

ELECTROMYOGRAPHIC PATTERN OF THE GULAR PUMP IN MONITOR LIZARDS

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ABSTRACT. Gular pumping in monitor lizards is known to play an important role in lung ventilation, but its evolutionary origin has not yet been addressed. To determine whether the gular pump derives from the buccal pump of basal tetrapods or is a novel invention, we investigated the electromyographic activity associated with gular pumping in savannah monitor lizards (*Varanus exanthematicus*). Electrodes were implanted in hyobranchial muscles, and their activity patterns were recorded synchronously with hyoid kinematics, respiratory airflow, and gular pressure. Movement of the highly mobile hyoid apparatus effects large-volume airflows in and out of the gular cavity. The sternohyoideus and branchiohyoideus depress, retract, and abduct the hyoid, thus expanding the gular cavity. The omohyoideus, constrictor colli, intermandibularis, and mandibulohyoideus elevate, protract, and adduct the hyoid, thus compressing the gular cavity. Closure of the choanae by the sublingual plicae precedes gular compression, allowing positive pressure to be generated in the gular cavity to force air into the lungs.

The gular pump of monitor lizards is found to exhibit a neuromotor pattern similar to the buccal pump of extant amphibians, and both mechanisms involve homologous muscles. This suggests that the gular pump may have been retained from the ancestral buccal pump. This hypothesis remains to be tested by a broad comparative analysis of gular pumping among the amniotes.

INTRODUCTION

Monitor lizards (genus *Varanus*) have recently been found to supplement their lung ventilation with gular pumping during locomotion (Brainerd and Owerko-

wicz, 1996). In a gular pump cycle, a monitor lizard first draws fresh air into its large pharyngeal (gular) cavity and then contracts its throat muscles to create positive pressure, thus forcing air into the lungs. Multiple gular pumps may occur in succession between costal breaths. Gular pumping has been shown to significantly increase both minute ventilation and aerobic capacity of savannah monitor lizards (*Varanus exanthematicus*) during exercise (Owerkowicz et al., 1999).

Little is known about the actual mechanism of gular pumping and its evolution. A highly expandable pharynx, supported by an elaborate hyobranchial basket, is a characteristic feature of monitor lizards. The large size and compressibility of the pharynx make it ideally suited for pumping large volumes of air. Smith (1986) studied the function of throat musculature in *V. exanthematicus* during feeding, and recorded hyobranchial muscle activity and hyoid movements. Bels et al. (1995: 99) provided a kinematic analysis of the throat threat display in *Varanus griseus*, "a ventilatory bucco-pharyngeal breathing pump (VBPPB)," consisting of alternating expansions and compressions of the gular cavity. These studies have documented the extreme excursions of the hyoid apparatus during a wide repertoire of monitor behaviors. However, the electromyographic (EMG) signature of the gular pump, as a ventilatory mechanism, has not been reported.

This study aims to determine how throat muscle activity is coordinated during gular pumping in *V. exanthematicus*. Which

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muscles are responsible for gular expansion, and which ones are responsible for compression? How is pressure generated in the gular cavity? What controls the air-flow pattern?

The evolutionary origin of the gular pump also presents an interesting dilemma. Squamates have been presumed to ventilate their lungs solely by means of costal aspiration (Gans, 1970; Carrier, 1987; but see Deban et al., 1994); they rely on contraction of intercostal muscles to create negative pressure in the pleural cavity to suck air into the lungs. The use of a pressure pump was thought to be reserved for air-breathing fish and amphibians (Liem, 1985; Brainerd et al., 1993). In this mechanism, air is gulped into the buccal (mouth) cavity, and subsequently the hyoid apparatus generates positive pressure, forcing air into the lungs. The gular pump of monitor lizards clearly qualifies as a pressure pump and therefore breaks with this traditional phylogenetic separation of breathing mechanisms. However, the gular pump differs from the buccal pump because the hyoid apparatus of monitor lizards is positioned posteriorly in the throat, whereas the hyoid apparatus of amphibians resides in the mouth cavity between mandibular rami. The presence of gular pumping behavior has not been rigorously investigated in other lizard genera, and it is unclear whether gular pumping is a uniquely derived trait of monitor lizards or whether its ancestry can be traced back to buccal pumping of basal tetrapods.

Therefore, this study attempts to address the origin of gular pumping from a functional perspective. How similar is the EMG pattern of the gular pump to that of the amphibian buccal pump? Is the gular pump a case of neuromotor conservatism in evolution, or has it evolved *de novo* in monitor lizards?

MATERIALS AND METHODS

Animals

Experiments were performed on four savannah monitor lizards (230–2,400 g)

during and immediately after locomotion on a motorized treadmill at speeds of 1–5 km/h. The animals were maintained at 25–40°C on a 14:10 hour light:dark photoperiod and were fed a diet of mice.

Terminology

This study follows the terminology of Smith (1986) in her description of the osteology and myology of the varanid gular region.

