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## Activity of Head Muscles During Feeding by Snakes: A Comparative Study<sup>1</sup>

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**SYNOPSIS.** The adaptive radiation of colubroid snakes has involved the development of numerous prey capture specializations combined with conservation of a swallowing mechanism characterized by independent movements of the right and left toothed bones of the skull. Synchronized electromyographic and cinematographic recordings of swallowing in *Nerodia*, *Elaphe*, *Heterodon* and *Aghkistrodon*, four diverse genera of colubroid snakes, allow a preliminary evaluation of the relationship between prey capture and swallowing. The results indicate that the movements of the palatopterygoid bar and advance of the mandible as closing of the jaws begins as well as patterns of muscle activity producing these movements are similar among the four genera. Conversely, the patterns of activity of external adductors and, to some extent, the depressor mandibulae differ among the four genera sampled. Analyses of bone movements during swallowing suggest that swallowing is effected primarily by the palatopterygoid bars. The mandibles and their connecting soft tissues mainly press the prey against the palatopterygoid teeth. The mandibular teeth evidently play little active role in swallowing. Also, the maxilla, which displays considerable morphological diversity among colubroid snakes, has little independent or direct function in swallowing, its teeth rarely contacting the prey. The data suggest that the heads of colubroid snakes have evolved two partially separated structural-functional units, a medial swallowing unit and a lateral prey capture unit.

### INTRODUCTION

Studies of cranial kinesis during swallowing by snakes have noted basic similarities in such diverse genera as *Elaphe* (Albright and Nelson, 1959b), *Bitis* (Bolt and Ewer, 1964), *Python* (Frazzetta, 1966) and *Aghkistrodon* (Kardong, 1977). The major feature shared by these diverse genera is the alternate advance of the right and left toothed bones over the surface of the prey, a phenomenon referred to as the "pterygoid walk" by Bolt and Ewer (1964). Authors commenting on specific features of bone displacement and suspected patterns of muscle activity (e.g., Dullemeijer, 1956; Liem *et al.*, 1971) have noted that similar mechanisms occur in a wide array of snake species. Thus, despite the existence of a few unusual swallowing mechanisms (Gans, 1952, 1972), the prevalent view is that swallowing is a conservative mechanism in advanced snakes (Colubroidea).

If swallowing is conservative, how is it

that the toothed bones of the head, the major effectors of swallowing, have become specialized for prey capture? Such specializations in snakes have elicited interest for centuries (e.g. Charas, 1669; Tyson, 1683), and recent work (e.g. Franz, 1977; Ruben, 1977a, b; Greene and Burghardt, 1978; Savitzky, 1981 and papers in this symposium) attests to the remarkable array of behavioral and morphological specializations associated with prey capture. Many of these innovations involve changes in the relationships of the cephalic bones and muscles. Thus, the head in advanced snakes may be viewed as a structurally diverse apparatus displaying a variety of prey capture mechanisms while maintaining a relatively conservative swallowing mechanism.

This apparent paradox may be resolved in at least three ways. The first solution assumes an error of assumption: Swallowing is not really conservative, but displays a variety of subtle specializations correlated in some manner with prey capture. The second solution assumes that swallowing is conservative but is functionally, and possibly structurally, separated from those aspects of the head devoted to prey capture. The third solution is that the mor-

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phological specializations associated with prey capture somehow retain all basic functions associated with swallowing. The following discussion considers this problem and attempts to define which solution is best supported by available data.

#### APPROACH

Swallowing behavior in representatives of four genera of colubroid snakes was analyzed using synchronized cinematography and electromyography. The basic methods employed for acquiring the data were described by Cundall and Gans (1979). Part of the data in that study was gained from snakes feeding during the terminal stages of recovery from anesthesia. All subsequent work has been based on animals feeding following complete recovery from anesthesia. Cinematographic comparisons of feeding in instrumented and untreated animals indicate that the procedures employed produce no changes in observable patterns of behavior.

The following treatment compares activity of nine selected cranial muscles, including three external adductors, one internal adductor, four dorsal constrictors and the depressor mandibulae. This sample includes those muscles that appear to be the major effectors of swallowing. Comparisons of the activity of these muscles are based on recordings from swallowing sequences in which the maximum prey diameter exceeded 50% of the potential gape (defined as  $1.5 \times$  mandibular length) of the snake. Swallowing of prey in this size range elicits very similar patterns of activity in individual muscles from one feeding sequence to the next. The swallowing of very small prey is characterized by different and more variable patterns of muscle activity.

In order to gain some measure of whether swallowing is conservative, it is necessary to compare species that differ in both prey capture strategies and major features of cephalic morphology. These considerations, combined with practical constraints of available published information on morphology and the availability of specimens, determined my ultimate choice of the species *Nerodia fasciata*, *N. rhombifera*,

*Elaphe obsoleta*, *Heterodon platyrhinos*, and *Agkistrodon piscivorus*.

