

## Drinking by the Common Boa, *Boa constrictor*

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The drinking cycle of the boa constrictor is composed of two stages. During the first, the expansion stage, the jaws and especially floor of the oropharyngeal cavity drop to expand the volume of the mouth and throat. The tips of the jaws part, and the tongue is withdrawn from the lingual canal through which water is aspirated into the oropharyngeal cavity. During the second, the compression stage, the jaws close, and the tongue moves into the lingual canal to plug it. The floor of the oropharyngeal cavity rises, and increasing pressure in the oropharyngeal cavity forces water to the back of the throat and into the esophagus. The expansion and compression stage of the oropharyngeal cavity floor occur in two distinguishable regions. Onset of each drinking stage begins in the anterior throat floor slightly before the posterior throat region, thus setting up front to back motion which functions as a buccal-pump mechanism, acting first to aspirate water into the mouth and then to force the water posteriorly past a sphincter into the esophagus.

**P**REY capture and swallowing have received widespread analysis in snakes (Dullemeijer, 1956; Albright and Nelson, 1959a, 1959b). However, the role of the jaw apparatus in drinking has so far received little attention. Drinking, together with feeding and defense, constitutes a major activity in which the jaw apparatus is involved. If explanations of cranial structure in snakes are to be proposed, then first we must analyze jaw structure and function during major activities performed by the skull (Dullemeijer, 1974; Homberger, 1988).

Our preliminary observations of water drinking by boas suggested a mechanism quite unlike that of other tetrapods. Although boas rhythmically protrude and withdraw their tongues as do dogs, boas do not curl their tongues to scoop water. Low, round, lateral papillae (McDowell, 1972) are present along the foretongue that possibly capture water by adhesion during tongue protrusion and carry it to the front of the mouth upon retraction. However, these papillae are small, few in number, and are carried into the tongue sheath, not the oropharyngeal cavity, upon tongue retraction. During prolonged drinking, boas do not regularly tip back their heads, as do some birds during drinking (Zweers, 1982). Unlike swallowing of food (Gans, 1952; Frazzetta, 1966), in which unilateral reciprocating motions (Gans, 1961) of jaws occur, both jaws move together and in synchrony during drinking by boas. Thus, deployment of the jaws, tongue, and oral cavity during drinking not only differs from other cranial activities, but the drinking mechanism appears distinct from that of many other tetrapods. To clarify the form-function basis of this unique mechanism, major bony elements and their relationships to

soft tissue anatomy of the oropharyngeal cavity were analyzed and subsequently matched with careful analysis of the buccal pressures and simultaneous motions of cranial elements during drinking by *Boa constrictor*. On the basis of these results, we propose an aspiration model of boa drinking that employs a buccal pump and a central role for the tongue.

### MATERIALS AND METHODS

Seven common boas (*Boa constrictor*), captive bred, were used ranging in size from 1.2–2.1 m, snout–vent length (SVL). Snakes were maintained at 23–28 C, fed mice or rats once every 10–20 days, but deprived of water and food for at least five days prior to experiments.

Intrabuccal pressure changes during drinking were recorded in four snakes, using Statham pressure transducers connected to the oropharyngeal cavity by fluid-filled catheters. Snakes were anesthetized with Halothane or immobilized by cooling. When tongue flicking or tail reflexes ceased, pressure catheters (PE 100) of equal length (40 cm) were inserted into two sites in the floor of the oropharyngeal cavity, one anterior near the glottis, and one posterior in the floor of the mouth between the angles of the jaws. This was done by passing a hollow syringe needle through the integument from the outside and into the oropharyngeal cavity at the desired position, taking care to avoid major blood vessels and nerves. The catheter was then inserted first into the beveled tip, down the barrel of the needle, and pushed through to the outside. The needle was then withdrawn leaving the catheter in place. An expanded collar at its tip prevented the catheter from being

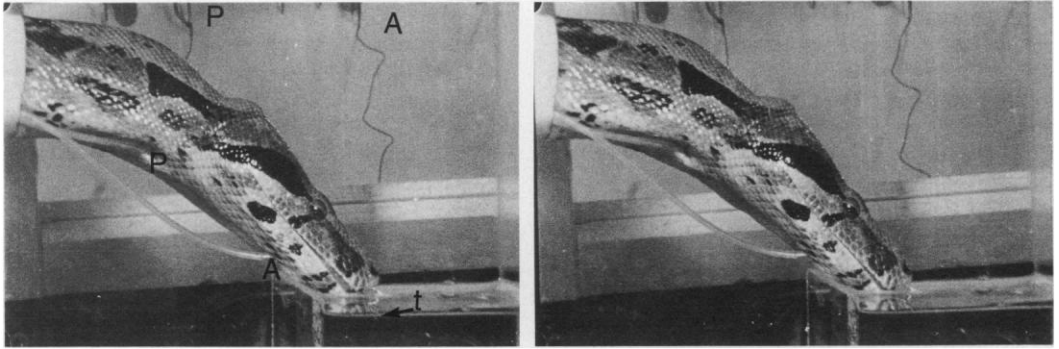


Fig. 1. Simultaneous motion pictures of drinking behavior and pressure recordings. Note placement of catheters as they enter the posterior (P) and anterior (A) oropharyngeal cavity. The respective pressure curves, traced on a chart recorder, appear in the mirror at the top of the picture. Picture at the left is during the expansion stage and at the right during compression stage. Tongue (t) is protracted at left, retracted at right.

pulled free by movements of the snake. Each catheter was connected to a pressure transducer held level with the tip of the catheter in the oropharyngeal cavity. Three-way valves allowed fluid filling and clearing of these catheters with distilled water. After the animal recovered from anesthesia, it was placed in a filming and recording cage. At one end, the cage was wide enough to accommodate the body of the snake, and at the other end, the cage was narrow and made of clear plastic (Plexiglas®) containing a built-in pool for water. Simultaneous filming of the snake and chart recorder permitted matching of motion with pressure events (Fig. 1). Filming took place before a photoflood lamp at 50 fps using a 16 mm Hycam camera (see Kardong, 1974). Colored food dye, injected into the water, allowed us to film then follow the frame-by-frame course of water flow into the mouth without disrupting the rhythmic drinking cycles. Some long-term drinking bouts of several minutes' duration were also filmed by video (Panasonic) and played back field by field with a Panasonic recorder.