Videoradiography

Videos of the lizards were taken with a Sony DCR VX1000 digital camcorder (60 fields/s at 1/250 s shutter speed) and the Siemens X-ray fluoroscope at the Museum of Comparative Zoology Laboratories at Harvard University. Video recordings were made separately in lateral and dorsoventral projections. Select video fields were imported into Adobe Photoshop on a Power Macintosh computer.

To better visualize movements of the floor of the mouth relative to the skull and hyoid, lead markers (1.6 × 0.5 mm) were placed unilaterally in the left sublingual plica and in the anterior epithelial border of the left choana. Marker implantation was performed percutaneously with a 20-gauge needle and plunger while the animals were under 1–2% halothane anesthesia.

Pneumotachography

Two animals were used to measure air-flow during gular pumping. A lightweight mask, fashioned from clear acetate and epoxy, was custom-fitted and taped over the lizard's snout to enclose the mouth and nostrils. A bias flow of humidified air (1,200 ml/min) was drawn through the mask. A pneumotachograph (8421 series 0-5 LPM, H. Rudolph, Kansas City, Missouri), connected to a differential pressure transducer (MP 45-1-871, Validyne, Northridge, California) downstream from the animal, measured airflow through the mask. The system was calibrated against

repeated injections of measured aliquots of air into the mask.

Pressure Recordings

Two animals (not used for airflow recordings) were instrumented to measure gular pressure during gular pumping. With the animal under 1–2% halothane gas anesthesia, a skin incision was made between the ceratohyal and ceratobranchial. The underlying muscles were carefully blunt-dissected and a 13-gauge needle was inserted through the pharyngeal epithelium into the gular cavity. A 20- to 30-cm-long polyethylene cannula (1.14-mm inner diameter, 1.57-mm outer diameter), previously sterilized and heat-flared at the distal end, was threaded through the hole and securely sutured to the lateral wall of the gular cavity. Before each recording session, the cannula was cleared of mucus to prevent capillarity artefacts and connected to a differential pressure transducer (PX138-0.3D5V, Omega Engineering, Inc., Stamford, Connecticut). The pressure transducer was calibrated against 10 cm H₂O after each recording session.

Electromyography

Electromyographic activity was recorded in the following muscles: constrictor colli, intermandibularis, mandibulohyoideus, omohyoideus, sternohyoideus, and branchiohyoideus. Patch and sew-through bipolar electrodes, as detailed by Loeb and Gans (1986) and Carrier (1996), respectively, were constructed of 0.28-mm-diameter Teflon-coated stainless steel wire (Cooner Wire Co., Chatsworth, California) and silastic-reinforced sheeting (Specialty Manufacturing, Inc., Saginaw, Michigan). In each electrode, the exposed portions of wires were 2 mm long and 1 mm apart. With the animal anesthetized, electrodes were surgically implanted and firmly anchored in the desired muscles. The electrode wires were then passed subcutaneously under the pectoral girdle to a single exit on the trunk's dorsum and soldered to connectors (Microtech, Inc., Boothwyn,

Pennsylvania). The signals were amplified 5,000–20,000 times (as appropriate for each channel) with Grass P511J amplifiers (Quincy, Massachusetts), with a bandpass of 100–1,000 Hz (with the 60-Hz notch filter in). The signals were acquired at 5,000 Hz and analyzed on a Power Macintosh computer using AcqKnowledge (BioPac Systems, Santa Barbara, California) and Igor Pro (WaveMetrics, Inc., Lake Oswego, Oregon) software. Electromyographic and pressure signals were temporally synchronized with video recordings by means of a light-emitting diode trigger (Thexton Unlimited, London, United Kingdom).

RESULTS

Kinematics

Four stages of hyobranchial movement characterize each gular pumping cycle (Fig. 1): resting, active expansion, early closure, and compression. The cycle usually begins with the expansion of the hyobranchial basket. From its resting position (Fig. 1A), the basihyoid and the lingual process are drawn slightly ventrad and caudad. The anterior processes are abducted and, pivoting on the basihyoid, swung laterad. The ceratohyals and ceratobranchials rotate to assume a more vertical orientation (Fig. 1B).

The compressive phase of the pump cycle begins with the elevation of the buccal floor to abut the palate, thereby closing off the mouth and nostrils. As highlighted by radiopaque markers, each choana is occluded by its ipsilateral sublingual plica. The glottis is located in the gular cavity, while the hyoid remains in a retracted and expanded configuration (Fig. 1C). Finally, the basihyoid is protracted and elevated, while the trachea slides rostrad in the gular cavity. The anterior processes are adducted, and the ceratohyals and ceratobranchials fold horizontally (Fig. 1D). The hyobranchium then relaxes and passively returns to its resting state (Fig. 1A); another pumping cycle may follow.

