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Cranial myology of the smalltooth sawfish (*Pristis pectinata*): implications for headshaking behaviors and entanglement in marine debris

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Abstract—The smalltooth sawfish (*Pristis pectinata*) was listed as endangered under the U.S. Endangered Species Act in 2003 because of a precipitous population decline primarily due to being taken as bycatch. The anatomy and internal morphology of this species and other sawfishes (Pristidae) are poorly documented but are important to understand from conservation and ecological perspectives. For example, entanglement in marine debris is frequently reported for this species and damages the cranial musculature, impeding feeding and ventilation through spiracles and gills. With improved understanding of its myology, we can identify how marine debris can damage the cranial musculature of individuals. We identified the cranial musculature of the smalltooth sawfish by examining freshly dead juvenile and adult specimens, and we describe it herein. The musculature differed little from that of guitarfish and wedgefish species; however, the defining muscular feature is the large, paired antorbitopectoralis muscles that anchor the lateral chondrocranium of pristids, and by proxy, their toothed rostrum, to the pectoral musculoskeletal system. On the basis of attachment characteristics and proximity to other muscles, we hypothesize that the large antorbitopectoralis muscles are used to actuate headshaking behaviors, such as those related to feeding, defense, and courtship. Finally, entanglement in marine debris has resulted in damage to 17 of the 24 cranial muscles associated with biological functions, including feeding and ventilation, damage that negatively affects fitness and may affect survivorship.

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Chondrichthyes (sharks, rays, and chimaeras) make up the sole extant sister clade to the other gnathostome clade of fish species and provide important perspectives on early vertebrate evolution (Maisey, 1980; Brazeau, 2009). Although not as species rich as the Osteichthyes (better known as *bony fishes*), the Chondrichthyes include some of the largest and longest-living vertebrates and occupy a range of habitats (e.g., Nielsen et al., 2016; Stein et al., 2018; Weber et al., 2020). As such, chondrichthyans have a suite of derived morphological characteristics, including a cartilaginous skeleton (Seidel et al., 2020; Atake and Eames, 2021). To better understand the role of chondrichthyans in gnathostome evolution, it is necessary to catalog and characterize the morphological diversity of extant species, including endangered species even though they can be difficult to study (Vaškaninová et al., 2020; Zhu et al., 2022).

One endangered taxon is the sawfishes (Rhinopristiformes: Pristidae), a group that comprises 5 species found in tropical seas and estuaries globally (Harry et al., 2024). Sawfishes have an elongated anterior rostrum or *saw* with numerous enlarged lateral denticles or *teeth* (Miller, 1995). Toothed rostra have evolved in sharks (the sawsharks, which compose the order Pristiophoriformes) and at least once in batoids (extant sawfishes and extinct sclerorhynchids; Underwood et al., 2016). The rostrum of sawfishes makes them susceptible to entanglement in marine debris, such as monofilament fishing line and rubber bands, and entanglement negatively affects fitness and has emerged as a conservation concern in recent years (Seitz and Poulakis, 2006; Yakich et al., 2024).

Like other batoids, sawfishes have ventral jaws that are suspended by paired, strut-like hyomandibular cartilages (Maisey, 1980). This euhyostylic jaw suspension, where the paired hyomandibulae are the sole elements articulating the jaws to the skull, is one of the defining features of batoids relative to sharks and coincides with an increasingly complex cranial musculature. For example, batoids have jaw muscles atop other jaw muscles (Kolmann et al., 2014), muscles "wrapped" around skeletal structures, perhaps to dissipate stresses over broader attachment areas (Kolmann et al., 2015), and systems of tendinous pulleys that reroute forces (Summers, 2000) or move jaws away from the cranium (Dean and Motta, 2004a, 2004b).

Links between musculoskeletal diversity and dietary specialization have been reported from studies of batoid musculature (Wilga and Motta, 1998; Kolmann et al., 2014; Ramírez-Díaz et al., 2023, 2025). For example, some batoid lineages have adapted their cranial morphologies for suction-feeding and extreme jaw protrusion and, therefore, are dietary specialists (e.g., *Narcine* spp.; Dean and Motta, 2004a), whereas others (e.g., *Rhinoptera* spp. and *Myliobatis* spp.) are known to crush shelled prey with forceful bites (Kolmann et al., 2015, 2023). In contrast, skates (Rajidae) and guitarfishes (Rhinobatidae) tend toward morphologies that balance biting and suction performance rather than those that specialize in either mechanism (Wilga and Motta, 1998; Wilga et al., 2012a). An extreme example of musculoskeletal modification is the rostrum of sawfishes.

The pristid rostrum is a long (up to one-third of total length; Bigelow and Schroeder, 1953), dorsoventrally flattened cartilaginous rod with socketed teeth that project laterally and are 2.5–5.0 cm long in adults. Sawfishes rapidly oscillate the rostrum from side to side to injure prey (Wueringer et al., 2012). They then swallow prey whole, although, like other batoids, they also trap injured prey between enlarged pectoral fins and the bottom until prey can be maneuvered to the mouth, a behavior called *tenting* (Wilga and Motta, 1998). However, whether the rostrum is actuated by cranial muscles or solely because of whole-body undulation is unknown. The antorbitopectoralis muscle, which connects the base of the rostrum to the pectoral girdle, is poorly described, yet its attachment to the skeleton indicates a role in feeding (Compagno, 1977; Nishida, 1990).

The smalltooth sawfish (*Pristis pectinata*) was listed as endangered under the U.S. Endangered Species Act in April 2003 (Federal Register, 2003), and its biology and ecology had been poorly understood (Brame et al., 2019). Since then, the species has become one of the best studied elasmobranchs, and recent research has identified it as a generalist piscivore that uses its toothed rostrum to stun bony fishes and other batoids (Poulakis et al., 2017; Lear et al., 2019). Documentation of the cranial myology of this species improves our understanding of its biology and feeding ecology, allowing comparisons to that of other batoids and assessments of damage caused by entanglement in marine debris. The goals of this study were 1) to identify and describe the cranial musculature of the smalltooth sawfish and 2) to determine how entanglement with marine debris, such as rubber bands and elastic bungee cords, negatively affects specific muscle function associated with biological functions, such as feeding and ventilation.