The displacements of the bones during drinking were directly inspected by cineradiography, generally following procedures described elsewhere (Kardong, 1986; Kardong et al., 1986). Both dorsoventral and lateral views were recorded separately at 85 kV using a Siemens fluoroscopic system with a 16 mm camera at 32 pps. Pressures in the cavity, recorded separately as described above, were matched to kinematic events evident in the cineradiography by finding similar displacement patterns in the opening and closing of the jaws. Cineradiographic films of drinking behavior were analyzed both on a frame-by-frame basis and at normal speeds. Because bones were dense in these large snakes,

motion could be followed easily without recourse to special osteological markers (e.g., Anker et al., 1967). However, bone sutures and fenestrae were not always evident in the cineradiographs; hence such details were determined directly from prepared skulls arranged in postures identical to those in the radiographs. Figure 5 was sketched directly from a skull so arranged. Functionally significant soft tissues, larynx, and tongue were followed radiographically by attaching or inserting into them tiny metal markers. Specifically a slender wound clip was attached to the side of the larynx, and the tip of a syringe needle was inserted into the tongue. All seven boas refused water laced with barium sulfate or other radiopaque fluids. However, when such fluids were injected directly into the mouth of a restrained boa via tubing (PE 350), occasional swallowing motions followed. More important for our results, the barium sulfate solution coated the esophagus giving it a temporary radiographic outline that could be observed directly when water alone was drunk next by the boa. These observations, records of bone kinematics, and a knowledge of anatomical relationships allowed an estimation of size and shape changes of the oropharyngeal cavity during water intake and swallowing.

Cycles, from about the midpoint of an immersion phase, were sampled from 14 different drinking bouts (four snakes). For each, the peak-to-peak time interval for mandibular displacement was divided into 100 units, and the proportion of this interval occupied by various drinking events was scored and totaled. This produced a frequency distribution of drinking events (Fig. 6). Because the snake often became obliquely oriented to the film or video camera, tongue protrusion might be visible when the

throat movement could not be scored. Nevertheless, the frequency distribution from the 14 drinking bouts gives a summary of the most common point in the drinking cycle that the event occurs. Terminology follows Haas (1973) for muscles; Kardong (1974) for ligaments; and Kardong (1972), McDowell (1972), and Groombridge (1979) for tongue and nose.

## RESULTS

*Anatomy.*—*Osteology:* The bones of the boid skull can be organized into three primary units that articulate with the braincase (Frazzetta, 1959, 1966; Gibson, 1966): snout, palatamaxillary, and mandibular units. The single snout unit includes paired nasals, septomaxillae, and vomers and a median premaxilla. A ventral, anteriorly directed process of each frontal fitted into a low depression in a respective posteriorly directed process on the ventral edge of each nasal. This nasofrontal articulation served as the point about which the snout unit rotated relative to the braincase.

Attachments of the palatamaxillary unit: The palatamaxillary unit included pterygoid, ectopterygoid, maxilla, and palatine which connected to other cranial elements at several sites (Fig. 2A). One site of attachment was via the prefrontal (pp in Fig. 2A), which served as the principal point from which the palatamaxillary unit was suspended (Frazzetta, 1966). In lateral view, the prefrontal appeared triangular in shape. One corner, the apex, was directed rostrally; a second corner, posterodorsally directed, established a hingelike articulation with the frontal; the third corner, ventrally directed, established an articulation with the palatamaxillary unit through three processes. Two of these processes, termed the lateral and medial foot processes, projected ventrally to meet the maxilla where they were received by respective recesses in the maxilla. The third process of the ventral prefrontal, the medial extension, was not a winglike extension as in pythons (Frazzetta, 1966), but was instead a stubby shelf that articulated with the palatine (Fig. 2A).

A second site of attachment with the braincase formed between the midpalatamaxillary unit and the anteroventrally projecting basiptyergoid process (bp in Fig. 2A). This attachment was established via a sheet of connective tissue that passed specifically from the basiptyergoid to the dorsomedial edge of the pterygoid. This connective tissue sheet permitted extensive excursions of the pterygoid relative to the basiptyergoid.

The third site of attachment of the palato-

maxillary unit was between the posterolateral end of the pterygoid and the medial condyle at the distal end of the quadrate (qp in Fig. 2A). These bones, pterygoid and quadrate, were joined firmly at this third site of attachment by the quadratopterygoid ligament and by the pterygoideus and pterygoideus accessorius muscles that passed across the site of articulation.

Other means of attachment of the palatamaxillary unit to the rest of the skull were also noted. Forward travel of the palatamaxillary unit brought the palatine into contact with the vomer, to which it had a ligamentous connection, but no joint was present. The long quadratamaxillary ligament joined the posterior end of the maxilla to the quadratomandibular joint. The postorbital ligament linked the anterolateral margin of the ectopterygoid to the ventral end of the postorbital bone.