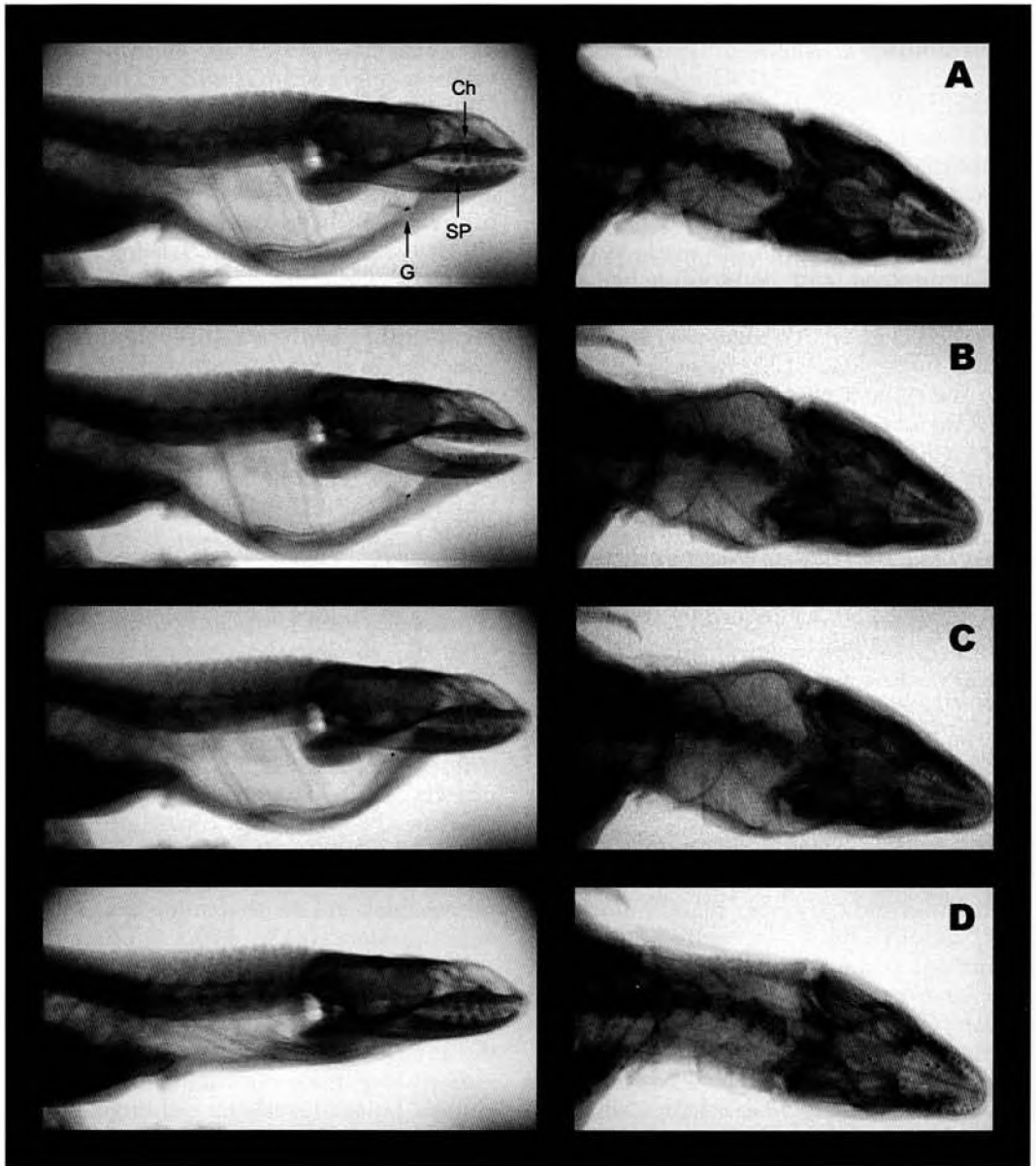


Figure 1. Still frames from an X-ray positive video (shutter speed 1/250 s) showing one gular pump cycle in *Varanus exanthematicus* (body mass = 600 g). The left column shows the animal in lateral projection, the right column in dorsoventral projection. Although not recorded simultaneously, frames in each row portray corresponding stages of a pump cycle. (A) Gular cavity relaxed. (B) Gular cavity expanded. (C) Buccal floor elevated. (D) Gular cavity compressed. Radiopaque markers (arrows) are placed at the choana (Ch), the sublingual plica (SP), and the glottis (G). Note the closure of the mouth and nares, which seals the gular cavity, as demonstrated by proximity of markers Ch and SP in (C).