Materials and methods

Eight fresh, intact specimens were studied after being found dead from unknown causes and reported by the public to the U.S. Sawfish Recovery Hotline (by phone, 1-844-4SAWFISH; email, sawfish@myfwc.com; or website form) (Table 1). Two specimens were fixed in 10% formalin and stored in 70% ethanol, then dissected. Specimens were skinned with a scalpel blade to reveal the musculature. Muscle terminology follows Compagno (1977), Nishida (1990), Miyake et al. (1992), Kolmann et al. (2014), and Ramírez-Díaz et al. (2023, 2025), and myological descriptions are organized by embryological and functional units for Chondrichthyes following Miyake et al. (1992) and Mallatt (1997) (Table 2).

Table 1

Summary of specimens of smalltooth sawfish (*Pristis pectinata*) that were collected from 2020 through 2024 in Florida and were used to map the cranial musculature of this species. STL=stretch total length; APM=antorbitopectoralis muscle.

Collection date	Sex	STL (mm)	Type of preservation	Location	Type of sample
15-Apr-2020	F	940	Preserved	St. Lucie River	Whole head
16-Jun-2022	M	1592	Fresh	Peace River	Whole head
22-Oct-2022	M	1242	Preserved	Everglades City	Whole head
9-Jan-2023	M	1152	Fresh	Caloosahatchee River	Whole head
8-May-2023	F	812	Fresh	Marco Island	Whole head
6-Feb-2024	F	4321	Fresh	Key West	Whole head
27-Mar-2024	M	4078	Fresh	Florida Bay	APM only
5-Apr-2024	M	4174	Fresh	Duck Key	APM only

Table 2

The abbreviations, origins, insertions, and functions of the 24 cranial muscles of the smalltooth sawfish (*Pristis pectinata*). In the second column, an asterisk (*) follows the name of each of the 17 muscles that were identified to have been damaged by marine debris.

Abbreviation	Muscle	Origin	Insertion	General function
AMLa	Adductor mandibularis lateralis	Palatoquadrate	Meckel's cartilage	Jaw closure
AMMa	Adductor mandibularis major	Palatoquadrate	Meckel's cartilage	Jaw closure
AMMe	Adductor mandibularis medialis	Palatoquadrate	Meckel's cartilage	Jaw closure
APM	Antorbitopectoralis*	Pectoral fin, propterygia	Antorbital cartilage	Stabilize and actuate rostrum?
CARC	Coracoarcualis*	Pectoral girdle	Coracomandibularis	Abducts jaws (with CM)
CB	Coracobranchiales	Coracoarcualis	Gill arches	Ventilation
CHD	Constrictor hyoideus dorsalis*	Medial 1st gill arch skeleton	Dorsal 1st gill arch skeleton	Ventilation
CHV	Constrictor hyoideus ventralis*	Medial 1st gill arch skeleton	Ventral 1st gill arch skeleton	Ventilation
CSD	Constrictor superficiales dorsalis*	Gill arch	Adjacent, posterior gill arch	Ventilation
CSV	Constrictor superficiales ventralis*	Gill arch	Adjacent, posterior gill arch	Ventilation
CU	Cucullaris	Scapulocoracoid	Synarcual	Elevates gill arches and pectoral girdle
DHYM	Depressor hyomandibularis*	Depressor rostri	Hyomandibular cartilage	Depresses hyoid arch
DLB	Dorso-longitudinalis*	Scapulocoracoid	Posterior chondrocranium	Raises and supports cranium
DM	Depressor mandibularis*	Coracomandibularis	Meckel's cartilage	Depresses Meckel's cartilage
DR	Depressor rostri*	Antimere, ventral midline	Pectoral propterygium	Lowers snout
ETM	Ethmoideo-parethmoidalis	Antorbital cartilage	Olfactory capsule	Unknown
CM	Coracomandibularis*	Coracoarcualis	Meckel's cartilage	Abducts jaws (with CARC)
CHY	Coracohyoideus*	Coracoarcualis	Basihyal, hypohyal cartilages	Expands oropharynx
CHYM	Coracohyomandibularis*	Antimere, ventral midline	Hyomandibular cartilage	Depresses hyoid arch
LHYM	Levator hyomandibularis*	Dorsal chondrocranium	Hyomandibular cartilage	Retracts hyoid cartilages
LP	Levator palatoquadrati	Preorbital, chondrocranium	Palatoquadrate	Jaw retraction
LR	Levator rostri*	Synarcual	Antorbital cartilage	Raises snout
SB	Suborbitalis*	Palatoquadrate	Meckel's cartilage	Jaw protrusion
SP	Spiracularis*	Postorbital, chondrocranium	Spiracular cartilage, palatoquadrate	Ventilation

We used Adobe Illustrator[1] 2023 and 2024 (vers. 27.9 and 28.5; Adobe Inc., San Jose, CA) to draw the musculature. First, muscle images from dissections were traced. Then, muscle fibers were added in the original directions, on the basis of observations during the dissections. Each muscle was labeled and colored, following Miyake et al. (1992), Kolmann et al. (2014), and Ramírez-Díaz et al. (2023). Cartilage elements were shaded in gray, and non-cranial muscles (i.e., pectorals) were shaded in beige to differentiate them.

We compared published photographs of smalltooth sawfish that were damaged by marine debris (Seitz and Poulakis, 2006; Yakich et al., 2024) to the mapped musculature from dissections to identify which muscles had been damaged.

This research was conducted under endangered species research permit number 25864 issued to the Florida Fish and Wildlife Conservation Commission.

