractaspis* usually contain several nestling mammals or single squamates (amphisbaenians snakes or fossorial lizards; Greene, 1977).

Records of 130 feeding events were analyzed. Of those records, 26 were observations of *Atractaspis microlepidota* feeding on neonate mice; eight were observations of *A. bibronii* feeding on snakes. None of the *A. microlepidota* and only three of the seven *A. bibronii* could be convinced to feed on snakes, even after prolonged fasting. One *A. bibronii*, on the other hand, took only snake prey. Video records were analyzed with a Panasonic AG-1970 S-VHS VCR. In 38 instances (Table 1) in which the fang was visible in lateral view just before it was jabbed into the prey we measured the angle formed between the long axis of the braincase and the axis of the fang to determine the extent of fang erection and thus maxillary rotation (Fig. 3A). The fang axis was chosen as the straight line from the center of the base of the fang to its tip because the fangs of *Atractaspis* are relatively straight and do not have recurved tips like the maxillary teeth of many other snakes (Kochva and Meier, 1986; Deufel and Cundall, 1999). When possible, angles between fang and braincase were also measured in ventral and anterior views to get a three-dimensional impression of fang rotation (Table 1). All angles were measured with a protractor to the nearest degree on still images displayed on a video monitor. We also measured how long the fang remained embedded in the prey.

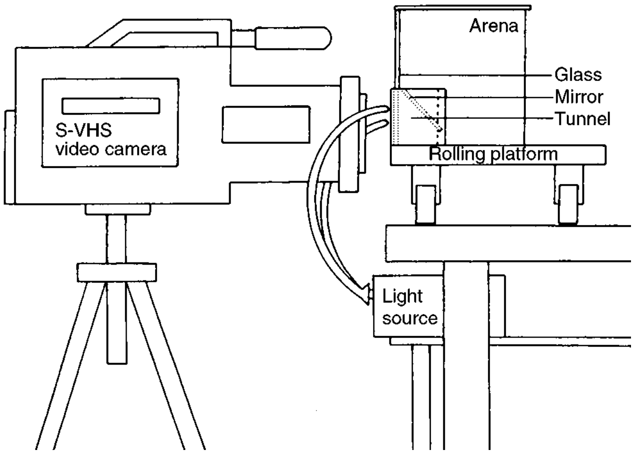

Fig. 2. Schematic diagram of the setup used to videotape feeding. The S-VHS video camera was used with its macro lens setting. The mirror forming the ceiling of the feeding tunnel that comes off the arena is at a 45° angle to the horizontal.

To compare movements of the entire head during prey transport with movements in other snake species we measured the extent of ventral bending of the head on the anterior trunk in lateral views (Fig. 3B). We further scored how many times each prey item was stabbed with a fang, how much time the snake spent with the prey item and how much of that time was actually spent in prey transport.

The effects of prey type on both number of fang penetrations and transport behavior (total time spent with the prey, total transport time, and braincase-vertebral column angle) in *Atractaspis bibronii* were tested using

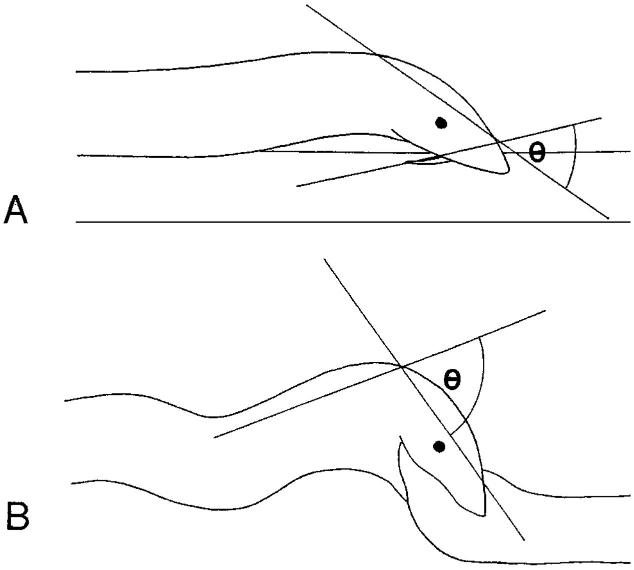

Fig. 3. Measurement of the angle between the long axis of the braincase and the long axis of the fang during prey envenomation **(A)**, and between the long axis of the braincase and the axis of the vertebral column during the compression phase of prey transport **(B)**.

Table 1. Angles of the fang axis to the long axis of the braincase during envenomation and angles of the long axis of the braincase to the axis of the vertebral column during the compression phase of bilateral prey transport. Numbers given in parentheses indicate the number of specimens included in the measurements.

	A. bibronii			*A. microlepidota*			$F_{1,36}$	p
	N	mean ± S.D.	range	N	mean ± S.D.	range		
fang-braincase (lateral view)	35 (6)	51 ± 8.7	31–70	3 (2)	47 ± 7.6	40–55	0.57	0.45
fang-braincase (lat., stimulation)	4 (1)	50 ± 11.6	35–63	–	–	–	–	–
fang-braincase (lat., dragging prey)	6 (5)	57 ± 10.2	45–70	–	–	–	–	–
	$F_{2,42} = 1.2$; $p = 0.31$							
fang-braincase (ventral view)	3 (2)	28 ± 7.8	23–37	–	–	–	–	–
fang-braincase (anterior view)	1	36 n/a	n/a	–	–	–	–	–
							$F_{1,100}$	p
braincase-vertebral column (mice)	72 (5)	65 ± 10.2	40–84	30 (3)	51 ± 10.2	25–72	37.3	< 0.01
braincase-vertebral column (snakes)	49 (3)	56 ± 10.7	33–86	–	–	–	–	–
	$F_{1,119} = 22.8$; $p = < 0.01$							

one-way analysis of variance, or a Mann-Whitney U-test when variances proved to be unequal. *A. microlepidota* refused to take snake prey.

Atractaspis bibronii and *A. microlepidota* were compared for fang-braincase angles, number of fang penetrations, total time spent with the prey and total transport times while feeding on neonate mice using one-way analysis of variance or a Mann-Whitney U-test when variances proved to be unequal.

Manipulations of live animals

Two *Atractaspis bibronii* were anesthetized using isoflurane and their dorsal constrictor muscles were stimulated through the oral mucosa with a bipolar needle electrode at a frequency of 3–40 Hz and a voltage sufficient to detect muscle contractions. During the stimulations, the animals were placed on their backs beneath a dissecting microscope and the camera was placed to record an oblique ventrolateral view of the roof of the mouth. Fang angle measurements were adjusted to account for the oblique view during the analysis of the videos. Muscles stimulated included the protractor pterygoideus, to test for maxillary rotation and fang erection, and the pterygoideus, to test for maxillary retraction. The retractor pterygoideus and retractor vomeris are so small that they had to be stimulated simultaneously, testing their effectiveness in retracting the palatine and moving the ventral snout elements, respectively. The levator pterygoideus was inaccessible because new fang generations fill the entire area between the ectopterygoid and the palatopterygoid bar.

To explore potential gape limits, we gently and slowly attempted to pull the two mandibular rami apart to determine the extensibility of the interramal region.

Manipulations of dead animals

Two specimens of *Atractaspis bibronii* that died during the study were manipulated and videotaped to determine maximal potential excursions of cranial elements. Both specimens were frozen after they died and thawed prior to examination. These manipulations included protraction and retraction of the pterygoid to determine the effects on the maxilla and (via the ligament connecting pterygoid and palatine) the palatine, protraction and retraction of the palatine to determine its potential excursions with respect to the snout, rotation of the maxilla to determine the direction and maximal extent of fang erection, retraction of the rectus capitus anterior tendons to determine the muscles' action, and spread of the interramal soft tissues to determine potential separation of the tips of the mandibles.

Anatomy

The behavioral data raised a number of questions about anatomical relationships not discussed in the literature. In particular, we investigated the attachment of the snout to the braincase to look for correlates with the use of the snout in burrowing, the shape of the palatine and its attachments to the snout that might relate to the palatine's disconnection from the pterygoid, and the configuration and ligamentous connections of the maxillary-prefrontal joint to explore potential constraints to maxillary rotation. We examined the arrangement of the muscles, connective tissues, and skin in the space between the mandibular rami by dissection and by examination of histological frontal sections of one *Atractaspis bibronii* (FMNH 81136), stained with a modified Van Gieson's stain, to find potential correlates with mandibular separation. Finally, we investigated the fiber architecture of the protractor pterygoideus muscle by

Table 2. Mean number of fang penetrations per prey item, total time spent with the prey, and time for prey transport for *A. bibronii* and *A. microlepidota* feeding on pink mice and for *A. bibronii* feeding on pink mice and hatchling/neonate snakes. Numbers given in parentheses indicate the number of specimens included in the measurenments.