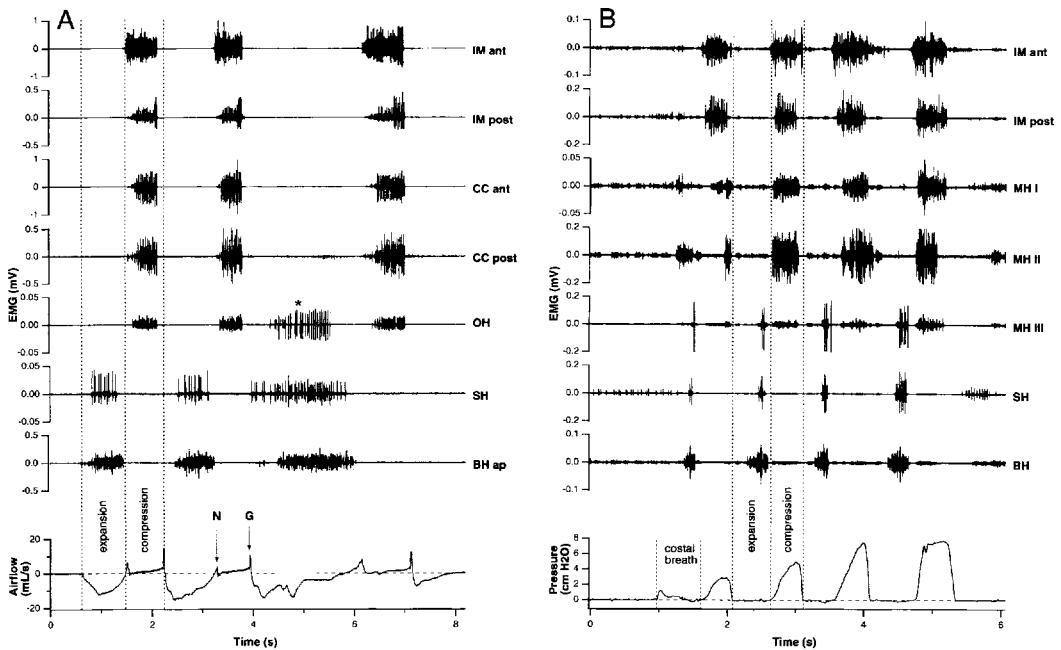


Figure 2. Raw electromyograms of hyobranchial muscles during gular pumping in *Varanus exanthematicus*. (A) Three gular pump cycles recorded simultaneously with airflow at the snout. Gular expansion (negative airflow) is initially passive because of the gravitational drop of the hyoid, and then active as the branchiohyoides and sternohyoides begin to contract. Gular compression occurs during the zero-flow plateau, as air is pressed into the lungs. Minimal air leakage occurs—note the spikes showing early closure of the nares (N) and the late closure of the glottis (G). The asterisk indicates unanticipated activity of the omohyoideus due to neck bending. (B) A costal breath followed by four successive gular pump cycles, recorded simultaneously with gular pressure. Gular expansion generates little negative pressure, but peak compressive pressures up to 15 cm H₂O have been recorded. *Abbreviations*: CC, m. constrictor colli; IM, m. intermandibularis; MH, m. mandibulohyoideus; BH, m. branchiohyoides (ceratohyoid head); BH ap, m. branchiohyoides (comuhyoid head); SH, m. sternohyoideus; OH, m. omohyoideus; ant, anterior; post, posterior.

Active expansion was not observed in every pump cycle. The animals often chose to proceed to closure and compression directly from the resting stage, in which case the volume of air pumped was not as great as when preceded by active expansion. Furthermore, resting gular volume was dependent on the positioning of the hyobranchial apparatus in the neck of the animal, which varied with the animal's posture and muscle tone of associated pectoral musculature (sternohyoideus and omohyoideus—see below).

Airflow

The airflow pattern at the animal's mouth and nostrils (Fig. 2A) is consistent with a biphasic nature of each gular pump, whereby a filling (expansive) phase is im-

mediately followed by an emptying (compressive) phase. Average filling volumes ranged from 6 to 15 ml, but individual gular inspirations up to 33 ml were also recorded. Early in the pump cycle, animals were observed to rely on passive filling of the gular cavity by gravitational drop of the hyoid (correspondent to the return of the hyoid from compressed to resting stage). Passive filling was followed by active expansion, as indicated by concomitant activity in the branchiohyoides and sternohyoideus, which resulted in faster (more negative) airflow and greater filling volumes.

Early in the filling phase, airflow into the gular cavity was rapid, as shown by the steep descent of the airflow trace to its minimum value. Late in the filling phase, inspiratory airflow gradually diminished to

nil. A slight overshoot of the zero-flow line (N in Fig. 2A) marked early closure of the mouth and nostrils, and the beginning of the emptying phase. A zero-flow plateau was recorded for the duration of the emptying phase, as air was forced from the gular cavity into the lungs. The emptying phase terminated in a small expiratory spike (0.5–1.0 ml), after the inferred closure of the glottis (G in Fig. 2A) and opening of the mouth and nares. Unless another pumping cycle occurred immediately afterwards, passive filling followed and a longer apnoic period ensued.

Pressure

Each costal breath was followed by as many as five gular pumps, with successive pump cycles generating increasingly positive gular pressures (Fig. 2B). Peak pressures up to 15 cm H₂O were recorded. With the onset of each compressive phase, gular pressure climbed steeply and reached peak pressure within 200 milliseconds. For most pumping cycles, gular pressure hovered within 5% of peak value for less than 100 milliseconds, although gular pressure would sometimes remain elevated at peak for up to 400 milliseconds. Thereafter, gular pressure dropped rapidly (within 100 milliseconds), often dipping to subatmospheric levels, and then equilibrated with the atmospheric pressure.

Gular pressure varied little from atmospheric pressure during the filling phase of a pump cycle. Active gular expansion generated only slightly subatmospheric pressures (–0.2 to –0.4 cm H₂O).

