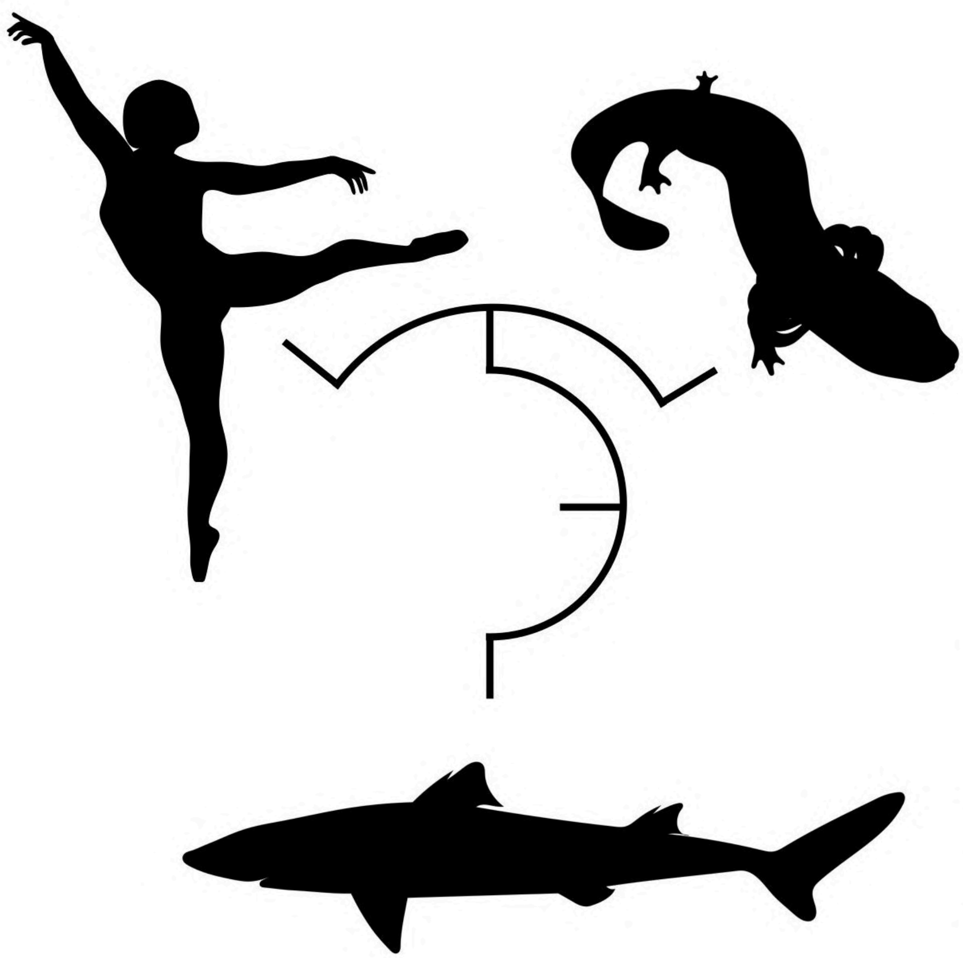
STUDENT GUIDE

Mapping the functional evolution of cranial nerves

Text and images by Aaron M Olsen, PhD



Description

In this module, you will compare and classify the shark cranial nerves and explain the functional evolution of some of the cranial nerves in vertebrates more broadly.

Introduction

At first, the vertebrate cranial nerves may seem like an arbitrary list of names and numbers, with seemingly no pattern uniting them. Seeing them only in this way will make it difficult for you to remember and understand them at a deeper level. While there is a certain arbitrariness to the way in which they were numbered and grouped, there are patterns in the functions of the cranial nerves and in the evolutionary conservation and modification of cranial nerves in different lineages of vertebrates.

In this module, you'll learn to recognize and explain these patterns. You'll also understand the broader functional and evolutionary context of the cranial nerves, and with this added context it will be easier for you to remember them.