	A. bibronii			*A. microlepidota*			
	N	mean ± S.D.	range	N	mean ± S.D.	range	p
# fang penetrations	85 (7)	1.56 ± 0.88	0–4	26 (3)	1.04 ± 0.66	0–2	<0.01
total time spent (min)	60 (7)	6.66 ± 3.43	2.25–18	27 (3)	7.80 ± 3.85	3–16	0.17
transport time (min)	89 (7)	3.42 ± 2.28	1–20.5	30 (3)	3.57 ± 1.57	1.33–8	0.74

	A. bibronii						
	Pink mice			Snakes			
	N	mean ± S.D.	range	N	mean ± S.D.	range	p
# fang penetrations	85 (7)	1.56 ± 0.88	0–4	8 (3)	5.88 ± 2.30	3–9	<0.01
total time spent (min)	60 (7)	6.66 ± 3.43	2.25–18	8 (3)	38.00 ± 25.41	2.25–80	<0.01
transport time (min)	89 (7)	3.42 ± 2.28	1–20.5	8 (3)	6.92 ± 2.82	4–12	<0.01

acid maceration (Gans and Gorniak, 1982) to determine the potential contraction distance of this muscle and thus the potential protraction of the pterygoid. To determine the pterygoid protraction necessary to fully rotate the maxilla, we measured the length of the rotational axis of the maxilla from the ectopterygoid attachment to the point of rotation between maxilla and prefrontal in five specimens. The length of the pterygoid was then measured, and the distance it would have to protract to rotate the maxilla through the average angle of rotation taken from the feeding records was calculated.

Skeletal structures and soft tissues were analyzed in preserved specimens (five *A. bibronii*: MCZ R-23467, MCZ R-53001, CAS 162591, CAS 173810, FMNH 81136) and in skeletal preparations of four specimens (three *A. bibronii*: AMNH 82071, LU 2366 plus one specimen A. Deufel, private collection; one *A. irregularis*: AMNH 12355). Institutional abbreviations are as in Leviton et al. (1985) except LU = Lehigh University.

In our correlation of morphology and function, we focused on establishing which characters are directly involved in producing fang rotation and the prey transport behaviors, and the potential evolutionary constraints and tradeoffs arising from participation of characters in more than one function.

Results

Behavior

Feeding

Fang use on live prey by *Atractaspis bibronii* is similar to the 'strikes' of *A. engaddensis* (synonym of *A. microlepidota*: David and Ineich, 1999) to a membrane during milking for venom (Golani and Kochva, 1988). *Atractaspis* stab live prey items with their fang while crawling alongside the prey. Fang erection and penetration into the prey last around 67–83 ms and are always unilateral; only one fang on one side is used. The fang emerges between the upper and lower labial scale rows while the jaws remain closed (Fig. 4A). Because the lower jaw is countersunk, ventrolateral movement of the fang as it emerges from the mouth pushes the edge of the supralabial scale row slightly laterally so that a bulge forms overlying the region of the maxillary-prefrontal joint.

At full extension, the angle formed between the long axis of the braincase and the fang axis averages 51° for *Atractaspis bibronii* and 47° for *A. microlepidota* (F = 0.574, df = 1, 36, p = 0.45; Table 1). The lateral rotational component of the fang is 36° for one *A. bibronii* (We did not obtain any anterior views of fang use by *A. microlepidota*). The extruded fang is jabbed into the prey by a sudden posteroventral jerk of the head toward the prey surface (Fig. 4B, C). The fang then remains embedded in the prey from anywhere between 0.2 sec to 2 min 40 sec (N = 24, mean = 17.9 sec). Presumably, venom is injected during this period.

Because 'strikes' are not launched from a distance of several head lengths, as they are in booids, vipers, and some colubrids (e. g., Kardong, 1974; Janoo and Gasc, 1992; Cundall and Deufel, 1999), the term 'strike' should not be used for this kind of behavior. We prefer to refer to it simply as fang stabbing.

The fang is extracted by moving the head anterodorsally, often as the snake crawls past the prey. Fang stabs usually produce a slit-like wound that bleeds profusely and is likely created by a posterior cutting edge opposite the discharge orifice for the venom (Kochva and Meier, 1986).

Frequently, *Atractaspis* stab the prey with the fang more than once (Table 2), and when several mice are presented simultaneously, usually all of them are stabbed with the fang before the snake begins to consume the first. When several mice were offered at the same time it became evident that envenomation actually occurs during the fang stabs. The mice that were consumed last had died because enough time had elapsed for the venom to act. In only two of ten trials did the snakes not envenomate all the neonate mice offered, although all were eaten. The mean number of fang stabs per prey item is significantly higher in *A. bibronii* (mean = 1.56) than in *A. microlepidota* (mean = 1.04, Mann-Whitney U-test: Z = –2.586, p < 0.05) and significantly higher for snake prey (mean = 5.88) than for neonate mice (mean = 1.56, Mann-Whitney U-test: Z = –4.846, p < 0.05; Table 2).

Atractaspis occasionally use their fang as a means to manipulate prey, hooking the fang into the prey like a gaff and then dragging it into a position to initiate transport more effectively (Fig. 5). Fang angles during dragging average slightly higher but are not significantly different from angles measured during initial fang penetrations (mean = 57°, F = 1.2, df = 2, 42, p = 0.31; Table 1).

When feeding on single neonate mice, both species always immediately begin prey manipulation and transport without waiting for the prey to die. With snake prey, transport is not begun until further fang pricks no longer elicit a response. After finding the head of the prey, the snake opens its mouth and begins forcing its head over the prey. During this initial stage, the snake uses head rotations around a vertical axis at the level of the orbits. Head rotation often also involves the anterior trunk. For example, as the snout swivels to the right, the anterior trunk swings to the left and sometimes the left mandibular ramus is protracted. Alternating mandibular motion is barely visible in *A. bibronii* and cannot be seen in all records that show a view of the mandibles. It is slightly more obvious in *A. microlepidota*. Frequently, the limited advance gained by the mandibles is lost by the prey slipping out of the snake's mouth during advances of the opposite side and during mouth closing. Movement of the head over the prey is greatly facilitated when the snake anchors the prey item against the walls of the tunnel or against coils of its body. The tips of the two mandibular rami do not separate appreciably to increase gape, and mandibular advance is not accompanied by maxillary movements during the initial stages of prey transport.

When the prey enters the esophagus, *Atractaspis* usually switches to a different mode of prey transport: bilaterally symmetrical head movements synchronized with anterior trunk compression and extension cycles (orocervical phase of Kley and Brainerd, 2002). During the compressive phase of the cycle, the mouth is tightly closed and the entire head is depressed. As the head rotates ventrally around the atlas, the anterior trunk appears to shorten, forming a few tight, low-amplitude horizontal bends (Fig. 6A). Head depression during transport is different from head depression during defensive displays in which ventral flexion occurs well posterior to the skull in the anterior trunk region (Golani and Kochva, 1988). In some records of the compressive phase, the ventral skin shows a constriction behind the enlarged gular scales or halfway between the posterior end of the gular scales and the first ventral scute. During head depression, the long axis of the braincase forms an average angle of 65° (*A. bibronii*) or 51° (*A. microlepidota*) with the axis of the anterior trunk (F = 37.27, df = 1,100, p < 0.01, Table 1). For *A. bibronii*, head depression is more pronounced for mouse prey than for snake prey (F = 22.76, df = 1, 119, p < 0.01; Table 1). After compression, the jaws open and the head and anterior trunk extend forward over the prey (Fig. 6B) to be followed by another compression cycle. During this phase of transport, there is no evidence of maxillary movements, unlike transport kinetics in snakes that use the pterygoid walk (Boltt and Ewer, 1964; Cundall, 1987). In two cases, *A. bibronii* violently shook its snake prey back and forth, commenced compression/extension cycles and followed each cycle by sideways whips of the head.

Prey handling and transport in *Atractaspis* are usually prolonged (Table 2). Total time spent with the prey is significantly higher for snake prey (mean = 38 min) than for mouse prey (mean = 6.66 min; Mann-Whitney U-test, Z = –4.459, p < 0.05; Table 2) because *Atractaspis* wait for snake prey to die before attempting to eat it. In the case of mouse prey, much time is spent in failed attempts to grasp the prey at what appears to be random locations on the prey's body. It appears that *Atractaspis* encounter the head of the prey by trial and error. After transport finally commences, records show numerous extension/compression cycles in which the prey slips out of the snake's mouth during the compression phase, presumably because the snake is unable to maintain a grip. This makes transport times highly variable (Table 2). However, transport can be rapid, especially when the snake continuously anchors the prey against the substrate or its own body. Transport times are not significantly different between the two species (mean = 3.42 min. for *A. bibronii*: mean = 3.57 min. for *A. microlepidota* feeding on mice; F = 0.113, df = 1, 117, p = 0.737; Table 2). However, transport times of elongate prey are significantly longer than transport times of mouse prey (mean = 6.91 min for snakes vs. mean = 3.42 min for mice; F = 16.5, df = 1, 95, p < 0.01; Table 2).