The mandibular unit included mandible, quadrate, and supratemporal. Relative motion was possible at both quadratomandibular and quadratosupratemporal joints. However, the firm supratemporal-braincase joint permitted very little displacement of the supratemporal relative to the braincase. The rostral tips of the mandibles did not enter into a distinct articulation, but these tips were joined by muscles to a medial mass of fibrous connective tissue embedded in the integument. The palatamaxillary and mandibular units were paired, but, in the absence of firm, direct articulations between the left and right sides, the units were capable of considerable independent motion.

The arcades of teeth borne by the palatine, dentary, and maxillary bones were sheathed in mucosal folds. The anterior tips of the paired maxillae and dentaries turned toward the midline, but neither tooth row met their partners of the opposite side. Thus, there was, at the anterior midline of the mouth, a tunnel, the lingual canal, through which the tongue could pass if the jaws were slightly parted.

*Lingual canal:* Closing and opening of the lateral seal to the mouth was accomplished by pressing together, or parting, complementary soft tissues of the roof and floor of the mouth. The mucosal folds, which followed along curved upper and lower tooth rows, extended far back into the oropharyngeal cavity to laterally seal the mouth when the jaws closed. Anteriorly, the raised mucosal folds followed the tooth rows to the front of the mouth but like the teeth did not reach the midline. The mucosal folds of the lower jaw made contact with sublingual plicae. However, medially between these plicae, a gap persisted that was the lower counterpart to a medial gap in mucosal folds along the roof of

the mouth above. When the jaws were nearly closed, the folds along the lower jaw were raised and fitted into a recess between lateral maxillary and medial palatopterygoid dental arcades. This closed all but the gap at the very anterior tip of the jaws. This remaining gap for the tongue was the lingual canal. Ventrally, the sublingual plicae, and dorsally, the tips of the maxillae marked the borders of this canal. Formally defined, the lingual canal was a narrow tunnel at the front of the mouth through which the tongue slipped during protraction/retraction movements. When the jaws were tightly closed, the lips around the anterior edges of the mouth were brought together to close even the opening to the lingual canal.

**Nose and oropharyngeal cavity:** The anterior border to the mouth was delimited by pliable lips comprised of upper and lower labial scales. No distinct anatomical feature marked the boundary between the mouth and the pharynx. Consequently, both contributed to an oropharyngeal cavity that extended posteriorly into the throat to just behind the angles of the jaws. Therefore, the anterior floor of the oropharyngeal cavity consisted of the soft tissue between mandibular rami; the posterior floor included the soft tissues of the throat.

Air inspired via the external nares passed first through the nasal vestibule before reaching the nasal chamber. A horizontal shelflike concha arising from the lateral wall divided the nasal chamber into dorsal and ventral regions. The concha, supported internally by a cartilaginous plate and bony extension of the septomaxilla, terminated in a narrow, posteriorly directed process. The nasal chamber opened posteriorly into the nasopharyngeal duct which led to the internal nares. The internal nares were defined laterally by the choanal arc, part of the roof of the oropharyngeal cavity (Fig. 2B).

The trachea rested in the floor of the oropharyngeal cavity above the tongue. Beginning the trachea was a specialized larynx. Entrance to the trachea was gained through a slitlike glottis, carried on the dorsal surface of the larynx, and controlled by intrinsic muscles (Kardong, 1972). Two pairs of long extrinsic laryngeal muscles arose outside the larynx, but inserted on or next to it. In *Boa constrictor*, the epiglottal process (Kardong, 1972) was expanded and bifurcated. Lateral and posterior to each bifurcation was a fleshy accessory epiglottal process.

*Drinking behavior—behavioral components.*—Even when presented with a deep water bowl, the boas usually submerged only the anterior end of the snout beneath the surface of the water.

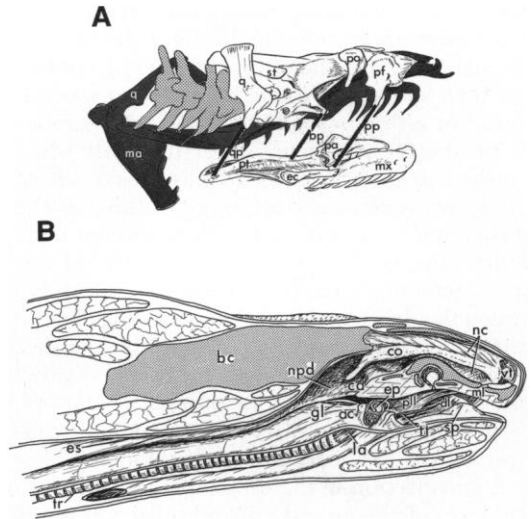


Fig. 2. Skull oronasal chambers of *Boa constrictor*. (A) Posterior three-quarter view of *Boa constrictor* skull. The right palatomaxillary unit—ectopterygoid (ec), pterygoid (pt), palatine (pa), maxilla (mx)—is dropped down from its various attachments with other elements of the skull. Straight, black lines show connections between elements, namely between the posterior-lateral pterygoid and the medial condyle of the quadrate (qp), between the basipterygoid process and the mediadorsal edge of the pterygoid (bp), and between prefrontal and anterior elements of the palatomaxillary unit (pp). The solid line (pp) from the maxilla connects to the medial foot process of the prefrontal; on either side of this process are the lateral foot process and medial extension. The right mandible is not shown. (B) Parasagittal view of nose and oropharyngeal cavity. The jaws are slightly parted to reveal the mucosal folds covering the palatine, dental, and maxillary tooth rows, pll, dl, ml, respectively. On its way to the lungs, air travels from the nasal vestibule (vt), through the nasal chamber (nc) and nasopharyngeal duct (npd) to enter the trachea via the glottis. When drinking, the larynx inserts into the nasopharyngeal duct plugging it and the nasal chamber. Other abbreviations: accessory epiglottal process (ac), braincase (bc), choanal arc (ca), concha (co), epiglottal process (ep), esophagus (es), tongue tips (tt), glottis (gl) opening into the larynx, mandible (ma), postorbital (po), prefrontal (pf), quadrate (q), sublingual plica (sp), trachea (tr).