Materials needed

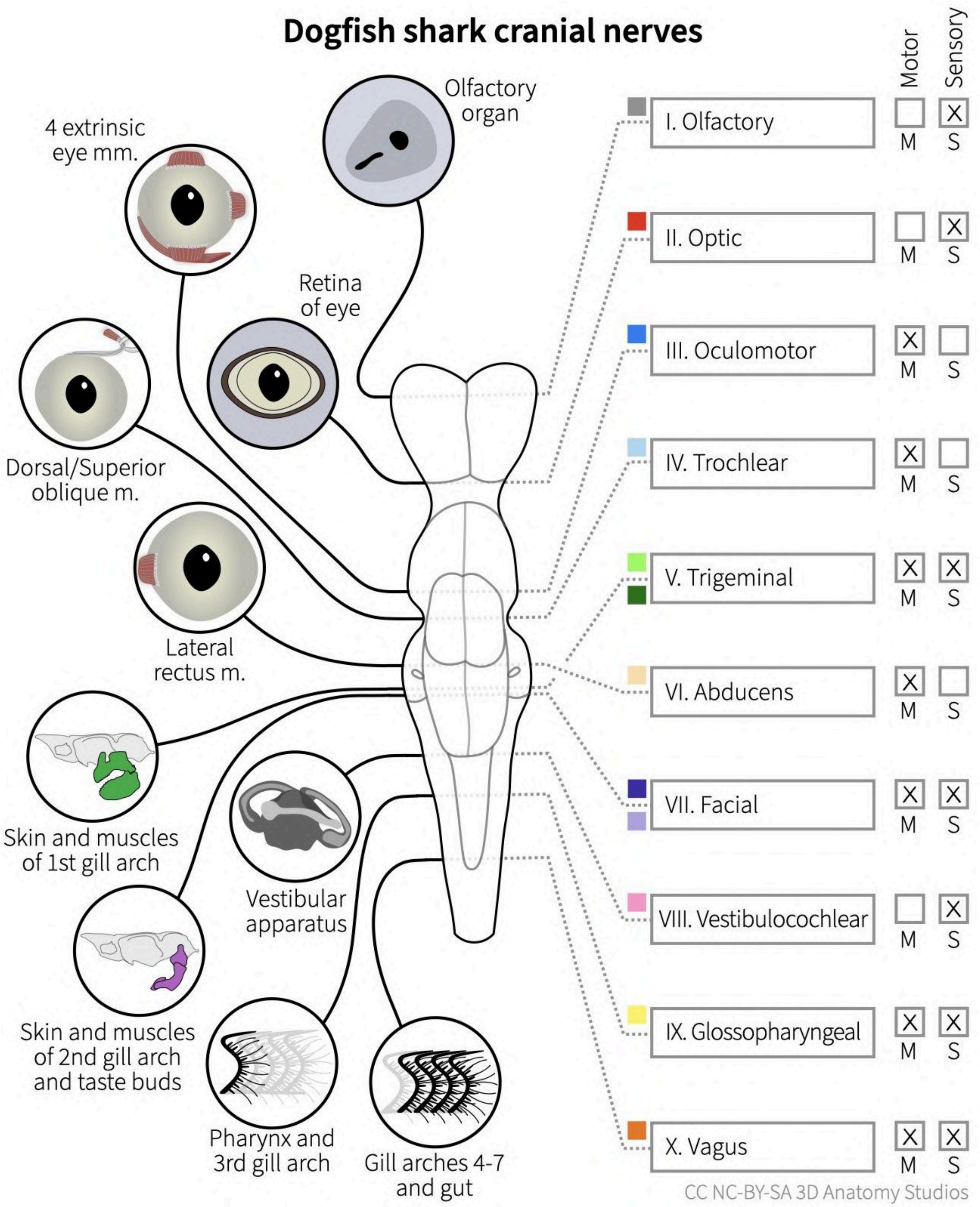
For this module, you'll need:

- The **Student Notebook** for this module (SA04).

You don't need any components from your shark kit. If you have the chondrocranium and brain with all of the cranial nerves (pipe cleaners) attached, they can be a handy reference.

Materials needed (continued)

For this module you can use the completed diagram from your **SA03 Student Notebook** or you can refer to the completed diagram below.



Section 1. How are the shark cranial nerves different or similar to one another?