Manipulations of live animals

Electrode stimulation of the protractor pterygoideus muscle to tetanus causes rotation of the maxilla on the prefrontal, carrying the fang ventrolaterally. The angle formed between the long axis of the braincase and the

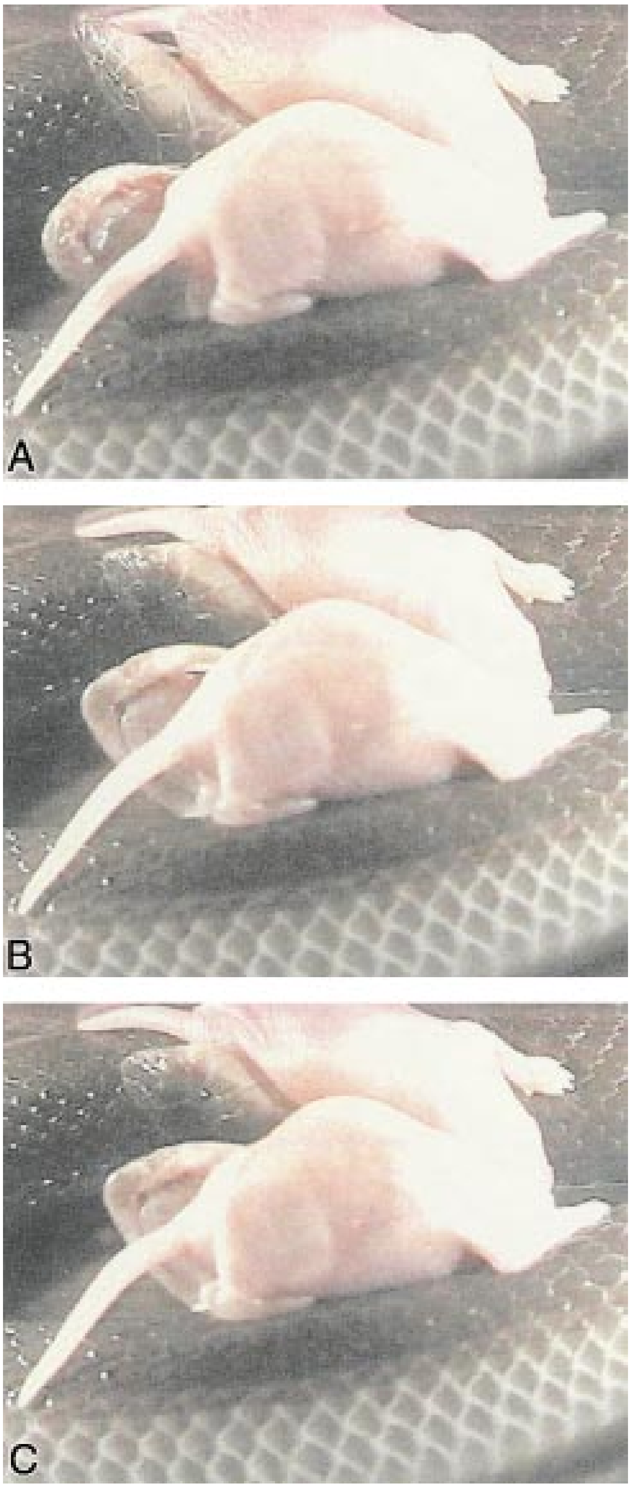

Fig. 4. Sequence of video frames of *Atractaspis bibronii* envenomating a pink mouse. **(A)** fang emerging between upper and lower labial scale rows, note the bulge in the upper labials overlying the maxillary-prefrontal joint, **(B, C)** fang penetration by a postero-ventral jerk of the head of the snake toward the prey. A mirror is placed at 45° to the picture plane.

Fig. 5. Fang use as a gaff to move and manipulate prey. *A. bibronii* is dragging the prey toward the left of the field.

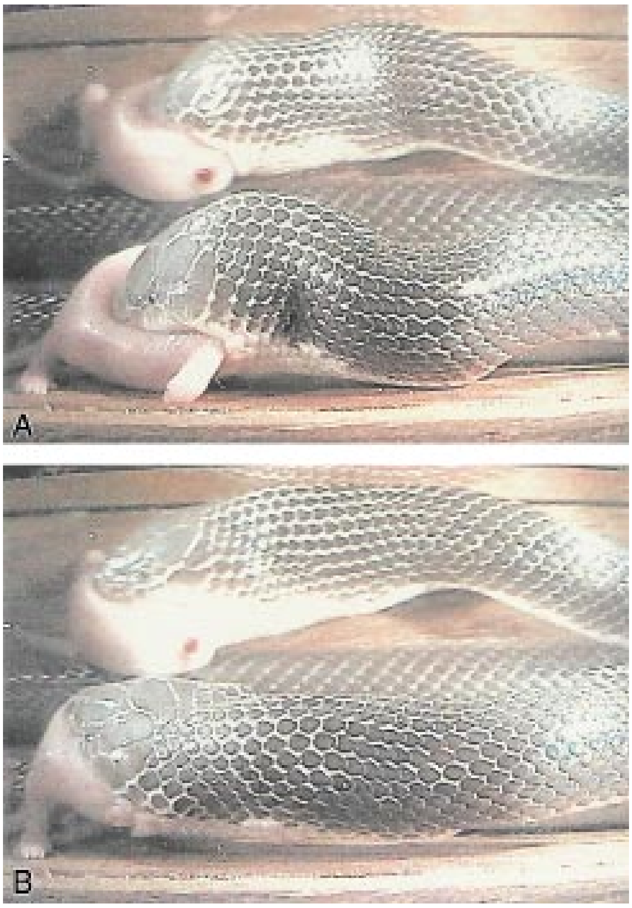

Fig. 6. Prey transport in *A. bibronii* by bilateral head and anterior trunk extension and compression cycles. **(A)** compression phase: the head is depressed onto the prey while the anterior trunk is drawn anteriorly and compressed into coils. **(B)** extension phase: the mouth is open and the head and anterior trunk extend over the prey.

fang axis does not exceed 63° (N = 4, mean = 50°). The rotating maxilla appears to pull on the maxillary process of the palatine via their ligamentous connection, moving the palatine very slightly anterolaterally. Because the large packet of new fang generations prevents access to the levator pterygoideus, we were unable to stimulate the levator and protractor pterygoideus simultaneously to simulate the likely action of those muscles during protraction of the palatomaxillary apparatus (Cundall and Gans, 1979).

We could not produce any visible muscle twitches in the retractor pterygoideus or the retractor vomeris, possibly because the contraction distance of these muscles is too small to be detected. Stimulation of the pterygoideus retracts the maxilla but could not adduct the mandibular rami because the lower jaw was held open in order to access the muscles in the roof of the mouth.

Stimulation of the rectus capitus anterior results in depression of the head on the anterior trunk. Tension applied to the interramal tissues by pulling the two mandibular rami apart produces separation no more than twice the resting distance between the tips of the rami.

Manipulations of dead animals

Manipulations of dead specimens confirmed our findings on bone mobility. Anterior movement of the pterygoid predictably results in rotation of the maxilla and extrusion of the fang. We reconfirmed that the rotation of the maxilla is constrained (Haas, 1931b; Visser, 1975). Anterior movement of the pterygoid has no effect on the palatine because the ligament connecting the two bones simply folds up. The palatine cannot be protracted appreciably because the distal tip of the choanal process abuts the posterior ventral processes of the vomers. The vomers themselves can be moved very slightly fore and aft with respect to each other and to the dorsal snout elements.

Retraction of the pterygoid retracts the fang and pulls on the rear end of the palatine via the ligament connecting the two bones. The movement is transmitted along the palatine to the vomeronasal capsule and the premaxilla by ligaments connecting the anterior end of the palatine to those structures. The palatine is prevented from moving posteriorly by its anterior ligamentous connections. Retraction of the rectus capitus anterior tendons results in depression of the entire head.

Attempts to elevate or depress the snout caused appreciable rotation at the fronto-parietal joint, not the prokinetic (naso-frontal) joint. The extent of movement (~20°) suggests that the ligaments connecting frontal and parietal (and frontal and parasphenoid) are either loose or subject to more rapid necrosis than the other cranial joints. A loose connection is also suggested in figures drawn from cleared and stained specimens of *Atractaspis irregularis* (Bourgeois, 1968).

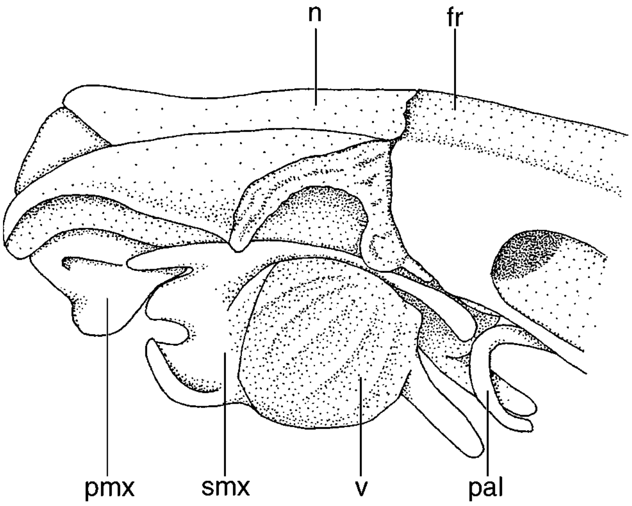

Fig. 7. Attachment of the snout to the braincase in *A. bibronii.* The left frontal bone is removed. Snout attachment occurs solely by a broad suture between the nasal and frontal bones. Septomaxilla and vomer do not participate in snout attachment. Abbreviations; fr, frontal; n, nasal; pal, palatine; pmx, premaxilla; smx, septomaxilla; v, vomer.

