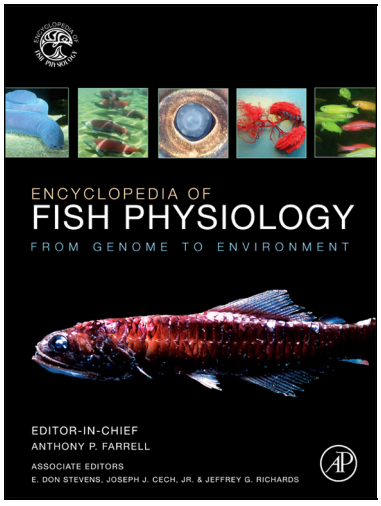

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MUSCLES, SKELETON, SKIN, AND MOVEMENT

The Muscles

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Cartilaginous Fishes Cranial Muscles

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Glossary

Branchiomeric Pertaining to muscles originating between the dorsal and ventral elements of the visceral arches of the skeleton.
Chondrocranium Cartilaginous cranium of the chondrichthyan fishes.
Epibranchial Pertaining to muscles lying dorsal to the branchial arches.
Hypobranchial Pertaining to muscles lying ventral to the branchial arches.
Meckel's cartilage Lower jaw of the chondrichthyan fishes.
Palatoquadrate Upper jaw of the chondrichthyan fishes.
Raphe A seam-like union between two halves of an anatomical structure having a sheet of connective tissue at the septum.
Scapulocoracoid Pectoral girdle of the chondrichthyan fishes.

Introduction

Study of the cranial musculature of the cartilaginous fishes has a long history owing to both the phylogenetic position of this clade and the dynamic nature of their predatory endeavors. Basal gnathostomes diverged from a common ancestor with the Teleostomi over 400 million years ago and thus the study of their cranial musculature promises insight into the proximate mechanisms underlying the transition of the anterior visceral arches from respiratory structures into those involved in active predation. While early studies focused on describing the cranial muscles and their relation to the visceral arches as a means of codifying the evolutionary history of jawed vertebrates, later studies focused on the range of function enabled by the diverse morphologies of the various chondrichthyan feeding (**see also Chondrichthyes**: Physiology of Sharks, Skates, and Rays, **Food Acquisition and Digestion:** Energetics of Prey Capture: From Foraging Theory to Functional Morphology, and **The Reproductive Organs and Processes:** Anatomy and Histology of Fish Testis) and respiratory mechanisms (**see also Ventilation and Animal Respiration**: Gill Respiratory Morphometrics).

Although taxonomically few, cartilaginous fishes possess a remarkable diversity of feeding mechanisms (six jaw

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suspension types, ram/biting/suction/filter feeding, jaw protrusion). While their respiratory mechanisms are not as diverse, they represent both predominant systems found in aquatic vertebrates, the suction-force pump and ram ventilation. The cranial muscles serve as the actuators of these mechanisms. Thus, studying their functional diversity provides critical links in our understanding of the relationship between the morphology, behavior and ecology in cartilaginous fishes, and the reconstruction of vertebrate evolutionary history. The following information is a basic guide to the cranial musculature of the three major radiations of extant cartilaginous fishes. Among the elasmobranchs, sharks are represented by the spiny dogfish *Squalus acanthias* and batoids by the southern guitarfish *Rhinobatos percellens*. The holocephalans are represented by the spotted ratfish *Hydrolagus colliei*. Hypobranchial and pharyngeal muscles are described in addition to cranial muscles, as these structures are also involved in feeding and respiration.

Shark Musculature

The muscles involved in feeding and respiration in cartilaginous fishes can be broadly categorized as epibranchial, branchiomeric, or hypobranchial. The epibranchial muscles form a cranial extension of the epaxial musculature, and as such retain the myomeric structure typical of the trunk. The epibranchial muscles originate on the epaxial muscle mass, insert onto the otic capsule of the chondrocranium, and elevate the cranium during prey capture (**Figures 1** and **2**, and **Table 2**).

The branchiomeric muscles adduct the dorsal and ventral elements of the visceral arches. As the visceral arches (I–VII) differentiated from respiratory structures into those suited for respiration and feeding (mandibular, hyoid, and branchial arches I–V), a concomitant differentiation of the branchiomeric muscles occurred. Branchiomeric muscles associated with the mandibular arch include the adductor mandibulae, preorbitalis, levator palatoquadrati, intermandibularis, and spiracularis. The adductor mandibulae originates on the palatoquadrate (upper jaw), inserts onto Meckel's cartilage (lower jaw), has multiple divisions, and is the primary jaw adductor in all cartilaginous fishes (**Figures 1–5** and **Table 2**). The preorbitalis originates on the chondrocranium, posterior to the nasal capsule, and inserts onto the median raphe, separating the dorsal and ventral divisions of the adductor mandibulae (**Figures 1** and **2**, and **Table 2**). It elevates the lower jaw, protrudes the upper jaw, and depresses the cranium.

The levator palatoquadrati originates on the otic capsule of the chondrocranium and inserts onto the palatoquadrate (**Figures 1, 2,** and **4**, and **Table 2**). It elevates the upper jaw into its resting position during the recovery phase of the gape cycle after the upper and lower jaws have been adducted. The intermandibularis is a thin sheet of muscle lying between the two halves of the lower jaw, with its right and left portions inserted upon the midventral raphe. It elevates the floor of the mouth during feeding and respiration, facilitating hydraulic transport through the oropharyngeal cavity (**Figure 3** and **Table 2**). Lastly, the spiracularis originates on the lateral wall of the chondrocranium, posterior to the levator palatoquadrati, and inserts onto and closes the spiracle (**Figures 1, 2,** and **4**).

Branchiomeric muscles of the hyoid arch include the interhyoideus, dorsal and ventral hyoid constrictors, hyoid trematic constrictor, and levator hyomandibulae. The interhyoideus is a thin muscle sheet lying dorsal to the intermandibularis. It originates on the ceratohyal cartilages of the hyoid arch, inserts onto the midventral raphe, and elevates the floor of the mouth (**Figures 2**

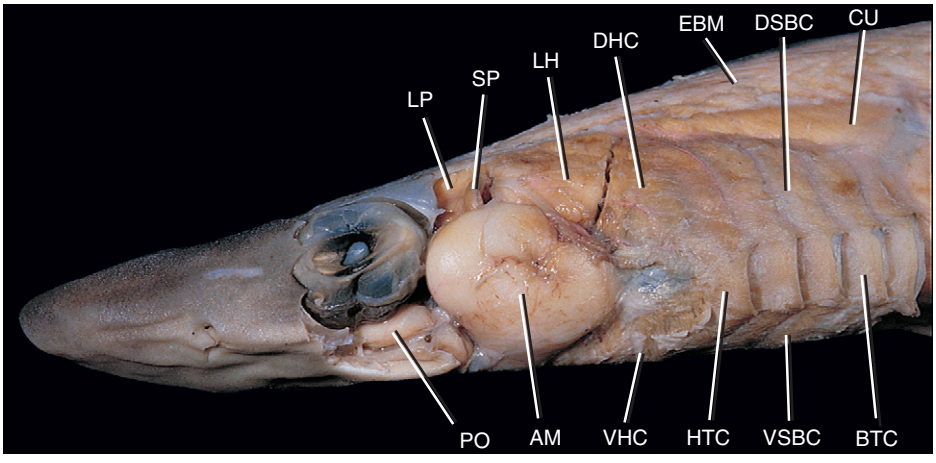

Figure 1 Epibranchial and branchiomeric cranial muscles of the spiny dogfish *Squalus acanthias* in lateral view. See **Table 1** for abbreviated terms. Modified from Fishbeck DW and Sebastiani AS (2008) *Manual of Vertebrate Dissection: Comparative Anatomy*, 2nd edn. Englewood, CO: Morton Publishing.

