RESEARCH ARTICLE

Drinking in Snakes: Resolving a Biomechanical Puzzle

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ABSTRACT

Snakes have long been thought to drink with a two-phase buccal-pump mechanism, but observations that some snakes can drink without sealing the margins of their mouths suggest that buccal pumping may not be the only drinking mechanism used by snakes. Here, we report that some snakes appear to drink using sponge-like qualities of specific regions of the oropharyngeal and esophageal mucosa and sponge-compressing functions of certain muscles and bones of the head. The resulting mechanism allows them to transport water upward against the effects of gravity using movements much slower than those of many other vertebrates. To arrive at this model, drinking was examined in three snake species using synchronized ciné and electromyographic recordings of muscle activity and in a fourth species using synchronized video and pressure recordings. Functional data were correlated with a variety of anatomical features to test specific predictions of the buccal-pump model. The anatomical data suggest explanations for the lack of conformity between a buccal-pump model of drinking and the performance of the drinking apparatus in many species. Electromyographic data show that many muscles with major functions in feeding play minor roles in drinking and, conversely, some muscles with minor roles in feeding play major roles in drinking. Mouth sealing by either the tongue or mental scale, previously considered critical to drinking in snakes, is incidental to drinking performance in some species. The sponge mechanism of drinking may represent a macrostomatan exaptation of mucosal folds, the evolution of which was driven primarily by the demands of feeding. *J. Exp. Zool. 317:152–172, 2012.* © 2012 Wiley Periodicals, Inc.

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Terrestrial animals acquire water in a variety of ways. Recently, studies of contact angle hysteresis during surface-tension transport of water in narrow-billed shore birds (Prakash et al., 2008) and the relative roles of inertia, gravity, viscosity, and capillarity during lapping in cats (Reis et al., 2010) and dogs (Crompton and Musinsky, 2011) have demonstrated the potential functional and structural complexity of drinking mechanisms. The analysis of cat drinking received popular attention (e.g., Gast, 2010; Brumfiel, 2010) because cats are pets and how they drink is puzzling. Reis et al. (2010) and Crompton and Musinsky (2011) demonstrated convincingly that cats and dogs do not use suction-based drinking mechanisms or the type of inertia-based mechanisms presumably involved in lapping in some other mammals. Other animals may drink using mechanisms that are equally unusual, and here we report on one of them.

How snakes drink has been described for one species of boid (*Boa constrictor*; Kardong and Haverly, '93) based on ciné, video, cineradiographic, and pressure recordings, and for one

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rear-fanged colubroid species (*Boiga irregularis*; Berkhoudt et al., '95) using similar movement and pressure recordings, plus electromyography (EMG) of selected cephalic muscles. These studies concluded that a two-phase buccal-pump model involving suction was the basis of snake drinking. A brief cineradiographic study by Bels and Kardong ('95) of a nonvenomous colubrid species (*Pantherophis alleghaniensis* [*Elaphe obsoleta quadrivittata* in their original description]) drinking barium-laced water demonstrated the presence of a functional sphincter separating the oropharynx from the esophagus, adding critical evidence in support of the two-phase buccal-pump model.

The buccal-pump model proposes that snakes alternate negative and positive pressures in the oropharyngeal cavity to produce a pulsed inflow of water. Opening the margins of the mouth and depressing the lower jaw creates negative pressure, which draws water into the oral cavity. As the mouth subsequently closes, intraoral pressure rises. Elevation of the lower jaw and buccal floor ultimately seals the margins of the mouth and increases the positive pressure, thereby forcing water posteriorly into the pharynx. Continued buccal pumping creates a pulsed flow of water through the oropharyngeal cavity that eventually crosses the sphincter into the esophagus. As long as pressure in the esophagus caudal to the sphincter does not exceed that generated during compression of the oropharyngeal cavity, the two-phase buccal pumping model explains how snakes manage to drink continuously without having to raise their heads to drain water accumulating in the pharynx or the esophagus (Bels and Kardong, '95; Berkhoudt et al., '95).

Elements of this model were questioned by Cundall (2000), who found that a number of species of snakes could drink without sealing the margins of their mouths. This left the mechanism for driving water flow in limbo, where it has remained. However, many years ago one of us (DC) collected data on muscle function during drinking in a few species of snakes that included data on muscles rarely recorded in any snake. Since then, DC has recorded drinking performance in a variety of snakes that provide additional insights into ophidian drinking mechanics. Finally, DC, ELB, AD, and NJK jointly recorded drinking in six watersnakes using synchronous pressure, kinematic, and performance measures. Here, we synthesize and summarize the kinematic, electromyographic, and pressure data for drinking in snakes that add to the results and interpretations reported by Kardong and Haverly ('93), Bels and Kardong ('95), and Berkhoudt et al. ('95).

Five elements of the buccal-pump model of drinking in snakes are tested here. First, we test that flow of water into the snake correlates with opening of the mouth. Second, we test the hypothesis that increased oropharyngeal pressure occurs during closing and peaks after the mouth is closed. Third, we test that pressure changes in the oropharyngeal and esophageal cavities are slightly out of phase, peaking in the oropharynx before the esophagus. This hypothesis is the logical extension of the esophageal sphincter model for regulating water flow (Bels and Kardong, '95) that is intrinsic to the two-phase buccal-pump model. Fourth, we test that bone movements during drinking are correlated with muscle activity patterns similar to those described previously (Berkhoudt et al., '95). Finally, we test the mouth-sealing model of pressure regulation during drinking (Kardong and Haverly, '93; Berkhoudt et al., '95)—basically, that moving water into the esophagus requires sealing the margins of the mouth.

After considering how our data relate to the buccal-pump model, we present a revised model of the mechanics of snake drinking based on all of our data combined with a revised interpretation of the oral anatomy of snakes.

MATERIALS AND METHODS

Drinking was studied through examination of the structure and function of the oropharyngeal and esophageal linings and of the bones and muscles forming the movable parts of the system, as well as through measures of movement, water flow, and pressure changes. This report is based on data acquired over 30 years using a variety of methods applied to different snakes.

Anatomy

The anatomy of the drinking apparatus was explored by a variety of techniques, including examination of prepared skulls, hemisected or serially transected (~1-cm thick sections) whole heads cut with a jeweler's saw (0.21 mm thick, 28 teeth/cm), and dissections of muscles and other soft tissues of the head and anterior trunk of all the snakes for which electromyographic and pressure data were obtained (Appendix 1). In addition, serial histological sections of the heads of various snakes were examined for details of connective tissue distributions and the form of the oropharyngeal and anterior esophageal cavities and their mucosal linings. All slides were prepared following the methods used by Cundall and Shardo ('95). Kardong and Haverly ('93) and Berkhoudt et al. ('95) both provided accounts of some anatomical features relevant to drinking and cite most critical past anatomical studies except Langebartel ('68), Parsons and Cameron ('77), Luppa ('77), and Groombridge ('79a,b).

Kinematics

Drinking was recorded from 1979 to 1981 in four *Agkistrodon piscivorus*, five *Heterodon platirhinos*, and seven *P. spiloides*. These kinematic data were recorded on strobe-illuminated Super-8 Kodachrome 40 film with a Canon 1014XLS camera at 24 fps (see below under "EMG"). The method for recording drinking behavior preceded that ultimately adopted in 1996 (Cundall, 2000). Snakes drank water from Petri dishes and there was no accurate measure of the volume consumed. Because regions of the snakes' heads visible on films varied, kinematic analyses concentrated primarily (except for *Heterodon*) on defining the point at which the snake shifted from opening, or expansion, to

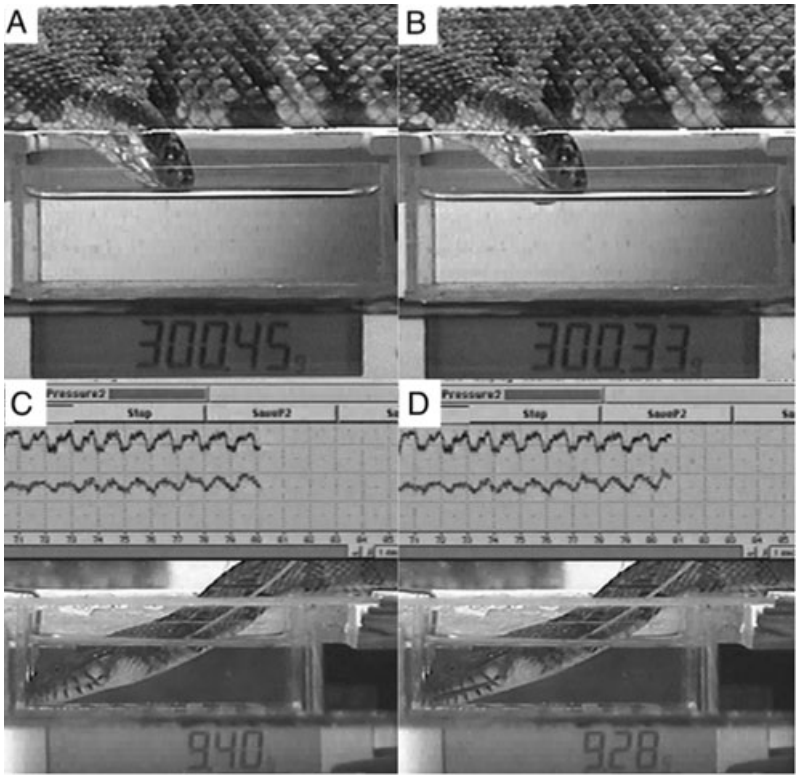

Figure 1. Video frames of drinking *Agkistrodon piscivorus* (A, B) and *Nerodia rhombifer* (C, D) during closed (A, C) and open (B, D) phases to show the nature of records analyzed for kinematics, performance, and, for C and D, pressure. In C and D, the top pressure trace was for oropharyngeal pressure, recorded by a transducer implanted in the cannula visible in the image on the snake's left side, and the bottom trace represented esophageal pressure recorded by a transducer in a cannula on the snake's right side at the level of the 7th rib (12th ventral scale).

closing, or compression, and vice versa, based on movements of the anterior end of the lower jaw. Drinking often lasted many minutes but filming was usually done in a series of relatively short segments (4–15 sec each).

Films of drinking by *H. platirhinos* were limited to those taken for EMG and we therefore measured movements for kinematic comparisons on projected images from the six rolls of film showing drinking in five individuals of this species. The one variable that may have been compromised by the recording technique is mandibular movement, which may have been limited by the shallowness of the Petri dishes.

Further kinematic analyses of drinking were done for 30 selected sequences drawn from video records (Fig. 1A, B) of 121 bouts (68 for two *A. piscivorus* and 53 for two *P. obsoletus*) recorded in 1996 and 1997 and reported on in Cundall (2000), and for selected sequences from 18 bouts for six *Nerodia rhombifer* recorded in 2000 (Fig. 1C, D: see below under "Pressure and Timing"). For *N. rhombifer*, 11 of the 18 bouts were recorded before catheters were implanted in these six snakes to record pressure changes in their oropharyngeal and esophageal cavities (Table 1), whereas seven bouts were recorded after catheter implantation. Selected video records of drinking for two *A. piscivorus,* two *P. obsoletus,* six *N. rhombifer*, one *N. sipedon*, and one *Crotalus mitchellii* were digitized and image sequences imported into the software package ImageJ to correlate movements with performance.

