

## Functional Morphology of Dewlap Extension in the Lizard *Anolis equestris* (Iguanidae)

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**ABSTRACT** The dewlap is an extendible flap of skin ordinarily folded under the throat. Lizards, particularly those in the genus *Anolis*, extend their dewlaps during interactions with conspecifics, other lizards, and potential predators. Dewlap extension is effected by movements of elements of the hyoid apparatus. This paper describes the anatomy of the hyoid and associated musculature in *Anolis equestris*, a large arboreal lizard with a prominent dewlap. A mechanism for dewlap extension is proposed based on results of morphological and experimental techniques.

Specializations of the hyoid skeleton for dewlap extension include elongated second ceratobranchials and highly movable joints between the ceratohyals and the hypohyals and between the first ceratobranchials and the body of the hyoid. A well developed *M. ceratohyoideus* extends between the ceratohyals and the first ceratobranchials of the hyoid apparatus. During dewlap extension, the hyoid apparatus acts as a first order lever. Contraction of *M. ceratohyoideus* pulls the ceratohyals posteriorly causing the hypohyals and the body of the hyoid to rotate dorsally around the first ceratobranchial/body joints. This movement results in the second ceratobranchials swinging forward and down, unfolding the dewlap. The relative immobility of the first ceratobranchials provides stability to the hyoid apparatus during dewlap extension. A comparison is made of dewlap extension and other hyoid displays.

The dewlap or gular fan, an extendible flap of skin under the throat, is a specialized display organ found in many lizards, especially agamids and iguanids of the genus *Anolis* (Carpenter and Ferguson, '77). The anoline dewlap is conspicuously extended during interactions with conspecifics, other lizards, and potential predators, often in concert with headbobbing and other bodily movements and postures (Jenssen, '77, '78). Because of its potential for inter- and intraspecific communication, the dewlap has long been a topic of interest (Greenberg and Noble, '44; Rand and Williams, '70; Crews, '75; Williams and Rand, '77; Echelle et al., '78; Sigmund, '83; Fitch and Hillis, '84; Losos, '85), yet few studies have examined the mechanism of dewlap extension in *Anolis*.

As early as 1826, Bell noted that the dewlap of *Anolis* is supported by the hyoid apparatus, a derivative of the hyoid arch and posterior branchial arches of fishes (Romer and Parsons, '77). However, Bell's interpretation of the mechanism of dewlap extension was based on an erroneous account of the hyoid anatomy. A more accurate description was published by von Geldern ('19), who proposed that dewlap extension in *Anolis*

*carolinensis* follows from contraction of a single pair of intrinsic hyoid muscles (i.e., *M. ceratohyoideus*). This action causes the elongated second ceratobranchials of the hyoid apparatus to swing forward unfolding the dewlap. Gnanamuthu ('30, '37) reviewed the anatomy of the buccal floor in a number of reptiles and concluded that contraction of *M. ceratohyoideus* and retraction of the tongue take an equal share in the extension of the dewlap. More recently, Bellairs ('70; p. 313) favored a similar explanation of the mechanism of dewlap extension.

One possible reason for this lack of agreement is that modern experimental techniques have not been applied to the study of the mechanism of dewlap extension. In this paper, we have examined the anatomy of the hyoid apparatus and associated musculature in *Anolis equestris*, a large lizard with a prominent dewlap, and reconsidered previous models of dewlap extension using electrical stimulation of muscles and nerves,

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electromyography, and denervation of selected muscles.

*Anolis equestris*, the Cuban knight anole, is a giant crown anole recently introduced into suburban Miami (King and Krakauer, '66; Williams, '69). Its behavior in the wild is poorly known, partly because of the species' highly arboreal habits (Ruibal, '64; Brach, '76). In the laboratory, dewlap extension is typically seen in conjunction with headbobbing displays, addressed to conspecifics or to the lizard's own reflection in a mirror. Headbobbing displays consist of stereotyped up-and-down movements of the forepart of the body. A study using multivariate clustering techniques identified five headbobbing display types (Font and Kramer, '89), four of which incorporate a single dewlap pulse of short duration. Occasionally, dewlap extension takes place independent of headbobbing movements as multiple dewlap pulses of variable duration ("dewlapping"; Jenssen, '77). This dewlapping is sometimes seen during shedding and presumably helps to get rid of loose pieces of skin. In contrast to headbobbing displays, defensive displays result from exposure to a threatening human. Similar displays in the wild are addressed to potential predators (Ruibal, '64). Defensive displays consist of lateral presentation, sagittal trunk compression, nuchal crest erection, gaping with the tongue partially extruded, and a combination of throat and dewlap extension lasting up to several minutes (Font and Kramer, '89). This paper offers an experimental analysis of the process of dewlap extension.

#### MATERIALS AND METHODS

##### *Experimental animals and maintenance*

Subjects were 19 adult *Anolis equestris* (49–106 gm; 132–166 mm snout-vent length) purchased through commercial dealers (Pet Farm Inc., Miami) and kept in the laboratory for up to 2 years prior to experimentation. Both male (N = 15) and female (N = 4) lizards were used in these experiments since *A. equestris* shows little sexual dimorphism in size or dewlap morphology (Collette, '61; Ruibal, '64).

The lizards were individually housed in 110 liter glass vivaria with sphagnum moss as ground litter and tree branches for perching. The vivaria were kept in a temperature controlled room (ca. 26°C). Ultraviolet supplemented lights (Vitalite, Duro-Test Corporation, North Bergen, New Jersey) above the vivaria provided a 14 hour daily photoperiod. The vivaria were sprinkled with water three times weekly and water was continuously available in shallow dishes. Food consisted of insects, baby mice and rats, and adult *Anolis carolinensis*.

##### *Morphological techniques*

With few exceptions, terminology used in this study follows the work of Throckmorton et al. ('85; see also Smith, '86). Available descriptions of the hyoid or its muscles in *Anolis* (mainly *A. carolinensis*) include those of Cope (1892), Willard ('15), von Geldern ('19), Gnanamuthu ('37), Kesteven ('44), Crews ('80), and Tanner and Avery ('82). However, these descriptions are not always in agreement and many lack appropriate illustrations.

The musculoskeletal components of the hyoid apparatus were examined by gross dissection in 12 *Anolis equestris* freshly killed or preserved in 10% formalin. Specimens included experimental animals and those drawn from the collection of N. Greenberg (University of Tennessee). Drawings of dissected material were done through a Wild binocular microscope using an iodine solution to increase contrast between muscles and surrounding tissue (Bock and Shear, '72). Comparative dissections were made of several specimens of *A. carolinensis* and *A. cybotes*, two related but much smaller species.