With regard to feeding strategies, *Nerodia* is a semiaquatic genus that feeds primarily on fish and anurans (Mushinsky and Hebrard, 1977; Kofron, 1978), capturing them by forward lunges or lateral sweeps of the head (Stoner, 1941; Evans, 1942; Trapido, 1943; Drummond, 1979). Prey are usually swallowed alive although some species of *Nerodia* (notably *N. rhombifera*) are known to feed on carrion (Cagle, 1937). *Elaphe obsoleta* is a terrestrial to semiarboreal species that feeds primarily on small mammals, birds and their eggs, lizards and anurans (Wright and Wright, 1957). *Elaphe* usually kills endothermic prey by constriction prior to swallowing. *Heterodon platyrhinos* is perhaps the most selective predator among the species examined, feeding almost exclusively on toads (*Bufo*), occasionally taking ranid frogs and salamanders (Platt, 1969). *Heterodon* appears to capture prey by lunging at it with the mouth open. Prey are characteristically swallowed alive, although the initial stages of swallowing frequently involve successive chewing movements on one side of the head during which the enlarged posterior maxillary teeth lacerate the skin of the prey. This has been suggested as a method of puncturing inflated toads (Ditmars, 1931; Smith and White, 1955), and as a method of envenomating the prey (Platt, 1969; Kroll, 1976). Taub (1967) noted that the Duvernoy's gland of *H. platyrhinos* contains predominantly serous cells but evidence suggests low toxicity of oral gland secretions in this species (McAlister, 1963; Grogan, 1974). *Agkistrodon piscivorus* is a semiaquatic pit viper with a highly specialized envenomating apparatus (Kardong, 1974) and highly toxic venom (Mebs, 1978). Despite these features, this species appears to feed on an extraordinary diversity of vertebrate and invertebrate prey, as well as carrion (Burkett, 1966). Prey capture strategies in *Agkistrodon* vary depending upon the type of prey being captured (Allen and Swindell, 1948).

The phylogenetic relationships of the four genera are quite distant based on morphological (Underwood, 1967), serological

(George and Dessauer, 1970; Minton and Salanitro, 1972) and karyological data (Baker *et al.*, 1972). Current systematic arrangements (Underwood, 1967; Dowling and Duellman, 1978) place these genera in separate subfamilies or families. However, as all four species are considered to be advanced snakes (Caenophidia or Colubroidea), they offer a reasonable possibility of obtaining a measure of the potential variability in the activity of cephalic muscles during feeding in this large and diverse assemblage.

Each of the species chosen has been the subject of previous work on cranial morphology. *Nerodia* has been described by Adams (1925) and Varkey (1979), *Elaphe* by Albright and Nelson (1959a, b), *Heterodon* by Weaver (1965) and Kroll (1976) and *Agkistrodon* by Kardong (1973, 1974).

#### COMPARATIVE FEATURES OF SKULL STRUCTURE

The skulls of the four genera have certain basic similarities in structural organization despite considerable differences in the forms of the various bones. Similarities include a mobile snout complex that attaches to the braincase at a functional prokinetic joint, independent right and left palatomaxillary arches that are ligamentously attached to mobile prefrontal bones, streptostylic quadrates and elongate, structurally independent mandibles.

Differences of varying magnitude are found in all four mechanical units (snout, braincase, palatomaxillary and mandibular) of the skull. The braincase in all four genera provides a rigid housing for the brain (Bellairs, 1949; Rieppel, 1980) but varies in the relative sizes of its orbital and postorbital regions thereby producing complex changes in muscle attachments and the precise direction of muscle action. The prefrontal bone, which forms the anterior wall of the orbit, lies above the palatomaxillary unit in *Nerodia*, *Elaphe* and *Heterodon* and rotates anterolaterally relative to the braincase, allowing the maxilla to swing forward and outward. In *Agkistrodon* the prefrontal lies medial to the maxilla but also rotates forward and outward (Kardong, 1974). The snout unit has much more

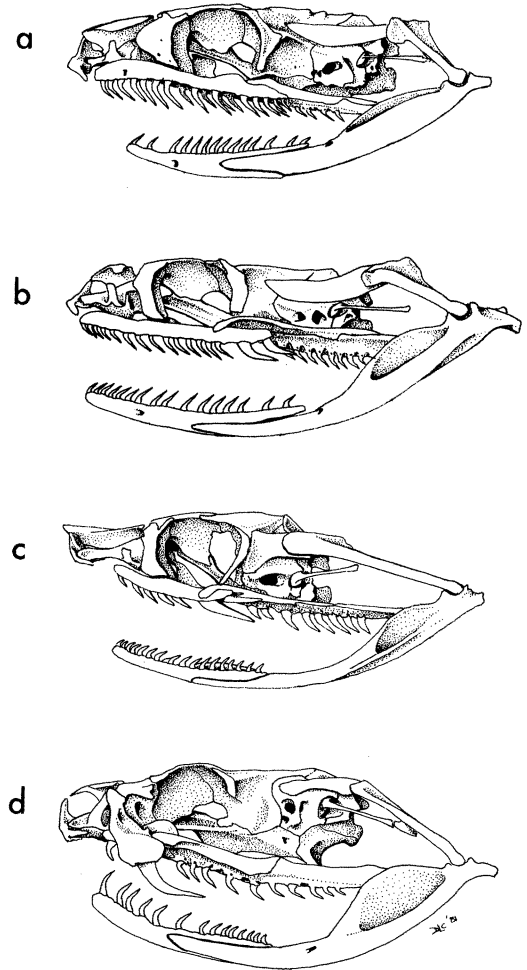


FIG. 1. Lateral views of the skulls of a) *Elaphe obsoleta*, b) *Nerodia fasciata*, c) *Heterodon platyrhinos* and d) *Agkistrodon piscivorus*.

