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Prey Transport Mechanisms in Blindsnakes and the Evolution of Unilateral Feeding Systems in Snakes[1]

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SYNOPSIS. **Most snakes ingest and transport their prey via a jaw ratcheting mechanism in which the left and right upper jaw arches are advanced over the prey in an alternating, unilateral fashion. This unilateral jaw ratcheting mechanism differs greatly from the hyolingual and inertial transport mechanisms used by lizards, both of which are characterized by bilaterally synchronous jaw movements. Given the well-corroborated phylogenetic hypothesis that snakes are derived from lizards, this suggests that major changes occurred in both the morphology and motor control of the feeding apparatus during the early evolution of snakes. However, most previous studies of the evolution of unilateral feeding mechanisms in snakes have focused almost exclusively on the morphology of the jaw apparatus because there have been very few direct observations of feeding behavior in basal snakes. In this paper I describe the prey transport mechanisms used by representatives of two families of basal snakes, Leptotyphlopidae and Typhlopidae. In Leptotyphlopidae, a mandibular raking mechanism is used, in which bilaterally synchronous flexions of the lower jaw serve to ratchet prey into and through the mouth. In Typhlopidae, a maxillary raking mechanism is used, in which asynchronous ratcheting movements of the highly mobile upper jaws are used to drag prey through the oral cavity. These findings suggest that the unilateral feeding mechanisms that characterize the majority of living snakes were not present primitively in Serpentes, but arose subsequently to the basal divergence between Scolecophidia and Alethinophidia.**

INTRODUCTION

Three fundamental modes of intraoral prey transport are recognized within Squamata. Most lizards use a hyolingual transport mechanism, in which cycles of tongue protraction and retraction serve to ratchet prey through the mouth and towards the pharynx (Smith, 1984; Herrel *et al.*, 1996; Schwenk, 2000). In some lizards, however, this lingual ratcheting mechanism is augmented or replaced by a cranioinertial transport mechanism, in which rapid movements of the entire head are used to propel prey through the oral cavity (Gans, 1969; Bramble and Wake, 1985). This mode of intraoral transport is of particular importance in varanid lizards (Smith, 1986; Elias *et al.*, 2000), which share with snakes a highly reduced tongue that lacks a frictional surface (McDowell, 1972; Schwenk, 1988). Finally, snakes use gnathic (jaw-based) transport mechanisms, in which kinetic elements of the jaw apparatus are used to ratchet prey into and through the mouth (Cundall and Greene, 2000). While both hyolingual and cranioinertial transport are common among tetrapods, gnathic transport mechanisms are unique to snakes (Bramble and Wake, 1985).

Nearly all of what is currently known about gnathic transport in snakes derives from studies of taxa belonging to Macrostomata (Fig. 1), a large and diverse clade that includes approximately eighty-five percent of the more than 2,500 species of extant snakes (McDiarmid *et al.*, 1999). These studies have shown that most macrostomatans ingest and transport their prey via a ‘‘pterygoid walk’’ mechanism (Boltt and Ewer, 1964), in which reciprocating ratcheting movements of the medial upper jaw arches, combined with lateral rotations of

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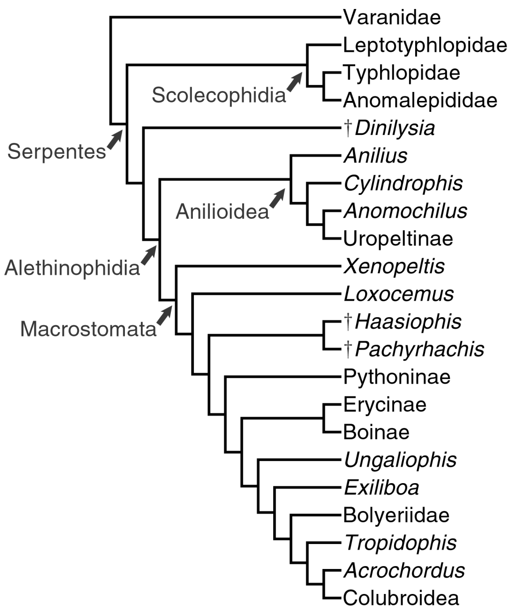


Fig. 1. Phylogenetic hypothesis of relationships of the major groups of snakes, modified from Tchernov *et al.* (2000). Interrelationships of the three scolecophidian families (Leptotyphlopidae, Typhlopidae and Anomalepididae) after Cundall *et al.* (1993). Fossil taxa are indicated by a dagger (†).

the entire head about the cranio-vertebral joint, serve to advance the snake's head over its prey (Dullemeijer, 1956; Albright and Nelson, 1959*a, b*; Frazzetta, 1966; Kardong, 1977; Cundall and Gans, 1979; Cundall, 1983; Kardong, 1986). Because this unilateral jaw ratcheting mechanism differs greatly from both the hyolingual and cranioinertial transport mechanisms of lizards (Kardong and Berkhoudt, 1998; Cundall, 1995), its origin has been somewhat enigmatic, and there have thus been numerous attempts made to determine the evolutionary steps through which it arose (*e.g.*, Gans, 1961; Rieppel, 1980; Lee *et al.*, 1999; Kardong and Bels, 2001). However, most studies that have addressed the evolutionary origin of unilateral feeding mechanisms in snakes have been conducted from an almost exclusively anatomical perspective because the actual feeding mechanisms used by basal snakes have remained largely unknown.

Recently, Cundall (1995) provided the first detailed account of feeding behavior in a basal snake, describing a prey transport mechanism that he termed ''snout shifting'' in the anilioid *Cylindrophis* (Fig. 1). Like the pterygoid walk, snout shifting involves unilateral movements of the toothed elements of the upper jaws, combined with side-to-side movements of the entire head, which together serve to advance the head over the prey. However, the upper jaws in *Cylindrophis* (and in other anilioids) remain tightly bound to the ventral elements of the bony snout (*e.g.*, vomers, septomaxillae) by several short, robust ligaments. These ligaments prevent extensive translational movements of the jaws such as those which are associated with the pterygoid walk in macrostomatans. Independent movements of the upper jaws are instead achieved through lateral rotations of the entire snout complex about the nasofrontal articulation (prokinesis; Frazzetta, 1962) and independent translational movements of the left and right septomaxilla-vomer complexes to which the upper jaws are bound (rhinokinesis; Cundall and Shardo, 1995). Thus, in certain respects, *Cylindrophis* represents an intermediate functional stage between lizards and macrostomatan snakes (Cundall, 1995); despite retaining a tight connection between the upper jaws and the snout (as in lizards), prey is transported via a unilateral jaw ratcheting mechanism (as in macrostomatans).