To compare kinematics among species, measurements were made of mandibular movement (measured at the position of the external nares), snout rotation around the prokinetic joint (angular displacement of the dorsal surface of the snout relative to the dorsal surface of the braincase), throat movement (dorsoventral excursion of the skin as a function of total head height at the angle of the jaws), and quadrate movement (measured as changes in width of the rear part of the head as seen in anterior or dorsal views) for 15 random cycles from two *A. piscivorus*, five *H. platirhinos* (see above), two *P. obsoletus*, and six *N. rhombifer*. Jaw movement frequency was also determined using measures of bout duration and cycle number for 20–22 bouts

Table 1. Kinematic and volumetric data for drinking bouts in six individuals of *Nerodia rhombifer* in which pressure data were recorded.

Snake	Sex	Body mass (g)	Number of drinking cycles	Volume of water (cm^3)	Volume/ cycle (cm^3)	Number of cycles analyzed	Volume/cycle analyzed (cm^3)	Head position[1]
N.r1	M	255	40	6.31	0.16	11	0.08, 0.30, 0.21	1
			23	2.43	0.11	6	0.13, 0.18	1
N.r2	M	320	63	15.69	0.25	8	0.03, 0.49	2
			75	9.04	0.12	8	0.14, 0.14	2
N.r3	M	265	92	9.87	0.11	8	0.20, 0.07	3
N.r4	F	500	69	2.27	0.03	10	0.00, 0.10	1
			198	27.10	0.14	7	—0.04[2]	2, 3
N.r5	F	510	57	17.30	0.30	14	0.34, 0.22, 0.31	1, 2
N.r6	F	845	88	24.29	0.28	9	0.64, 0.19	2
Means			78.3	12.7	0.17			
Ranges			23–198	2.3–27.1	0.03–0.30		—0.04–0.64	

For each bout, 3–6 drinking cycle segments were analyzed, total number of cycles/bout listed in "Number of cycles analyzed" column, and average volume/cycle for each analyzed segment is listed in "Volume/cycle analyzed" column. See also Figures 1, 8, and 9.
[1]Head position: 1, head above surface with only tip of mouth in water; 2, head horizontal with lower jaw submerged completely; 3, entire head submerged completely.
[2]Transducers implanted in this snake (N.r4) registered no pressure changes after the first 30–40 cycles of the second bout until near the end of that bout.

for untreated individuals of three of the four species recorded and for 15 bouts representing seven *H. platirhinos* with EMG electrodes implanted.

Pressure and Timing

To record pressure changes during drinking, catheters were inserted into six *N. rhombifer* that previously had been recorded drinking twice at weekly intervals. Snakes were anesthetized with isoflurane. A 14-gauge needle was then passed through the body wall immediately ventral to the ribs and into the gut at the appropriate level. A measured length (15.5 cm) of 1.27-mm o.d. polyethylene catheter tubing was passed through the needle into the gut and then the end of the catheter in the gut was flared to produce a collar about 3 mm in diameter. The needle and catheter were then gently pulled back until the flared catheter end rested against the gut mucosa, and then the needle was removed. Each catheter was attached to the snake's skin with one or two sutures caudal to the point at which the catheter emerged. Calibrated Millar Microtip SPR-407 pressure transducers (Millar Instruments, Inc., Houston, TX) with a measured lead were then threaded into the premeasured catheter. Transducer output was amplified 50 times with a Tektronix AM502 DC amplifier (Tektronix, Inc., Beaverton, OR) and most drinking bouts were recorded at 100 Hz with a GW Instruments (GW Instruments, Inc., Somerville, MA) data acquisition board in a Macintosh computer with SuperScope II software. Final analysis was based on output processed with a low-pass filter set at 10 Hz.

All snakes had one transducer tip placed in the posterior portion of the oropharyngeal cavity. Five of the snakes also had a second transducer inserted in a catheter in the lateral wall of the esophagus at the approximate level of the 9th–12th ventral scales. Split-screen video records of drinking showed pressure traces over images of a snake drinking from a reservoir placed on a digital balance. Using mirrors, the LED screen of the digital balance was reflected immediately below the image of the snake drinking (Fig. 1C, D). Hence, pressure, performance (i.e., volume of water transported), and kinematics were recorded in the same image. Precise timing of events was determined from short (100–140 frame) digitized segments of video records analyzed with ImageJ software.

The position of the snake's head influenced pressure profiles and baselines dramatically. Because previous models depend on knowing whether a pressure at a particular moment in time represents a positive or negative pressure, this is not a trivial problem. Obtaining a zero ambient setting for pressure during drinking was impossible because of electrical drift and varying surface interactions at the transducer face. However, prior calibration of the transducers allowed accurate measures of relative pressure changes. Our interpretations depend on sequential records with transducers at the same level for the same snake both drinking and not drinking, and on knowing approximate rates and directions of water flow at the same time.

To determine the phase relationships of mandibular motion and oropharyngeal pressure, we cross-correlated the waveforms using the xcov function in MATLAB (R2008b; MathWorks, Natick, MA). This procedure shifts one wave relative to the other to search for the maximum similarity (correlation) between the waves. The output is the optimum lag time and maximum correlation coefficient.

Electromyography

Synchronized electromyograms were obtained from four to seven muscles for each individual of the three species of snakes (*A. piscivorus*, *H. platirhinos*, and *P. spiloides*) used for EMG. Data were obtained from 89 chronically implanted bipolar fine-wire electrodes representing 20 different cephalic muscles (Table 2). All electrodes listed recorded analyzable activity during feeding, although only 61 of the electrodes showed activity during drinking. Muscle terminology follows Langebartel ('68), Haas ('73), Groombridge ('79b), and Zaher ('94), and illustrations of the muscles listed in Table 2 and Figures 5 and 6 can be found in Cundall and Gans ('79) and Cundall and Greene (2000).

All electrodes were implanted using long 24-gauge hypodermic needles inserted through small (1 mm) incisions 2–3 cm caudal to the head of animals anesthetized with an intraperitoneal injection of sodium pentobarbital (30 mg/kg body weight). Free ends of the electrodes were then run under the skin to emerge on the surface approximately 20 cm caudal to the snake's head. They were then soldered to a harness of earphone wire sutured to the skin. The free end of the harness ended in a multipin Amphenol connector (Amphenol Connex Corp., Moorpark, CA) that could be plugged into leads from preamplifiers. Remaining surgical and recording methods were as described by Cundall and Gans ('79) and additional EMG records of prey transport for some of these snakes were given in Cundall ('83) and Cundall and Greene (2000). Electrode placements (shown for *A. piscivorus* in Cundall and Greene [2000]) were confirmed by dissection of animals sacrificed with an overdose of anesthetic after the last recording session, fixed in 10% buffered formalin, and stored in 70% ethanol.

Synchronization of ciné and EMG records was based on the output of a photocell in front of one of the strobe lights used for illumination. Muscle activity from chart records was plotted against kinematic patterns determined from frame-by-frame analysis of ciné records projected using a Lafayette Super-8 Analyzer (Lafayette Instrument Co., Lafayette, IN). All muscle activity events are plotted against the times at which the mouth began to open or close. Use of relatively short sequences on the films facilitated matching film sequences to the photocell outputs on EMG records.

The electromyographic data presented in this article were recorded on tapes that are no longer available. All of the EMG analysis is based on chart-paper records, one set made during recording sessions and another one or two clean sets made at paper-drive speeds that showed photocell output clearly.

Table 2. Head and neck muscles and species of snakes sampled in this study via electromyography (EMG). *N* = number of snakes containing electrodes for the muscle.

Muscle	Number of electrodes	Species	*N*
Adductor mandibulae externus superficialis	2	*Agkistrodon piscivorus*	1
		Heterodon platirhinos	1
Adductor mandibulae externus profundus	4	*Pantherophis spiloides*	4
Adductor mandibulae externus medialis	7	*Agkistrodon piscivorus*	4
		Heterodon platirhinos	2
		Pantherophis spiloides	1
Adductor mandibulae posterior	6	*Heterodon platirhinos*[1]	3
		Pantherophis spiloides	2
Compressor glandulae	2	*Agkistrodon piscivorus*	2
Pseudotemporalis	1	*Agkistrodon piscivorus*	1
Pterygoideus	6	*Agkistrodon piscivorus*	1
		Heterodon platirhinos	1
		Pantherophis spiloides	4
Levator pterygoidei	6	*Heterodon platirhinos*	2
		Pantherophis spiloides[1]	3
Protractor pterygoidei	8	*Agkistrodon piscivorus*	2
		Heterodon platirhinos[1]	3
		Pantherophis spiloides	1
Protractor quadrati	4	*Heterodon platirhinos*	2
		Pantherophis spiloides	2
Retractor pterygoidei	2	*Heterodon platirhinos*[1]	1
Intermandibularis anterior, pars posterior	4	*Agkistrodon piscivorus*[1]	2
		Heterodon platirhinos	
Transversus branchialis	1	*Pantherophis spiloides*	1
Intermandibularis posterior, pars anterior	2	*Agkistrodon piscivorus*	1
		Pantherophis spiloides	1
Intermandibularis posterior, pars posterior	3	*Agkistrodon piscivorus*	1
		Heterodon platirhinos	2
Depressor mandibulae	9	*Agkistrodon piscivorus*	2
		Heterodon platirhinos[1]	2
		Pantherophis spiloides[1]	3
Cervicomandibularis	5	*Agkistrodon piscivorus*	1
		Pantherophis spiloides	4
Neurocostomandibularis	12	*Agkistrodon piscivorus*	4
		Heterodon platirhinos	2
		Pantherophis spiloides[1]	5
Cervicoquadratus	2	*Heterodon platirhinos*	2
Constrictor colli	3	*Heterodon platirhinos*	3

[1]One or more individuals of this species had two electrodes implanted in this muscle.

RESULTS

Anatomy

The oropharyngeal and esophageal cavities of snakes are flattened at rest and have small resting volumes (Figs. 2 and 3). Berkhoudt et al. ('95) provided a simplified view of this complex

