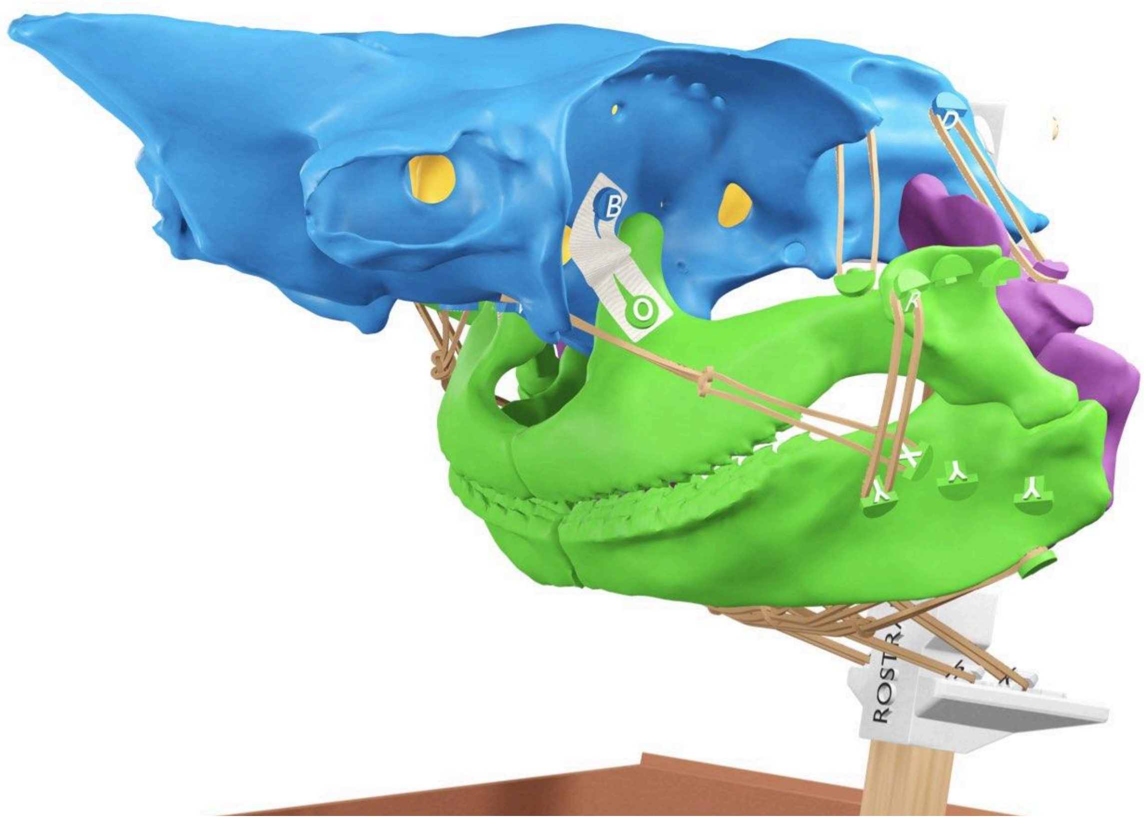
STUDENT GUIDE

Simulating the motions of your shark's jaws

Text and images by Aaron M Olsen, PhD



Description

In this module, you will identify and attach jaw muscles to the skeleton of your spiny dogfish shark (*Squalus acanthias*) and figure out the actions of each muscle by using your model to simulate the motions of the jaws.

Introduction

After learning the skeletal elements of the shark skull, you may be thinking: relative to sharks, humans have a much simpler cranial skeleton! Excluding the tiny middle ear bones, we only have two moving cranial bones: our mandible and hyoid. In this sense, the human cranial skeleton is **less kinetic** (i.e., capable of moving in fewer ways) than the shark cranial skeleton. With so few moving bones, how do we bite, chew, suck, process, and swallow food?

Our trick to achieving all of these complex motions is having a highly kinetic **tongue**. Just three or so muscles are associated with moving the mandible but more than seven muscles make up and attach to the human tongue. This gives the tongue a high degree of mobility that, in coordination with the mandible and hyoid, helps us perform complex manipulations.

Although sharks process their food differently from us, they still need to manipulate their food in complex ways to eat (e.g., moving food around inside their mouth, reducing its size, moving it toward the stomach to swallow). Yet, if you were to look inside a shark's mouth you wouldn't see a tongue. The floor of their mouth and pharynx can move up and down but it's nothing like a tongue. How do sharks achieve these manipulations without a tongue?

Sharks, such as this white shark (*Carcharodon carcharias*), don't have a tongue. Modified from a photograph by Bernard Dupont licensed under CC BY-SA 2.0.

Whereas humans have a highly kinetic *tongue*, sharks have a highly kinetic *cranial skeleton*. Sharks have nine separate jaw cartilages that make up the first and second arches of their jaws and that connect together to form a **linkage mechanism** (an engineering term for rigid elements connected by mobile joints). Sharks move their jaw cartilages to manipulate and transport food and water through their mouth rather than using a tongue (Dean, Wilga & Summers 2005). How do sharks use their jaw muscles to drive this complex cranial linkage mechanism? In this module, you will figure this out for yourself, by attaching muscles to your shark skeleton, simulating jaw motions, and discovering which muscles drive which motions.

Materials needed

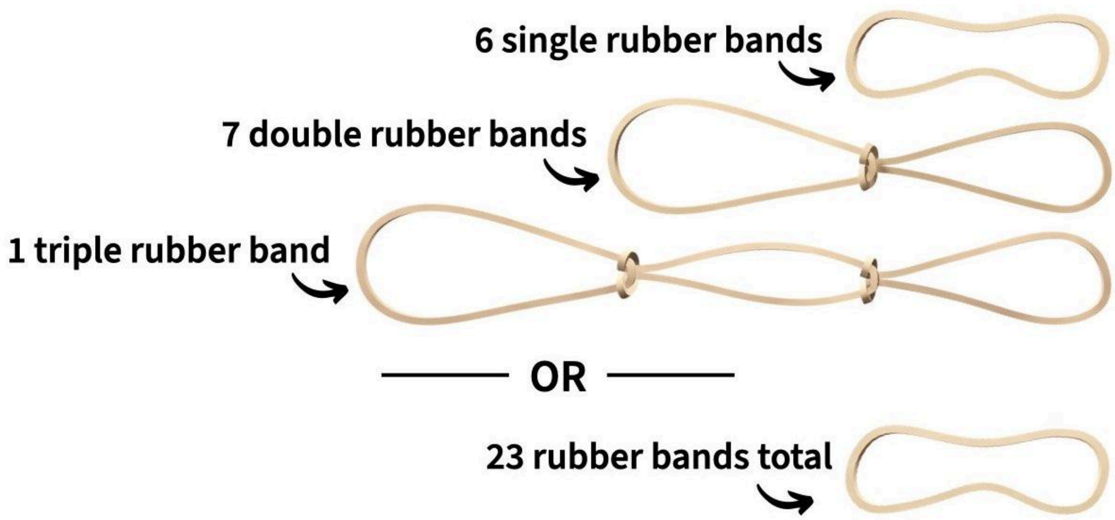
For this module, you'll need:

- The **Student Notebook** for this module (SA05).
- To first complete the module **Building the skeleton of your shark skull** (SA01). In that module, you'll mount your chondrocranium and brain to the stand and attach all of the jaw cartilages. After completing that module, your shark skull will look like the image below and you'll be ready to start this module.

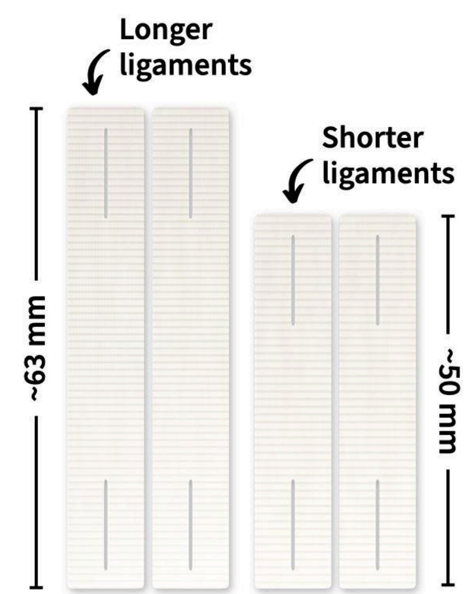
If your skull has the branchial arches attached, it's fine to leave them in place; you may need to remove and reattach them as you complete this module to attach some muscles.

Materials needed (continued)

- The **rubber bands** (#14) from your kit box (there should be more in your kit than you need for this module). Your rubber bands may be all single rubber bands or some may be knotted together (if your kit has been used before). Either is OK- if you need double or triple rubber bands, you'll make them as a part of this module.



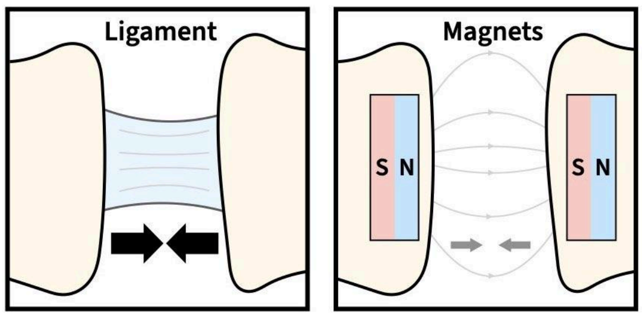
- The **ribbons** from your kit box with slits at each end. For this module, you'll only use the two shorter ribbons (~50 mm in length; see image below).



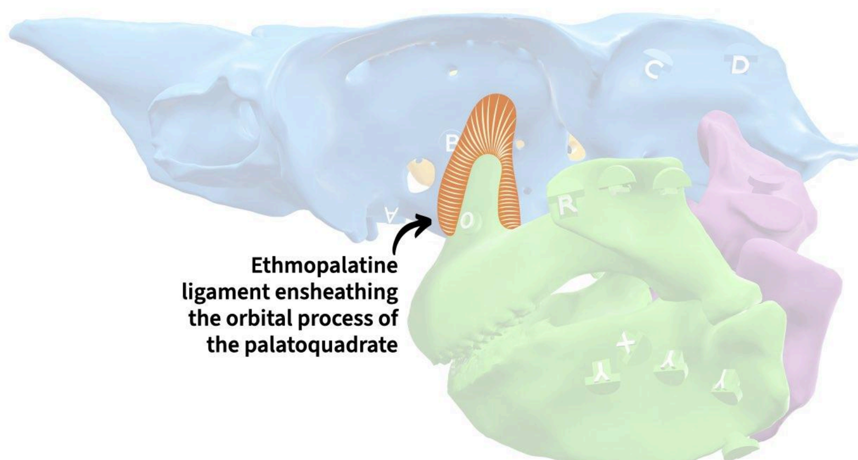
- **OPTIONAL** "Dressing forceps" (not "rat tooth" or "tissue" forceps) can be helpful for attaching the ligaments and muscles, though they are not necessary.

Adding ligaments to stabilize your shark's jaws

Recall that from the **Building the skeleton of your shark skull** module, each pair of attracting magnets in your jaw cartilages represents one or more ligaments. Ligaments function in holding together but also limiting the motion of skeletal elements. However, these magnetic connections are *much* weaker than real ligaments and they can only act over a short distance.



A key ligament limiting the motion of your shark's jaws is the **ethmopalatine ligament**.

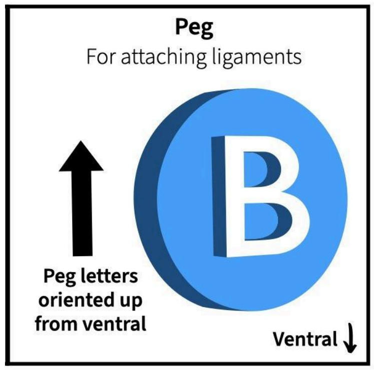


This ligament prevents the **palatoquadrate** from moving too far from the **chondrocranium**. To make your simulations more realistic and to help keep your jaw cartilages from coming apart, you can add a more realistic ethmopalatine ligament (i.e., a ribbon) to your shark. It's easier to add this ligament *before* adding any muscles, so if you add it, it's best to do that now.

Before you add any ligaments, read through the **Build note** on the next page. If you're having trouble attaching the ligaments, you can just complete this module without attaching them.

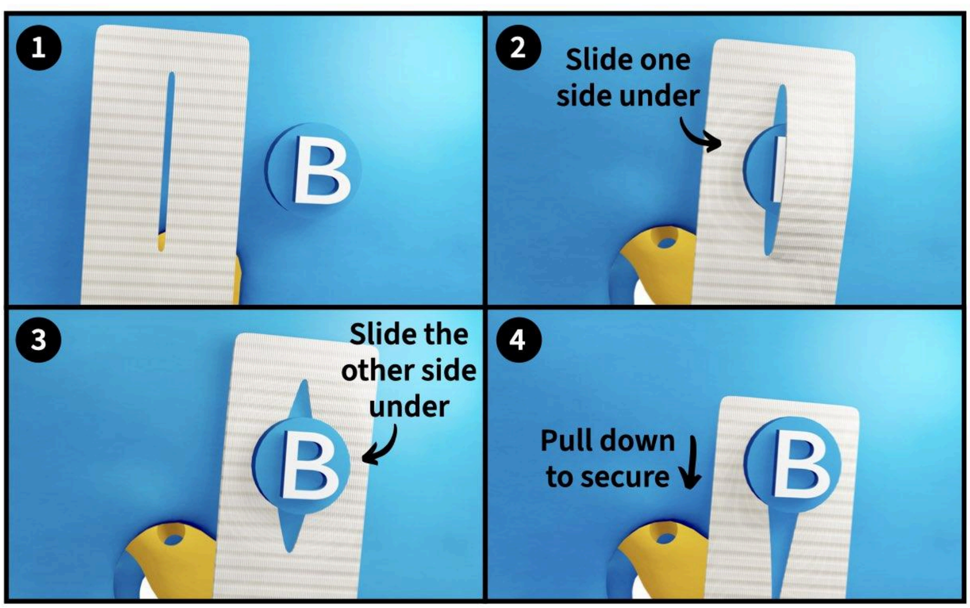
BUILD NOTE: Attaching ligaments

The 3D printed pieces in your kit have small hooks and pegs with raised letters on them: the hooks are for attaching muscles and the pegs are for attaching ligaments (ribbons). Each peg has a unique letter on it oriented approximately with the bottom pointing **ventrally**.