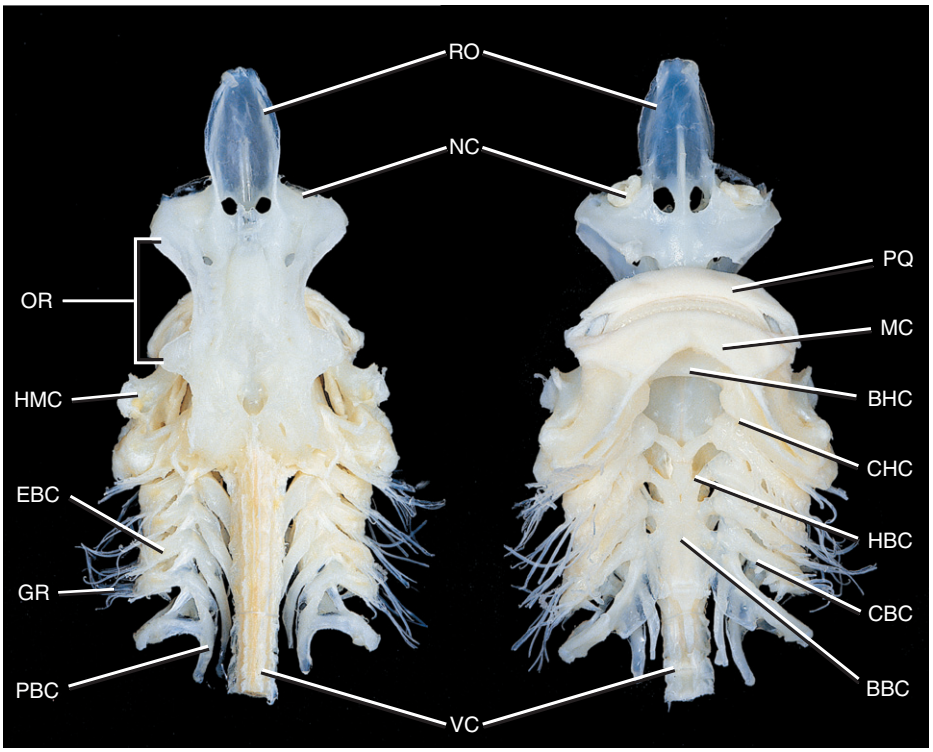

Figure 2 Dorsal and ventral views of the visceral arches and chondrocranium of the spiny dogfish *Squalus acanthias*. See **Table 1** for abbreviated terms. Modified from Fishbeck DW and Sebastiani AS (2008) *Manual of Vertebrate Dissection: Comparative Anatomy*, 2nd edn. Englewood, CO: Morton Publishing.

Table 1 List of terms and abbreviations of the cranial musculature of cartilaginous fishes

AM	Adductor mandibulae	HTC	Hyoid trematic constrictor
AMA	*Adductor mandibulae anterior*	HMC	Hyomandibular cartilage
AML1	*Adductor mandibulae lateral 1*	HYP	*Hypaxialis*
AML2	*Adductor mandibulae lateral 2*	HBC	Hypobranchial cartilage
AMM	*Adductor mandibulae medial*	IB	*Interbranchial*
AMP	*Adductor mandibulae posterior*	IH	*Interhyoideus*
BBC	Basibranchial cartilage	IM	*Intermandibularis*
BHC	Basihyal cartilage	LA	*Labialis anterior*
BA	*Branchial adductor*	LI	*Lateral interarcual*
BTC	*Branchial trematic constrictor*	LR	*Lateral rectus*
CBC	Ceratobranchial cartilage	LAOA	*Levator anguli oris anterior*
CHC	Ceratohyal cartilage	LAOP	*Levator anguli oris posterior*
CC	*Coracoarcualis*	LVH	*Levator hyoideus*
CB	*Coracobranchialis*	LH	*Levator hyomandibulae*
CH	*Coracohyoideus*	LP	*Levator palatoquadrati*
CHM	*Coracohyomandibularis*	LVR	*Levator rostri*
CM	*Coracomandibularis*	MC	Meckel's cartilage
CU	*Cucullaris*	MR	*Medial rectus*
CP	*Cucullaris profundus*	NC	Nasal capsule
CS	*Cucullaris superficialis*	OR	Orbit
DM	*Depressor mandibularis*	PQ	Palatoquadrate
DPR	*Depressor rostri*	PBC	Pharyngobranchial cartilage
DHC	*Dorsal hyoid constrictor*	POP	Post-orbital process
DI	*Dorsal interarcual*	PO	*Preorbitalis*
DO	*Dorsal oblique*	RO	Rostrum
DOC	*Dorsal opercular constrictor*	SCC	Scapulocoracoid cartilage
DR	*Dorsal rectus*	SPV	Spiracular valve
DSBC	*Dorsal superficial branchial constrictor*	SP	*Spiracularis*
EP	*Epaxial*	VHC	*Ventral hyoid constrictor*
EBM	*Epibranchial*	VOC	*Ventral opercular constrictor*
EBC	Epibranchial cartilage	VSBC	*Ventral superficial branchial constrictor*
EHC	Epihyal cartilage	VC	Vertebral column
GR	Gill rays		

Table 2 Origins, insertions, and actions of the cranial muscles of sharks

Muscle	*Origin*	*Insertion*	*Action*
Adductor mandibulae	Palatoquadrate cartilage	Meckel's cartilage	Adduct lower jaw
Branchial adductor	Epibranchial cartilage	Ceratobranchial cartilage	Adduct gill arch
Branchial trematic constrictor	Tendinous sheath of gill slit	Gill slit	Compress gill pouch
Constrictor hyoideus dorsalis	Chondrocranium, cucullaris	Tendinous sheath of hyomandibular cartilage	Compress first gill pouch
Constrictor hyoideus ventrails	Raphe of first gill slit	Tendinous sheath of hyomandibular cartilage	Compress first gill pouch
Coracoarcualis	Scapulocoracoid cartilage	Coracomandibularis, corachyoideus	Expand oropharyngeal cavity
Coracobranchialis	Coracoarcualis, pectoral girdle	Basihyal, hypobranchial, and basibranchial cartilages	Abduct hyoid and branchial arches
Coracohyoideus	Coracoarcualis	Basihyal cartilage	Abduct hyoid arch
Coracomandibularis	Coracoarcualis	Meckel's cartilages	Abduct lower jaw
Cucullaris	Epibranchial	Pectoral girdle	Elevate pectoral girdle
Dorsal interarcual	Pharyngobranchial cartilage	Pharyngobranchial cartilage	Adduct gill arch
Dorsal oblique	Chondrocranium	Eyeball	Rotate eyeball
Dorsal rectus	Chondrocranium	Eyeball	Rotate eyeball
Dorsal superficial branchial constrictor	Cucullaris	Tendinous sheaths of gill slits	Compress gill pouches
Epibranchial	Epaxialis	Chondrocranium	Elevate chondrocranium
Hyoid trematic constrictor	Tendinous sheath of hyomandibular cartilage	First gill slit	Compress first gill pouch
Interbranchial	Gill rays	Gill rays	Adduct gill arches, move interbranchial septa
Interhyoideus	Ceratohyal cartilage	Midventral raphe	Elevate floor of mouth
Intermandibularis	Meckel's cartilage	Midventral raphe	Elevate floor of mouth
Lateral interarcual	Pharyngobranchial cartilage	Epibranchial cartilage	Adduct gill arch
Lateral rectus	Chondrocranium	Eyeball	Rotate eyeball
Levator hyomandibulae	Chondrocranium, epibranchial muscles	Hyomandibular cartilage	Elevate hyomandibular cartilage
Levator palatoquadrati	Chondrocranium	Palatoquadrate cartilage	Elevates upper jaw
Medial rectus	Chondrocranium	Eyeball	Rotate eyeball
Preorbitalis	Chondrocranium	Adductor mandibulae	Adduct lower jaw, protrude upper jaw
Spiracularis	Chondrocranium	Spiracle	Close spiracular valve
Ventral oblique	Chondrocranium	Eyeball	Rotate eyeball
Ventral rectus	Chondrocranium	Eyeball	Rotate eyeball
Ventral superficial branchial constrictor	Coracoarcualis	Tendinous sheaths of gill slits	Compress gill pouches