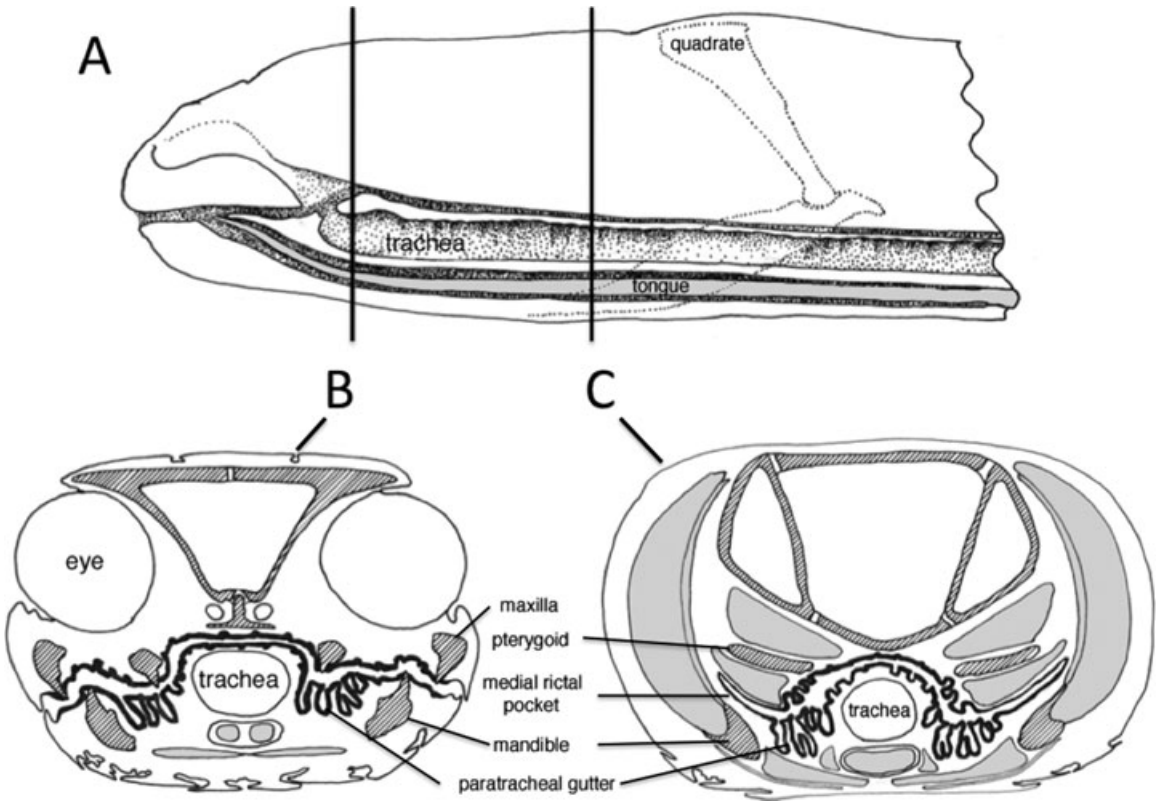

Figure 2. Anatomy of the oral cavity and oropharynx in snakes. (A) Diagrammatic lateral phantom view of the head and anterior trunk of a colubrid snake to show the shape and limited resting volume of the oral cavity and oropharynx. (B and C) Cross-sectional views at the levels shown in A to illustrate variations in mucosal form and folding in the roof of the oral cavity and oropharynx, linguotracheal ridge, and paratracheal gutter. Hatched regions in B and C are bones, whereas solid-shaded regions are muscles.

cavity (their Fig. 10). In many snakes, the lining tissues of the cavity are capable of extraordinary stretch, particularly those in the region between the mandibles. Expansion comes about primarily by unfolding of pleated epithelia. Most of the mucosa is simple columnar epithelium with abundant mucus cells. A stratified squamous epithelium lines only the margins of the oral cavity and limited longitudinal strips of presumed ectodermal origin line the anterior part of the mouth. In life, all parts are coated with mucus.

The mouths of snakes are unusual in having the tongue enclosed in a sheath lying ventral to the larynx and trachea (McDowell, '72), and in having the larynx and glottis situated immediately caudal to the opening of the tongue sheath, but near the anterior part of the lower jaw. Technically, the esophagus in most snakes should begin approximately at the level of the eyes, a short distance behind the glottis. We (and most other treatments of snake anatomy) assume that the esophagus begins caudal to the jaw joint, the point at which the mucosal lining and its underlying connective tissues lose close association with the bones and skeletal muscles of the jaw apparatus. However, moving the opening of the tongue sheath and the glottis to the anterior region of the oral cavity produces a prominent longitudinal linguotracheal ridge on the floor of the mouth. When the mouth is closed, this ridge lies in an equally prominent groove in the roof of the mouth immediately behind the internal nares, bounded laterally by the medial upper jawbones (palatines and pterygoids). In most snakes the palatines and pterygoids bear teeth, which lie at rest in a trough in the soft tissues of the lower jaw, between the mandible and the linguotracheal ridge (Figs. 2B and 3A). We here name this trough the paratracheal gutter (Figs. 2B and 3A). The paratracheal gutter extends through the oropharyngeal cavity and into the esophagus. The dentary teeth on the lower jaw similarly fit into a groove between the maxillary and palatopterygoid teeth (Fig. 2B). When the mouth is closed, the epithelial surfaces of the upper and lower jaws are therefore very close throughout their width, and in sectioned material of snakes preserved in a resting condition, the oropharyngeal region may have little or no appreciable cavity anywhere.

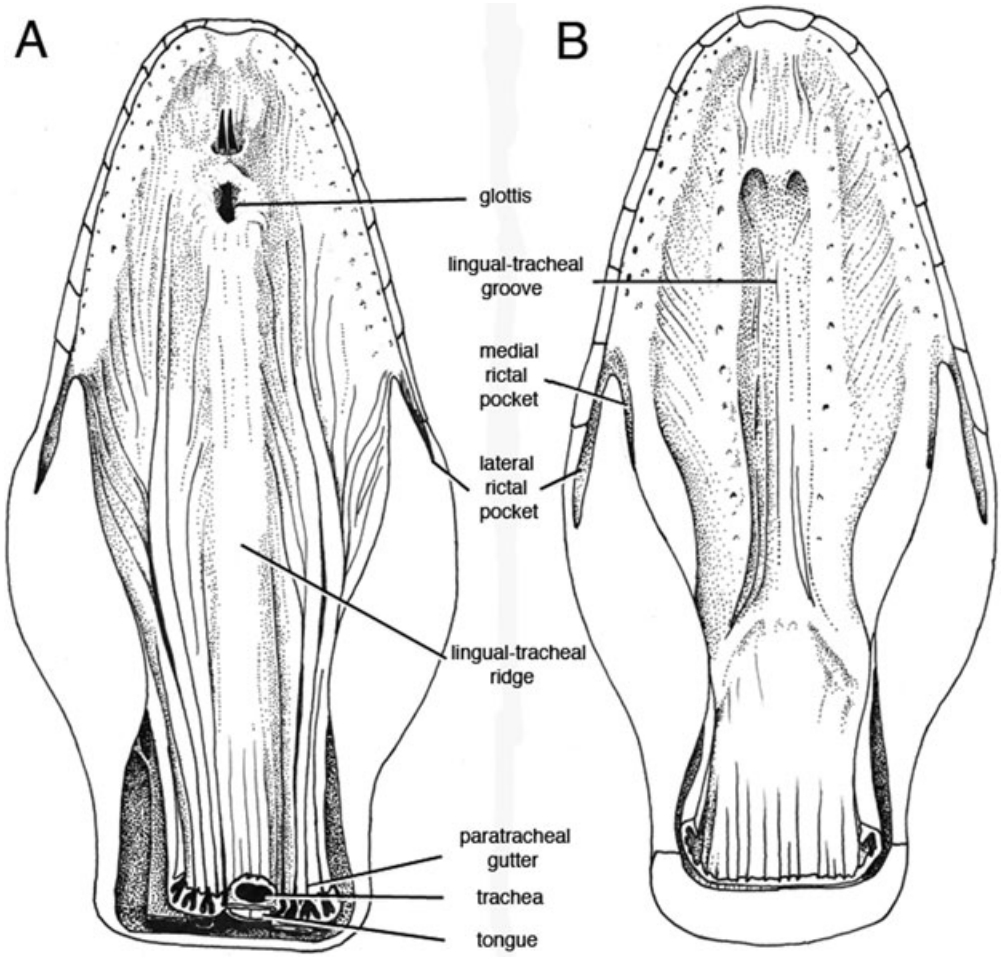

Figure 3. Gross morphology of the floor (A, in dorsal view) and roof (B, in ventral view) of the oral cavity, oropharynx, and esophagus in a generalized colubrid snake to show the major patterns and positions of mucosal folds.

At the angle of the mouth are two pocket-like invaginations. One lies lateral to the adductor muscles and receives ducts of the rictal glands (McDowell, '86; Underwood, 2002). The more medial one is rarely discussed and varies in depth. It can be seen in histological sections to extend along the lateral surface of the pterygoideus muscle, becoming shallower as the pterygoideus nears its attachment to the mandible. Folds in the mucosa at the anterior edge of this medial pocket connect with the paratracheal gutter. This latter pocket lies between the pterygoideus and the mandible and its associated medial adductor muscles (pseudotemporalis, adductor mandibulae posterior; see Figs. 2C and 3A, B). To distinguish the two pockets, we suggest calling them lateral and medial rictal pockets (the former of which contains the venom or Duvernoy's glands in venomous colubroid snakes). The mucosa lining the medial pocket is either not folded or minimally folded and exhibits few goblet (mucus) cells. It is attached both to the mandible and to the surfaces of both the pseudotemporalis (laterally) and the pterygoideus (medially). These attachments suggest that the volume of the pocket can be actively changed through movements of the mandible and contractions of the pterygoideus and pseudotemporalis.

The dorsal mucosa of the esophagus, like that of the oropharyngeal cavity, bears numerous relatively shallow folds (Fig. 3B). Folding of the esophageal wall deepens lateral to the edge of its attachment to the overlying musculoskeletal body wall. In the snake species we examined, the anterior part of the esophagus is attached by connective tissues to the subvertebral and subcostal muscles and has a few shallow folds. The width of esophageal attachment diminishes to a narrow strip within about ten body segments in most species, with folding of the mucosa of the esophageal roof increasing as the width of attachment decreases. However, the deepest folding occurs at the ventrolateral edges of

the esophagus near the distal tips of the ribs (Fig. 3A). Hence, in the anterior trunk, the esophagus is draped over the trachea and tongue with its most folded regions lying alongside the trachea.

A critical feature of the snake mouth is the exact form of its lining at different points. The oral mucosa is underlain by a thin layer of connective tissue, which attaches to surrounding structures at relatively few points, with attachment regions diminishing in size caudally. In other words, as one proceeds posteriorly through the mouth, the attachment points between the mucosa and surrounding structures decrease. The mucosa has shallow folds over the trachea and over the dental ridges of all toothed bones, but is deeply grooved in the paratracheal gutter, particularly in the region underlying the pterygoideus muscle. In contrast, the mucosa covering the pterygoideus muscle is relatively smooth (Figs. 2C and 4A, B). Immediately caudal to the posterior margins of the pterygoid bones, ventrally directed folds extend obliquely across the roof of the gut (Fig. 3B). These folds may represent the esophageal sphincter proposed by Bels and Kardong ('95).

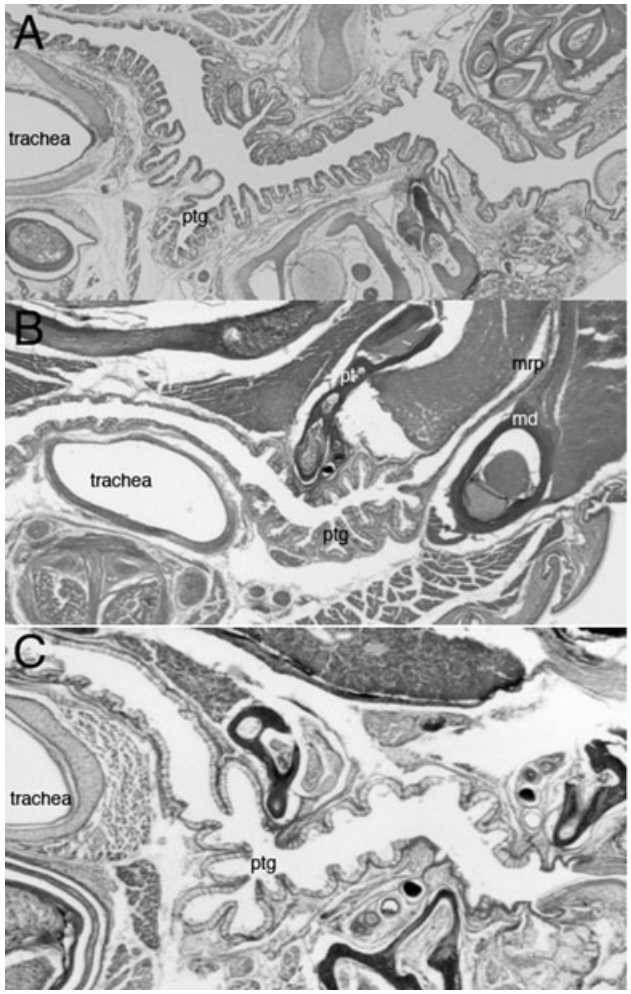

Figure 4. Photomicrographs of the oral mucosa for one half of the head of (A) *Heterodon platirhinos*, level of posterior orbit, (B) *Regina septemvittata*, level of otic region, and (C) *Thamnophis sirtalis*, mid-orbital region, to show increased fold depths in the region of the paratracheal gutter. The pterygoideus muscle lies against the medial side of the medial rictal pocket in B. md, mandible; mrp, medial rictal pocket; pt, pterygoid; ptg, paratracheal gutter. Actual widths of regions shown, to the nearest 0.1 mm, are: (A) 4.0 mm, (B) 3.0 mm, and (C) 2.0 mm.