The composition of the hyoid apparatus was examined in two *Anolis equestris* by sectioning and histological staining. The hyoids and adjacent tissue were embedded in paraffin and sectioned in the transverse plane at 10  $\mu$ m using a microtome. Alternate sections were stained either with Milligan trichrome stain, which distinguishes muscle and connective tissue, or alizarine red S, specific for calcium deposits (Humason, '79). Sections were studied and drawn using an Olympus microscope. Similarly stained sections from the hyoids of three *A. carolinensis* were available for comparison.

##### *Electromyography*

Experiments using synchronous video and electromyographic (EMG) recordings were performed on two large male *Anolis equestris*. The animals were anesthetized by intramuscular injection of ketamine hydrochloride at dosages of 180–200 mg/kg (Font and Schwartz, '89). Incisions were made in the intermandibular region to expose the musculature of the buccal floor. Because previous models suggested that it plays a crucial role in dewlap extension (von Geldern, '19; Gnanamuthu, '30, '37), recording electrodes were implanted in *M. ceratohyoideus* and in another, easily accessible muscle (*M. omohyoideus*, lateral portion). Technical constraints prevented recording of more than two EMG signals at a time. Bipolar hook electrodes were constructed with 60  $\mu$ m insulated electromagnet copper wire and inserted into the muscles using

22-gauge hypodermic needles (Loeb and Gans, '86). Electrode wires were run subcutaneously to connectors in the animal's back. Proper electrode placement was confirmed by electrical stimulation at the time of surgery and by post-mortem examination.

After recovery from surgery the animals were presented in their home vivaria with a conspecific intruder or a mirror to elicit headbobbing displays. Their behavior was observed using a closed-circuit TV and video recording system. During recording, a light-weight cable with a swivel mechanism joined the connectors in the animal's back to the EMG amplifier. The wires did not appear to impair the lizards' behavior. EMG signals were amplified by a Phipps and Bird amplifier with an integral oscilloscope (low frequency cutoff = 10 Hz, high frequency cutoff = 30,000 Hz), and recorded on a Teac A-3440 reel-to-reel tape recorder. The signal from *M. ceratohyoideus* was simultaneously recorded on the audio track of the video tape to allow synchronization of video and EMG recordings as in Rome et al. ('84).

The overall gain (approximately 3,000) of the EMG amplifier and tape recording system was calibrated with a 1 mV, 1 kHz sine wave. A hard copy of the EMGs was obtained by playing the tape into a Nicolet 4094 Digital Oscilloscope and plotting them with a Hewlett Packard digital plotter. This procedure avoided the decreased amplitude obtained at high frequencies with mechanical recording systems. Video films were analyzed frame-by-frame using a TV projection system (Miami Flock Equipment Co.). For each display, the position of the lizard's snout and the extent of dewlap extension every 33 msec were plotted onto graph paper (Jenssen, '78; Jenssen and Gladson, '84). In order to correlate behavior and muscle activity patterns, headbobbing displays were graphed on the same time scale as the EMG recordings.

Headbobbing displays were also analyzed from video and super-8 films collected on five additional lizards. The results of this analysis are discussed more fully elsewhere (Font and Kramer, '89).

#### *Nerve transection*

In lizards, *M. ceratohyoideus* is innervated by a branch of the ramus pharyngo-laryngeus (RPL), a combined nerve carrying fibers from several cranial nerves (Willard, '15; Oelrich, '56). No other hyoid muscles are innervated by this branch of RPL. The effects of interrupting the nerve supply to *M. ceratohyoideus* on dewlap extension were studied in six *Anolis equestris*. In

these animals, the RPL on one side was surgically transected at the posterior end of *M. ceratohyoideus*. Dewlap extension was elicited as described above.

#### *Electrical stimulation*

The actions of hyoid muscles were investigated by electrical stimulation in three *Anolis equestris*. In these animals, the musculature of the buccal floor was exposed by dissection under deep ketamine anesthesia. Tetanic stimulation (2–3 V) was applied to individual muscles and nerves using a Grass S44 stimulator and tungsten needles.

### RESULTS

#### *External morphology of the dewlap*

The dewlap is a longitudinal fold of elastic skin located along the midventral line of the throat. The dewlaps of *Anolis* lizards differ greatly in relative size, shape, and coloration (Echelle et al., '78; Fitch and Hillis, '84). A presumed benefit of dewlap extension is the increased conspicuousness and apparent body size it accords a displaying lizard (Williams and Rand, '77; Chiszar, '78; Greene, '87). Planimetric measurements indicate that dewlap extension increases the lateral profile of a displaying *A. equestris* by as much as 20%. However, the dewlap is barely visible when folded, thus reducing the risk of predation associated with conspicuousness and enhanced visibility.

The extended dewlap has a characteristic semicircular outline due to the flexibility of cartilaginous second ceratobranchials that unfold it. In *Anolis equestris* the dewlap skin is almost devoid of scales. Only four to six horizontal rows of scattered gorgetals and sternals (terminology of Fitch and Hillis, '84) are visible across the dorsal one third of the dewlap. This results in large portions of bare skin being exposed when the dewlap is extended. In the Miami population of *A. equestris* the bare skin between dewlap scales is pale pink (2.5-5R 9/2; Munsell book of color), probably due to the presence of pteridine pigments (Ortiz et al., '63), and contrasts sharply with the bright green-blue of the head, dorsum, limbs, and tail.

#### *The hyoid skeleton*

The hyoid apparatus of *Anolis equestris* is embedded in the tissue of the buccal floor, of which it forms the skeletal framework. The hyoid and its musculature are separated from the oropharyngeal cavity by a sheet of mucosa containing abundant melanocytes. The hyoid apparatus is cartilaginous except for the first cerato-

branchials, and is surrounded by a dense tendinous sheath which provides a surface for insertion of hyoid muscles.

Directly beneath the larynx is the central portion, or body of the hyoid (Fig. 1). Anteriorly, the body is continuous with the entoglossal process. The entoglossal is short and stylet-like, separated from the musculature of the tongue by a fluid filled sac. Paired hypohyals project anteriorodorsally from the body and run for a short distance parallel to the entoglossal process. Slender ceratohyals and first ceratobranchials articulate with the distal ends of the hypohyals and with the body of the hyoid, respectively, by movable synovial joints (Fig. 2). Ceratohyals and first

ceratobranchials extend posteriolaterally from their respective attachments, reaching around the sides of the head. Proximally, the first ceratobranchials are located ventral to the ceratohyals. Distally, they are dorsal to them due to the sharp curvature of the ceratohyals around *M. pterygoideus*. Short, cartilaginous epihyals and first epibranchials attach by fibrous joints to the distal ends of ceratohyals and first ceratobranchials, respectively. Posteriorly, the body of the hyoid is continuous with paired second ceratobranchials. The two lay in close apposition and share a common perichondrial sheath throughout most of their length, tapering considerably as they extend away from the body of the hyoid (Fig. 1).