Results

The smalltooth sawfish has 24 cranial muscles in 6 series—epaxial, branchial, hyoid, precranial, mandibular, and hypaxial—and at least 17 of these muscles were found to have been damaged by entanglement in marine debris (Table 2). Muscles from all 6 series have been damaged, and the 17 muscles that have been damaged are associated with jaw movement, ventilation through spiracles and gills, and general head movements. The muscles that were found to have been damaged are indicated by asterisks in the text in this section and in Table 2.

Epaxial series

This series has one paired bilateral muscle: the dorso-longitudinalis* (Fig. 1). The dorso-longitudinalis elevates the chondrocranium relative to the synarcual and post-cranial skeleton.

This muscle (previously known as the *dorsal longitudinal bundles*; Kolmann et al., 2014) originates from the anterodorsal face of the scapulocoracoid cartilage. It is formed by individual epaxial muscle fibers, which run parallel to the synarcual cartilage. It inserts on the dorsal side of the otic capsules of the chondrocranium.

Branchial series

This series has 3 paired bilateral muscles, the dorsal and ventral superficial branchial constrictor muscles and the cucullaris. These muscles compress the gill arches or elevate and compress the entire gill chamber (Table 2).

Constrictor superficiales dorsalis* and ventralis* There are 5 pairs each of these thin, sheet-like branchial constrictor muscles (constrictor superficiales dorsalis 1–5 and constrictor superficiales ventralis 1–5). The origin of each muscle is the gill arch anterior to it, and the insertion is the gill arch posterior to it. Each constrictor superficiales dorsalis constricts the dorsal region of each adjacent gill arch pair, and the constrictor superficiales ventralis muscles do the same for the ventral half of these arches (Figs. 1 and 2).

Cucullaris This muscle originates from the anterodorsal face of the scapulocoracoid cartilage and runs beside the dorso-longitudinalis at a slight angle to insert on the synarcual cartilage process in the mid-hypaxial region (Fig. 1).

Hyoid series

This series has 7 paired bilateral muscles: levator hyomandibularis, levator rostri, constrictor hyoideus dorsalis, constrictor hyoideus ventralis, depressor hyomandibularis, depressor mandibularis, and depressor rostri. Most of these muscles reorient, rotate, and translate the hyomandibular cartilage (Table 2). The levator rostri and depressor rostri elevate and depress the rostrum, respectively, and the depressor mandibularis depresses the Meckel's cartilage (MK) (Ramírez-Díaz et al., 2025).

Levator hyomandibularis* This muscle is short and falcate in shape. It originates from the lateral otic capsule wall posterior to the spiracularis origin. The levator hyomandibularis narrows before inserting on the laterodorsal surface of the hyomandibular cartilage (Fig. 1).

Levator rostri* This sickle-shaped muscle originates from the dorsal surface of the cervicothoracic synarcual, just adjacent to the origin of the dorso-longitudinalis. The levator rostri narrows considerably before inserting with a long tendon on the dorsoposterior side of the antorbital cartilage. Its long tendon overlies several muscles and runs taut across the dorsal side of the adductor mandibularis major (Fig. 1).

Constrictor hyoideus dorsalis* and ventralis* The paired constrictor hyoideus dorsalis and ventralis are thin, sheet-like muscles. The constrictor hyoideus dorsalis originates from the dorsal medial septum of the first branchial arch and inserts medially on a membrane shared with the constrictor hyoideus ventralis. The constrictor hyoideus ventralis originates from the ventral hypobranchial septum at the center of the first branchial arch. Both muscles form a wall between the hyoid and branchial muscle regions (Figs. 1 and 3).

Depressor hyomandibularis* This muscle is paired, triangular, and sheet-like, originating beside the coracomandibularis. Proceeding toward the exterior insertion, the muscle narrows, and a thin tendon inserts on the lateral ventral surface of the hyomandibula (Fig. 3).

Depressor mandibularis* This muscle originates from fascia covering the lateral surface of the coracomandibularis and the dorsal surface of the depressor rostri. The origin is broad

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA, or the Florida Fish and Wildlife Conservation Commission.