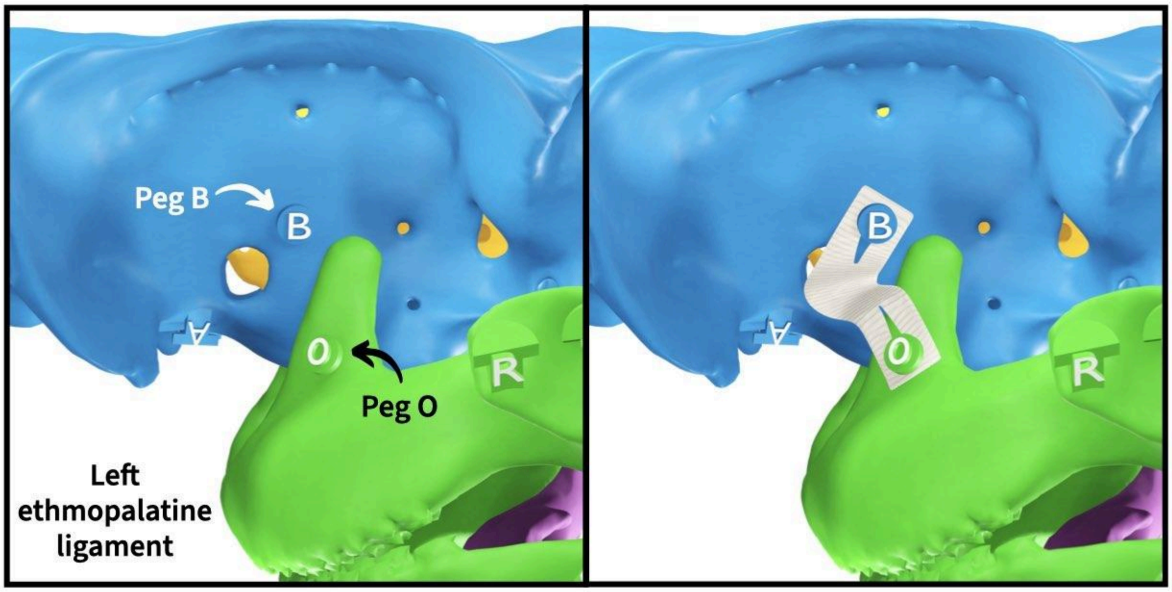
Each ligament has a slit cut in either end, like a buttonhole. To attach a ligament, attach each end to a peg, like to buttoning a button (a pair of dressing forceps can be helpful):

1. Position one end of the ligament next to one of the pegs.
2. Slide one edge of the slit under one side of the peg.
3. Pull the other edge of the slit across and under the peg.
4. Carefully pull the ligament down to secure it in place.

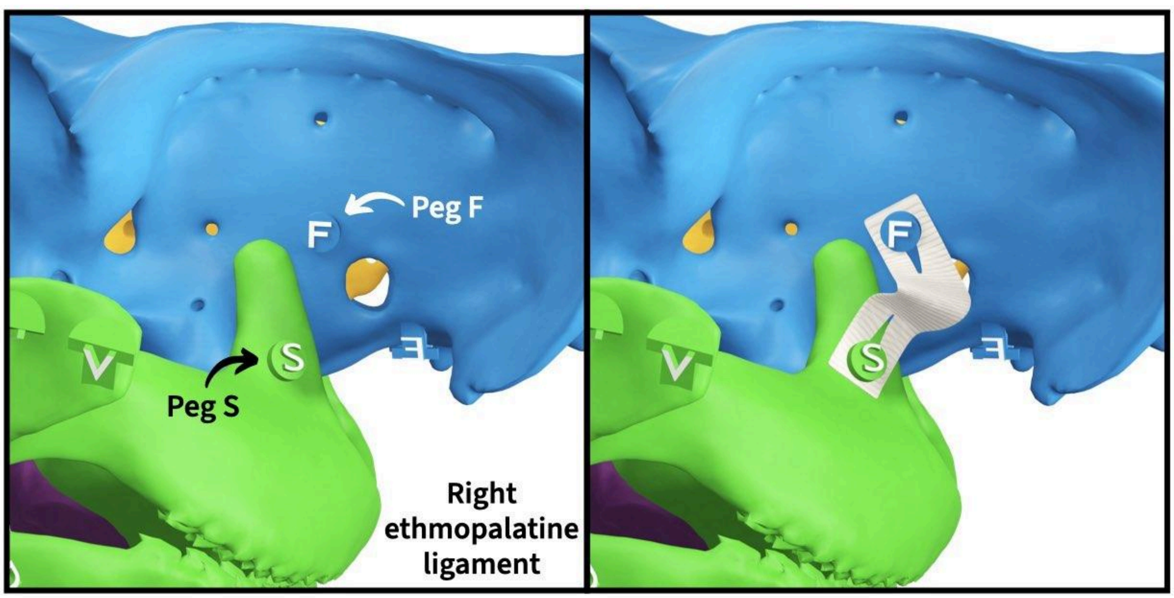


To detach the ligament, just follow the same steps in reverse.

Using the **Build note** on the previous page, attach one of the two *shorter* ribbons in your kit to the "O" peg of the left palatoquadrate and the "B" peg on the wall of the left orbit of the chondrocranium. It may be easier to remove the palatoquadrate to attach the ligament to the "O" peg; you should be able to carefully remove the left palatoquadrate while keeping all the other jaw cartilages connected.



Repeat this on the right side, attaching the second shorter ribbon to the "S" peg of the right palatoquadrate and the "F" peg on the wall of the right orbit of the chondrocranium.

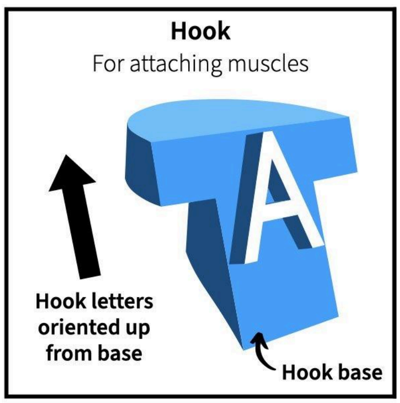


Section 1. What are the shark jaw muscles?

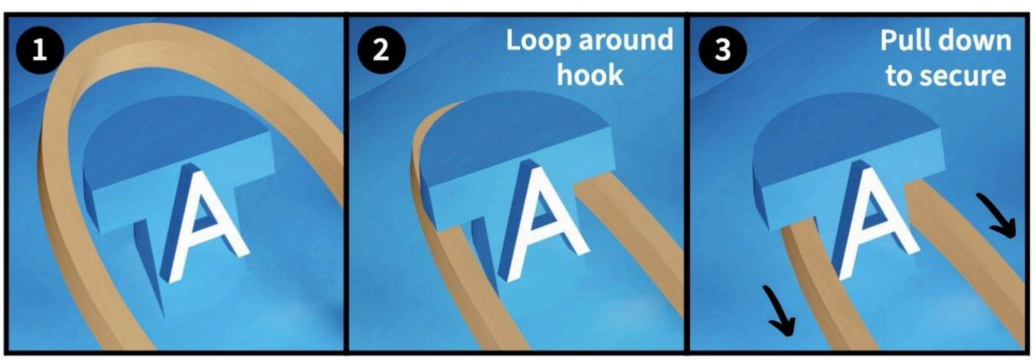
Muscles are the motors of animals. Every intrinsically driven movement of an animal (driven by the animal itself, not externally) is driven by a muscle. So to fully understand how an animal can (and cannot) move, you need to understand the attachments and orientations of the muscles that drive those movements. In this section, you'll attach eight muscles that drive most of the motion of your shark's jaws. For how to attach muscles, see the **Build note** below.

BUILD NOTE: Attaching muscles

The hooks on the 3D printed pieces in your kit are for attaching muscles (rubber bands). Each hook generally has a unique letter and every hook letter is oriented with the bottom toward the base of the hook, as shown in the image below.



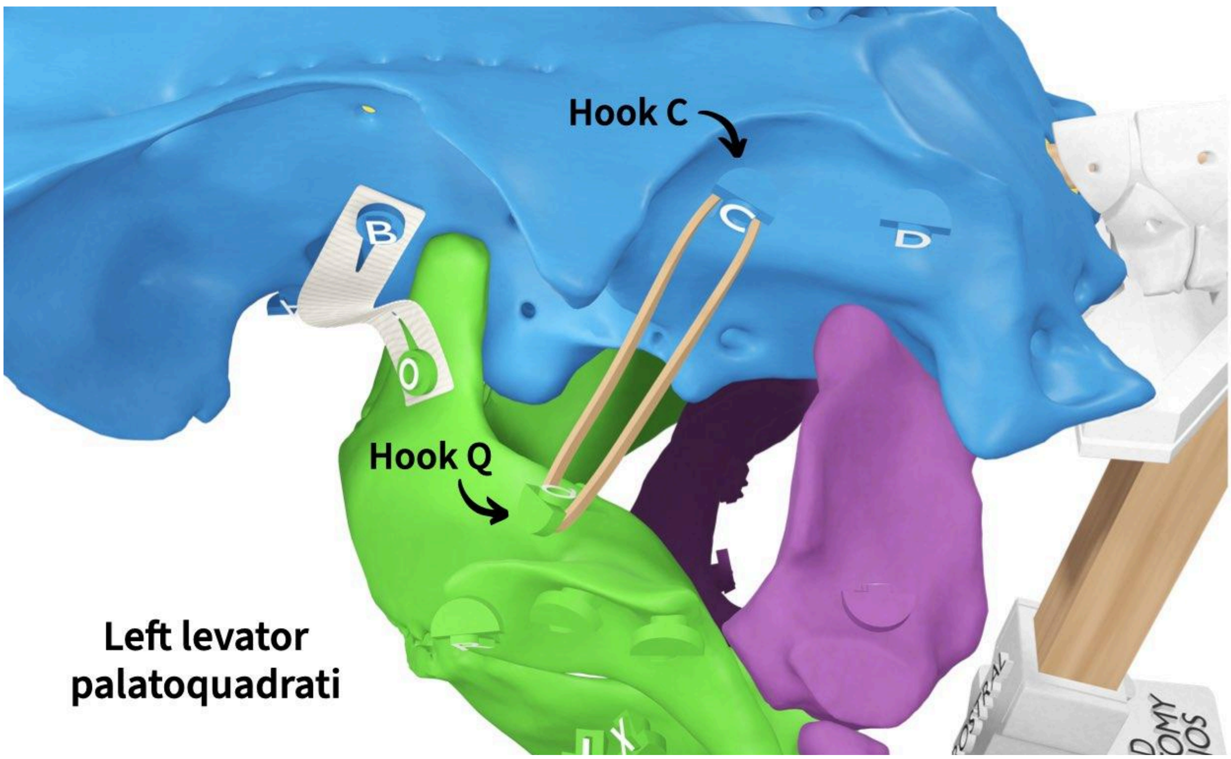
Attach each muscle by looping the rubber band around the hook and secure it by pulling it down around the base of the hook (a pair of dressing forceps can be helpful for this).



Once attached at both ends, the rubber band should be tight enough to stay in place.

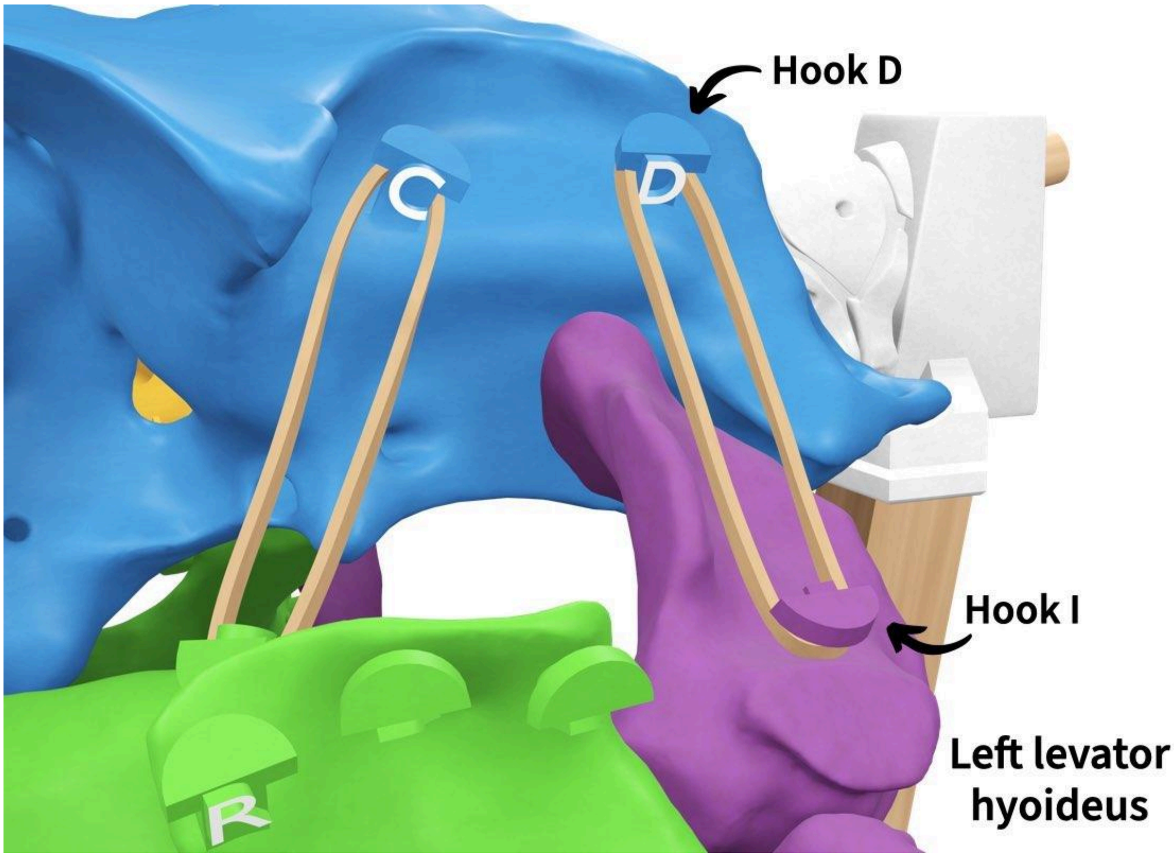
The levators

The first two muscles you'll add are both "levators," so named because their actions include **elevation**. The first is **levator palatoquadrati**, which originates on the chondrocranium and inserts on the palatoquadrate. Add the left levator palatoquadrati to your shark skull by attaching one end of a single rubber band to hook "C" on the left side of the chondrocranium and attaching the other end to hook "Q" on the left palatoquadrate.