Kinematics

We first give a general description of the kinematics of drinking in snakes and then consider kinematic differences among *A. piscivorus, N. rhombifer,* and *P. spiloides.*

The basic kinematic pattern exhibited by drinking snakes entails a rocking motion, in which the anterior end of the lower jaw is depressed as its posterior end is elevated. The whole mandible then falls and the jaw joint moves ventrally and slightly medially and anteriorly, the upper jaw moves medially, and the ventral skin overlying the throat region falls. The anterior part of the lower jaw starts rising while the posterior end is still moving ventrally and medially, and then the entire lower jaw is elevated, usually after its anterior end has already contacted the snout. The posterior end of the lower jaw moves dorsally and laterally as closing continues, and continues this trajectory until the anterior end of the mandible begins moving downward again.

The taxa we examined differed in both subtle and obvious aspects of their drinking kinematics. In *Nerodia* and *Pantherophis*, each mandible appears to move largely through a simple dorsoventral rotation around the jaw joint, with little detectable rotation around its long axis. Rotation around the long axis was described for both *Boa* (Kardong and Haverly, '93) and *Boiga* (Berkhoudt et al., '95). In *Pantherophis*, there is no independent movement of the infralabial or mental scales and the snout shows little or no movement during drinking. In contrast, the mental scales and anterior infralabials of both *Agkistrodon* and *Nerodia* are elevated as mouth closing begins, as in *Boiga* (Berkhoudt et al., '95), and after the mental scale hits the rostral scale of the snout, it shows a distinct ventral flip in *Agkistrodon* but not in *Nerodia*. In the latter, the snout is elevated as the mental and anterior infralabial scales move upward and slightly forward.

Opening involves depression of the intermandibular soft tissues, which is achieved partly by adduction of the distal ends of the quadrates. Medial movement of the quadrates allows depression of the skin between the posterior ends of the mandibular rami. In *Agkistrodon*, *Nerodia*, and *Pantherophis*, opening the mouth depresses the anterior skin, including the mental scale,

and the distal tips of the mandibles. Although it seems likely that the mandibles undergo rotation around their long axes at the end of the close phase in most species, as shown by Kardong and Haverly ('93) for *B. constrictor*, rotation could not be seen in any of the ciné or video records and must occur when the mandibular tips are not visible.

In *A. piscivorus*, the mandible is strongly curved and, at rest, the curve is directed ventromedially. When opening begins, the posterior end of the mandible moves dorsomedially and the anterior end moves ventrally and slightly laterally but the middle does not appear to move at all. As opening progresses, the jaw (quadrate articular) joint moves ventrally along with the rest of the lower jaw and the posterior end of the upper jaw, and this movement is often accompanied by medial or ventromedial movement of the upper jaw, making the head appear slightly narrower.

Agkistrodon also shows complex and marked movements of the mental and anterior infralabial scales. The first sign of mouth opening is a rapid ventral flip of the mental scale, termed a retraction by Berkhoudt et al. ('95), which is followed by slight ventromedial movement of the anterior infralabials that exposes the dental mucosa over the anterior dentary teeth. When closing begins, the mental scale lifts rapidly and as the lower jaw rises, it contacts the rostral scale, usually lifting the snout slightly. The anterior infralabials are also raised to fit within the margins of the anterior supralabials.

The ventral skin of the posterior lower jaw and anterior trunk also moves during drinking, presumably powered by muscles associated with the hyoid apparatus and by intrinsic cutaneous muscles. The movement patterns vary but generally involve dorsoventral and slight anteroposterior excursions. Based on 12 quantified short sequences for four *N. rhombifer* and for two sequences for *A. piscivorus*, the throat begins rising at the same time as does the mandible and its elevation peaks as the mouth closes or shortly (0.03–0.13 sec) thereafter. *Pantherophis spiloides* displays a slightly different movement pattern, with the ventral skin starting to rise well before the lower jaw starts to close, and continuing to rise until mouth opening begins. Quadrate and throat movements are potentially related. Apart from topographic proximity, the quadrate movements measured reflect changes in distance across the throat that could result in dorsoventral movements of the ventral skin, which could change pressures in the paratracheal gutters immediately dorsal to the skin (Fig. 2).

Analysis of extent of movement of the mandibles, throat, quadrates, and snout for the four species revealed significant differences in all but throat movement (Table 3). Intraspecific variation for all variables was relatively high. The results of this analysis suggest that movement of water is not constrained by specific kinematic patterns and that, unlike inertial methods of drinking (Prakash et al., 2008; Reis et al., 2010), the mechanism used by snakes involves much slower cycles of force application (Table 4).

Electromyography

Representative electromyograms are shown in Figure 5 and summaries of muscle activity patterns across all three species studied (*A. piscivorus*, *H. platirhinos*, and *P. spiloides*) are given in Figures 6 and 7. Two features of muscle activity during drinking

Table 3. Means ± SDs, ANOVA, and SNK post-hoc results for measurements of movements of the mandible, throat, quadrate, and snout during drinking in four species of snakes. $N = 15$ cycles for all species.

Variable	*Agkistrodon piscivorus*	*Heterodon platirhinos*	*Nerodia rhombifer*	*Pantherophis obsoletus*	*F*	*P*
Mandible	0.31 ± 0.07	0.18 ± 0.04	0.34 ± 0.07	0.21 ± 0.06	23.7	<0.01
Throat	0.08 ± 0.03	0.09 ± 0.03	0.07 ± 0.03	0.09 ± 0.03	0.96	0.42
Quadrate	0.04 ± 0.01	0.10 ± 0.04	0.10 ± 0.03	0.09 ± 0.04	13.07	<0.01
Snout angle	0.60 ± 0.51	0.00 ± 0.00	0.53 ± 0.64	1.67 ± 0.62	27.92	<0.01
SNK						
Mandible	*Heterodon*	*Pantherophis*	*Agkistrodon*	*Nerodia*		
Quadrate	*Agkistrodon*	*Pantherophis*	*Nerodia*	*Heterodon*		
Snout Angle	*Heterodon*	*Nerodia*	*Agkistrodon*	*Pantherophis*		

Table 4. Summary kinematic data for drinking in four species of snakes. For each kinematic variable, the mean ± standard deviation is given, followed by the range (in parentheses).

Species	*N*	Bout duration (s)	Number of cycles/bout	Cycle frequency (s^{-1})
Agkistrodon piscivorus	22	121 ± 91 (43–463)	90 ± 64 (32–326)	0.77 ± 0.10 (0.62–1.07)
Heterodon platirhinos	15	65 ± 62 (21–265)	49 ± 56 (16–233)	0.70 ± 0.16 (0.47–1.06)
Nerodia rhombifer	20	244 ± 264 (6–1147)	194 ± 204 (3–859)	0.78 ± 0.09 (0.50–0.90)
Pantherophis obsoletus	20	162 ± 79 (25–281)	137 ± 63 (13–258)	0.85 ± 0.15 (0.52–1.13)

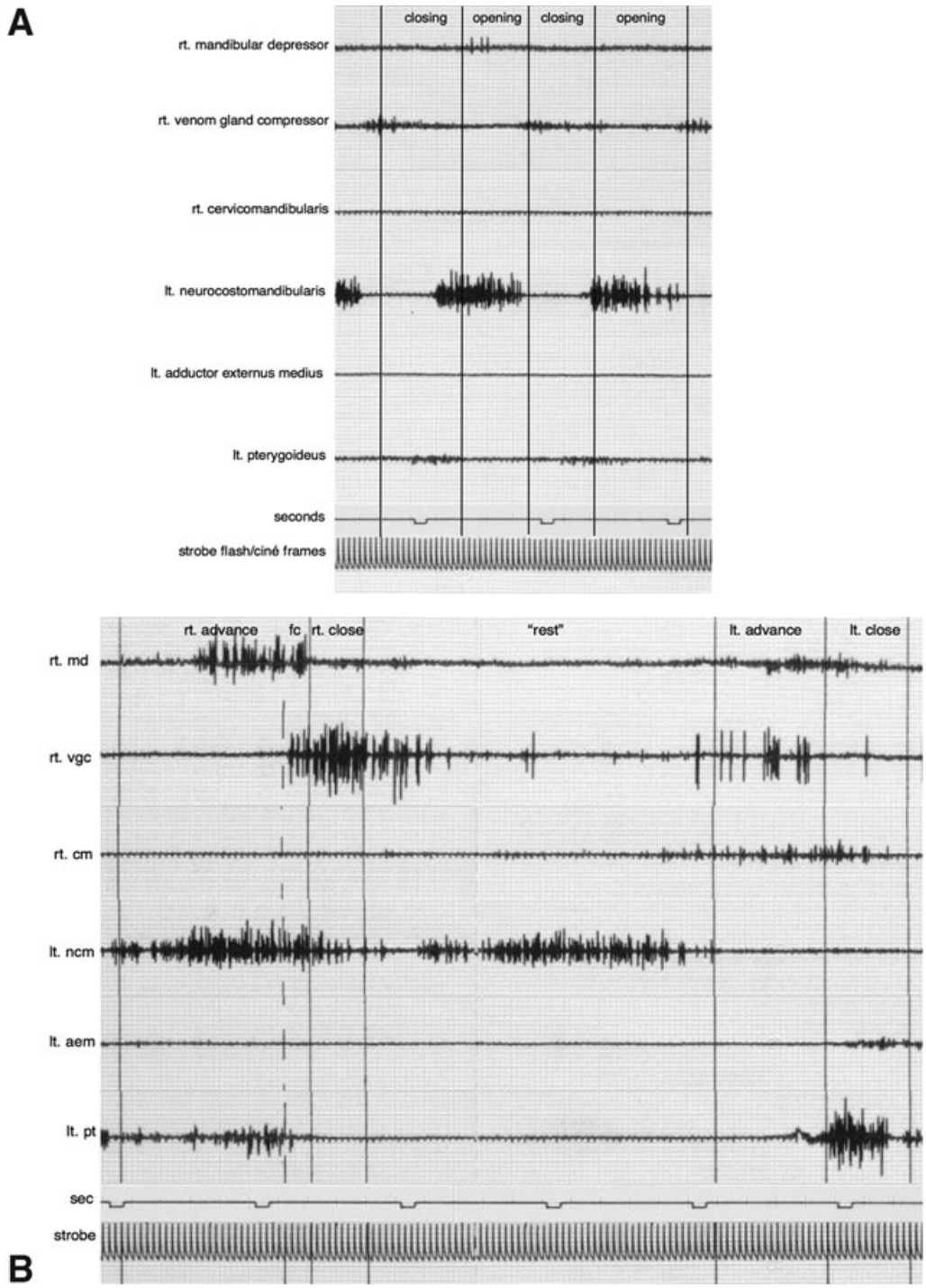

Figure 5. Representative electromyograms for six muscles during drinking (A) and intraoral transport of a fish (B) in a single individual of *Agkistrodon piscivorus*. The EMGs for prey transport were recorded about an hour after the drinking record and show different levels of activity of the same muscles during the two behaviors. The snake had struck and swallowed a small mouse shortly after drinking and immediately prior to eating the fish. Fc, fast close, a behavior that involves protraction of the lower jaw and retraction of the fang on the advancing side due to contraction of the pterygoideus (see Cundall [1983] for more details).