The discovery of snout shifting in *Cylindrophis,* and its likely presence in other anilioids such as *Anilius* (Gans, 1961; Cundall, 1995), suggests that the pterygoid walk is unique to Macrostomata, but that the unilateral jaw displacement pattern common to both snout shifting and the pterygoid walk is primitive for Alethinophidia (Fig. 1). Whether this unilateral jaw displacement pattern is unique to Alethinophidia is unknown, however, because the feeding mechanisms of the three families of blindsnakes (Scolecophidia; Fig. 1) have remained largely unknown (Kardong *et al.*, 1997). The feeding behavior of these tiny, secretive snakes is known only from a few brief accounts (Smith, 1957; Reid and Lott, 1963; Thomas, 1985; Webb and Shine, 1993*b*; Kley and Brainerd, 1999), and thus a detailed understanding of feeding mechanics in the group is lacking. In this paper

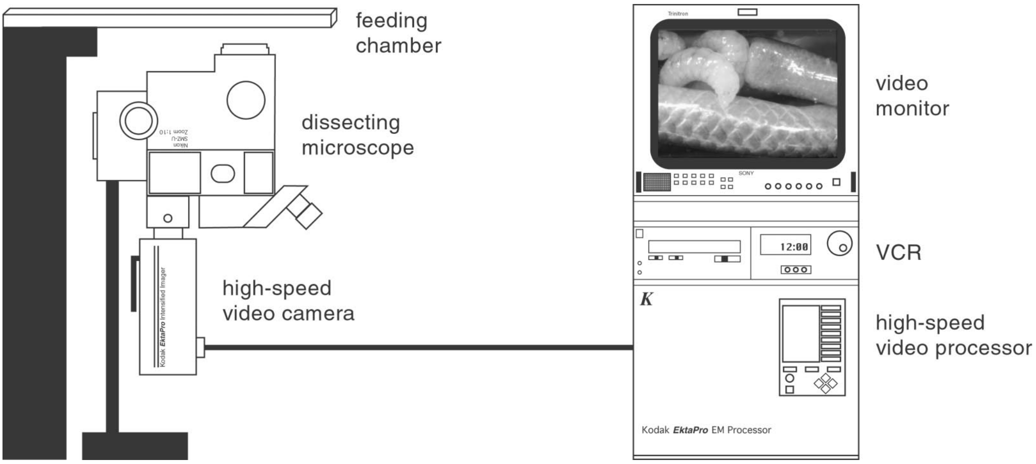


FIG. 2. Schematic diagram of the apparatus used for magnified high-speed videography.

I describe the prey transport mechanisms used by representatives of two families of Scolecophidia (Leptotyphlopidae and Typhlopidae) in an effort to elucidate the phylogenetic origin of unilateral feeding mechanisms in snakes.

MATERIALS AND METHODS

The blindsnakes used for this study were purchased from commercial herpetological suppliers. Feeding behavior was observed in one species of Leptotyphlopidae (*Leptotyphlops dulcis* (Baird and Girard), n = 20) and two species of Typhlopidae (*Typhlops lineolatus* Jan, n = 5; *Rhinotyphlops schlegelii* (Bianconi), n = 5). The snakes were fed larvae and pupae of several species of ants (most frequently species of *Camponotus*, *Formica* and *Acanthomyops*) collected in the vicinity of Amherst, Massachusetts. Ant pupae ranged in size from 1.3 × 3.0 mm to 3.4 × 8.4 mm, while the larvae were generally smaller, often less than 1 mm in diameter.

Feeding trials for 10 individuals of *Leptotyphlops dulcis* and 1 individual of *Typhlops lineolatus* were recorded using magnified high-speed videography (Fig. 2). (Unfortunately, all but one of the typhlopids observed during this study refused to feed under the conditions required for this technique.) Several hundred feedings were recorded for each species. Because the mouth in blindsnakes is subterminal and countersunk into the ventral surface of the head, feeding trials were recorded from a ventral perspective. The snakes were fed in a clear acrylic filming chamber (6 × 13 × 34 mm) positioned above an inverted Nikon SMZ-U dissecting microscope that was coupled to a Kodak EktaPro high-speed video system. Feeding sequences were recorded at 250 fps (shutter speed, 1/500 sec) and then transferred to S-VHS videotape using a Panasonic AG-1970 VCR. Selected video sequences were digitized using Adobe Premiere software on a Power Macintosh G3 computer and jaw movements were analyzed frame-by-frame using NIH Image software. Additional feeding trials were recorded at 60 fps with a Sony DCR VX700 digital camera. Finally, several feeding trials for *T. lineolatus* were recorded using videofluoroscopy. X-ray videos were recorded at 60 fps using a Sony DCR VX1000 digital camera that was coupled to a Siemens radiographic unit equipped with a Sirecon image intensifier. In these feeding trials, ant pupae were injected with an aqueous barium sulfate solution so that they could be visualized throughout intraoral transport and swallowing.

The cranial morphology of all three species of blindsnakes was studied primarily through microdissections and the examination of cleared and stained skeletal preparations. Microdissections were performed on 5 *Leptotyphlops dulcis*, 4 *Typhlops li-*

neolatus and 3 *Rhinotyphlops schlegelii* to examine the myology of the jaw apparatus in each species. Because of the extraordinarily small size of *L. dulcis* (2.2–3.0 mm head diameter, mean = 2.6 mm), specimens of this species were generally dissected in water or in 70% ethanol, and the entire head of each specimen was frequently immersed in Lugol's iodine solution (Weigert's variation) to facilitate differentiation between closely apposed muscle layers (Bock and Shear, 1972). Following these dissections, 5 *L. dulcis*, 3 *T. lineolatus* and 2 *R. schlegelii* were cleared and stained according to a protocol modified from Hanken and Wassersug (1981) and 2 *L. dulcis*, 1 *T. lineolatus* and 1 *R. schlegelii* were prepared as dried skeletons using small dermestid beetle larvae. The bones, cartilages, ligaments and joints of the jaw apparatus were examined and manipulated in each of these skeletal preparations under a Nikon SMZ-U stereo dissecting microscope. In addition, the heads of 3 specimens of *L. dulcis* were decalcified, dehydrated and embedded in low-viscosity nitrocellulose (Thomas, 1983) and serially sectioned at 30 μm in transverse, frontal and sagittal planes. Sections were stained with Hematoxylin and Picro-Ponceau (Humason, 1979; Thomas, 1983) and examined using a Zeiss Axioskop compound microscope to verify the relationships of cranial elements determined from alcoholic and cleared and stained specimens.

RESULTS

Magnified high-speed videography revealed that both *Leptotyphlops dulcis* and *Typhlops lineolatus* ingest and transport their insect prey using rapid jaw ratcheting mechanisms. However, the transport mechanisms used by these species differ radically from one another, and neither resembles the unilateral jaw ratcheting mechanisms used by alethinophidian snakes.

