Mechanics of drinking in the brown tree snake, *Boiga irregularis*

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Summary

The drinking cycle of the brown tree snake was studied with the use of cineradiography, electromyography, high-speed cinematography, and pressure transducers to determine the morphological basis and mechanism of water intake. The drinking cycle is composed of two phases, open and close. During the open phase, the lower jaw is depressed and the quadrato-mandibular joint moves inward enlarging the oropharyngeal cavity. Through the parted anterior corners of the mouth, water is drawn into the mouth. During the close phase, these displacements are reversed, the edges to the mouth close, volume of the mouth decreases, pressure in the oropharyngeal cavity therefore rises, and water is driven past the esophageal sphincter into the esophagus. Unlike the drinking in primitive snakes, the tongue does not rhythmically protrude from and retract into the mouth during the drinking cycle, but instead the lingual canal is closed by soft tissues (oral mucosa, labial scales) and opened when these part. We propose that drinking is based upon a buccal-pump mechanism that aspirates water into the mouth, then drives it into the esophagus. This permits prolonged drinking bouts without requiring head tipping or the use of gravity for water intake or intraoral transport.

Drinking behavior and the mechanics of intraoral water movement have only recently received detailed analysis in tetrapods. In birds, these studies report a variety of drinking mechanisms. In some birds, the tongue and larynx scoop water; in other(s) tongue-scoop and head tip-up move water (Heidweiller and Zweers,1990); in the mallard, a double capillarity and pressure mechanism passes water around lingual elements (Kooloos and Zweers 1989); in the domestic chicken, water adhesion to beak tips and capillarity initially collect water followed by use of tongue and larynx (Zweers 1992; Heidweiller *et al.* 1992), but this

mechanism is affected by aspects of scaling (Heidweiller and Zweers 1992).

Among squamates, two modes of drinking have been recognized so far for lizards. In one (iguanian and scleroglossan), water delivery to the mouth is primarily by the tongue (Smith 1984; Bels *et al.* 1993). In the other *(Varanus)*, the whole snout is submerged in the water followed by complex action of the hyoid apparatus apparently to draw in water (Auffenberg 1981; Smith 1986). Outside of anecdotal comments about "gulping", information on drinking mechanics in snakes is scant. The only detailed description of drinking mechanics is for the primitive boid snake, *Boa constrictor* (Kardong and Haverly 1993). In the boa, the rhythmic rise and fall of the mandibles and floor of the oropharyngeal cavity between them form the basis for a buccal-pump mechanism that aspirates water into the mouth then forces it into the esophagus; synchronized with this pump is the regular protraction and retraction of the tongue, itself contributing to the closing and opening of the front of the mouth.

Observation of drinking by members of advanced families of snakes revealed a different mechanism. The tongue does not establish aprotraction/ retraction cycle synchronized with buccal cycles. The purpose then of this study was to carefully characterize this undescribed drinking mechanism and to propose a model of drinking that would contribute to comparative studies of drinking in tetrapods.

Materials and methods

We examined drinking behavior in five brown tree snakes, *Boiga irregularis,* collected in Guam and held in captivity for six months. They ranged in size from 120 to

210 cm, snout-vent length. Snakes were deprived of food and water for one to four days prior to experimental trials. Each trial consisted of first strike and swallowing of mice followed by a drinking session. Surgery to implant electrodes and affix instrumentation was performed in the morning and experimental trials conducted in the evening of the same day.

Anesthesia

Insertion of electrodes, attachment of gape sensor, and implantation or attachment of radiographic markers were all done when the snake was under inhalation anesthesia. Isoflurane (Forene R, Abbott, U.K.) was administered by endotracheal intubation with a vaporizer (TILC fluothane vaporiser, Loosco, Amsterdam, Netherlands) in a concentration of 1.5% in a gas flow of 0.7 liters/minute (200 cc O_2 and 500 cc NO_2) which exited via a syringe needle inserted into the posterior lung sac thereby establishing a unidirectional anesthetizing system (de Cock Buning 1983).

Motion analysis

Cineradiography was done with an X-ray system (Gigantos, Siemens-Reiniger AG, Erlangen, Germany) using Kodak Ortho G, 35 mm film at 48 fps. During separate drinking episodes, both dorsoventral and lateral radiographic films were made. These were accompanied by simultaneous light 16 mm films made with a Bolex Paillard camera (Video News Film, Eastman Kodak, type 7240) placed lateral to the snake operated at 50 fps. Camera shutter recordings sent electronically to the tape recorder (EMI, 7 1/2 ips) permitted synchronization of kinematic and electromyographic records. Gape displacement was recorded directly using a magneto-restrictive sensor (type KMZ 10, Philips, Eindhoven, Netherlands) affixed to the dorsum of the head over the parietal bone. This sensor detected the position of a small (2×10 mm) permanent magnet glued externally to the chin of the snake next to and between the anterior tips of the dentaries. The sensor produced an output waveform proportional to actual gape displacement. This produced results more sensitive (Philips Technical publication 102) than the conventional Hall-effect sensor described for a similar application in pigeons (Deich et al. 1985). Cine films were examined frame-by-frame (NEC 16 mm analysis projector) to gather qualitative information and used in descriptions of basic kinematic events.

Electromyography

Implantation of bipolar electrodes (copper, 50 micrometer) was done while snakes were anesthetized. Skin over the desired muscle was opened with a small incision, the muscle was gently exposed, and the electrode pair inserted into the belly of the muscle while visually viewing implantation under an operating microscope following techniques of Zweers (1974) and Heidweiller et al. (1992). By gently separating superficial muscles, even deeper muscles could be exposed via a lateral route without requiring entry through the oral cavity. After each implantation, correctness of the electrode position was further verified by sequential back stimulation through the recording electrodes using a Grass S-66 stimulator and PSIU (photo-electric stimulus insulation unit). Electrode pairs were placed near the origin of each muscle, slightly bent to add slack, and the incision closed by suture and tissue glue (cyanocrylate). Externally, electrodes were run across and glued to the surface of the skin to reach the nape of the neck. Here the electrodes were bundled together into a single cord by glue and loosely tied to a strong string sutured to the neck that carried the tension from snake to outside the cage. Immediately following surgery and later after drinking trials, the snakes were radiographed to confirm position of electrodes. Snakes were brought out of anesthesia by switching from isoflurane/O_2 mixture to O_2 run unidirectionally through the lungs. The snakes struck and swallowed offered dead mice and drank offered water within 4–8 hrs after surgery. Four to ten electrode pairs were implanted during one experimental trial along with the gape sensor and filming analysis.