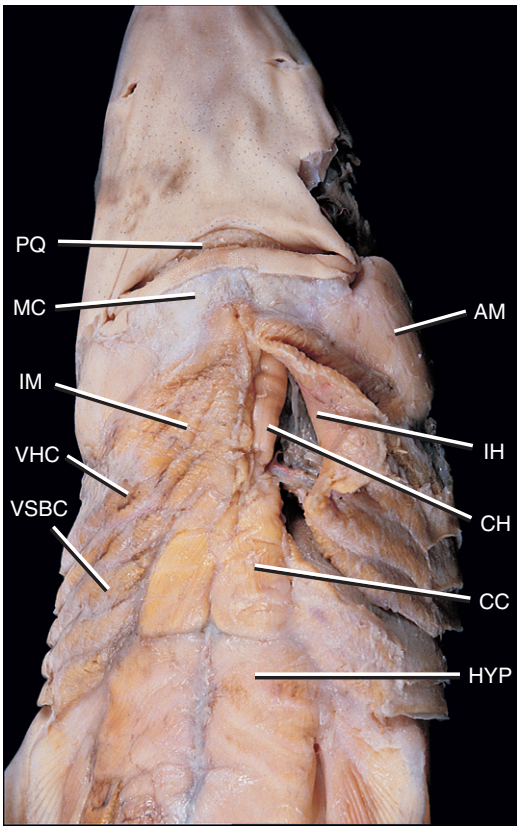

Figure 3 Branchiomeric and hypobranchial cranial muscles of the spiny dogfish *Squalus acanthias* in ventral view. The intermandibularis and interhyoideus have been partially reflected to show the coracohyoideus. See **Table 1** for abbreviated terms. Modified from Fishbeck DW and Sebastiani AS (2008) *Manual of Vertebrate Dissection: Comparative Anatomy*, 2nd edn. Englewood, CO: Morton Publishing.

and 3, and **Table 2**). The dorsal and ventral hyoid constrictors as well as the hyoid trematic constrictor compress the first gill pouch, assisting in hydraulic transport during respiration and feeding. Both the dorsal and ventral hyoid constrictors insert onto the tendinous sheath overlying the hyomandibular cartilages. The former originates from the otic capsule of the chondrocranium and cucullaris muscle, whereas the latter originates adjacent to the interhyoideus along the raphe of the first gill slit (**Figures 1–4** and **Table 2**). The hyoid trematic constrictor originates on the tendinous sheath overlying the hyomandibular cartilages and inserts onto the first gill slit (**Figure 1** and **Table 2**). The levator hyomandibulae originates on the otic capsule of the chondrocranium and epibranchial musculature, inserts onto the hyomandibular cartilages, and elevates these cartilages following a gape or respiratory cycle (**Figures 1** and **2**, and **Table 2**).

The branchiomeric muscles of the branchial arches include the dorsal and ventral superficial branchial constrictors, branchial trematic constrictors, dorsal and lateral interarcual, branchial adductor, interbranchial, and cucullaris muscles. The dorsal and ventral superficial branchial constrictors lie above and below the gill slits in positions comparable to the respective hyoid constrictors. The dorsal superficial branchial constrictor originates on the cucullaris and extends downward to meet its ventral counterpart at a series of tendinous intersections on each gill slit. The ventral division originates on the fascia of the coracoarcualis muscle (**Figures 1** and **3–5**, and **Table 2**). The branchial trematic constrictor muscles originate on the

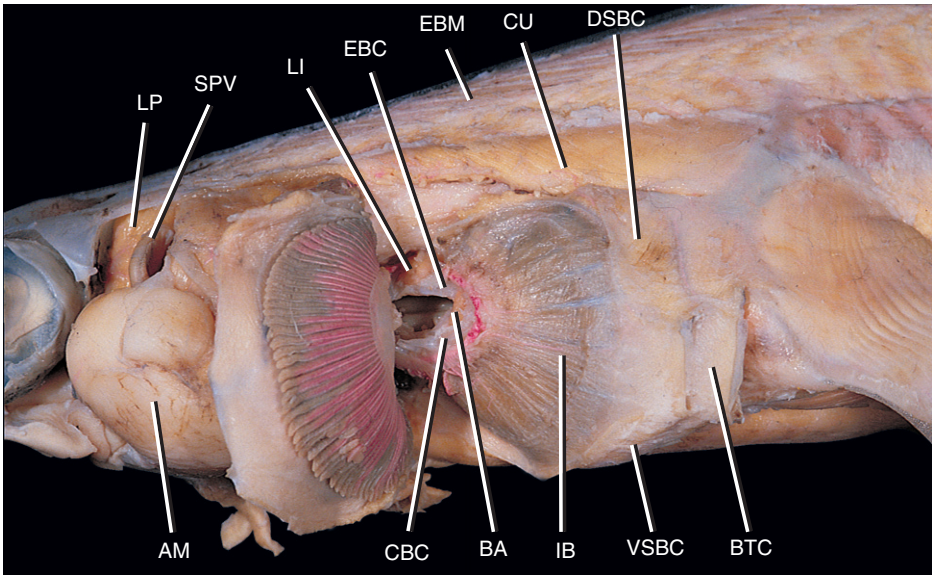

Figure 4 Epibranchial and branchiomeric cranial muscles of the spiny dogfish *Squalus acanthias* in lateral view with the gills reflected to show the deep branchial muscles. See **Table 1** for abbreviated terms. Modified from Fishbeck DW and Sebastiani AS (2008) *Manual of Vertebrate Dissection: Comparative Anatomy*, 2nd edn. Englewood, CO: Morton Publishing.