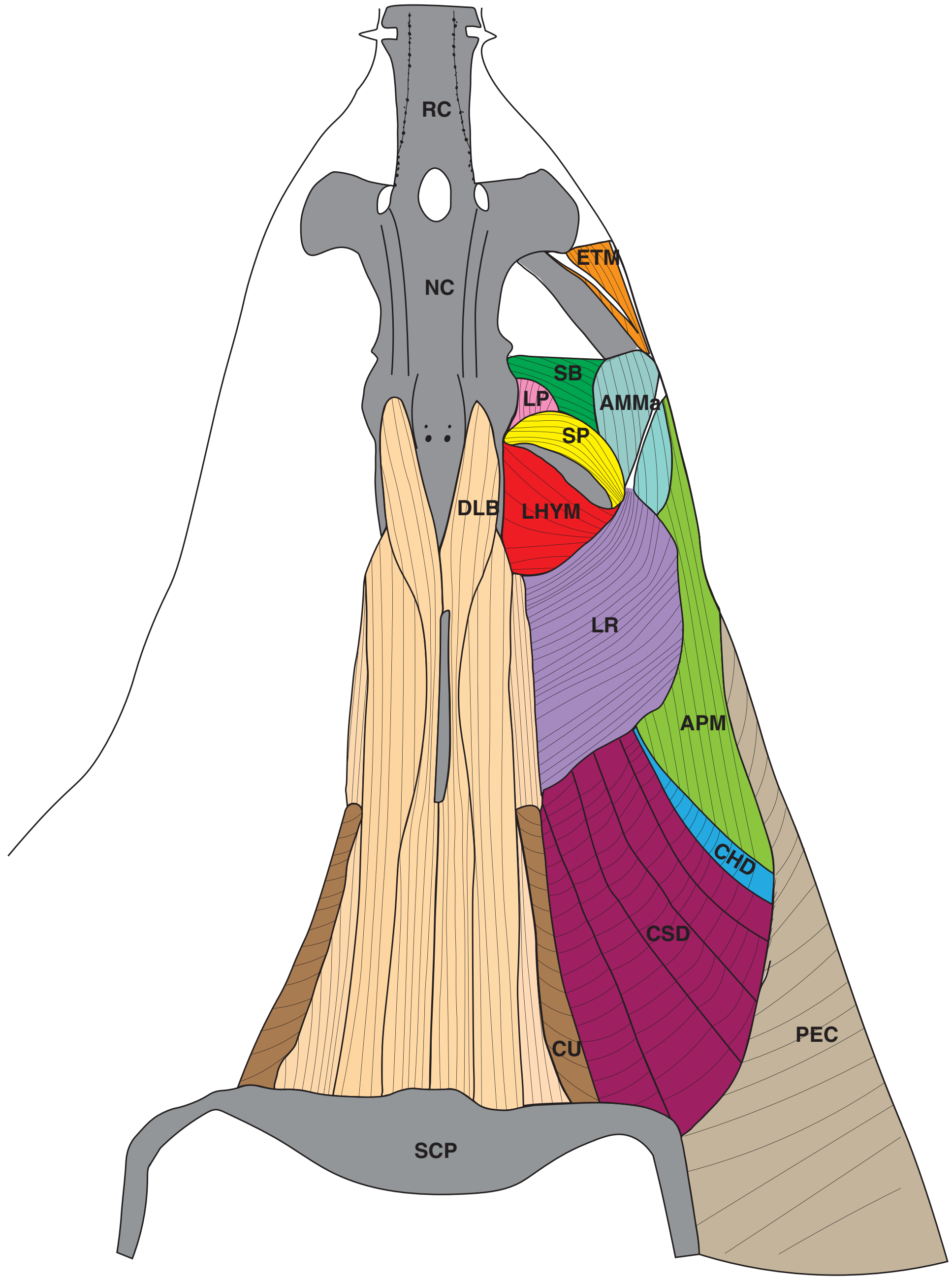

Figure 1

Superficial dorsal view of the cranial musculature of the smalltooth sawfish (*Pristis pectinata*), with skin removed. The cranial muscles (in colors) are as follows: ethmoideo-parethmoidalis (ETM), suborbitalis (SB), levator palatoquadrati (LP), adductor mandibularis major (AMMa), spiracularis (SP), dorso-longitudinalis (DLB), levator hyomandibularis (LHYM), levator rostri (LR), antorbitopectoralis (APM), constrictor hyoideus dorsalis (CHD), constrictor superficiales dorsalis (CSD), and cucullaris (CU). Cartilage (in gray) and non-cranial muscles (in beige) are as follows: rostral cartilage (RC), nasal capsule (NC), scapulocoracoid (SCP), and pectoralis muscles (PEC, non-cranial).

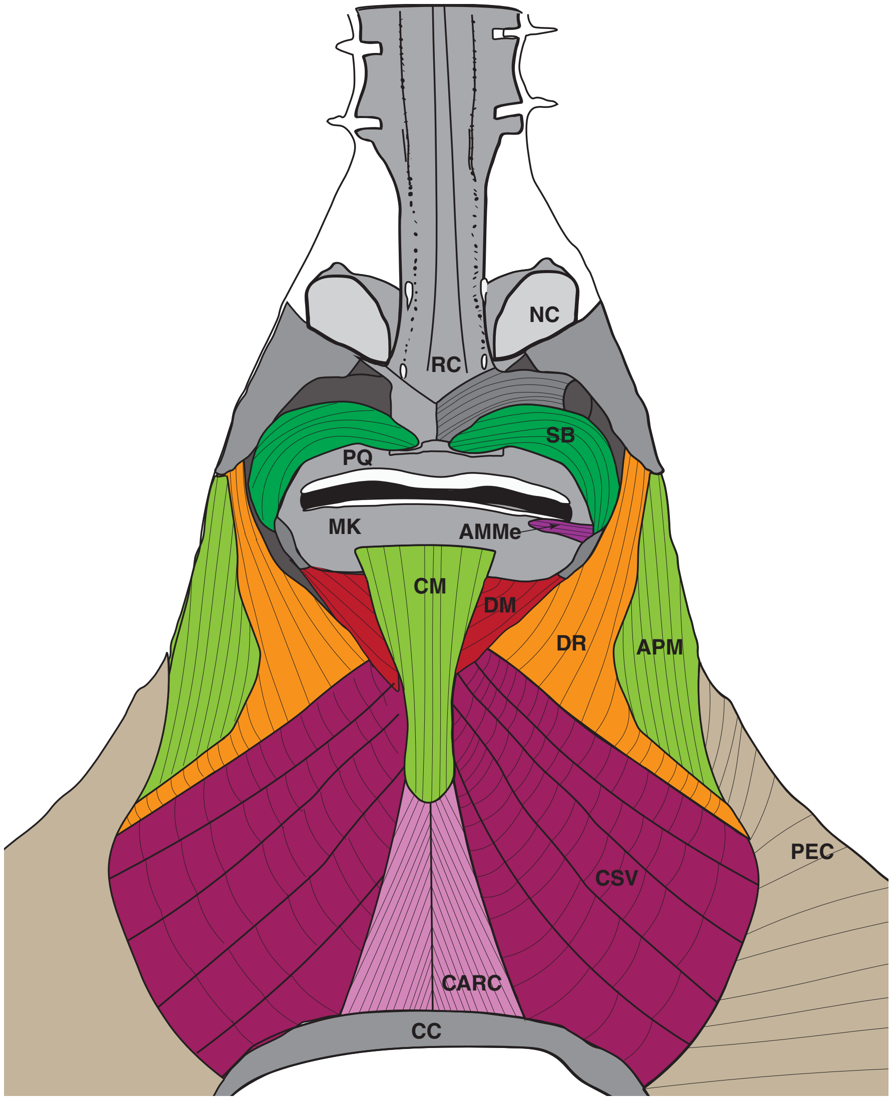

Figure 2

Superficial ventral view of the cranial musculature of the smalltooth sawfish (*Pristis pectinata*), with skin removed. The cranial muscles (in colors) are as follows: suborbitalis (SB), adductor mandibularis medialis (AMMe), coracomandibularis (CM), depressor mandibularis (DM), depressor rostri (DR), antorbitopectoralis muscle (APM), coracoarcualis (CARC), and constrictor superficiales ventralis (CSV). Cartilage (in gray) and non-cranial muscles (in beige) are as follows: rostral cartilage (RC), nasal capsule (NC), palatoquadrate (PQ), Meckel's cartilage (MK), pectoralis muscles (PEC, non-cranial), and coracoid bar (CC).

and narrows to a tendon before inserting on the lateral margin of the MK. The tendon inserts at a 45° angle and forms a shared insertion with the suborbitalis tendon (Fig. 3).