This left the lateral edges of the mouth and paired nostrils out of the water. The floor of the throat rose and fell in rhythmic cycles accompanied by protrusion and withdrawal of the tongue. Once begun and if left undisturbed, the slow alternating pumping cycles of the throat region with synchronized tongue protrusion usually continued for several minutes. The drinking movements were bilaterally symmetrical and simultaneous. A drinking bout consisted of four phases of unequal duration—ap-

proach, immersion, emersion, withdraw phases. Movement about the cage brought the head of the snake close to the water (approach); contact between snout and water (immersion) was followed in a thirsty snake by a variable number of drinking cycles; when interrupted or when finished drinking, the head was raised out of the water (emersion), although pulsing of the throat and tongue movements continued for a short time, 5–10 more cycles; retreat of the snake from the vicinity of the water (withdraw) ended the drinking bout. Characteristically, the immersion phase consisted of a variable number of cycles each of which, in turn, was divided into expansion and compression stages marked, respectively, by the fall (expansion) or rise (compression) of the anterior tips of the mandibles.

A constriction in the esophagus, posterior to the level of the quadratomandibular joint, was evident radiographically. A catheter tip introduced through the mouth was forced past this esophageal constriction and barium sulfate injected posterior to it. This fluid accumulated in and swelled the esophagus posterior to the constriction, but this esophageal constriction effectively prevented any significant amount of fluid from reentering the mouth from the esophagus. We observed no peristalsis (e.g., Dullemeijer, 1959) nor bends in the axial column (e.g., Kardong, 1986) as is characteristic of snakes swallowing prey. Visual inspection of this esophageal region in a preserved boa under a dissecting scope failed to detect any significant associated extrinsic striated muscle. Thus, this constriction was likely produced by intrinsic musculature within the wall of the esophagus.

**Expansion stage:** During the expansion stage, the mandibles were depressed carrying downward the anterior floor of the oropharyngeal cavity between them. Shortly after mandibular tips began to fall, the posterior floor of the oropharyngeal cavity began to descend. This descent of the posterior oropharyngeal cavity continued to extend caudally to involve next a similar fall of the floor of the throat just posterior to the quadratomandibular articulation. The tongue, already occupying the lingual channel at the start of the expansion stage, was withdrawn as this stage continued. Although the quadratomandibular joint moved medially, it experienced only very slight vertical displacement. Depression of the mandible parted the lips at the anterior end of the snout, and water entered the oropharyngeal cavity via the tip of the snout but not along the lateral edges of the lips.

**Compression stage:** The compression stage began with elevation of the mandibles. Simultaneous with the onset of jaw closure, the quadratomandibular joint began to swing laterally. This joint continued to move outward about its proximal articulation with the supratemporal throughout the remainder of the stage. The anterior floor of the oropharyngeal cavity lifted, both because it was carried upward by the closing mandibles, and because of internal changes (flattening) in its shape. Throat elevation began as soon as, or immediately after, the mandibles started to close. The tongue once again occupied the lingual canal.

The anterior (between dentaries) and posterior (between and just posterior to the quadratomandibular joints) floor of the oropharyngeal cavity (Fig. 3) rose and fell slightly out of phase with one another. The anterior oropharyngeal cavity initiated both the expansion and compression stages to be followed immediately by the posterior portion of the oropharyngeal cavity and throat. Thus, the anterior floor of the oropharyngeal cavity reached its lowest and highest points of excursion slightly before the posterior floor. This produced an alternating wavelike motion traveling rostral-to-caudal within the floor of the oropharyngeal cavity. Metal clips attached to the side of the larynx confirmed in radiographs that during both phases of drinking, the larynx was inserted into the internal nares and held there continuously throughout drinking.

On four separate occasions one boa, 2.1 m SVL, was allowed to drink continuously from a container of water of known volume, its swallowing cycles were counted, and the volume of water remaining when finished drinking was immediately measured. Volume per cycle ranged from 0.09 to 0.265 ml/cycle ( $\bar{x}$  = 0.181 ml/cycle).

*Drinking behavior—kinematic components.*—During drinking bouts, the braincase was held in a fixed position over the water. Both the mandibular and the palatamaxillary units moved rhythmically, but the snout unit exhibited no rotations about its articulation with the braincase. The quadrate rotated, in a transverse plane, about its articulation with the supratemporal. This was an oscillating motion in which the quadratomandibular joint swung in and out (medial–lateral) describing a shallow arc (Fig. 4). This inward-outward motion alternately carried the posterior ends of the mandibles toward, then away from one another. However, the anterior mandibular tips remained more or less