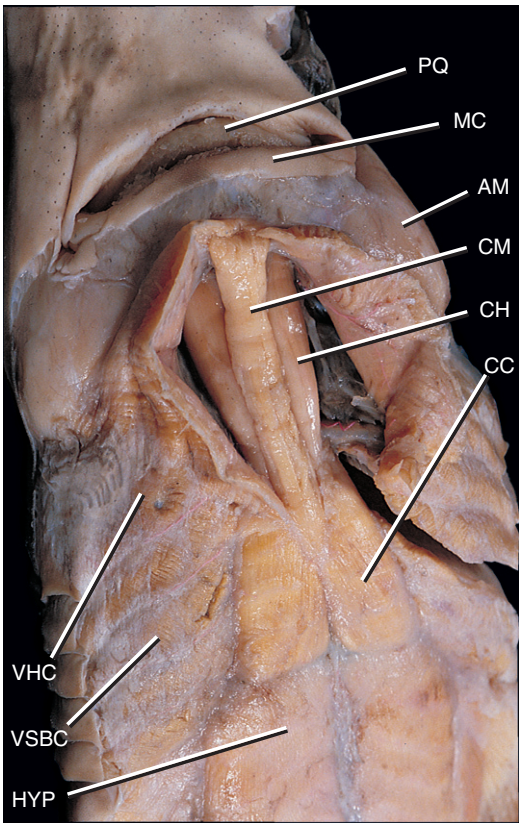

Figure 5 Branchiomeric and hypobranchial cranial muscles of the spiny dogfish *Squalus acanthias* in ventral view. The intermandibularis and interhyoideus have been removed to show the coracomandibularis and coracohyoideus. See **Table 1** for abbreviated terms. Modified from Fishbeck DW and Sebastiani AS (2008) *Manual of Vertebrate Dissection: Comparative Anatomy*, 2nd edn. Englewood, CO: Morton Publishing.

tendinous intersections of the dorsal and ventral superficial branchial constrictors, and they insert onto each of the gill slits (**Figures 1** and **4**, and **Table 2**). Collectively these muscles compress the gill pouches.

The gill arches are moved by the dorsal and lateral interarcual, branchial adductor, and interbranchial muscles. The dorsal interarcual muscles are located between the pharyngobranchial cartilages of adjacent branchial arches and control the distances between these elements. The lateral interarcual muscles originate, and insert upon, the pharyngobranchial and epibranchial cartilages of the same branchial arch. They adduct these elements. The branchial adductors originate, and insert upon, the epibranchial and ceratobranchial cartilages of the same branchial arch. They adduct these elements as well. The interbranchial muscles are an extensive series of circumferential fiber bundles that span between adjacent gill rays on each branchial arch (**Figures 2** and **4**, and **Table 2**). They control the orientation of the interbranchial septa and adduct the branchial arches. Lastly, the cucullaris originates on the epibranchial musculature, and inserts onto, the scapulocoracoid cartilage of the pectoral girdle, which it elevates (**Figures 1** and **4**, and **Table 2**).

The hypobranchial muscles are largely associated with the abduction of the visceral arches, resulting in expansion of the oropharyngeal cavity. The coracomandibularis and coracoarcualis lie in series in the floor of the mouth, with the former immediately deep to the interhyoideus (**Figures 3** and **5**, and **Table 2**). The coracohyoideus is a paired muscle lying deep to the coracomandibularis, both of which originate on the fascia of the coracoarcualis. The coracomandibularis and coracohyoideus insert onto, and abduct, the lower jaw and basihyal cartilage of the hyoid arch, respectively. The paired, segmented coracoarcualis muscles originate upon the scapulocoracoid cartilage. They assist the coracomandibularis and coracohyoideus in their functions (**Figures 2**, **3**, and **5**, and **Table 2**). The segmented coracobranchialis muscles originate on the coracoarcualis and coracoid bar, and insert onto and abduct the ventral elements of the hyoid and branchial arches.

The positions of the eyes are controlled by six extrinsic muscles, all of which originate on the chondrocranium. The lateral, medial, dorsal, and ventral rectus muscles insert onto the eyeball orthogonal to the viewing plane, while the dorsal and ventral oblique muscles insert onto the eyeball from an acute angle. The same arrangement of extrinsic eye muscles is found among all cartilaginous fishes (**Figure 6** and **Table 2**).

Coordinated Muscle Activity in Feeding and Respiration

Like other aquatic vertebrates, sharks typically capture prey by expansive, compressive, and recovery phases of the gape cycle (**see also Chondrichthyes**: Physiology of Sharks, Skates, and Rays, **Food Acquisition and Digestion:** Energetics of Prey Capture: From Foraging Theory to Functional Morphology, **Ventilation and Animal**

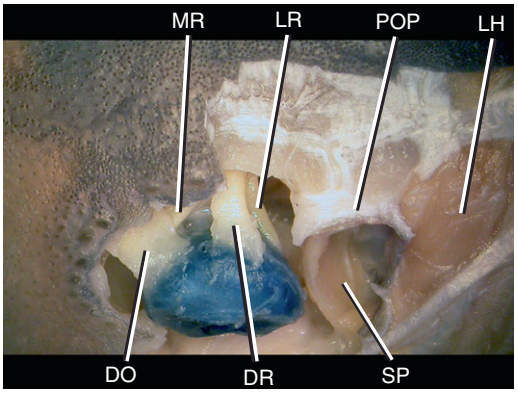

Figure 6 Extrinsic eye muscles of the southern guitarfish *Rhinobatos percellens* in dorsal view (rostrum toward the left). See **Table 1** for abbreviated terms.

Respiration: Gill Respiratory Morphometrics, **Buoyancy, Locomotion, and Movement in Fishes:** Feeding Mechanics, and **The Muscles:** Bony Fish Cranial Muscles). The expansive phase is characterized by cranial elevation via the epibranchial musculature and abduction of the ventral elements of the visceral arches. The coracomandibularis, coracohyoideus, coracoarcualis, and coracobranchialis are activated in rapid succession resulting in a posteriorly directed wave of abduction, which facilitates hydraulic transport of food and water (**Figure 7**, **Video Clip 1**). The compressive phase is characterized by contraction of the adductor mandibulae followed by the preorbitalis, which adducts both jaws while protruding the upper. Head depression occurs via relaxation of the epibranchial musculature. The palatoquadrate and hyomandibular cartilages are returned to their resting positions during the recovery phase via the levator palatoquadrati and levator hyomandibulae muscles (**Figure 7**, **Video Clip 1**).

Respiration in *S. acanthias* occurs via a suction-force pump. While experimental evidence of muscle activity patterns during shark respiration is lacking, the plausible mechanism is described as follows. The external gill slits are closed via the branchial trematic constrictors, and then water is drawn into the oropharyngeal cavity and parabranchial chambers through the mouth and spiracles as the hypobranchial muscles expand the floor of the mouth (suction pump). The mouth and spiracles are then closed via the adductor mandibulae and spiracularis muscles. The branchial chambers are then compressed via the dorsal and ventral branchial constrictors, dorsal and lateral interarcual, and branchial adductor muscles as the external gill slits open, thereby forcing water out (force pump; **Figure 8**). In addition to the suction-force pump, many sharks rely upon ram ventilation in which the mouth is held open during forward movement, resulting in water flow across the gills.

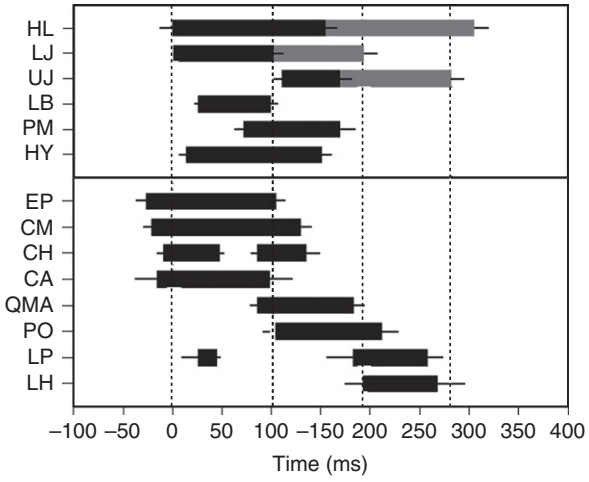

Figure 7 Kinematic (top) and motor (bottom) patterns during prey-capture in the spiny dogfish *Squalus acanthias.* Black and gray bars for kinematic events indicate onset, peak, and end of activity. Black bars for motor events indicate onset and duration of muscle activity. Dashed vertical lines indicate the onset of the expansive, compressive, and recovery phases and the end of the recovery phase. HL, head lift; HY, peak hyoid depression; LB, labial extension; LJ, lower jaw movement; PM, prey movement; QMA, quadratomandibularis anterior (subdivision of the adductor mandibulae); UJ, upper jaw movement. **Table 1** provides information on those terms not listed in the figure caption. From Wilga CD and Motta PJ (1998) Conservation and variation in the feeding mechanism of the spiny dogfish *Squalus acanthias*. *Journal of Experimental Biology* 201: 1345–1358.