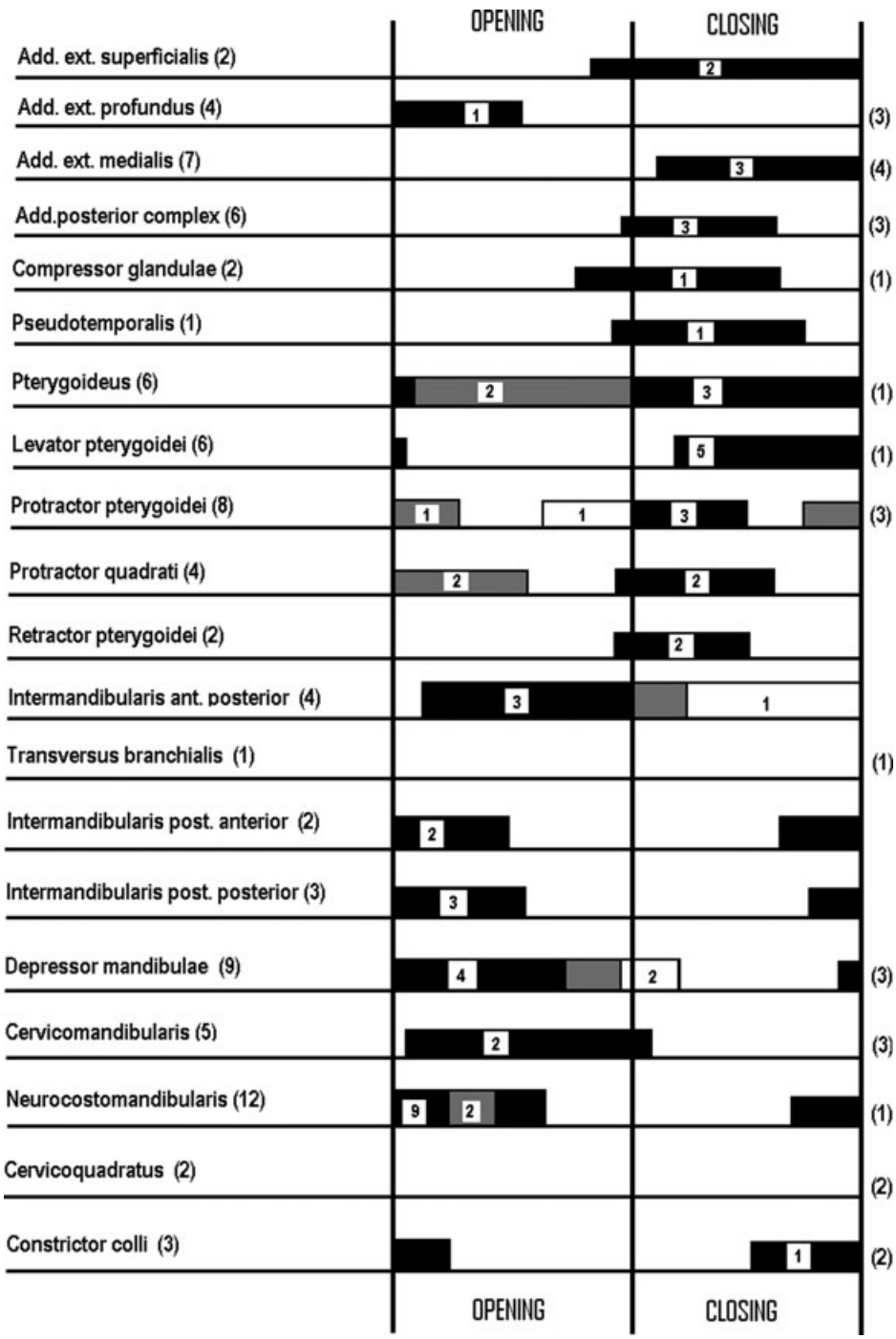

Figure 6. Summary of activity periods of muscles recorded during drinking for *Agkistrodon piscivorus, Heterodon platirhinos,* and *Pantherophis spiloides.* Black blocks represent the most frequent pattern, white blocks represent a less frequent pattern, and gray blocks represent periods of overlap between the two patterns. Numbers next to muscle names represent the total number of electrodes for that muscle yielding data during drinking or feeding, numbers within the blocks represent the number of electrodes that produced each pattern, and numbers to the far right represent the number of electrodes that recorded no activity during drinking. Block heights approximate average relative EMG amplitudes.

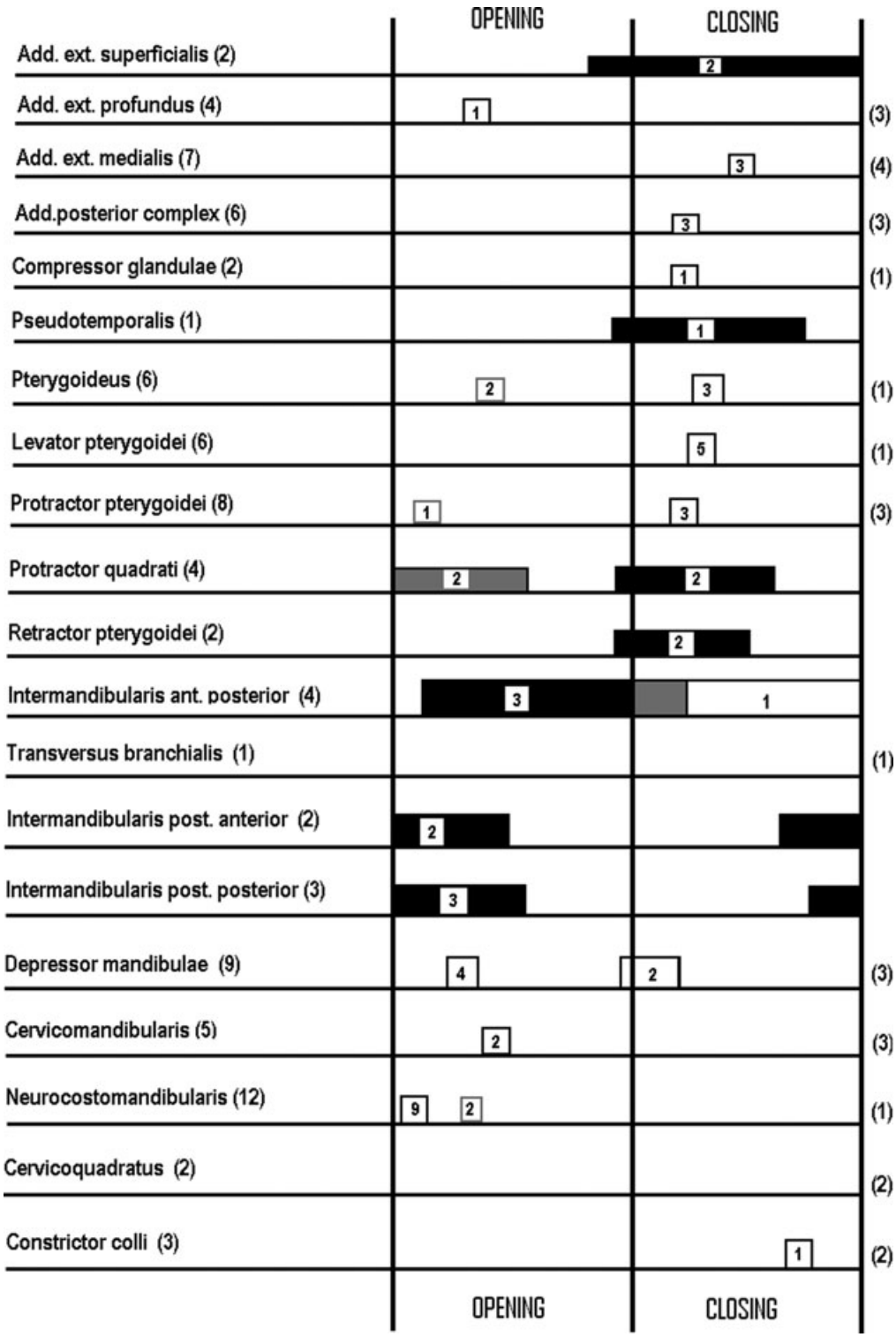

Figure 7. Electromyographic summary for drinking in which those electrodes that showed no activity during drinking are given preference. This summary diagram shows that relatively few muscles, or parts of muscles, show consistent activity during drinking.

differ from those during feeding. First, all muscles showing activity were typically active on both sides for all cycles. Second, for most snakes, the amplitude of activity of most muscles during drinking was less than that observed during feeding (compare Fig. 5A, B). Exceptions to this pattern were observed in the activity levels recorded from the intermandibular muscles.

During opening, activity was seen irregularly in about half the muscles recorded—notably those muscles that serve partly as constrictors of the posterior oropharyngeal cavity (i.e., neurocostomandibularis, cervicomandibularis, constrictor colli, and intermandibular muscles), the depressor mandibulae, and the dorsal constrictors that elevate and protract the upper jaw (Fig. 6). Medial movement of the jaw joint could be powered partly by contractions of the protractors of either the quadrate or pterygoid, a pattern of activity that occurred in the protractor quadrati muscles of *Pantherophis* but not of *Heterodon*. In some sequences, activity of a few closing muscles began at the end of opening as did activity of the major elevators and protractors of the upper jaw, the protractor pterygoidei, protractor quadrati, and levator pterygoidei. Activity of the latter usually ceased early in opening but that of the other two muscles sometimes continued well into the following opening phase.

Anterior intermandibular muscles were active throughout opening whereas the more posterior intermandibular muscles were active through the latter half of closing and into the first half of opening. This pattern suggests activity to prevent lateral flaring of the anterior tips of the mandibles and compression of the posterior intermandibular space after filling of the available space in the paratracheal gutter and posterior oral cavity. These muscles showed activity primarily during drinking in *Agkistrodon* and *Heterodon* (Cundall, unpublished data) and at the end of prey transport in *Nerodia* (Cundall and Gans, '79).

During closing the oral cavity is compressed either from anterior to posterior, as in *Boiga* (Berkhoudt et al., '95), *Nerodia,* and *Pantherophis*, or uniformly, as in *Agkistrodon* and *Crotalus*. Electrodes in the mandibular adductors showed variable patterns of activity, some (12 of 28) showing no activity during drinking (Fig. 7) but high-amplitude activity during feeding (two shown in Fig. 5B). Of those that did show activity during drinking, it was of low amplitude and occurred primarily during closing. The two patterns of closing are reflected in the timing of elevation of the anterior part of the lower jaw relative to the throat: either synchronous, as in *Agkistrodon* and *Crotalus,* or sequential, from anterior to posterior, as in *Pantherophis*.