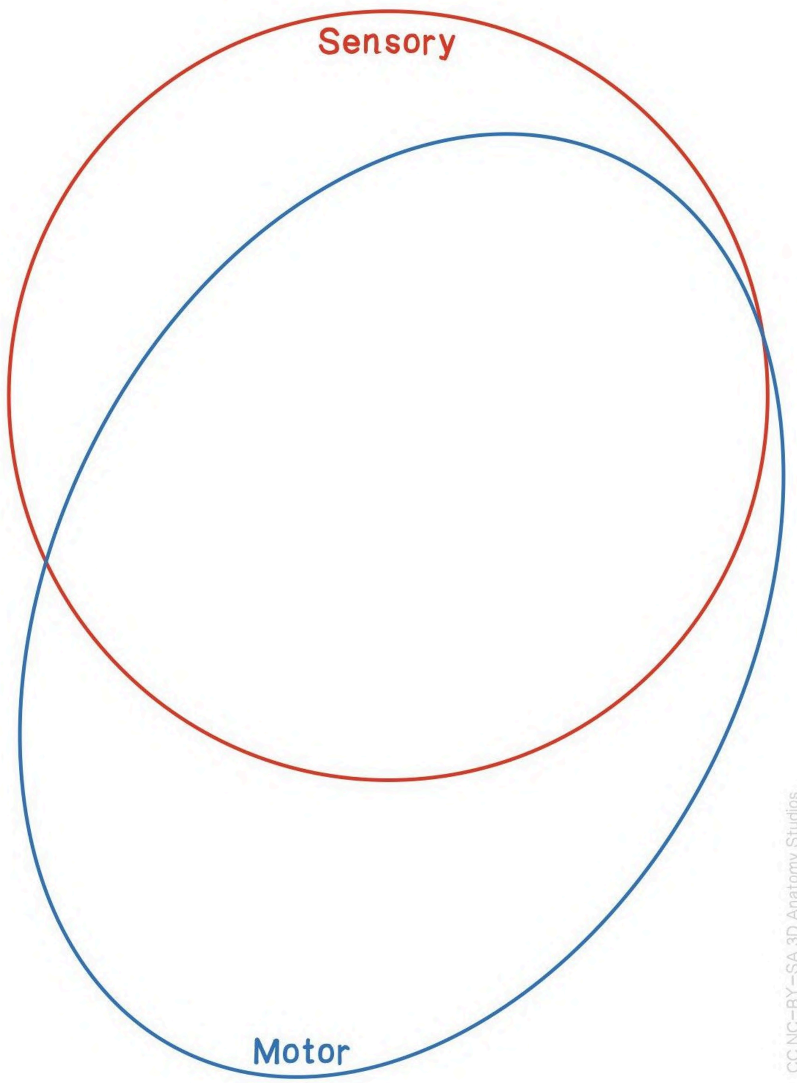
The 10 cranial nerves of the shark have similarities and differences with one another. On page 1 of your **Notebook**, create a Venn diagram of the shark cranial nerves forming groups of two or more cranial nerves based on any characteristics you'd like. You can use the diagram on the previous page as a reference. To give you as much space as possible, just use the roman numerals for each cranial nerve (e.g., "I", "II", "III"), rather than the full name.

Before you draw any ovals, you might want to make a list of potential groups and the nerves in those groups first; you should be able to come up with at least six groups. That will help you plan the positions and sizes of your ovals. As you plan the groupings, you may find that your ovals need to be repositioned or resized; you may also want to create a few drafts on scratch paper before drawing the final version on page 1.

If you need some help getting started, check out the hint on the following page.

HINT: Start with sensory vs. motor

One classification that applies to all cranial nerves is whether they have a sensory component, motor component, or both. If you were to draw two large, overlapping ovals, one for sensory and one for motor (see image below), which cranial nerves would you put in each oval and in the overlapping space?



When you've completed your Venn diagram, what grouping did you use? Which groupings are structural? Which groupings are functional? Thinking of the cranial nerves within these conceptual groups is one technique that will help you learn and remember them.

Section 2. What cranial nerves and functions are ancestral versus derived in vertebrates?

The cranial nerves of vertebrates are, in general, highly conserved through evolution. For example, most of the cranial nerves are present in some form in all vertebrates, including in sharks and humans. However, just as with any anatomical system, throughout vertebrate evolution there have been losses and gains of cranial nerves and cranial nerve functions depending on the selective pressures and evolutionary histories of particular lineages.