Batoid Musculature

Phylogenetic relationships among the different groups of sharks and rays (Batoidea) are still debated, although little doubt exists that elasmobranchs are monophyletic. Molecular data suggest that sharks and rays are sister groups (i.e., sharks are monophyletic), whereas morphological data suggest that rays are derived sharks (i.e., sharks are not monophyletic) and part of the Squalomorphii, a large group including the six- and seven-gill sharks, bramble sharks, dogfishes, and the superorder Hypnosqualea (sawsharks, angelsharks, and rays). Patterns in the cranial muscles corroborate the latter hypothesis because there are many subdivided muscles among species of Batoidea that are derived from the patterns seen in squalomorph sharks (e.g., in the adductor mandibulae complex).

In batoids, the epaxial musculature inserts directly onto the chondrocranium and elevates the head (**Figure 9** and **Table 3**). The branchiomeric muscles of the mandibular arch include the adductor mandibulae complex, preorbitalis, levator palatoquadrati, and spiracularis muscles. The adductor mandibulae complex adducts the jaws and is composed of three divisions, all of which originate on the palatoquadrate (upper jaw) and insert onto Meckel's cartilage (lower jaw). The medial division surrounds the mouth opening, with lateral divisions 1 and 2 adjacent to it along the mandibular arch (**Figures 10** and **11**, and **Table 3**). There is great variation in the adductor mandibulae complex among batoids, with both fusions and further subdivisions common among these divisions.

The adductor mandibulae complex is partially overlain by the preorbitalis, which originates on the nasal capsule and inserts onto the lower jaw via a tendon that joins the adductor mandibulae complex (**Figures 10** and **11**, and **Table 3**). The preorbitalis both adducts the lower jaw and protrudes the upper. The levator palatoquadrati and the spiracularis originate on the otic region of the chondrocranium. The levator palatoquadrati inserts onto and elevates the upper jaw. The spiracularis inserts onto the spiracular cartilage and distal tip of the hyomandibular cartilage to form the anterior

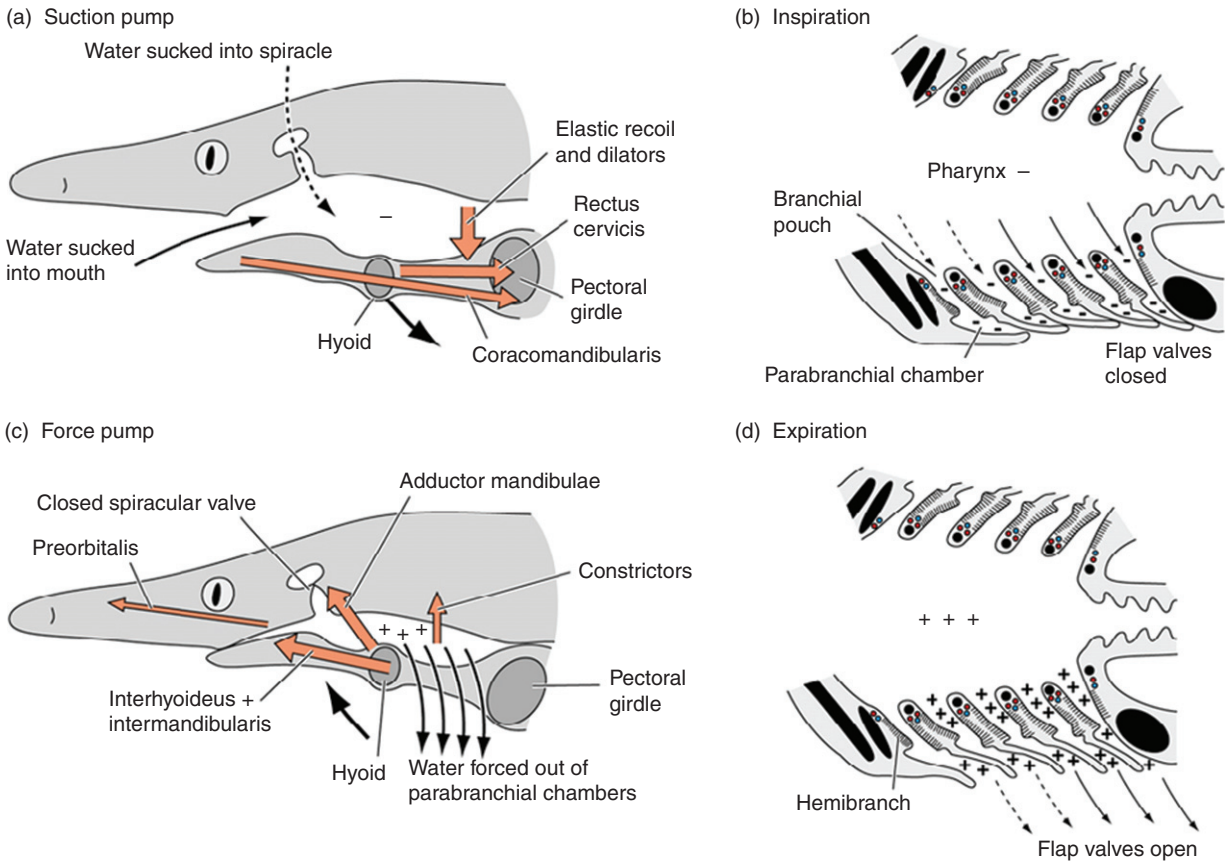

Figure 8 Mechanics of gill ventilation via the suction-force pump in the spiny dogfish *Squalus acanthias* seen in lateral (a, c) and frontal (b, d) sections of the pharynx. Relative pressures are indicated by + and –. Narrow black arrows indicate the flow of water that entered the pharynx through the mouth, while dashed black arrows indicate that which has entered through the spiracle. Orange arrows indicate muscle activity and wide black arrows depict movements of the hyoid. From Liem KF, Bemis WE, Walker WF, Jr., and Grande L (2001) *Functional Anatomy of the Vertebrates: An Evolutionary Perspective*, 3rd edn. Belmont, CA: Brooks/Cole-Thomson Learning.

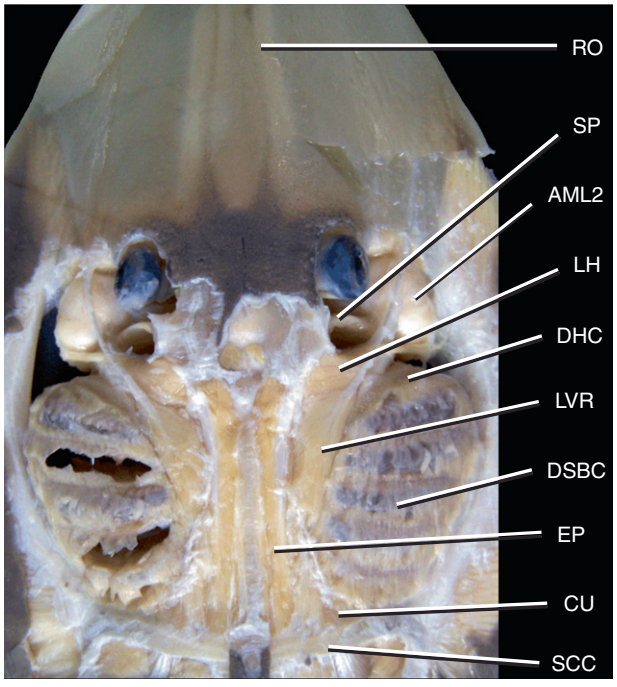

Figure 9 Epaxial and branchiomeric cranial muscles of the southern guitarfish *Rhinobatos percellens* in dorsal view. See **Table 1** for abbreviated terms.