intimate associations with the maxilla in *Elaphe* and *Nerodia* than it does in either *Heterodon* or *Agkistrodon*. The mandibular unit exhibits major differences in the size, position, and degree of attachment of the supratemporal to both the braincase and quadrate. Quadrates of the four genera differ in relative sizes of muscle attachment surfaces and relative total lengths. These differences may influence displacements of the angle of the mouth and thus the relative size of the gape (Gans, 1961). The palatomaxillary units of the four genera differ in a variety of features (Fig. 2). *Elaphe* has a relatively long maxilla with regularly

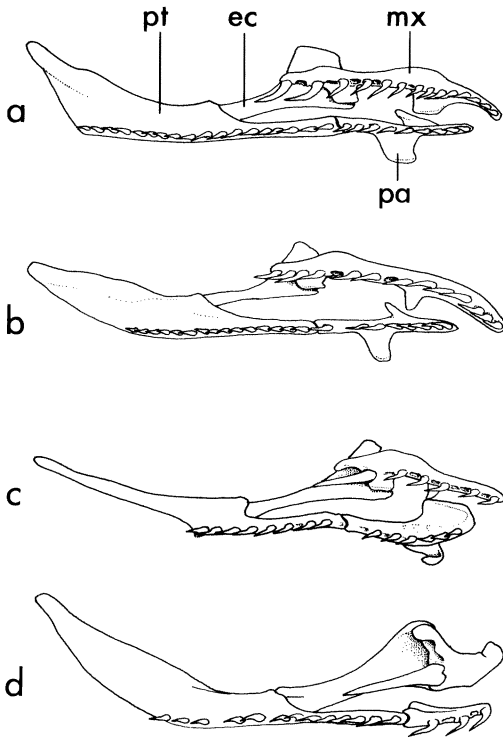


FIG. 2. Ventral views of the right palatomaxillary arches of a) *Nerodia fasciata*, b) *Elaphe obsoleta*, c) *Heterodon platyrhinos* and d) *Agkistrodon piscivorus*.

spaced teeth that become progressively shorter toward the rear end. Maxillary form is similar in *Nerodia* but most species display enlarged posterior teeth with a blade-like edge similar to that described for *Thamnophis elegans* by Wright *et al.* (1979). In *Heterodon* the front of the maxilla lies further from the tip of the snout than in *Elaphe* or *Nerodia* and the posterior teeth are greatly enlarged. *Agkistrodon* has a typical viperid maxilla (Anthony, 1955; Brattstrom, 1964) that is very short and contains only one or two functional teeth that are modified as long, recurved tubular fangs. Differences of the remaining bones of the palatomaxillary arch are illustrated in Figure 2. Whereas palatine and pterygoid tooth patterns are more conservative than maxillary tooth patterns, *Heterodon* is unusual among the four genera in possessing relatively large posterior pterygoid teeth (see Fig. 1).

#### BONE DISPLACEMENTS DURING SWALLOWING

As noted above, virtually all previous authors on the subject have described swallowing in snakes as an alternate advance of the right and left toothed bones of the head over the surface of the prey. This process may be divided into behavioral phases (Kardong, 1977; Cundall and Gans, 1979) describing one complete cycle of movements for both sides of the head. The phases are designated as ipsilateral advance, ipsilateral close, ipsilateral relaxation, contralateral advance, contralateral close and contralateral relaxation. During the ipsilateral advance phase, the ipsilateral mandible drops while the ipsilateral palatomaxillary unit is elevated and protracted. This process is frequently aided by rotation of the braincase. Ipsilateral close follows ipsilateral advance, beginning when the palatomaxillary unit is depressed, coming into contact with the prey surface, and the mandible is protracted and adducted. Ipsilateral closing ends when mandibular adduction ceases. It is followed by ipsilateral relaxation, a phase of varying length during which there are no detectable movements of cephalic bones and minimal muscle activity. The end of this relaxation phase marks the start of the contralateral advance phase during which the snake begins to advance the contralateral palatomaxillary unit and mandible while the ipsilateral side retains its position relative to the prey. This is followed by a contralateral close phase and a contralateral relaxation phase that is followed by the beginning of another cycle. For either side, the entire period between the end of ipsilateral close and the beginning of the next ipsilateral advance is designated as an ipsilateral hold period which contains the last four behavioral phases listed above, namely ipsilateral relaxation, contralateral advance, contralateral close, and contralateral relaxation. The activity of muscles is described for the ipsilateral side only. Thus descriptions of muscle activity during contralateral advance, for example, refer to the activity of ipsilateral muscles while the bones of the opposite side of the head are being protracted.

Swallowing tends to be a more or less continuous process and therefore establishing boundaries between separate phases attributes a neatness of function that the system rarely exhibits. In comparing patterns of muscle activity, I have emphasized differences occurring at the end of advance and the beginning of close phases because behavioral events during this period are quite distinct and readily visualized.

