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RESEARCH ARTICLE

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The velar chord and dynamic integration of the gular valve in crocodylians

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Abstract

Crocodylians evolved a unique gular valve that is capable of creating a water-tight seal between the oral and pharyngeal cavities, allowing the animal to safely submerge with an open mouth. The gular valve has traditionally been described as consisting of two separate parts: an active mobile ventral portion (consisting of the tongue and portions of the hyolingual apparatus) and a dorsal portion, which is a static fold on the hard palate (often termed the palatal velum). The results of the present study argue that the two portions of the gular valve are functionally integrated, not separate, and that the dorsal portion (herein the dorsal gular fold) is a dynamic element the shape and tension of which are influenced by active and passive forces. Using gross dissection, histology, and DiceCT, the present study documents a previously underscribed component of the gular valve, the velar chord, which links the hyolingual apparatus to the dorsal gular fold, functionally integrating the two halves of the gular valve. Through endoscopic videography and a variety of manipulations on living crocodylians, this study demonstrates that changes in the tension on the velar chord directly alter the shape and tension of the dorsal gular fold. The shape changes observed in the dorsal gular fold could be accommodated by a shallow depression in the ventral surface of the palatine bones, herein termed the velar fossa. The velar fossa is a prominent feature of *Alligator mississippiensis* and was observed in other crocodilians; however, a survey of living and fossil crocodylians demonstrated that the velar fossa is not a universal feature in this clade. Understanding the functional linkage between the dorsal and ventral portions of the gular valve has implications beyond the dive reflex of crocodylians, since active manipulation of the dorsal gular fold likely plays a role in a variety of behavioral and physiological processes such as deglutition and vocalization.

KEYWORDS

Alligator, gular fold, hard palate, velum palatini

1 | INTRODUCTION

Crocodylians possess a unique gular valve which allows the animal to safely open its mouth while submerged. The basic structure and functional role, of the gular valve, have long been recognized; there is little difference in the descriptions provided by Owen (1849) and Nevarez (2009). The dorsal gular fold is suspended from the hard palate; the larger ventral gular fold is elevated from the base of the tongue to abut the rostral surface of the dorsal fold. Though the dorsal gular fold is just rostral to the internal nares on the hard palate, the fold does not regulate airflow; crocodylians have well-developed sphincter muscles around the external nares which allow them to occlude the respiratory tract while submerged (Bellairs & Shute, 1953; Klassen et al., 2020). The apposition of the ventral gular fold against the dorsal gular fold forms a watertight seal across the oropharynx, allowing the submerged crocodile to gape without swallowing or inhaling water.

The ventral gular fold, which is frequently termed the basihyal valve, is a specialization of the hyobranchial apparatus (e.g., Li & Clarke, 2015). Structural features of this fold, particularly the associated muscles, have been repeatedly described (e.g., Cleuren & De Vree, 2000; Putterill & Soley, 2006; Schumacher, 1973). Johnston (2023) provided a detailed description of the mechanics involved in the elevation of the ventral gular fold, in particular, the role of the ceratobranchial as the instigating lever. Yoshida et al. (2021) were able to use the presence of a dorsal deflection in a shortened ceratobranchial to argue for aquatic adaption in a Crocodylomorpha ancestor to the crocodylians. Compared to the literature of the ventral gular fold, that of the dorsal gular fold (or velum palatini) is more diverse and even contradictory. Some workers (e.g., Ferguson, 1979; Taguchi, 1921) describe the dorsal gular fold as having intrinsic skeletal muscle, while others (e.g., Bellairs, 1969; Jones, 1940; Putterill & Soley, 2006) argue that it is amuscular. Johnston (2023) followed Göppert (1937) in describing the dorsal gular fold as fixed; while Grigg and Gans (1993) state that it is “rigid.” One of the reasons for the diversity of names applied to the gular folds has been that some researchers treat the dorsal and ventral folds as an integrated valve (e.g., Putterill & Soley, 2006), while others treat them as independent structures (e.g., Goodrich, 1930) and typically avoid the term “gular valve.” Chiasson (1962) argued that the dorsal gular fold was a paired structure; Putterill and Soley (2006) noted that the presence of a midline (and shallow) apical notch does not indicate a paired origin.

For several years, the senior author (BAY) has been using the American alligator (*Alligator mississippiensis*) as a model organism. Some of the studies performed involved anesthetizing the alligator with an inhalatory anesthetic (isoflurane). Following standard practice (e.g., Fleming, 2014), the alligator's jaws were bound around a bite tube or pad, allowing for safe endotracheal intubation. With the bite pad or tube secured, the gular valve could be directly manipulated by hand or with a laryngoscope. This was done before any anesthesia. When the ventral gular fold was deflected, not only did the defensive hisses produced by the alligator change (Britton, 2001; Herzog & Burghardt, 1977; Reber et al., 2017), but the dorsal gular fold could be seen (and felt) to move, suggesting a mechanical linkage between the two gular folds.

The current study was undertaken with three goals. Firstly, to test the hypothesis that the shape and tension of the dorsal gular fold are dynamic, not rigid or static. Secondly, to describe the mechanical linkage between the ventral and dorsal gular folds. And thirdly, to describe any osteological features that might be associated with the dorsal gular fold and, as such, could provide evidence for the evolutionary history of the gular valve.

2 | MATERIALS AND METHODS

2.1 | Behavioral observations

To determine if the dorsal gular fold was rigid or static, young *Paleosuchus palpebrosus* and *Paleosuchus trigonatus* were gently held aloft and photographed performing their characteristic open-mouth display. Each animal was then induced to bite a bite tube which was securely taped in place. A portable digital endoscope (NTS150RS, Teslong) was then threaded through the bite tube into the oral cavity. With the endoscopic camera in place, the gular valve was photographed and filmed (from a rostral perspective) while the animals produced defensive hisses or responded to the ventral gular fold being gently palpated. To determine if the dorsal gular fold would change shape or tension during feeding, a mock behavioral trial was performed using a previously frozen head of a 178 cm (total length) specimen of *Alligator mississippiensis*. This isolated head had been frozen with the mouth fully closed. Once the head was thawed, the endoscopic camera could be threaded up the severed esophagus to the level of the gular valve. With the camera in place, a midline incision was made in the rostral portion of the lower jaw. The head was suspended (horizontally) in the air to prevent compression on the gular region. A previously frozen adult rat was thawed, shaved (to improve visualization of the dorsal gular fold), and inserted into the oral cavity through the ventral incision. Using placental forceps, the rat could be pushed caudally using the natural resistance of the soft tissue of the lower jaw to guide the rat along the surface of the hard palate and over the dorsal gular fold.

To test the influence of the ventral gular fold/hyolingual apparatus on the shape and tension of the dorsal gular fold, the contours of the dorsal gular fold were photographed during manual manipulation of the hyolingual apparatus. To do this, the lower jaw of a freshly euthanized 176 cm total length specimen of *Alligator mississippiensis* was strapped to a heavy board, and a second strap was used to safely create a large gape angle with the hyolingual apparatus fully depressed (due to the euthanasia). It was then possible to manipulate the position of the hyolingual apparatus (using external manual pressure on the surface of the lower jaw) and document the changes in dorsal gular fold photographically.

All care and use of live crocodylians followed all established guidelines and were approved by the Institutional Animal Care and Use Committee of A.T. Still University (Protocol #175, approved November, 2023).

2.2 | Anatomical studies

Gross dissection was performed on the gular valve from three previously frozen *Alligator mississippiensis* (total lengths of 145, 163, and 172 cm). The best approach to the dorsal gular fold (df) was obtained by making a midline incision through the soft tissue of the lower jaw (including the ventral gular fold and hyobranchial complex) and then partially freeing the soft tissue of the lower jaw from the medial margin of the mandibles. In this way, the soft tissue of the lower jaw could be reflected like an open book, leaving intact both the df and the lateral pharyngeal wall with the velar chord. These dissections were documented using a digital camera (Nikon D3100) or a dissecting microscope (Leica M80) using the IC80HD digital camera (Leica).

Histological analyses were performed on the dorsal gular folds from two specimens of *Alligator mississippiensis* (38 and 29 cm total length), one *Paleosuchus palpebrosus* (22.5 cm total length), one *Caiman crocodilus* (38 cm total length), and one *Paleosuchus trigonatus* (43 cm total length). The *A. mississippiensis* was obtained from the Louisiana Department of Wildlife and Fisheries; the *C. crocodilus* was obtained from the Vertebrate Zoology collection at Truman State University, while the two *Paleosuchus* were obtained commercially. In each specimen, a bone saw was used to excise the df and surrounding tissue as a block including the underlying hard palate. The excised blocks were decalcified (RDO Rapid Decalcifier) for 48 h, then smaller blocks (each containing a region of the df) were isolated using razor blades. The small tissue blocks were dehydrated through an ethanol series prior to paraffin embedding. Sections were cut at 10 μm; most sections were in a parasagittal plane, but frontal and transverse sections were also made. Hematoxylin and eosin staining was used for general tissue identification and orientation. Masson's trichrome stain was used to determine the composition of the velar chord, particularly between collagen (green staining) and skeletal muscle (magenta staining). This distinction was confirmed using phosphotungstic acid hematoxylin (PTAH) staining in which the skeletal muscle is a deep blue while the collagen fibers are red. Microscopic anatomy was documented using a DM 4000B microscope (Leica Microsystems Inc.).