Leptotyphlops

Morphology of the jaw apparatus. Only a brief description of the relevant structures of the jaw apparatus of *Leptotyphlops* is presented here. A more detailed account of the cranial morphology of *L. dulcis* will be published elsewhere (Kley, in preparation). Descriptions of the cranial anatomy of other species of *Leptotyphlops* are provided by Haas (1930, 1959), McDowell and Bogert (1954), List (1966), Brock (1932), and Abdeen *et al.* (1991*a*, *b*, *c*).

One of the most peculiar features of the jaw apparatus in *Leptotyphlops dulcis* is the complete lack of teeth in the upper jaws (viz., the maxillae, palatines and pterygoids; Fig. 3A). Within Serpentes, this condition is unique to Leptotyphlopidae (Greene, 1997). Furthermore, the upper jaw arches are relatively immobile due to tight ligamentous connections between the maxillae and other elements of the rigid snout complex (especially the premaxilla and prefrontals). As a result, ratcheting movements of the upper jaws like those associated with prey transport in alethinophidian snakes are not possible in *Leptotyphlops*. Also, in contrast to most alethinophidians, the ligamentous connection between the posterior part of the pterygoid and the distal part of the quadrate is extremely weak, visible only in histological sections as a faint band of loosely arranged connective tissue. Thus, the lower jaw is functionally decoupled from the upper jaws in *Leptotyphlops*.

In contrast to the upper jaws, however, the lower jaw of *Leptotyphlops* bears teeth and is highly kinetic. The mandible itself is relatively short and is suspended from the braincase by the exceptionally long, anteroventrally directed quadrates (Fig. 3A). The proximal end of each quadrate articulates with the braincase in a relatively loose sliding joint. A single row of four or five teeth is present on each dentary, representing the only teeth in the skull. Because of the somewhat cupped shape of the enlarged lateral flanges of the dentaries, these tooth rows are oriented nearly transversely across the anterior margin of the lower jaw (Fig. 3B, left). Moreover, each mandibular ramus is divided into separate anterior and posterior halves by a highly mobile intramandibular joint. This joint is formed by contact between the posterior end of the splenial, which is closely applied to the ventromedial surface of the dentary, and the anterior end of the angular, which runs along the ventrolateral surface of the compound bone (Fig.

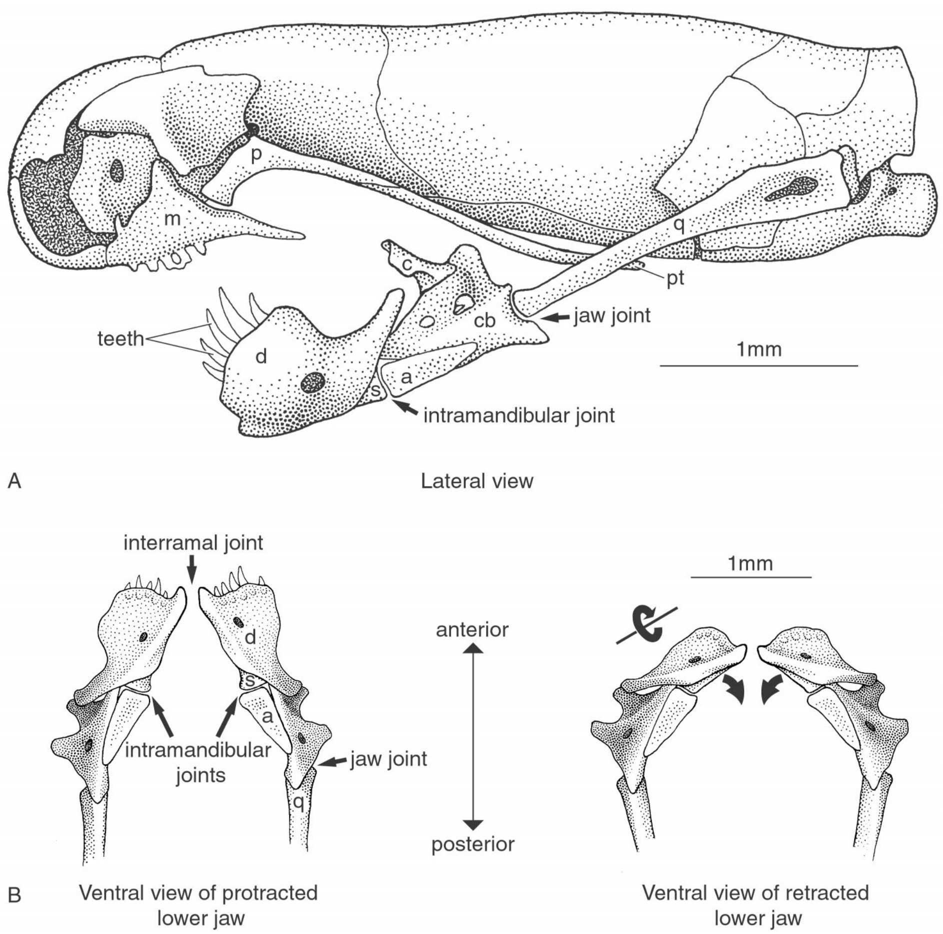


FIG. 3. Cranial morphology and jaw mechanics in *Leptotyphlops dulcis*. Drawings were made from a cleared and stained adult specimen. A. Left lateral view of the skull. Note the well-developed intramandibular (splenial-angular) joint and the absence of teeth on the upper jaw elements (pterygoid, palatine and maxilla). (The ventrally directed projections on the maxilla are features of the bone itself, and the size and form of these projections vary widely between individuals.) B. Ventral view of the lower jaw during protraction (left) and retraction (right). Note that during retraction, the dentary-splenial complex rotates medially about the intramandibular joint and also caudally about its own long axis. Abbreviations: a, angular; c, coronoid; cb, compound bone; d, dentary; m, maxilla; p, palatine; pt, pterygoid; q, quadrate; s, splenial. Modified from Kley and Brainerd (1999).

3A). Because of the rounded articular facets on both the splenial and angular, and the reduced dorsal contact between the dentary and post-dentary bones (*e.g.*, coronoid and compound bone), the anterior half of each mandibular ramus (dentary + splenial) is capable of extensive rotation about the intramandibular joint in all planes. However, lateral and ventral rotations of the dentary-splenial complex are checked by several ligaments that span the intramandibular joint.