Electromyograms (EMGs) were amplified 1000 times with preamplifiers and stored on magnetic tape (14 channel, SE Labs/EMI, U.K.) along with motion data. Filtering occurred at two frequencies: a high pass filter at −3 db at 100 Hz and a low pass filter −3 db at 10 kHz. These data were also viewed simultaneously during recording on an 8 channel memory oscilloscope (Model VM 680 G, Nihon Kohden, Tokyo) and a thermal array recorder (model WS-681G, Nihon Kohden, Tokyo). A custom encoder/decoder produced and stored on a separate channel experimental data and real and elapsed times (hr, min, sec).

Oropharyngeal pressures

To help assess the relative importance of forces derived from capillarity compared to muscle generated forces, intraoral pressures were recorded separately in two snakes, 163.1 and 210.5 cm snout-vent length during one drinking session each. In addition to affixing a magnetic sensor as described above a polyethylene pressure catheter (PE 100, 40 cm length) was inserted into anesthetized snakes through the floor of the throat into the middle of the oropharyngeal cavity and slightly lateral to the midline thereby positioning it next to the trachea and avoiding major blood vessels or nerves (see Kardong and Haverly 1993, for details of the procedure). An expanded beveled collar at the tip of the catheter both prevented it from being pulled free and held the catheter opening about 3 mm above the oral epithelium next to the trachea. The catheter was connected to a liquid pressure transducer (Statham) held level with the tip of the catheter in the oropharyngeal cavity. Three-way valves allowed fluid filling and clearing of the catheter with distilled water. Both pressure (catheter) and jaw displacement (magnetic sensor) were recorded simultneously during the drinking session as adjacent traces on a galvanometer-driven chart recorder (Bell and Howell).
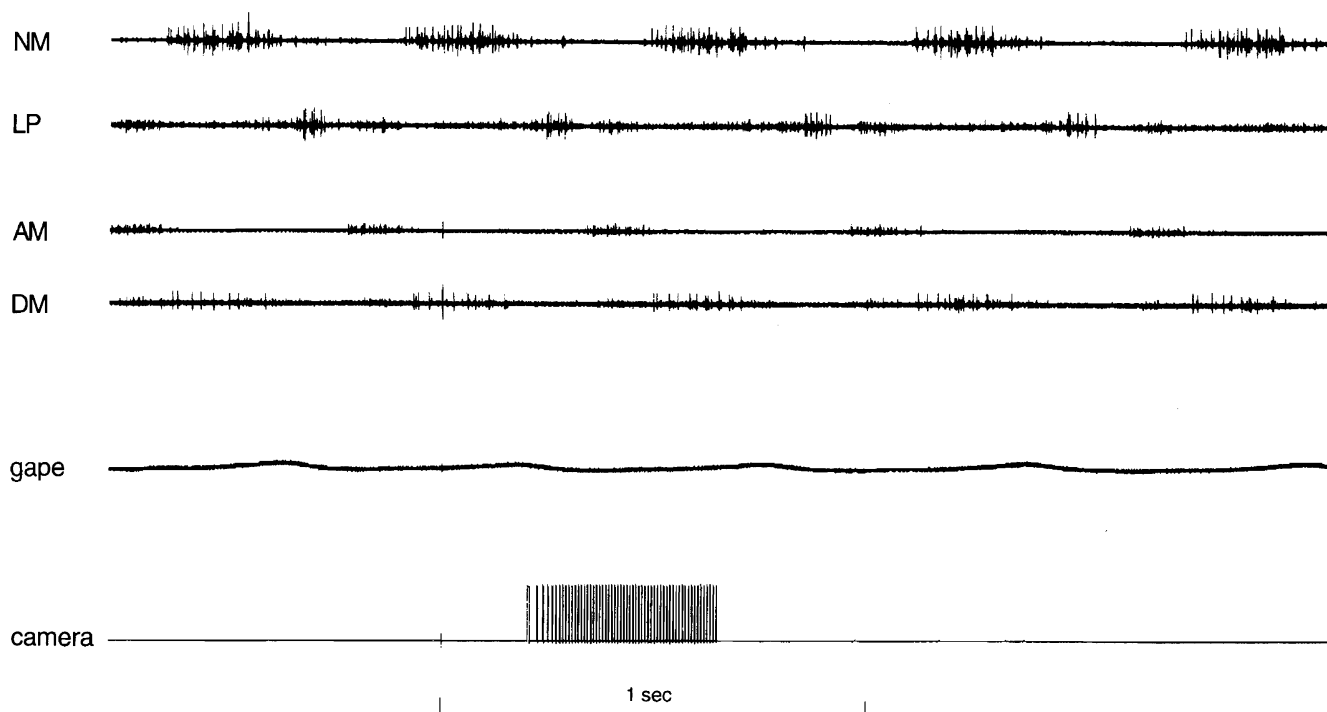
Fig. 1. Representative activity of four cephalic muscles shown in register with shallow, rhythmic displacement of the jaws, gape, through five drinking cycles. A short burst of simultaneous high-speed film was made during the beginning of the sequence, each of the one hundred eleven frames represented by a spike. Traced here, gape peaks are maximum open representing a distinctive feature of jaw displacements and used to synchronize muscle activity between separate experiments. The high-speed filming sampled a short duration of the drinking cycles and helped verify the synchronization of muscle activity and gape.

AM, M. adductor mandibulae externus medialis, DM, M. depressor mandibulae, NM, M. neuro-costo-mandibularis, LP, M. levator pterygoidei.

Data representation, reduction, and statistical analysis

Electromyograms were examined initially by play-back of original recordings together with simultaneous film frame pulses and gape sensor outputs at one-quarter of recorded speed. The distinctive peaks and valleys produced by the gape trace (magnetic sensor) were common to all experiments, and were used as the common reference to synchronize data between separate experiments. Four representative electromyographic traces are shown in Figure 1, accompanied by simultaneous traces of the gape and a short burst of spikes from the shutter of the high-speed camera. This allowed synchronization of motion and muscle activity. Further analysis of these activities was done by rectifying and integrating a/d converted electromyographic signals at 0.5 ms intervals. These were stored on an Epson AT microcomputer and Asystant data acquisition software used to correct EMG records for their off-set voltage. Drinking bouts were of variable length, from 40 to 85 cycles during our experimental trials. To compare drinking mechanics during water intake, the time of first contact with the water to when the snout was lifted out of the water was divided into three intervals – early, middle, late. Early and late intervals were defined as the events during the first and

last 15% of the drinking bout; middle was approximately half way between them. Three complete, adjacent cycles during each of these intervals were sampled and scored. All selected gape and rectified/integrated electromyo-

Table 1. Summary of F-tests for significance of drinking phases (early, middle, late) on muscle and gape variables.