Electromyographic Activity

Recordings from hyobranchial muscles produced a consistent activity pattern during gular pumping (Fig. 2A, B). Although they remained quiescent during passive filling, branchiohyoideus (both cerato- and cornuhyoid heads), sternohyoideus, and mandibulohyoideus III were turned on during active gular expansion. Onset of the branchiohyoideus was followed in 50–200

milliseconds by almost simultaneous activation of the sternohyoideus and mandibulohyoideus III. The intensity of their firing remained roughly constant while these muscles were active. All three muscles were turned off before the end of the filling phase, with activity in the branchiohyoideus persisting for up to 150 milliseconds after the offset of the sternohyoideus and mandibulohyoideus III.

Gular compression began with a burst of activity in the intermandibularis anterior, which was followed within 100 milliseconds by contraction of the constrictor colli, intermandibularis posterior, and all three heads of mandibulohyoideus. The intensity of their firing generally increased from onset to offset. Activity ceased in all muscles together, once gular pressure had peaked.

The activity of the mandibulohyoideus III was biphasic; it contracted during gular expansion and compression, but not continuously (Fig. 2B). It was briefly (50–100 milliseconds) silent between the two phases of the pumping cycle.

The omohyoideus was usually quiescent during gular pumping. When participating in gular pumping, the omohyoideus was predominantly active during gular compression. However, it might occasionally fire during gular expansion (° in Fig. 2A), which tended to decrease the gular filling volume. In such instances, activity of the omohyoideus was correlated with changes in posture and/or neck bending by the animal.

During locomotion, regular phasic activity was observed in most hyobranchial muscles, but was especially prominent in the sternohyoideus and omohyoideus. The rate of discharge was the same as the foot-fall frequency, and in the latter two muscles the signal amplitude was greater than in stationary animals.

DISCUSSION

Hyobranchial Muscle Function

The role of individual muscles involved in the gular pump can be inferred by con-

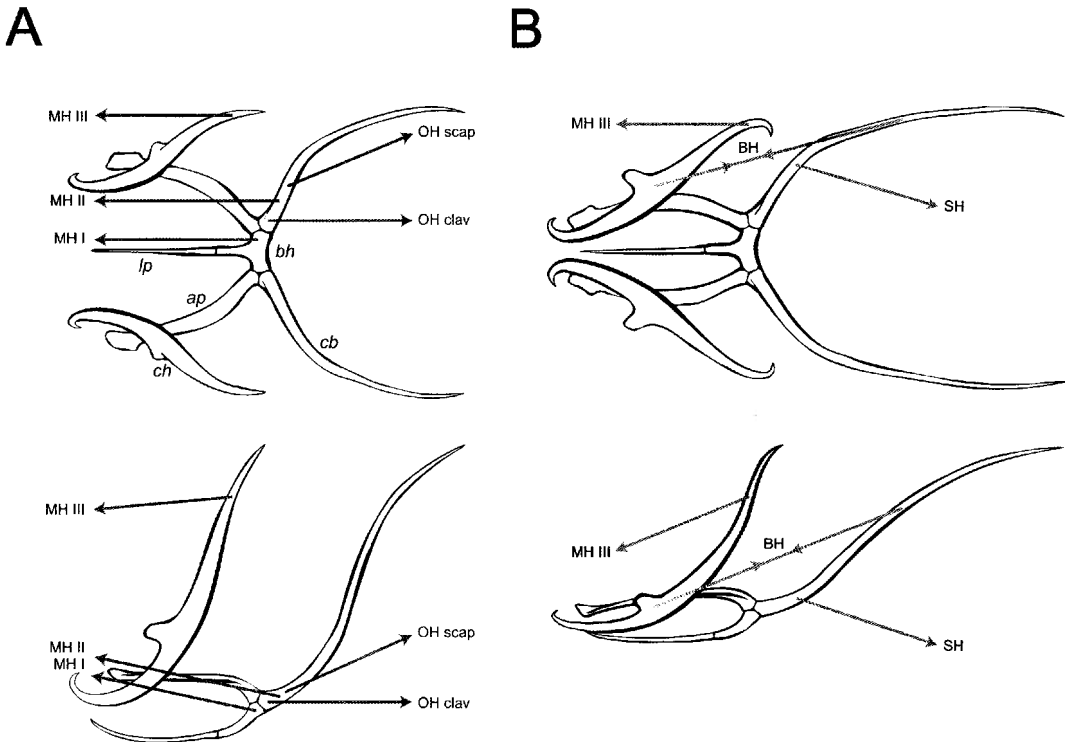


Figure 3. The hyobranchial apparatus of *Varanus exanthematicus*, in ventral (top row) and lateral (bottom row) views. Force vectors (gray arrows) show the sites of insertion and lines of action of the hyobranchial muscles, as measured in dissected specimens. (A) The hyoid in its expanded configuration; contraction of musculi (mm.) mandibulohyoideus and omohyoideus will result in hyoid compression. Constrictor colli and intermandibularis are not shown, because they do not insert directly on the hyoid. (B) The hyoid in its compressed configuration; contraction of the branchiohyoideus, sternohyoideus, and mandibulohyoideus III will result in hyoid expansion. *Abbreviations:* ap, anterior process; bh, basihyoid; cb, ceratobranchial; ch, ceratohyal; clav, clavicular; lp, lingual process; scap, scapular; others as in Figure 2.

sidering their insertion sites on the hyoid apparatus (Fig. 3), the patterns of their EMG activity, and the kinematics of the hyoid elements during each gular pump cycle.