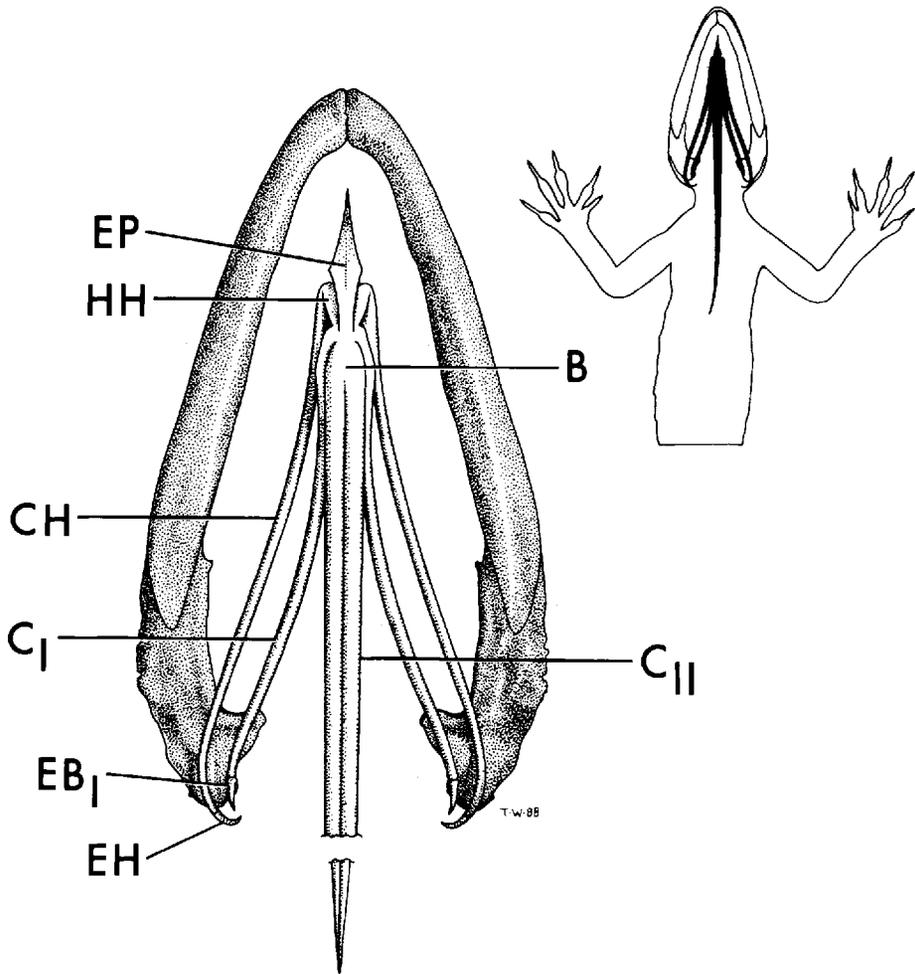


Fig. 1. Ventral view of the hyoid skeleton of *Anolis eques-tris*. **Insert** shows hyoid apparatus in situ. Abbreviations: B, body of the hyoid; CH, ceratohyal; CI, first ceratobranchial;

CII, second ceratobranchial; EB I, first epibranchial; EH, epihyal; EP, entoglossal process; HH, hypohyal.

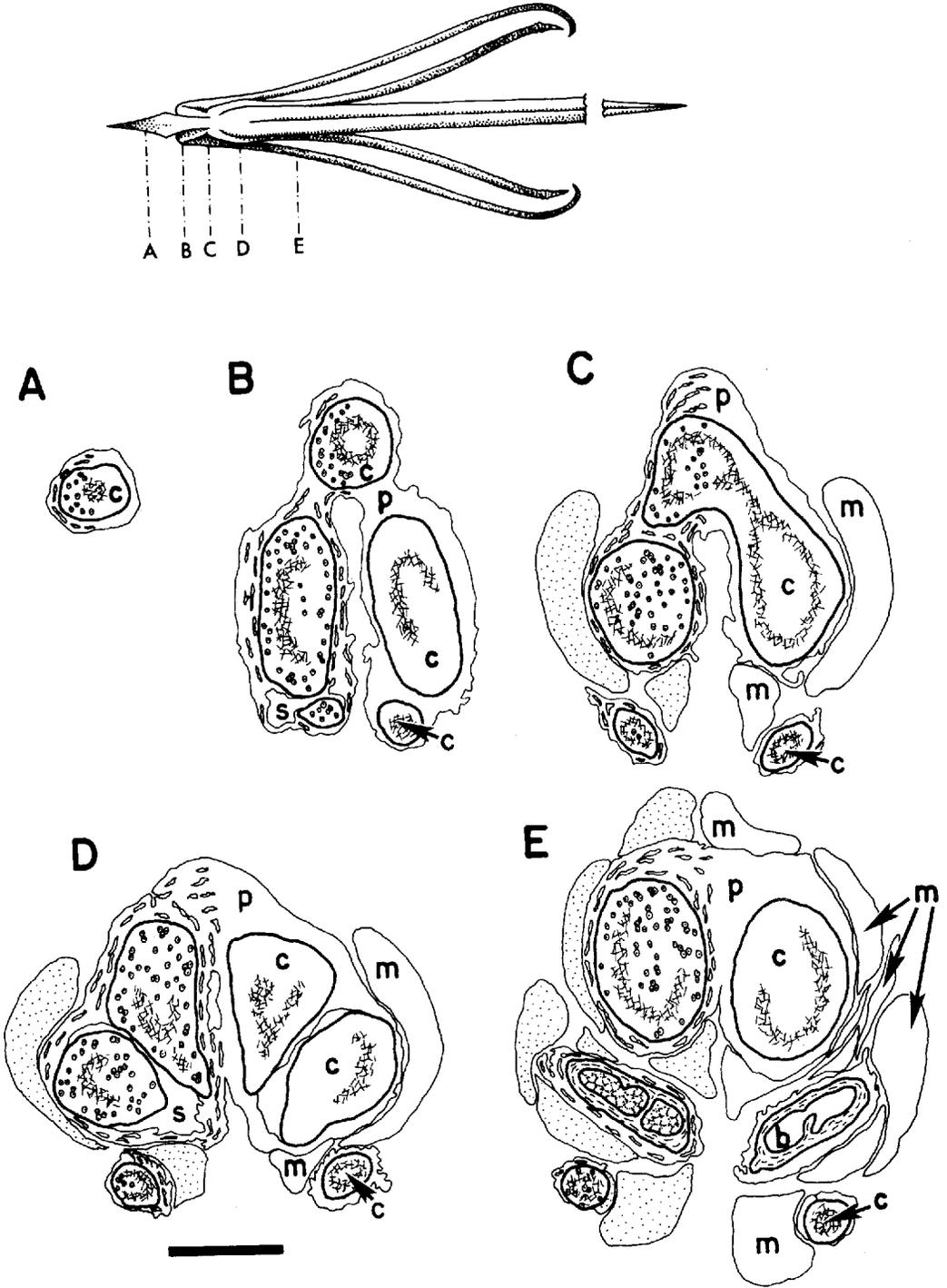


Fig. 2. Histologic composition of the hyoid apparatus of *Anolis equestris*. A-E: Camera lucida drawings of transverse sections stained with Milligan trichrome stain or alizarine red S (ventral side is up). Note the presence of calcium deposits in