Anatomy

Skull

The skull of *Atractaspis bibronii*, like other species of *Atractaspis* (Phisalix, 1912; Bourgeois, 1961, 1963, 1968; Parker and Grandison, 1977), has an elongate braincase, no postorbitals and small supratemporals (Kochva, 1987; Underwood and Kochva, 1993). Premaxilla and nasals are firmly united, with a triangular process of the premaxilla reaching dorsally between the two nasals. The nasals have extensive ligamentous attachments with the frontals along their entire posterior edge, including their dorsal and vertical laminae, and hence form the primary attachment of the snout to the rest of the braincase (Fig. 7). Each septomaxilla has a long posterior process that passes ventral to the frontal and lateral to the trabecular commissure. Although slender, this process would resist dorsoventral rotation of the snout. The vomer lies completely ventral to the prokinetic joint.

There is a remarkable reduction in the dental armature. The slender pterygoid has no teeth, and the palatine and dentary each bear only two small teeth. The short maxilla bears only the fangs (Phisalix, 1912; Bourgeois, 1963, 1968; Underwood and Kochva, 1993). The fangs are relatively long, approximately 1/4 to 1/3 of the length of the head, which places them in the middle of the range of relative fang lengths between elapids and viperids but closer to viperids (Visser, 1975; Kochva and Meier, 1986). Palatine and pterygoid are separated by a gap spanned by a flexible ligament (e.g., McDowell, 1986). The anterior end of the palatine is truncated. It does not project beyond the anterior edges of its choanal and maxillary processes. The palatine has ligamentous connections to the vomeronasal capsule and the premaxilla. A ligament attaches to the anteroventral end of the palatine, extends anteriorly, attaching to the choanal cartilage of the vomeronasal capsule, and continues along the joint between vomer and septomaxilla to insert ventrolaterally on the connective tissue at the posteroventral edge of the premaxilla. As the ligament approaches the rear end of the premaxilla, it gives rise to a medial branch that runs along the posteroventral process of the premaxilla to meet its partner in the midline (Fig. 8). These ligamentous connections tie the palatine very tightly to the snout and prevent it from being retracted. The small maxillary process of the palatine lies in the connective tissue of the maxillary-prefrontal joint, and the choanal process attaches to the caudal edge of the vomer (Phisalix, 1912; Fig. 8), preventing any rostral displacement of the palatine.

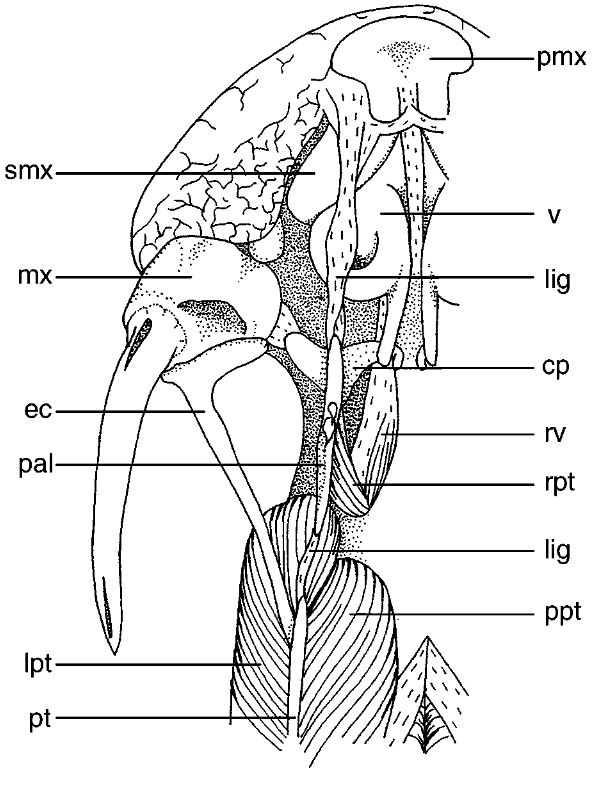

Fig. 8. Ventral view of a dissection of the anterior roof of the mouth of *A. bibronii.* The palatine is suspended by the retractor vomeris and ligaments to the snout, pterygoid, and maxillary-prefrontal joint. Abbreviations: cp, choanal process; ec, ectopterygoid; lig, ligament; lpt, levator pterygoideus; mx, maxilla; pal, palatine; pmx, premaxilla; ppt, protractor pterygoideus; pt, pterygoideus; rpt, retractor pterygoideus; rv, retractor vomeris; smx, septomaxilla; v, vomer.

The pterygoid is a thin, narrow bone that ends only slightly anterior to its attachment to the ectopterygoid. Its rear end is not ligamentously connected to the distal end of the quadrate. As a result, movements of the quadrate (and mandibular rami) are independent of pterygoid movements.

The maxilla is short and bears only the fangs. The two fang sockets lie in the transverse plane, and only one is usually filled with an ankylosed fang. A slender ligament connects a process on the anterolateral maxilla to the lateral process of the premaxilla, limiting maxillary retraction. The maxillary-prefrontal joint is usually described as a ball-and-socket joint (Haas, 1931b; Golani and Kochva, 1988), with the convex distal end of the prefrontal forming the ‘ball’ of the joint. A ball-and-socket joint generally al-

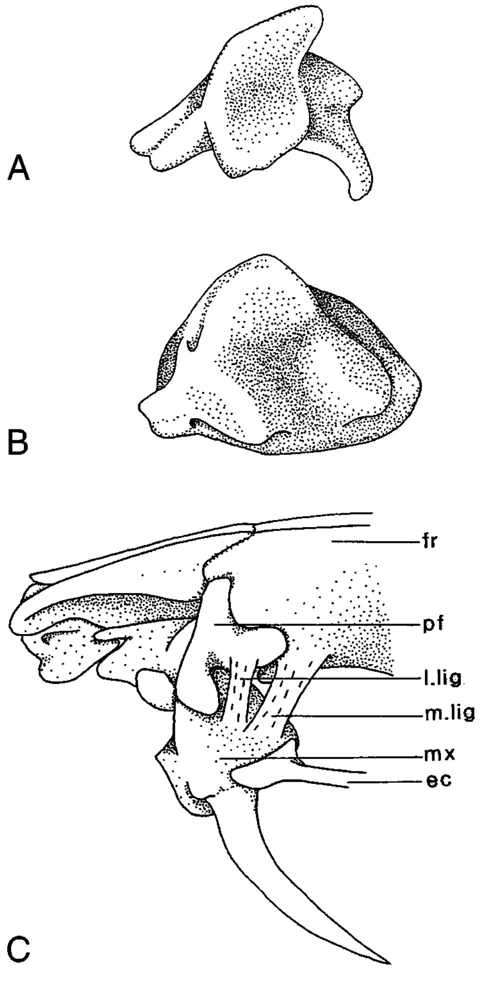

Fig. 9. Left maxillary-prefrontal joint of *Atractaspis bibronii.* **(A)** ventral view of prefrontal, **(B)** dorsal view of maxilla, **(C)** slightly postero-lateral view of the joint showing the ligaments constraining maxillary rotation: the lateral ligament connects the maxilla to the prefrontal whereas the medial ligament connects the maxilla directly to the frontal. Abbreviations: ec, ectopterygoid; fr, frontal; l. lig, lateral ligament; m. lig, medial ligament; mx, maxilla; pf, prefrontal.

lows rotations in many directions, as in the human shoulder or hip joints. However, maxillary rotation in *Atractaspis* is constrained to one rotational axis because the articular surfaces of the maxillary-prefrontal joint are more complex than 'ball-and-socket' suggests. The dorsal surface of the maxilla is concave, the cavity being formed by three dorsal projections that reach around the distal end of the prefrontal. All projections are rounded, one of them is medial, two are lateral. The distal end of the prefrontal is saddle-shaped, with the axis of the saddle being oriented obliquely from anteromedial to posterolateral. The orientation of the saddle-shaped distal end of the prefrontal is also the rotational axis of the maxillo-prefrontal joint, allowing the fang-tip to swing ventrolaterally only. The medial end of the saddle is pierced by the lacrimal foramen and fits into the central concavity of the maxilla (Fig. 9A, B). The lateral end of the saddle projects between the two lateral projections on the maxilla. Excursion of the maxilla beyond approximately 50° (Table 1) is constrained by two strap-like ligaments on the posterior aspect of the joint dorsal to the ectopterygoid attachment (Fig. 9C). The lateral ligament spans the maxillary-prefrontal joint, reaching from the posterior surface of the tip of the posterolateral projection of the maxilla to a posterolateral process of the prefrontal behind its saddle-shaped distal end. The medial ligament connects the maxilla directly to the frontal, anterior to the origin of the dorsal and ventral oblique extrinsic ocular muscles. The medial ligament runs from the center of the posterior face of the maxilla, along a shallow depression between the maxilla's medial and posterolateral dorsal projections, to the frontal directly medial to the posterolateral attachment of the prefrontal. The lacrimal duct passes between the two ligaments.

The quadrate is long, slender and curved. Its head overlaps almost the entire length of the short supratemporal. The supratemporal is connected to the rest of the braincase by a triangular occipital ligament (Underwood and Kochva, 1993) that arises from the entire length of the supratemporal. The mandibular rami are slender with a very short retroarticular process. There is only enough bone to cup the distal end of the quadrate.