For DiceCT, the head of a 63 cm (total length) specimen of *Alligator mississippiensis* was pre-treated in 5% Lugol's solution for 6 weeks and then scanned at the University of Texas High-Resolution X-ray CT Facility using a custom-

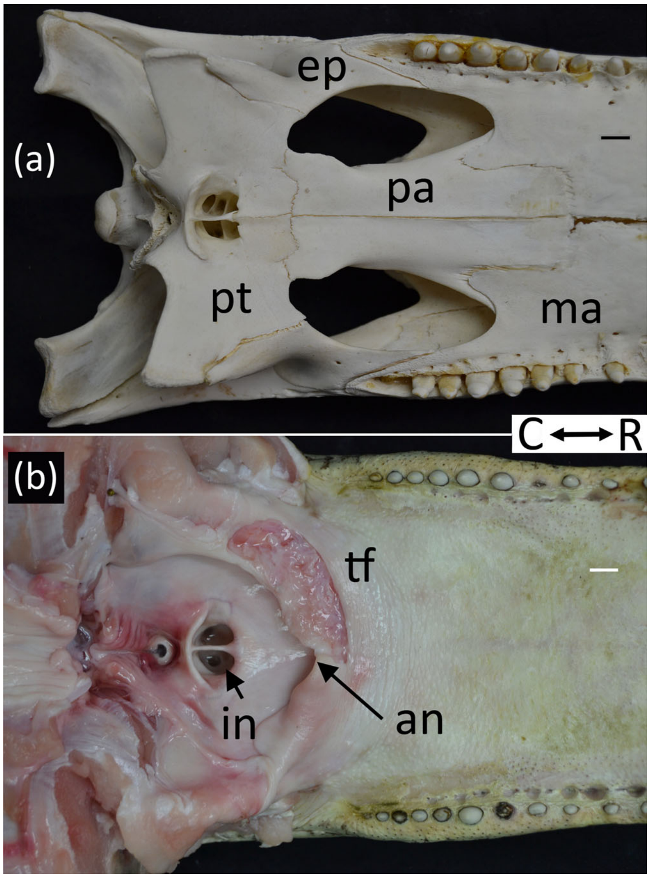

FIGURE 1 Palatal view of the skull (a) and dorsal gular fold (b) of a 172 cm total length specimen of *Alligator mississippiensis*. The apical notch (an) of the dorsal gular fold (df) is rostral to the suture between the pterygoid (pt) and palatine (pa) bones, occurring near the caudal extent of the maxillary (ma) dentition. The dorsal gular fold is located rostral to the internal nares (in) or choanae, and the median pharyngeal valve. Transverse folds (tf) are evident along the rostral surface of the dorsal gular fold. The epithelium has been removed from the right-hand side of the dorsal gular fold to reveal the submucosal parenchyma. Scale bars = 1 cm. ep, ectopterygoid.

built North Star Imaging scanner in volume mode. The X-ray source was set to 130 kV and 0.14 mA with an aluminum foil pre-filter. A total of 3600 projections were acquired over 360 degrees of rotation at 1 frame per second with no frame averaging and no detector binning. A beam-hardening correction of 0.25 was applied; the resulting slices measured 1979 × 1979 pixels and had a voxel resolution of 9.65 microns. The resulting DICOM images were examined using Dragonfly (Object Research Systems).

2.3 | Comparative osteology

Through the kind cooperation of the Field Museum of Natural History, the palatal morphology of a number of recent and fossil crocodylians was examined (listed as: scientific name; museum catalog number, binomial authority, and total skull length in cm) including: *Alligator mississippiensis*, 31011, (Daudin, 1802), 46; *Alligator sinensis*, 229974, (Fauvel, 1879), 31; *Alligator sinensis*, 31302,

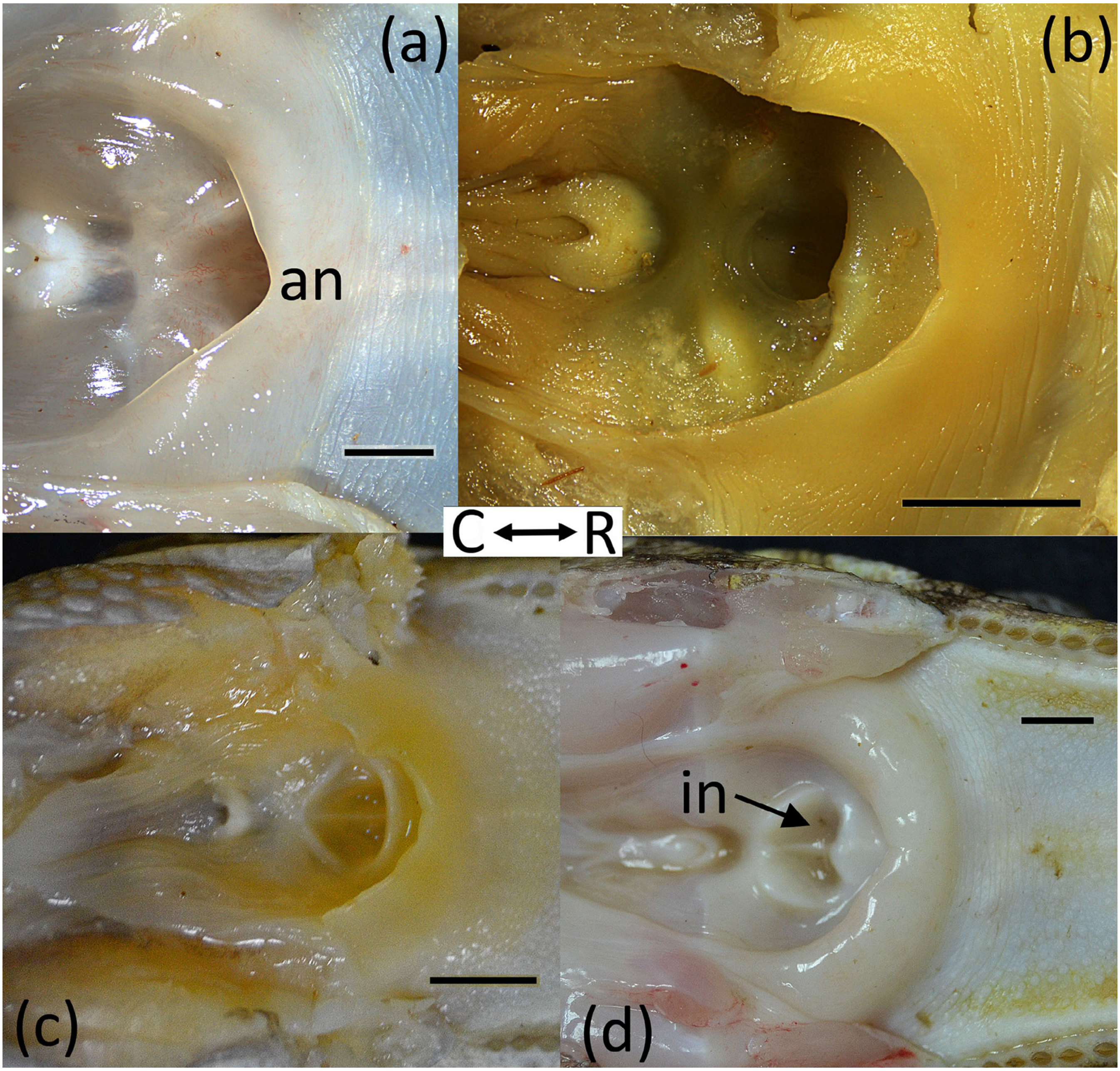

FIGURE 2 Palatal view of the dorsal gular folds from a 38 cm total length *Alligator mississippiensis* (a), a 38 cm total length *Caiman crocodilus* (b), a 22.5 cm total length *Paleosuchus palpebrosus* (c), and a 43 cm total length *Paleosuchus trigonatus* (d). While the position, general shape, and size of these dorsal gular folds are similar, there is variation in the relative prominence of the apical notch (an) and the relative width of the ventral or free edge of the fold. Scale bars = 0.5 cm. in, internal nares.

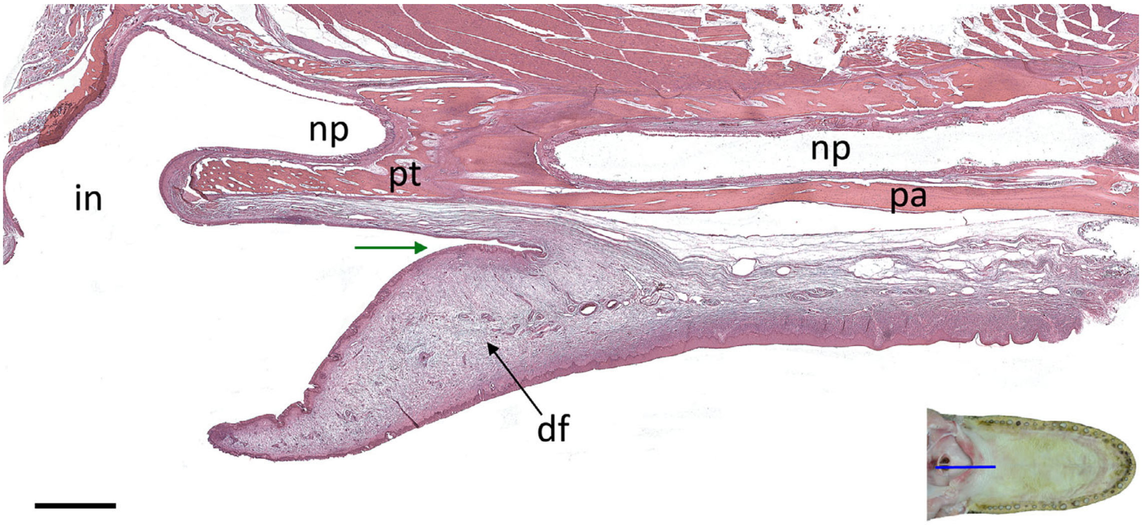

FIGURE 3 Parasagittal section, with hematoxylin and eosin staining, of the dorsal gular fold (df) of *Alligator mississippiensis*; the inset figure shows the position and extent of this section. This section demonstrates the relationship of the df to the internal nares (in), the epithelial transition over the df, the relatively uniform parenchyma within the df, and the "pocket" on the caudal surface of the df (green arrow). The submucosa is more closely attached to the pterygoid (pt) than it is to the palatine (pa). Note that there is no evidence of a velar chord in this section. Scale bar = 1 mm. np, naso-paharyngeal duct.