most hyoid elements (crosshatching). The level of the cross sections is indicated at the top. Abbreviations: b, bone and marrow cavity; c, hyaline cartilage; m, muscle; p, perichondrium; s, synovial capsule. Bar = 1 mm.

The second ceratobranchials support the dewlap during dewlap extension; they are the longest elements of the hyoid (40% of the lizards' snout-vent length) and reach as far back as the middle of the sternum. In three animals examined, old fractures were present in the second ceratobranchials.

With the hyoid in a resting position, the epihyals and the distal ends of the ceratohyals curve around the retroarticular process of the mandible. During dewlap extension they bend laterally and distend the skin alongside the posterior border of the mandible.

The hyoid skeleton of *Anolis carolinensis* resembles that of *A. equestris* in its major components. In *A. carolinensis* the entoglossal process is longer relative to the size of the hyoid. This results in the body of the hyoid being located further back along the intermandibular space. Only a narrow constriction marks the transition between hypohyals and ceratohyals. As in *A. equestris*, the first ceratobranchials articulate with the body of the hyoid by movable synovial joints. No epihyals are present in the hyoid of *A. carolinensis*.

The hyoid skeleton of two male *Anolis cybotes* was also examined. As in *A. carolinensis*, the entoglossal is long and slender. The second ceratobranchials are remarkably long (67% of the lizards' snout-vent length), reaching as far caudally as the pelvic girdle. The ceratohyals consist of a proximal cartilaginous portion, which is dorsoventrally flattened, and a distal ossified portion. Long epihyals attach to the distal ends of the ceratohyals.

#### *Histologic composition of the hyoid apparatus*

The first ceratobranchials are the only ossified elements of the hyoid apparatus in *Anolis equestris*. They provide insertions for six different pairs of hyoid muscles (see below). In cross section, the first ceratobranchials appear dorsoventrally flattened (Fig. 2). They are hollow, with a prominent marrow cavity which in *A. equestris*, but not in *A. carolinensis*, is traversed by numerous transverse septa. The remaining portions of the hyoid are made of hyaline cartilage. The cellular elements or chondrocytes in this cartilage are arranged in clusters of four (isogenic groups), presumably arising from mitotic divisions of a single cell (Junqueira et al., '77). The acellular matrix contains heavy calcium deposits, occupying the core of most cartilaginous elements of the hyoid (except epihyals and epibranchials). Calcium deposits in the second ceratobranchials are arranged in a semicircle open ventrally (Fig. 2E). The effect of such calcification upon the structural properties of the hyoid remains to be studied.

#### *Musculature of the buccal floor*

The muscles of the buccal floor are classified into six groups according to their origins and insertions (von Geldern, '19; Smith, '84). The superficial throat musculature consists of thin muscles with no connection to the hyoid skeleton. Supra- and infrahyoid musculature refers to those muscles with insertions on the hyoid and origins in the mandible or the shoulder girdle. The intrinsic hyoid musculature consists of a single paired muscle, *M. ceratohyoideus*, extending between two arms of the hyoid. Of the tongue musculature, only the extrinsic muscles bear connections with the hyoid and might be involved in the mechanism of dewlap extension (see below). Descriptions of the intrinsic tongue muscles in lizards can be found in McDowell ('72), Smith ('84, '86, '88), and Schwenk ('86).

#### *Superficial throat musculature*

The superficial throat muscles in *Anolis equestris* are the *Mm. intermandibularis anterior* and *posterior*, and the *M. constrictor colli* (Fig. 3). The *Mm. intermandibularis* are thin, sheet-like muscles; they are the most superficial muscles on the ventral aspect of the rostral two thirds of the head. Both *Mm. intermandibularis* insert along a midline connective tissue raphe except for two distinct bundles of *M. intermandibularis anterior* attached to the symphyseal region of the mandible (Fig. 3). Beneath the body of the hyoid, a few superficial fibers from *M. intermandibularis anterior* insert on the underlying skin.

The *M. intermandibularis posterior* arises from ventral and ventrolateral borders of the mandible, superficial to *M. pterygoideus*. Caudally, a small bundle of fibers detaches from the main portion of *M. intermandibularis posterior* and passes dorsal to the second ceratobranchials of the hyoid apparatus to join fibers from the opposite side (Fig. 3). This bundle overlaps the anterior fibers of *M. constrictor colli*.

The *M. intermandibularis anterior* arises from the ventromedial border of the rostral half of the mandible, deep to the insertions of *M. hyomandibularis* and *M. ceratomandibularis externus*. It interdigitates with the latter muscle before reaching a superficial position on the ventral aspect of the buccal floor. The *M. intermandibularis anterior* can be divided into superficial and deep portions, the fibers of which run at almost right angles to each other.

The *M. constrictor colli* is the most superficial muscle of the neck. It originates on fascia of the skin in the cervical region and inserts along a midline raphe, dorsal to the second ceratobranchials. The muscle is exceedingly thin in *Anolis equestris* (Fig. 3).