Table 3 Origins, insertions, and actions of the cranial muscles of batoids

Muscle	*Origin*	*Insertion*	*Action*
Adductor mandibulae lateral 1	Palatoquadrate cartilage	Meckel's cartilage	Adduct lower jaw
Adductor mandibulae lateral 2	Palatoquadrate cartilage	Meckel's cartilage	Adduct lower jaw
Adductor mandibulae medial	Palatoquadrate cartilage	Meckel's cartilage	Adduct lower jaw
Branchial trematic constrictor	Propterygium of pectoral fin	Gill slits	Compress gill pouch
Coracoarcualis	Scapulocoracoid cartilage	Coracomandibularis, corachyoideus	Expand oropharyngeal cavity
Coracohyoideus	Coracoarcualis	Basihyal cartilage	Abduct hyoid arch
Coracohyomandibularis	Hypobranchial muscles and raphe	Hyomandibular cartilage	Abduct hyomandibular cartilage
Coracomandibularis	Coracoarcualis	Meckel's cartilages	Abduct lower jaw
Cucullaris	Scapulocoracoid cartilage	Propterygium of pectoral fin	Elevate pectoral fin
Depressor hyomandibularis	Hypobranchial muscles and raphe	Hyomandibular cartilage	Abduct hyomandibular cartilage
Depressor mandibulae	Hypobranchial muscles and raphe	Meckel's cartilage	Abduct lower jaw
Depressor rostri	Hypobranchial muscles and raphe	Rostrum	Depress rostrum
Dorsal hyoid constrictor	Dorsal superficial branchial constrictor	First Gill pouch	Compress gill pouch
Dorsal oblique	Chondrocranium	Eyeball	Rotate eyeball
Dorsal rectus	Chondrocranium	Eyeball	Rotate eyeball
Dorsal superficial branchial constrictor	Cucullaris	Dorsal hyoid constrictor	Compress gill pouches
Epaxialis	Scapulocoracoid cartilage	Chondrocranium	Elevate chondrocranium
Interbranchial	Hypobranchial muscles	Gill arch	Adduct gill arch
Lateral rectus	Chondrocranium	Eyeball	Rotate eyeball
Levator hyomandibulae	Chondrocranium	Hyomandibular cartilage	Elevate hyomandibular cartilage
Levator palatoquadrati	Chondrocranium	Palatoquadrate cartilage	Elevate upper jaw
Levator rostri	Chondrocranium, epibranchial musculature	Rostrum	Elevate rostrum
Medial rectus	Chondrocranium	Eyeball	Rotate eyeball
Preorbitalis	Chondrocranium	Meckel's cartilages	Adduct and elevate jaws, protrude upper jaw
Spiracularis	Chondrocranium	Spiracular and hyomandibular cartilages	Close spiracular valve
Ventral hyoid constrictor	Ventral superficial branchial constrictor	First Gill pouch	Compress gill pouch
Ventral oblique	Chondrocranium	Eyeball	Rotate eyeball
Ventral rectus	Chondrocranium	Eyeball	Rotate eyeball
Ventral superficial branchial constrictor	Propterygium of pectoral fin	Ventral hyoid constrictor	Compress gill pouches

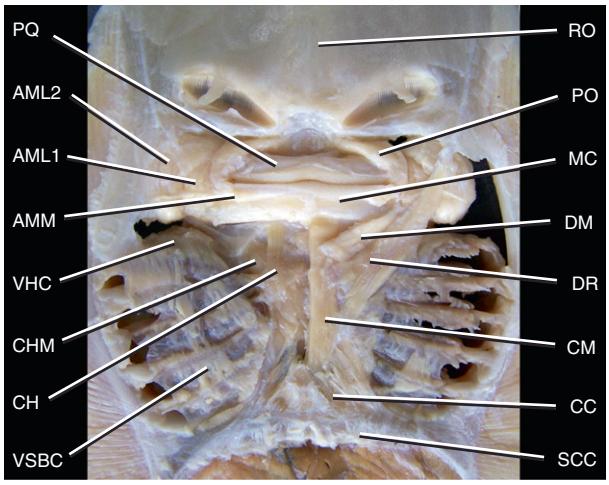

Figure 10 Branchiomeric and hypobranchial cranial muscles of the southern guitarfish *Rhinobatos percellens* in ventral view. See **Table 1** for abbreviated terms.

wall of the spiracle, which is closed via contraction of this muscle (**Figures 6** and **9**, and **Table 3**).

The branchiomeric muscles of the hyoid arch include the dorsal and ventral hyoid constrictors, levator hyomandibulae, depressor rostri, levator rostri, depressor mandibularis, and depressor hyomandibularis. The dorsal and ventral hyoid constrictors originate on the respective superficial branchial constrictors, and they unite medially to form the anterior wall of the branchial chamber, which they compress (**Figures 9** and **10**, and **Table 3**). The levator hyomandibulae originates on the otic region of the chondrocranium and inserts onto the hyomandibulae, which it retracts following a gape cycle (**Figures 6** and **9**, and **Table 3**). The rostrum is moved by the depressor and levator rostri muscles. Dorsally, the levator rostri originates on the epaxial musculature and otic capsule, and it inserts via a stout tendon between the nasal capsule and rostral cartilage. The depressor rostri originates along the ventral surface of the hypobranchial musculature and hypobranchial raphe, and it inserts onto the rostrum via a long tendon (**Figures 9–11** and **Table 3**). The depressor mandibularis appears to be a division of the depressor rostri, which inserts onto and assists in the abduction of the lower jaw (**Figures 10** and **11**, and **Table 3**). The depressor hyomandibularis originates along the ventral surface of the hypobranchial musculature, inserts onto the distal tips of the hyomandibular cartilages, and abducts these structures.

The branchiomeric muscles of the branchial arches include the dorsal and ventral superficial branchial constrictors, branchial trematic constrictor, interbranchial, and cucullaris muscles. The dorsal and ventral superficial branchial constrictors surround the gill arches. The ventral division originates on the propterygium of the pectoral fin, whereas the dorsal division originates on the cucullaris. These muscles insert onto each other and their respective hyoid constrictors, and they compress the gills (**Figures 9–11** and **Table 3**). Laterally, the branchial trematic constrictor originates under the propterygium, inserts onto the superficial branchial constrictors, and also compresses the gills. The interbranchial muscles originate on the coracohyoideus and coracohyomandibularis, and insert onto and adduct the gill arches. The cucullaris originates on the scapulocoracoid, inserts on the fifth dorsal superficial branchial constrictor, and elevates the pectoral fin (**Figure 9** and **Table 3**). Although not found in *R. percellens*, many batoids possess branchial adductor muscles that originate and insert upon the epibranchial and ceratobranchial cartilages, and adduct these structures.