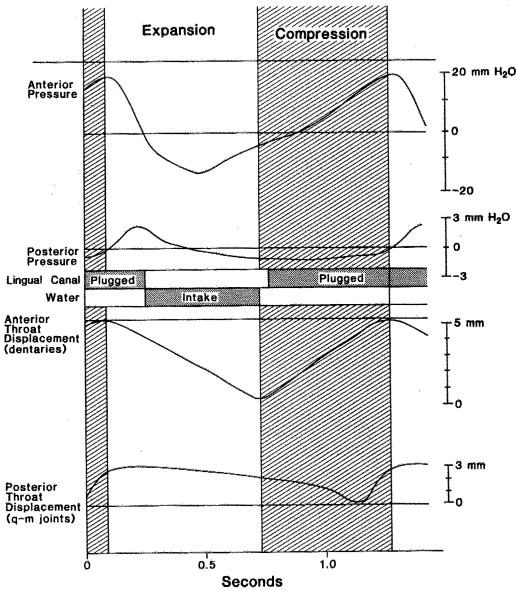


Fig. 3. Representative pressures and displacements. Plot of simultaneous changes in oropharyngeal cavity pressures and motion events from cine films. Two moving points were followed through both phases of a drinking cycle—a point on the anterior tip of the dentaries (Anterior Throat Displacement) and a point riding on the midventral floor of oropharyngeal cavity in line with quadrato-mandibular joints (Posterior Throat Displacement). Where jaw closure and the tongue seal the mouth during this cycle, the shaded area central indicates the extent of the cycle where the lingual canal is plugged. With these events, the simultaneous pressures experienced in the anterior (in front of the larynx) and posterior (between the quadrato-mandibular joints) pressures inside the oropharyngeal cavity are plotted. This is one of 88 cycles during a continuous drinking bout. The division of the cycle into expansion and compression stages is indicated by open and cross-hatch, respectively. Quadratomandibular joints (q-m joints).

fixed in position relative to each other. Thus, as viewed dorsally, the mandibles appeared to rotate about their anterior tips, so that their posterior ends alternately flared then drew inward during repeating cycles.

Besides this pronounced bellowslike mandibular displacement in a transverse plane, the mandible rotated first into a depressed and then into an elevated position during the drinking cycle. During the expansion stage, the anterior tips of the mandibles thus rotated downward, whereas their posterior ends were carried in a shallow arc ventromedially (Fig. 4). These motions were reversed during compression. Mandibular depression and elevation was accompanied by slight rotation of each mandible about

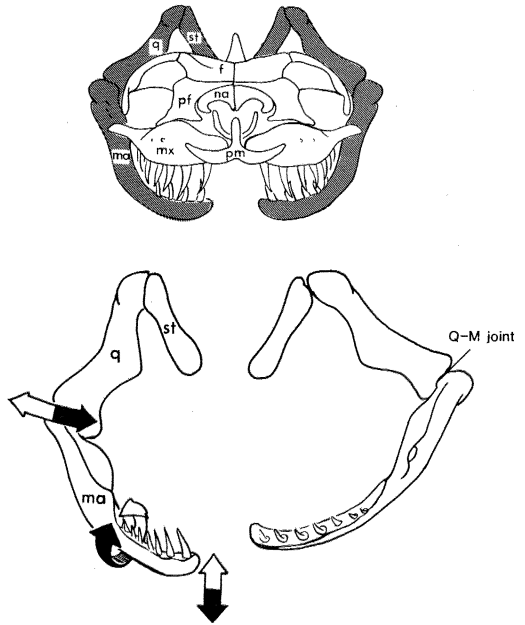


Fig. 4. Displacements of the mandibular unit during drinking. Above: Front view of skull of *Boa constrictor*. The shaded bones constitute the paired mandibular units composed of supratemporal (st), quadrato (q), and mandible (ma). Below: Isolated mandibular units. The left mandibular unit is accompanied by arrows showing the planes of rotation for the quadratomandibular (Q-M) joint, anterior tip of the mandible, and about the long axis of the mandible. The dark half of each arrow indicates direction of displacement or rotation during the expansion stage; the light half of each arrow indicates motions during compression state. Although displacements are exaggerated here for emphasis, the mandibular unit at the right is elevated (compression), and the mandibular unit at the left is depressed (expansion). Other abbreviations: frontal (f), maxilla (mx), nasal (na), prefrontal (pf), premaxilla (pm).

its long axis through about 10 degrees. Specifically, long axis rotation swung mandibular tooth tips laterally upon compression (elevation) and inward during the expansion (depression) stages (Fig. 4). Cineradiography confirmed that the supratemporal remained motionless relative to the braincase.

During drinking cycles, the palatomaxillary unit pivoted horizontally about its suspension from the prefrontal. The distal end of the quadrato accompanied the posterior pterygoid in these oscillations. Consequently, during expansion, posterior elements of the palatomaxillary unit (pterygoid, ectopterygoid) swung inward and anterior elements (palatine, maxilla) swung outward (Fig. 5), whereas the reverse occurred during the compression stage.