On page 2 of your **Notebook** you'll find an evolutionary tree with three **extant** (living) **taxa**: dogfish shark, common mudpuppy (an amphibian), and human. Below the names of each **taxon** (the singular form of taxa), you'll find information for each taxon related to some of the cranial nerves and their functions. And in the tree, you'll find "trait change summary boxes," numbered 1-5, at each branching point within the tree, with a subset of cranial nerves. These boxes summarize changes in these nerves at different points of time in the evolutionary history of these three taxa.

In this module, you'll use the information supplied for each extant taxon (in the top half of the page) to infer the trait changes in the tree (in the bottom half of the page). This tree does not contain *all* of the cranial nerves nor does it contain *all* of their functions- if it did, the figure would not fit on a single page. These are just a subset of the cranial nerves and their functions for you to learn *some* of the major evolutionary changes in vertebrate cranial nerves.

Understanding tree relationships

To get you oriented toward tree thinking, first observe the branching pattern of the tree. Based on the branching, are mudpuppies more closely related to sharks or to humans? Once you think you know the answer, check the solution on the following page.

ASSESS: Our cousin, the mudpuppy

If you answered "humans," you are correct! In this tree, mudpuppies and humans are **sister groups** that have a **most recent common ancestor** (MRCA) at the dot labeled "2"; think of them like two siblings, closely related. The MRCA of mudpuppies and humans at "2" does not include sharks. Sharks are then related to mudpuppies and humans as a group and all three taxa share a MRCA at the dot labeled "1"; if mudpuppies and humans are like siblings, sharks are like a cousin to both. Thus, you and a mudpuppy are more closely related to each other than either of you is to a shark.

Lateral line nerves

Now that you understand the evolutionary relationships depicted in the tree, it's time to start filling in the sequence of trait changes, starting with the first nerve in the list: the **lateral line nerves** (abbreviated "LL"). These are a set of cranial nerves that connect to the brain at several points and carry mechanical and, sometimes, electrical information detected by sensory organs on the skin underwater. Use the information provided at the top of the tree on page 2 of your **Notebook** to guess the changes (if any) in the summary boxes at points 1-5 on the tree.

Refer to the "Possible trait changes" box on page 2 of your **Notebook** for examples of all the possible trait changes that can occur at each point. If the nerve evolves at a particular point in the tree, add a "+" to the circle; if the nerve is lost, add a "-" to the circle. If the nerve gains a function, add a "+" to the box; if the nerve loses a function add a "-" to the box. And if there is no change, leave the circle and box empty.

If you're unsure how to proceed, check out the hints on the following page!

HINT: Two gains or a gain and a loss?

Note that both dogfish sharks and common mudpuppies can sense mechanical and electrical stimuli via their lateral lines (Bullock, Bodznick & Northcuttet 1983). This raises two possible scenarios: either lateral lines evolved independently in each lineage (at points 3 and 4 in the tree) or evolved once in the ancestor of both sharks and mudpuppies (point 1) and were lost after the split between mudpuppies and humans in the lineage that includes humans (point 5). Which of these two scenarios do you think is most likely?

HINT: More about lateral lines

As you fill in the trait changes for this nerve, you're facing one of the major challenges of inferring changes within a tree given only information (and *limited* information!) from living taxa, the taxa "at the tips" of the tree. Depending on how easy it is to evolve versus lose a trait, either of the scenarios mentioned in the hint above are likely. Here's some additional information:

- Lateral lines are found throughout fishes and some aquatic vertebrates
- Fossils that are descendants of the most recent common ancestor of sharks and mudpuppies, at point 1 in the tree, show evidence of lateral lines (they leave indications in bone)

ASSESS: Lateral lines mapped

Because of the widespread distribution of lateral lines among aquatic vertebrates and their ancestors, lateral lines likely evolved once at point 1 and were later lost. The lateral line is only useful for gathering sensory information underwater. This explains why mudpuppies *retain* their lateral line from their ancestors, while more terrestrial vertebrates lost their lateral line.

Optic nerve (CN II)

Next, complete the trait changes for the second nerve in the list: the **optic nerve (CN II)**. Though it is not included in the bulleted lists above the tree, note that all of the taxa on the list have an optic n. that sends visual perception information to the brain. Check your work against the solution on the following page.