(Fauvel, 1879), 13; *Boverisuchus vorax*, PR 399, (Troxell, 1925), 41; *Caiman crocodilus chiapasius*, 73710, (Bocourt, 1876), 15.5; *Caiman crocodilus chiapasius*, 73687, (Bocourt, 1876), 20; *Caiman crocodilus*, 73440, (Linnaeus, 1758), 18.5;

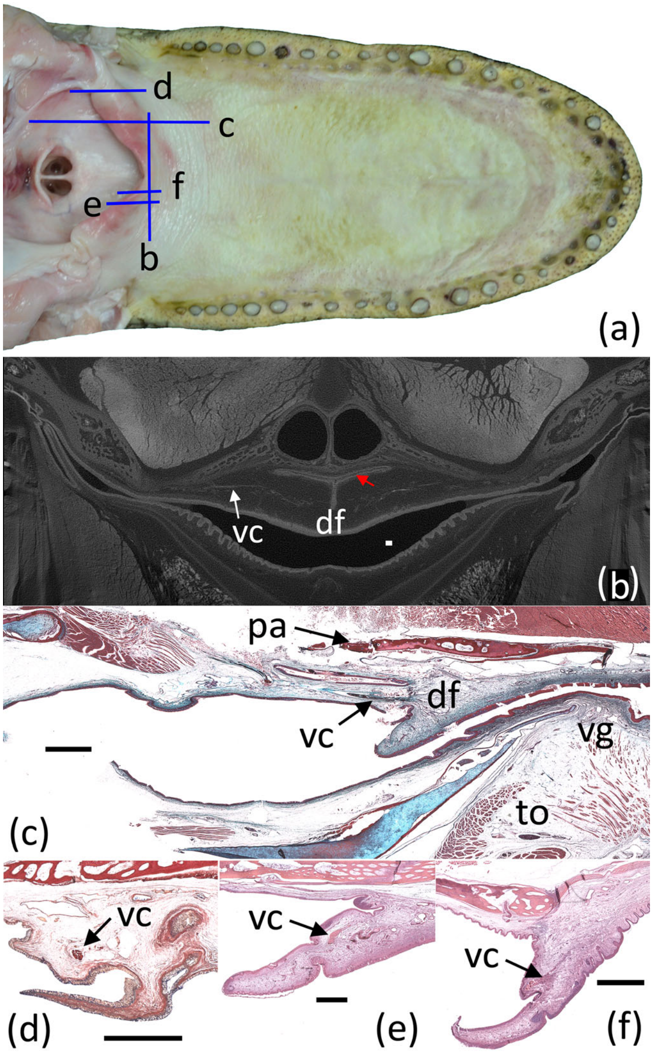

FIGURE 4 Morphology of the dorsal gular fold. (a) Palatal view of *Alligator mississippiensis*; the planes and extent of the sections in this figure are indicated with blue lines. (b) Transverse DiceCT image of the head, showing the velar chord (vc) in the lateral portion of the df. This section is near the caudal border of the apical region of the df, so the caudal pockets in the epithelium are evident (red arrow). (c) Parasagittal section with Masson's trichrome staining through the closed mouth of *Alligator mississippiensis*, showing the approximation of the ventral gular fold (vg) and the dorsal gular fold (df) and the velar chord (vc) coursing into the df. (d) Parasagittal section with PTAH staining through the dorsal gular fold of *Paleosuchus palpebrosus*; this section is lateral (close to the pharyngeal wall) and shows the velar chord (vc) at the base of the df. (e) Parasagittal section, with hematoxylin and eosin staining, of the dorsal gular fold of *Alligator mississippiensis*; this section is at a plane medial to (C) but lateral to (Figure 3). In this plane, the velar chord (vc) is a distinct bundle of dense connective tissue near the dorsal-ventral midpoint of the df. (f) Parasagittal section, with hematoxylin and eosin staining, of the dorsal gular fold of *Paleosuchus trigonatus*; the velar chord is present as a distinct bundle of dense connective tissue. The morphological features of the velar chord evident with hematoxylin and eosin staining, combined with the specific staining reactions of the velar chord to Masson's trichrome and PTAH stains, demonstrate that the tissue composition of the velar chord is collagen not skeletal muscle. Scale bars: 1 mm. pa, palatine; to, tongue.

Caiman latirostris, 9713, (Daudin, 1801), 30; *Caiman latirostris*, P 15029, (Daudin, 1801), —-; *Ceratosuchus burdoshi*, P 15576, (Schmidt, 1938), 23; *Crocodylia*?, PR 490, —-, —-; *Crocodylus acutus*, 59070, (Cuvier, 1807), 62; *Crocodylus affinis*, PR 12202, (Marsh, 1871), 55 est.; *Crocodylus intermedius*, 75657, (Graves, 1819), 53; *Crocodylus mindorensis*, 21904, (Schmidt, 1935), 17.5; *Crocodylus niloticus*, 17157, (Laurenti, 1768), 46; *Crocodylus novaeguineae*, 14047, (Schmidt, 1928), 28.5; *Crocodylus palustris*, 51691, (Lesson, 1831), 28.5; *Crocodylus porosus*, 13969, (Schneider, 1801), 51; *Crocodylus porosus*, 13219, (Schneider, 1801), 53; *Gavialis gangeticus*, 98864, (Gmelin, 1789), 23.5; *Melanosuchus niger*, 45653, (Spix, 1825), 28; *Osteolaemus tetraspis*, 44410, (Cope, 1861), 30; *Paleosuchus palpebrosus*, 69875, (Cuvier, 1807), 12; *Paleosuchus palpebrosus*, 98961, (Cuvier, 1807), 12.5; *Paleosuchus trigonatus*, 69877, (Schneider, 1801), 12; *Tomistoma schlegelii*, 206755, (Müller, 1838), 42.5. Additional osteological observations were made on multiple skulls of *Alligator mississippiensis* and other crocodylians from the private collection of BAY.

3 | RESULTS

3.1 | Shape and location of the dorsal gular fold

The dorsal gular fold (df) is near the caudal border of the hard palate. In all the specimens examined, it was distinctly arched, with a rostral convex surface, the apex of which is roughly aligned with the caudal extent of the maxillary dentition (Figure 1). The apical surface of the df rests over the caudal portion of the palatine, while the lateral portion of the fold courses over the palatine foramen and generally aligns with the ectopterygoid/pterygoid suture (Figure 1). The caudal concave surface of the df opens into the flattened smooth terminal portion of the hard palate where the paired internal nares are located immediately rostral to the median pharyngeal valve (Figure 1). The rostral apex of the df has the shortest ventral projection, though the extent to which this results in a distinct apical "notch" varies by species and age (Figure 2). The junction between the palatal mucosa and the df on the rostral side is marked by a series of loose transverse folds or pleats (Figures 1 and 2). In smaller specimens, the ventral edge of the df is sharply defined; as the df increases in size, this edge gets broader and often "folds over" caudally but not rostrally (Figures 1 and 2). The base of the df is narrower (rostral-caudal) than the adjacent free (ventral) portion, so there is naturally a pocket or infolding along the caudal base; this pocket is more prominent laterally (Figure 3).

3.2 | Composition of the dorsal gular fold

The epithelium of the df is similar to the adjacent palatal epithelium; so there is a transition from oral epithelium on the rostral surface to respiratory epithelium on the caudal surface (Figure 3). Deep to the epithelium, the "flesh" of the df is all submucosa, with a rich vascular supply, abundant innervation, and exocrine glands (Figure 3). Coursing in the lateral portion of the df is a prominent band of dense connective tissue herein termed the velar chord (Figure 4). The velar chord was present in every specimen examined (Figure 4); whether examined histologically or through gross dissection, there was no medial attachment to the velar chord (Figures 3 and 4). No skeletal muscle fibers were observed in the df or in any portion of the velar chord.

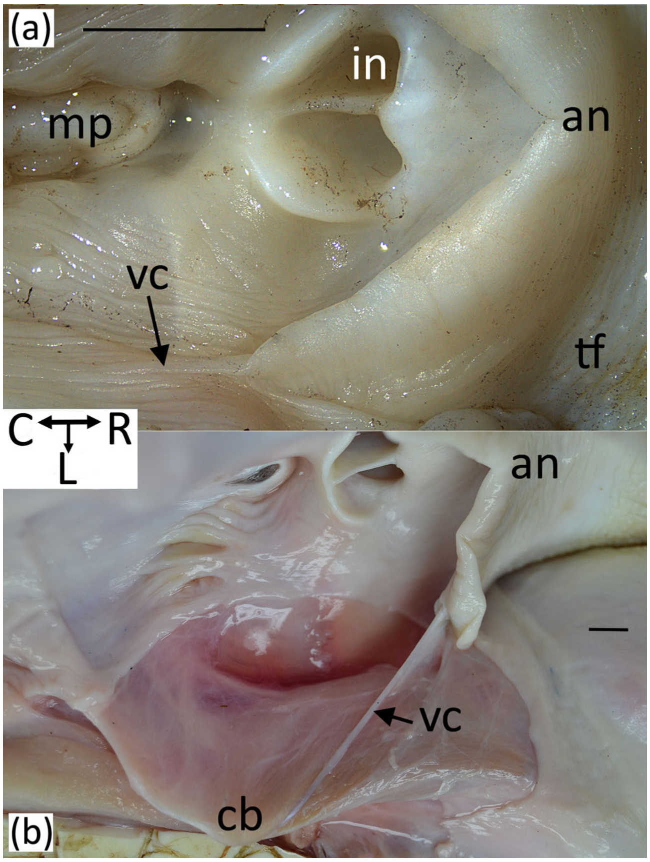

FIGURE 5 Morphology of the velar chord in *Alligator mississippiensis*. (a) Intact palatal surface of a 38 cm total length specimen; the velar chord (vc) extends from the caudolateral surface of the dorsal gular fold blending into the epithelial folds of the pharyngeal wall. (b) Superficial dissection of the velar chord (vc) from a 163 cm specimen; note that to get this perspective the hyolingual apparatus has been bisected then rotated so the exposed surface of the ceratobranchial (cb) is actually the dorsal surface. Scale bars: 1 cm. an, apical notch; in, internal nares; mp, median pharyngeal valve; tf, transverse folds.