Independent variable: phase (early, middle, late)

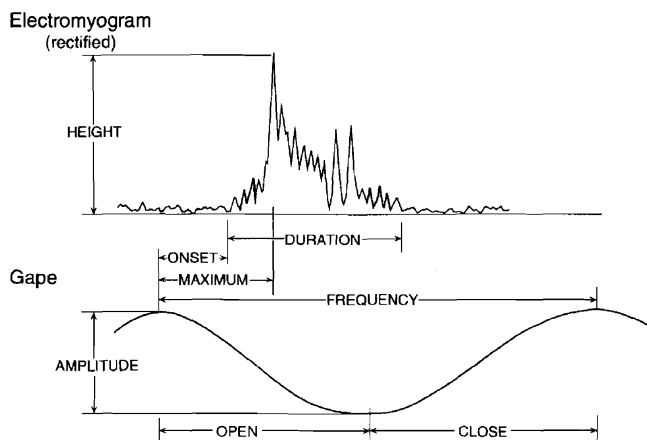| Dependent variable	F-ratio
Gape	
AMPLITUDE	19.77**
FREQUENCY	185.78**
Electromyograms	
HEIGHT	0.03
DURATION	0.43
ONSET	0.50
MAXIMUM	0.59
AREA	10.55**

* $p < 0.05$, ** $p < 0.001$

Fig. 2. Variables of electromyograms (rectified) and of recorded gape displacement. The HEIGHT, DURATION, and AREA of each electromyogram was measured as well as the time of its ONSET and MAXIMUM relative to the beginning of a gape cycle. The AMPLITUDE and FREQUENCY of the gape cycle was measured. These variables were scored and averaged for three adjacent cycles during early, middle, and late parts of a drinking bout.

gram sequences were played back from the tape recorder to the thermal chart recorder at equivalent paper speeds to produce an inscribed record. Measurements were made directly on this chart recording to calculate (0.1 mm) the variables listed in Table 1 and shown in Figure 2. For the gape cycle itself, two variables were scored: peak-to-peak frequency (FREQUENCY) and maximum amplitude (AMPLITUDE). The maximum height (HEIGHT), duration (DURATION), and area (AREA) of each rectified electromyogram were scored. Each rectified electromyogram was scored relative to its respective gape cycle producing two further variables, the time of onset of each electromyogram relative to gape peak, jaws closed (ONSET), and maximum electromyogram relative to onset of the gape cycle when jaws began to open (MAXIMUM).

Results

Morphology

Osteology: In general, the skull of *Boiga irregularis* is typical of colubrid snakes (Albright and Nelson 1959; Cundall 1981, 1983; Kardong 1986), Figure 3. The bones of the skull can be organized into three primary units that articulate with the braincase (Albright and Nelson 1959; Frazzetta 1959, 1966). The single snout unit included paired nasals, septomaxillae, and vomers and a single median premaxilla. The nasofrontal articulation established the point about which the snout unit rotated on the braincase.

The paired palatomaxillary units included pterygoid, ectopterygoid, maxilla, and palatine. The left
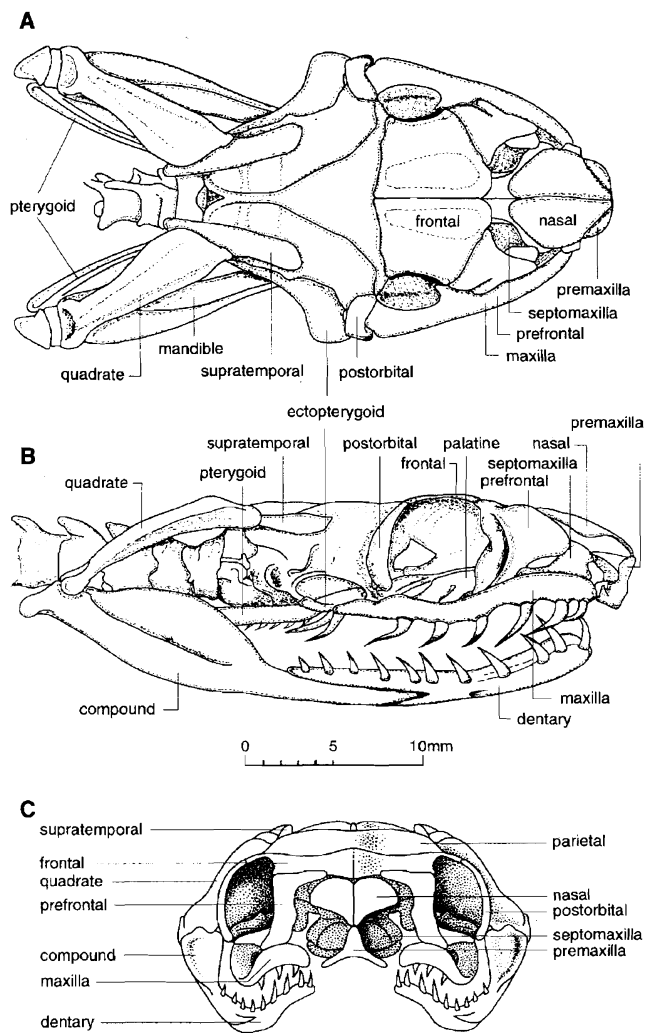

Fig. 3. Skull of *Boiga irregularis* as seen in dorsal **(A)**, lateral **(B)**, and frontal **(C)** views.

and right sides were not directly joined and each was independently suspended from three primary sites. Foremost was the suspension from the prefrontal. Viewed laterally, the prefrontal was roughly triangular in shape with each edge establishing an important functional relationship with other bones of the skull. The dorsal corner was widened into an edge that articulated with the frontal of the braincase; this articulation was very firm and prevented significant movement of the prefrontal relative to the braincase. The anterior corner and edge of the prefrontal dorsal to it served as a site of origin of a broad ligament that reached to the posterior edge of the nasal. The ventral corner of the prefrontal established an articulation with and so suspended the palatomaxillary unit; specifically, its medial side made contact with the palatine, and its lateral side was firmly attached to the mid shaft of the maxilla.

The second suspension site of the palatomaxillary unit was from the postorbital via a very strong

ligament, the L. maxillo-postorbitale. This ligament together with the firm prefrontal suspension checked displacement of the maxilla restricting its motion to slight rotation about the prefrontal, but preventing any significant horizontal sliding in an antero-posterior direction.

The third suspension site was established between quadrate and pterygoid, specifically from the medial condyle of the distal quadrate to the posterior tip of the pterygoid. These two bones did not form an articulation but were joined by a ligament, L. quadrato-pterygoidale, and by the pterygoid and accessory pterygoid muscles that spanned the distance between the bones. This permitted some relative motion between quadrate and pterygoid similar to that reported in other colubrids (Cundall and Gans 1979; Kardong 1986).