The distal tips of the dentaries are rounded and do not contact one another anteriorly (Fig. 3B). However, Meckel's cartilage, which persists throughout nearly the entire length of the lower jaw, provides a tight linkage between the mandibular rami. The left and right halves of this cartilage exit the distal tips of the dentaries, curve dorsomedially, and fuse together to form a robust cartilaginous nodule at the midline. This cartilaginous linkage severely limits both lateral separation and independent anteroposterior excursions of the tips of the mandibular rami, but allows extensive rotation between the left and right anterior mandibular segments. In addition, this nodule of cartilage between the tips of the mandibular rami serves as the site of origin for the extraordinarily robust median tendon of the *M. genioglossus*. A large slip of this muscle extends caudally beyond the lingual sheath to insert onto the posteriorly positioned, Y-shaped hyoid which, on average, is located between the 14th and 19th precaudal vertebrae in *Leptotyphlops dulcis*. This hyoid portion of the *M. genioglossus* (a likely homologue of the *M. mandibulohyoideus* II of lizards) is unique to Leptotyphlopidae among snakes (Langerbartel, 1968; Groombridge, 1979).

Feeding mechanics and behavior. When presented with ant larvae and pupae, individuals of *Leptotyphlops dulcis* quickly began to exhibit characteristic frenzied feeding behavior. The snakes began to feverishly sway their heads and necks from side to side in an attempt to locate potential food items. Once the snout contacted an ant larva or pupa, the snake would slide the ventral surface of its snout over the top of the prey until the prey item was positioned at or near the front of the mouth. In some instances, the snake would actually pin its prey against the substrate with its snout prior to initiating ingestion, but this was not a necessary pre-requisite for successful ingestion. Once the snake had positioned its mouth near the prey, it would then open its mouth widely and grasp the prey between its jaws.

In all feedings that were observed, *Leptotyphlops dulcis* ingested and transported ant larvae and pupae using a rapid mandibular raking mechanism (Kley and Brainerd, 1999). Immediately following mouth opening, the snakes initiated bilaterally synchronous cycles of lower jaw flexion in which the toothed anterior mandibular segments were rapidly (2–3 Hz) rotated in and out of the mouth to drag prey into and through the oral cavity (Fig. 3B). This mandibular raking mechanism involved complex movements at the intramandibular joints. Each anterior mandibular segment (dentary + splenial) was rotated medially in a horizontal plane about the splenial-angular (intramandibular) joint. As a result of this movement, both the intramandibular joints and the distal ends of the quadrates were forced laterally. At the same time, however, each anterior mandibular segment was also rotated caudally about its own long axis (Fig. 3B, right). The combined result of these movements was that the transversely oriented dentary tooth rows were rotated caudally into the mouth, thereby dragging the prey toward the snake's esophagus.

The rapid jaw movements associated with ingestion and prey transport in *Leptotyphlops* were usually augmented by synchronized movements of the anterior portion of the trunk. During jaw protraction, the neck was flexed slightly in the vertical plane, forming a shallow arch over the substrate. Then, during subsequent jaw retraction, the neck was straightened, thereby pushing the braincase anteriorly as the lower jaw was pulling the prey caudally. Thus, as in alethinophidian snakes, movements of the anterior trunk supplement jaw movements during prey transport in *Leptotyphlops*. In contrast to the concertina-like movements seen in alethinophidians (Cundall, 1995; Kley and Brainerd, 1996; Moon, 2000), however, axial bending during prey transport in *Leptotyphlops* is restricted to the vertical plane. Finally, it should be emphasized that while the ventroflexion associated with prey transport in *Leptotyphlops* may result in the prey being forced against the substrate, this is neither a necessary nor a common aspect of feeding behavior in these snakes (*contra* Reid and Lott, 1963).

Once the prey was transported to the rear of the mouth, *Leptotyphlops dulcis* initiated swallowing with a forceful compression of the pharynx. After the prey was forced into the esophagus through pharyngeal compression, swallowing appeared to occur entirely through peristalsis. No axial bending was observed during swallowing.

Muscular control of jaw movements. Leptotyphlopid snakes are among the most highly miniaturized tetrapods. Even in the largest species of *Leptotyphlops*, maximum head diameter rarely exceeds 5 mm. Thus, electromyography of head muscles in these snakes was not feasible. However, micromanipulations of both fresh and cleared and stained specimens provided useful, albeit limited, insight into the muscular control of the mandibular raking mechanism.

The results of these manipulations strongly suggest that jaw retraction in *Leptotyphlops* is powered primarily by the long and robust *M. genioglossus*, *pars hyoidea*, which runs from the cartilaginous nodule between the distal tips of the mandibular rami to the posteriorly positioned hyoid apparatus. Indeed, by applying a caudally directed force to the tendon of the *M. genioglossus*, the movements of the anterior mandibular segments that were observed during feeding were replicated almost precisely. In contrast, jaw protraction in *Leptotyphlops* appears to be powered mainly by the *M. geniohyoideus*. This complex strap muscle has a lateral head, originating from the lateral surface of the trunk muscles in the cervical region, and a medial head, originating from the hyoid. Both heads converge to insert via tendons onto the ventroposterior surface of the dentary. The action of the *M. geniohyoideus* is to rotate the anterior mandibular segments laterally about the intramandibular joints and also rostrally about their own long axes, thus rotating the dentary tooth rows outwards to their resting position. It is likely, however, that contraction of the *M. intermandibularis* complex and elastic recoil of Meckel's cartilage also contribute to jaw protraction.

Typhlops *and* Rhinotyphlops

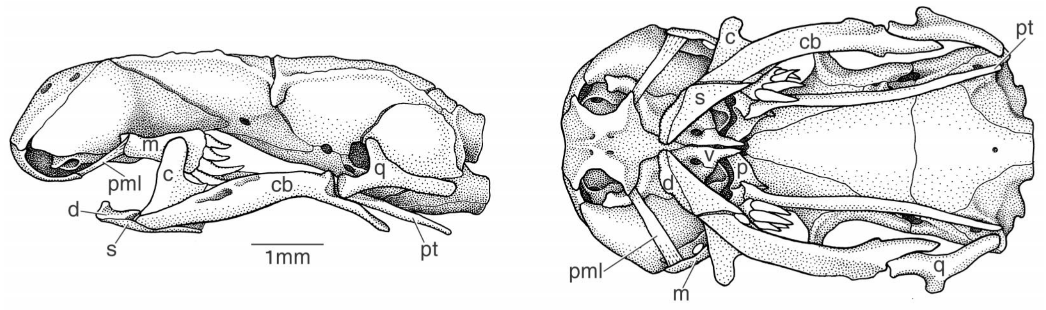
Morphology of the jaw apparatus. As for *Leptotyphlops*, only a brief description of the typhlopid jaw apparatus will be presented here. More comprehensive treatments of the cranial anatomy of other typhlopid species are provided by Haas (1930), Smit (1949), List (1966) and Iordansky (1997).

In nearly every major respect, the morphology of the jaw apparatus of *Typhlops lineolatus* was found to agree completely with that of *Rhinotyphlops schlegelii*. However, the jaw morphology of both of these taxa differs profoundly from that of *Leptotyphlops dulcis*. Most significantly, the lower jaws of *Typhlops* and *Rhinotyphlops* are toothless and relatively rigid, whereas the upper jaw arches bear teeth and are highly mobile.