Depressor rostri* This superficial, sickle-shaped muscle originates from the anterodorsal surface of the branchial constrictor superficiales ventralis and inserts on the posterior inferior margin of the antorbital cartilage through a long tendon (Fig. 2).

Precranial series

This series has 3 paired bilateral muscles: the ethmoideoparethmoidalis (Fig. 1), suborbitalis (Fig. 3), and antorbitopectoralis muscles. We include the antorbitopectoralis in this section for convenience; however, the embryological origins of this unique pristid muscle are unknown. The suborbitalis aids in retraction and stabilization of the jaws after jaw protrusion. The function of the

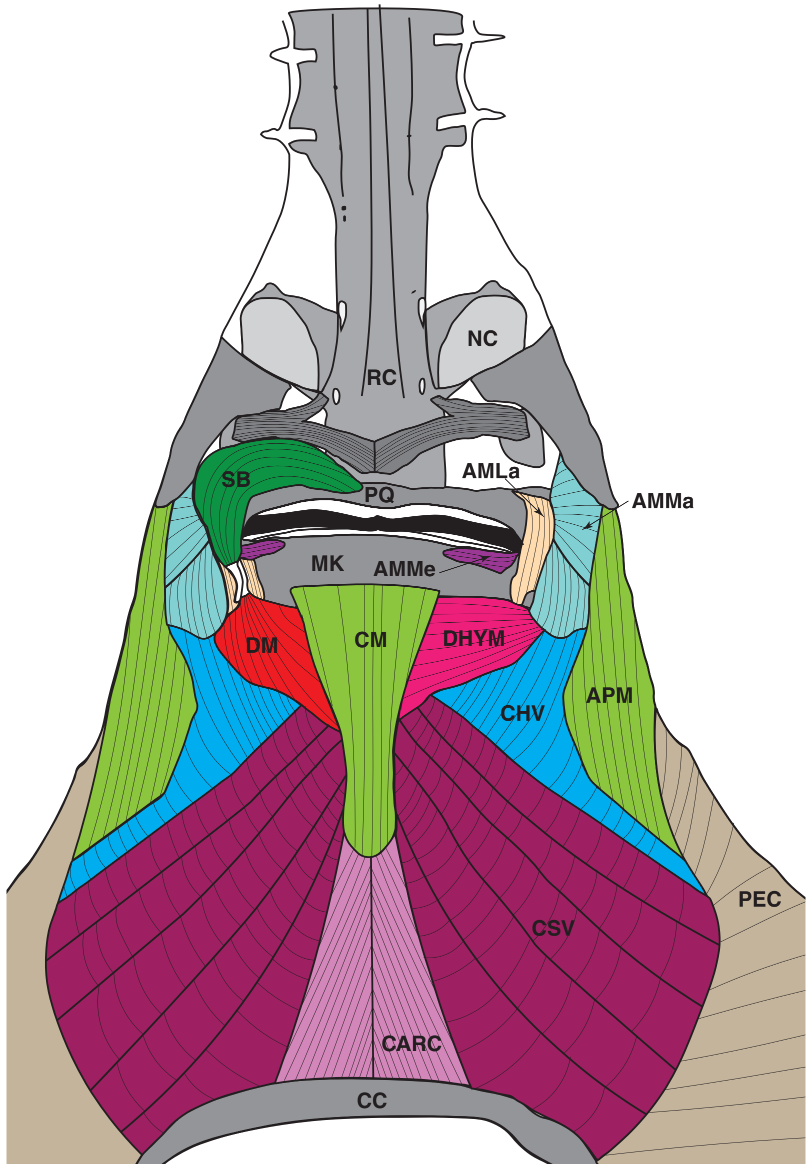

Figure 3

Superficial and medial ventral views of the cranial musculature (in colors) of the smalltooth sawfish (*Pristis pectinata*), with skin removed. On the left, the superficial layer is shown, with depressor rostri removed (see Figure 2). On the right, the medial layer is shown, with suborbitalis (SB) and depressor mandibularis (DM) removed (see left side); the muscles are as follows: adductor mandibularis lateralis (AMLa), adductor mandibularis major (AMMa), adductor mandibularis medialis (AMMe), coracomandibularis (CM), depressor hyomandibularis (DHYM), constrictor hyoideus ventralis (CHV), antorbitopectoralis muscle (APM), coracoarcualis (CARC), and constrictor superficiales ventralis (CSV). Cartilage (in gray) and non-cranial muscles (in beige) are as follows: rostral cartilage (RC), nasal capsule (NC), palatoquadrate (PQ), Meckel's cartilage (MK), pectoralis muscles (PEC, non-cranial), and coracoid bar (CC).

ethmoideo-parethmoidalis is unclear (Kolmann et al., 2014), but given the attachment, it presumably serves a purpose in maintaining articulation between the chondrocranium and propterygia. The function of the antorbitopectoralis muscle is explored later in this section. Note that the precranialis, another precranial muscle, is lacking in the smalltooth sawfish and appears to be present only in myliobatiforms (Ramirez-Diaz et al., 2023, 2025).

Ethmoideo-parethmoidalis These small muscles originate from the medial posterior surface of the antorbital cartilage and insert on the lateral anterior surface of the olfactory capsule (Fig. 1).