The paired mandibular unit included supratemporal, quadrate, and mandible consisting of compound, splenial, and dentary bones. The attachment of the supratemporal to the parietal was firm, allowing very little relative movement between supratemporal and braincase. The ligaments across the supratemporal-quadrate joint permitted extensive motion so that the quadrate experienced considerable freedom of rotation about this joint in both antero-posterior and mediolateral planes. The quadrato-mandibular joint allowed the greatest rotation of the mandible in a dorso-ventral plane, but much less freedom of rotation laterally about this joint. The anterior tips of the mandibles did not meet at the midline, but these tips were joined by muscles to an interramal pad, a medial mass of fibrous connective tissue embedded in the dermis of the chin. The highly supple kinematic connection to the braincase and absence of direct connections between left and right sides permitted the paired halves of the mandibular unit considerable independent motion.

Oral Morphology: The arcades of teeth carried in the maxillae (upper) and dentary (lower) arched forward but did not meet at the midline thus leaving an anterior gap in the tooth rows at the front of the mouth (Figure 4). This gap, the lingual canal, together with slight parting of the lips offered an opening through which the tongue was protracted from the mouth during chemosensory activity. Externally, entrance to the lingual canal was guarded by rostral (upper) and mental (lower) integumental scales. The rostral scale was firmly affixed to the underlying premaxilla. However, the mental scale was suspended in the integument between the mandibular tips. Muscles moved the mental scale dorsally to close or ventrally to open the entrance to the lingual canal. Lateral to these scales, the lips continued around the borders of the mouth formed by upper and lower rows of labial scales. Along their ventromedial border, the upper row of labial
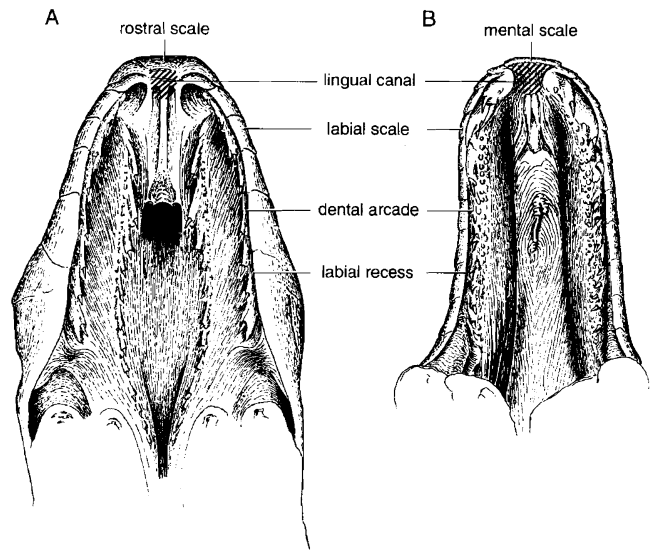

Fig. 4. Anterior oral cavity of *Boiga irregularis*. **A.** Roof of oropharyngeal cavity. Rostral scale and several adjacent upper labial scales form the outer rim of the mouth and hold on their medial side an oral groove, the upper labial recess, that receives the rim of the lower labial scales when the mouth is closed. The oral mucosa covering the maxillary tooth row is indicated, the dental arcade. The anterior oropharyngeal cavity defines the lingual canal. The upper gap between maxillary teeth forms the top half and lower dentary teeth define the edges of the bottom half of the lingual canal, the route through which the tongue is protruded from and withdrawn into the mouth. **B.** Floor of oropharyngeal cavity. Mental scale and adjacent lower labial scales form the outer rim to the mouth; the oral mucosa covers the anterior tooth arcade of the dentary teeth and between this dental arcade and the labial scales forms the lower labial recess. Complementary areas of the lingual canal are labeled and indicated by slanted cross-hatching.

scales formed a continuous parallel groove, the labial recess; the lower labial scales formed along their free border a labial ridge. When the jaws closed, ridge fitted into recess to seal the sides of the mouth. Further, the medial palatine tooth rows were sheathed in pliable mucosal folds. Consequently, when the jaws closed, the dental and maxillary arcades pressed together to contribute also to the lateral sealing of the oropharyngeal cavity.

Lateral Jaw Musculature: The lateral jaw musculature of *B. irregularis* conforms to that of most other colubrids (Cowan and Hick 1951; Albright and Nelson 1959; Cundall 1986), so only the general features germane to drinking mechanics will be mentioned here and their lines of action indicated (Figure 5).

Three primary muscles arose on the braincase and inserted on the palatomaxillary unit (Figure 5A). M. levator pterygoidei took its origin from a low fossa on the posterior face of the postorbital
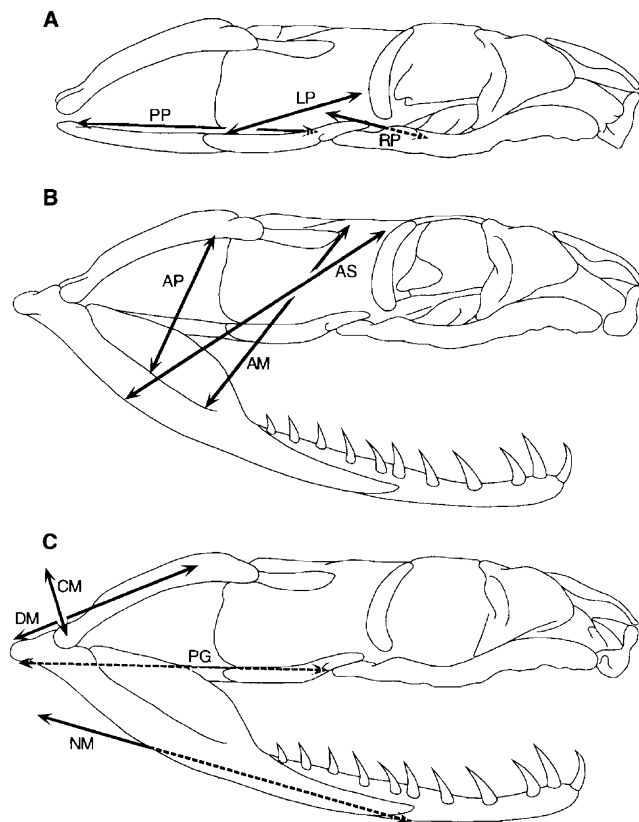
Fig. 5. Lines of action of major jaw muscles. **A.** Major muscles originating on the braincase and inserting on the palatomaxillary unit. **B.** Jaw adductor muscles. **C.** Muscles arising outside the mandibular unit and inserting to it.

AM – M. adductor mandibulae externus medialis; AP – M. adductor mandibulae externus profundus; AS – M. adductor mandibulae externus superficialis; CM – M. cervico-mandibularis; DM – M. depressor mandibulae; LP – M. levator pterygoidei; NM – M. neuro-costo-mandibularis; PG – M. pterygoideus; PP – M. protractor pterygoidei; RP – M. retractor pterygoidei.

process of the parietal and ran in a ventro-posterior direction to insert across the medial and lateral edges of the mid-pterygoid. M. protractor pterygoidei originated within a fossa on the sphenoid midventrally and ran almost horizontally reaching caudally to insert on the dorsal, posterior end of the pterygoid. M. retractor pterygoidei originated in a well defined fossa on the ventro-lateral wall of the braincase and ran in an antero-ventral direction to insert on the dorsal, posterior end of the palatine.