Repeat this on the right side of your shark's skull by attaching a single rubber band to hook "G" on the chondrocranium and hook "U" on the right palatoquadrate. On page 1 of your **Notebook**, fill in the "Attachments" column for levator palatoquadrati with the two elements this muscle attaches to.

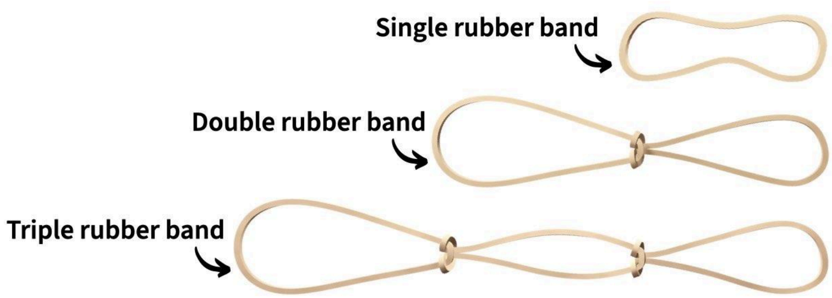
The second levator is the **levator hyoideus**, which originates on the chondrocranium and inserts on the hyomandibula. Add the left levator hyoideus by attaching a single rubber band to hook "D" on the left side of the chondrocranium and hook "I" on the left hyomandibula.



Repeat this on the right side by attaching a single rubber band to hook "H" on the chondrocranium and hook "J" on the right hyomandibula. On page 1 of your **Notebook**, fill in the "Attachments" column for levator hyoideus.

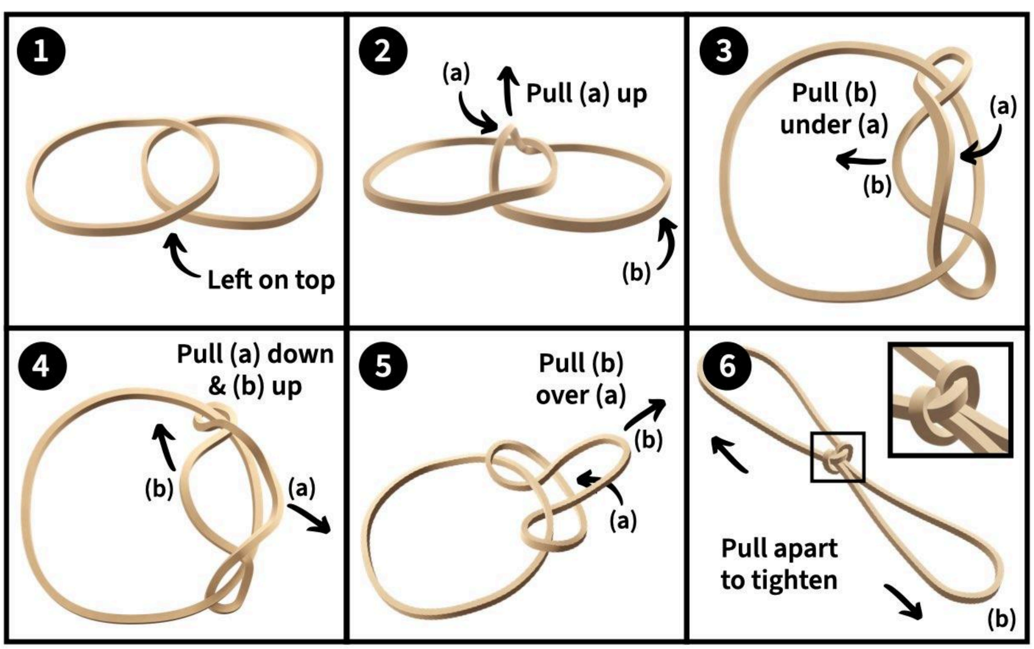
BUILD NOTE: Making a longer muscle

Your kit includes rubber bands of just one length but your shark's muscles are different lengths. To make longer muscles, you'll loop together two and three rubber bands.



If your kit already has rubber bands looped together, sort them into separate piles. If not, follow the instructions and image to form square knots between the rubber bands.

1. Place two rubber bands on your work surface so they are slightly overlapping.
2. Pull the left-most part of the right rubber band (a) up.
3. Insert the right-most part of the right rubber band (b) through the gap.
4. Pull loop (a) down to the right and loop (b) up.
5. Continue pulling loop (b) up and over (a) toward the right.
6. Pull apart to tighten the knot but *don't pull it too tight* or the length will be off.

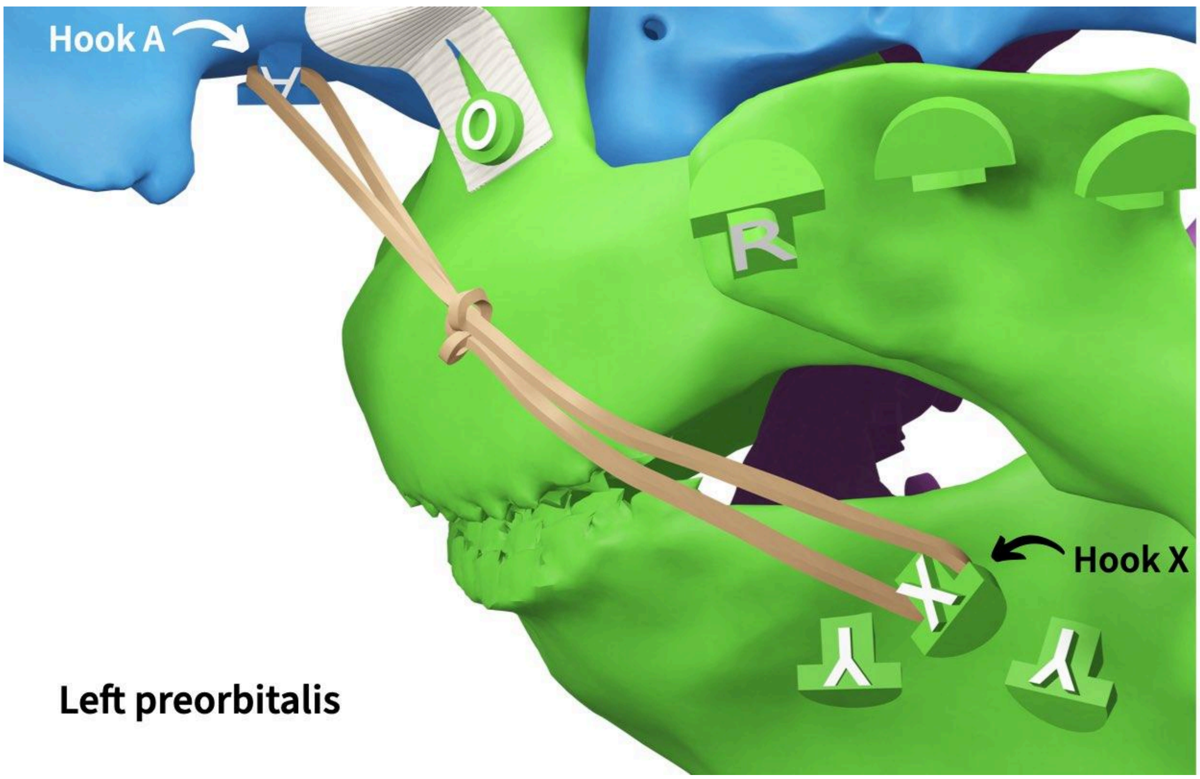


To create a triple rubber band, just repeat these steps with a second rubber band.

The adductor mandibulae complex

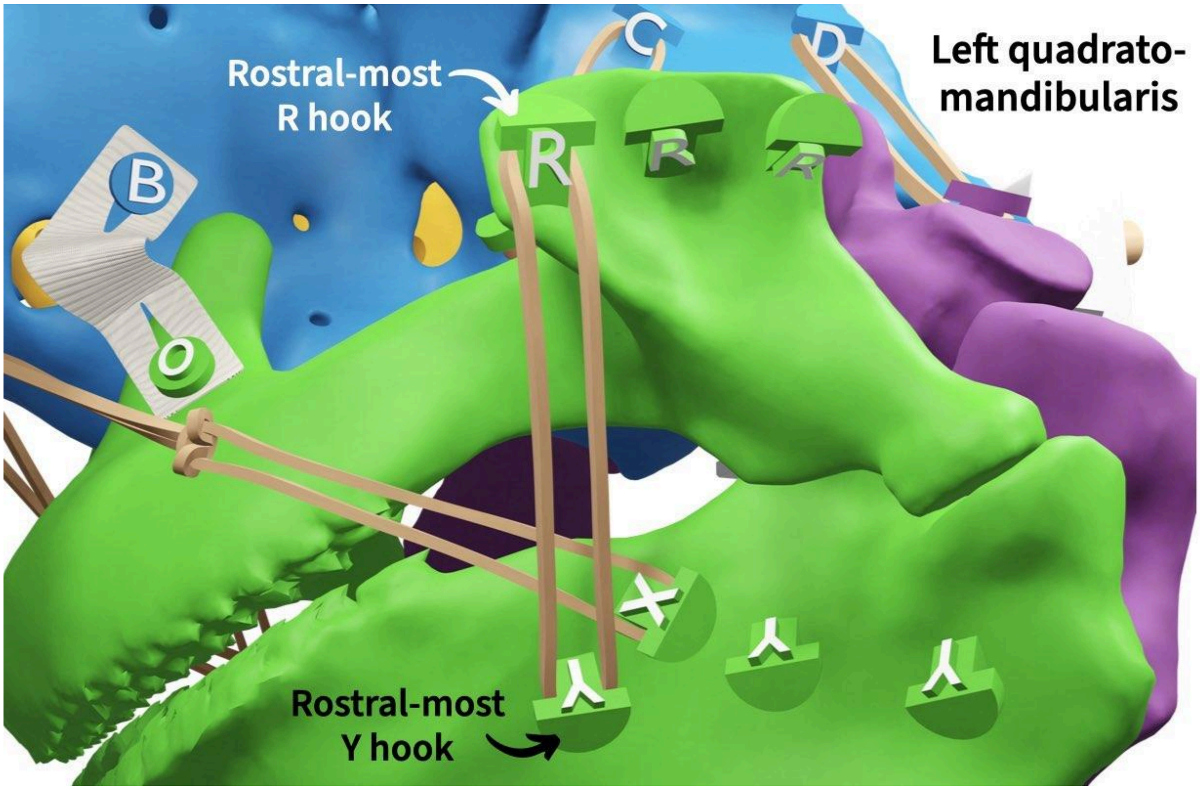
The next two muscles you'll add are part of what's called the **adductor mandibulae complex**. To **adduct** means to bring together, whereas **abduct** means to pull apart. The first is **preorbitalis**, which originates on the chondrocranium and inserts on the **mandible**. The preorbitalis is longer than the previous two muscles so you'll need to use a double rubber band; if your kit doesn't already have these made, use the build note on the previous page to make them.

Add the left preorbitalis to your shark skull by attaching a *double* rubber band to hook "A" on the left side of the chondrocranium and to hook "X" on the left mandible.



Repeat this on the right side by attaching a *double* rubber band to hook "E" on the chondrocranium and hook "d" on the right mandible. On page 1 of your **Notebook**, fill in the "Attachments" column for preorbitalis.

The second muscle of the adductor mandibulae complex is the **quadratomandibularis**, which originates on the palatoquadrate and inserts on the mandible. Add the left quadratomandibularis by attaching a *single* rubber band to the rostral-most "R" hook on the palatoquadrate and the rostral-most "Y" hook on the left mandible. The other hooks are alternate attachment sites for this muscle (thus the repeat letters) that you'll use in another module.



Notice how you added the quadratomandibularis muscle "on top of" the preorbitalis muscle? This matches the layering in an actual shark skull: the quadratomandibularis is **superficial to** the preorbitalis, meaning closer to the external surface of the body. An equivalent way to say this is that preorbitalis is **deep to** the quadratomandibularis.