Muscles

As noted in the introduction, the lateral jaw muscles of *Atractaspis* have been well described, but they explain few of the unusual functional properties of the feeding apparatus. Muscles that correlate with particular aspects of feeding behavior include some spinally innervated muscles of the anterior trunk, the facially innervated mandibular depressors, and the trigeminally innervated dorsal constrictors, pterygoideus, and interramal muscles.

The three spinally innervated muscles that influence feeding mechanics are the superficial cutaneous complex, the neurocostomandibularis, and the rectus capitus anterior. The superficial cutaneous muscle complex forms a sheet of muscle covering much of the caudal head region, anteriorly attaching on the internal posterior edges of the large head scutes as well as on the skin between the two mandibular rami, just posterior to the angle of the mouth (Fig. 10). It runs posteriorly to merge with the intrinsic cutaneous musculature that attaches to all but the dorsalmost three scale rows (Buffa, 1904). With the exception of the dorsal gap between the right and left segments of this muscle, it is similar to that described for *Anomochilus* (Cundall and Rossman, 1993). Fibers of the cervicoquadratus and costocuta-

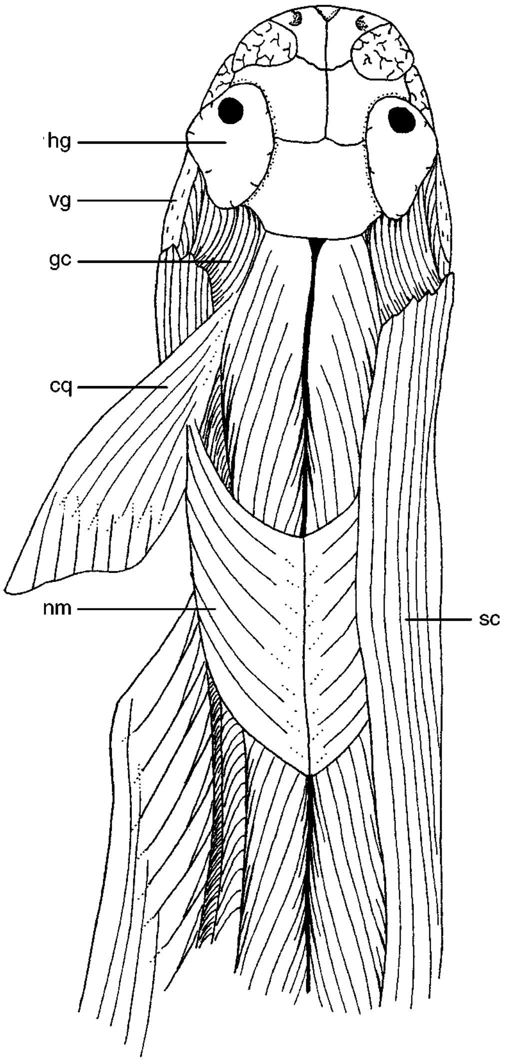

Fig. 10. Dorsal view of *A. bibronii* showing the superficial cutaneous muscle and its relationships. The muscle is bisected and reflected on the left side of the animal. Anteriorly, the muscle inserted on the skin at the angle of the mouth and on the rictal plate. Abbreviations: cq, cervicoquadratus; gc, gland compressor; hg, harderian gland; nm, neuromandibularis; sc, superficial cutaneous muscle; vg, venom gland.

neous superior merge medially on the superficial cutaneous muscle, caudal to the head, and superficial fibers of the neurocostomandibularis merge with the ventral part of the cutaneous muscle in the lower jaw. A muscle similar to the superficial cutaneous muscle was illustrated for *Atractaspis corpulentus* (Haas, 1931b) and *A. dahomeyensis* (Underwood and Kochva, 1993), but in the latter case, the muscle was labeled as constrictor colli. We have found no evidence of a constrictor colli in *A. bibronii*. The longitudinal arrangement of the fibers in the superficial cutaneous sheet allows this muscle to shorten the skin during the compression phase of prey transport. This is facilitated by loss of attachment of the skin of the anterior trunk region to the neural spines of the vertebrae and by the gap between the anterior and posterior attachments of the cutaneous muscle to the underlying muscles.

Atractaspis is unusual in having only a single muscle running from the cervico-costal region to the mandible. In *A. bibronii* the muscle originates aponeurotically from the dorsal fascia overlying the spinalis-semispinalis at the level of vertebrae five to ten. It descends rostrally, passes the corner of the mouth where some of its fibers insert on the rictal plate, and inserts on the lateral and ventral surfaces of the mandible. Haas (1931b) described this muscle in *A. corpulentus*, identifying it as neurocostomandibularis and proposing the absence of the cervicomandibularis. Underwood and Kochva (1993), on the other hand, stipulated the presence of a cervicomandibularis and the absence of the neurocostomandibularis in *A. engaddensis*, whereas McDowell (1986) proposed possible fusion of the two muscles based on its anterior fibers inserting on the angle of the mouth. Based on its location medial to the cervicoquadratus and its innervation solely by spinal nerves two to four in *A. bibronii*, we conclude that the muscle in question is the neurocostomandibularis. The neural (neuromandibularis) and costal (costomandibularis) heads of the neurocostomandibularis merge anteriorly with each other and with fibers arising from the hyoid apparatus and the midventral fascia (ceratomandibularis**:** see Fig. 11).

The last of the spinal muscles relevant to the feeding behavior is the rectus capitus anterior, a large subvertebral muscle that attaches to the floor of the braincase (Pregill, 1977). In contrast to most colubroid snakes, the muscle in *Atractaspis* inserts well forward on the basisphenoid, reaching almost to the level of the anterior end of the pterygoid (Fig. 12). It is pinnate and forms a prominent, broad tendon that can be followed caudally to vertebra 35–37. The rostral insertion of this muscle suggests that it is responsible for the forceful depression of the head that occurs during feeding.

Among the facially innervated muscles, the only modification that relates to feeding behavior is reduction of the depressor mandibulae. The depressor mandibulae is feebly developed and inserts on a tiny retroarticular process. Reduction of the depressor correlates with the absence of fast abduction of the lower jaw during envenomation. We agree with Haas (1931a) that jaw opening is probably achieved by contraction of the neurocostomandibularis and ceratomandibularis. In most snakes, the depressor mandibulae is situated to maximize the speed of jaw abduction during rapid strikes, essentially by exerting a large force on a short in-lever. Although the muscle is still present in *Atractaspis*, it appears to be a vestigial structure incapable of generating appreciable force.

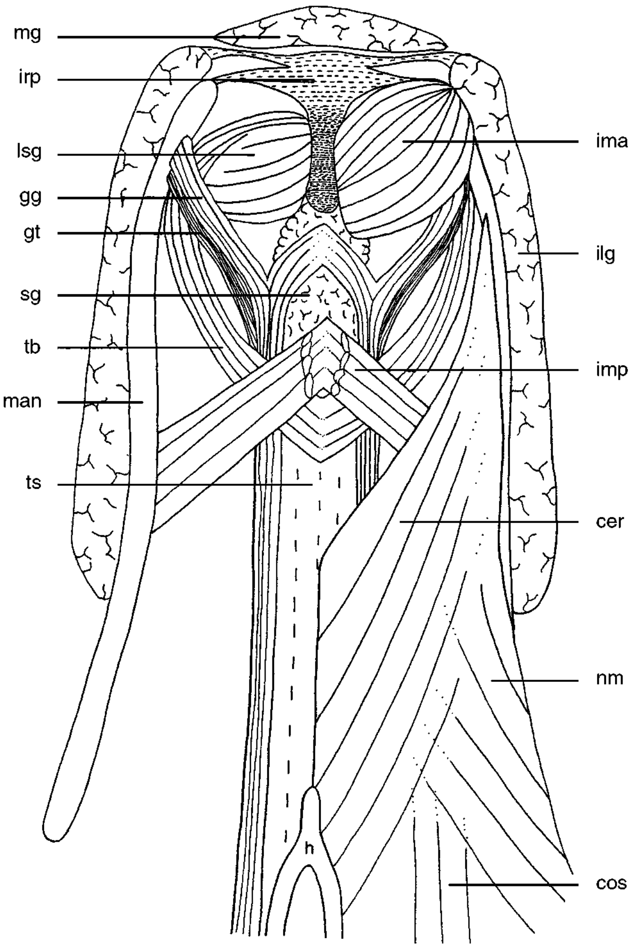

Fig. 11. Schematic diagram of the arrangement of structures in the interramal space of *A. bibronii*. Neuromandibularis, costomandibularis, ceratomandibularis, and intermandibularis anterior have been removed on the left. The geniotrachealis inserts on the wall of the trachea (not shown) at the level of the posterior end of the sublingual gland. Abbreviations: cer, cervicomandibularis; cos, costomandibularis; gg, genioglossus; gt, geniotrachealis; h, hyoid; ilg, infralabial gland; ima, intermandibularis anterior; imp, intermandibularis posterior; irp, interramal pad; lsg, lateral sublingual gland; man, mandible; mg, mental gland; nm, neuromandibularis; sg, sublingual gland; tb, transversus branchialis; ts, tongue sheath.