The three major adductor muscles were examined in this study, the Mm. adductor mandibulae externus profundus, medialis, and superficialis (Figure 5B). The adductor profundus originated along the anterior edge of the quadrate and passed as a large wall of muscle to the mandibular fossa where

its insertion occupied the edges of this fossa. The adductor superficialis and adductor medialis originated adjacent to each other along the parietal ridge on the dorsal braincase. The adductor medialis inserted on the mandible anterior to the adductor profundus. The adductor superficialis developed as a broad fan of muscle passing superficial to the others and terminated in an aponeurosis that inserted along the ventral, lateral edge of the mandible; the center of this insertion laid below the middle of the mandibular fossa.

Four other major muscles were examined that ran to or within the mandibular unit (Figure 5C). Both Mm. cervico-mandibularis and neuro-costo-mandibularis arose outside the unit along the neck near the dorsal midline. The cervico-mandibularis, the most anterior of these two, narrowed as it slanted forward and ventrally to insert laterally along the distal end of the quadrate and on to the retroarticular process of the mandible. The neuro-costo-mandibularis was a broad sheet of muscle that swept forward and ventrally traveling around the angle of the jaws, into the throat, and finally established an insertion along the ventral edge of the dentary. The M. pterygoideus also arose outside the mandibular unit, but from the lateral process of the ectopterygoid via a very prominent tendon. It passed posteriorly becoming a very large, pinnate muscle that bulged below the angle of the jaw just as it reached its insertion on the ventral surface of the retroarticular process. This course gave it an almost horizontal line of action. The M. depressor mandibulae arose within the mandibular unit from the dorsal surface of the quadrate, especially from its proximal end, and narrowed ventrally as it approached its insertion on the dorsal surface of the retroarticular process.

Drinking behaviour

• Phases

A drinking bout consisted of four phases of unequal and varying duration – approach, immersion, emersion, and withdraw (Figure 6).

Approach Phase: During the approach phase, the snake reached its head into various parts of the cage. This probing of the head about the cage was accompanied by tongue flicks. These tongue flicks were similar in basic motion as those described for *Boa constrictor* (Ulinski 1972). During tongue flicks, the tines of the protruded tongue spread forming a Y-shape, swept the space in front of the snout, then the tines came together as the tongue returned to the mouth. If the snake was close to the substrate, the tongue tines made contact and rolled forward so that their tips, espe-

Fig. 6. Drinking Phases. *Approach phase:* the thirsty snake moves about the cage exhibiting irregular tongue flicks until it makes contact with the water. *Immersion phase:* drinking cycles begin involving repeated opening and closing stages drawing water into the mouth; here a meniscus lifts up to adhere to the lingual canal, but more often the anterior tip of the snout is actually submerged just beneath the surface of the water. *Emersion phase:* the snake lifts its head from the water, drinking cycles decline, then stop. *Withdraw phase:* the snake moves away from the water.
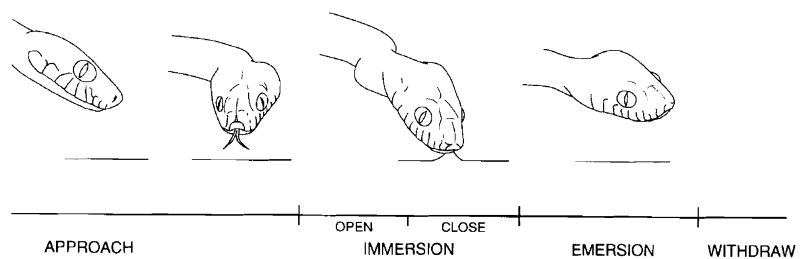
cially their dorsal surfaces, were in contact with the surface before retraction. Eventually the snake came into contact with the water, usually first by tongue contact. If the snake was going to drink, then movements of the head about the cage ceased upon contact with the water and drinking motions immediately began.

Immersion Phase: First contact of the tongue or snout with the water marked the beginning of the immersion phase. Rhythmic cycles of depression and elevation of the mandible followed, accompanied by expansion and compression of the oropharyngeal cavity in the region of the quadratomandibular joints. Cycles of tongue protraction from the mouth occasionally continued into the early onset of the emersion phase. But, as the rhythmic mandibular cycles became established, all tongue protrusion ceased and these tongue cycles were absent from subsequent drinking movements. If tongue flicks began again, they did not appear until the very conclusion of immersion or at the onset of the emersion phase. During these drinking cycles, the head was held in a fixed position above the water so that the snout was in contact with the water. Occasionally, the snout would be pushed to a depth so that water covered the nostrils. However, the snake usually kept the nostrils out of the water, and contact with the water could be quite modest. The usual position was for the chin to be in contact with the water, but for the capillarity of the water to draw up a meniscus to the front of the mouth where water then entered through the lingual canal. When drinking drops of water, this capillarity was important in bringing water to the lingual canal, although the actual movement into the oropharyngeal cavity was by the active pumping action of the jaws.

Emersion Phase: When the head was lifted, contact between water and snout was broken. This ended immersion and marked the beginning of the emersion phase. Despite loss of contact with the water, the rhythmic movements of the jaws and throat continued for several cycles. If the water

container was below the level of the body, then during emersion the snake returned its head to a level approximately level with the rest of the body. There was no marked "head tipping" as occurs in some birds (Heidweiller and Zweers 1990; Zweers 1992) and some lizards (Bels *et al.* 1993). Occasionally, the snake would return to the water and start a second immersion phase of drinking. However, usually the snake departed and did not immediately resume drinking.

Withdraw Phase: The departure of the head of the snake from the vicinity of the water marked the onset of the withdraw phase.

• **Water displacement**

Water entered the mouth during the immersion phase. The immersion phase consisted of a variable number of cycles composed of opening and closing stages.

Opening stage: During the opening stage, the anterior tips of the mandibles were slightly depressed. This was accompanied by retraction of the mental scale and adjacent labial scales away from the lingual canal. This retraction of scales along the tip of the lower jaw together with slight mandibular depression opened the lingual canal and immediately adjacent margins of the mouth. Water now entered the mouth flowing in at the anterior tip of the snout (Figure 7). As anterior mandibular tips depressed, descent of the region of the oropharyngeal cavity between posterior ends of the mandibles deepened the throat. The overall result was to enlarge the volume of the oropharyngeal cavity.