#### MUSCLE ORGANIZATION AND ACTIVITY

##### *The external adductor muscles*

The externus group is composed of three to five anatomically separate muscles that arise from the anterior surface of the quadrate and dorsolateral edge of the postorbital braincase (Lakjer, 1926; Haas, 1973). These muscles vary in their precise form and attachments among snakes as described by Phisalix (1914, 1922), Haas (1931*a, b*, 1952, 1962), Cowan and Hick (1951), Dullemeyer (1959), Kochva (1962) and Varkey (1979) among others. The external adductors of *Nerodia* and *Elaphe* have a similar pattern (Fig. 3a) in which the M. adductor externus superficialis inserts predominantly over the lateral surface of the M. adductor externus profundus via a broad aponeurosis, sending a few fibers around the angle of the mouth to insert on the dermis of the skin and directly on the mandible at the rear end of the dentary. In *Heterodon* (Fig. 3b), all the superficialis muscle curves around the angle of the mouth to insert directly on the mandible (Weaver, 1965). A more complex situation exists in *Agkistrodon* in which the superficialis is divided into two muscles (Kochva, 1962; Kardong, 1973); a superficial portion passes medial to the venom gland to form an aponeurotic insertion over the profundus portion of the externus group, and a deeper muscle (M. levator anguli oris) inserts on the dermis of the skin covering the angle of the mouth and on connective tissue associated with the rear end of the dentary and infralabial gland. The M. adductor externus medialis arises from the parietal behind the superficialis and passes ventrally to insert on the mandible immediately posterior to the dentary; its relationships are similar for all four genera

although this muscle is reduced in relative size in both *Agkistrodon* and *Heterodon*. The M. adductor externus profundus arises from the quadrate and inserts over most of the lateral surface of the compound bone lying between the quadratomandibular articulation and the posterior tip of the dentary in all genera except *Agkistrodon* in which the insertion is limited to the region of the mandibular fossa. A derivative of this muscle, the M. compressor glandulae (Haas, 1962; Kochva, 1958, 1962, 1963), forms a major component of the external adductors in *Agkistrodon*, arising from the dorsal surface of the venom gland and inserting on the mandible between the profundus and the posterior tip of the dentary (Fig. 3c).

The anatomical positions of the external adductors limit their actions to adduction of the mandible. However, the orientations of the fibers of the different externus muscles allow forces to be generated in various directions (Fig. 3) during adduction. Electromyographic recordings indicate that all of the external adductors recorded are active at some time during ipsilateral closing (Fig. 4) in all four genera. Generally, activity starts at low amplitude during the late advance phase and is strongest during the latter two thirds of closing. The low total activity of the external adductors during the early part of ipsilateral closing coincides with extensive medial and ventral movement of the palatopterygoid joint and continued protraction of the mandible. Marked mandibular adduction begins at the point when activity of the external adductors increases.

As ipsilateral closing ceases, the activity of the external adductors falls and typically terminates at some point early during ipsilateral relaxation (Fig. 4, period 3). However, in *Heterodon* the profundus continues to be moderately active throughout the relaxation period. In all genera, some of the external adductors are slightly to moderately active during contralateral advance and during the early part of contralateral close. They may prevent opening of the ipsilateral side of the mouth via its elastic connection with the active side.

The continuous activity of the profun-

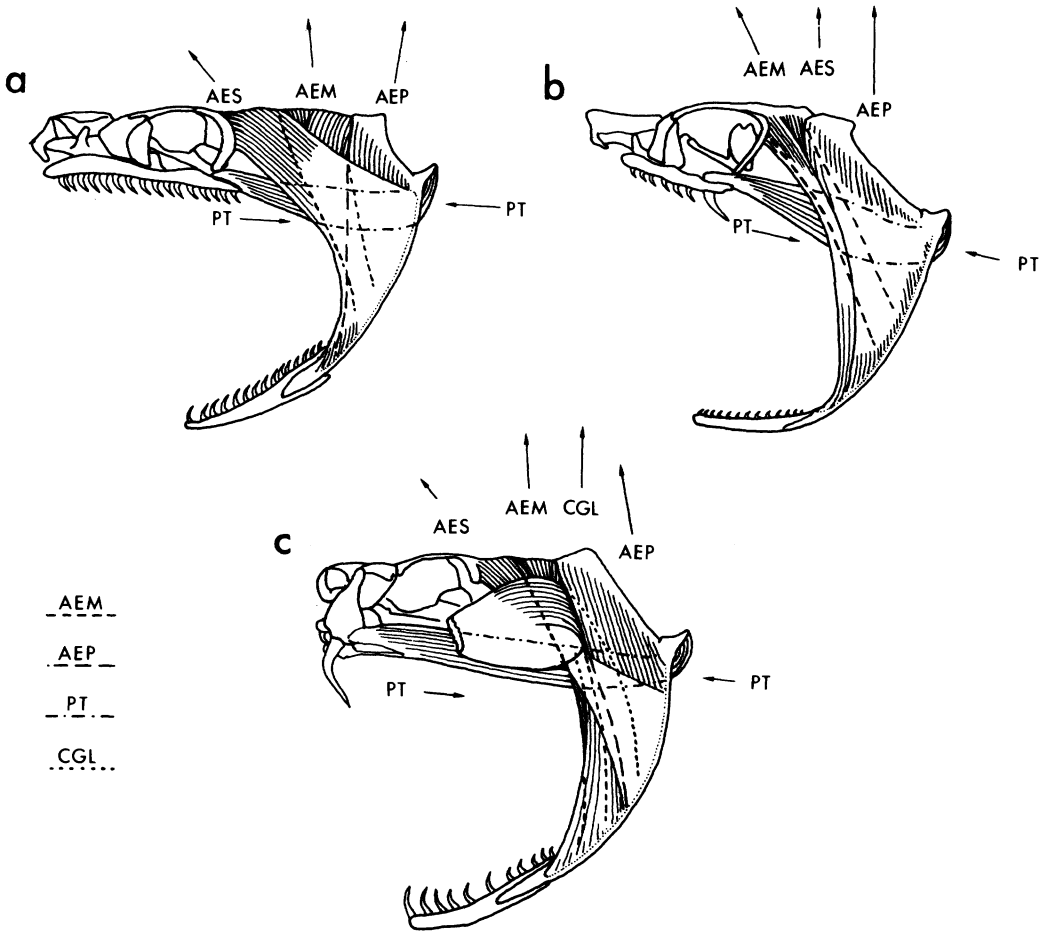


FIG. 3. Relationships of external adductor and pterygoideus muscles in a) *Nerodia* and *Elaphe*, b) *Heterodon* and c) *Agkistrodon*. Arrows indicate direction of forces applied to the mandible or maxilla during contraction of the muscle indicated. Abbreviations: AEM—adductor externus medialis; AEP—adductor externus profundus; AES—adductor externus superficialis; CGL—compressor glandulae; PT—pterygoideus.