Suborbitalis* The comma-shaped suborbitalis originates from the chondrocranial basal plate above the center of the palatoquadrate (PQ). This muscle has a narrow tendon inserting on the MK. The tendon fuses with the depressor mandibularis tendon, forming a common insertion (Fig. 3). We note that the suborbitalis is exceptionally large and thick, relative to that of other rhinopristiforms and other batoids. The size and thickness of this muscle indicate that it plays an important role in feeding by protruding and retracting the jaw.

Antorbitopectoralis* This robust, tubular muscle is unique to pristids (Nishida, 1990) and originates from the anterior tip of the pectoral-fin muscle, adjacent to the levator rostri, depressor rostri, and adductor mandibularis major. It inserts onto the posterior surface of the antorbital cartilage with a thick tendon and attaches directly with muscle fibers. Although, as expected on the basis of the pectoral-fin musculature, this muscle does not encase internal radial cartilages. It provides an empty and flexible gap between the propterygium and antorbital cartilage (Fig. 1), which may allow lateral movement of the rostrum and the associated anterior skeleton.

Mandibular series

This series has 5 paired bilateral muscles spanning superficial, medial, and deep layers of the cranium: levator palatoquadrati, spiracularis, adductor mandibularis medialis, adductor mandibularis major, and adductor mandibularis lateralis (Figs. 1–4). The adductor mandibularis generally adduct (close) the jaws, and all muscles are involved with feeding and ventilation (Kolmann et al., 2014; Table 2).

Levator palatoquadrati This triangular muscle originates from the lateral wall of the otic capsule, anterior to the spiracularis origin. It inserts on the anterodorsal face of the PQ near the medial symphysis and posterior to the insertion of the suborbitalis (Fig. 1).

Spiracularis* This muscle originates from the lateral wall of the otic capsule and almost entirely envelopes the spiracular cartilage. It inserts along the spiracular cartilage, extending to the distal edge of the anterodorsal surface of the hyomandibular cartilage (Fig. 1).

Adductor mandibularis medialis This thin, fusiform muscle originates on the PQ at the corner of the mouth through loose connective tissue. It inserts on the MK, just posterior to the overhanging dentition, encircling the entire corner of the mouth (Figs. 2 and 4).

Adductor mandibularis major This large, pennate muscle is one of the largest muscles in the mandibular series. In general, it originates on the PQ and partially inserts on the MK, entirely covering the jaw joint. However, its origin extends beyond the ventral face of the PQ and also extends to the dorsal surface of the PQ (Fig. 3). The insertion extends beyond the MK to also insert on the medial surface of the antorbital cartilage.

Adductor mandibularis lateralis This muscle originates from the PQ and inserts on the MK, medial to the insertion of the adductor mandibularis major (Fig. 4).

Hypaxial series

This series has 5 muscles spanning superficial, medial, and deep layers: the single, medial coracomandibularis and the paired bilateral coracohyoideus, coracoarcualis, coracohyomandibularis, and coracobranchiales (Figs. 2–4). In general, these muscles pull the feeding and respiratory apparatus posteriorly and ventrally to assist with opening of the jaw and oropharyngeal expansion (Miyake et al., 1992; Mallatt, 1997; Table 2).

Coracomandibularis* This long, delta-shaped muscle originates on the anterior (insertion point) of the coracoarcualis, overlying the esophageal tract. It broadens as it nears its insertion onto the medial symphysis of MK, specifically onto the posterodorsal surface of the medial symphysis (Fig. 3).

Coracohyoideus* This slender muscle originates on the anterior, curved tip of the first branchial membrane and on the coracoarcualis (see below) and inserts on the basihyal and possibly on hypohyal cartilages (Fig. 4).

Coracoarcualis* This triangular muscle originates at the anteroventral surface of the scapulocoracoid cartilage. It narrows anteriorly toward its insertion on fascia shared with the coracomandibularis and overlying the esophageal tract (Fig. 4).

Coracohyomandibularis* This strap-shaped muscle originates on the midline fascia, which forms the ventral side of the oropharyngeal cavity. The origination also extends to the basihyal cartilages embedded within this fascia. It then inserts through a tendon on the ventral surface of the hyomandibular cartilage (Fig. 4).

Coracobranchiales (not illustrated) These long, thin muscles originate from the anterodorsal surface of the coracoid, lateral to the heart. They run along the pericardium and narrow as they approach the gill chamber, with the antimeres joining at the midline near the conus arteriosus.