Closing stage: Elevation of the anterior mandibular tips marked the beginning of the closing stage, and together with protraction of the lower lip (mental scale plus adjacent labial scales) closed the sides of the mouth and lingual canal, respectively. Slightly following the onset of jaw closure, the posterior part of the oropharyngeal cavity began to flatten as the throat elevated. Flaring now
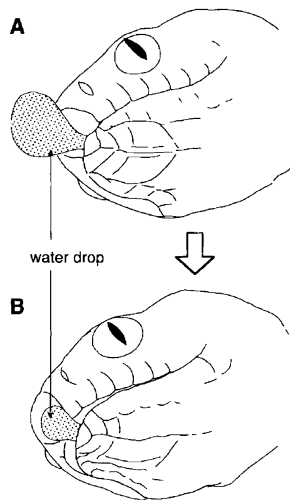
Fig. 7. Drinking a droplet of water. As shown here in ventral view, the snake is drinking a water droplet from a clear glass plate so that the action of the lips can be observed. In A, the mouth is closed. In B, note that the mental and adjacent lower labial scales are retracted to part the front of the mouth. The mandible is also slightly depressed and the water droplet is drawn in via the lingual canal.

of the quadrato-mandibular joints resulted in widening of the posterior throat region at the angles of the jaws.

• Drinking kinematics

During the opening stage, the anterior tip of each mandible was depressed, rotating about its articulation with the quadrate (Figure 8). From both high-speed films and cineradiography, we confirmed that during opening the quadrato-mandibular joint swung inward describing a shallow arc in a medio-ventral direction. No motion was evident in the supratemporal that remained in a fixed position throughout all cycles of drinking. During the closing stage, these displacements were reversed. The anterior tip of the mandible was elevated; the quadrato-mandibular joint rotated outward along a dorso-lateral arc. Although the mandibular units were independently suspended from the braincase, these displacement cycles of opening and closing were synchronous between left and right units.

Because the posterior end of the pterygoid was tethered to the quadrate, the pterygoid tended to follow the inward and outward swings of the quadrate. This imparted motion to the palatomaxillary unit gently rotating it in a horizontal plane about its suspension from the prefrontal. No significant motion was detectable in the snout unit (high-speed and cineradiography).
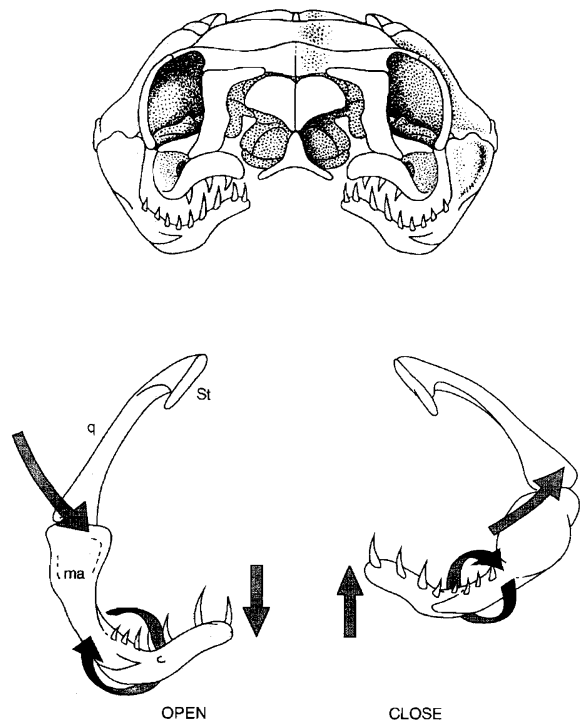

Fig. 8. Displacements of the mandibular unit. At the top of the figure, a frontal view of the skull of *Boiga irregularis* is shown; the right mandibular unit is shaded. At the bottom of the figure, the isolated and enlarged mandibular units of each side are shown; the one positioned on the left of the page is in an open position, the one on the right side of the page is in a closed position. The positions are exaggerated to illustrate displacements. During opening, the quadrato-mandibular joint swings ventro-medially, the tip of the mandible is lowered; and the mandible itself rotates clockwise about its long axis. During closing, these motions are reversed.

ma – mandible; q – quadrate; St – supratemporal.

Gape displacement significantly increased in frequency from early, middle, to late in the drinking bout whereas gape amplitude significantly decreased (Table 1).

• Muscle activity

Two muscles were silent during drinking, the adductor profundus and cervico-mandibularis, although both had shown significant activity during prey swallowing behavior immediately preceding drinking. Only activity of the adductor superficialis was restricted to one stage, the closing stage. All other active muscles tended to exhibit activity during parts of both opening and closing stages, although the maximum activity usually occurred during one stage (Figure 9).

During the opening stage, the muscles reaching their most prominent activity included the depres-
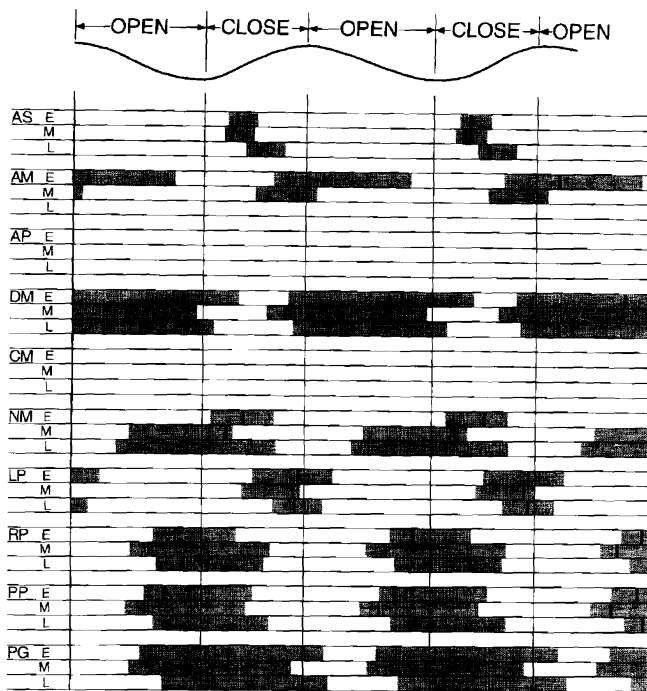
Fig. 9. Block electromyograms of the major jaw muscles during drinking. The displacement of the lower jaw is plotted along the top of the figure, divided into open and close stages. For each muscle, the electromyograms are shown from early (E), middle (M), and late (L) in the drinking sequence. The solid vertical line within each block represents the point at which the electromyogram reaches its maximal peak.

AM − M. adductor mandibulae externus medialis; AP − M. adductor mandibulae externus profundus; AS − M. adductor mandibulae externus superficialis; CM − M. cervico-mandibularis; DM − M. depressor mandibulae; LP − M. levator pterygoidei; NM − M. neuro-costo-mandibularis; PG − M. pterygoideus; PP − M. protractor pterygoidei; RP − M. retractor pterygoidei.

sor mandibulae and neuro-costo-mandibularis. During the closing stage, the most active muscles were the adductor superficialis and adductor medialis. The other muscles tended to have peak activity initiated during one stage but continued into the early parts of the next. For instance, onset of activity in the levator pterygoideus (LP) began late in the closing stage but was significant into the early part of the next open stage; beginning in late open and continuing activity into early close were the retractor pterygoideus (RP), protractor pterygoideus (PP), and pterygoideus (PG) muscles (Figure 9).