Variation in levels of muscle activity occurred in some immersions, with muscles occasionally becoming active during opening that had been silent during early cycles, but a more common trend was one of a gradual decline in amplitude throughout the course of individual drinking bouts.

Pressure Changes

Pressure profiles for the six *N. rhombifer* studied varied among individuals and within bouts of each snake (Figs. 8 and 9). Generally, pressure changes were correlated with movements of the lower jaw; however, although counterintuitive, neither pressure changes nor jaw movements were directly linked to water flow. Esophageal pressure changes were generally smaller than those in the oropharynx but in some snakes the pressure changes in the two regions were approximately equivalent and synchronous, whereas in others pressure changes in the esophagus were delayed 0.03–0.25 sec.

In four of the five snakes for which we have synchronized oropharyngeal pressure and mandibular motion data, pressure and motion were out of phase, such that pressure was dropping as the mandible was elevating (Fig. 8). Cross-correlation analysis showed that the oropharyngeal pressure waveform lagged slightly behind mandibular motion by 0.13 ± 0.034 sec (mean $\pm$ SEM; $n = 9$ sequences from N.r1–4). Shifting the pressure traces forward yielded a negative correlation coefficient between the waveforms of -0.72 ± 0.031, indicating that the waves were close to half a cycle out of phase. In N.r5, correlations between the waveforms were weaker and less consistent; one correlation was positive (with a coefficient of 0.69), one was weakly negative (–0.39), and one trace (Fig. 9) showed similar positive and negative correlations (lag of 0.17 sec and correlation coefficient of 0.51; lag of –0.10 sec and correlation coefficient of –0.58).

Three patterns of pressure changes in the oropharynx and esophagus were recorded. In one (N.r3), recorded in a snake with its entire head underwater, pressures in both the oropharynx and esophagus were similar in magnitude and in phase, increasing at the end of mouth closure, remaining high throughout mouth opening, then dropping rapidly as mouth closure began (Fig. 8A). Pressure and mandibular movement were out of phase. Lowest pressures occurred in the middle of mouth closure and pressure rose at the end of the close phase and remained high throughout mouth opening, falling as mouth closure began. In a second pattern, seen in two snakes (N.r1 and N.r4) with only the tips of their mouths in the water, oropharyngeal pressures followed the pattern just described but esophageal pressures either did not change or were essentially out of phase with oropharyngeal pressures, falling as the latter rose and vice versa (Fig. 8B). Among the remaining three snakes that had much of their lower jaws submerged and their heads oriented nearly horizontally while drinking, one had no esophageal transducer (N.r2). However, another (N.r6) had the oropharyngeal transducer placed at the approximate position of the proposed esophageal "sphincter" and showed low or no fluctuations in pressure while drinking 24.3 cm^3 over 88 cycles with most of the lower jaw submerged. In a second bout, the same snake showed oropharyngeal pressure changes correlated with jaw and throat movements. Its neck and lower jaw were immersed and its external nares were out of the water, but it imbibed only 1.3 cm^3 of water over

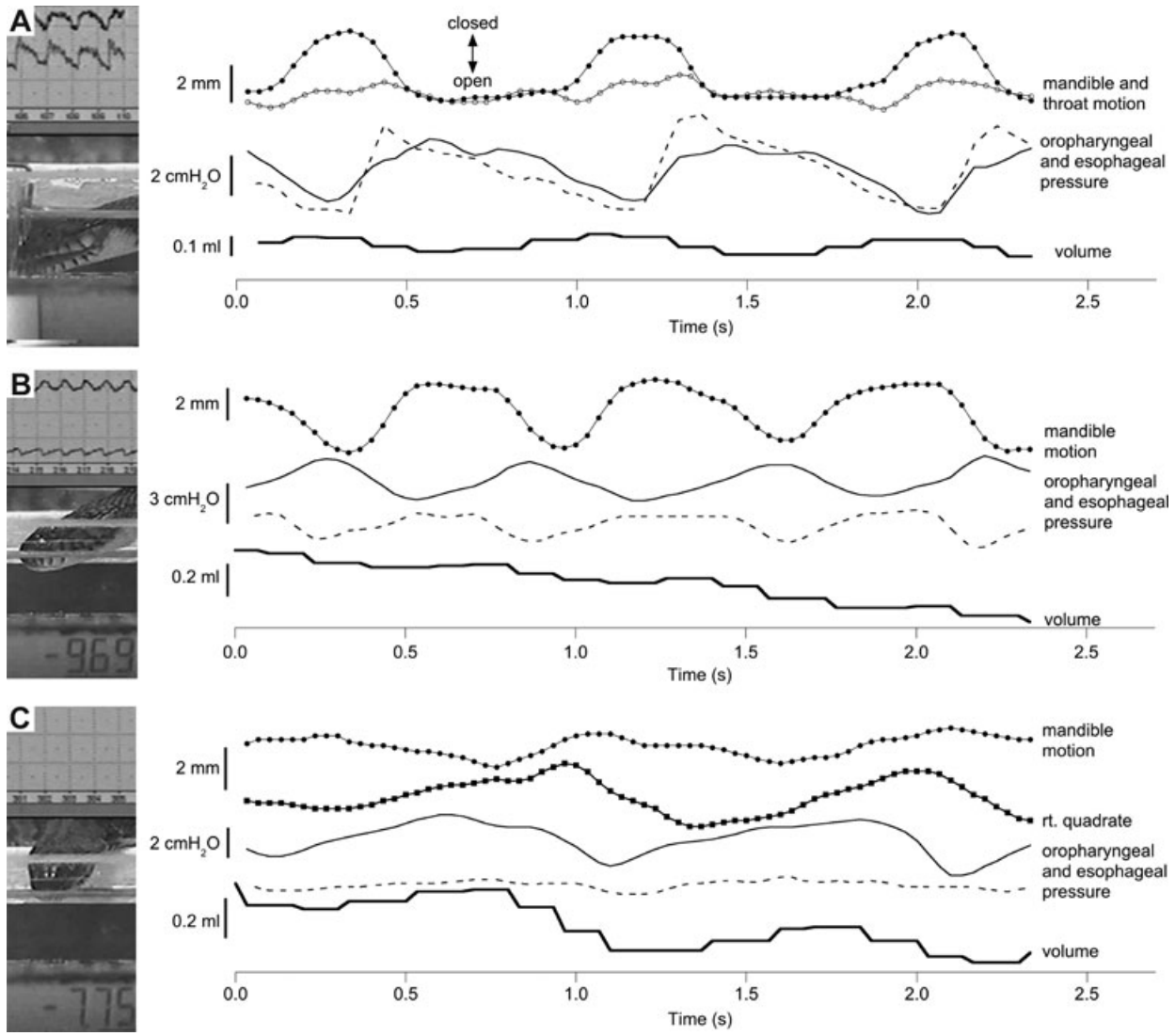

Figure 8. Representative pressure, kinematic, and volume profiles for three individuals of *Nerodia rhombifer*, showing variations in timing of intraoral and esophageal pressure changes relative to mandibular movement and water transport. The images on the left represent the initial frames from the video sequence from which kinematic, pressure, and volume changes were plotted on the right. Volume traces are all corrected for time lag by 20 frames. (A) N.r3, head completely submerged, (B) N.r4, head at surface, only tip of lower jaw in water, (C) N.r1, only tip of lower jaw in water. In all three representative profiles (A–C), thick solid lines represent volumes of water transported, thin solid and dashed lines represent oropharyngeal and esophageal pressures, respectively, and traces of mandibular movements are denoted by solid circles. In A, throat movements are denoted by open circles, and in C, movements of the right quadrate are denoted by solid squares, increasing values representing adduction (medial movement) of the quadrate.

approximately 150 cycles of mouth movements. In both snakes with functioning oropharyngeal transducers, multiple high pressure peaks occurred during each cycle. In one snake, the highest pressure occurred immediately following mouth closure, followed by a rapid drop in pressure, in the other the highest peak appeared in the middle of mouth opening (Fig. 8C). Lowest pressures occurred either at or just prior to mouth closure.

In one snake (N.r1), timing of pressure changes in the oropharyngeal and esophageal cavities varied during the course of a bout, and this variation correlated with fluid-flow volumes.

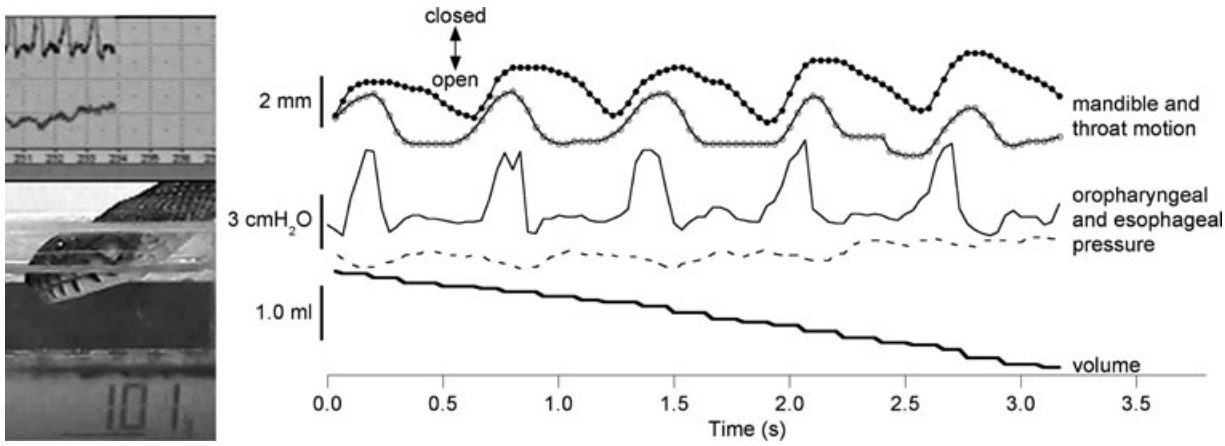

Figure 9. Pressure, kinematic, and volume profiles for a short segment of a drinking bout in a single individual of *Nerodia rhombifer* (N.r5), showing continuous inflow of water, suggesting independence of, or loose functional ties between, pressure changes and flow. Movements of the mandible and throat are denoted by solid and open circles, respectively.

During out-of-phase pressure changes, there was low net flow of water into the snake, but when pressure changes were in phase in the two cavities, volumes imbibed increased, the opposite of events shown for N.r3 (Fig. 8A) and N.r4 (Fig. 8B).

Our pressure records show that pressure changes are complex, rapid, and relatively small. Maximum pressure differentials rarely exceeded 4 cm H_2O. Because we have no way to determine exactly where ambient pressure was in our records, we cannot determine if the snakes ever generated suction in either the oropharynx or esophagus, or measure the pressure differential between the oropharyngeal cavity and the esophagus. However, with respect to models of pressure change and kinematic activity, we have accurate measures of the timing of both kinematic and pressure events that show that decreases in oropharyngeal pressure rarely accompany mouth opening.

Performance and Water Flow

The performance of the drinking apparatus varied so widely that accounting for all volume change patterns with a simple model seems impossible. For those six individuals of *N. rhombifer* for which we have kinematic, pressure, and performance data, flows were pulsed in 12 of 19 sequences analyzed (Fig. 8 and Table 1) within the nine bouts for which pressure data are available and not pulsed in seven (Fig. 9). In 18 of 19 sequences, water entered the snake, whereas in one sequence, there was continuous flow out of the snake over four cycles. Pulsed flow apparently involved flow in both directions (see also Cundall, 2000, for additional examples of pulsed and nonpulsed flow and changes in direction of flow).