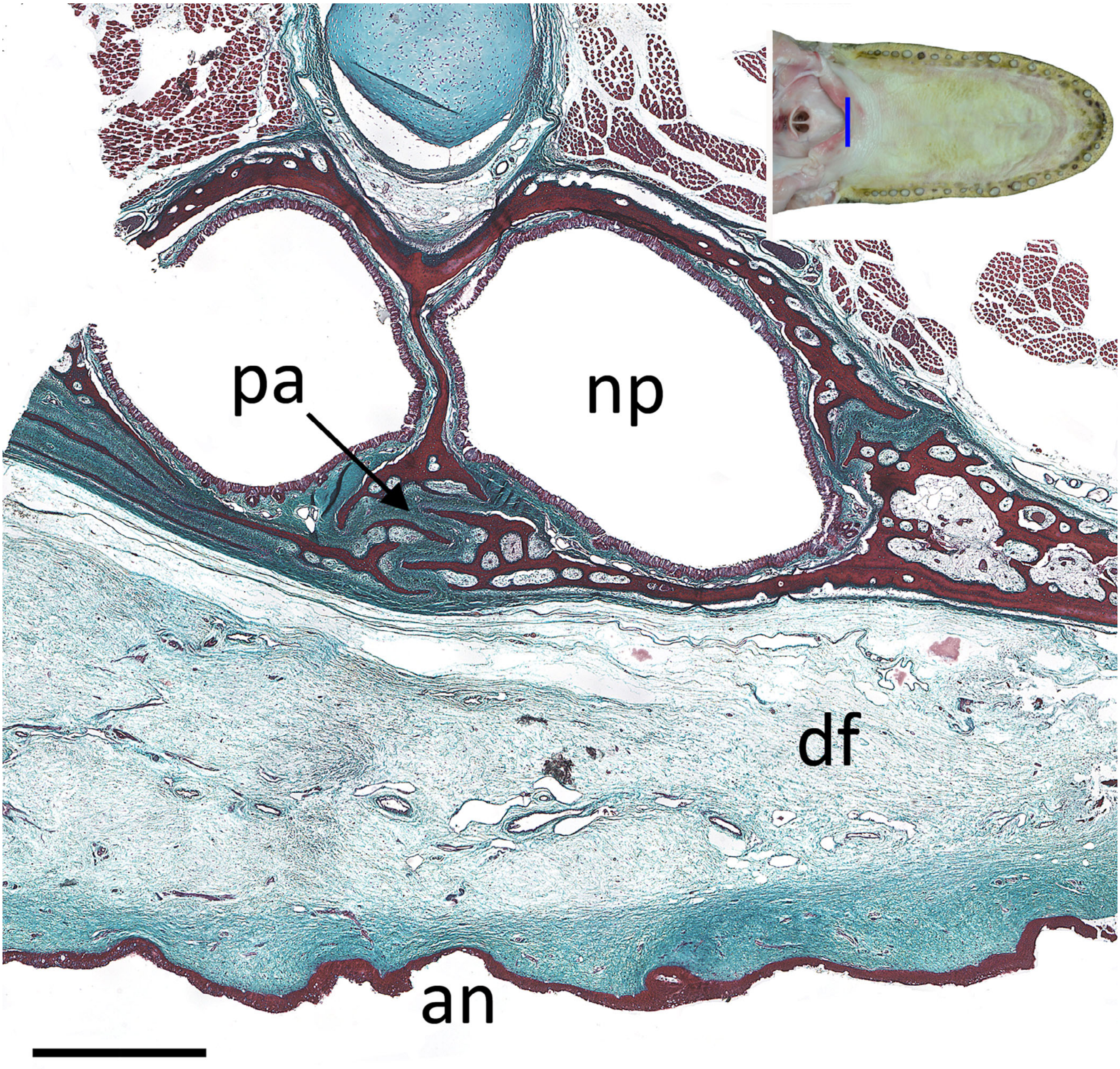

FIGURE 6 Transverse section, with Masson's trichrome stain, through the dorsal gular fold of a 38 cm total length *Caiman crocodilus*. Inset is a palatal view of *Alligator mississippiensis*; the plane and extent of this section is indicated by the blue line. This section is in the region of the apical notch, so no velar chord is evident. The parenchyma of the df is uniform save for the presence of the vascular elements. Note the relative separation between the submucosa of the df and the periosteum of the palatine bones. The specificity of the Masson's trichrome clearly demonstrates the absence of skeletal muscle tissue within the parenchyma of the df. Scale bar = 1.0 mm. an, apical notch; np, naso-pharyngeal duct; pa, palatine.

3.3 | Attachments of the dorsal gular fold

The velar chord attaches to the medial surface of the ceratobranchial, near the junction with the caudal ossified tip of that hyolingual cartilage. The velar chord extends rostrodorsad, roughly parallel to the caudal tip of the ceratobranchial (Figure 5), to enter into the lateral margin of the df. As the velar chord courses mediad through the df it decreases in size (through fibrous attachment with the parenchyma of the df) until it terminates lateral to the midline of the df. The epithelium over the lateral margin

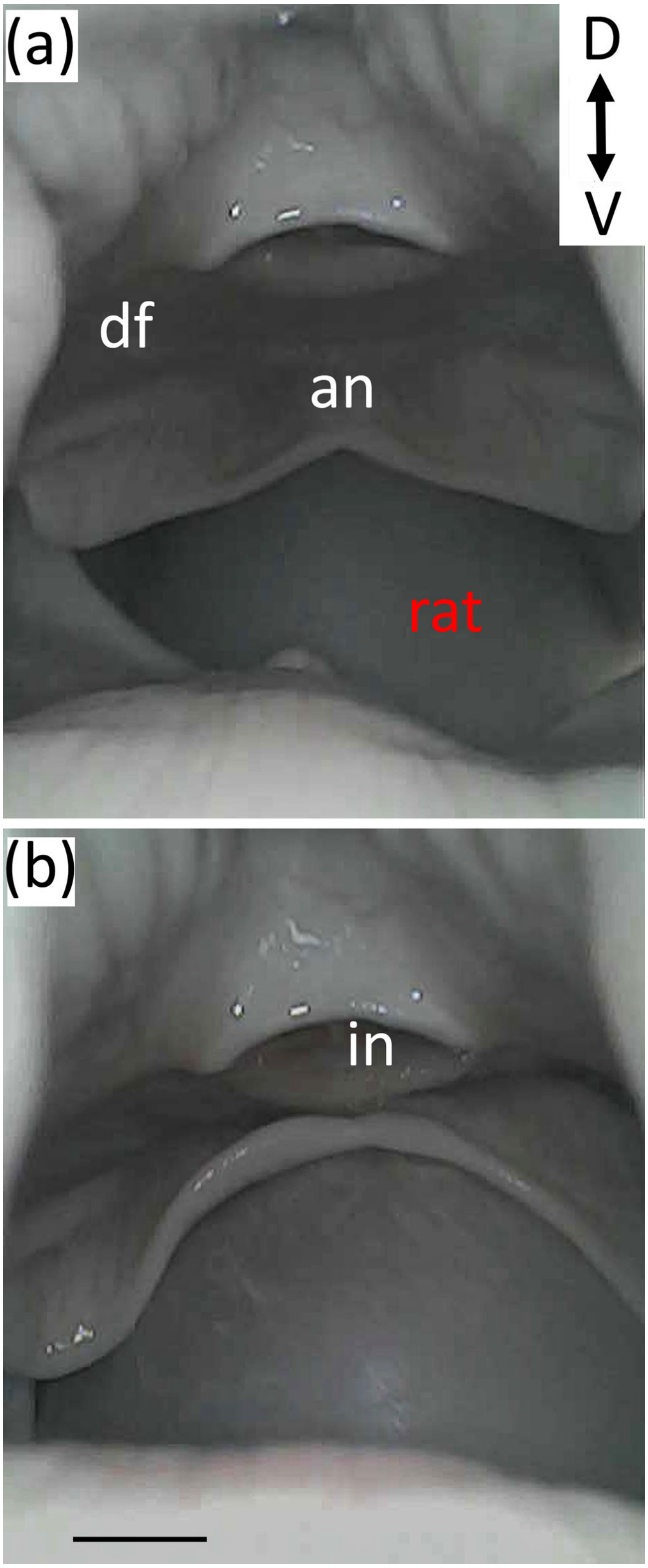

FIGURE 7 Isolated frames from the endoscopic video of mock deglutition in *Alligator mississippiensis*. (a) is at first contact between the prey item and the df. As the prey item continues to move caudally (b) the df is compressed dorsal-ventrally (especially the apical notch) and folds over caudally. Scale bar = 1 cm. an, apical notch; in, internal nares.

of the df (on both the rostral and caudal surface) is continuous with the epithelium of the oral and pharyngeal cavities, respectively. The fleshy parenchyma of the df does not extend laterally into the wall of the pharyngeal cavity; accordingly, the df is relatively thinner (and more mobile) along the lateral margin. On either the rostral or caudal side of the df the collagen fibers in the submucosa of the hard palate form a tightly laminar structure binding the epithelium to the underlying periosteum (Figure 3). In contrast, the portion of the submucosa immediately deep to the df is more open and lacks a clear integration with the underlying periosteum (Figures 3 and 6).

No sexual dimorphism was observed in the position, composition, or attachments of the df or velar chord.

3.4 | Movements

This study documented three distinct movements of the df, associated with deglutition, exhalation, and ceratobranchial displacement. During deglutition, any large prey item, or even a small prey item that is pressed against the palatal surface by the tongue or lower jaw, will move over the df. The caudad movement of a prey item causes both dorso-ventral compression of the df, and tends to bend or fold the free ventral edge of the df caudally (Figure 7). During strong exhalatory bursts, such as during defensive hissing, the rostral contours of the df change (Figure 8). The transverse folds or pleats at the junction between the df and the palatal mucosa are not tightly attached to the underlying hard palate, so the exhalatory airstream leaving the internal nares expands the df away from the palatal surface. This exhalatory billowing of the df also appears to change the tension on the thinner, more membranous, lateral margins of the df. Elevation of the caudal end of the ceratobranchial (where the velar chord attaches) reduces the tension in the velar chord resulting in increased caudal folding in the df. Conversely, depression of the caudal end of the ceratobranchial increases velar chord tension pulling the lateral margins of the df further ventrad and increasing the definition of the apical notch (Figure 9). Though observed independent of radiographic evidence for ceratobranchial displacements, similar changes in the df were observed in live unanesthetized specimens (Figure 10).

With a freshly euthanized *A. mississippiensis* held in a gaping position, the gular chords were clearly visible and the df was tensed, depressed, and symmetrical (Figure 11a). If the hyolingual apparatus was manually elevated, the contours (tension) of the velar chord and df were reduced, a change that was particularly clear when unilateral (Figure 11b).