Gular expansion results from the coordinated activity of the sternohyoideus, branchiohyoideus, and mandibulohyoideus III. The sternohyoideus pulls the ceratobranchial in a caudoventrad direction, giving it a more vertical orientation. This action tends to retract and depress the basihyoid, while pointing the lingual process ventrad. With the ceratobranchial stabilized by the sternohyoideus, the branchiohyoideus tends to abduct the anterior process and retract the ceratohyal. However, the proximal end of the anterior pro-

cess pivots about the basihyoid, and the ceratohyal has its distal end anchored to the lower jaw by the mandibulohyoideus III. The broad, loose nature of articulation between the ceratohyal and the anterior process allows sliding to occur between these two elements. Thus, as the anterior process swings laterad, it pushes against the ceratohyal, the angle between these two elements increases, and the ceratohyal assumes a more vertical orientation. Altogether, these muscles tend to expand the gular cavity in the lateral and dorsoventral dimensions.

Gular compression begins with the early closure of mouth and nostrils. The intermandibularis anterior, positioned under the sublingual plicae, contracts to elevate

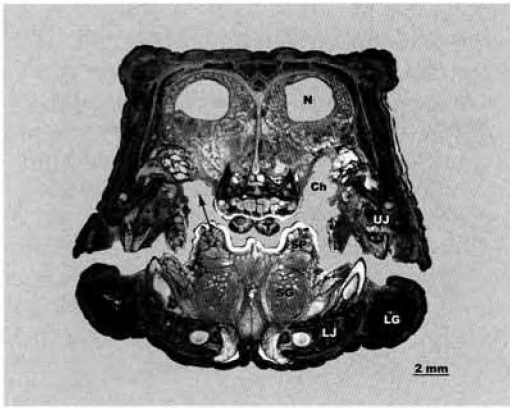


Figure 4. Cross section of the snout of *Varanus exanthematicus* at the anterior border of the choanae. Each nasal passage connects to its ipsilateral choana just posterior to this plane. Elevation of the mouth floor allows the sublingual plica to plug the choana above. The congruent outlines of the lower and upper jaws allow an airtight closure of the mouth, sealed with saliva from labial and sublingual glands. *Abbreviations:* Ch, choana; LG, labial gland; LJ, lower jaw; N, nasal passage; SG, sublingual gland; SP, sublingual plica; UJ, upper jaw.

the buccal floor and push the plicae against the choanae (SP → Ch in Fig. 4), thus blocking airflow through the nasal passages. Although no recordings were taken from the adductor mandibulae, this muscle is most likely to be responsible for keeping the mouth closed, while the thick, fleshy gums (Auffenberg, 1981) seal the oral margins with secretion of salivary glands lining both lingual and labial aspects of the lower jaw. The gular cavity is effectively made airtight for the duration of gular compression.

Muscles responsible for gular compression include the omohyoideus, constrictor colli, intermandibularis posterior, and mandibulohyoideus. The clavicular and scapular heads of the omohyoideus attach the ceratobranchials to the respective parts of the pectoral girdle, and their contraction retracts and elevates the basihyoid. The constrictor colli encircles the floor and sides of the gular cavity, forming a sleeve in which the hyobranchial basket is suspended. Together with its anterior extension, the intermandibularis posterior, this superficial transverse muscle elevates the

hyoid apparatus. On the other hand, the mandibulohyoideus connects the hyoid to the lower jaw and, along with the sternohyoideus and omohyoideus, controls its anteroposterior position in the neck. As the basihyoid is protracted, the ceratohyals and ceratobranchials assume a more horizontal orientation, in effect folding the hyobranchial basket. The orthogonal orientation of muscle fibres in the constrictor colli and intermandibularis to the mandibulohyoideus means that their synchronous activity will squeeze the air out of the gular cavity.

With the onset of locomotion, most hyobranchial muscles show bursts of activity in phase with the footfall pattern. This is particularly pronounced in the sternohyoideus and omohyoideus; their firing intensity during locomotion is several times greater than at rest. Yet it is hard to imagine their acting as locomotor muscles. It is more likely that with every retraction of the forelimb these muscles are stretched and fire reflexively to stabilize the hyoid, keeping it in position for pumping. Low-intensity phasic activity detected in other hyobranchial muscles is probably an artefact of cross-talk from the underlying axial muscles of the neck, participating in the lateral bending of the neck during locomotion.