Apparent pulsing of flow is a function of fluctuations in the total mass resting on the balance. Because the balance is measuring both the mass of water in the reservoir plus the mass of whatever part of the snake's head is displacing water in the reservoir, any change in the amount of the snake's head that is actually immersed causes changes in apparent mass. Thus, cyclical movements of the lower jaw can cause cyclical changes in mass that would appear to reflect changes in flow. It is clear from records in which flow rates are low that apparent decreases in flow, or even apparent reversals of flow, may occur when more of the snake is added to the mass of the reservoir. For records in which the whole head or entire lower jaw were under water, mass decreases are not pulsed but apparently more or less continuous. Combining all records, including those without pressure data, and taking into account the position of the head, drinking can clearly involve nonpulsed flow, as was suggested in Figure 5 of Cundall (2000).

Behavior

Agkistrodon, *Heterodon*, and *Pantherophis* usually drink by bending their heads down so that just the tip of the mandible and snout touch the water. *Nerodia*, on the other hand, uses a number of postures, frequently immersing its entire head in the water. Lower jaw movement varies considerably, the same snake showing different excursions of the mandible in different bouts, and different species showing marked differences in the extent of mandibular movement, as shown in Table 3. These differences in posture are critical to one's expectations of how the snake can be driving water flow. Snakes that keep their heads and bodies above the water, the mouth nearly closed, and move the tongue in and out of the lingual groove present a mechanical problem different from snakes that drink by immersing their entire head in the water and using large movements of the lower jaw but never actually closing the mouth.

DISCUSSION

Our data suggest that the mechanisms invoked to explain how snakes drink depend on behavioral features as well as physical events. Kardong and Haverly ('93) analyzed drinking by a number of boas that immersed only the tip of the snout and lower jaw in the water and moved their tongue tips in and out of the lingual groove. Their explanation, supported by pressure data and kinematic data from films and radiographs, was that the snakes used a buccal pump—alternating suction and compression—to drive water into the esophagus. Further study of *Boiga* (Berkhoudt et al., '95) did little to raise serious questions about the buccal-pump model because *Boiga* drinks in a manner similar to *Boa*, but without tongue movement and with more marked opening and closing of the mouth. Only the *Boa* study examined performance of the system, but the performance data were not considered in the model. All other data supported a suction and compression mechanism.

Our EMG, kinematic, pressure, and performance records show that when other species of snakes drink, they use a limited number of muscles to generate small cyclic movements that move limited amounts of water. The volumes of water moved per cycle argue against sole use of the suction-compression buccal-pump model of Kardong and Haverly ('93) and Bels and Kardong ('95). As noted previously (Cundall, 2000), water flow can be unidirectional and continuous, bidirectional and cyclic, and have net inward or, more rarely, outward flow. Opening and closing movements of the jaws vary among species but appear less variable than water flow. Combining all our data, we can provide tests of the hypotheses outlined in the introduction that grew out of the buccal-pump model.

Tests of Previously Proposed Hypotheses

The first hypothesis, that flow of water into the mouth correlates with mouth opening, is consistent with some but not all of our data. For parts of some immersions, flow is essentially continuous. Hence, an alternating suction-compression mechanism cannot be operating some or all of the time. The second hypothesis, that pressure increases during mouth closing, was also not supported by our records of pressure changes in *N. rhombifer*. As shown in Figure 8, oropharyngeal pressure could peak during opening, the opposite of predictions from the buccal-pump model. The third hypothesis, that oropharyngeal and esophageal pressure changes are slightly out of phase, was not supported. Our records show that relationships between the two cavities are complex and the timing of pressure changes is variable, even within a single bout. The fourth hypothesis, that bone movements are correlated with muscle activity patterns, is largely supported by our data, which also emphasize how little activity is actually required of most jaw adductors during drinking and how some muscles, such as the pterygoideus, may be activated to serve partly as solid pressure plates (see "Sponge Model of Drinking in Snakes" below). Our data for intermandibular muscles suggest that the posterior ones appear to act as elevators/compressors of the floor of the mouth during drinking, whereas the anterior ones may serve to prevent lateral abduction of the mandibular tips by pterygoideus activity. Finally, although some snakes appear to seal the margins of the mouth for short periods, others never close the mouth and yet inward flow of water continues. Hence, mouth sealing appears not to be necessary for driving water flow.

Sponge Model of Drinking in Snakes

Our data show that snakes drink using a variety of kinematic patterns but with generally similar patterns of bone movement. To account for all of the data at hand, a model that does not necessitate sealing the mouth is needed. We suggest that, in addition to periodic use of the buccal-pumping mechanism proposed by Kardong and Haverly ('93), part of the mouth of snakes acts like a sponge. Rhythmic squeezing and relaxation of the sponge drives water, the direction of water movement being dependent on the distribution and dynamics of fluid pressure in the system. Hence, the key to drinking in snakes lies in the anatomy of the oropharyngeal and esophageal cavities and their associated structures, just as chemical transfer from tongue tips to squamate vomeronasal organs appears to depend critically on the anatomy and hydraulic properties of the anterior oral cavity (Filoramo and Schwenk, 2009).

Elements of the model are as follows. The region of the mouth anterior to the rictus oris (angle of the mouth, which lies at the anterior edge of the adductor muscles, well anterior to the jaw joint) serves as the entry area and functions largely in channeling water to the rear half of the oral cavity. In some snakes, only the lingual groove in the mental scale need be in contact with water to allow entry into the anterior channels of the paratracheal gutter. The rear half of the mouth contains expanded sponge-like regions of the paratracheal gutters, which are overlain by the pterygoids and pterygoideus muscles. As shown in Figure 4, the dorsal mucosa around the pterygoid tooth row is folded, providing an increased sponge volume when pushed against the paratracheal gutter. Sponge filling will occur by a combination of forces, including those arising from expansion of spaces among mucosal folds. Sponge compression will drive water out of the sponge in directions determined by the organization of channels, which run predominantly anteroposteriorly, and by the direction in which compressive forces are applied. If compression occurs from anterior to posterior, it will tend to drive water posteriorly. Simply squeezing the posterior part of the oral cavity should tend to force water both rostrally and caudally. Some of the water forced caudally will enter the esophagus, the amount presumably being dependent on the volume of water already in the esophageal paratracheal gutter.

To drive water through the oral cavity against the force of gravity should require pressure. Given the width of the oral

cavity and esophagus in all of the snake species examined, gut-like peristalsis is not likely to operate. Instead, simple dorsoventral and mediolateral movements of the floor and roof of the cavities must suffice to squeeze their sponge-like mucosal linings. A simple model made from microscope slides and a piece of sponge showed that water is readily moved uphill by simply compressing the sponge in an uphill direction (Fig. 10). It is therefore useful to note that the posterior intermandibular muscles fire after the anterior intermandibular muscle at the end of closing and beginning of opening, which should clear water out of the posterior oropharynx. This might also explain why pressure in the posterior part of the oral cavity could rise as opening occurred. However, as expansion of the region occurs later in opening, water will be drawn from more anterior regions. Compression in any part of the sponge system would force water along channels of lower pressure, as suggested by the hydraulic model for stage I chemical delivery in squamate vomeronasal systems (Filoramo and Schwenk, 2009). We think that the mouth of snakes uses its compressive ability in both mediolateral and dorsoventral planes to modulate water flow.

Our data—and those of Kardong and Haverly ('93) and Berkhoudt et al. ('95)—suggest that mandibular movement drives sponge filling and draining. The anterior tips of the mandibles appear to move only dorsoventrally. However, the caudal ends of the mandibles move dorsoventrally and mediolaterally, and the mandibles rotate around their long axis. Because the mandibles of most alethinophidian snakes are curved to varying degrees (Cundall and Irish, 2008), long-axis rotation of the mandibles shown in radiographs (Kardong and Haverly, '93) would allow the middle of the mandibles to regulate mediolateral compressive forces on the sponge area between the mandibles and the linguotracheal ridge (Fig. 11), independently of the anterior and posterior ends of the former. Fluid flow would depend on combined effects of bone and muscle excursions on changing volumes of spaces between mucosal folds and between the roof and floor of the mouth.

Although the oral mucosa has a number of properties distinctly not sponge like, its arrangement of spaces matches some features of sponges, suggesting it may behave in a similar physical manner. Very small spaces allow adhesion and flow driven by surface tension (capillarity), whereas larger spaces are filled only when external forces exceed those of surface tension and adhesion. The key to sponge behavior apparently lies in the relative distribution of large and small spaces and the compressibility of the entire volume; that is, the material housing small spaces must be as compressible when loaded with fluid as is the material around large spaces. Although there appears to be little published information on the physical properties of simple elastic sponges and the forces involved in acquiring and releasing fluids (Vogel '81, 2003), our simple tests with artificial sponges (Fig. 10) and with rates of water movement in capillary tubes suggest that the frequency of jaw cycling during drinking

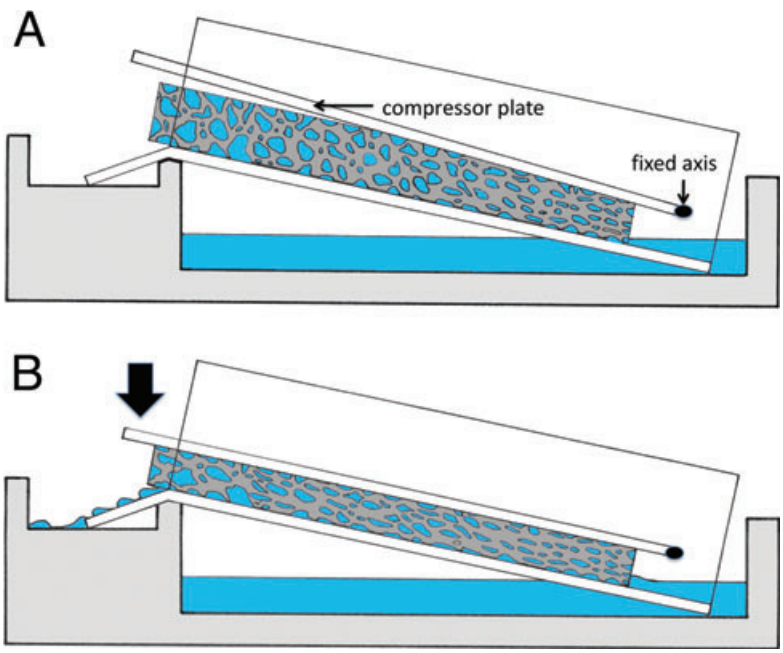

Figure 10. A sponge model of water transport in snakes. By keeping the lower end of the sponge partially compressed, simple up-and-down movement of the other end of the compressor plate drives water upward and over the edge of the floor of the sponge chamber.