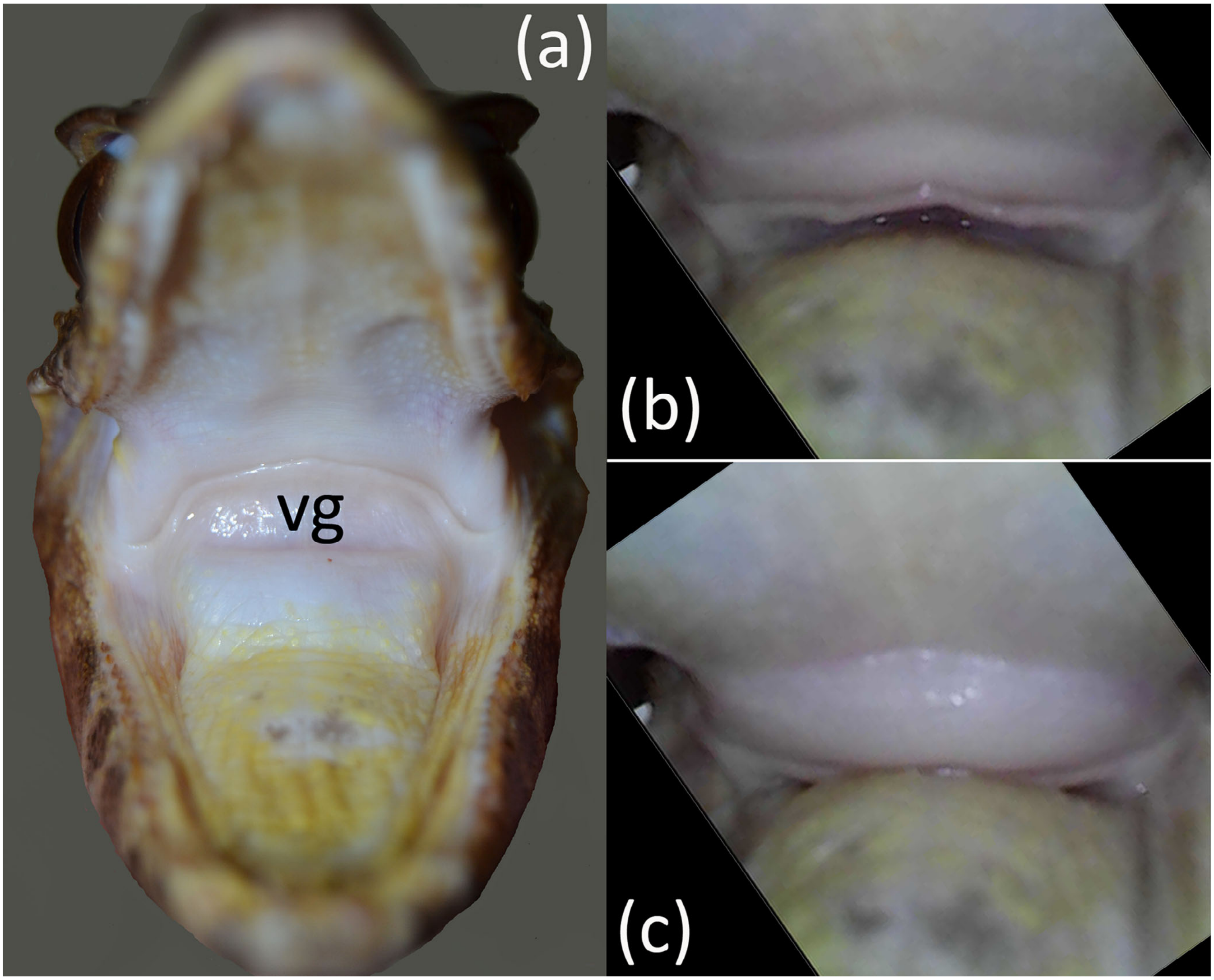

FIGURE 8 Dynamics of the gular valve in *Paleosuchus trigonatus*. (a) During the defensive gape display the gular valve is typically shut, so the ventral gular fold (vg) obscures the more caudal dorsal gular fold. (b) Endoscopic image of the closed gular valve with the animal at "rest". (c) subsequent image taken while the animal is performing a defensive hiss. The hiss is being expelled through the nares, not the oral cavity (the gular valve is still closed). The exhalent airstream is strong enough that it causes movement or billowing of the df relative to the palatal surface.

3.5 | Mechanical model

Johnston (2023) modeled the elevation of the ventral gular fold (our terminology) as a two pivot system: a rostral pivot between the basihyal and the tongue and a caudal pivot between the ceratobranchial and the basihyal. If the certabranchial is depressed and protracted, primarily through the action of the branchiohyoideus and branchiomandibularis visceralis muscles (Johnston, 2023), not only will the ventral gular fold be elevated, but the tension on the velar chord will be increased leading to tension and ventral displacement in the df (Figure 12). If the ventral gular fold is depressed and the ceratobranchial returned to an elevated and retracted position (primarily by the actions of the genioglossus and coracohyoideus muscles, Johnston, 2023) the tension in the velar chord will be decreased leading to a dorsal shift and likely folding in the df (Figure 12). The velar chord is not a continuous connective tissue band connecting the two contralateral ceratobranchials; each velar chord terminates within the df before reaching the midline. A consequence of this morphology, clearly evident in Figures 5 and 11, is that unilateral ceratobranchial displacement leads to changes only in the ipsilateral df. Bilateral changes in the dorsal gular folds require changing the tension of both velar chords, which requires the displacement of both ceratobranchials.

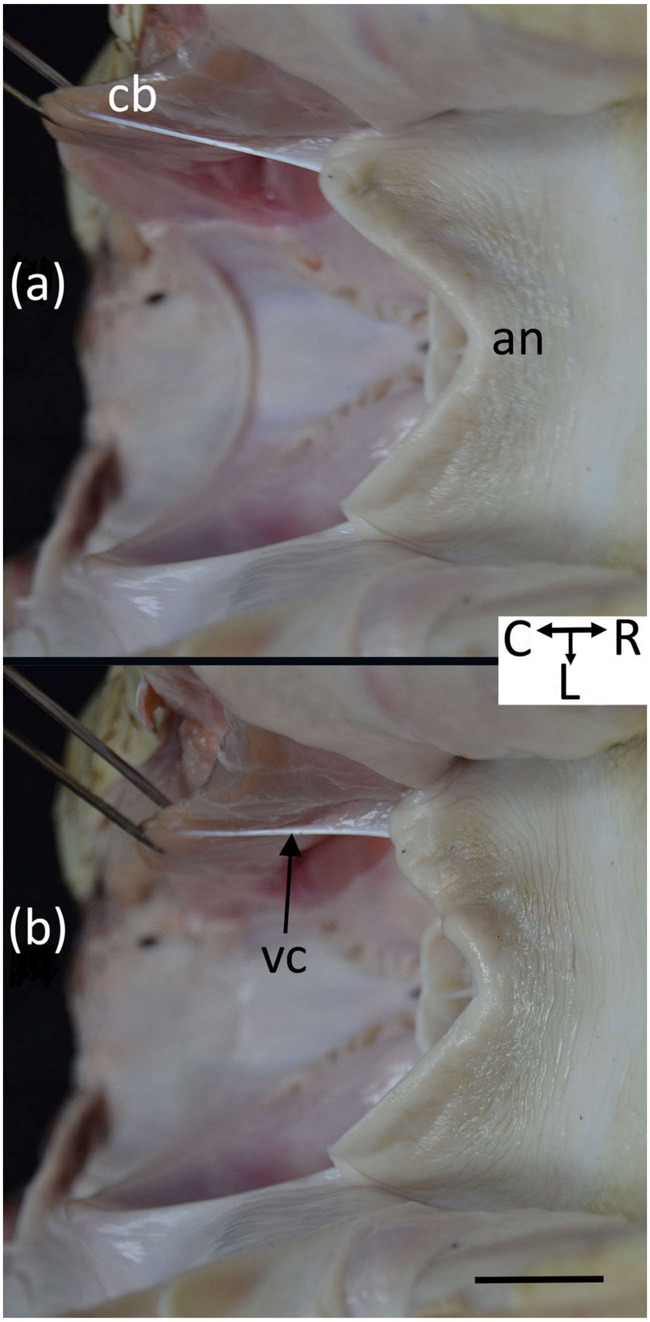

FIGURE 9 Mechanical linkage of the dorsal gular fold in *Alligator mississippiensis*. The lateral portion of the velar chord was exposed, then these two images taken roughly 15 s apart. By manual manipulation of the ceratobranchial the tension on the velar chord could be increased (a) or decreased (b) leading to changes in the appearance of the df. Note that because the velar chord does not course continuously through the df, these unilateral manipulations did not influence the contralateral side of the df. Scale bar = 1 cm. an, apical notch; cb, ceratobranchial; vc, velar chord.

3.6 | Osteological association

In *Alligator mississippiensis*, on the ventral surface of the palatines, immediately deep to the region of the apical notch of the df, there is a shallow medial-lateral depression, herein termed the velar fossa (Figure 13). While the velar fossa is more prominent in larger specimens of *A. mississippiensis*, its presence is not purely size-related, as evident from its absence in some of the large crocodylian skulls examined (Figure 14).

The velar fossa was well-developed in *Alligator mississippiensis*, *Alligator sinensis*, *Boverisuchus vorax*, *Caiman crocodilus chiapasius*, *Caiman latirostris*, *Ceratosuchus burdoshi*, *Crocodylus intermedius*, *Crocodylus mindorensis*, *Crocodylus porosus*, *Paleosuchus palpebrosus*, and *Tomistoma schlegelii*. In *Osteolaemus tetraspis* the velar fossa took the form of a transverse groove (Figure 15), while in *Melanosuchus niger* there was a midline ridge coursing through the fossa. The velar fossa was weakly developed, or absent, from the skulls of *Caiman crocodilus chiapasius*, *Caiman crocodilus*, *Caiman latirostris*, *Crocodylus acutus*, *Crocodylus affinis*, *Crocodylus niloticus*, *Crocodylus novaeguineae*, *Crocodylus palustris*, *Crocodylus porosus*, *Gavialis gangeticus*, *Paleosuchus palpebrosus*, and *Paleosuchus trigonatus* (Figure 15).