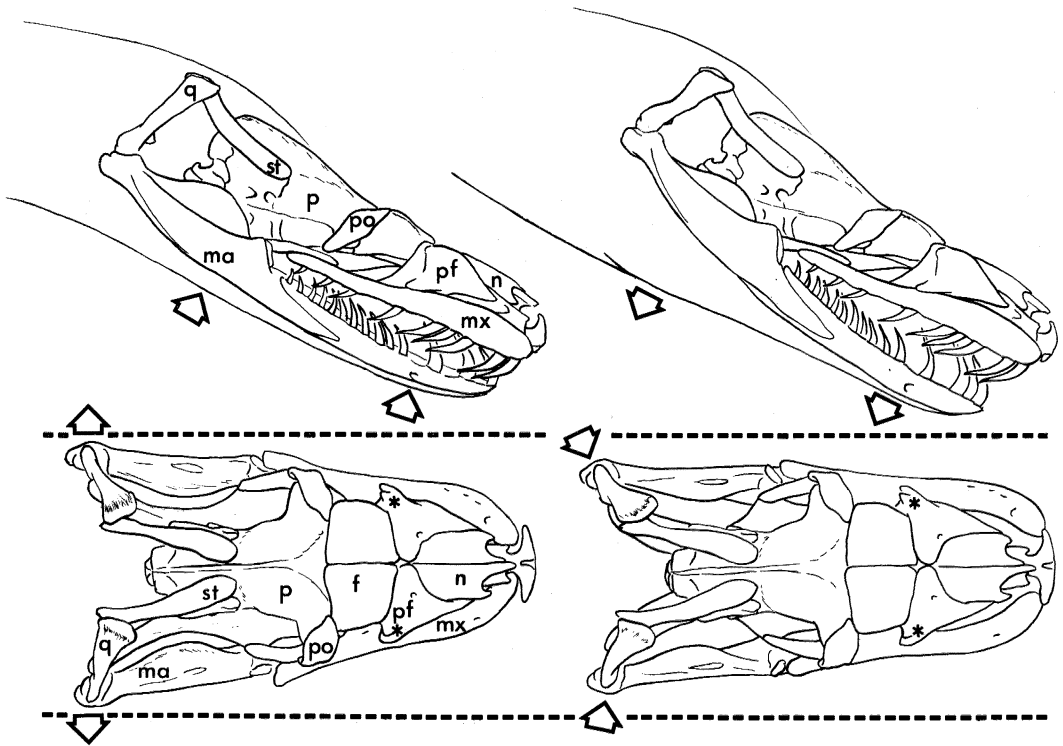


Fig. 5. Kinematics of boa drinking. The positions and motions of cranial elements during drinking are shown in lateral (top) and dorsal (bottom) views. In each view, the skulls at the left are completing the compression stage and next will be entering the expansion stage, right. The movement completed is indicated by small, open arrows. The asterisks mark the vertical axis of rotation of the palatamaxillary arch about its major articulation with the prefrontal. Cranial events pictured are based upon cineradiographic sequences of drinking. Abbreviations: frontal (f), nasal (n), mandible (ma), maxilla (mx), prefrontal (pf), pterygoid (pt), postorbital (po), quadrate (q), supratemporal (st).

*Pressure changes.*—Negative and positive pressures, relative to atmospheric, were recorded in the oropharyngeal cavity during drinking (Figs. 3, 6). The actual pressures reached seemed to depend upon the effort exerted by the snake. During one brief bout (seven cycles), amplitudes as great as 120 mm H<sub>2</sub>O were recorded from the anteriorly placed catheter. During a longer bout (88 cycles without interruption), an initial amplitude of 28 mm H<sub>2</sub>O in the anterior mouth was established and rose to 45 mm H<sub>2</sub>O shortly before (20 cycles) termination of the drinking bout. However, the basic pattern of pressure fluctuation was similar regardless of amplitudes attained. One of these pressure cycles, matched to throat displacements, is shown in Figure 3. Beginning in midexpansion stage, the pressure in the anterior oropharyngeal cavity, though still negative, began to rise. It continued to rise throughout the compression stage. As the cycle again entered the expansion stage, the anterior buccal pressure precipitously declined reaching a minimum value at about midstage. The tongue

protruded from the mouth and remained out from the moment just before the anterior pressure peaked, through its peak, and subsequent decline. The tongue was withdrawn into the mouth at about the moment the anterior buccal pressure began to rise.

Pressure in the posterior oropharyngeal cavity cycled in a regular pattern; but the pattern was slightly delayed, and pressures reached were smaller compared to anterior oropharyngeal cavity pressures. For instance, in a representative cycle (Fig. 3), the posterior pressure fluctuated between about  $\pm 3$  mm H<sub>2</sub>O whereas anterior buccal pressures varied between about  $\pm 20$  mm H<sub>2</sub>O. Rates of rise and fall in posterior buccal pressures were slower than for anterior pressures. For instance, posterior pressure rose at an average rate of 4.8 mm H<sub>2</sub>O/second and fell at 18 mm H<sub>2</sub>O/second (Fig. 3). The comparative values for the anterior oropharyngeal cavity were higher (51.3 and 133.3 mm H<sub>2</sub>O/second rise and fall rates, respectively).

In Figure 6, a frequency distribution is pre-

sented of 14 drinking bouts that summarize behavioral events. Notice that during some drinking cycles, the tongue was protracted from the mouth by about midcompression and in others it was out into early compression, but tongue-out occurred mostly during expansion stage. Generally, posterior events lagged behind anterior events. For example, the lowest pressure recorded from the anterior oropharyngeal cavity (Anterior Pressure Valley) usually occurred during expansion stage, whereas the lowest pressure in the posterior cavity (Posterior Pressure Valley) usually occurred next during the compression stage. Vertical displacement of the throat tended to reach its highest level (Throat High) at the end of the compression stage and its lowest level (Throat Low) after the expansion stage, in each case slightly lagging behind vertical displacements of the anterior tip of the mandibles (Displacement Mandibles).

#### DISCUSSION

Variations in the relationships between anterior and posterior pressures, and in their amplitudes were observed. For example, on one occasion, pressure in the anterior oropharyngeal cavity began to drop after the posterior pressure, and the tongue was protruded and withdrawn on a slightly different schedule than shown in Figure 3; the range of pressure fluctuations on two occasions shifted so that the posterior, rather than anterior, oropharyngeal cavity experienced greater oscillations. In all these exceptional cases, the chin or throat rested on the edge of the water dish or the head against the side of the cage. Variation in tongue protrusion pattern could be expected if the opening to the lingual canal was pressed against the side of the water dish. If, however, drinking patterns were recorded when only the tip of the snout was placed beneath the water and the head remained unobstructed (Fig. 1), then a regular and repeating schedule of drinking events emerged. A drinking model, based on these conditions, is proposed.