In both *Typhlops* and *Rhinotyphlops*, the mandible is much longer than in *Leptotyphlops*, and is suspended from the braincase via the relatively short quadrates (Fig. 4A). The dentary is greatly reduced and lacks teeth, a condition that is unique to typhlopids among snakes. As in *Leptotyphlops*, the left and right halves of Meckel's cartilage are bound together by an expanded interramal cartilaginous nodule, an arrangement which prevents independent movements of the left and right mandibular rami. However, in sharp contrast to the condition seen in *Leptotyphlops*, there is extensive contact between the relatively long splenial and the large, triangular coronoid. Thus, the intramandibular joint is bridged completely by the splenial (Fig. 4A), and consequently, the lower jaws of *Typhlops* and *Rhinotyphlops* are relatively rigid and akinetic.

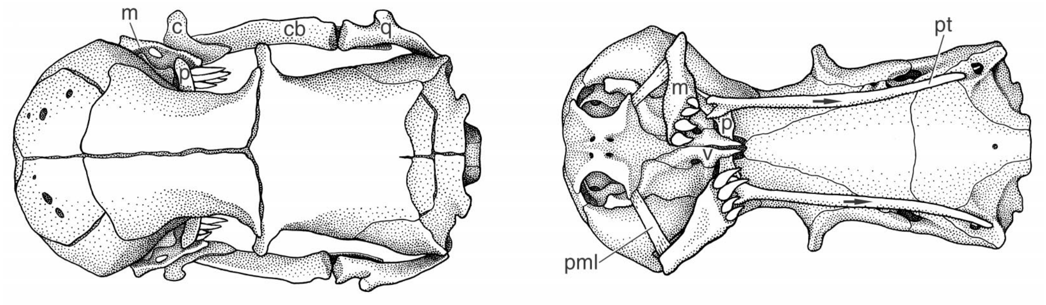
In contrast to the lower jaw, the upper jaws of both *Typhlops* and *Rhinotyphlops* are exceptionally kinetic. The maxillae lie horizontally against the roof of the mouth with their transversely oriented tooth rows directed posteriorly (Fig. 4A, B, C), and are suspended largely by ligaments and muscles rather than through bony articulations. In particular, a robust ligament running from the canaliculate anterior end of the maxilla to the posterolateral margin of the premaxilla (the premaxillo-maxillary ligament) anchors the anterior end of the maxilla (Fig. 4A, C). Posteriorly, the maxilla is suspended by the *M. retractor maxillae*, a large muscle that takes its origin from the lateral surface of the braincase and inserts onto the posterodorsal surface of the maxilla.

The palatine is the only bone that contacts the maxilla directly. This bone has a complex arched shape, with a medial process that articulates with the posterolateral margin of the vomer (Fig. 4C), and a lateral process that curves ventrally to insert into a shallow groove on the dorsal surface of the maxilla (Fig. 4B). Near the midpoint of the palatine, there is a slight ventral process that is embraced by the forked anterior end of the pterygoid (Fig. 4C). As in *Leptotyphlops*, the pterygoid in *Typhlops* and



A Lateral view

C Ventral view



B Dorsal view

D Ventral view, lower jaw removed

FIG. 4. Cranial morphology and jaw mechanics in *Typhlops lineolatus*. Drawings were made from a cleared and stained adult specimen. A. Left lateral view of the skull. Note the horizontally positioned maxillae and the absence of teeth on the lower jaw. B. Dorsal view of the skull, showing the sliding articulation between the lateral process of the palatine and the dorsal surface of the maxilla. C. Ventral view of the skull, showing the articulation between the medial process of the palatine and the posterolateral edge of the vomer. Note the robust premaxillo-maxillary ligaments which anchor the anterior ends of the maxillae. D. Ventral view of the skull during maxillary raking, showing asynchronous retraction of the maxillae. The lower jaw has been removed to permit an unobstructed view of the upper jaws. Abbreviations: c, coronoid; cb, compound bone; d, dentary; m, maxilla; p, palatine; pml, premaxillo-maxillary ligament; pt, pterygoid; q, quadrate; s, splenial; v, vomer.

Rhinotyphlops is a long and slender bone that is widely separated from the quadrate (Fig. 4C). Thus, the upper and lower jaws are functionally decoupled as in *Leptotyphlops*. In both *Typhlops* and *Rhinotyphlops*, the pterygoid is suspended from the ventral surface of the braincase by the robust *M. protractor pterygoidei*, which originates from the ventral surface of the braincase and courses posteroventrally to ensheathe the posterior end of the pterygoid.

Feeding mechanics and behavior. Like *Leptotyphlops*, *Typhlops* and *Rhinotyphlops* exhibited somewhat frenzied feeding behavior when presented with ant brood. Soon after a snake detected the presence of prey (presumably via chemosensory cues obtained through tongue-flicking), it initiated a tactile search for individual prey items by rapidly sweeping its head from side to side in an erratic fashion as it progressed forward. Once the snake's head contacted an ant larva or pupa, the snake maneuvered its head so that its mouth was positioned directly over the prey. The snake would then open its mouth to initiate capture and ingestion.

In all feedings that were observed, *Typhlops lineolatus* and *Rhinotyphlops schlegelii* ingested and transported their prey using a rapid maxillary raking mechanism. As the mouth was opened over an ant larva or pupa, the snake initiated ratcheting movements of the upper jaws in which the toothed maxillae were rapidly (3–5 Hz) rotated in and out of the mouth. These maxillary raking movements served to drag the prey caudally into the mouth and towards the throat.

The jaw movements associated with maxillary raking in *Typhlops* and *Rhinotyphlops* were more variable than those involved in the mandibular raking mechanism of *Leptotyphlops*. Most frequently, both ingestion and intraoral transport were characterized by asynchronous jaw movements in which the left and right maxillae were protracted and retracted slightly out of phase with one another (Fig. 4D). In some instances, however, only a single maxilla was used during ingestion. This generally occurred when a snake was attempting to ingest an ant larva or pupa that was positioned to one side of its mouth rather than directly below it, or when a snake was trying to extract prey from a narrow, confined space.

Movements of the lower jaw were also somewhat variable. In the majority of feedings observed, ingestion was completed with a single maxillary retraction. In such instances the lower jaw was abducted during maxillary protraction and then adducted during maxillary retraction. However, ingestion of larger prey required several maxillary protraction-retraction cycles. In these instances, the lower jaw remained partially adducted throughout most of the maxillary protraction phase, presumably to prevent the advancing maxillae from pushing the prey back out of the mouth. Finally, during the rapid ingestion of large numbers of relatively small prey, movements of the lower jaw were largely independent of upper jaw movements. Under these circumstances, the lower jaw generally remained abducted as the maxillae continued to rake prey into the mouth. In this manner, multiple prey items were often ingested simultaneously.