ASSESS: Optic nerve mapped

There is no loss of the optic n. (CN II) nor changes to its function indicated for any of the taxa in the information at the top of the tree. So the most likely scenario is that the optic nerve evolved once at the base of the tree (at point 1) without any losses or changes in its function at any other point in the tree. The optic n. actually evolved even earlier than at point 1, but since your tree doesn't go further back in time, this is the best place to put it for this activity.

Trigeminal nerve (CN V)

Next, complete the trait changes for the third nerve in the list: the **trigeminal nerve (CN V)**. Note that all of the taxa have a trigeminal n. that provides motor and sensory innervation to structures derived from the **first gill arch**. Check your work against the solution on the following page.

ASSESS: Trigeminal nerve mapped

There is no loss of the trigeminal n. (CN V) indicated for any of the taxa at the top of the tree. So it's most likely that this nerve evolved once at the base of the tree (point 1) or earlier. However, there are changes to its function. Unlike mudpuppies and humans, sharks are able to protrude their upper and lower jaws, in part, due to the **orbitalis muscle**, innervated by the trigeminal n. And in humans, the trigeminal n. provides general sensation for the muscular tongue (in amphibians, tongue general sensation appears to come from spinal nerves, not cranial nerves; Anderson & Nishikawa, 1997). Since these are different functions, it's most likely that the trigeminal n. gained these functions independently at points 3 and 5 in the tree.

Abducens nerve (CN VI)

Complete the trait changes for the next nerve in the list: the **abducens nerve (CN VI)**. Note that all of the taxa have an abducens n. that innervates the **lateral rectus** extrinsic eye muscle. Check your work against the solution on the following page.

ASSESS: Abducens nerve mapped

There's no loss of the abducens n. (CN VI) indicated. So it's most likely that this nerve evolved once at point 1 or earlier. However, there are changes to its function: in common mudpuppies, and some other amphibians, the **retractor bulbi** pulls the eyeball backward in the orbit. When animals swallow in air (versus water), they can't rely on water to help push back the food. And in amphibians, no bony structures separate the eyeball and mouth, only soft tissue. It's thought that the eyeball is pulled by the retractor bulbi to physically push the food down the throat. This also explains why a frog's eyeballs move when it swallows (Levine, Monroy & Brainerd 2004).

The retractor bulbi muscle is innervated by the abducens nerve and the most likely scenario is that this nerve gained this function once at point 4 in the tree.

Facial nerve (CN VII)

Complete the trait changes for the next nerve in the list: the **facial nerve (CN VII)**. Note that all of the taxa have a facial n. that provides motor and sensory innervation to structures derived from the **second gill arch**. Check your work against the following page.

ASSESS: Facial nerve mapped

There's no loss of the facial n. (CN VII) indicated, so the most likely scenario is that this nerve evolved once at the base of the tree (point 1) or earlier.

However, functions of the facial n. specific to each taxon are listed. In sharks, the facial n. innervates the **levator hyomandibulae** muscle, which helps retract and elevate the upper and lower jaws. In mudpuppies and other amphibians, the facial n. innervates the **depressor mandibulae** muscle, which depresses the **mandible**. And in humans and other mammals, the facial n. innervates the **muscles of facial expression**. Given the differences among these functions, each function mostly likely evolved independently at points 3, 4, and 5 in the tree.

Vestibulocochlear nerve (CN VIII)

Complete the trait changes for the second to last nerve in the list: the **vestibulocochlear nerve (CN VIII)**. Check your work against the solution on the following page.

ASSESS: Vestibulocochlear mapped

In all of the taxa, the vestibulocochlear n. (CN VIII) carries sensory information from the **vestibular system** to the brain. The vestibular system helps all vertebrates sense orientation and acceleration. So the most likely scenario is that this nerve evolved once at the base of the tree (point 1).

However, there are functions of this nerve indicated for mudpuppies and humans that are not indicated for sharks. In sharks and some other aquatic vertebrates, the vestibular system can also function in hearing by perceiving sound vibrations that are transmitted from the water into the body. However, for vertebrates that live in air (above water), a different type of hearing system is required because sound vibrations (i.e., waves) do not easily pass from the air into the body.