dus when *Heterodon* swallows living toads and frogs suggests that this adductor functions as a more or less permanent restraining mechanism. However, the large quadramandibular angle (Fig. 3b) combined with the very small size of the dentary teeth (Fig. 1) suggest that the dentary teeth play little if any role during swallowing. Instead, the mandible appears to function solely in keeping the prey pressed against the palatopterygoid bar. The absence of ipsilateral or contralateral adductor activity during much of the relaxation periods when *Nerodia* and *Agkistrodon* swallow large prey

suggests that the larger dentary teeth may provide passive restraint in these genera.

The available EMG evidence permits one to make several general points concerning the function of the external adductors. First, these muscles clearly act in adducting the mandible. This includes the M. compressor glandulae which has an activity pattern similar to the other adductors during swallowing (Fig. 4). Second, one or more of the external adductors may control and stabilize mandibular position during the late stages of ipsilateral advance. At this time they are sometimes active for more

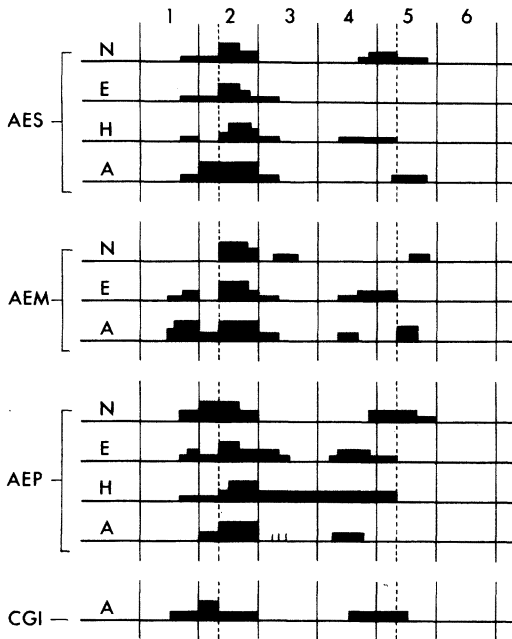


FIG. 4. Patterns of external adductor activity during swallowing in N—*Nerodia*, E—*Elaphe*, H—*Heterodon*, and A—*Agkistrodon*. Column 1—ipsilateral advance phase; 2—ipsilateral close; 3—ipsilateral relaxation; 4—contralateral advance; 5—contralateral close; 6—contralateral relaxation. Muscle abbreviations as for Figure 3.

than one second when antagonistic muscles are firing strongly. Third, most of the external adductors exhibit asymmetric bilateral activity, asymmetry occurring in both the amplitude of activity and the firing pattern. This suggests that one or more of the external adductors maintain closure of the ipsilateral jaws when the contralateral jaws are advancing.

At the end of ipsilateral advance and the beginning of ipsilateral close the activity of the adductors clearly differs among the four genera. As displacements of the mandible during this part of swallowing are very similar in all four genera, it seems that a conservative pattern of mandibular motion (and apparently quadrate and supratemporal motion as well) is being produced by different patterns of adductor activity. Comparison of adductor activity between *Nerodia* and *Elaphe* makes it clear that this

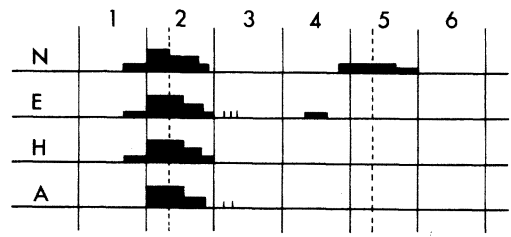


FIG. 5. Patterns of pterygoideus activity during swallowing in the four genera examined. Abbreviations and column designations as for Figure 4.

activity bears no simple relationship to adductor form and attachments.

*The pterygoideus muscle*

In most advanced snakes, the M. pterygoideus extends from the distal end of the ectopterygoid to the posteromedial surface of the mandible (Fig. 3). Additional connections may exist at both the origin and insertion. In *Agkistrodon*, the origin includes the lateral edge of the maxilla, the fang sheath and the anteroventral capsule of the venom gland. In *Heterodon*, the pterygoideus inserts on both the mandible and the rear end of the pterygoid (the latter attachment is not mentioned by Weaver, 1965). Stimulation of the pterygoideus causes the anterior tips of the mandible to swing dorso-laterally and effects marked outward rotation of the dentary tooth row. In *Heterodon*, stimulation of the pterygoideus results in similar mandibular movements combined with marked ventromedial displacement of the palatopterygoid joint.