It should be emphasized that no appreciable protraction of the lower jaw was ever observed in either *Typhlops lineolatus* or *Rhinotyphlops schlegelii*, and the mandible was never used to scoop prey off of the substrate as predicted by Iordansky (1981, 1990, 1997). However, prey items that were initially positioned unfavorably for efficient ingestion were in some instances reoriented by the mandible. During maxillary retraction, prey were frequently flipped up over the anterior margin of the lower jaw, an action that tended to align the long axis of the prey with that of the snake's head.

Unlike the smaller *Leptotyphlops*, *Typhlops* and *Rhinotyphlops* often ingested multiple prey items before swallowing them. Once the pharynx was filled, the snake initiated swallowing with a forceful contraction of the throat muscles immediately ventral to the pharynx, followed by wavelike muscular contractions propagated along the ventral surface of the neck. The prey was then rapidly propelled along the remainder of the esophagus, presumably via peristalsis. Like *Leptotyphlops*, *Typhlops* and *Rhinotyphlops* exhibited no axial bending during swallowing.

Muscular control of jaw movements. Several previous studies have analyzed the potential movements of the jaw apparatus in typhlopids and their muscular control (Haas, 1930; Evans, 1955; Iordansky, 1997). However, all of these studies were based exclusively on anatomical evidence. My observations of feeding in live *Typhlops lineolatus* and *Rhinotyphlops schlegelii*, combined with the brief accounts of Thomas (1985) and Webb and Shine (1993*b*) for *Typhlops richardi* and *Ramphotyphlops nigrescens*, respectively, provide some corroboration of the functional hypotheses generated through these morphological investigations.

High-speed video recordings of *Typhlops lineolatus* reveal that the tooth-bearing posterior ends of the maxillae are rotated through an arc of greater than 90° during jaw protraction. Given that neither of the muscles inserting onto the maxillae (*M. retractor maxillae* and *M. pterygoideus*) have origins that are anterior to the maxillae, the observed rotations of these elements are inferred to be produced indirectly through movements of the pterygoid and palatine bones. As noted by Evans (1955), the application of an anteriorly directed force to the pterygoid causes the arched palatine to pivot about its medial connection with the vomer, resulting in the lateral process of the palatine being displaced anteriorly and ventrally, thereby erecting the maxilla. The only muscle capable of producing this anterior translation of the pterygoid is the *M. protractor pterygoidei*, which originates from the ventral surface of the braincase and courses posteroventrally to ensheathe the caudal end of the pterygoid. Thus, as suggested by previous authors (Haas, 1964; Cundall and Rossman, 1993; Iordansky, 1997), erection of the maxilla appears to occur through the action of the *M. protractor pterygoidei*.

My observations of the cranial musculature of *Typhlops lineolatus* and *Rhinotyphlops schlegelii*, together with those of Haas (1930) for *T. punctatus*, *T. lumbricalis* and *Ramphotyphlops bituberculatus* and those of Iordansky (1997) for *T. lumbricalis* and *T. vermicularis* strongly suggest that the primary retractor of the upper jaw is the *M. retractor maxillae*. This is a very large muscle of uncertain homology (Lakjer, 1926; Haas, 1930, 1973) that is unique to Typhlopidae. It has a broad origin over the lateral surface of the braincase and inserts onto the posterodorsal portion of the maxilla. While other muscles are likely to participate in upper jaw retraction (*e.g.*, *M. pterygoideus* and *M. retractor pterygoidei*), the size, position and fiber orientation of the *M. retractor maxillae*, together with its direct insertion onto the maxilla, suggest that it is largely responsible both for retracting the upper jaw and rotating the maxilla back to its resting position.

DISCUSSION

Although the foraging strategies (Watkins *et al.*, 1967; Gehlbach *et al.*, 1971; Webb and Shine, 1992) and dietary habits (Punzo, 1974; Webb and Shine, 1993*a*; Webb *et al.*, 2000; Torres *et al.*, 2000) of scolecophidian snakes have been studied in some detail, the feeding behavior of these diminutive serpents has been known only from a few brief accounts (Smith, 1957; Reid and Lott, 1963; Thomas, 1985; Webb and Shine, 1993*b*; Kley and Brainerd, 1999). The actual mechanisms by which blindsnakes capture, ingest, transport and swallow their prey have remained largely unknown (Cundall and Rossman, 1993; Greene, 1997). However, previous studies of the cranial morphology of scolecophidians have proposed three different feeding mechanisms that might be used by these snakes: 1) suction feeding (Haas, 1964, 1968; Groombridge, 1979); 2) lingual transport (McDowell, 1972); and 3) gnathic (jaw-based) transport (Haas, 1930, 1962, 1964, 1968; Iordansky, 1981, 1997). Neither suction feeding nor lingual feeding have ever been documented in any snake and I found no evidence for either in *Leptotyphlops*, *Typhlops* or *Rhinotyphlops*. Instead, all three species observed during the course of the present study used their jaws to capture, ingest and transport their insect prey. However, both the mandibular raking mechanism of *Leptotyphlops* and the maxillary raking mechanism of *Typhlops* and *Rhinotyphlops* differ significantly from the jaw ratcheting mechanisms of alethinophidian snakes.

Mandibular raking

The mandibular raking mechanism of *Leptotyphlops* differs profoundly from the feeding mechanisms of other snakes in that prey is transported by bilaterally synchronous movements of the lower jaw rather than by independent movements of the upper jaws. Among the more than 2,500 living species of snakes, mandibular transport mechanisms are known elsewhere only in a small number of cochleophagous (snail-eating) colubrids of the subfamilies Dipsadinae and Pareatinae (Cundall and Greene, 2000). In these taxa, the mandible is used to pull snails from their shells. However, the snail extraction mechanisms used by these highly specialized colubrids involve unilateral ratcheting movements of the left and right mandibular rami (Sazima, 1989) and thus bear little resemblance to the bilaterally synchronous mandibular raking mechanism of *Leptotyphlops*. Furthermore, bilaterally synchronous jaw movements are generally restricted to prey capture in alethinophidians (*e.g.*, Frazzetta, 1966; Kardong, 1974; Cundall, 1987; Cundall and Deufel, 1999). Only rarely do such movements occur during prey transport, and when they do, it is only during the transition between intraoral transport and swallowing, a period during which the prey is moved not by the jaws, but by concertina-like movements of the trunk in the cervical region (Cundall, 1995; Kley and Brainerd, 1996; Kardong and Berkhoudt, 1998).