*Drinking model.*—Water entry: The soft tissues of the oral mucosa and the tongue form a seal around the edges of the mouth when the jaws close. For water to enter, this seal is broken by parting the jaws and retracting of the tongue from the lingual canal. During depression, each long mandible, hinged far posteriorly at the quadrate, describes the greatest arc of displacement at its anterior tip and progressively less displacement backward toward its articulation with the quadrate. Consequently, soft tissues

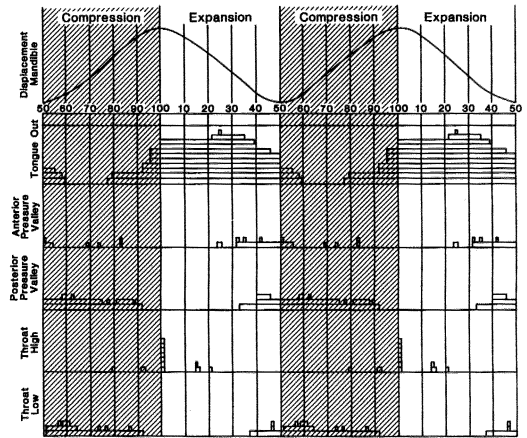


Fig. 6. Frequency distribution of drinking events. Five characteristics of the drinking cycle were scored during 14 drinking bouts: tongue protrusion, low points in buccal pressure (Anterior Pressure Valley, Posterior Pressure Valley), and vertical displacement of the throat at its peak (Throat High) or lowest point of expansion (Throat Low). Peak-to-peak (Displacement Mandible) time interval for each cycle was divided into 100 equal units (100 percent) and its percentage duration scored. These were then added to produce this frequency diagram of each variable. The stippled areas thus represent the summary of each variable's most frequent occurrence within a cycle.

along the anterior margins of the mouth are disengaged first, and depression proceeds only to the point where the seal here, anteriorly, is broken. Water enters the anterior tip of the mouth following the differential pressure gradient between external water pressure (high) and buccal pressure (low) as a result of depression of the anterior floor of the oropharynx.

*Intrabuccal transport:* Water entering the anterior oropharynx continues into the posterior part of the oropharynx following the pressure gradient resulting from the depression of the posterior part of the throat. This brings the pulse of water into the vicinity of the entrance to the esophagus.

*Swallowing of water:* Once in the oropharyngeal cavity, water has three possible portals of exit—the esophagus, the mouth, and through the paired internal nares. The larynx is fitted into the internal nares to stopper them and so prevent escape of water out that pair of openings. When the mandibles are elevated, the soft oral epithelium and mucosal folds of upper and lower tooth rows meet to close the sides of the mouth and the protracted tongue plugs the lingual canal. Although only visibly protruding



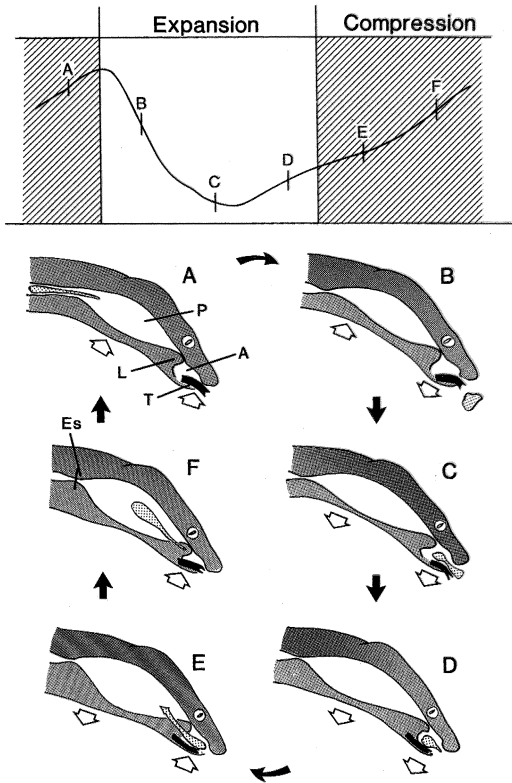


Fig. 7. Drinking model for the boa. A general trace of anterior buccal pressure is indicated (top) with approximate positions of six stages in the model. (A) Late compression stage, tongue protruded, pressure near peak. (B) Early expansion stage, tongue protruded, buccal pressure starting to fall. (C) Midexpansion stage, tongue beginning retraction, water starts to enter (aspiration), pressure fall ceases and begins to climb. (D) End of expansion stage, tongue fully retracted, water pulse completes entry into anterior oropharyngeal cavity. (E) Early compression stage, tongue retracted, water pulse in mouth follows pressure gradient around glottis. (F) Late compression stage, mouth closing and sealing, tongue starts protraction and occludes lingual canal. A, again. Finally, compression stage nearly complete, tongue fully protracted, pressure rises, pulses of water forced past esophageal sphincter. Anterior (A) and posterior (P) regions of the oropharyngeal cavity. Esophageal sphincter (Es), larynx (L), tongue (T).

from the mouth for part of each drinking cycle, the tongue affects water flow over a longer time interval of each cycle. With the onset of mandibular depression, the seal is broken and water enters even before the tongue has been retracted fully out of view. The lingual canal is functionally blocked (by tongue and mandibular closure), often before the tongue tips emerge from the mouth. Thus, of the three portals, two are blocked at appropriate points in the drinking

cycle—the internal nares by the larynx, the edges of the mouth by mandibular elevation and by the tongue. This leaves only the unobstructed esophagus open, and as pressure in the oropharyngeal cavity builds, it forces water into the esophagus.

A constriction, an “esophageal sphincter,” is an important part of the drinking mechanism. It remains constricted during a drinking bout. It is only forced open briefly when oropharyngeal pressure is near its peak of each cycle. At this peak, water under pressure squirts through, but continued constriction prevents retrograde gravity flow to the mouth even when the head is tilted down and the esophagus is above the level of the oropharyngeal cavity.