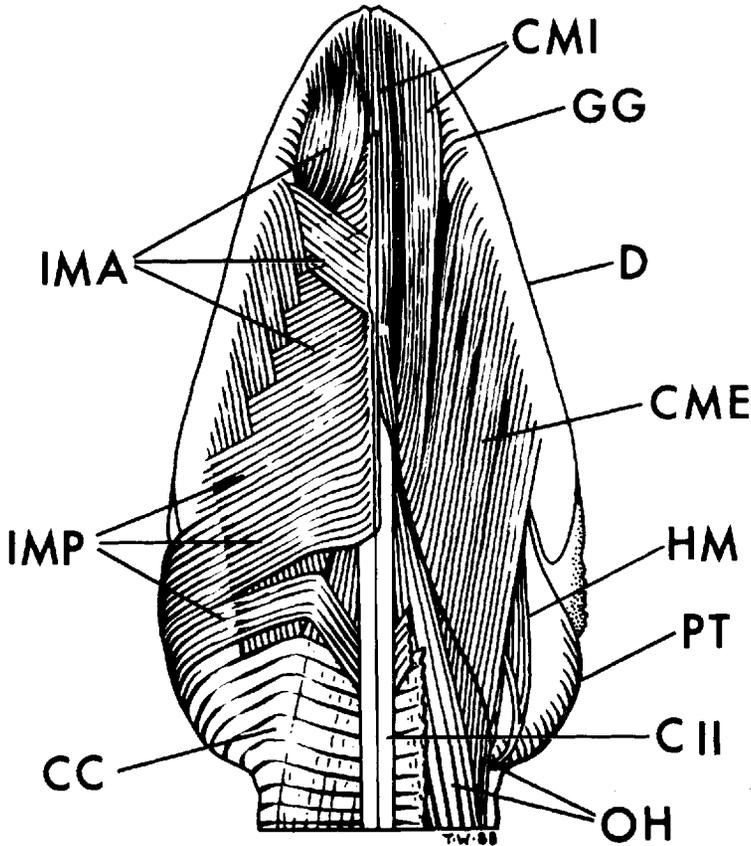


Fig. 3. Ventral view of the superficial layer of hyoid muscles in *Anolis equestris*. Mm. intermandibularis anterior and posterior and M. constrictor colli have been cut on the right to expose underlying muscles. Abbreviations: CC, M. constrictor colli; CME, M. ceratomandibularis externus; CMI, M. cerato-

mandibularis internus; CII, second ceratobranchial; D, dentary; GG, M. genioglossus; HM, M. hyomandibularis; IMA, M. intermandibularis anterior; IMP, M. intermandibularis posterior; OH, M. omohyoideus; PT, M. pterygoideus.

Abundant connective tissue present between the superficial throat musculature and the skin in the gular region may contribute to the adherence of the skin to the buccal floor when the dewlap is folded.

#### Suprahyoid musculature

The suprahyoid musculature consists of three muscles: Mm. ceratomandibularis internus and externus, and M. hyomandibularis. The M. ceratomandibularis internus includes medial and lateral portions (Fig. 3). The medial portion is a thin, ribbon-like muscle bundle arising from the mandibular symphysis and the skin in the symphyseal region. It inserts on the hyoid apparatus, at the transition between the body and the second ceratobranchials. The lateral portion of M. ceratomandibularis internus arises from the ventral border of the mandible, lateral to the symphysis and deep to M. intermandibularis ante-

rior, and inserts on the proximal one third of the ipsilateral first ceratobranchial. The M. ceratomandibularis externus arises as a broad sheet from the ventromedial border of the mandible, interdigitates with M. intermandibularis anterior, and inserts on the distal two thirds of the first ceratobranchial.

The origin of M. hyomandibularis is on the ventromedial border of the mandible, deep to M. ceratomandibularis externus. The muscle then courses posteriorly between M. ceratomandibularis externus and M. intermandibularis anterior, and inserts on the distal one third of the ipsilateral ceratohyal (Figs. 3, 4).

#### Infrahyoid musculature

Two muscles, M. omohyoideus and M. sternohyoideus, form the infrahyoid musculature (Fig. 4). The M. omohyoideus has medial and lateral portions originating from the shoulder girdle

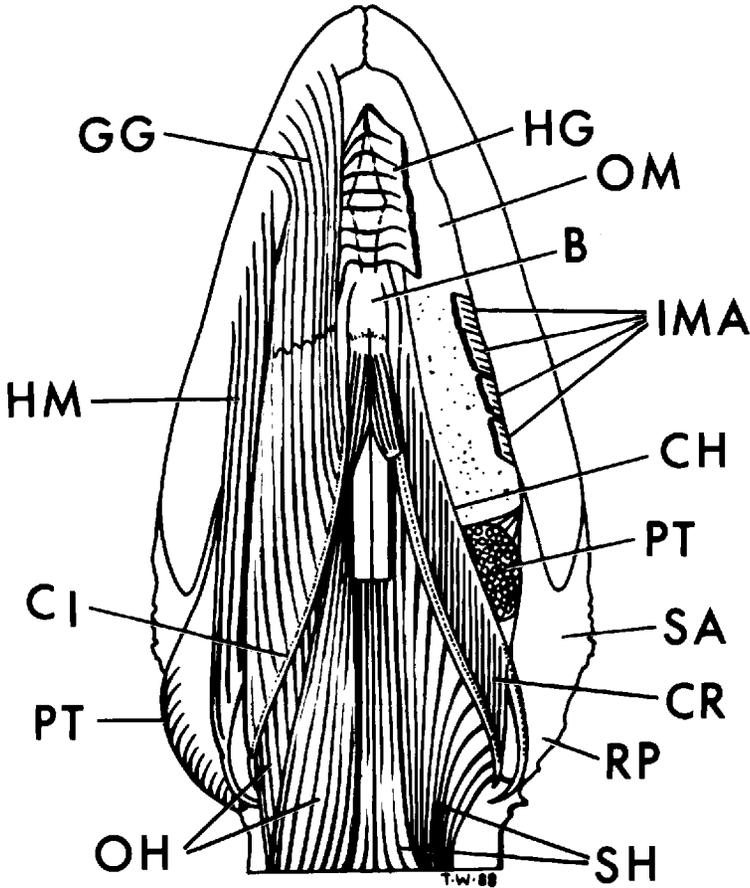


Fig. 4. Deep view of hyoid muscles in *Anolis equestris*. The superficial throat musculature has been removed bilaterally, as has *M. ceratomandibularis*. The *Mm. genioglossus* and *hyomandibularis* have been removed on the right to expose *M. ceratohyoideus*. Abbreviations: B, body of the hyoid; CH, ceratohyal; CR, *M. ceratohyoideus*; CI, first cera-

tobranchial; GG, *M. genioglossus*; HG, *M. hyoglossus*; HM, *M. hyomandibularis*; IMA, *M. intermandibularis anterior*; OH, *M. omohyoideus*; OM, oral mucosa; PT, *M. pterygoideus*; RP, retroarticular process; SA, supra-angular; SH, *M. sternohyoideus*.

(clavicle and anterior border of the suprascapula) and inserting on the hyoid. The medial portion is broad near its origin and tapers as it extends anteriorly to insert at the base of the second ceratobranchial, caudal to the insertion of *M. ceratomandibularis internus*. The lateral portion of *M. omohyoideus* inserts along the ventral aspect of the first ceratobranchial of the hyoid apparatus. Fibers from *M. intermandibularis posterior* and *M. constrictor colli* conceal both portions of *M. omohyoideus* along most of their course.