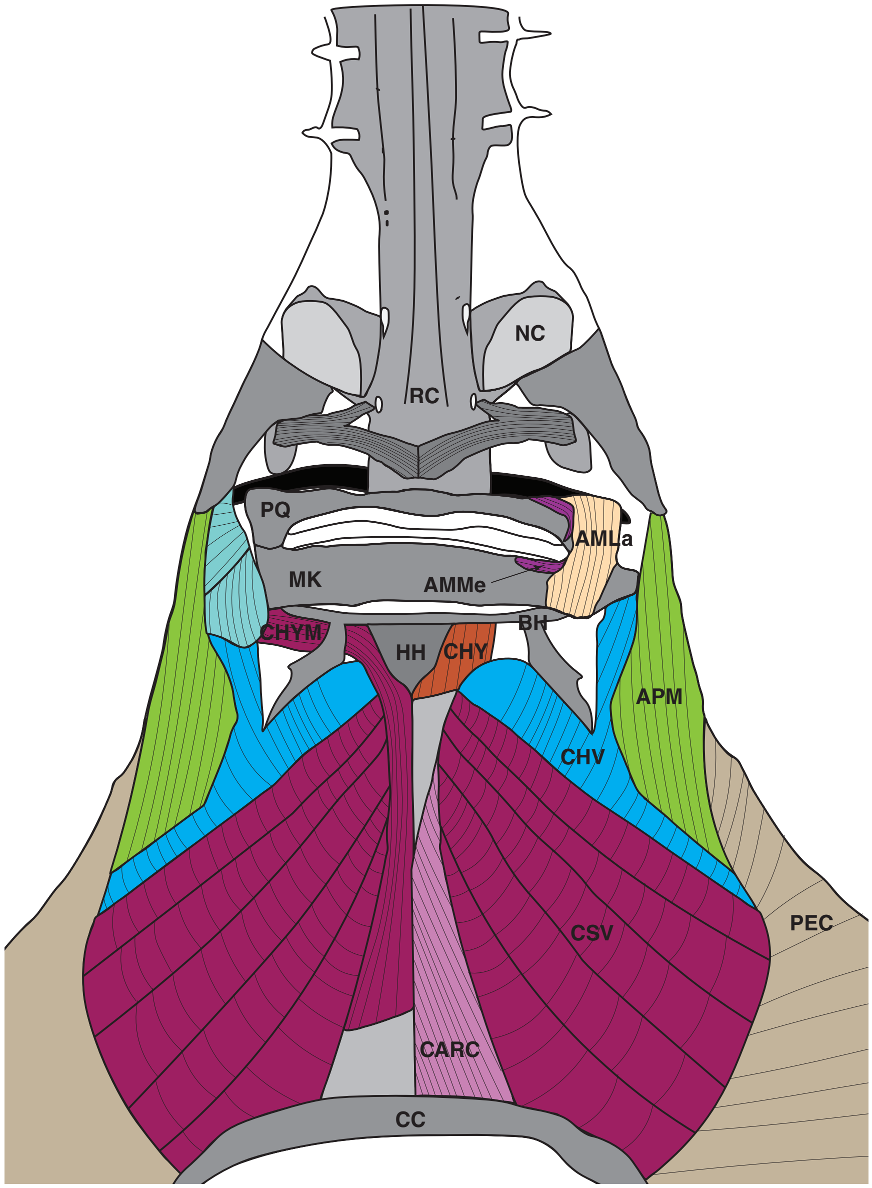

Figure 4

Medial and deep ventral views of the cranial musculature (in colors) of the smalltooth sawfish (*Pristis pectinata*), with skin removed. On the left, the deep layer is shown, with coracohyoideus (CHY), coracoarcualis (CARC), and fascia removed (see right side). On the right, the medial layer is shown, with coracomandibularis, depressor hyomandibularis, and adductor mandibularis major removed (see Figure 3); the muscles are as follows: adductor mandibularis medialis (AMMe), adductor mandibularis lateralis (AMLa), coracohyomandibularis (CHYM), CHY, constrictor hyoideus ventralis (CHV), antorbitopectoralis muscle (APM), CARC, and constrictor superficiales ventralis (CSV). Cartilage (in gray) and non-cranial muscles (in beige) are as follows: rostral cartilage (RC), nasal capsule (NC), palatoquadrate (PQ), Meckel's cartilage (MK), basihyal (BH), hypohyal (HH), pectoralis muscles (PEC, non-cranial), and coracoid bar (CC).

Then they insert on the second hypobranchial cartilage as they do in other species (e.g., Motta and Wilga, 1995).

Discussion

Unlike that of some sharks and other rays, most of the cranial musculature (i.e., mandibular and hyoid series) of the smalltooth sawfish is not specialized for feeding on specific prey (Motta and Wilga, 1999; Huber et al., 2005; Kolmann et al., 2023). Instead, the cranial musculature has similarities to guitarfishes and wedgefishes (Rhinopristiformes; Wilga and Motta, 1998; Kolmann et al., 2014), except for the presence of large, paired antorbitopectoralis muscles that connect the rostrum to the pectoral girdle. *Pristis* sawfishes also have wide jaws without labial cartilages, characteristic of other piscivorous rays, such as species of *Gymnura*, *Paratrygon*, and *Pteroplatytrygon* (Magnuson et al., 2024). Like guitarfishes and some generalist myliobatiforms, the smalltooth sawfish has small, molariform teeth and lacks hypertrophied jaw adductors, possibly because it targets soft-bodied prey, such as small teleosts (Poulakis et al., 2017; Hancock et al., 2019). Overall, the cranial musculature and unspecialized jaw of the smalltooth sawfish combines the high-performance protrusion, suction, and crushing morphologies of other batoids (Dean et al., 2007).

Batoids use various appendages to aid feeding. For example, cownose rays (*Rhinoptera* spp.) use cephalic lobes to increase prey capture efficiency (Mulvany and Motta, 2014), and butterfly rays (*Gymnura* spp.) stun fish with their pectoral fins (Henningsen, 1996). In fact, most batoids use some manner of tenting behaviors (i.e., behaviors in which they use their large pectoral fins to corral and trap prey during feeding) (Wilga et al., 2012b; Kolmann et al., 2016). Skates and guitarfishes also use their pectoral fins during feeding but do so in coordination with the rostral cartilage to direct water flow beneath the disc (Wilga et al., 2012b). The ability of sawfishes to laterally shake their head is another example of elaboration on the coordination between batoid head- and body-derived musculoskeletal systems. Given that the antorbitopectoralis muscle is presumably derived from pectoral muscle, use of the rostrum in feeding by sawfishes and other batoids demonstrates coordination between the cranial and appendicular musculoskeletal systems that is unlike the feeding mechanisms of most other vertebrates.

A musculoskeletal hypothesis for rostral function in sawfishes

Despite the elongated rostrum of sawfishes being a cranial appendage, its function might be facilitated by pectoral musculature, even indirectly (e.g., by depressor rostri and antorbitopectoralis; see Figures 1 and 2). In the smalltooth sawfish and other pristids, the pectoral propterygium does not directly articulate with the chondrocranial skeleton. Most batoids have propterygia that surround and potentially constrain lateral expansion of the cranium (Kolmann et al., 2014, 2015; Ramírez-Díaz et al., 2023). However, in the smalltooth sawfish, the antorbitopectoralis muscle is a pliable element that bridges the gap between the antorbital and propterygial skeletons. This means that sawfishes, unlike other batoids, can move their heads laterally. This ability to move their heads laterally presumably reflects the ability of sawfishes to oscillate their rostrum both vertically and horizontally (Wueringer et al., 2012). We hypothesize that the antorbitopectoralis muscle 1) actuates lateral strikes by contributing force directly to headshaking, 2) modulates lateral strikes, ensuring that overextension does not occur by preventing lateral hyperextension, or 3) does some combination of both. This ability presumably supports important headshaking behaviors used by sawfishes during feeding, defense, and courtship (e.g., precopulatory rostral strikes; G. Poulakis, unpubl. data; Grubbs[2]).