4 | DISCUSSION

Gadow's (1901) treatise, *Amphibia and Reptiles*, described the crocodylian gular valve as, “The hinder margin of the tongue is raised into a transverse fold, which, by meeting a similar fold from the palate, the velum palatinum, can shut off the mouth completely.” (p. 443). This description, like virtually all previous and subsequent treatments of the gular valve, treats the valve as two separate units (the dorsal and ventral gular folds in the terminology used herein). The major finding of the present study is that the velar chord forms a mechanical and functional linkage between the ventral and dorsal gular folds, such that the gular valve is best recognized as a single integrated morphological complex (Figures 11 and 12). Putterill and Soley (2006) appear to have seen the velar chord on histological sections through the df of *Crocodylus niloticus*; they described the presence of a bundle of dense regular connective tissue but did not explore the structure further. Taguchi (1921) working on the same species, appears to have also noted the velar chord, but he described it as skeletal muscle (the tensor palatini) without providing any details regarding the origin or insertion.

Tension in the velar chord and df is likely less than the muscle forces acting on the ceratobranchial; accordingly, it seems more likely that the ceratobranchial displacement influences the df more than the converse. Increasing upper jaw rotation and increasing the gape angle, increase the tension on the velar chord. One

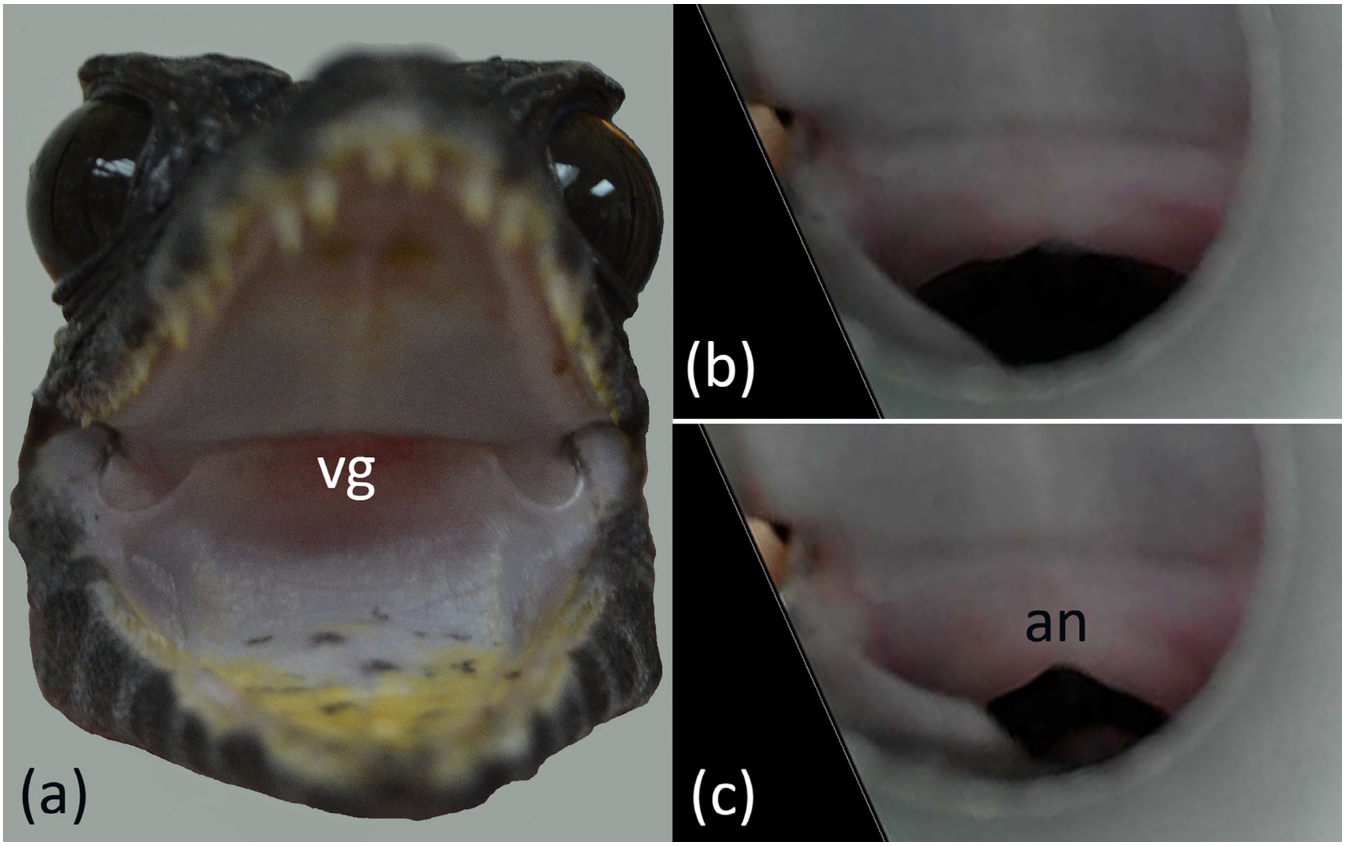

FIGURE 10 Dynamics of the gular valve in *Paleosuchus palpebrosus*. (a) During the defensive gape display the gular valve is typically shut, so the ventral gular fold (vg) obscures the more caudal df. (b) Endoscopic image of the open gular valve with the animal at "rest". (c) subsequent image taken while palpating the ventral gular valve. Note the change in the contour of the df, and the change in the prominence of the apical notch, between frames b and c.

consequence of this can be seen in head-on photos of crocodylians. There is a distinct inverse correlation between the elevation of the hyobranchial system and the prominence of the df, particularly the apical notch. This relation is evident in photos of individuals lifting up the upper jaw of anesthetized or dead crocodylians (in which the hyobranchial skeleton is depressed due to lack of muscle tone) but can also be seen in yawning crocodylians (Figure 11, see, Figure 3.2 in Johnston, 2023).

The manipulation of the hyobranchial apparatus in an anesthetized or dead crocodylian clearly demonstrates the mechanical linkage between the df and the ceratobranchial. The ceratobranchial and the rest of the crocodylian hypobranchial apparatus supports a series of antagonistic skeletal muscles (e.g., Johnston, 2023; Li & Clarke, 2015; Schumacher, 1973) which means that the animal has the ability to fine tune or modulate the velar chord and df. This modulation, which can be demonstrated by palpating the ventral gular fold (Figure 10) presumably enables crocodylians to ensure a good seal between the dorsal and ventral gular folds during submergence.

The same mechanism of dorsal gular fold modulation through hyobranchial adjustment may play an important role in crocodylian vocalization. The transition from a closed gular valve/narial hiss to an open gular valve oral hiss would change the format of the call due to the structural/volume differences between the nasal and oral cavities. Note that the open gular valve oral hiss would have different acoustic properties depending on the gape angle. The ventral gular fold is not likely to influence the acoustics of crocodylian calls given its size and shape; the elements are so large that they are unlikely to be vibratory. The df seems more likely to be vibratory, especially the lateral portion and the epithelium at the transition from the df to the lateral pharyngeal wall. This is exactly the same portion of the df that is most malleable during ceratobranchial displacement. Accordingly, in at least some species or size classes of crocodylians, the df may play a role not only in shaping the format of the call (see Reber et al., 2017), but also in providing a dynamic harmonic component (see Britton et al., 2001).

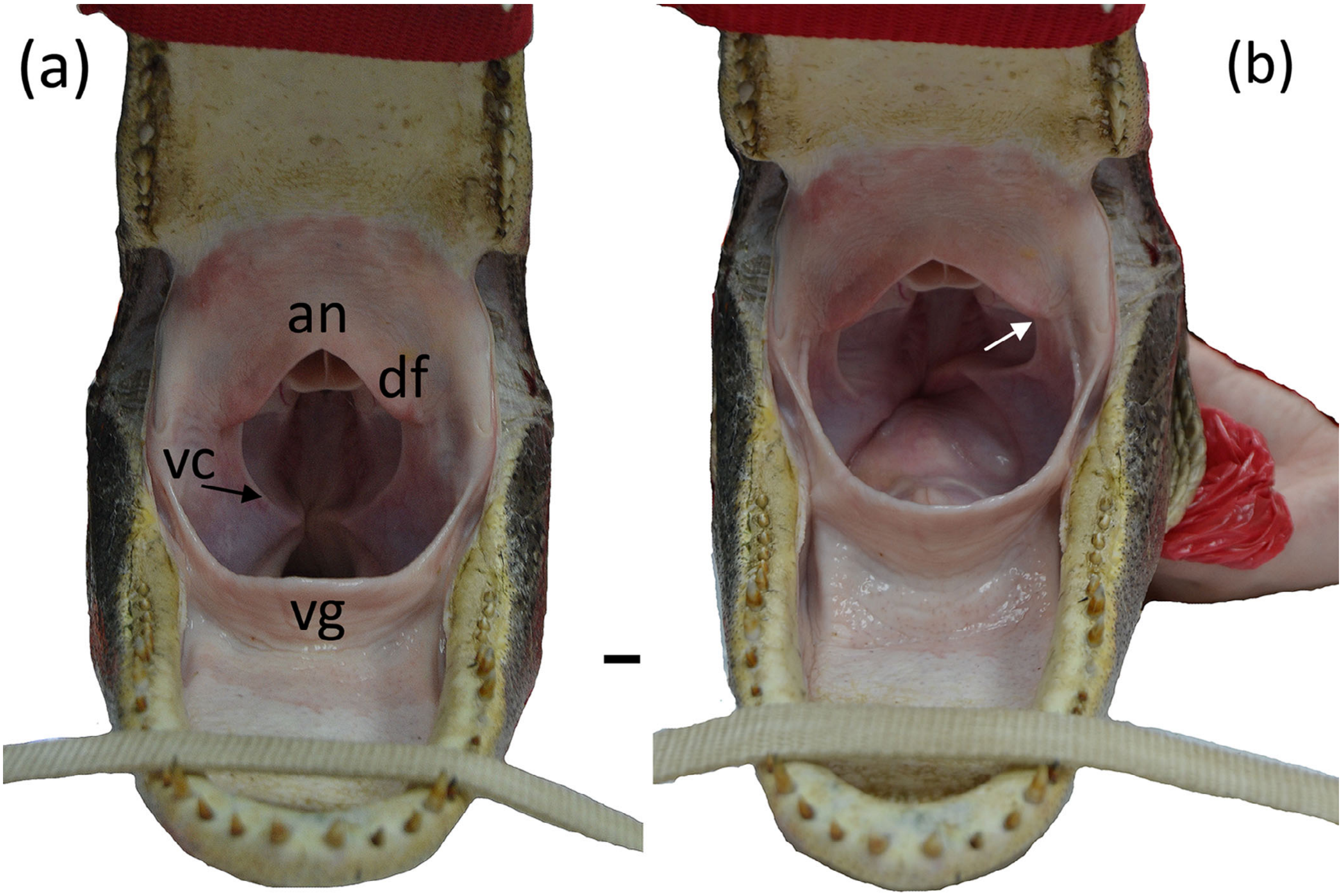

FIGURE 11 Frontal view of the gape of a 176 cm total length specimen of *Alligator mississippiensis*. In this specimen the hyolingual apparatus was fully depressed which, when combined with the large gape (a), accentuated the tension in the velar chord (vc) and the df. By manually elevating one side of the hyolingual complex (b), the tension and contours of the velar chord and df were altered (white arrow). Scale bar = 1 cm. an, apical notch; df, dorsal gular fold; vc, celar chord; vg, ventral gular fold.