Water does not gradually collect in the oropharynx during a drinking bout. Instead, each expansion/compression cycle results in transport of a pulse of water through the oropharynx, past the esophageal sphincter, and into the anterior esophagus. Here the pool of water gradually grows with the addition of a new pulse of water during each cycle. This pool of water eventually moves from the esophagus to the stomach during emersion and withdraw phases as the head is lifted, perhaps aided by the few cycles that continue after the head is raised out of the water.

**Buccal-pump model:** Based upon these structural elements (larynx, oropharyngeal cavity, tongue, esophageal sphincter, and cranial bones) and their functions (kinetic actions, expansion/compression), the following six-stage model of a drinking cycle in boa constrictors is proposed (Fig. 7). Slightly before anterior oropharyngeal pressure peaks, the tongue is out and compression ends (Fig. 7A). Next, the mandibles begin depression and the oropharyngeal cavity starts to expand initiating a drop in pressure (Fig. 7B). Outside water enters next (Fig. 7C) when the jaws have parted (top open the anterior mouth) and the tongue starts to retract (to open the lingual canal). These events continue late into expansion stage (Fig. 7D), and water continues to enter, following the pressure gradient from the relatively high external to the low buccal pressure. Thus, during these stages (Fig. 7C–D), a pulse of water is aspirated into the oropharyngeal cavity, reversing the pressure drop, and so contributing to the initial rise of pressure (D, top of Fig. 7). The onset of compression (Fig. 7E) begins first in the anterior oropharyngeal cavity with mandibular elevation followed by the onset of tongue protrusion (Fig. 7F). Water in the mouth follows the pressure gradient from front to back of the oropharyngeal cavity, pass-

ing around the partially obstructing larynx. Finally (Fig. 7A), elevation of the slightly lagging posterior oropharyngeal cavity increases pressure here sufficiently to force the mass of water past the esophageal sphincter.

This model emphasizes two features of drinking by the boa. First, the basic feature used to generate low pressure to draw water in and then high pressure to swallow it is the floor of the oropharyngeal cavity. Swallowing is thus accomplished by a buccal-pump mechanism. A lapping or gulping motion is not a major mechanism of intraoral water movement. Instead, the buccal pump creates a temporary negative pressure that draws water into the mouth by aspiration. Second, critical to the operation of this buccal pump is the proper closure of the mouth. This is accomplished by closure of the sides of the mouth, occlusion of the internal nares by the larynx, and the plugging of the lingual canal by the tongue. The sides of the mouth are momentarily sealed when the pliable, thick mucosal folds surrounding the upper and lower tooth rows are brought together. The tongue, by blocking the lingual canal, prevents water from squirting back out of the oropharyngeal cavity during compression. However, it further prevents the entrance of water from the outside until a negative pressure is established during expansion. This means that, when the tongue retraction finally opens the lingual canal, water is actually aspirated into the mouth. The tongue, therefore, does not itself directly transport significant amounts of water into the oropharyngeal cavity.

With the larynx raised to plug the internal nares, it also partially divides anterior from posterior regions of the oropharyngeal cavity, leaving constricted but open channels at its base narrowly connecting front with back of the oropharyngeal cavity. In water-breathing fish, the gill curtain has been proposed to act as an adjustable resistance between buccal and opercular chambers allowing differential pressures to build between the two chambers in response to configurational changes in the mouth walls (Hughes and Ballintijn, 1965; Ballintijn, 1969; Liem, 1985). We suggest that an analogous system operates in the boas to move water during drinking. The slightly out of phase changes in the buccal floor, front to back, together with the resistance presented by the larynx allow temporary dynamic pressure differentials to develop between anterior and posterior oropharyngeal compartments of the mouth. Higher pressure anteriorly ensures, together with closure of the lingual canal by the tongue, that water here will flow next into the posterior com-

partment. Near the end of the compression phase this water is forced next past the esophageal sphincter and into the esophagus.

Careful descriptions of tetrapod drinking exist for several species of birds, but the mechanisms of water intake and transport are quite varied. In some birds, the tongue and larynx scoop water; in others tongue-scoop and head tip more 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, 1982; Heidweiller et al., 1992), but this mechanism is affected by aspects of scaling (Heidweiller and Zweers, 1992).

Outside of anecdotal comments about lapping and gulping, information on drinking mechanics in snakes is surprisingly scant. We know of no detailed, published study done on ophidians that addresses the mechanical basis of their drinking. So far, only three modes of drinking have been recognized in lizards. In two of these (iguanian and scleroglossan), water delivery to the mouth is primarily by the tongue (Smith, 1984; Bels et al., 1992). In the third (*Varanus*), the tongue is not used, but instead the whole snout is inserted directly into the water where the complex use of the hyoid is apparently involved (Auffenberg, 1981; Smith, 1986).

Why the tongue directly participates in such a drinking mechanism in boas is not clear. More derived species of snakes, such as members of the Colubroidea, do not exhibit cyclic tongue protrusions from the mouth during drinking (pers. obs.). Tongue protrusions in boas may be part of a drinking mechanism that confines water intake to a restricted region of the mouth, around the lingual canal, and thus permits efficient intake of small droplets of water as might be available in the form of dew. Possibly, use of the tongue represents retention of a plesiomorphic characteristic, lost in derived snakes. Without further comparative studies, this issue cannot be addressed. The buccal-pump mechanisms of drinking in the boa constrictor described herein seems then to be the first such analysis of snake drinking and reports a mechanism that is distinct from other squamates.

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