Activity of the pterygoideus (Fig. 5) is remarkably uniform among the four genera. In all genera except *Agkistrodon*, the muscle exhibits low amplitude activity at the end of ipsilateral advance. The pterygoideus becomes very active during the initial phases of ipsilateral closing. Its activity gradually declines in amplitude during the remainder of closing. Low amplitude activity during late contralateral advance and closing is characteristic of *Nerodia*. *Elaphe* typically exhibits activity of very low amplitude during contralateral advance.

The size, position and timing of activity of the pterygoideus suggests that it is one



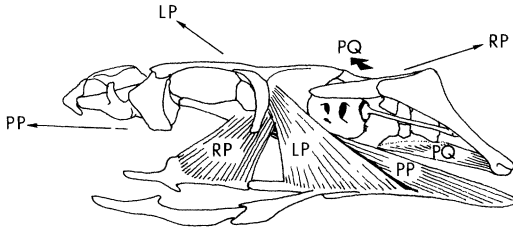


FIG. 6. General pattern of dorsal constrictor arrangement in colubroid snakes. Arrows indicate approximate directions of forces applied to the palatimaxillary apparatus and quadrate during contraction of the muscle indicated. Abbreviations: LP—levator pterygoidei; PP—protractor pterygoidei; PQ—protractor quadrati; RP—retractor pterygoidei.

of the primary effectors of the complex bone movements seen in early ipsilateral closing. In *Nerodia*, *Elaphe* and *Heterodon*, these movements include depression and medial displacement of the rear end of the maxilla combined with medial rotation of the maxillary tooth row, medial (*Elaphe*) or ventromedial (*Nerodia* and *Heterodon*) movement of the palatopterygoid joint, protraction of the distal end of the quadrate and mandible combined with lateral rotation of the dentary tooth row and, occasionally, slight adduction of the mandible. In *Agkistrodon*, pterygoideus activity correlates with retraction of the maxilla and fang as the palatopterygoid joint swings ventromedially. Thus, when the palatopterygoid bar contacts the prey, the fang is already retracted; like the condition in other viperid genera it does not usually participate in swallowing (Dullemeijer, 1956; Boltz and Ewer, 1964).

#### The dorsal constrictor muscles

Snakes are unique among vertebrates in the complexity of their mandibular dorsal constrictor musculature. In the four genera examined, as in most colubroid snakes described to date, the dorsal constrictor plate forms five pairs of muscles extending from the floor of the braincase to the snout, palatimaxillary arch, and quadrate or quadratomandibular region. EMG recordings are presently available for four of the five muscles.

Three of the dorsal constrictors extend

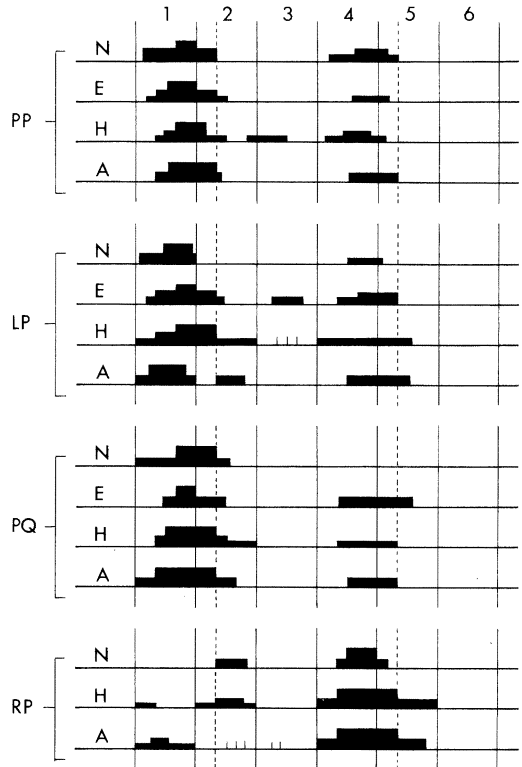


FIG. 7. Patterns of dorsal constrictor activity during swallowing among the four genera examined. Generic abbreviations and column designations as for Figure 4. Muscle abbreviations as for Figure 6.

posteriorly from their origins on the floor of the braincase and collectively effect protraction of the palatimaxillary arch and mandible (Fig. 6). These are: 1) the M. protractor pterygoidei which arises from the floor of the braincase below (*Agkistrodon*) or immediately behind (remaining genera) the orbit and inserts on the rear end of the dorsal surface of the pterygoid; 2) the M. levator pterygoidei which arises from the side of the braincase immediately behind the orbit and passes down and back to insert on the dorsolateral edge of the pterygoid around and behind the ectopterygo-ptyerygoid joint; and 3) the M. protractor quadrati which arises from the region of the basioccipital and associated cervical vertebrae at the rear of the braincase and extends posterolaterally to insert on the distal end of the quadrate (*Agkistrodon*, *Het-*

*erodon*) or the retroarticular process of the mandible (*Elaphe*, *Nerodia*).

All three muscles become active at some point during ipsilateral advance in all four genera (Fig. 7). Activity of high amplitude is maintained through the latter part of advance phase and correlates with protraction of the ipsilateral palatomaxillary arch and the distal end of the quadrate. The movements are remarkably similar among the four genera and collectively result in maximum anterolateral displacement of the anterior part of the ipsilateral palatomaxillary apparatus.

At the initiation of closing, the protractor pterygoidei and protractor quadrati continue firing. The activity of the levator pterygoidei is more variable. The cessation of its activity at the end of ipsilateral advance in both *Nerodia* and *Agkistrodon* is correlated with rapid ventromedial displacement of the palatopterygoid joint in these two genera. In both *Elaphe* and *Heterodon* displacement of this joint is slower, suggesting that the levator pterygoidei controls the rate of movement of the joint by resisting the action of the pterygoideus.