The muscle activity patterns associated with mandibular raking in *Leptotyphlops* remain completely unknown. Given the bilaterally synchronous jaw movements that characterize this mechanism, it seems likely that bilateral activation of the hypoglossal muscles powering jaw retraction (*M. genioglossus*, *pars hyoidea*) and protraction (*M. geniohyoideus*) is involved. Regardless of muscle activity patterns, however, movements of the lower jaw in *Leptotyphlops* are morphologically constrained to be bilaterally synchronous. As in typhlopids (Bellairs and Kamal, 1981; Young, 1998), the left and right halves of Meckel's cartilage in *Leptotyphlops* extend beyond the distal tips of the mandibular rami and fuse together to form a robust interramal nodule of cartilage. This cartilaginous link between the tips of the mandibular rami permits hinge-like rotations between the dentaries, but allows almost no lateral or anteroposterior separation of the mandibular tips. In addition, during jaw retraction, caudally directed forces generated through contraction of the *M. genioglossus* are distributed evenly between the left and right distal mandibular segments because this muscle originates from a median tendon that arises from the interramal cartilaginous nodule. For these reasons, independent movements of the left and right halves of the lower jaw are not possible in *Leptotyphlops*.

Maxillary raking

Like mandibular raking in *Leptotyphlops*, maxillary raking in *Typhlops* and *Rhinotyphlops* represents a highly specialized mechanism for the rapid ingestion and transport of large numbers of small insect prey. In contrast to mandibular raking, however, maxillary raking bears at least some similarity to the feeding mechanisms of alethinophidian snakes. In particular, prey is transported into and through the mouth via independent ratcheting movements of the upper jaws. However, many more differences than similarities can be found between the feeding mechanisms of typhlopids and alethinophidians.

Perhaps the most striking differences between the feeding mechanisms of typhlopids and alethinophidians relate to the morphology and function of the upper jaws in the two groups. The vast majority of alethinophidian snakes have a continuous row of relatively long, recurved teeth along each medial upper jaw arch. In most taxa, reciprocating translational movements of these toothed palatopterygoid arches are primarily responsible for transporting prey through the oral cavity (Cundall and Greene, 2000). In typhlopids, however, the pterygoids and palatines are toothless and translational movements of the pterygoids serve only to protract and retract the toothed maxillae. Prey transport in typhlopids is thus brought about exclusively through rotational movements of the highly mobile maxillae.

Other important differences between the feeding mechanisms of typhlopids and alethinophidians relate to the structure of the lower jaw and its functional association with the upper jaws. In alethinophidian snakes, the distal tips of the dentaries are quite separate from one another and are joined together only by highly variable arrays of connective tissues (Young, 1998; Bellairs, 1984). Although the biomechanical properties of these interramal connective tissues have not yet been critically examined, in most taxa they permit considerable separation between the distal tips of the mandibular rami. Consequently, each half of the lower jaw can be protracted or retracted independently of the other. Furthermore, due to a ligamentous connection between the caudal tip of the pterygoid and the quadratomandibular joint (the pterygoquadrate ligament), unilateral movements of the upper and lower jaws on each side of the head are at least partially coupled to one another in most taxa (*e.g.*, Albright and Nelson, 1959*b*; Cundall and Gans, 1979). In contrast, the interramal connection in typhlopids is quite rigid. As noted previously by Bellairs and Kamal (1981), the two halves of Meckel's cartilage are bound together in the interramal region by an enlarged cartilaginous nodule, thereby preventing independent movements of the left and right mandibular rami. However, the rigidity of the lower jaw in typhlopids does not impede movement of the upper jaws. Due to the relatively wide separation between the pterygoid and quadrate and the loss of the pterygo-quadrate ligament (Iordansky, 1997), the upper and lower jaws are functionally decoupled in Typhlopidae.

Finally, it is important to emphasize that the synchronization of jaw movements is different in typhlopids and alethinophidians. Alethinophidians generally use unilateral ratcheting movements of their jaws to drag themselves forward over their prey (Gans, 1961). The upper and lower jaws on one side of the head are opened and protracted, and then closed and retracted. These movements are then mirrored by the contralateral jaws. In contrast, typhlopids most commonly drag prey into and through the mouth using asynchronous movements of the upper jaws. That is, the maxillae are protracted and retracted slightly out of phase with one another rather than in an alternating, reciprocating pattern.

The neuromuscular control of maxillary raking in typhlopids remains unexplored. Given the degree to which feeding kinematics (especially patterns of maxillary protraction and mandibular abduction) are modulated according to prey size and position, it is likely that the motor patterns associated with maxillary raking exhibit considerable variability as well. Unlike Leptotyphlopidae, however, Typhlopidae includes a small number of ‘‘giant’’ species (*e.g., Rhinotyphlops schlegelii, Typhlops punctatus*) that reach nearly 1 m in length and more that 2.5 cm in diameter (FitzSimons, 1962; Roux-Estève, 1974). Large adults of such species might afford the opportunity to use electromyography to study the activity of head muscles during feeding in these snakes. EMG data from typhlopids would not only provide a more detailed understanding of the maxillary raking mechanism itself, but could also be compared with similar data from alethinophidian snakes (*e.g.,* Cundall and Gans, 1979; Kardong and Berkhoudt, 1998) and scleroglossan lizards (*e.g.,* Smith, 1982; Herrel *et al.*, 1999) in an attempt to elucidate the modifications in motor control patterns that were associated with the shift to jaw-based prey transport mechanisms in the early evolution of snakes. Finally, the sensory pathways involved in the modulation of feeding kinematics in typhlopids remain unknown and are likely to represent a profitable line of inquiry in future studies of typhlopid feeding. Given that ingestion in *Typhlops* and *Rhinotyphlops* is usually initiated only after the snake’s snout has come into contact with the prey, it seems likely that the integumentary mechanoreceptors present on the head scales of typhlopids (Aota, 1940; Young and Wallach, 1998) represent an important source of sensory feedback during feeding. Denervation experiments could provide insight into the role of these cutaneous tactile organs in modulating feeding behavior.

The origin of unilateral feeding in snakes

As discussed above, the leptotyphlopid mandibular raking mechanism and the typhlopid maxillary raking mechanism both differ in significant ways from the snout shifting and pterygoid walk mechanisms of anilioids and macrostomatans, respectively. In particular, neither mandibular raking nor maxillary raking are characterized by the unilateral pattern of jaw displacement that underlies the feeding mechanisms of alethinophidians. Although feeding behavior in the third scolecophidian family, Anomalepididae, remains entirely unknown, the close phylogenetic relationship between anomalepidids and typhlopids (Cundall *et al.*, 1993; Tihen, 1945; Robb and Smith, 1966; List, 1966), and the similar form and position of the maxillae in these two families (List, 1966), suggest that anomalepidids also transport prey using a maxillary raking mechanism. Furthermore, many of the morphological features that facilitate unilateral feeding in Alethinophidia (*e.g.,* loose interramal connection, kinetic snout, pterygoquadrate ligament, etc.) are absent in Anomalepididae (Haas, 1964, 1968), as they are in Leptotyphlopidae and Typhlopidae. Thus, available evidence suggests that, among extant snakes, unilateral feeding is present only in Alethinophidia.