Amphibians (which are generally only partially aquatic) and mammals (which are generally terrestrial) have evolved different solutions to this. Amphibians, which includes mudpuppies, have a limited ability to detect sounds in air and these signals are carried by the vestibulocochlear nerve (Christensen et al., 2015). Humans and other mammals have evolved a specialized hearing system, the **cochlea**, which is also innervated by the vestibulocochlear nerve.

Since these functions are different, the most likely scenario is that this nerve gained functions at points 4 and 5 in the tree. However, since these functions involve the same nerve and auditory sensation, it's also likely that the vestibulocochlear n. of the most recent common ancestor of mudpuppies and humans (at point 2 in the tree) also had some kind of new function. So you could also add a gain in function for VIII at point 2 (indicated as "optional" by gray font).

Hypoglossal nerve (CN XII)

Complete the trait changes for the last nerve in the list: the **hypoglossal nerve (CN XII)**. Check your work against the solution on the following page.

ASSESS: Hypoglossal mapped

As was mentioned previously with the retractor bulbi muscle and abducens nerve, once vertebrates started feeding in air (as opposed to water), they had to find additional ways to move food into and through their mouth that didn't rely on being underwater all the time. One way is to use a muscular tongue to capture and transport food. Both the mudpuppy and human have a tongue that is at least partially muscular (the human tongue is entirely muscular while the amphibian tongue has a skeleton, derived from the posterior gill arches).

Despite the very different structure and function of these tongues, the tongue muscles of the mudpuppy and human are both innervated by the hypoglossal nerve (Anderson & Nishikawa, 1997). This nerve is considered a *spinal* nerve in amphibians because it emerges from the **central nervous system** (CNS) within the *spine* and a *cranial* nerve in humans because it emerges from the CNS within the skull. However, both nerves are thought to be **homologous**; that is, the hypoglossal nerve that is present in humans and in mudpuppies is the same nerve that is present in their most recent common ancestor, at point 2 in the tree.

Since this nerve is absent in sharks, it's most likely that the hypoglossal nerve evolved at point 2 in the tree.

Your story of cranial nerve evolution in vertebrates

You've now created a picture of *some* of the evolutionary changes in vertebrate cranial nerves (see the full, completed tree on the following page). Even though your tree only has three vertebrate taxa, only seven cranial nerves, and just a handful of the cranial nerve functions, it still captures many of the major evolutionary changes. If you were to explain the main takeaways of this evolutionary tree to someone, what would you say? What would you conclude are some of the principal narratives in cranial nerve evolution, based on the tree you just filled in?

Jot down at least three brief bullet points that you would use to construct your narrative on page 3 of your **Notebook**. If you get stuck, check out the hint on the next page.

HINT: Questions to spur ideas

If you're having trouble thinking of takeaways, answer one or more of the following questions:

- What are the different patterns of trait changes that you see at points 1-5 in the tree (including gains and losses of a structure and gains and losses of function)?
- Do two or more of the changes in cranial nerve functions have anything in common?
- Do evolutionary gains and losses of cranial nerves (e.g., the hypoglossal nerve, lateral line nerves) have anything in common?

References cited

- Bullock, Theodore Holmes, David A. Bodznick, and R. Glenn Northcutt. "The phylogenetic distribution of electroreception: evidence for convergent evolution of a primitive vertebrate sense modality." *How do Brains Work?* (1993): 581-602. DOI: 10.1007/978-1-4684-9427-3_46.
- Levine, Robert P., Jenna A. Monroy, and Elizabeth L. Brainerd. "Contribution of eye retraction to swallowing performance in the northern leopard frog, *Rana pipiens*." *Journal of Experimental Biology* 207.8 (2004): 1361-1368. DOI: 10.1242/jeb.00885.
- Anderson, Curtis W., and Kiisa C. Nishikawa. "The functional anatomy and evolution of hypoglossal afferents in the leopard frog, *Rana pipiens*." *Brain research* 771.2 (1997): 285-291. DOI: 10.1016/S0006-8993(97)00803-2.
- Christensen, Christian Bech, et al. "Better than fish on land? Hearing across metamorphosis in salamanders." *Proceedings of the Royal Society B: Biological Sciences* 282.1802 (2015): 20141943. DOI: 10.1098/rspb.2014.1943.