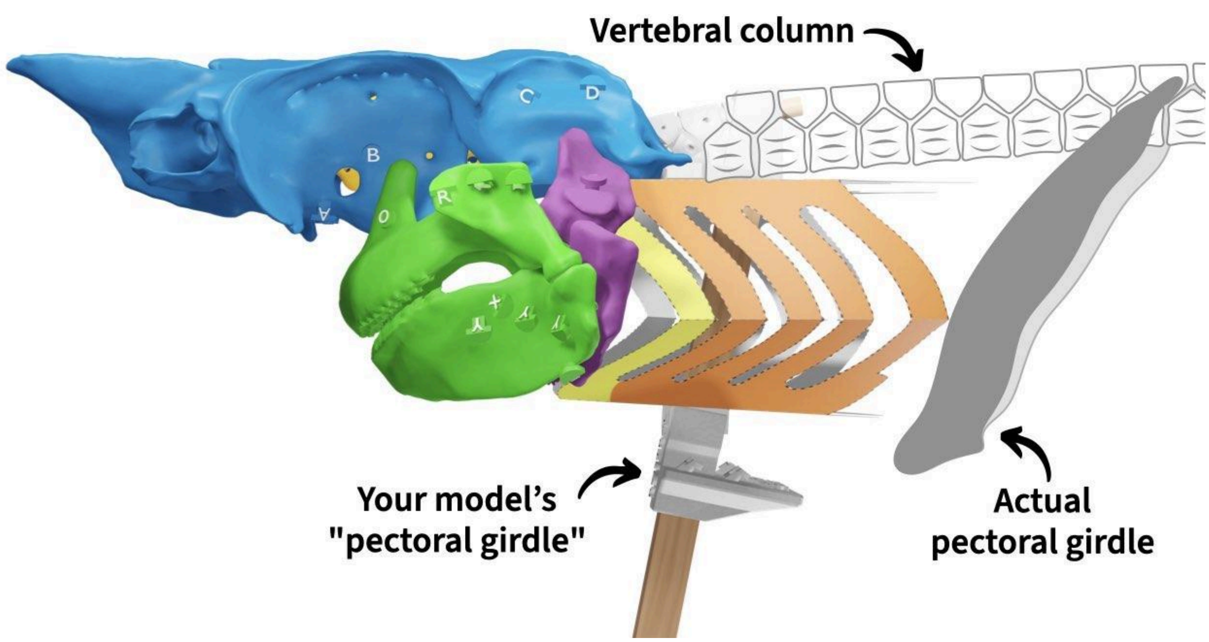
Repeat this on the right side by attaching a single rubber band to the rostral-most "V" hook on the right palatoquadrate and the rostral-most "e" hook on the right mandible. On page 1 of your **Notebook**, fill in the "Attachments" column for quadratomandibularis.

The "coraco" muscles

The next muscles you'll add could be collectively called the "coraco" muscles: all these muscles attach directly (or indirectly) to the **coracoid**, the main element that makes up the **pectoral girdle** (or **shoulder girdle**). The first is the **coracomandibularis**, which originates on the pectoral girdle (specifically, the coracoid part) and inserts on the mandible.

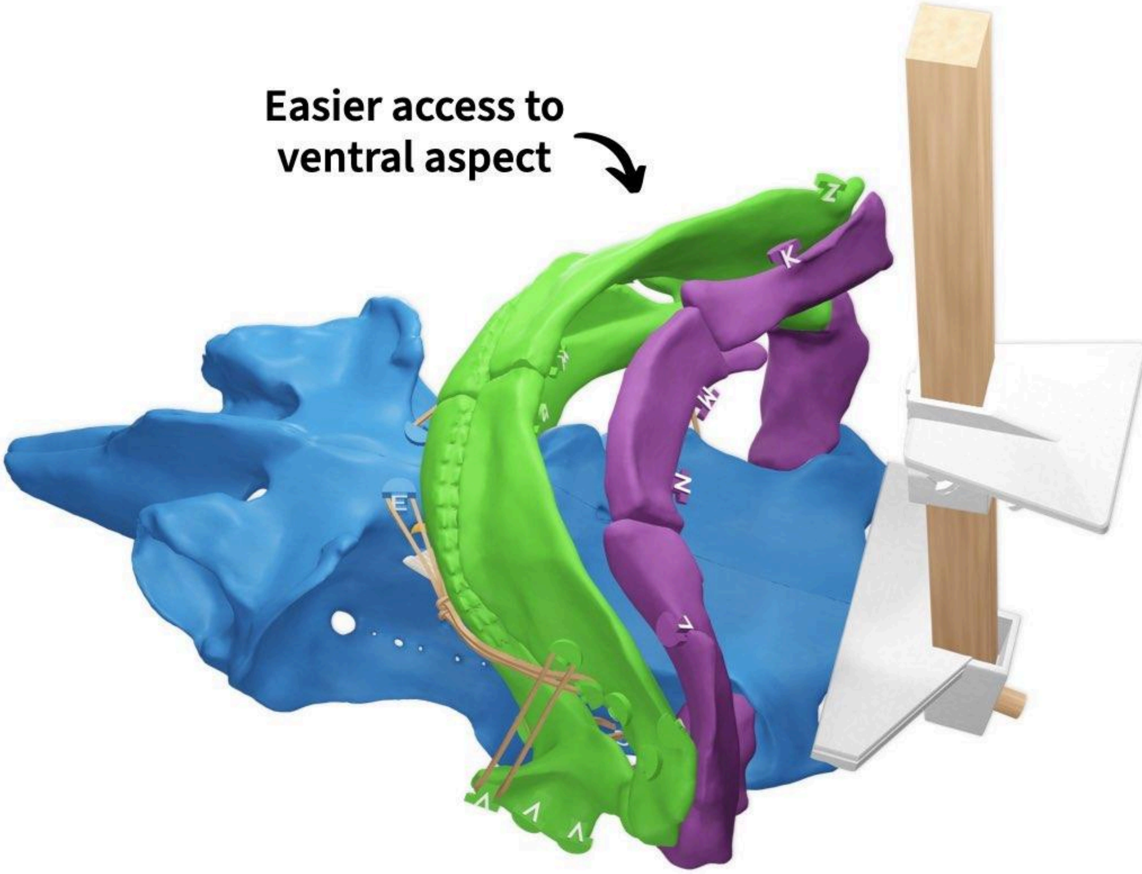
BUILD NOTE: A shoulder stand-in

The middle 3D printed piece of the stand rod in your kit serves as an approximate stand-in for the pectoral girdle. Although the stand rod is located more rostrally than in an actual spiny dogfish shark, the **dorsoventral** position (i.e., its height) is approximately the same.

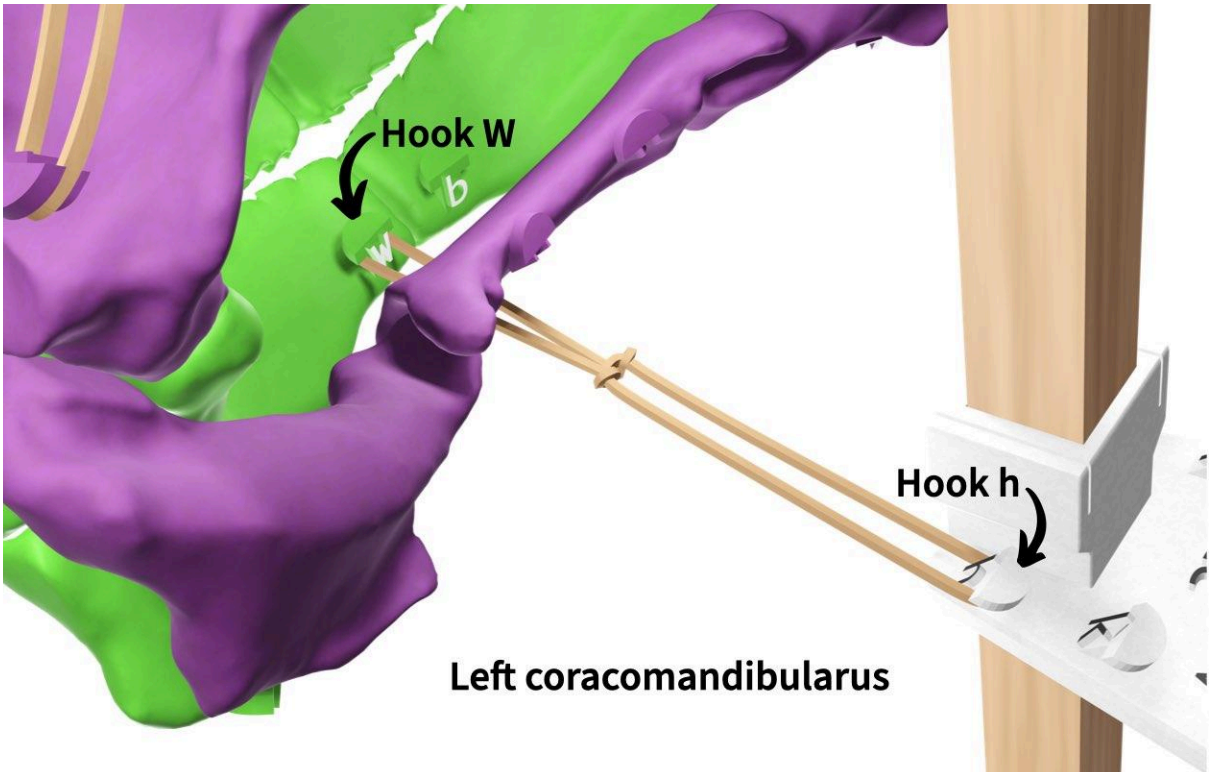


BUILD NOTE: Flipping your shark

Since the coraco muscles are on the ventral aspect of your shark skull, you might find it easier to flip your shark upside down. To do this, remove the stand rod plus shark skull from the stand base, flip it over, and set the skull upside down onto your work surface.



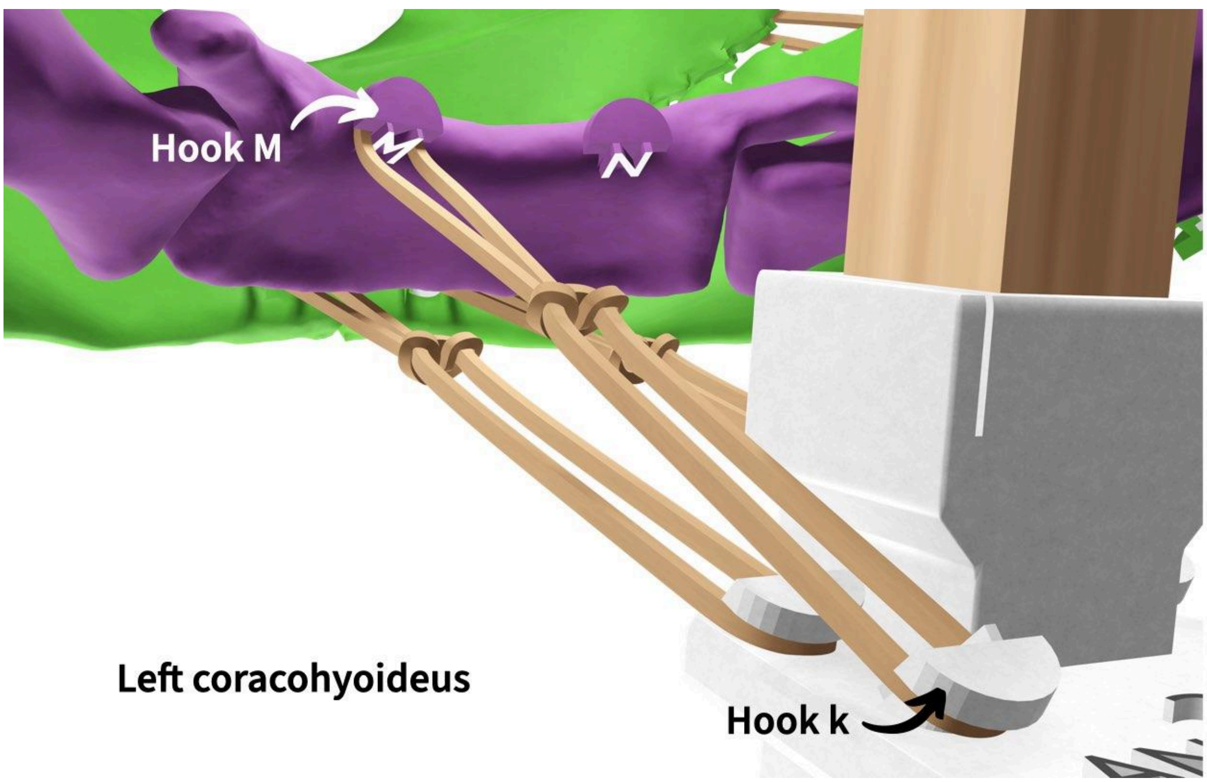
Add the left coracomandibularis to your shark skull by attaching a *double* rubber band to hook "W" on the left mandible and hook "h" on the middle piece of the stand rod.



Repeat this on the right side by attaching a *double* rubber band to hook "b" on the right mandible and hook "m" on the stand rod. On page 1 of your **Notebook**, fill in the "Attachments" column for coracomandibularis.

The other two coraco muscles are the **coracohyoideus** and **coracoarcualis**. These two muscles form something like a "muscle chain": the coracoarcualis originates on the pectoral girdle and inserts on the coracohyoideus *muscle*, and the coracohyoideus originates on the coracoarcualis *muscle* and inserts on the **basihyal cartilage** of the **hyoid arch**. (The coracomandibularis actually attaches to the coracoarcualis too, in addition to the pectoral girdle - it's just been simplified for your shark skull model.)

Because these muscles connect to each other, you'll add them together as a double rubber band. Add the left "coracohyoideus + coracoarcualis" to your shark skull by attaching a *double* rubber band to hook "M" on the basihyal and hook "k" on the stand rod. The double rubber band may not be very tight once it's attached; that's OK - if you secure the band by pulling them around the hooks, it should stay attached.