When the feeding mechanisms of scolecophidian snakes are placed within a phylogenetic context (Fig. 5), two hypotheses emerge concerning the evolution of unilat-

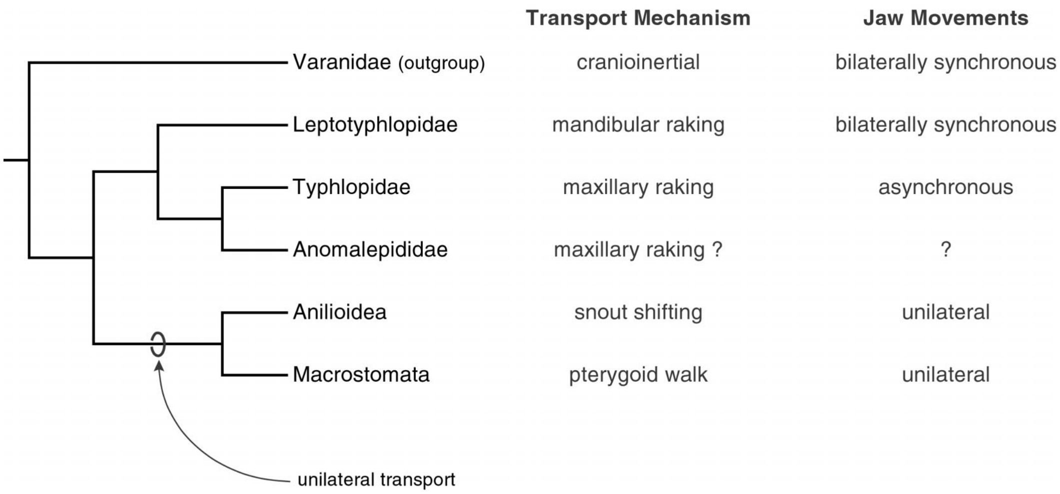


FIG. 5. The phylogenetic distribution of prey transport mechanisms in snakes. Phylogenetic hypothesis adapted from Tchernov *et al.* (2000) and Cundall *et al.* (1993). Fossil taxa are excluded.

eral feeding: (1) unilateral feeding arose in the common ancestor of Anilioidea and Macrostomata (*i.e.*, within Alethinophidia); or (2) unilateral feeding arose in the common ancestor of Scolecophidia and Alethinophidia (*i.e.*, it is primitive for Serpentes), and was subsequently lost in Scolecophidia. It is clear that the feeding mechanisms of blindsnakes are highly derived and doubtless differ considerably from those of ancestral snakes. Therefore neither of these two hypotheses can be strongly rejected based on the morphological and behavioral data that are currently available. However, when the criterion of parsimony is used to evaluate these hypotheses, the first scenario is favored over the second. For this reason, I accept the hypothesis that unilateral feeding evolved within Alethinophidia (Fig. 5).

Why unilateral feeding mechanisms are unique to Alethinophidia remains unknown. Perhaps the most conspicuous difference in feeding biology between Scolecophidia and Alethinophidia relates to the prey on which these snakes feed. Scolecophidians feed predominantly on social insects. In most species for which detailed dietary information is available, ant larvae and pupae represent the most important food resource (Webb and Shine, 1993*a*; Webb *et al.*, 2000). In some species, termites are also frequently consumed (Punzo, 1974; Brattstrom and Schwenkmeyer, 1951). In contrast, most alethinophidians feed on relatively large vertebrate prey (Greene, 1983, 1997). It might therefore be inferred that unilateral transport evolved as an adaptation for handling large and potentially dangerous prey, as this mode of transport ensures that a constant grip is maintained on struggling prey as it is ratcheted through the mouth. Indeed, many non-venomous colubroid snakes ingest and transport their prey while it is still alive, and in the case of large colubrids such as *Drymarchon*, formidable prey such as large rats and small rabbits can be eaten safely in this manner (unpublished observation, N.J.K.). However, constriction appears to have arisen very early in alethinophidian evolution (Greene and Burghardt, 1978) and basal alethinophidians rarely ingest their prey without first killing it through suffocation. Thus, it appears unlikely that unilateral transport arose as an adaptation for the transport of live, struggling prey.

It might also be hypothesized that the unilateral pattern of jaw displacement seen in alethinophidians arose simply as a byproduct of the structural modifications of the skull associated with the ingestion of large-diameter prey in these snakes. For instance, the liberation of the mandibular tips has long been recognized as an important morphological innovation in the early evolution of snakes that served to increase potential gape size (Gans, 1961). However, loosening of the interramal linkage not only allowed the tips of the mandibular rami to spread apart laterally, but also permitted the left and right halves of the lower jaw to be protracted and retracted independently of one another. Therefore, if mandibular liberation occurred as a result of selection for increased gape size, its role in unilateral transport would be interpreted as being exaptive rather than adaptive (*sensu* Gould and Vrba, 1982). Like the adaptive hypothesis presented above, however, this exaptive hypothesis seems unlikely in the light of available evidence. First, the evolution of increased gape size in Alethinophidia has occurred primarily through structural modifications of the lower jaw, suspensoria and intermandibular soft tissues (Gans, 1961; Lee *et al.*, 1999; Cundall and Greene, 2000). In contrast, many of the modifications in cranial morphology that facilitate unilateral feeding have occurred in the upper jaws, and therefore have had little effect on gape size. Second, although nearly all alethinophidians feed on relatively massive prey, the ability to ingest exceptionally large-diameter prey is restricted primarily to certain clades within Macrostomata (*e.g.*, Viperidae, Pythonidae, Boidae, etc.); basal alethinophidians feed predominantly on relatively narrow, elongate prey such as eels, caecilians, amphisbaenians, other snakes, and earthworms (Greene, 1983; Rajendran, 1985). Thus, unilateral transport evolved before many of the structural modifications associated with increased gape size arose within Macrostomata.

While the adaptive significance of unilateral transport remains unclear, its apparent absence in Scolecophidia suggests that it is a uniquely alethinophidian innovation. Future studies of the evolution of unilateral feeding mechanisms in snakes should therefore be focused on functional comparisons of the feeding apparatus in basal alethinophidians and closely related scleroglossan lizards. In particular, electromyographic studies using bilateral electrode placement would be especially valuable in assessing the degree to which motor patterns became modified in association with the shift to a unilateral jaw displacement pattern.

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