The hypobranchial muscles include the coracoarcualis, coracohyoideus, coracomandibularis, and coracohyomandibularis. The coracoarcualis originates on the scapulocoracoid cartilage, and provides support for the origin of the coracohyoideus and coracomandibularis muscles, assisting these muscles in abducting the oropharyngeal

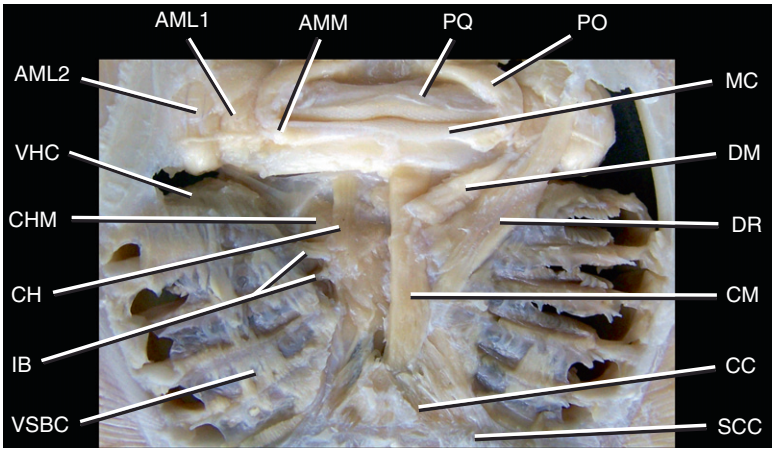

Figure 11 Close-up of the branchiomeric and hypobranchial cranial muscles of the southern guitarfish *Rhinobatos percellens* in ventral view. See **Table 1** for abbreviated terms.

cavity (Figures 10 and 11, and Table 3). The coracohyoideus and coracomandibularis insert onto, and abduct, the basihyal cartilage and lower jaw, respectively (Figures 10 and 11, and Table 3). The coracohyomandibularis originates along the hypobranchial musculature and raphe ventral to the gill arches, and it inserts through a tendon onto the hyomandibulae, further aiding the depressor hyomandibularis in abducting the structures (Figures 10 and 11, and Table 3).

Holocephalan Musculature

The epibranchial muscles of holocephalans fishes originate upon the epaxial muscle mass and insert onto the chondrocranium (Figures 12–14 and Table 4). They contribute minimally to cranial elevation owing to the relatively akinetic cranial skeleton of holocephalans. The branchiomeric muscles of the mandibular arch include the labialis anterior, intermandibularis, levator anguli oris anterior and posterior, and adductor mandibulae anterior and posterior. The labialis anterior originates, and inserts upon, the premaxillary and superior maxillary cartilages, respectively. The intermandibularis originates upon the inferior maxillary cartilage and inserts onto the premandibular cartilages, a pair of fibrocartilaginous masses located at the lower jaw symphysis (Figure 12 and Table 4). Contraction of these muscles protracts the upper and lower sets of labial cartilages. The levator anguli oris anterior and posterior muscles originate upon the antorbital crest of the chondrocranium and insert onto the superior maxillary cartilage, from where they retract the labial cartilages via a series of ligamentous attachments (Figure 12 and Table 4). Deep to the levator anguli oris muscles, the adductor mandibulae anterior has a broad origin across the surface of the preorbital region of the chondrocranium. It is the primary jaw adductor and inserts via a stout tendon that wraps beneath the lower jaw. The adductor mandibulae posterior originates upon the suborbital ridge of the chondrocranium and its tendon merges with that of the adductor mandibulae anterior (Figures 13 and 14, and Table 4).

Branchiomeric muscles of the hyoid arch include the dorsal and ventral opercular constrictors, levator hyoideus, and interhyoideus muscles. The dorsal opercular constrictor originates from the vertebral column and pectoral girdle. The ventral opercular constrictor originates via the midventral raphe on the ventral surface of the pharyngeal cavity and inserts with the dorsal division onto the tendinous sheath overlying the opercular flap from where they compress the pharyngeal cavity (Figure 12 and Table 4). The levator hyoideus originates from the ventral surface of the chondrocranium beneath the orbit and inserts onto the epihyal cartilage (Figures 13 and 14, and Table 4). The interhyoideus originates upon the symphysis of the lower jaw and inserts onto the ceratohyal cartilages (Figure 13 and Table 4). These muscles abduct the hyoid arch. The

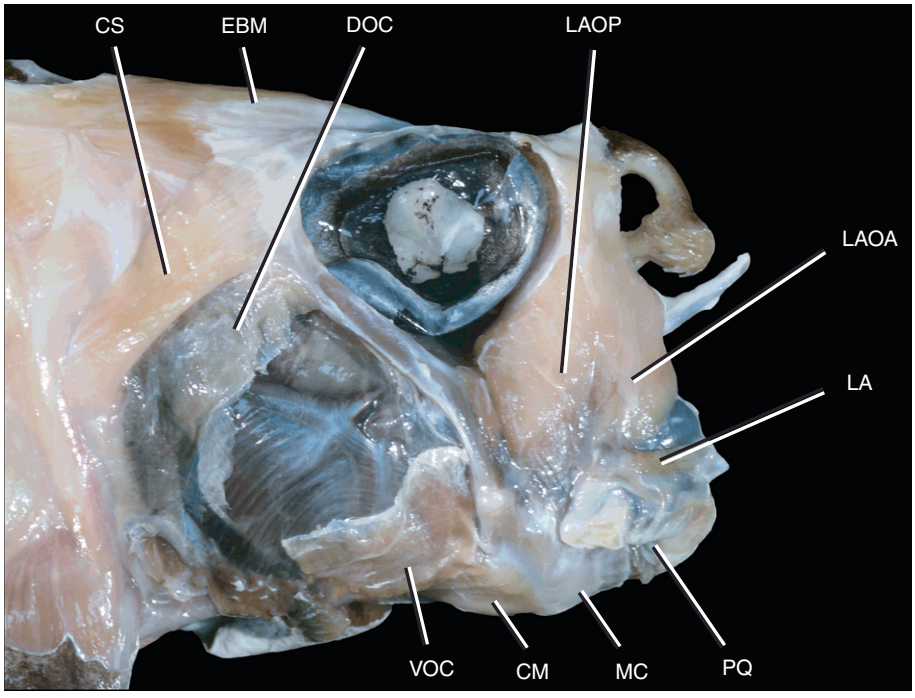

Figure 12 Epibranchial and superficial branchiomeric cranial muscles of the spotted ratfish *Hydrolagus colliei* in lateral view. See Table 1 for abbreviated terms.

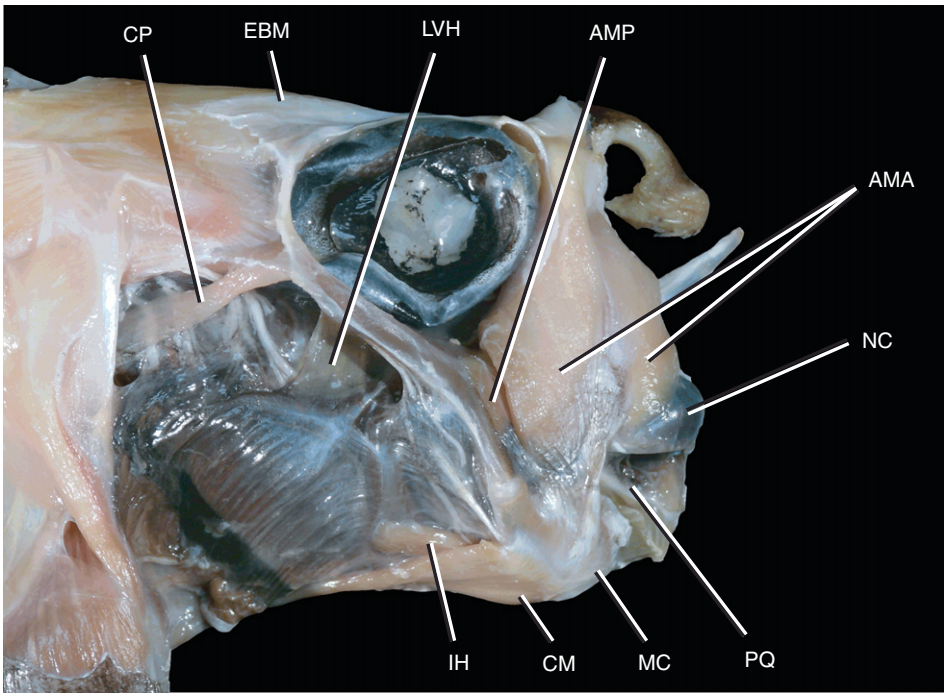

Figure 13 Epibranchial and deep branchiomeric cranial muscles of the spotted ratfish *Hydrolagus colliei* in lateral view. See **Table 1** for abbreviated terms.