The trigeminally innervated muscles responsible for retraction of the palatomaxillary apparatus are all reduced in some manner (Haas, 1931a). These include the retractor pterygoideus, the retractor vomeris, and the pterygoideus. The two former muscles arise from the floor of the braincase, between the fronto-parietal joint and the caudal edge of the palatine. In conjunction with their reduction in size, the origins of these muscles are small and distinctly separate from the origin of the protractor pterygoideus. The retractor pterygoideus inserts only on the middle third of the palatine and does not reach the rear edge of the choanal process as in many other snakes (e. g. Albright and Nelson, 1959a; Dullemeijer, 1959; Cundall, 1986). As in other colubroids, the retractor vomeris inserts on the dorsal-most rear end of the vomer (Figs. 8, 12). The persistence of these small muscles reflects either phylogenetic inertia or suggests that both the palatine and the ventral snout are capable of moving despite our failure to demonstrate this through stimulation of the muscles.

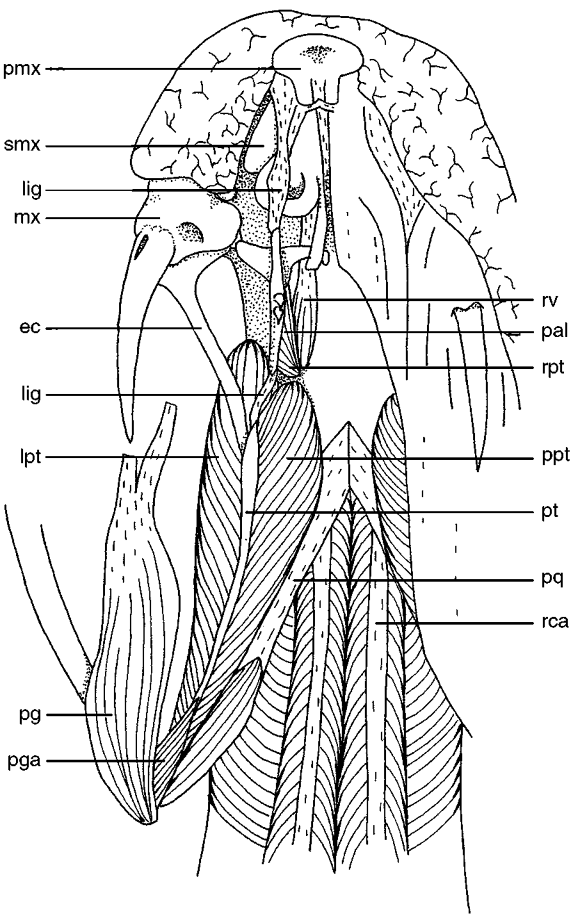

Fig. 12. Ventral view of a dissection of the roof of the mouth of *A. bibronii* with most of the mucosa removed. Abbreviations: ec, ectopterygoid; lig, ligament; lpt, levator pterygoideus; mx, maxilla; pal, palatine; pg, pterygoideus; pga, pterygoideus accessorius; pmx, premaxilla; ppt, protractor pterygoideus; pq, protractor quadratus; pt, pterygoid; rca, rectus capitus anterior; rpt, retractor pterygoideus; rv, retractor vomeris; smx, septomaxilla.

Both elements of the pterygoideus complex appear reduced in cross-sectional area relative to their condition in most colubroid snakes. In the case of the pterygoideus, no fibers arise directly from the palatomaxillary arch. Instead, they arise at the caudal edge of a long, complex tendinous apparatus that comprises more than half the length of the muscle. This tendon attaches medially on the supralabial gland, on the venom duct at the level of the eye, and rostrally on the lateral and medial faces of the maxilla via slips incorporated in the vagina dentis (Haas, 1931b; Kochva, 1962). Caudally, the pterygoideus attaches to the ventral surface of the tiny retroarticular process of the mandibular ramus. Shortening of contractile pterygoideus length is matched by shortening of the pterygoideus accessorius connection between the rear end of the pterygoid and the quadrate-mandibular joint. Despite the wide separation between the rear end of the pterygoid and the jaw joint, the accessorius fibers arise only from a short region of the caudal end of the pterygoid. In a similar pattern that reflects limited excursion of the jaw joint relative to the braincase, the protractor quadratus is unusual in that it is fleshy only in its caudal third, near its insertion on the quadrate. The rest of the muscle consists of a flat tendon attached to the basisphenoid at the cranial end of the rectus capitus anterior insertion, a point well rostral to its typical colubroid position near the rear end of the skull (Fig. 12).

In contrast to the retractors, the muscles that directly protract the palatomaxillary arches are well developed (Haas, 1931a). The levator pterygoideus originates in a small area on the lateral parietal behind the orbit where one would normally find the postorbital. Its fibers fan ventrally and posteriorly to insert on most of the dorsal surface of the pterygoid except the medial edge. The protractor pterygoideus originates on the basisphenoid lateral to the insertion of the rectus capitus anterior tendon, at the level of the rear end of the palatine. Its medial anterior fibers fan ventrally and posteriorly to insert on the dorsal surface of the pterygoid medial to the insertion of the levator pterygoideus (Fig. 12). The lateral anterior fibers run postero-ventrally to insert on the posterior third of the pterygoid. The anteriormost fibers of the protractor pterygoideus, running from the anteriormost point of origin to the anterior end of the pterygoid, are the shortest fibers of the muscle. Fibers originating along the lateral origin are the longest. Assuming the preserved muscle was at its resting length and that the muscle is able to contract about 30–50% of its resting length (Ramsey and Street, 1940; Gordon et al., 1966), the longest fibers of the protractor pterygoideus are able to protract the pterygoid about 17–28% of the latter's length. Pterygoid displacement necessary to rotate the maxilla through 50° is only around 17% (based on measurements of five specimens, min = 14.9%, max = 21.8%) because of the short rotational radius of the maxilla (Fig. 13).

Because of the observed limits to separation of the tips of the two mandibular rami, we examined the arrangement of the interramal muscles. The interramal muscles of *Atractaspis bibronii* are similar to those in elapids (Fig. 11), characterized by the absence of the intermandibularis posterior superficialis. Fibers of the intermandibularis posterior insert on the skin approximately at the level where some records show a constriction of the skin during the compression phase of bilateral transport. The similarity of the arrangement of the interramal muscles of *A. bibronii* to snakes with large gape suggests that the muscles of the interramal space are not gape-limiting but that gape is limited by connective tissue elements or the skin.

Young (1998; 1998/99) investigated the interramal connective tissue elements of a large number of taxa. In *Atractaspis*, he found a symphyseal connection by a lateral band of connective tissue of poor or moderate density connecting the ventrolateral surfaces of the anterior tips of the two dentaries. Young (1998) proposed that this type of arrangement facilitates separation of the tips of the mandibular rami compared to a more perpendicular arrangement of the connective tissue found in other taxa. In our examination of one set of Young's slides, we found that the interscale regions between the anterior infralabial scales and between the first infralabial scale and the mental scale are not highly folded as they are in some other snakes. The interscale region in *Atractaspis* is a simple, shallow inpocketing of keratinized epidermis and the underlying dermis. Straightening of the interscale regions on either side of the mental and gular scales can account for the approximate doubling of the distance between the tips of the mandibular rami observed during feeding and manual distension. Anterior ends of the two rami are connected to each other by a thin strand of collagenous connective tissue lying along the anterior edge of the intermandibularis anterior muscle. A similar strand of connective tissue connects the capsules of the infralabial glands on either side of the jaw, possibly representing Young's (1998) lateral band. Both strands of connective tissue converge on an interramal pad in the midline. The anterior end of the interramal pad is relatively wide and consists mainly of transversely oriented, loosely packed, thin bands of collagen fibers with relatively few visible nuclei. The posterior region of the interramal pad is narrower and rodlike, consisting of thick bundles of transversely oriented collagen fibers surrounding spaces of clear ground substance containing round nuclei. Tendons of the lateral sublingual gland compressor portion of the intermandibularis anterior muscle insert on and merge with the collagen fibers of the posterior region of the interramal pad. Connective tissue arrangements suggest that gape is limited mainly by the reduced interscale regions between the scales on the perimeter of the anterior lower jaw and by the collagenous interramal pad.

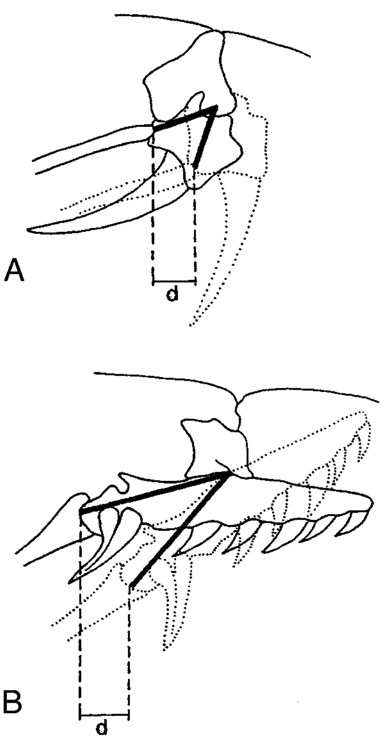

Fig. 13. Effect of the length of the maxilla on its rotatability. Shortening of the maxilla in *Atractaspis* **(A)** compared to its rear-fanged relatives like *Xenocalamus mechowi* **(B)**, allows *Atractaspis* to rotate its fang through a larger angle for the same pterygoid-ectopterygoid protraction *d*.