The "billowing" of the df (Figure 8) during strong exhalation is due, in part, to the spatial alignment between the df and the glottal opening of the larynx. A strong exhalatory stream causes rostrad rotation of the ventral edge of the df; this movement is easy because of the infolding or "pocket" present on the caudal margin of the df. Continued force on the df from the exhalent airstream can cause a slight ventral displacement of the df; this displacement is possible due to the relatively weak connection between the submucosa of the df and the underlying palatine periosteum (Figures 3 and 6) as well as the transverse pleats on the rostral margin of the df (Figures 1 and 2). Within the context of the "billowing" of the df, it is worth noting that Taguchi (1921) referred to the df as the palatal sails ("Gaumensegels"), though this appears to be based on the angular shape of the df, rather than the df's expansion during exhalation.

Crocodylians are generally recognized as opportunistic predators; while the diets of some species/size classes contain small prey items, most species and nearly all adults, are capable of ingesting relatively large prey items (Erickson et al., 2012; Gignac & Erickson, 2016). Prey items are first positioned/manipulated using inertial transport, which is far more effective in air than in water. Crocodylians have a relatively reduced hyoid apparatus, which has traditionally been interpreted as a specialization for ingesting large prey items (Li & Clarke, 2015). Earlier workers argued that in crocodylians the tongue and hyolingual system did not play a role in oral transport or swallowing; more recent work has documented cyclic displacement of the hyolingual system and an important role of the hyoid and tongue in pushing the prey item against the dorsal palate (Busbey III, 1989; Cleuren & de Vree, 1992, 2000; Li & Clarke, 2015). The proposed movements of the hyolingual apparatus during deglutition would have the effect of lowering tension in the velar chord, and thus increasing mobility of the df. The reduced tension in the velar chord, the presence of a caudal epithelial infolding or "pocket" on the df (Figure 3), and the relatively loose connection between the df and the

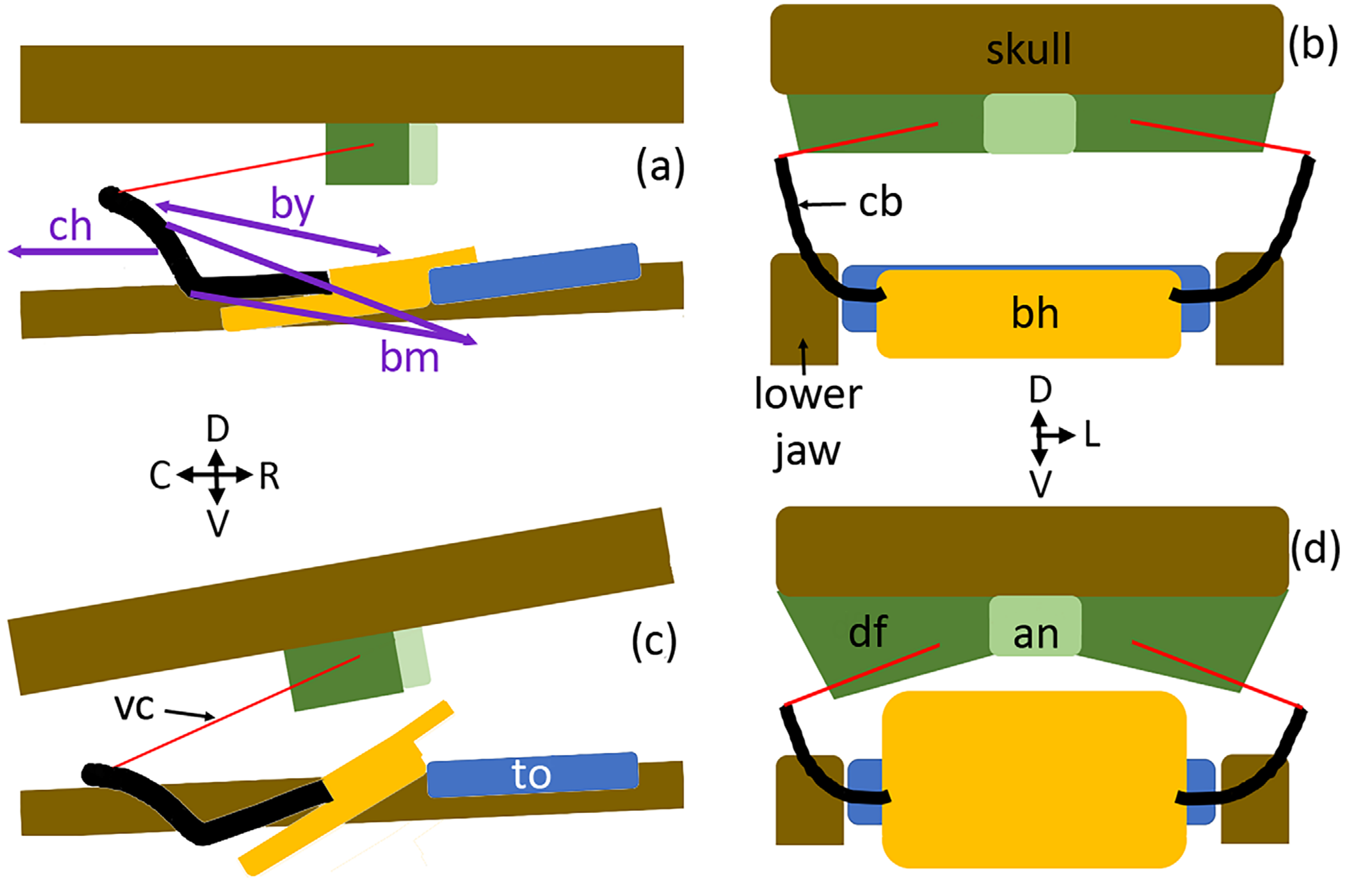

FIGURE 12 Proposed mechanical model of the gular valve. The valve is schematically illustrated in the open condition (above) from the lateral (a) and caudal (b) perspective, and in the closed condition (below) from the lateral (c) and caudal (d) perspectives. The palate/skull and lower jaws are illustrated by the olive bars; the tongue (to) is illustrated in blue. Protraction and rotation of the ceratobranchial (cb, black) has two results: (1) it causes the rotation of the basihyal (bh, yellow) about the caudal end of the tongue thereby elevating the ventral gular fold; and (2) it increases the tension on the velar chord (vc, red) which causes increased tension and depression of the dorsal gular fold (df, green). The apical region (light green) of the dorsal gular fold is considered a more passive anchoring point. The anatomical attachments and lines of pull of the primary muscles responsible for opening and closing the gular valve are shown in purple; bm, branchiomandibularis; by, branchiohyoideus; ch, coracohyoideus.

underlying palatine periosteum (Figures 3 and 6) all combine to allow the df to shift and deform during the oral transport and swallowing of a prey item (Figure 7).

The ability of the df to shift and deform does not appear to be uniform across the medial-lateral span of this feature. The central region, marked by the apical notch, has a smaller epithelial infolding or "pocket" and is not directly connected to the velar chord. The fact that the central portion of the df is perpendicular to the long axis of the pharynx, as opposed to the more oblique orientation of the lateral portions of the df (Figures 1 and 2), makes the central portion particularly vulnerable to shear forces during ingestion of a large prey item.

The present study was undertaken, in part, to test the hypothesis that the shape and tension of the dorsal gular fold are dynamic. This hypothesis was supported by observing changes in the shape of the df during behavioral displays in living crocodilians (Figures 8 and 10), following contact with a food item during mock deglutition (Figure 7), and during manual manipulation of the hyolingual apparatus (Figure 11). This study was also intended to describe any mechanical linkage between the ventral gular fold and the df. By connecting the ceratobranchial to the df, the velar chord can effectively alter the tension acting on the df as was demonstrated in both intact (Figure 11) and dissected (Figure 9) *A. mississippiensis*.