The *M. sternohyoideus* is very thin in *Anolis equestris*. Like *M. omohyoideus*, it has medial and lateral portions (Fig. 4). The lateral portion (*M. sternohyoideus* of other authors; e.g., Gnan-

amuthu, '37) arises from the clavicle, interclavicle, and sternum, and inserts along the first ceratobranchial, dorsal to the insertion of *M. omohyoideus*. A medial bundle can sometimes be distinguished running along both sides of the trachea to insert dorsally at the base of the ipsilateral second ceratobranchial, opposite the insertion of the medial portion of *M. omohyoideus*.

#### Intrinsic hyoid musculature

This musculature consists of a single paired muscle in *Anolis equestris*. The *M. ceratohyoideus* is a thin muscle sheet extending between the first ceratobranchials and the ceratohyals on either side of the hyoid apparatus. With the hyoid in a resting position, the fibers of *M. cera-*

tohyoideus run roughly parallel to the second ceratobranchials (Fig. 4).

#### Extrinsic tongue musculature

The extrinsic tongue muscles are *M. genioglossus* (tongue protractor) and *M. hyoglossus* (tongue retractor) (Fig. 4). The two fuse into a single muscle complex in lizards (Oelrich, '56). The *M. genioglossus* arises from the ventral border of the mandible, lateral to the symphysis, and inserts on the ventral surface of *M. hyoglossus*. Deeper fibers insert on the lateral edge of the tongue.

The fibers of *M. hyoglossus* originate along the distal two thirds of the first ceratobranchial, dorsal to the insertion of *M. ceratomandibularis externus*, and pass anteriorly around the body of the hyoid to merge with the intrinsic tongue musculature.

#### *Dewlap extension*

A single dewlap pulse accompanies 52% of the headbobbing displays of *Anolis equestris*. The duration of this dewlap pulse is variable; in a sample of 19 displays from three lizards it ranged from 2.82 to 8.82 seconds ( $\bar{x} = 5.30$ ;  $SD = 1.77$ ). An unusual feature of the headbobbing displays of *A. equestris* is a lateral side-to-side movement of the head that signals the end of the display (Fig. 5). The dewlap is typically extended sometime during the first or second headbob and folded during the lateral head movement at the end of the display. Maximum dewlap extension is achieved in an average of 0.15 seconds ( $SD = 0.06$ ). Dewlap folding is slower and appears to take an average of 0.34 seconds ( $SD = 0.18$ ). However, measurements of the duration of dewlap folding were complicated by the presence of the lateral head movement at the end of the display. Occasionally, the dewlap does not fold completely and remains partially extended after the termination of the headbobbing display.

#### *Electromyography*

Activity in *M. ceratohyoideus* and *M. omohyoideus* (lateral portion) was assessed by electromyography. Simultaneous EMG and video recordings were made of 27 headbobbing displays given to conspecifics or mirrors. Of the 27 headbobbing displays, *M. ceratohyoideus* was electrically active during each of the 14 displays that included dewlap extension. An original recording is shown in Figure 5 to illustrate the nature of muscle activity. Activity in *M. ceratohyoideus* starts at or immediately precedes the onset of dewlap extension. This activity continues while

the dewlap is maximally extended and may persist while the dewlap is folding back. However, precise timing of dewlap folding in relation to the EMG pattern was difficult to assess due to the side-to-side movement of the head at the end of the display. Activity is also present in *M. ceratohyoideus* during feeding, drinking, and chemosensory tongue protrusion, but we did not perform a complete analysis of these behaviors.

During headbobbing displays the lateral portion of *M. omohyoideus* shows bursts of activity coinciding with the lateral head movement at the end of the display (Fig. 5). Since this activity is also present in displays lacking dewlap extension and there is no electrical activity while the dewlap is extended (Fig. 5), the muscle probably does not participate in the mechanism of dewlap extension.

#### *Effects of denervation of M. ceratohyoideus*

Unilateral transection of the RPL proximal to the *M. ceratohyoideus* on that side of the throat results in the dewlap extending obliquely, rather than perpendicularly to the buccal floor. In every case the dewlap was angled toward the side that had its nerve supply interrupted. This would be expected if simultaneous contraction of both *Mm. ceratohyoideus* is required for normal dewlap extension.

#### *Electrical stimulation*

Direct electrical stimulation of *M. ceratohyoideus* or of the RPL lifts the second ceratobranchials away from the buccal floor. Simultaneous stimulation of both the left and right muscles emulates normal dewlap extension, however stimulation of just one side results in an oblique display. Fibers from *M. intermandibularis posterior* bunch up over the body of the hyoid as the muscle is pushed forward by the erecting second ceratobranchials. Simultaneously, the ceratohyals slide posteriorly and their distal ends with the attached epiphyseals bend laterally stretching the skin alongside the posterior margins of the mandibles. No other single hyoid muscle yields dewlap extension upon stimulation.

Stimulation of suprahyoid muscles protracts the entire hyoid apparatus, whereas stimulation of infrahyoid muscles retracts it. Abduction of ceratohyals and first ceratobranchials is produced by stimulation of *M. hyomandibularis* and *M. ceratomandibularis externus*, respectively. Stimulation of *M. omohyoideus* and *M. sternohyoideus*, on the other hand, causes the first ceratobranchials to adduct about their joints with the body of the hyoid.