All of the protractor complex exhibits low amplitude activity during contralateral advance and early contralateral closing. Sporadic activity is occasionally seen during ipsilateral relaxation (Fig. 7). Generally, the activity patterns of these muscles are very similar, both to each other and among the four genera.

The retractor pterygoidei arises from the floor of the braincase and extends anteroventrally to insert on the palatine (*Nerodia* and *Elaphe*) or the palatine and anterior pterygoid (*Heterodon* and *Agkistrodon*). Its activity during ipsilateral bone movements is quite variable and never reaches high amplitude (Fig. 7). In contrast, the high amplitude activity of this muscle during contralateral advance and closing is considerably less variable. The pattern of activity indicates that this muscle plays little if any role in retracting the palatomaxillary apparatus during ipsilateral closing. Rather, it protracts the braincase relative to the ipsilateral side during contralateral advance and advances the braincase relative to the prey.

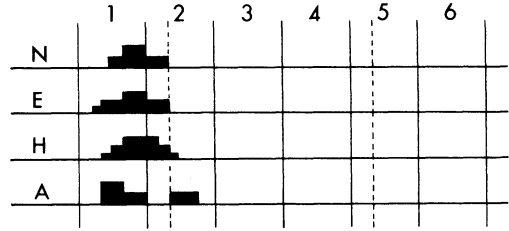


FIG. 8. Patterns of depressor mandibulae activity among the four genera examined. Generic abbreviations and activity periods as for Figure 4.

*The depressor mandibulae*

The depressor mandibulae arises from the rear surface of the quadrate (and associated areas of the supratemporal and supraoccipital in *Heterodon* and *Agkistrodon*) and inserts on the retroarticular process of the mandible. When stimulated, its only action is depression of the mandible. The depressor becomes active about half way through ipsilateral advance, remains strongly active until or just after closing begins, and then typically ceases firing during the beginning of mandibular adduction (Fig. 8). The pattern is different in *Agkistrodon*; its depressor mandibulae exhibits no activity during the initial part of ipsilateral close but then shows low amplitude activity as mandibular adduction begins. This change in activity pattern is not correlated with any detectable difference in mandibular movement. Nevertheless, it is clear that depressor activity is not conservative among the four genera.

INTERACTIONS OF THE MUSCLES

The firing patterns of the muscles indicate a broad overlap in activity of antagonistic muscles. Whereas information on muscle cross-sectional areas, length-tension curves, sarcomere lengths and fiber composition are not available for most cephalic muscles of snakes, the present data suggest that the transition from advance to closing phases is mediated by nearly all of the muscles applying forces in various directions at a number of points in the system.

Original expectations that the cephalic musculature of snakes might not exhibit excessively complex patterns of activity (Gans, 1961) have been met. The system

operates with characteristics of muscle activity similar to those described for feeding in teleost fishes (*e.g.*, Liem, 1978, 1980; Lauder, 1981), birds (Zweers, 1974) and mammals (*e.g.*, Kallen and Gans, 1972; Herring and Scapino, 1973; Gorniak, 1977) with one notable difference. Antagonistic overlap in other vertebrate systems tends to occur over short time intervals (a few milliseconds to as much as a tenth of a second) because mandibular movements are quite rapid. In snakes, antagonistic overlap may extend to periods in excess of 1 sec, although the relative period of antagonistic overlap does not differ from that in teleost fishes and mammals. Thus, snakes have retained the basic temporal characteristics of antagonistic activity despite the fact that their swallowing apparatus typically operates at only a fraction of the speed characteristic of deglutitional mechanisms in other vertebrates.

#### DISCUSSION

The question of whether snakes have retained a conservative swallowing mechanism during an adaptive radiation characterized by the development of numerous prey capture specializations is not readily answered by electromyographic evidence alone. Clearly, some muscles have retained conservative patterns of activity and others have not. Considering patterns of bone displacement, movements of the palatopterygoid bar and mandible are similar while movements of the maxilla are not. These inconsistencies provide a clue to one possible interpretation of functional and structural relationships in the heads of colubroid snakes.

Swallowing in snakes is a process of successive advance of the toothed bones of the head, as emphasized by Kardong (1977). Retraction, implying retraction of the prey relative to the braincase and body of the snake, may occur but is neither a necessary nor common feature of the system. If palatopterygoid advance is one of the basic functional components of the system, we would expect conservation of both basic anatomical relationships and activity of the muscles responsible for this process. This appears to be the case.

Virtually all descriptions of swallowing in snakes refer to a period of retraction during the closing phase (*e.g.*, Dullemeijer, 1956; Bolt and Ewer, 1964; Gans, 1974). An apparent retraction does occur in nearly all snakes and often involves a rotation of the braincase that appears to pull back the palatomaxillary arch of the closing side. Careful examination of the position of the prey relative to some point on the braincase indicates that the prey usually retains a fixed position relative to the braincase. Closing is therefore not a retraction process but a method of fixing the palatopterygoid on the prey surface.

This conclusion is supported by activity of the elements of the system presumed to function as retractors, such as the retractor pterygoidei, which are most active during advance of the toothed bones of the opposite side. Such activity serves to advance the braincase over the surface of the prey, not to draw the prey into the esophagus. While the end result may be the same, in the first case the snake employs only the energy required to move its head while in the second case the snake must employ sufficient energy to overcome the inertia of the prey. When prey weight exceeds the weight of the snake's head, it is clearly advantageous to move the head rather than the prey.