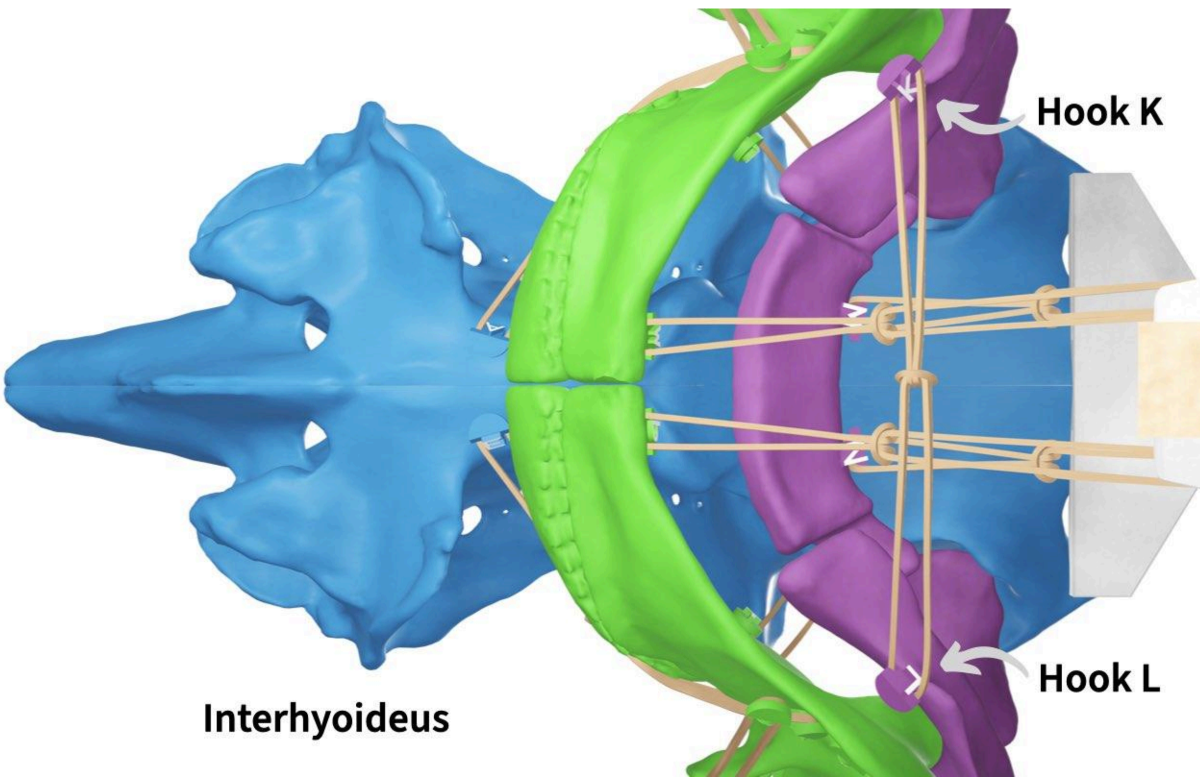


Repeat this on the right side by attaching a *double* rubber band to hook "N" on the basihyal and hook "n" on the stand rod. On page 1 of your **Notebook**, fill in the "Attachments" column for the combined "coracohyoideus + coracoarcualis."

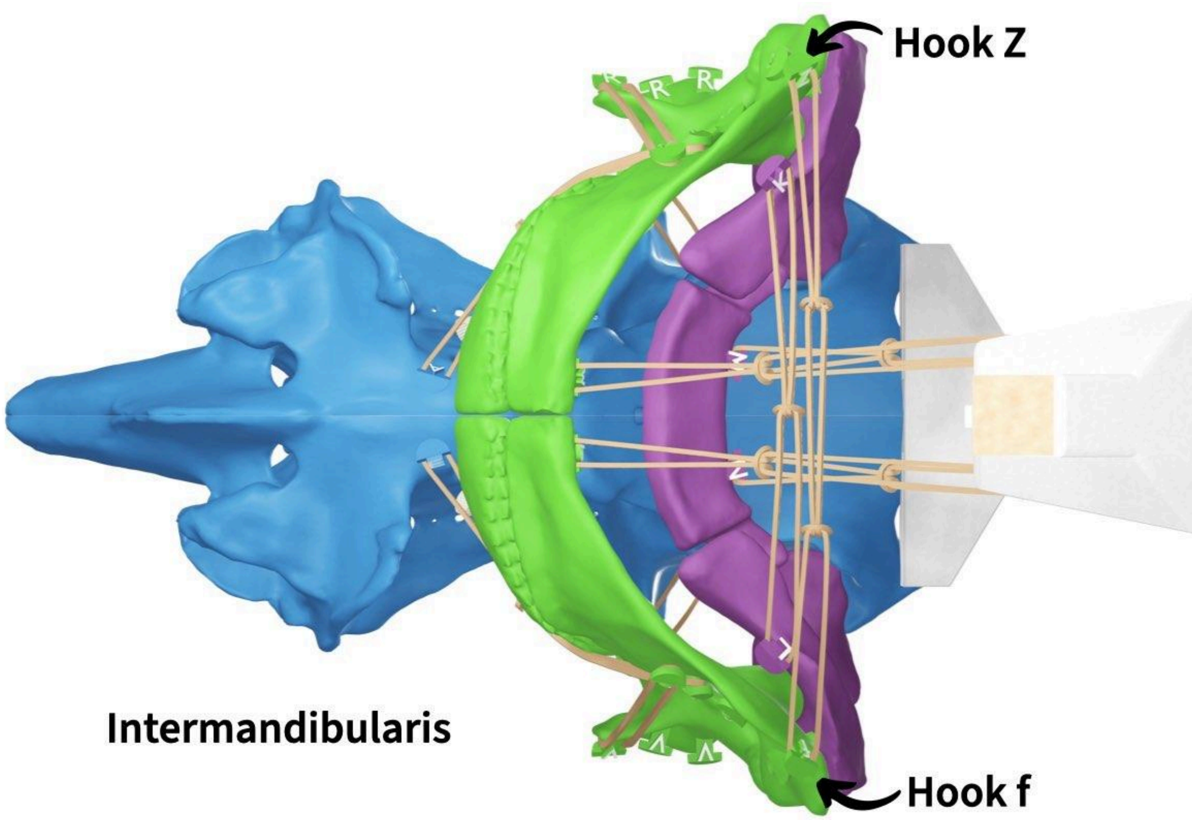
The ventral sheet muscles

The last two muscles you'll add could be called the "ventral sheet muscles." These muscles are broad, thin sheets of muscles that cover most of the ventral surface of the shark's skull and are superficial to the coraco muscles. So keep in mind that the rubber bands just represent the approximate orientation of these muscles, not their shape. For these muscles, it will probably be easiest to remove and flip your shark skull again so you can more easily access the ventral aspect of the skull.

The deepest of these two is the **interhyoideus**. The interhyoideus runs between ("inter") the two left and right **ceratohyals** of the hyoid arch. Add the interhyoideus to your shark skull (superficial to the coraco muscles) by attaching a *double* rubber band to hook "L" on the left ceratohyal and hook "K" on the right ceratohyal.



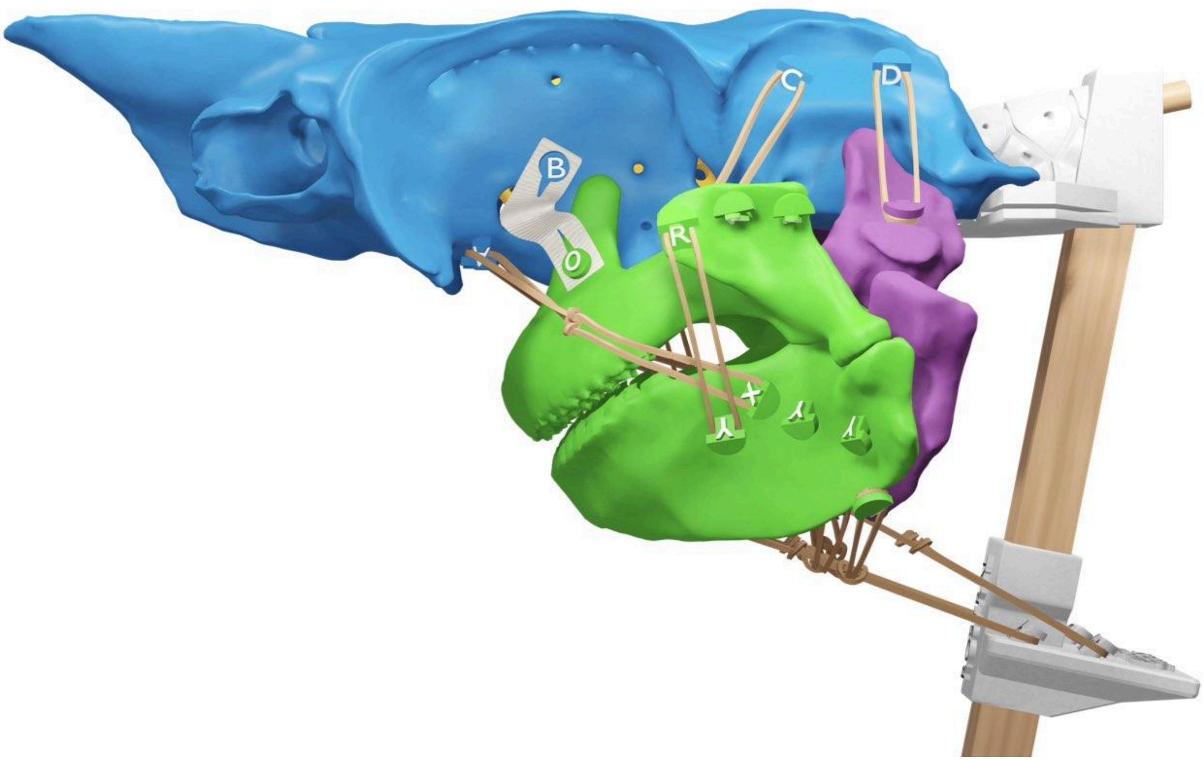
Superficial to the interhyoideus is the **intermandibularis**. Analogous to the interhyoideus, the intermandibularis runs between the left and right mandibles. Add the intermandibularis by attaching a *triple* rubber band to hook "f" on the left mandible and hook "Z" on the right mandible.



On page 1 of your **Notebook**, fill in the "Attachments" columns for interhyoideus and intermandibularis. Once you've finished, check that you have all of your muscles attached correctly by comparing your shark with the image on the following page.

ASSESS: Muscles added

With all the jaw muscles added, your shark should look like the image below.

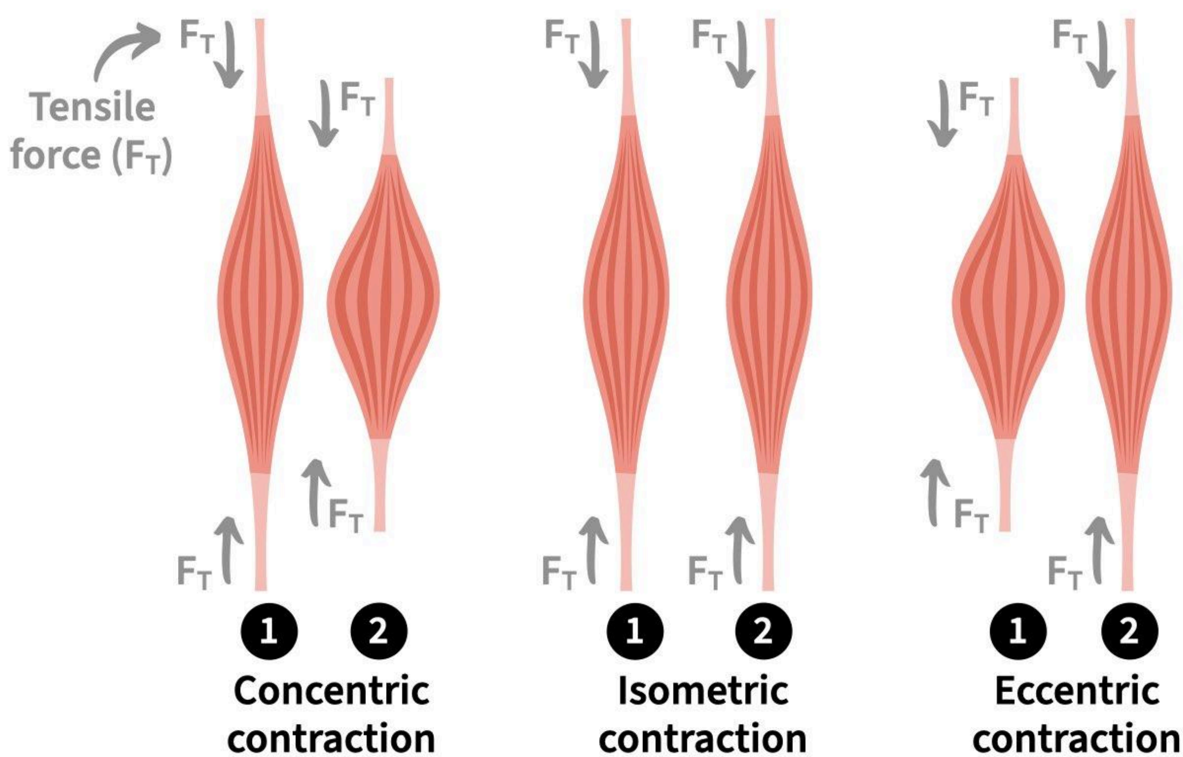


Section 2. How can your shark's jaws move and which muscles drive those motions?