From a developmental perspective, the embryological origin of the unique antorbitopectoralis muscle is unknown; however, we propose 2 possibilities. Given its origin, it could be a derivation of the pectoralis (fin) muscle. If true, like the cephalic lobes of myliobatids and mobulids, it is an example of pectoral-fin muscles of batoids that have been adapted for novel roles in feeding (Mulvany and Motta, 2013, 2014). Alternatively, it could be derived from precranial muscles. The association, positionally and with respect to attachment, of the antorbitopectoralis with both the cranial and pectoral skeletons is similar to that of precranial muscles like the ethmoideo-parethmoidalis. The function and origin of precranial muscles is still uncertain; Mallatt (1997) proposed that the precranial muscles are holdovers from the "oral" mouth, a vestige of a mouth before jaws, of the original vertebrates (i.e., agnathans). Kolmann et al. (2014) suggested that muscles, such as the precranialis and ethmoideo-parethmoidalis, have a role in articulating the skull, propterygia, and jaw skeletons together. If the antorbitopectoralis is derived from the precranial muscle series, it indicates recapitulation, a return of ancient muscles to a more direct and active role during feeding.

Marine debris and its effects on cranial muscle function

The rostrum and flattened head make sawfishes vulnerable to entanglement, particularly for juveniles that remain in estuaries for their first few years (Poulakis et al., 2011). Entanglement in marine debris, such as rubber bands and elastic bungee cords, poses a garroting threat to the smalltooth sawfish (and other large marine vertebrates; Seitz and Poulakis, 2006). These pollutants enter waterways (e.g., during hurricanes) and sink to the bottom where sawfishes live. As a sawfish swims along the bottom, its rostrum may move through and become encircled by debris, and the debris then moves down the rostrum and stops where the head widens. As the entangled fish grows, the encircling debris squeezes the body, impeding muscle function and leading to behavioral and respiratory inhibition and even to death (Yakich et al., 2024).

[2] Grubbs, D. 2025. Unpubl. data. Coast. Mar. Lab., Fla. State Univ., 3618 Coast. Hwy. 98, St. Teresa, FL 32358.

Yakich et al. (2024) reported that many cases of entanglement of smalltooth sawfish with marine debris involved damage to the head and branchial region, and in our research, we identified at least 17 individual cranial muscles that have been damaged by marine debris (see Table 2). The importance of the well-developed antorbitopectoralis for feeding may make injury to this muscle especially lethal for sawfishes because damage from encircling debris often occurs on both sides of the head. We suggest that entanglement in marine debris, especially by elastic bands, interferes with the following biological functions by arresting muscle action: 1) elevation of and lateral movements of the rostrum, 2) protrusion of the jaws, 3) suction-feeding through oropharyngeal expansion, and 4) gill ventilation. Future research in which electromyography is used is needed to confirm these effects.

Conclusions

Cranial muscle anatomy of the smalltooth sawfish resembles that of guitarfishes and wedgefishes, with one key distinction: the presence of unique, large, paired antorbitopectoralis muscles that connect the rostrum to the pectoral girdle. These muscles are unique to pristids and presumably help stabilize and actuate the toothed rostrum during the headshaking behaviors related to feeding, defense, and courtship. Use of the antorbitopectoralis during feeding is an example of how batoids incorporate appendicular structures, such as the pectoral fins, into prey capture. Entanglement in marine debris is problematic for a variety of biological functions (e.g., vision, feeding, defense, courtship, and ventilation), particularly when it impairs the function of the antorbitopectoralis muscles and, by extension, the rostrum. Encircling marine debris has damaged over two-thirds of the cranial muscles of the smalltooth sawfish, joining capture as bycatch and habitat loss as ongoing threats to this endangered species.

Resumen

El pez sierra de dientes pequeños (*Pristis pectinata*) fue incluido en la lista de especies en peligro de extinción de la Ley de Especies en Peligro de Extinción de los Estados Unidos en 2003 debido a un abrupto declive de su población causado principalmente por la captura incidental. La anatomía y la morfología interna de esta especie, y de otros miembros de la familia Pristidae, están poco documentadas, pero es importante comprenderlas desde una perspectiva ecológica y de conservació. Por ejemplo, se han registrado numerosos casos de enredos en residuos marinos de esta especie, dañando la musculatura craneal y dificultando la alimentación y la ventilación a través de los espiráculos y las branquias. Mejorando la comprensión de su miología, podemos identificar cómo los desechos marinos pueden dañar la musculatura craneal de los individuos. En el presente estudio, identificamos y describimos la musculatura craneal del pez sierra de dientes pequeños examinando cadáveres frescos de juveniles y adultos. La musculatura difiere poco de la de las especies de pez guitarra y pez cuña; sin embargo, la característica muscular definitoria son los grandes músculos antorbitopectorales pareados que anclan el condrocráneo lateral de los pristidos y, por analogía, su rostro dentado, al sistema musculoesquelético pectoral. Basándonos en las características de fijación y la proximidad a otros músculos, planteamos la hipótesis de que los grandes músculos antorbitopectorales se utilizan para accionar comportamientos de sacudida de la cabeza, como los relacionados con la alimentación, la defensa y el cortejo. Por último, el enredo en los desechos marinos afectó 17 de los 24 músculos craneales asociados a funciones vitales, como la alimentación y la ventilación, pudiendo afectar su salud física y la supervivencia.

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