If swallowing is largely a process of advancing the palatopterygoid bars, what is the function of the mandible? Apparently, the mandible serves primarily to tense the intermandibular soft tissues and keep the prey item against the roof of the mouth. Bolt and Ewer (1964) noted that the mandible moves very little during the swallowing of large prey. My observations show that the limited mandibular movement that does occur is protraction during the early part of closing. This serves to bring the mandibular tip forward under the prey and keeps the mandible under the palatopterygoid bar.

Dullemeijer (1956) suggested that the adductor musculature of snakes evolved to effect manipulation and retraction of the prey during swallowing. If this is the case, amplitude of activity of the various adductors should be higher during swallowing

than during prey capture and should bear some relationship to prey weight. Among the genera studied, adductor activity is greatest during prey capture and exhibits little relationship to prey weight for prey exceeding approximately 5% of the weight of the snake. It should also be noted that many of the adductors exhibit a decrease in activity during that part of closing when retraction movements are most obvious, and exhibit their greatest activity at or just following the point when the palatopterygoid teeth contact prey. The electromyographic results are therefore consistent with the idea that the adductors collectively function in fixing the teeth of the palatopterygoid bar on the surface of the prey.

The external adductors vary in both form and activity pattern among the four genera examined. It is difficult to evaluate the influence that this variability may have on mandibular movements during swallowing. However, given the nature of adductor activity during prey capture, it seems possible that the source of this variability is associated with demands of prey capture, not swallowing.

The pterygoideus muscle is primarily responsible for mandibular protraction at the beginning of closing. The position of this muscle in most colubroid snakes is quite unusual. Rather than arising from the pterygoid, as it does in boid snakes (Gibson, 1966; Frazzetta, 1966), lizards (Oelrich, 1956; Frazzetta, 1962; Avery and Tanner, 1971) and most other tetrapods, the origin has shifted laterally, lying on the distal end of the ectopterygoid closely associated with the rear end of the maxilla. This shift allows the muscle to impart a medially directed force to the pterygoid, a posteroventrally directed force to the maxilla and an anteriorly directed force to the retroarticular process of the mandible. Thus, the pterygoideus is the major effector of medial movement of the palatopterygoid joint and of protraction of the mandible during the closing phase of swallowing. The association of this muscle with these two critical events during swallowing combined with its uniform pattern of activity among the four genera studied lends support to the

notion that swallowing is conservative in colubroids.

One final clue that sheds further light on the structural and functional relationships between swallowing and prey capture involves the action of the maxilla. Much of the detailed literature on cranial kinesis during swallowing in snakes has dealt with viperids (Haas, 1929; Dullemeijer, 1956, 1959; Bolt and Ewer, 1964; Liem *et al.*, 1971; Kardong, 1977). These studies have demonstrated that the maxillary fangs of viperids are not employed during the swallowing process despite the fact that they are typically erected, or partially erected, during the advance phase. Contraction of the pterygoideus at the beginning of closing usually retracts the fang before it penetrates the prey. In natricine and colubrine snakes, such as *Nerodia* and *Elaphe*, the maxilla is relatively unspecialized. Albright and Nelson (1959b) postulated that the maxilla of *Elaphe* would be dragged ventromedially and caudally by the contraction of cervical muscles acting through the quadratomaxillary ligament. They also comment that the maxillary teeth are reengaged in the surface of the prey during closing. While the motions they describe are substantially correct, these motions are actually produced by contractions of the pterygoideus; generally, the maxillary teeth do not reengage the prey. Even when the maxillary teeth do contact the prey, they do so after engagement of the palatopterygoid teeth. Because the maxilla and palatopterygoid bar are linked by the ectopterygoid, their movements are similar in extent and timing. Therefore, the only function that the maxilla could have during swallowing is one of restraint.

The function of enlarged posterior maxillary teeth, such as those found in *Heterodon*, is complex. Observations show that these enlarged teeth are used during prey capture and manipulation, as suggested by Platt (1969), Kroll (1976) and Kardong (1979, 1980). In addition, these teeth are used to lacerate the prey. *Heterodon*, unlike most snakes, exhibits successive unilateral chewing motions during which the enlarged posterior maxillary teeth are raked against the prey, often producing

large wounds and copious bleeding. However, when swallowing actually begins, the maxillary teeth usually remain visible throughout the process. Thus, the maxilla appears to be of little functional significance during swallowing in *Heterodon*, as in most colubroids.

#### SUMMARY

It is evident that swallowing in the four genera of colubroid snakes examined here is dependent upon very similar movements of the palatopterygoid bar. The mandible acts only to keep the prey pressed against the palatopterygoid teeth and the maxilla plays little if any direct role in swallowing. Electromyographic evidence shows that the most conservative activity patterns are found among the palatopterygoid protractors and the pterygoideus, a muscle responsible for critical palatopterygoid and mandibular movements. These characteristics indicate that swallowing is indeed a conservative process. They also suggest that swallowing and prey capture are functionally and, to some extent, structurally separated. The upper jaw is functionally separated into a medial swallowing device and a lateral prey capture device. These functional entities are structurally connected both to each other and to the mandible which functions, albeit in different manners, in both prey capture and swallowing. Functional separation of the maxilla from a direct and necessary role in swallowing has apparently allowed it to respond to selection pressures associated largely with prey capture strategies.

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