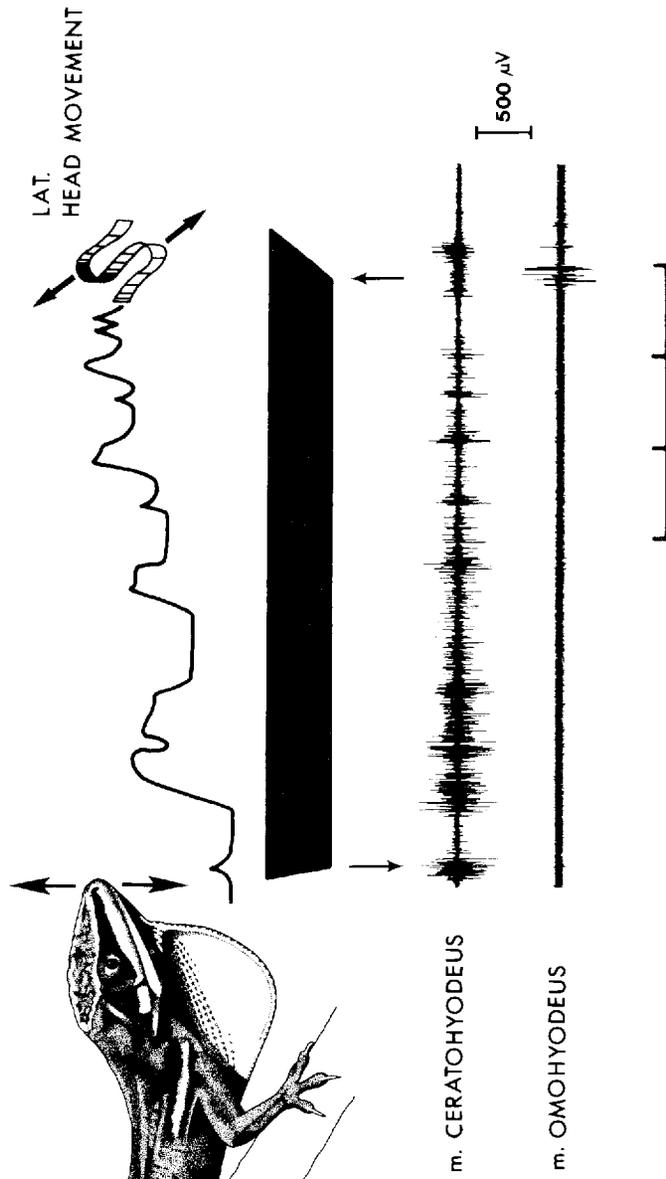


Figure 5

DISCUSSION  
*Hyoid anatomy*

From a primitive role as a support for the gills, the hyoid apparatus has undergone pronounced evolutionary change in all vertebrate taxa (Corsy, '33; Romer and Parsons, '77). The hyoid apparatus of modern lizards is used in feeding, drinking, respiration, chemoreception, and possibly sound reception (Gnanamuthu, '37; Arechaga et al., '77; Smith, '84, '86). In addition, the hyoid supports "morphological adjuncts" (Greene, '87) displayed during interactions with conspecifics, other lizards, and potential predators, such as the dewlap of *Anolis* and other lizards, and the frills of the agamids *Chlamydosaurus kingii* and *Amphibolurus barbatus* (= *Pogona barbata*) (Kent, 1895; Beddard, '05; Throckmorton et al., '85).

The hyoids of lizards differ both in the relative dimensions of their parts and in the presence or absence of certain hyoid elements (e.g., plates III–VI in Cope, 1892). Within anoline lizards, the hyoids are structurally similar (Etheridge, '59). They are elongated, rather than broad, and possess one pair each of ceratohyals, first ceratobranchials, and second ceratobranchials. Epiphyals and epibranchials are also present in some forms. The second ceratobranchials are long and slender, a feature presumably related to the possession of a dewlap. Elongated second ceratobranchials occur in other iguanid and agamid lizards that have dewlaps (Tanner and Avery, '82) and have been retained by all species of *Anolis*, including those, like *A. agassizi* and *A. hendersoni*, that have secondarily lost their dewlaps (Etheridge, '59).

The hyoid musculature of *Anolis* resembles that of other iguanid lizards (Kesteven, '44; Oelrich, '56; Avery and Tanner, '71). Elongated and roughly parallel ceratohyals and first ceratobranchials provide broad surface for insertion of a

well developed *M. ceratohyoideus*. A *M. ceratohyoideus* in this position represents the primitive condition for lizards (Rieppel, '78). More recently evolved lizards (e.g., *Varanus*) have more than one pair of intrinsic hyoid muscles that contribute to complex movements of the hyoid during feeding (McDowell, '72; Smith, '84, '86).

*Previous models of dewlap extension*

The earliest model of dewlap extension is Bell's (1826). This author proposed that the dewlap of *Anolis* is extended ("when the animal is excited with anger or desire," p. 192) by a backward pull of *M. sternohyoideus* on the hyoid apparatus. According to Bell, the distal ends of the second ceratobranchials attach to the skin in the abdomen, so that retraction of the hyoid would cause them to become arched, thus extending the dewlap "like the fabric that stretches over the ribs of an opened umbrella" (Bell, 1826; p. 193–194).

Chemin (1899) attributed dewlap extension in the agamid *Calotes versicolor* to a downward pull of *M. sternohyoideus* on the hyoid apparatus, and to air swallowing. According to Chemin, *M. ceratomandibularis internus* forms a raphe with its counterpart of the opposite side. This "strap" of tissue prevents the entoglossal process from moving down, so that a downward pull by *M. sternohyoideus* would make the whole apparatus pivot around the body of the hyoid and extend the dewlap (Chemin, 1899).

These early models of dewlap extension were challenged by von Geldern ('19) and Gnanamuthu ('30, '37), who noted that the second ceratobranchials are not fixed in the skin, nor does *M. ceratomandibularis internus* form a midline raphe in any of the species they studied. Moreover, contraction of *M. sternohyoideus* pulls the hyoid back rather than down, and dewlap extension is independent of air swallowing.

Von Geldern ('19) proposed that dewlap extension in *Anolis carolinensis* is achieved through contraction of *M. ceratohyoideus* alone. In contrast, Gnanamuthu ('30, '37) stated that simultaneous contraction of *M. ceratohyoideus* and retraction of the tongue are necessary for dewlap extension in *A. carolinensis*, and in the agamids *Calotes versicolor* and *Sitana ponticeriana*. According to Gnanamuthu, *M. hyoglossus* (an extrinsic tongue muscle) inserts on the entoglossal process. Therefore, retraction of the tongue would cause the entoglossal to be pulled upward and backward. Insofar as the entoglossal is continuous with the rest of the hyoid, this movement would supplement the action of *M. ceratohyoideus* and aid in dewlap extension.

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Fig. 5. Representative data from experiments in which video recordings were synchronized with EMG recordings of two hyoid muscles (right side) during headbobbing displays in *Anolis equestris*. Upper graph depicts vertical displacement of the head (i.e., headbobs) through time, including the side-to-side movement of the head at the end of the display (display type A2; Font and Kramer, '89). Blackened block represents dewlap extension through time. Small vertical arrows enclose period of maximum dewlap extension. There was no electrical activity in *M. ceratohyoideus* prior to the beginning of dewlap extension. However, this is not shown because the Nicolet could digitize only 8 seconds of EMG at one time without a reduction in quality (time resolution) of the trace. Note also activity in *M. omohyoideus* (lateral portion) coinciding with lateral head movement. Time scale is in seconds.