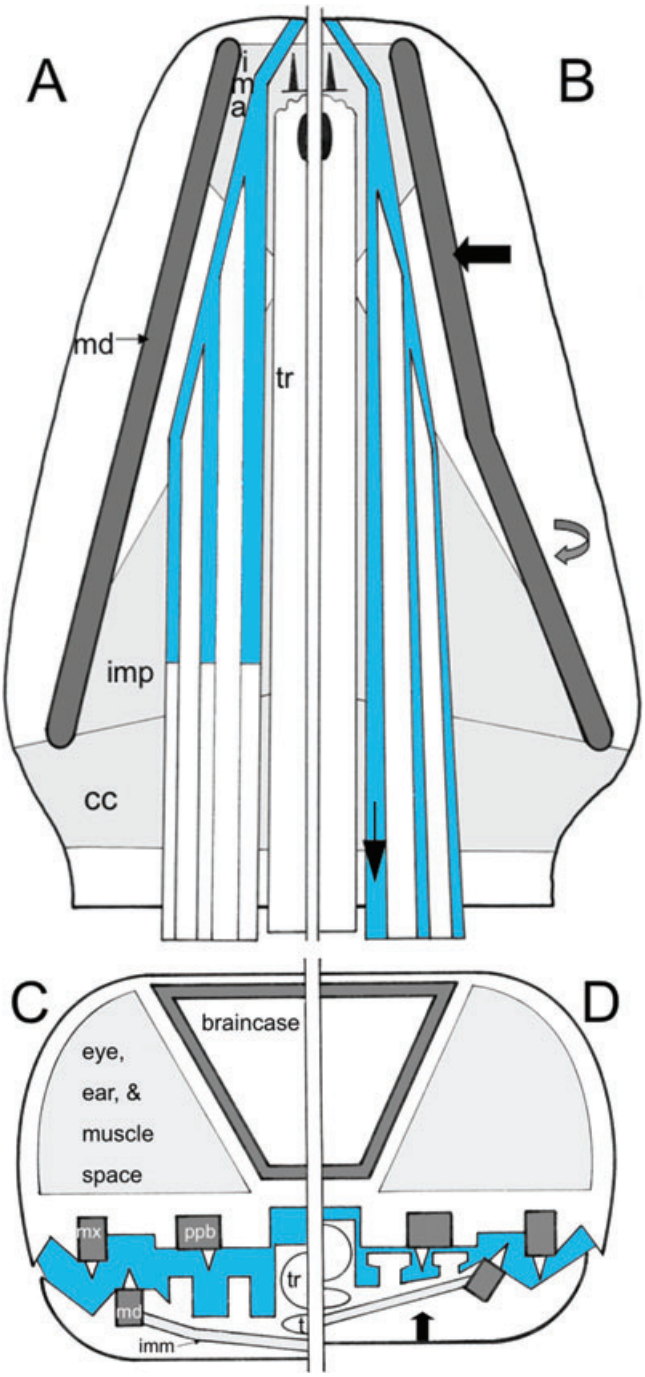

Figure 11. Diagrammatic summary of the sponge model of snake drinking. (A and B) The lower jaw and associated soft tissues in dorsal view, (C and D) cross-sectional views of the middle of the head. Bone is shown in dark gray, muscle and some other soft tissues in light gray, and the water medium in blue. In A, water has filled the anterior part of the paratracheal gutter. In B, constriction of the anterior paratracheal gutter has forced water caudally. Water may flow through smaller spaces in the paratracheal gutter by capillarity, and fill larger spaces through hydrostatic pressure arising from compression of the oropharyngeal and intermandibular spaces through muscle contraction. The model links kinematic, electromyographic, and pressure data with the anatomical data presented in Figures 2–4. A and C show the opening phase, during which water fills the paratracheal gutter and part of the oropharyngeal space. Closing the mouth (B and D) constricts the intermandibular space and raises the floor of the mouth, compressing the paratracheal gutter and oropharyngeal cavity against the roof of the mouth, which may be stiffened by slight contraction of the dorsal constrictors and pterygoideus (not shown). Anterior-to-posterior directed increases in hydrostatic pressure force water caudally along the gutter and into the esophagus. cc, constrictor colli muscle; ima, intermandibularis anterior muscle complex; imm, intermandibularis muscles; imp, intermandibularis posterior muscle complex; md, mandible; mx, maxilla; ppb, palatopterygoid bar; ptg, paratracheal gutter; t, tongue sheath and tongue; tr, trachea.

in snakes (Table 4) is a function of the time required for optimal sponge filling and clearance. The snake mouth presents a much more elaborate problem than these models in that its lining is not only elastic but also coated with mucus, which must influence water flow across the surface.

Sponge filling occurs when any externally applied compressive force is released. Releasing compression in one area allows flow from more compressed areas. Although it seems unlikely that snake mouths behave like glass capillary tubes, simple tests with capillary tubing suggested that, at angles approximating those assumed by snakes when drinking, water moves 2 cm up

a tube with an inner diameter of 0.4 mm in approximately 0.7–1.4 sec. In the snake mouth, the sponge-like floor and roof of the posterior oropharyngeal cavity can be compressed by combinations of tensing the pterygoideus, depressing the pterygoid, and raising the floor (Fig. 11). In effect, the medial upper jaws (i.e., palatopterygoid bars) and pterygoideus muscles act as a dorsal compressor plate, the intermandibular muscles, constrictor colli, neurocostomandibularis, and hyoid apparatus act as a series of ventral compressor plates, the mandibles act as lateral compressor plates, and the trachea and tongue act as a medial compressor plate (Fig. 11). Mouth closure is accompanied by lateral movements of the quadrates and posterior ends of the mandibles combined with activity of the posterior intermandibular muscles in the latter part of closing. Activity of the anterior intermandibular muscles during most of opening and early closing may tense the anterior intermandibular space but, more importantly, may prevent lateral movements of the tips of the mandibles that might reduce the potential of the anterior paratracheal gutters to act like a wick.

Angled transverse ridges of mucosa that might act as valves at the posterior margins of the pterygoids appear to lie well anterior to the level of the esophageal sphincter proposed by Bels and Kardong ('95), a feature that, like Bels and Kardong, we could find no structural evidence for. The paratracheal gutter is continuous from the oropharyngeal cavity to the esophagus, but, during drinking, we assume the width of the grooves is varied dynamically, primarily in the region from the rictus oris to the jaw joint. Caudal to the jaw joint the esophagus remains flattened, broad, and draped over the trachea and tongue. The mid-dorsal region of the anterior esophageal mucosa is not highly folded, with folding being most prominent ventrolaterally. However, it is probably sponge-like in behavior throughout its collapsed length. Illustrations in Bels and Kardong ('95) suggest that fluid fills the width of the esophagus. Their Figure 1C suggests that the posterior oropharynx is periodically cleared of most fluid, a feature that should not occur if the region were behaving like a sponge. An alternative is that compression of this postrictal region is more efficient than we currently assume to be possible.

To summarize our model, water enters the mouth during depression of the anterior part of the lower jaw and flows into the grooves between the major folds of the mucosa in the paratracheal gutter (Fig. 11A, C). Initial medial movements of the pterygoid and posterior part of the lower jaw at the beginning of opening compress the caudal sponge region medially but continued adduction of the quadrate combined with ventrolateral rotation of the middle of the mandible gradually relax tension on the inferior oral mucosa and allow filling of the space beneath the pterygoideus. As the mouth closes and begins compression of the anterior sponge region, the posterior part of the oropharyngeal cavity is compressed by being stretched laterally as the quadrates move laterally and by shortening of the anterior trunk constrictors (e.g., neurocostomandibularis, constrictor colli) that raise the floor of the mouth. As this happens, the anterior grooves are squeezed by the palatopterygoid dental mucosa being pushed against the paratracheal gutter (Fig. 11B, D). During the terminal phases of closure, the posterior intermandibular muscles aid in raising the floor of the oropharynx while at the same time providing some of the force driving the jaw joint medially during the beginning of mouth opening.

The difference between the timing of pressure changes in our recordings as compared to those of Kardong and Haverly ('93) undoubtedly relate to exact placement of the transducer tips. Their anterior transducers were well anterior to the rictus oris, whereas our oropharyngeal transducers were located near the caudal edge of the postrictal sponge region. This location is just anterior to Kardong and Haverly's posterior transducers, which, judging from their Figure 1, lay in the extreme anterior part of the esophagus. Berkhoudt et al. ('95) show no original pressure data but give pressure values for the middle and end of the immersion. Their summary diagram of the buccal-pump model shows pressure as a sine wave, a waveform we never recorded in *Nerodia* in either the oropharynx or esophagus.

Most of the records for the snakes recorded in this study reflect effects of a limited size range that characterize many species of snakes (Boback and Guyer, 2003). As snakes become larger, the effectiveness of the sponge-like nature of the paratracheal gutter may decrease and some of the features of the suction-compression buccal-pump model should be recruited. However, *Varanus* with heads about twice the length of the heads of the snakes used in our study drank about 0.5 mL/cycle (Smith, '86), volumes roughly equivalent to those of snakes. The mucosa of the buccal floor of some lizards is moderately folded (Schwenk, '88), and this folding was considered an integral part of the mechanism of drinking in *Lacerta*, although performance was not measured (Bels et al. '93). Both *Lacerta* and *Varanus* depend on head elevation and gravity to drain the oropharyngeal cavity. Regardless of size, performance measures will be critical in evaluating models of drinking.

Critical features in support of our model are the slow rate of jaw cycling and the small volumes of water moved per cycle. Other recorded vertebrate mechanisms for overcoming the effects of gravity (Prakash et al., 2008; Reis et al., 2010) require much faster cycling rates. In all cases, however, the critical behavioral properties of the animals are constrained by the unique features of the structures involved in water transport. In the case of macrostomatan snakes, much of the anatomy of the lower jaw apparatus appears to have evolved in response to the demands of increasing surface area to surround large prey. The extraordinary folding of the mucosal floor of the oropharyngeal cavity that provides the sponge-like properties of their drinking apparatus suggests that the sponge mechanism likely represents an exaptation (Gould and Vrba, '82) of a tissue region that evolved primarily to stretch around relatively large prey. Drinking in

basal (i.e., nonmacrostomatan) snakes might allow tests of this hypothesis.

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Appendix 1

Histological material (Lehigh University microscope slide collection; slide series numbers after species names)—*Agkistrodon piscivorus*, late embryo 290, juvenile 339; *Heterodon platirhinos*, juveniles 332, 335; *Nerodia fasciata*, juvenile 314; *N. sipedon*, juvenile 179; *Pantherophis spiloides/alleghaniensis*, 125–126. Related taxa examined: *Regina septemvittata*, 175, 176, 206–207; *Thamnophis sauritus*, juvenile 168; *Thamnophis sirtalis*, juveniles 131, 155–156, 163, 171–172. (Most slide series are serial sections.)

Gross anatomical material (LU = Lehigh University; MC = Matthew Close personal research collection)—Skeletal specimens studied: *Agkistrodon piscivorus* (LU 2156, 2167); *Heterodon platirhinos* (LU 844, 1121, 1426); *Nerodia rhombifer* (LU 2291, 2293); *Pantherophis alleghaniensis/spiloides* (LU 1427, 2175, 2269). Alcoholic specimens dissected: *Agkistrodon piscivorus* (LU 2223–24, 2515); *Heterodon platirhinos* (LU 2456–61); *Nerodia rhombifer* (LU 2338–41, 2374–76); *Pantherophis spiloides* (LU 2525–2528); *Broghammerus* (= *Python*) *reticulatus* (MC PYRE 02, 04). Alcoholic specimens sectioned: *Agkistrodon piscivorus* (LU 2320, 2321, 2529); *Crotalus atrox* (LU 2524); *Farancia abacura* (LU 2330); *Nerodia fasciata* (LU 2322); *N. rhombifer* (2517, 2518); *N. sipedon* (LU 2519); *Pantherophis spiloides* (LU 2530); *Python bivittatus* (LU 1093); *Xenopeltis unicolor* (LU 2400).