Slight differences occurred in the onset of activity of the same muscle during early, middle, and late points in the drinking sequence. Except for the neuro-costo-mandibularis, all active muscles showed earlier onset of activity during the middle of the drinking sequence compared to their onset during either the early or late part of the sequence.

In Table 1, the F-test of muscle and gape variables are shown for statistical variation during the three phases of drinking − early, middle, and late. During a drinking bout, the AMPLITUDE of lower jaw oscillations tended to decrease, but FREQUENCY increased. Although the maximum height and length of electromyograms did not significantly change the total area of electromyograms decreased during a drinking bout.

For the two large snakes tested, the oropharyngeal pressures peaked during the middle of the emersion phase (2.0 +/− 0.8 cm H_2O) and declined near the end (1.5 +/− 0.6 cm H_2O) just before the snake lifted its head from the water.

Discussion

Drinking by *Boiga irregularis* involves the cyclical generation of low and high pressures within the oropharyngeal cavity accompanied by the synchronous opening and closing of the margins of the mouth. This seal to the margins of the mouth is formed by the engagement of upper and lower labial scales along with the meeting of upper and lower tooth arcades lined with oral mucosa. When the jaws close these soft tissues are brought together, sealing the sides of the mouth, and preventing either intake or loss of water along the sides of the mouth. The lingual canal at the tip of the snout is closed by the mental scale and several adjacent lower labial scales that are protracted forward and dorsally to meet and close with the rostral and several adjacent upper labial scales. With the mouth sealed, rising positive pressure in the oropharyngeal cavity forces water past the esophageal sphincter and into the esophagus (D in Figure 11).
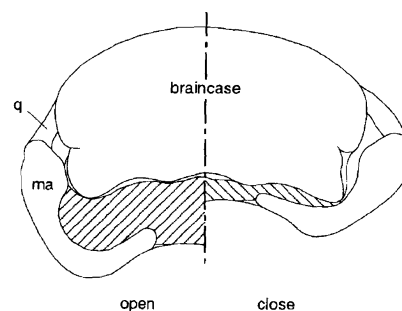

Fig. 10. Volume changes in the oropharyngeal cavity during open and close stages of drinking. Note that during opening, the cross-sectional area defined by the oropharyngeal cavity (cross hatching) is larger than when the jaws are closed. This results from geometric changes in the oropharyngeal cavity due to displacements of the mandibular unit and to changes in position of the throat.
ma − mandible; q − quadrate.
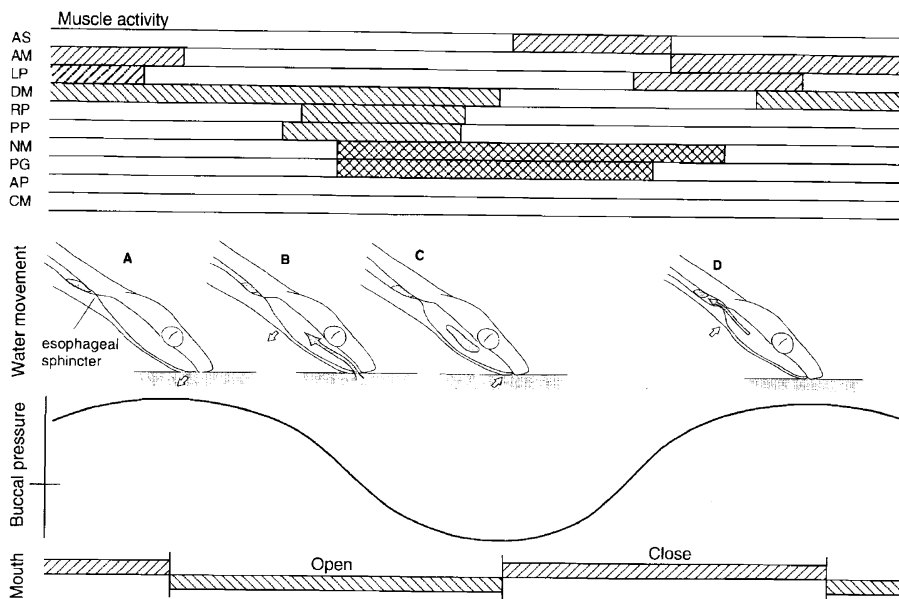
AM – M. adductor mandibulae externus medialis;
AP – M. adductor mandibulae externus profundus;
AS – M. adductor mandibulae externus superficialis;
CM – M. cervico-mandibularis;
DM – M. depressor mandibulae;
LP – M. levator pterygoidei;
NM – M. neuro-costo-mandibularis;
PG – M. pterygoideus;
PP – M. protractor pterygoidei;
RP – M. retractor pterygoidei.

Fig. 11. Buccal-Pump Model. The proposed model of drinking by *Boiga irregularis* is summarized in four steps. **A.** Initial opening characterized by lower jaw depression and opening of the lingual canal. **B.** Enlargement of the oropharyngeal cavity produces a negative pressure aspirating ambient water. **C.** Initial closing characterized by elevation of lower jaws, closure of the lingual canal, and meeting of tooth arcades along the sides of the mouth. **D.** Rise in oropharyngeal pressure drives the imbibed water (arrow) past the esophageal sphincter (constriction) and into the beginning of the esophagus to join the growing pool of water drunk earlier in the drinking bout. During close, the superficialis (AS) and medialis (AM) are active, the profundus (AP) is silent; the pterygoid levator (LP) becomes active well into close. The depressor mandibulae becomes active near the end of close and remains active throughout the open phase. During open it is joined by the retractor pterygoidei (RP) and protractor pterygoideus (PP). The neuro-costo-mandibularis (NM) and pterygoideus (PG) are active from the open into the close phases.

Slight depression of the mandibles together with retraction of the mental scale breaks the oral seal around the anterior tip of the mouth. Negative pressure within the oropharyngeal cavity encourages the aspiration of ambient water into the oropharyngeal cavity (B in Figure 11). Once drawn into the oropharyngeal cavity, the jaws close re-establishing the oral seal, pressure rises, and the water is swallowed completing the cycle.

Rising and falling pressures are produced in the oropharyngeal cavity by a combination of events. During the opening stage, the depression of the mandible together with the accompanying inward swing of the quadrato-mandibular joint change the geometry of the oropharyngeal cavity so as to enlarge its volume. This volume is increased further by depression of the throat, the posterior floor of the oropharyngeal cavity. Enlarging the oropharyngeal cavity decreases pressure within and this encourages the entry of water (Figure 10).