### Mechanism of dewlap extension

The results of the present study confirm and expand von Geldern's ('19) conclusions about the mechanism of dewlap extension. During dewlap extension the hyoid of *Anolis equestris* functions as a first order lever (Fig. 6). The hypohyals are the short or power arm, the second ceratobranchials are the weight arm, and the first ceratobranchial/body joints act as the fulcrum. Dewlap extension occurs in two phases. Initially, a slight depression of the buccal floor straightens the ceratohyals and brings them to a position dorsal and roughly parallel to the first ceratobranchials (Fig. 6B). During the second phase of dewlap extension, contraction of *M. ceratohyoideus* pulls the ceratohyals posteriorly. The first ceratobranchials provide insertions for *M. ceratohyoideus* and five additional pairs of hyoid muscles. The relative immobility afforded by these muscle attachments prevents protraction of the first ceratobranchials during contraction of *M. ceratohyoideus* and stabilizes the hyoid apparatus. Retraction of the ceratohyals causes the hypohyals and the body of the hyoid to rotate dorsally around the first ceratobranchial/body joints while the second ceratobranchials swing ventrally extending the dewlap (Fig. 6C).

Although the *Mm. ceratohyoideus* on both sides of the hyoid usually work together, a relative independence is also possible. This permits

some angling of the dewlap away from the mid-sagittal plane, as when an animal displays toward an antagonist positioned above or below its horizontal plane.

Since EMG activity was recorded from two muscles only, participation of hyoid muscles other than *M. ceratohyoideus* and *M. omohyoideus* in the mechanism of dewlap extension cannot be fully evaluated. However, the results of EMG, electrical stimulation, and denervation experiments are in agreement with von Geldern's ('19) hypothesis about the key role of *M. ceratohyoideus* in dewlap extension.

Participation of the tongue musculature in the mechanism of dewlap extension, as suggested by other authors (Gnanamuthu, '30, '37; Bellairs, '70; p. 313), is unlikely. Our results indicate that the entoglossal is not attached to the musculature of the tongue. Furthermore, during defensive (i.e., antipredator) displays of *Anolis equestris*, the tongue is usually protruded, not retracted, in concert with a combination of throat and dewlap extension (see below).

Dewlap folding is likely due to contraction of the medial portions of *Mm. omohyoideus* and *sternohyoideus*. Because they insert at the base of the second ceratobranchials, contraction of these muscles will pull the extended second ceratobranchials back to a horizontal position. Relaxation of *M. ceratohyoideus* and the elastic nature of the second ceratobranchials and dewlap skin may also contribute to restoring the hyoid to a resting position.

### Other hyoid displays

In addition to dewlap extension, displaying *Anolis* lizards often exhibit throat extension, a conspicuous ventral expansion of the buccal floor (Stamps and Barlow, '73; Greenberg, '77; Jensen, '79). In *A. equestris*, throat extension involves simultaneous depression and protraction of the hyoid apparatus as a whole. When the hyoid moves forward, the entoglossal and the body of the hyoid push the skin beneath the mandibular symphysis, giving the lizard the appearance of possessing a chin (Fig. 3A in Font and Kramer, '89). According to Oelrich ('56), throat extension in *Ctenosaura pectinata* (Iguanidae) is accomplished by contraction of the suprahyoid musculature.

Throat and dewlap extension may occur simultaneously, indicating a complex pattern of muscle activation. This is usually seen during defensive (i.e., antipredator) displays in which the second ceratobranchials sweep ventrally while the hyoid is held in a protracted position. The combination of throat and dewlap extension results in the dewlap being located farther rostrally than during headbobbing displays. Also,

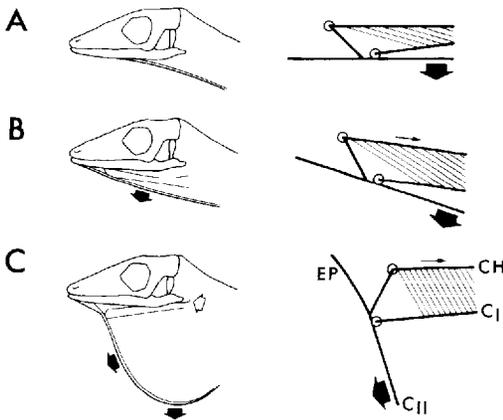


Fig. 6. Diagrams illustrating hyoid movements during dewlap extension in *Anolis equestris*. For clarity, only one side of the hyoid is shown. The circles on the right identify movable synovial joints between the ceratohyal and the hypohyal and between the first ceratobranchial and the body of the hyoid. The *M. ceratohyoideus* is drawn as lines running between the ceratohyal and the first ceratobranchial. The arrows indicate the direction of movement. A: Resting position. B: Immediately preceding dewlap extension the entire hyoid is slightly depressed. C: Moment of maximum dewlap extension. Note bending on distal end of ceratohyal (open arrow). Abbreviations as in Figure 1.

this combination of throat and dewlap extension may last for up to several minutes; this contrasts with the short dewlap pulse attending headbobbing displays.

A variation of the mechanism of dewlap extension may be found in the South Indian flying lizard, *Draco dussumieri* (Agamidae). In this species, the medial bundle of *M. ceratmandibularis internus* is well developed and inserts along the proximal one third of the second ceratobranchials (Gnanamuthu, '37; John, '72). This is unlike the condition in *Anolis*, where the muscle is thin and has a smaller insertion on the body of the hyoid. In *Draco*, contraction of *M. ceratmandibularis internus* may assist the action of *M. ceratohyoideus* by pulling forward on the second ceratobranchials (Gnanamuthu, '37; John, '72). This is supported by the observation that, when the dewlap of *Draco* is fully extended, the second ceratobranchials project well beyond the lizard's snout (Hairston, '57), farther rostrally than in the majority of anoles.

In addition to a dewlap in the usual position, *Draco dussumieri* has lateral cutaneous expansions on either side of the neck (John, '72). During dewlap extension these "wattles" are stretched by the first ceratobranchials of the hyoid apparatus, which in this species are longer than the ceratohyals (Gnanamuthu, '37; John, '72). Similar expansions seen alongside the posterior border of the mandible in displaying *A. equestris* are produced by a lateral bending of the epihyals and of the distal ends of the ceratohyals.

The hyoid displays of some Australian agamids differ greatly from dewlap extension due to divergent hyoid morphology. *Chlamydosaurus kingii* and *Amphibolurus barbatus* lack second ceratobranchials of the hyoid apparatus, possessing instead elongated first ceratobranchials that support a conspicuous frill (Kent, 1895; Beddard, '05; Throckmorton et al., '85). Throckmorton et al. ('85) studied frill extension in *A. barbatus* and concluded that *Mm. ceratmandibularis*, *ceratohyoideus*, *hyomandibularis*, and *hyoglossus/genioglossus* participate in the mechanism of frill extension. Unlike the dewlap of *Anolis* and other lizards, which extends in a ventral direction, the frills of *Amphibolurus* and *Chlamydosaurus* extend laterally. In accordance with their predominant orientation, frills are used in concert with frontal, rather than lateral displays. The different appearance of frills and dewlaps attests to the plasticity of the hyoid and its potential for producing widely contrasting displays.

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