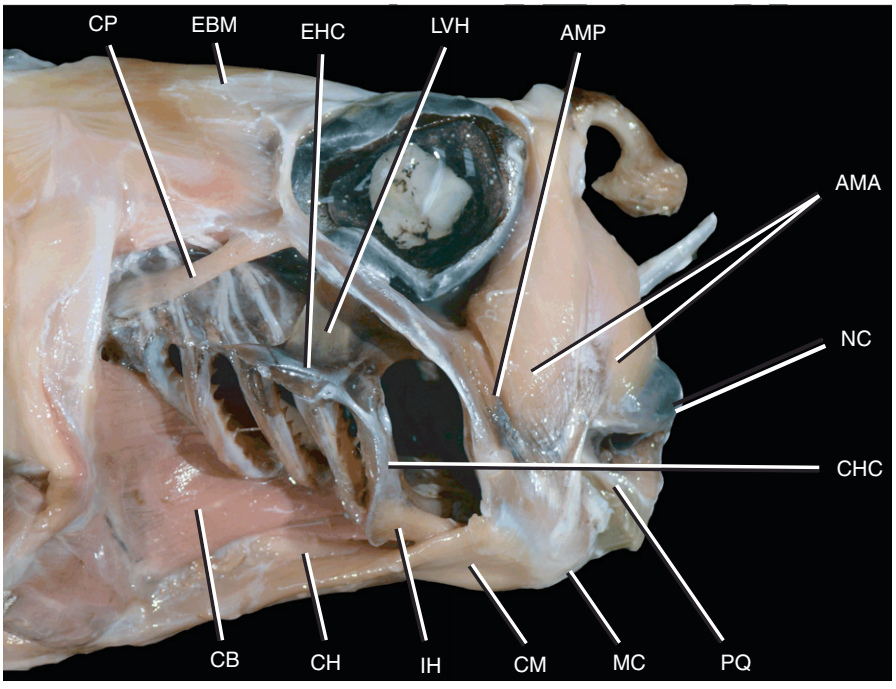

Figure 14 Epibranchial, deep branchiomeric, and hypobranchial cranial muscles of the spotted ratfish *Hydrolagus colliei* in lateral view. See **Table 1** for abbreviated terms.

levator hyoideus may assist in returning the hyoid arch to its resting position following a gape or respiratory cycle.

Branchiomeric muscles of the branchial arches include the constrictor branchialis, adductor arcuum branchialium, cucullaris superficialis, and cucullaris profundus. The constrictor branchialis originates, and inserts upon, the epibranchial and ceratobrancial cartilages of the first three branchial arches, respectively. The adductor

Table 4 Origins, insertions, and actions of the cranial muscles of Holocephalans

Muscle	*Origin*	*Insertion*	*Action*
Adductor arcuum branchialium	Epibranchial, pharyngobranchial cartilages	Ceratobranchial cartilage	Adduct gill arch
Adductor mandibulae anterior	Chondrocranium	Meckel's cartilage	Adduct lower jaw
Adductor mandibulae posterior	Chondrocranium	Meckel's cartilage	Adduct lower jaw
Constrictor branchialis	Epibranchial cartilag	Ceratobranchial cartilage	Adduct gill arch
Constrictor operculi dorsalis	Vertebral column, pectoral girdle	Tendinous sheath of operculum	Compress phayrngeal cavity
Constrictor operculi ventralis	Midventral raphe	Tendinous sheath of operculum	Compress phayrngeal cavity
Coracobranchialis	Pectoral girdle	Ceratobranchial cartilages	Abduct branchial arches
Coracohyoideus	Coracomandibularis	Basihyal cartilage	Abduct hyoid arch
Coracomandibularis	Pectoral girdle	Meckel's cartilage	Abduct lower jaw
Cucullaris profundus	Chondrocranium	Pectoral girdle	Elevate and rotate pectoral girdle
Cucullaris superficialis	Chondrocranium	Pectoral girdle	Elevate and rotate pectoral girdle
Dorsal oblique	Chondrocranium	Eyeball	Rotate eyeball
Dorsal rectus	Chondrocranium	Eyeball	Rotate eyeball
Epibranchial	Epaxialis	Chondrocranium	Elevate chondrocranium
Interhyoideus	Meckel's cartilage	Ceratohyal cartilage	Abduct hyoid arch
Intermandibularis	Inferior maxillary cartilage	Premandibular cartilage	Protract labial cartilages
Labialis anterior	Premaxillary cartilage	Superior maxillary cartilage	Protract labial cartilages
Lateral rectus	Chondrocranium	Eyeball	Rotate eyeball
Levator anguli oris anterior	Chondrocranium	Superior maxillary cartilage	Retract labial cartilages
Levator anguli oris posterior	Chondrocranium	Superior maxillary cartilage	Retract labial cartilages
Levator hyoideus	Chondrocranium	Epihyal cartilage	Elevate epihyal cartilage
Medial rectus	Chondrocranium	Eyeball	Rotate eyeball
Ventral oblique	Chondrocranium	Eyeball	Rotate eyeball
Ventral rectus	Chondrocranium	Eyeball	Rotate eyeball

arcuum branchialium has a complex origination from the epibranchial and pharyngobranchial cartilages, and inserts onto the ceratobranchial cartilages of the first four branchial arches. Both of these muscles adduct the branchial arches. The cucullaris superficialis and profundus originate upon the postorbital region of the chondrocranium, and insert onto the scapular process of the pectoral girdle, which they elevate and rotate (**Figures 12–14** and **Table 4**).

The hypobranchial muscles of holocephalans include the coracomandibularis, coracohyoideus, and coracobranchialis. The coracomandibularis originates on the coracoid bar of the pectoral girdle, and inserts onto, and abducts the lower jaw (**Figures 12–14** and **Table 4**). The coracohyoideus originates on the coracomandibularis and inserts onto the basihyal cartilage, which it abducts. The coracobranchialis has multiple divisions that originate on the coracoid bar, insert onto the ceratobranchial cartilages, and abduct the branchial arches (**Figure 14** and **Table 4**).

See also: **Buoyancy, Locomotion, and Movement in Fishes**: Feeding Mechanics. **Chondrichthyes**: Physiology of Sharks, Skates, and Rays. **Food Acquisition and Digestion**: Energetics of Prey Capture: From Foraging Theory to Functional Morphology. **The Muscles**: Bony Fish Cranial Muscles. **The Reproductive Organs and Processes**: Anatomy and Histology of Fish Testis. **Ventilation and Animal Respiration**: Gill Respiratory Morphometrics.

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