Airflow and Pressure Changes

The pneumotachograph and the pressure transducer provide complementary information about the patterns of airflow and pressure generation outside and inside the gular cavity. During gular expansion, pressure drops only slightly below the atmospheric level. The lizard's mouth and nares are wide open (Fig. 1B) and provide little resistance to airflow into the gular cavity. Gular expansion, whether passive or active, is too slow for gular pressure to turn more negative; instead, it quickly equilibrates with atmospheric pressure.

Inspiratory airflow ceases when the mouth and nares are shut (see above). The "corking" of the choanae by the sublingual

placae expels an aliquot of air from the nasal passages (N in Fig. 2A). The gular pressure increases from this point on and air is pressed through the open glottis into the trachea and lungs. The plateau at zero-flow indicates the efficacy of the oral seal.

Only at the very end of compression does a puff of air leak out of the mouth and nares at a high flow rate (G in Fig. 2A). The hyobranchial muscles have already turned off by this time, yet their contraction clearly persists for approximately 120 milliseconds (a reasonable time period for slow-twitch fibers in isometric contraction) and gular pressure remains elevated. This expiratory "gular leakage" possibly represents excess air, which was not pressed into the lungs. The fact that this occurs at the end of every pumping cycle indicates that the glottis always closes before the nares open. Such carefully coordinated timing suggests that this may be a hard-wired mechanism designed to prevent air escaping from the lungs, which have been pressurized by gular pumping.

Origin of Gular Pumping

The gular pump of monitor lizards bears striking resemblance to the buccal pump of extant amphibians, in function and in mechanism. Both pumps generate positive pressure to force air from the pharyngeal cavity into the lungs. Both employ the hyobranchial apparatus to produce volumetric changes of the buccal and gular cavities. This similarity suggests that buccal pumping and gular pumping may be homologous behaviors. However, the derived morphology of the monitor lizards and their deeply nested position in the squamate phylogeny (Estes et al., 1988) suggest the possibility that gular pumping, as ventilatory behavior, may have evolved independently in monitor lizards. This alternative hypothesis would be supported by finding that the gular and buccal pumps are powered by nonhomologous muscles, or that the patterns of their activation are markedly different.

Lepidosaurs, especially the highly de-

rived varanids, do not necessarily possess the same ensemble of hyobranchial muscles found in Lissamphibia, and even among the latter, the muscular organization of the throat is highly variable. However, muscle homologies can be established with a fair degree of certainty by determining their anatomical relations and motor nerve supply (Fürbringer, 1888, in Cunningham, 1890). The constrictor colli of lizards and the interhyoideus of amphibians seem to be homologous, by virtue of having a common precursor in the constrictor hyoideus, as found among the Dipnoi (Edgeworth, 1935). Except for its lateralmost third head with a disparate motor innervation and therefore origin (Rieppel, 1978), the mandibulohyoideus is clearly a highly differentiated version of the geniohyoideus, ubiquitous among the vertebrates. The rectus cervicis of caecilians is homologous with the sternohyoideus in both frogs and monitor lizards. Lacking a pectoral girdle, caecilians lack an omohyoideus.

The branchiohyoideus is found in neither anurans nor caecilians. Its putative homologue, subarcualis rectus I (not the larval branchiohyoideus externus; Edgeworth, 1935, contra Smith, 1920), is present in urodeles, but the EMG activity of this muscle during buccal pumping is yet to be investigated. Nevertheless, EMG evidence from feeding studies in *Ambystoma* (Lauder and Shaffer, 1985; Reilly and Lauder, 1991) shows that the subarcualis rectus I is active during buccal expansion in aquatic and terrestrial prey capture, and its role in generating buccal expansion during suction feeding has been deduced from its anatomical position and fiber orientation in various salamanders (Erdman and Cundall, 1984; Lauder and Shaffer, 1988; Lorenz-Elwood and Cundall, 1994). This suggests that the subarcualis rectus I functions in much the same way in the buccal pump of salamanders as does the branchiohyoideus in the gular pump of lizards.