During the closing stage, these displacements are reversed. The mandibles are elevated, the quadrato-mandibular joint swings outward, and the throat lifts upward, all of which decreases the volume of the oropharyngeal cavity raising the pressure within (C in Figure 11).

As the pressure begins to rise, water in the oropharyngeal cavity does not escape because the edges of the mouth seal during the closing stage as upper and lower lips and dental arcades are brought together. Escape through the nostrils is assumed to be prevented by the larynx that is inserted into the internal nares. This maintains respiratory continuity during prolonged drinking sequences and also closes the nasal passage during drinking. Consequently, this elevated oropharyngeal pressure serves to move water from the oropharyngeal cavity, past the esophageal sphincter, and into the esophagus.

Unlike boid snakes (Kardong and Haverly 1993), the tongue does not exhibit synchronous protraction/retraction cycles from/into the mouth during drinking. Drinking mechanisms in birds involve forces derived from capillarity (Zweers 1992). However the role of capillarity in snakes is difficult to evaluate. Capillarity depends on surface tension across a small space. When the floor and roof of the oropharyngeal cavity are held close together, the space between these complementary regions is small and so capillarity could draw up a line of water. However, when the oropharyngeal cavity enlarges during cycles of the immersion phase,

this space enlarges and the further involvement of capillarity becomes unlikely. On some occasions, the snake did not submerge its anterior snout, but only made sufficient contact with the water for surface tension to lift up a meniscus of external water to the lingual canal. Similarly, when drinking water droplets, the surface tension caused adhesion between the external water droplet and the lingual canal. This adhering water droplet did not actually enter the oropharyngeal cavity until the cavity expanded. This may imply that the negative pressures generated within the cavity, and not capillarity, were responsible for actual movement of the water into the mouth. Further, compared to capillarity forces, these forces generated in the oropharyngeal cavity were relatively substantial, representing the equivalent of 2 to 3 cm of water pressure. Perhaps in small snakes capillarity might be a more significant contributing force to water movement into and through the oropharyngeal cavity. But, the primary forces aspirating water first into the oropharyngeal cavity then moving it into the esophagus were generated by active kinematic changes in jaw displacements accompanied by action of the floor of the oropharyngeal cavity.

On the basis of these conclusions, the following four-step drinking model is proposed for *B. irregularis.*

Buccal-pump model

Opening Stage: Onset of the opening stage, the first step in drinking, is marked by depression of the anterior tips of the mandibles. This, together with opening of the lingual canal by retraction of the mental scale, breaks the seal around the mouth (Figure 11A). During the next step (Figure 11B), a pulse of ambient water is aspirated into the mouth following the lower pressure within the oropharyngeal cavity produced by enlargement of the oropharyngeal cavity.

Closing Stage: The third step, and onset of the closing stage, begins with closure of the sides of the mouth by elevation of the mandibles, engagement of the soft oral mucosa along upper and lower tooth arcades, and protraction of the mental scale to close the lingual canal (Figure 11C). The fourth step is accompanied by a decrease in oropharyngeal cavity volume due to continued closure of the mandibles and elevation of the throat (Figure 11D); this increases intraoropharyngeal pressure driving the just aspirated pulse of water into the esophagus, the only currently open exit route from the oropharyngeal cavity.

These cycles continue without interruption so that pulses of water are added to the growing pool of water behind the esophageal sphincter. Eventually the head is lifted and the water collected in the esophagus moves under gravity's force to the stomach.

This buccal-pump mechanism of drinking depends upon producing negative then positive pressures relative to ambient to draw water into the mouth and then force it past the esophageal sphincter. This mechanism of intraoral transport relies on active volume changes in the oropharyngeal cavity produced by muscle action and geometric changes in jaw kinematics. It does not require the lifting of the head after imbibing each pulse of water to take advantage of gravity to move water to the esophagus. This mechanism can also gather in small quantities of water, such as droplets that might form as morning dew. This is possible because the opening to the oropharyngeal cavity is kept small and generated pressures thus localized.

Muscle Activity: These buccal pump displacements are produced by the jaw musculature (Figure 11). During the close phase, the large adductor profundus (AP) remains silent, but the adductor superficialis (AS) and adductor medialis (AM) lateral jaw muscles are active. In this model, both adductor superficialis and adductor medialis cause jaw elevation at this point in the drinking bout. The levator pterygoideus (LP) is also active during mid to late close making it a muscle that stabilizes the palatomaxillary arch during the close phase. Depression of the lower jaw is caused by the depressor mandibulae, but actual opening occurs only after jaw adductors (superficialis, medialis) become silent. The depressor mandibulae and jaw adductors act antagonistically, rotating the lower jaw in opposite directions about its articulation with the quadrate. Although activity of the depressor mandibulae begins late in the close phase overlapping with the adductors, it has a short lever arm compared to the adductors. Therefore, the depressor mandibulae produces no jaw depression until the adductors cease contracting antagonistically. The pterygoid retractor (RP) and pterygoid protractor (PP) are active once the open phase is well underway and thereby they impart rotation in a horizontal plane to the palatomaxillary arch such that the posterior end of the arch travels inward (Figure 8).

Both the neuro-costo-mandibularis (NM) and pterygoideus (PG) begin activity well into open phase and remain active well into the close phase. This makes both "bridging" muscles, those that are active primarily during the transition from one phase to the next. Both muscles reach peak activity at this transition (pterygoideus) or just into the close phase (neuro-costo-mandibularis). This pattern of activity is similar to their activities during swallowing wherein they are active during the end of ipsilateral opening and into closing (Cundall and Gans 1979; Cundall 1983; Kardong *et al.* 1986). The pterygoideus reaches peak activity at this tran-

sition between open and close, then continues throughout most of the close phase. It is silent during early opening. The pterygoideus is a large, complex muscle with multiple effects on jaw displacements (Cundall 1983). But its most important activity in our model is as a contributor to jaw closure, a role documented in other snakes (Kardong *et al.* 1986) and in lizards (Smith 1982).

From its origin on the sides of the neck, the neuro-costo-mandibularis sweeps around the angles of the jaws, ventrally into the throat and spreads forward to find its insertion on the anterior ends of the mandibles near the chin. Its peak activity occurs during jaw closure contributing, like the pterygoideus, to jaw elevation. However, in our model it also contributes directly to pumping water from the mouth into the esophagus. As the neuro-costo-mandibularis passes the angles of the jaws, it spreads as a muscular sheet along the floor of the buccal cavity in the throat. Therefore, when it contracts, it elevates and thereby flattens the bulged floor of the throat. This, together with geometric changes in the jaws (lateral flaring, jaw elevation, mouth closure), elevates the intraoropharyngeal pressure that in turn drives the water within the mouth past the esophageal sphincter and into the esophagus.

Acknowledgements

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