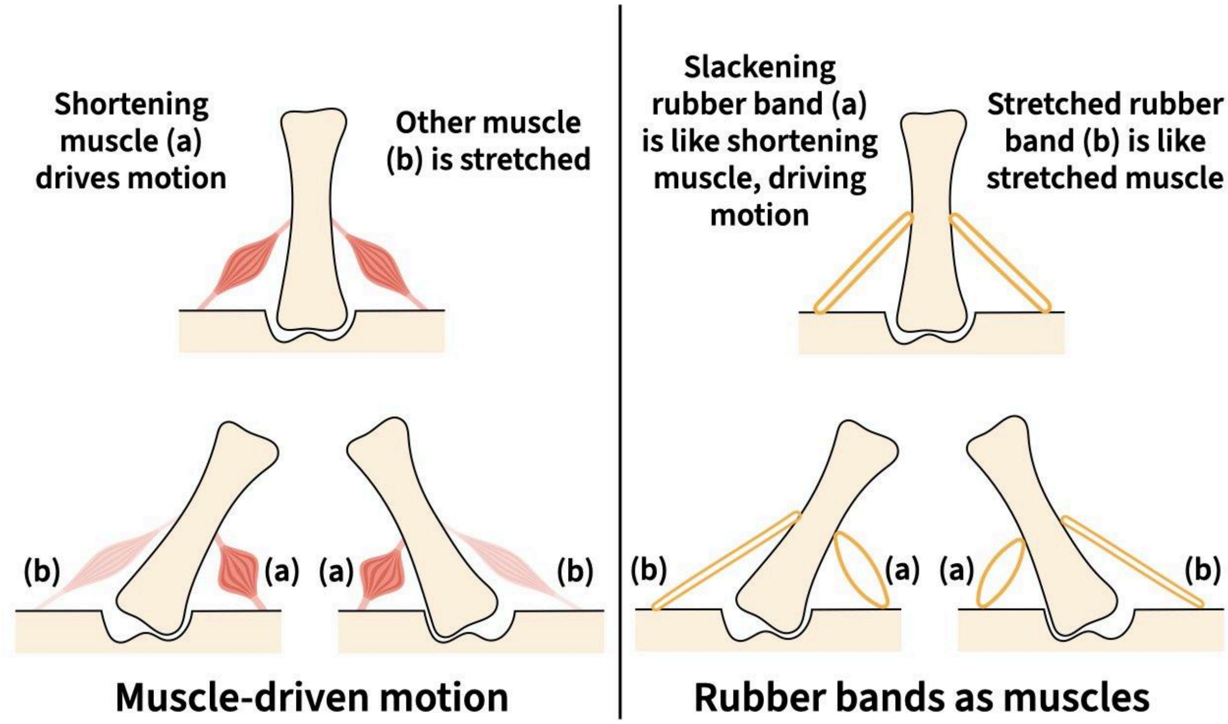
Now that you've added all of the jaw muscles to your shark, you're ready to simulate some motion and figure out which muscles drive which motions! Before you do that, however, it's important to talk about how to infer muscle actions from simulated motion and the limitations of those inferences.

How to infer muscle action from simulated motion

At the cellular level, muscles can only produce **force in tension** (also called a **tensile force**). This means, basically, that muscle cells can only pull, not push. It is possible for whole muscles composed of cells in multiple orientations to effectively push (one example is your tongue), but that's not relevant for this module. Muscles can produce tension while they are shortening (**concentric contraction**), staying the same length (**isometric contraction**), or lengthening (**eccentric contraction**; Dickinson et al. 2000). For this module, we'll just consider muscle actions from concentric contractions.



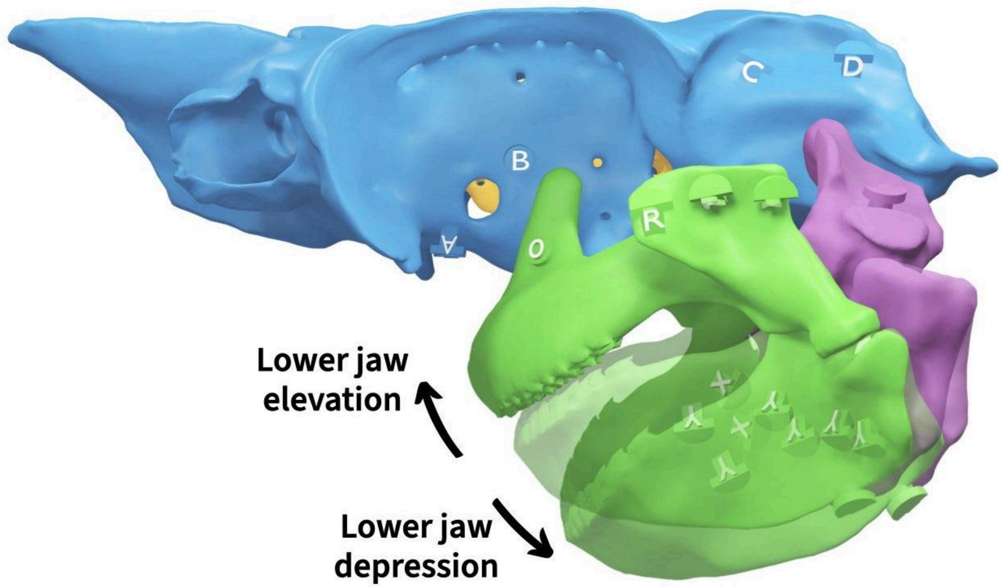
To infer the actions of muscles with your shark skull, you'll simulate a particular motion (i.e., action) of the jaws and observe which rubber bands shorten or slacken during that motion; the rubber bands that shorten correspond to muscles that could drive that motion.



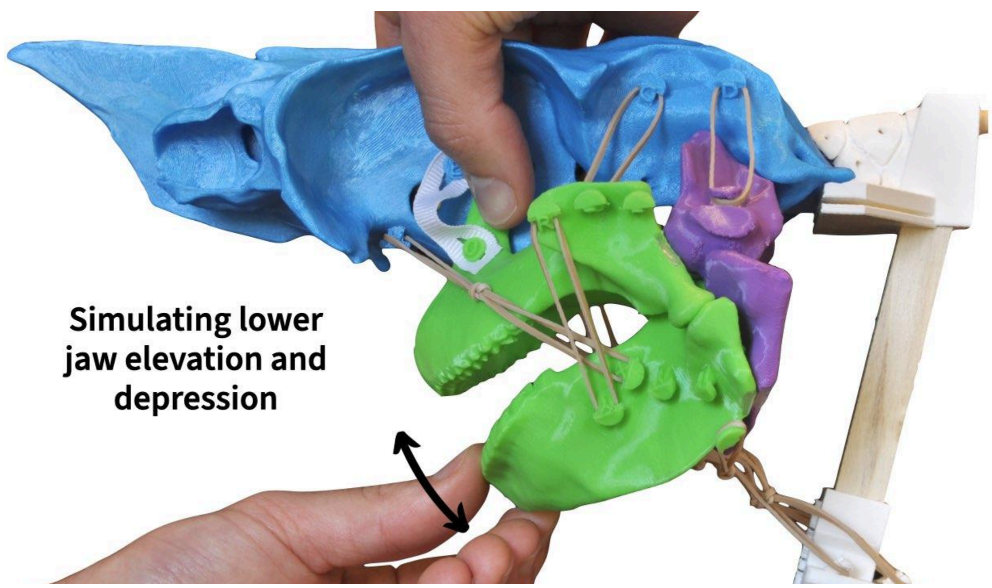
Be aware, however, that just because a muscle *could* drive a motion doesn't mean that it *does*. To actually prove a muscle's action, you need to show that it is **active** during that action in a live animal. This is done by recording electrical signals from the muscle, a technique called **electromyography (EMG)**. EMG experiments have actually been performed for the spiny dogfish shark by Wilga and Motta 1998 and, despite your more basic approach, the results of your simulations will be very similar to their results.

Lower jaw elevation and depression

The first action you'll simulate is elevation-depression of the lower jaw (mandible).



Since all the jaw cartilages are connected, if you try to just move the lower jaw, it will move other elements too. To simulate motion of only the lower jaw, use your right hand to secure the palatoquadrates and use your left hand to elevate and depress the lower jaw.

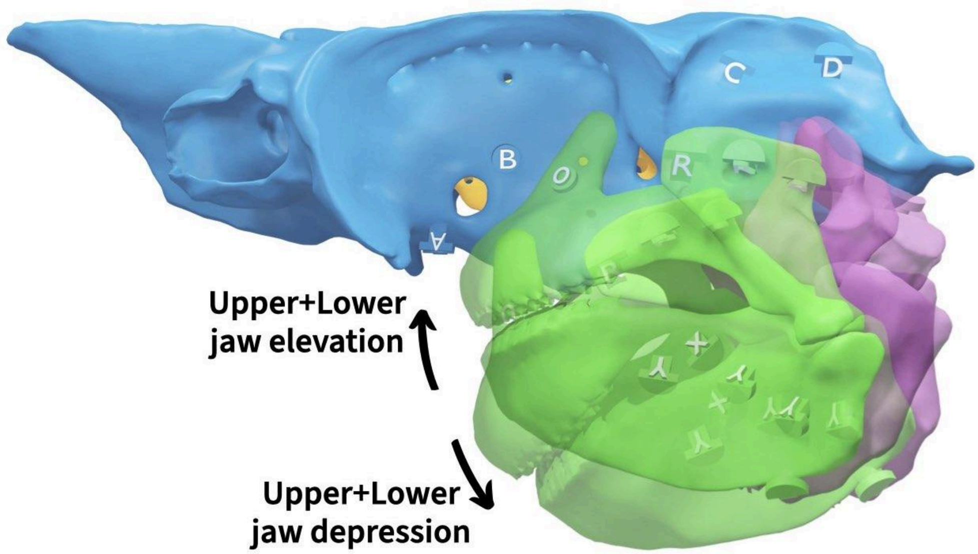


Which muscles shorten or slacken during each action? On page 1 of your **Notebook**, indicate the muscles that could potentially drive these motions by filling in the corresponding column(s) with an "X.

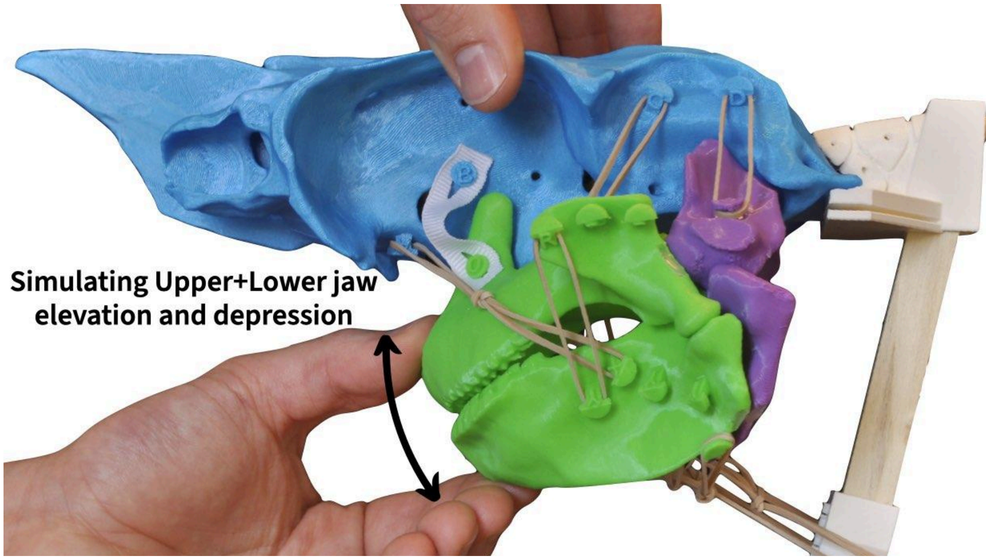
You may have noticed how the hyoid arch moves along with the lower jaw. This is partially due to how your model is put together but also due to ligaments connecting the mandible and the ceratohyal at the caudal end of these elements (the magnets in your kit reproduce this to some extent). These connections can produce *variable* coupling between the hyoid and **mandibular arch** (the upper+lower jaw), potentially allowing the coracohyoideus to indirectly depress the lower jaw. However, this coupling is not absolute nor is it fully understood in spiny dogfish sharks.

Upper+Lower jaw elevation and depression

You just simulated elevation and depression of the *lower* jaw but sharks can also elevate and depress their upper and lower jaw together; you could call this "jaw elevation and depression" (without the "lower"). This motion is primarily along the dorsoventral axis.



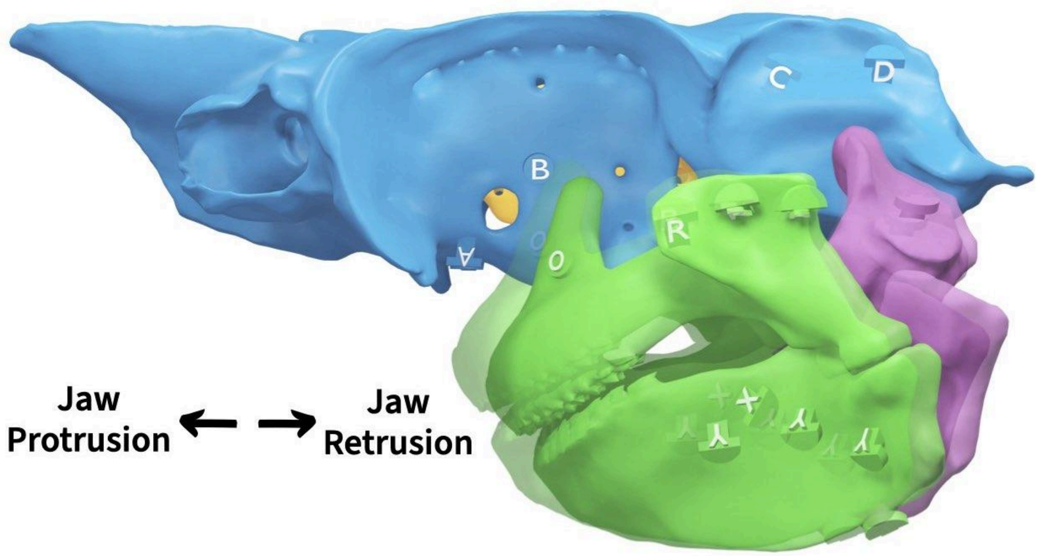
Simulate elevation and depression of the upper+lower jaw by holding the chondrocranium in place with one hand and, with your other hand, gripping the upper and lower jaw together at the **symphysis** (where the left and right side connect at the midline).