Discussion

Maxillary kinetics

Our analysis of fang use on live prey confirms anecdotal reports (Corkill et al., 1959; Visser, 1975; Kochva and Meier, 1986) and Golani and Kochva's (1988) analysis of *Atractaspis engaddensis* 'strikes' to a device covered by a rubber membrane. *Atractaspis* envenomate prey by a unilateral, close-mouthed, backward stab of the fang. The stab is kinematically similar to unilateral chewing movements described for some rear-fanged snakes such as *Heterodon*, *Xenodon*, and *Oligodo*n that envenomate and manipulate prey by repeated unilateral fang stabs or slashes driven by maxillary rotations (Boulenger, 1915; Cundall, 1983; Coleman et al., 1993). Because many of the proposed relatives of *Atractaspis* are rear-fanged (Bourgeois, 1968; Underwood and Kochva, 1993), *Atractaspis* may have modified the prey capture strategy of a rear-fanged ancestor to operate in the confines of a burrow simply by eliminating mouth opening. Fang protrusion may be facilitated by the countersunk lower jaw that allows the fang to pass between the upper and lower labial scale rows (Fig. 4). The loss of rapid mouth opening during the stab is also reflected in the reduction of the depressor mandibulae and retroarticular process. The countersunk lower jaw and the longitudinally arranged superficial cutaneous musculature, shared with other fossorial species (Cundall and Rossman, 1993), both correlate with a burrowing lifestyle. Although the duration of fang extrusion in *Atractaspis* (beginning of stab to beginning of fang penetration) is equivalent to the duration of the extension phase of the strike of crotalines (Kardong and Bels, 1998), the stab is slow because, in contrast to crotalines, *Atractaspis* initiates the stab when very close to the prey. Maxillary rotation in *Atractaspis* is limited compared to vipers, and correlates with the unique strategy of directing the fang tip posteroventrally to envenomate prey. Maxillary rotation in *Atractaspis* is achieved by modest protraction of the pterygoid because the rotational radius of the maxilla is small (Fig. 13).

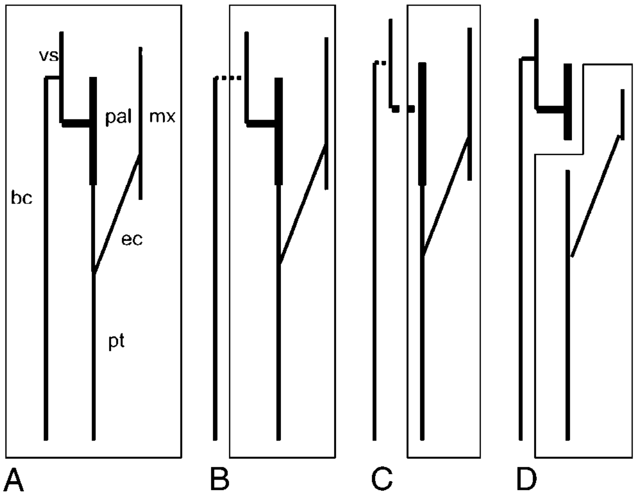

Fig. 14. Schematic diagram of the various ways snakes have modified ancestral palato-pterygoid attachments to increase kinetics. The palato-maxillary apparatus is only shown on the right side of the braincase. Dotted lines represent loosened attachments. Boxes are drawn around feeding functional units. **(A)** lizard; **(B)** basal alethinophidians like cylindrophiids, aniliids, and uropeltids; **(C)** most derived colubroids like vipers, elapids, and colubrids; **(D)** atractaspidids. See text for further explanation. Abbreviations: bc, braincase; ec, ectopterygoid; mx, maxilla; pal, palatine; pt, pterygoid; vs, ventral snout elements.

The evolution of the alethinophidian palatomaxillary apparatus has been viewed as a gradual loosening and detachment of palatine, pterygoid, ectopterygoid, and maxilla from the rest of the braincase and snout to increase the kinetics of the apparatus. Increased kinetic potential eventually resulted in the unique pterygoid walk prey transport mechanism that allows snakes to eat large prey items (Cundall and Greene, 2000) and facilitated the evolution of envenomation systems based on rotatable maxillae. In scleroglossan lizards, among which presumably lie the ancestors of snakes (Rieppel, 1988**;** Pough et al., 2001), palatomaxillary elements are linked to the braincase through tight connections with the ventral snout bones. The feeding functional unit includes the entire palatomaxillary apparatus as well as the snout and braincase (Fig. 14A). Cranial kinesis, if present, occurs around a mesokinetic joint between the frontal and parietal bones (Frazzetta, 1962). In basal alethinophidians the palatomaxillary apparatus attains limited mobility by loosening the ventral snout elements (septomaxillae and vomers) from the rest of the snout while the palatine remains attached to those ventral elements by short, sturdy ligaments (Cundall, 1995). The feeding functional unit no longer includes the braincase (Fig. 14B). Slight anterolateral palatomaxillary displacements are facilitated by the shifting of ventral snout elements with respect to the dorsal snout (snout-shifting). The prey transport mechanism of these primitive alethinophidians can be viewed as a 'proto-pterygoid walk', including limited alternating anterolateral and posteromedial movements of the palatomaxillary arches and ventral snout bones.

In derived alethinophidians (vipers, elapids, colubrids and most atractaspidids), the palatomaxillary apparatus is further modified to perform the pterygoid walk and, in vipers, elapids, and some colubrids and atractaspidids, to envenomate prey. The ventral snout elements are no longer critical to the mechanics of the feeding functional unit (Fig. 14C). Whereas the medial elements of the palatomaxillary apparatus comprise the functional unit performing prey transport, the lateral linkage of pterygoid, ectopterygoid and maxilla comprises the prey envenomation functional unit (Cundall, 1983). In derived alethinophidians, the connection of the palatine to the ventral snout elements is relatively loose and the palatopterygoid joint is modified to facilitate flexion, allowing increased anterior-posterior excursion of the palatopterygoid bar for efficient pterygoid walk prey transport and maxillary rotation (Cundall, 1983; 1995).

Atractaspis retains a tight connection between the palatine and the snout and between the snout and the braincase (Bourgeois, 1968; McDowell, 1986, Fig. 7). This arrangement correlates with the fossorial habits of *Atractaspis* (Bourgeois, 1968; Broadley, 1983; Spawls and Branch, 1995; Chippaux, 1999). Tight attachment of the palatine to an immobile, or nearly immobile, snout, however, impedes excursions of the palatopterygoid bar. Thus, in *Atractaspis,* and presumably some of its relatives, the pterygoid is mobilized by detachment from the palatine-snout complex (Figs. 14D, 8).

The different patterns of liberating the pterygoid to allow its protraction suggest that there were a number of evolutionary experiments with jaw design in early alethinophidians and that atractaspidids may be an early radiation of colubroids, as suggested by McDowell (1986).

Prey transport

Ideas of how colubroid snakes transport prey are based on anatomical, radiographic, electromyographic, and film or video analyses of a relatively small number of species (Dullemeijer, 1956; Albright and Nelson, 1959a, b; Boltt and Ewer, 1964; Kardong, 1977; Cundall and Gans, 1979; Cundall, 1983) combined with less detailed observations of many other species. Most macrostomate snakes employ the 'pterygoid walk', in which the right and left palatopterygoid bars are alternately advanced over the prey, using the teeth to ratchet the snake's head forward. Having teeth on the pterygoid is critical for this process. The absence of maxillary rotation or fang movement during any stage of transport in *Atractaspis* suggests that the pterygoid does not move. It is possible that increased fang length resulted in immobilization of the pterygoid during transport because fang movements possibly get in the way, essentially decoupling both pterygoid and maxilla from prey transport functions.

Atractaspis transports prey with a mechanism convergent on those of some basal alethinophidians (e.g., *Cylindrophis*: Cundall, 1995). The mechanism relies on cervical compression-extension during orocervical and cervical phases of transport, a feature widespread among alethinophidians (Kley and Brainerd, 2002).

Initiation of transport in *Atractaspis* appears similar to *Cylindrophis*; both begin prey transport mostly by forcing their head over the prey by lateral rotations (Cundall, 1995). In contrast to *Cylindrophis,* however, motion of the mandibular rami was minimal in both species of *Atractaspis,* a feature that correlates with short fiber lengths of the protractor quadratus and pterygoideus accessorius. Orocervical transport occurs by bilateral compression/extension cycles of the head and anterior trunk. Forceful head depression onto the prey during the compression phase was presumably caused by the anterior-inserting rectus capitus anterior. The motion may press the small palatine teeth into the skin of mouse prey or help the teeth catch behind the scales of reptilian prey, creating friction to prevent the prey from slipping. This may account for the retention of teeth on a bone that is immobilized by its tight attachment to the nearly immobile snout. The small retractor vomeris and retractor pterygoideus may serve to orient the tiny palatine teeth on the surface of the prey. Formation of a constriction in the skin of the lower jaw during compressive periods of the orocervical phase of transport suggests that *Atractaspis* may use the intermandibularis posterior, which inserts slightly posterior to the enlarged gular scales, to hold the prey.