The present study also sought to document any osteological correlates of the dorsal gular fold; these results were not clear cut. The dorsal-ventral compression of the central portion of the df that was observed in the presence of a large prey item (Figure 7) may be accommodated, in part, by the shallow depression in the underlying surface of the palatines, what is herein termed the velar fossa (Figures 13–15). The velar fossa was a

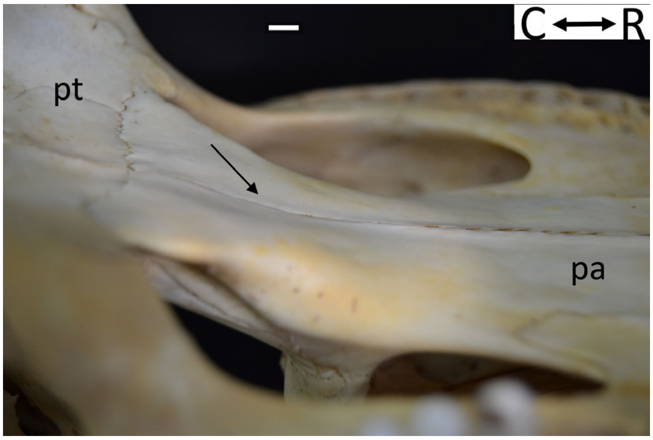

FIGURE 13 Lateral view of the velar fossa from a 29 cm skull length specimen of *Alligator mississippiensis*. The velar fossa (arrow) is a medial-lateral depression in the ventral (palatal) surface of the palatines; the fossa is slightly cranial to the palatine/pterygoid suture and is roughly aligned with the caudal extent of the maxillary dentition (a position that corresponds to the apex of the df). Scale bar = 1 cm. pa, palatine; pt, pterygoid.

consistent feature in every specimen of *Alligator mississippiensis*; however, intraspecific variation was found in *Caiman crocodilus chiapasius*, *Caiman latirostris*, *Crocodylus porosus*, and *Paleosuchus palpebrosus*. The dorsal gular fold and the velar fossa may be epiphenomena with no mechanical connection. The considerable morphological variation in the hard palate of crocodylians (Dollman & Choiniere, 2022) may result in different force lines acting in this region of the palatine bones, which could influence the development of a velar fossa. There could also be a complex relationship between the size of the dorsal gular fold, the gape angle and size of the pharynx, and the diameter of the common prey items, which influences the relative prominence of the velar fossa.

5 | CONCLUSION

Perhaps the most important finding to emerge from this study is the recognition that, contrary to earlier claims, the dorsal gular fold is neither fixed nor static but is a dynamic part of the oral/pharyngeal cavity. The present study demonstrated that the df varied in shape and tension when subjected to a variety of influences ranging from tension on the velar chord to the compressive forces of deglutition. One influence not explored in the present study was the influence of the ventral gular fold. Our results suggest that the closing of the gular valve involves more than just the elevation of the ventral gular fold; rather, we hypothesize that the elevation of the ventral gular fold is associated with active changes in the dorsal gular fold which maximize the efficacy of the seal of the gular valve.

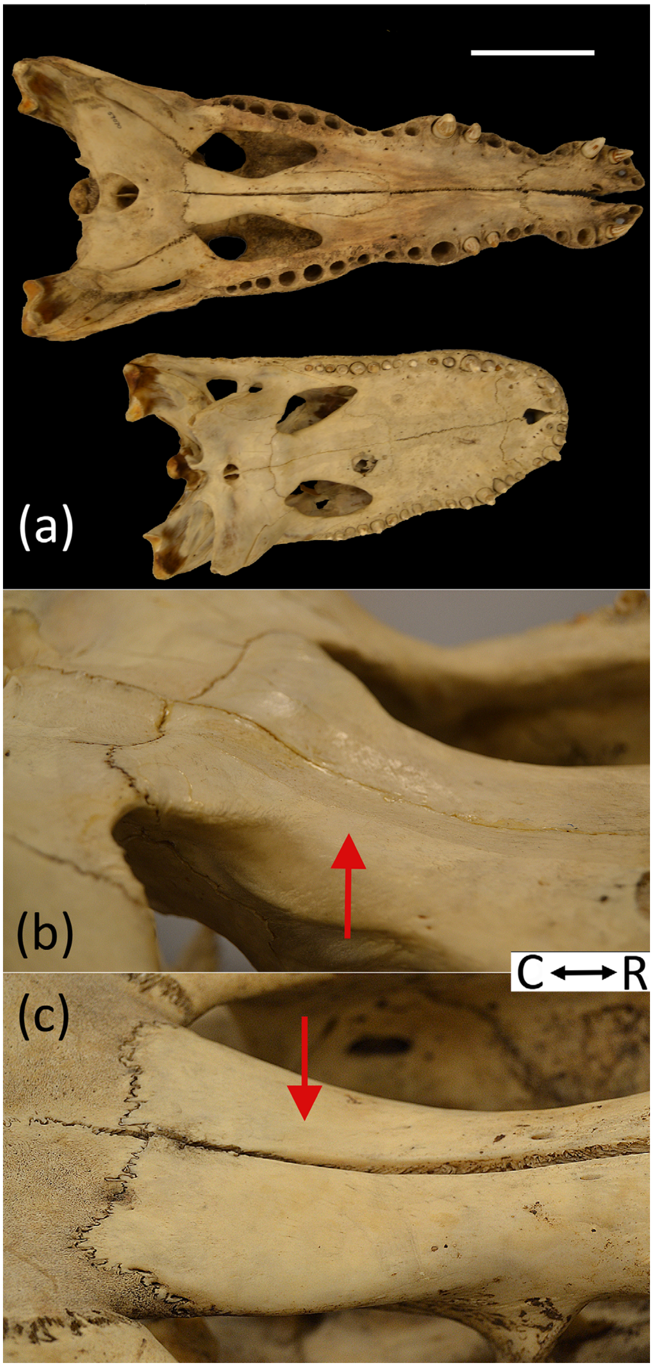

FIGURE 14 (a) Palatal views of (top) a 62 cm skull length *Crocodylus acutus* (FMNH 59070) and (bottom) a 46 cm skull length *Alligator mississippiensis* (FMNH 31011). (b) The velar fossa (arrow) from the *A. mississippiensis* skull. (c) The same region (arrow) of the palatal surface from the *C. acutus* skull; note that despite being larger, the *C. acutus* lacked a velar fossa. Scale bar = 10 cm.

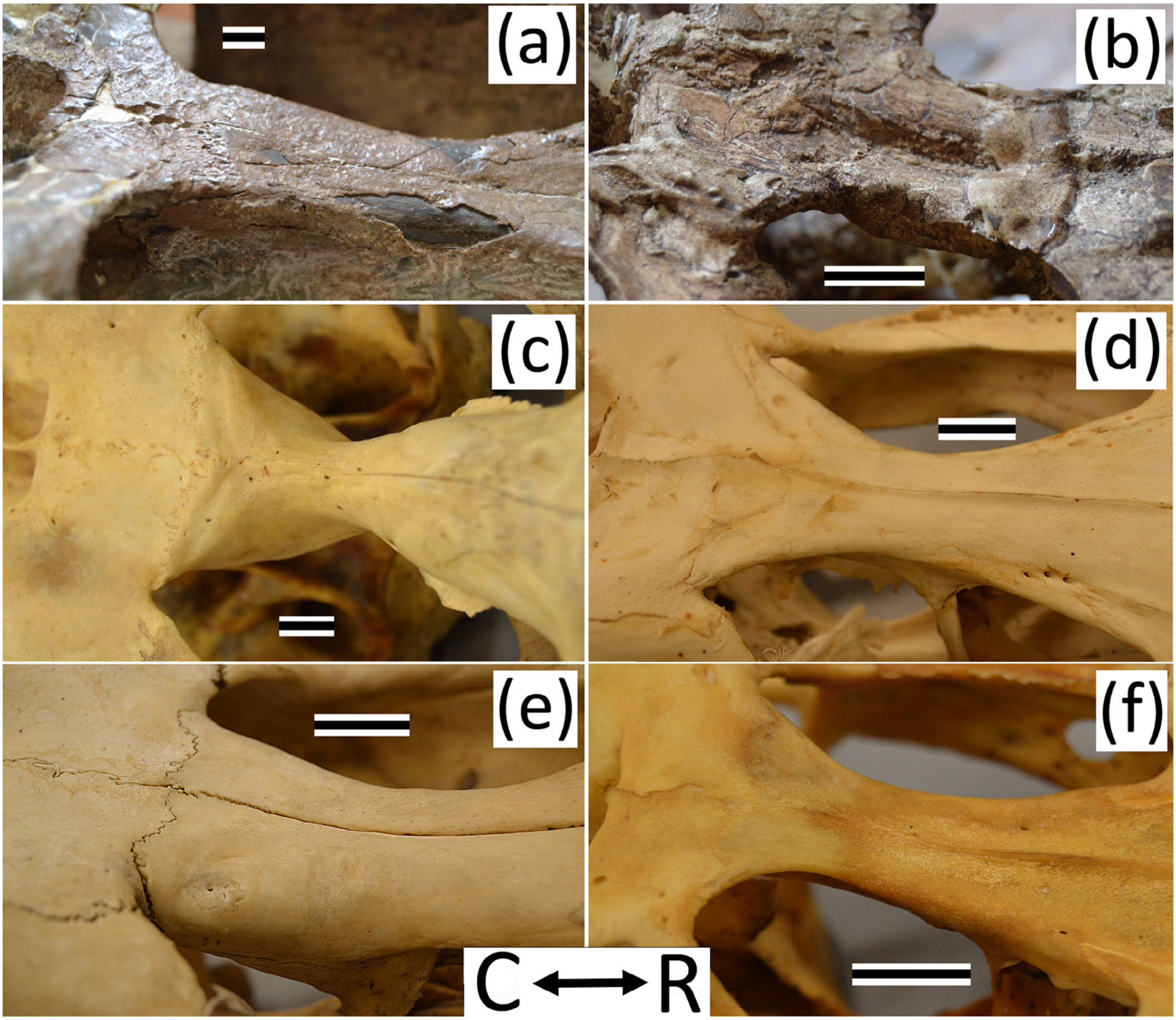

FIGURE 15 Variation in the velar fossa among crocodylians. A clear velar fossa is present in (a) *Boverisuchus vorax* (FMNH PR399) and (b) *Ceratosuchus burdoshi* (FMNH P15576). An unusual transverse fossa was observed in (c) *Osteolaemus tetraspis* (FMNH 44410). The velar fossa of (d) *Melanosuchus niger* (FMNH 45653), though clear, had a midline ridge through it. No clear velar fossa was found in either (e) *Crocodylus niloticus* (FMNH 17157) or (f) *Paleosuchus palpebrosus* (FMNH 98961). Scale bars = 1 cm.

AUTHOR CONTRIBUTIONS

Bruce A. Young: Conceptualization; investigation; writing – original draft; methodology; validation; visualization; formal analysis; project administration; data curation; supervision; resources. **Michael Cramberg:** Investigation; methodology; writing – review and editing; visualization; formal analysis. **Olivia G. Young:** Investigation; visualization; writing – review and editing; formal analysis.

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