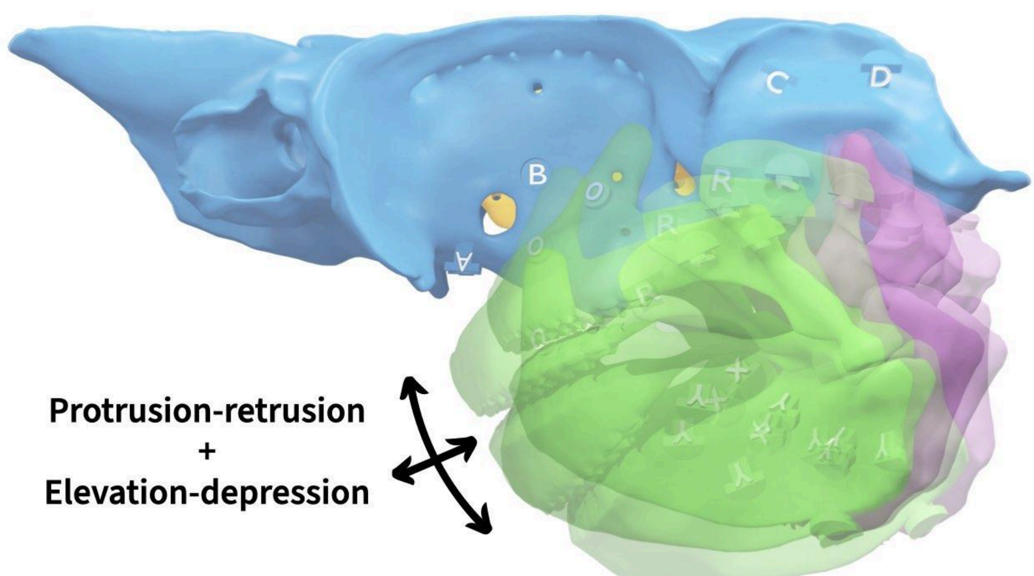
Which muscles shorten or slacken during each of these actions? Fill in the table on page 1 of your **Notebook** with your results.

Upper+Lower jaw protrusion and retrusion

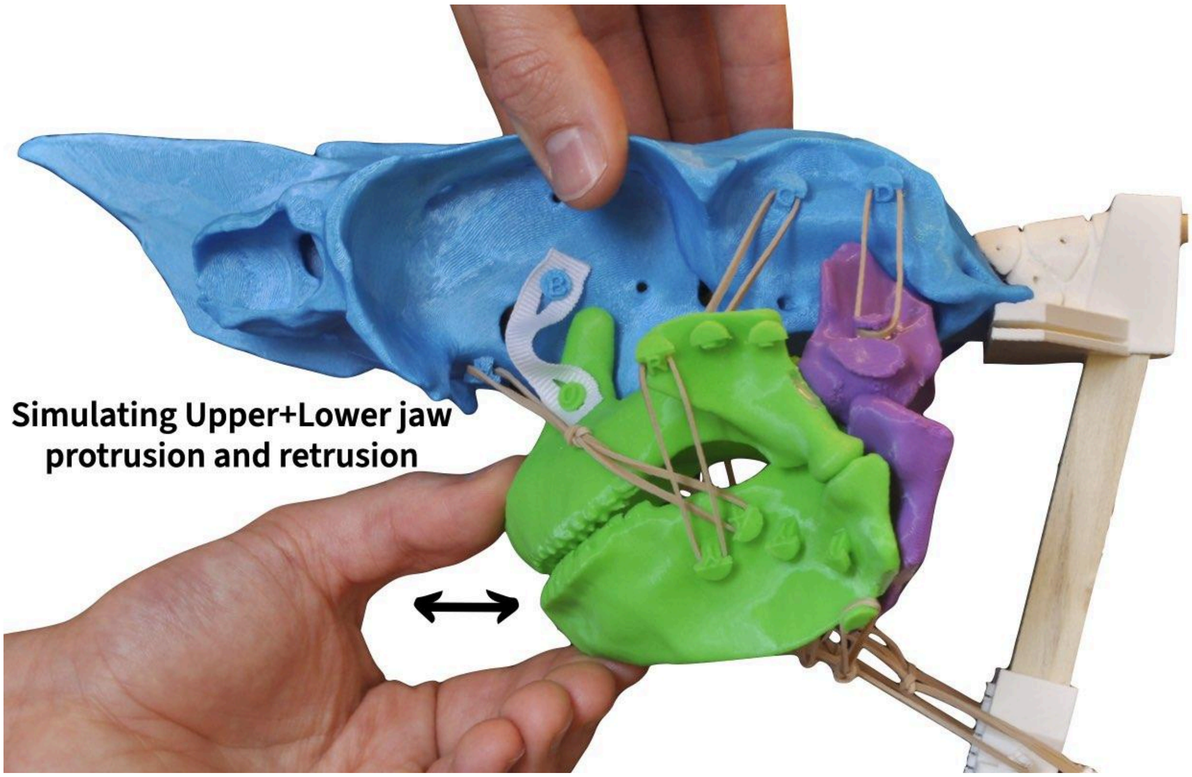
What is traditionally called **jaw protrusion** in sharks is actually a *combination* of two different motions: up-and-down motion and forward-and-back motion. When you simulated upper+lower jaw depression-elevation previously, you simulated the up and down motions (primarily along a dorsoventral axis). The second motion, forward-and-back, occurs primarily along the **rostrocaudal axis**. In this module, we'll call this rostrocaudal motion **protrusion** and **retrusion** (to match the terms used in other animals, such as mammals).



When combined, these two axes allow the jaws to move up, down, forward, and backward.



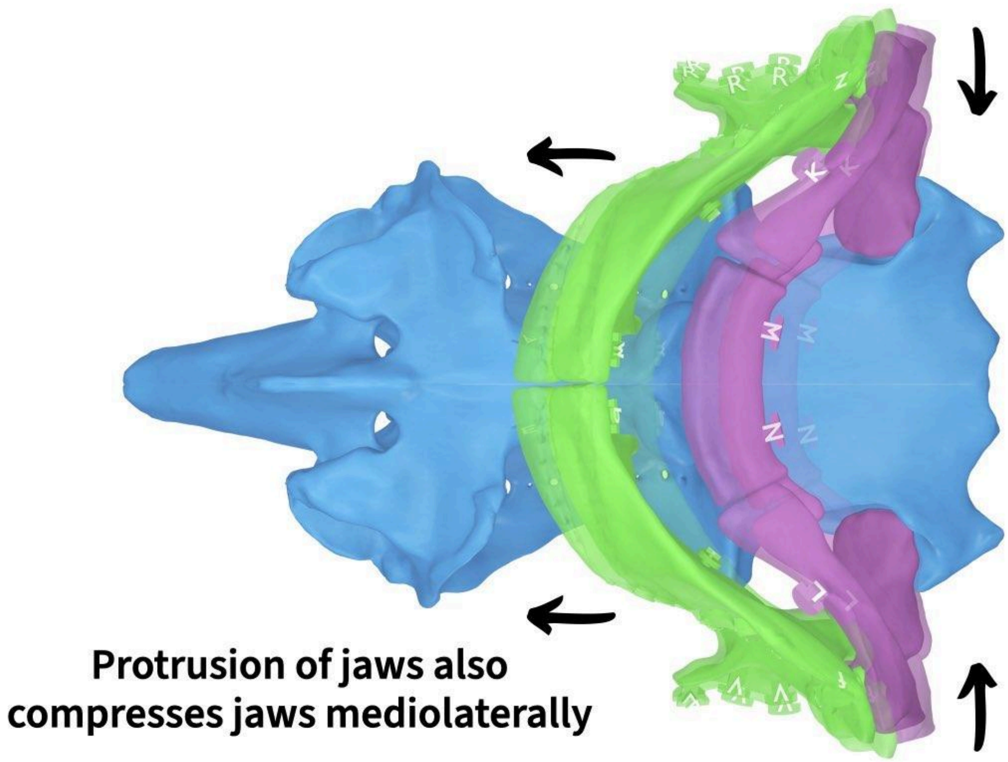
For the purposes of determining muscle actions, however, it's simpler to break this complex motion down into two axes. Simulate protrusion and retrusion of the upper+lower jaw similar to how you simulated elevation-depression, but this time pull the jaws rostrally *by just a couple millimeters*. Note that the jaws move *much* less rostrocaudally than they do dorsoventrally.



Which muscles shorten or slacken during each of these actions? Because the motions are relatively small, the length changes are subtle. Fill in the table on page 1 of your **Notebook** with your results. This one is a bit more challenging so use the following two hints to help you.

HINT: Try a ventral view

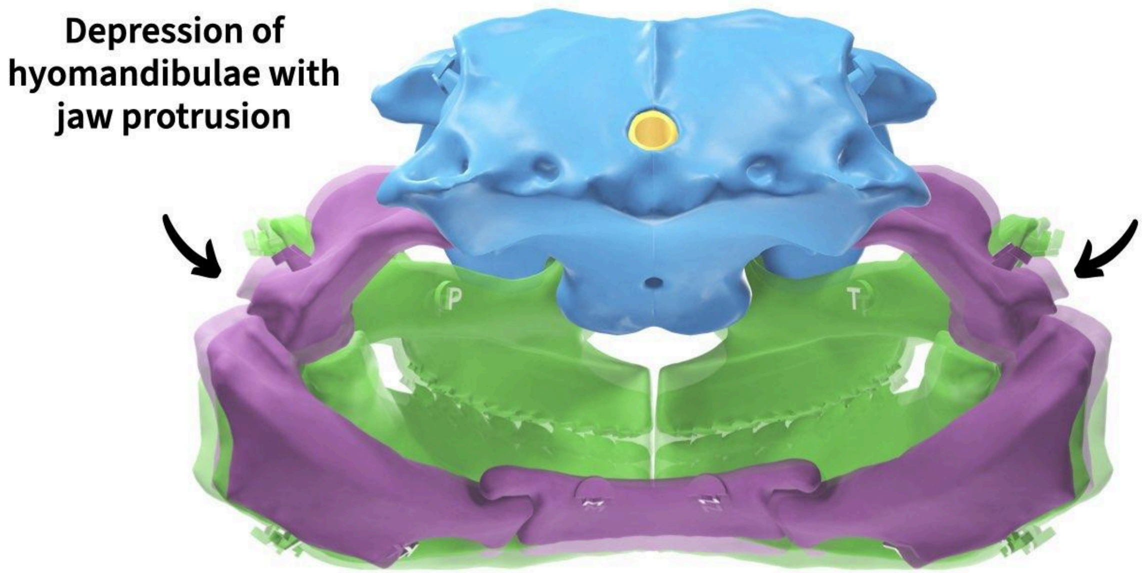
If you view the ventral aspect of your skull as you simulate protrusion, you can observe that as the jaws protrude rostrally, they also narrow (are compressed) **mediolaterally** (along the left-right axis).



What muscle(s) could drive this mediolateral expansion or compression?

HINT: Try a caudal view

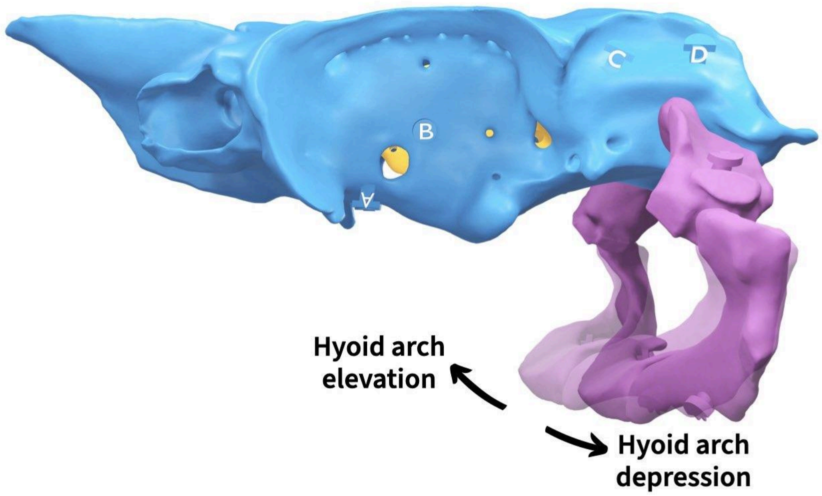
If you view your skull caudally as you simulate protrusion, you can observe that as the jaws protrude rostrally, the hyomandibulae adduct (rotate inward).



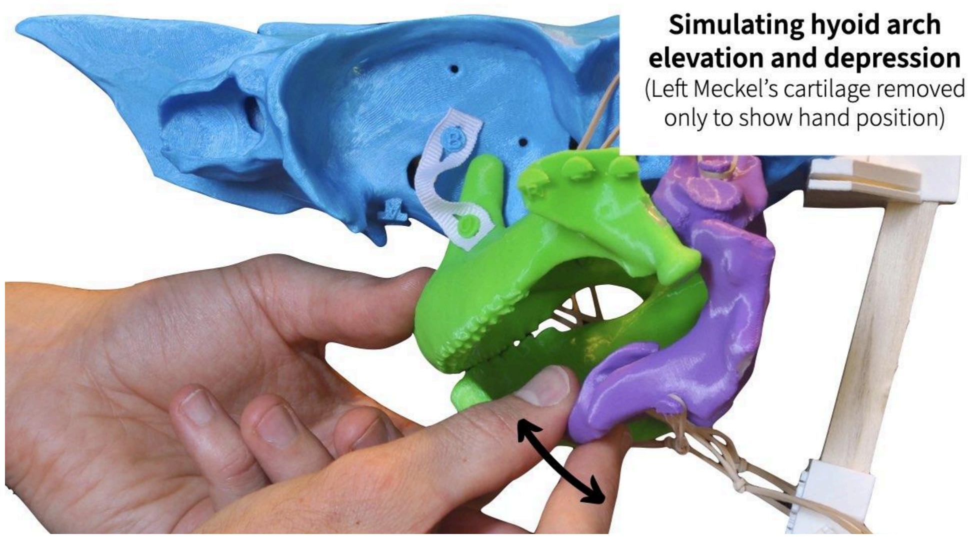
What muscle(s) could drive this depression or elevation of the hyomandibulae?