Many alethinophidian snakes commonly employ lateral concertina bending of the anterior trunk region, similar to that seen in *Atractaspis,* as soon as prey enter the esophagus (Moon, 2000; Kley and Brainerd, 2002). They use it in addition to pterygoid walk prey transport. This lateral bending is not a derived feature, but occurs in *Xenopeltis* (Kley and Brainerd, 2002), basal alethinophidians (Cundall, 1995), and in lizards (Moon, 2000). Head depression during the contraction phase of concertina swallowing has also been observed in lizards (Condon, 1987; Elias et al., 2000) and in snakes (Cundall, 1995; Kley and Brainerd, 2002). Cundall (1995) reports head depression in *Cylindrophis* around 31–46º from the horizontal plane. This number does not account for the angle between the anterior trunk and the horizontal and is thus difficult to compare to our data (head-anterior trunk angles around 51–65º, Table 1). However, judging from the figure in Cundall (1995), head-anterior trunk angles in *Cylindrophis* are similar to those observed in *Atractaspis*.

In our feeding trials, we observed only limited separation of the tips of the mandibular rami to about twice their resting distance during ingestion or transport, effectively restricting gape size to a prey diameter only slightly larger than the diameter of the snake. Morphological correlates of fossoriality include limited skull kinesis and gape (Gans, 1968; Rieppel, 1984). Morphological evidence suggests that extensibility of the anterior interramal space is limited, a finding supported by records of feeding and lower jaw manipulations. Absence of appreciable separation of the tips of the mandibles limits gape to a size defined by mandible length. Although the mandibles of *Atractaspis* are relatively long, field and museum records of prey size (Greene, 1977; Broadley, 1983) indicate that *Atractaspis* typically consume prey of relatively small diameter.

Fang use and transport were similar in both species of *Atractaspis* tested, with the exception of the number of fang stabs per prey item and the degree of head depression during the compression phase of transport. *Atractaspis bibronii* stabbed neonate mice significantly more often than *A. microlepidota,* possibly reflecting a lower venom output of the smaller *bibronii*. However, *A. bibronii* venom is considerably more toxic than that of *A. microlepidota* (Kochva, pers. comm.). Head depression was significantly less pronounced in *A. mi-*

crolepidota although this did not impact on transport times. In *A. bibronii*, head depression was more pronounced when they were feeding on mice, possibly because the long snake prey made bending of the head on the trunk more difficult.

Prey handling and early transport in *Atractaspis* appears inefficient compared to other snakes. This is largely due to long delays before the snakes began transport. It appeared that the snakes could not easily 'find' the head of the prey. Once orocervical transport commenced, however, it progressed rapidly in many cases. Transport times were, on average, twice as long for snake prey than for mouse prey simply because snake prey were much longer. The long times *Atractaspis* spend with their prey suggests a lack of selection for feeding efficiency in a subterranean environment.

An evolutionary hypothesis

Molecular and morphological systematic analysis suggests that *Atractaspis* shares an ancestor with a number of fossorial African genera (Bourgeois, 1968; Heymans, 1975; McDowell, 1986, 1987; Underwood and Kochva, 1993; Zaher, 1999), possibly including the front-fanged *Homoroselaps* (Vidal and Hedges, 2002). We suggest that the selective advantage of the envenomation strategy of *Atractaspis* over con-familial rear-fanged snakes lies in four factors: Firstly, greater envenomation efficiency resulting from the longer, canaliculate fang; secondly, envenomation without having to open the mouth, allowing envenomation during head contact with any part of the prey; thirdly, capacity to envenomate and rapidly release the prey; and fourthly, potential for effective defensive envenomation against adult rodents. Most prey consumed by *Atractaspis* (amphisbaenians, fossorial skinks, typhlopid snakes; Greene, 1977) are also selected by some other atractaspidids (e.g., *Amblyodipsas*, *Xenocalamus*, *Chilorhinophis*, *Macrelaps*: Broadley, 1983). The fact that none of these taxa have long fangs suggests that all of the prey types can be caught and eaten without the use of long fangs. Thus, none of the squamate prey selected by *Atractaspis* can be considered the sole driving force behind selection for its envenomating apparatus. However, the diet of *Atractaspis* includes nestling rodents (Greene, 1977; 1997), prey items rare or absent in the stomachs of most other atractaspidids (Broadley, 1983). We feel it is unlikely that the evolution of the unusual morphology of *Atractaspis* was driven by selection of rodent prey alone because nestling rodents can be eaten easily, even without envenomation. On the other hand, the absence of mammals in the stomachs of other atractaspidids and the large geographic range of the genus *Atractaspis* suggest that the success of the clade is partly attributable to the use of the envenomating apparatus on mammals. Possibly the ability of *Atractaspis* to rapidly envenomate and kill all mammal nestlings before ingesting any may also allow defense against attacks by attending adult mammals.

The fact that the envenomating system of *Atractaspis* works well in confined spaces hardly explains its use in mammal nesting chambers (Nowak, 1999). However, because *Atractaspis* envenomates prey without opening its mouth, it is able to secure prey in tunnels with diameters only large enough to fit predator and prey (Fig. 15). The ability to inject incapacitating quantities of venom in confined spaces may allow *Atractaspis* to exploit greater diversity and size ranges of squamates as well as nestling mammals. The fact that *Atractaspis* never attempted to ingest snake prey until the prey no longer responded to fang pricks suggests that squamates may be more dangerous to the predator than nestling mammals. Hence, the capacity to efficiently envenomate and release potentially dangerous prey and the ability to kill a variety of prey types in subterranean environments may be the selective factor underlying the evolution of an envenomating system at the expense of its prey transport functions. Like *Dasypeltis* (Gans, 1952), *Atractaspis* still manage to transport dead or immobile prey with a jaw apparatus having only a few tiny teeth.

Eliminating mouth-opening for envenomation was facilitated by the completely countersunk mouth, also correlating with a fossorial lifestyle. Envenomation without mouth opening is facilitated by a long fang on a short, rotatable maxilla. Even though a short fang would likely also protrude from a closed mouth, elongation of the fang increases the chance of penetrating and remaining embedded in a struggling prey. Liberation of the pterygoid from the palatine was a solution to mobilizing the palatomaxillary apparatus while the palatine remained tightly connected to a nearly immobile snout used for burrowing. The size of the fang may have led to the elimination of pterygoid protraction because fang rotation would interfere with transport. The

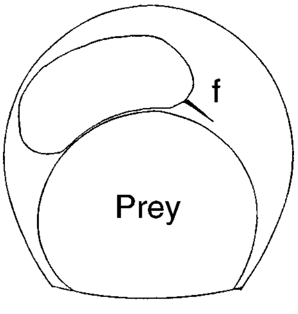

Fig. 15. Tunnel cross-section showing *Atractaspis* and prey. The ability to extrude a fang from a closed mouth allows *Atractaspis* to envenomate prey in confined spaces. Abbreviations: f, fang.

absence of pterygoid movements during transport made the evolutionary retention or reappearance of teeth on that bone unnecessary. *Atractaspis* relies on a prey transport mechanism that is convergent on mechanisms seen in primitive alethinophidians. The loss of normal pterygoid-walk transport is not detrimental, possibly because *Atractaspis* is relatively protected from predation in its subterranean environment.

Functional units and potential tradeoffs

Functions such as the pterygoid walk are performed by a collection of structures working together in a concerted manner. Such suites of structures may not only be shaped by external adaptive selection or phylogenetic constraints, but also by internal functional interactions (Wagner and Schwenk, 2000). Wagner and Schwenk (2000) propose that structures participating in a biological function can vary only within certain thresholds because the function of the entire system has to be maintained or fitness will decrease. Variation within those thresholds still allows evolution of the entire suite of structures in response to a changing environment. However, modification of any one structure in a functional linkage that puts it outside those thresholds will result in a total breakdown of system function (Schwenk, 2001). The liberation of the palatopterygoid connection, loss of pterygoid teeth, and elongation of the fang in *Atractaspis* may represent such an event. *Atractaspis* cannot perform the pterygoid walk with its modified palatomaxillary apparatus, but uses the entire head and anterior trunk in a way that ultimately performs the same biological role of getting food into the stomach of the snake.

Haas (1931b) interpreted the loss of a direct bony link between pterygoid and palatine in *Atractaspis* as an extreme form of the solenoglyph *Bauplan*. The lateral envenomation portion of the palatomaxillary apparatus is emphasized by excluding the palatine from the linkage system. In most venomous snakes, both fang erection and prey transport are driven by protraction of the pterygoid: maxilla and fang are rotated by protraction of the pterygoid and attached ectopterygoid, whereas protraction and retraction of the palatopterygoid bar characterizes the ‘pterygoid walk’ prey transport mechanism (Boltt and Ewer, 1964). Thus there is significant overlap between the suites of characters involved in performing both behaviors. Characters participating in multiple functions may potentially be subject to conflicting demands. If selection acting on one of these characters is stronger for one function than for another, selection for the second function may be ineffectual. It is conceivable that optimization of one function will then be to the detriment of the other (Schwenk and Wagner, 2001). In *Atractaspis*, the evolution of a long fang that allowed envenomation with a closed mouth in very narrow burrows (Fig. 15) resulted in the loss of palatomaxillary function during transport. Functional tradeoffs between the demands of burrowing, envenomation in a confined space, defense, and prey transport have ultimately favored the prey envenomation function.

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