Having established the homology of hyobranchial muscles of amphibians and

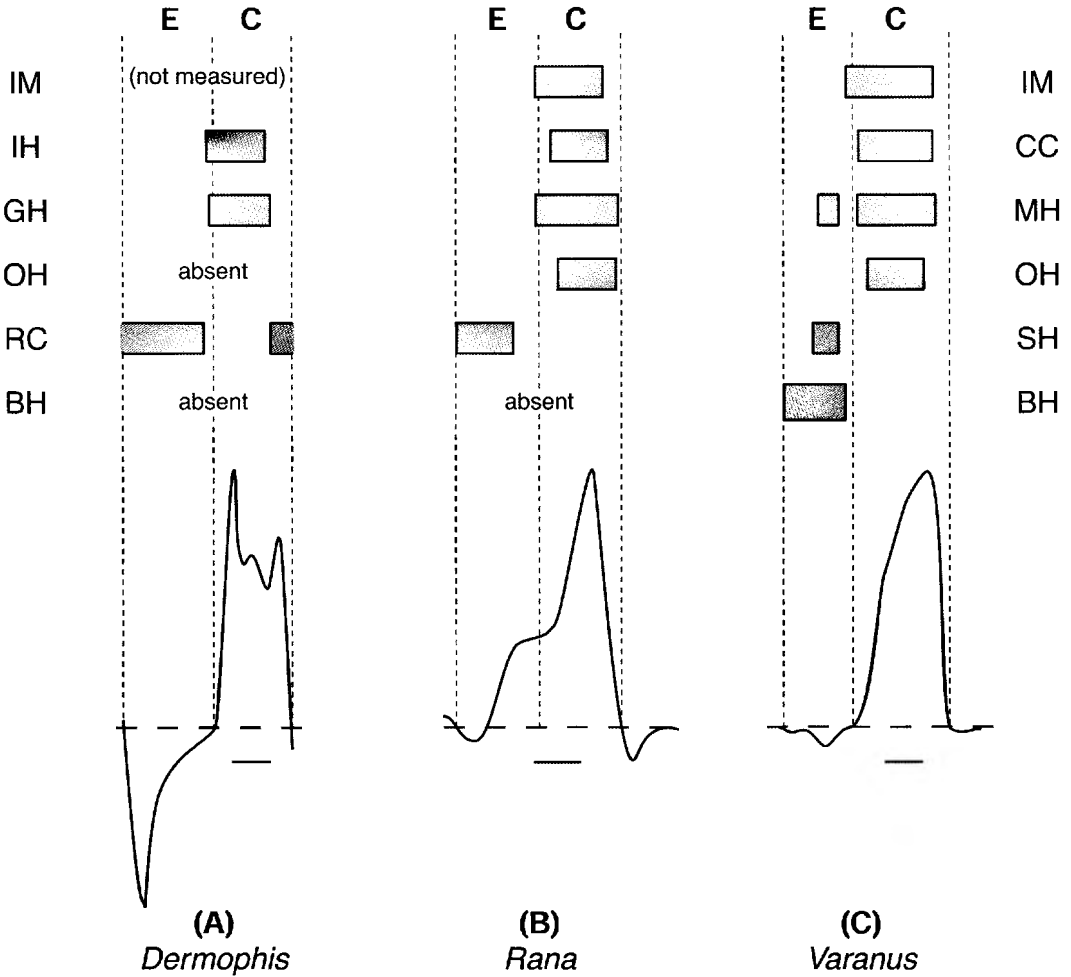


Figure 5. Comparison of hyobranchial muscle activity patterns during a single pressure pump cycle in (A) a caecilian (*Dermophis*), (B) a frog (*Rana*), and (C) a monitor lizard (*Varanus*). Homologous muscles are shown in the same row. Each pumping cycle (E + C) has been scaled to the same duration time (the scale bars are 0.2 seconds). Pressures (bottom trace) have been scaled to the same peak value; maximum peak pressures range from 4 cm H₂O (frog) to 15 cm H₂O (caecilian and monitor lizard). *Abbreviations*: E, active expansion; C, compression; GH, m. geniiohyoideus; IH, m. interhyoideus; RC, m. rectus cervicis; others as in Figure 2. (A) is modified from Carrier and Wake (1995); (B) is a composite of de Jongh and Gans (1969) and West and Jones (1974); and (C) is from this study.

lizards, it is possible to directly compare their activity patterns in the gular pump of *V. exanthematicus* and in the buccal pump of a caecilian (Carrier and Wake, 1995) and an anuran (de Jongh and Gans, 1969; West and Jones, 1974). Differences in pressure profiles aside, all three neuromotor patterns clearly are similar (Fig. 5). This suggests that homologous hyobranchial muscles function in much the same

way in these distantly related clades. Therefore, the homology of the gular and buccal pumping behaviors cannot be rejected.

Nevertheless, analysis of the present data does not allow us to conclude with confidence that the gular and buccal pumps are homologous behaviors. Neuromotor similarity is not sufficient to claim that a behavioral mechanism has been

conserved in evolution (Smith, 1994). Unlike other situations in which the neuromotor pattern is conserved despite functional divergence (e.g., in the evolution of terrestrial and aerial locomotion; Goslow et al., 1989), the gular pump may represent functional convergence with the buccal pump by using homologous structures. The question of homology in the case of the gular pump is made even more complex by the fact that cycles of gular expansion and compression are also used in feeding (Smith, 1986), gular flutter (Heatwole et al., 1973), and throat displays (Bels et al., 1995). One or more of these behaviors could have retained the ancestral motor pattern for hyobranchial movement and this pattern could have been co-opted for lung ventilation (with appropriate modification of narial and glottal valving). The next study undertaken to explore the homology of buccal and gular pumping should be a broad comparative analysis to map the character of gular pumping (its presence or absence) on the phylogeny of Amniota. Preliminary investigations within Squamata indicate that gular pumping is widespread among nonserpentine squamates (Deban et al., 1994; Al-Ghamdi et al., 2001; Brainerd and Owerkowicz, personal observation). This result, combined with our finding of neuromotor similarity in the pumping mechanisms of monitor lizards and amphibians, suggests that the gular pump of lizards may have been retained continuously from a buccal pumping ancestor.

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