Hyoid arch elevation and depression

Elevation and depression of the hyoid arch is how fish compress and expand, respectively, their throat to create suction for drawing prey into their mouth and for moving water over their gills. As mentioned when you simulated lower jaw elevation-depression, the hyoid arch has some coupling with the mandibular arch (the "hyoid arch" here refers primarily to the ceratohyals and basihyal, since the hyomandibulae move in a different way). However, this coupling is not absolute: the hyoid arch can also move independently of the mandibular arch.



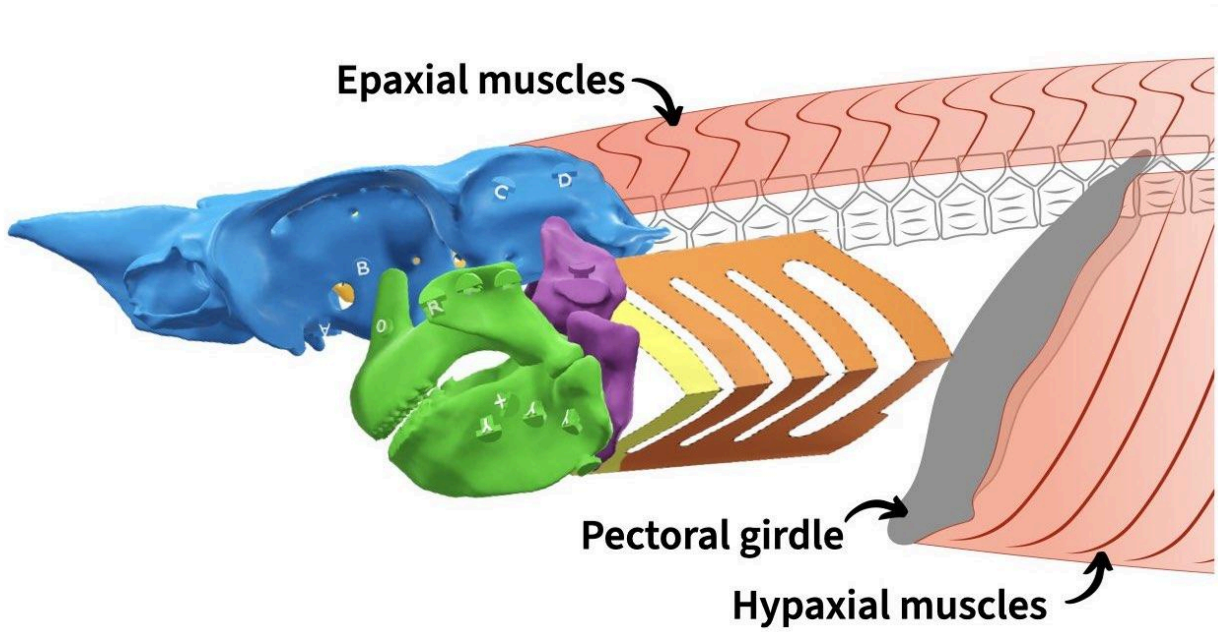
To simulate hyoid elevation-depression, hold the lower jaw in place with one hand and use your other hand to push and pull the basihyal dorsally and rostrally.



Which muscles shorten or slacken during each of these actions? Fill in the table on page 1 of your **Notebook** with your results.

Section 3. How do sharks use body muscles to open their mouth?

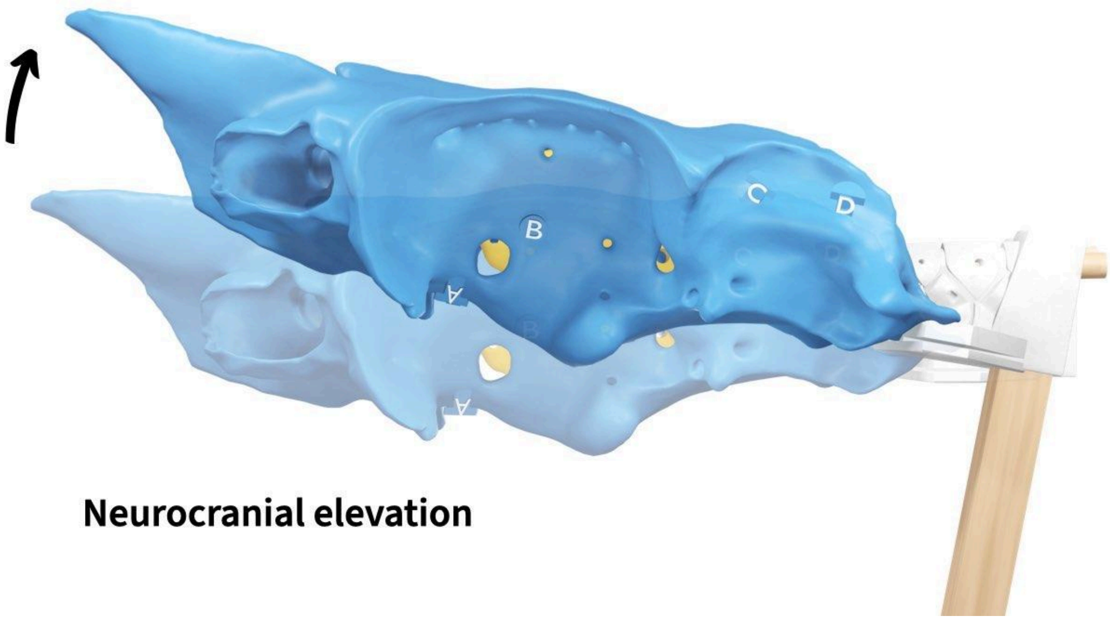
You've added all of the major jaw muscles to your shark skull, however, there are two additional muscles (groups of muscles really) that have an essential role in jaw opening: the **epaxial** and **hypaxial** muscles. The epaxials (also called **epaxialis**) are essentially the "back muscles," whereas the hypaxials (also called **hypaxialis**) are essentially the "belly muscles." At their rostral-most points, the epaxials insert on the caudal surface of the chondrocranium, whereas the hypaxials insert on the pectoral girdle.



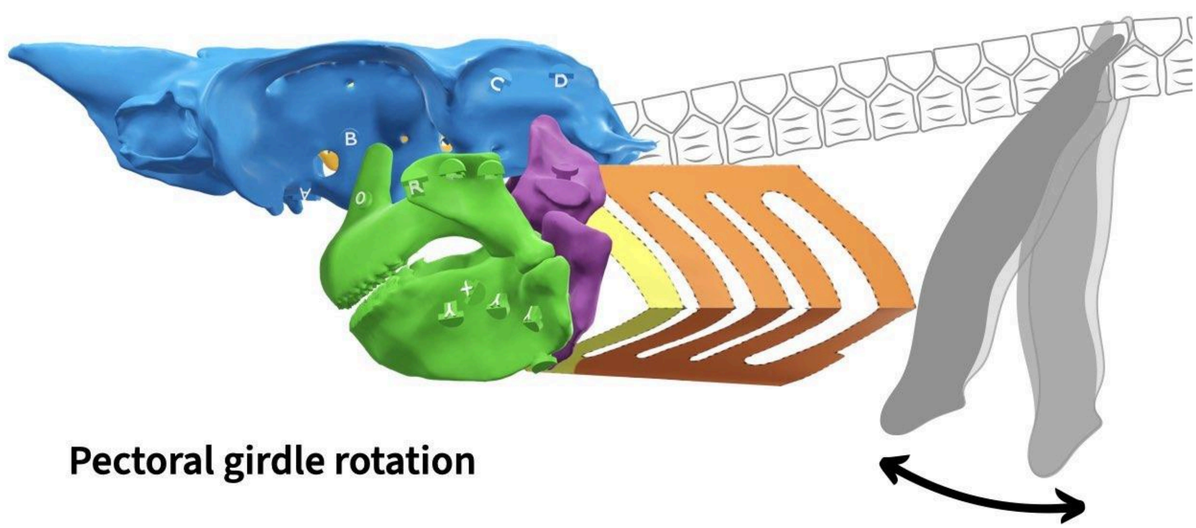
Why are these *body* muscles essential to opening the mouth? The answer is related to **power** (energy per unit time). Fish need a lot of power to open their mouth quickly against the resistance of water and generate a strong suction force that will capture prey. And the power a muscle can generate is directly related to its volume: the larger the muscle volume, the greater the power. By using the largest muscles in their body to open their mouth, fish are able to generate much more power than they would if they were to rely solely on their cranial muscles (Camp et al. 2017).

Using your shark skull to perform simulations, can you explain *how* fish can use their body muscles to open their mouth *and* generate suction? Write your explanation on page 2 of your **Notebook**; feel free to use bullet points.

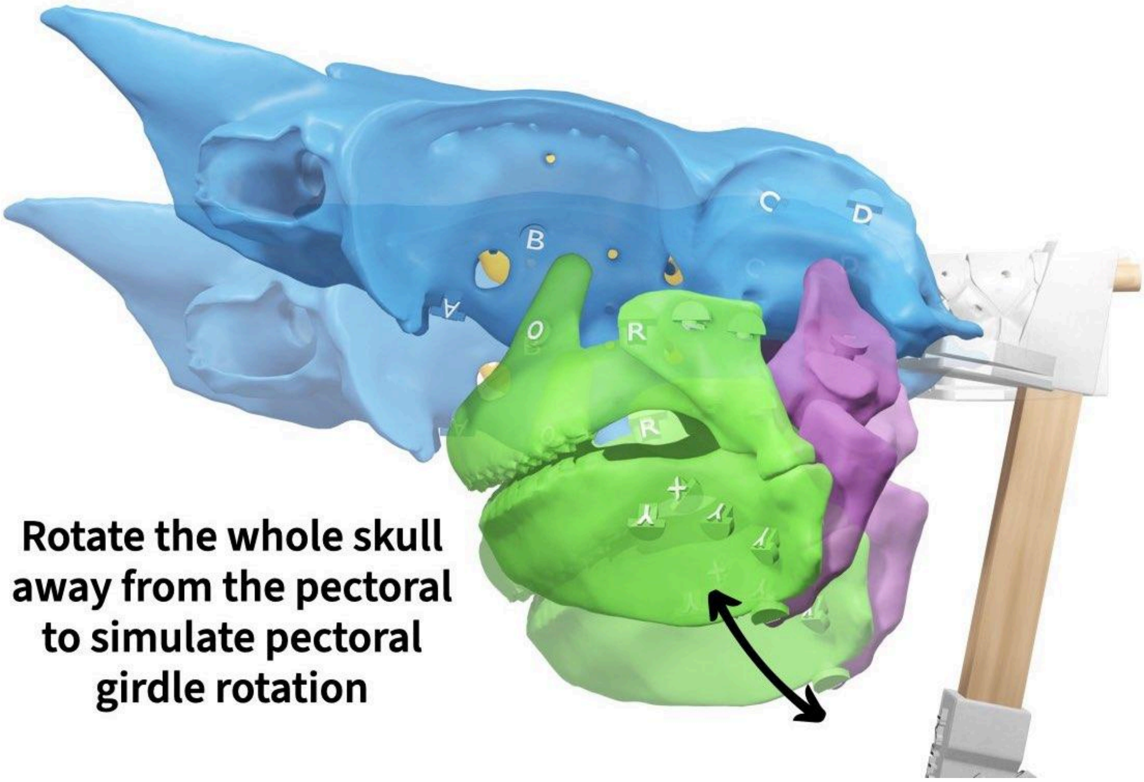
Your explanation should include which muscles are involved and their role. To help you figure this out, your stand mount rotates up to simulate neurocranial elevation.



Also, recall that the middle piece of your stand rod represents the pectoral girdle. In your model, the pectoral girdle is fixed to the stand but in an actual fish it can rotate rostrally and caudally.



Even though your shark's pectoral girdle is fixed, you can simulate motion of all the other elements relative to the pectoral girdle, which is similar.



If you need some help, check out the hint below. Then check your work on the next page.

HINT: It takes coordination

The epaxials and hypaxials don't act alone. Their actions are coordinated with those of the jaw muscles.

Section 4. How do sharks manipulate their food without a tongue?

Based on what you now know about the motions and muscles of your shark's jaws, can you explain how sharks are able to manipulate their food without a tongue? In other words, if someone were to say, "sharks can't manipulate food and water in complex ways because they don't have a tongue," how would you counter this argument? Write your explanation on page 2 of your **Notebook**; feel free to use bullet points.

In this module, you've learned how to use physical models to perform simulations and predict biomechanical function. While simulations are just one tool in your toolbox, they are invaluable for testing our understanding of systems and generating hypotheses. You've learned how muscles can drive complex motions of biomechanical systems through concentric contraction, acting through linkage mechanisms, and coordination. And you've learned that just because sharks are humans' distant relatives or just because they're fish, doesn't mean that their feeding system is any less complicated. The jaws of sharks are a mix of specialized (e.g., jaw suspension) and conserved (e.g., using body muscles for added power) features, like for any vertebrate feeding system.

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