MAMMAL AND REPTILE SKULLS AS EVIDENCE FOR EVOLUTION BY NATURAL SELECTION I

LAB 2

(many thanks to Kathleen Smith for letting us borrow from several Biology 330L labs!)

INTRODUCTION

This week in lab we will continue our investigations of the evidence for evolution by natural selection by exploring how this process generates **adaptation, convergence** of distantly related species, and **divergence** of closely related species. Specifically, we will carefully examine the skulls of many different modern mammalian species and compare the structure and function of different skull traits, including aspects of their teeth and jaws. As we learned in class and in the plant lab last week, when we compare different living species in terms of their morphology, physiology, and behavior we often observe that some traits exhibit patterns of underlying similarity whereas other traits reveal specific patterns of differences. There are two basic ways that we might explain these patterns. For example, we might postulate that the similarities among species are due to a shared evolutionary history (common inheritance) whereas the differences are due to specializations (adaptations) to different environments. Alternatively, we might suggest that the similarities are due to convergent evolution in response to similar environmental conditions, whereas the differences are due to the species being only very distantly related to each other, with very different evolutionary histories. The only way to distinguish between these two hypotheses is to examine the patterns of trait similarities and differences in the context of a well-supported **phylogeny** (evolutionary tree) of the species that reveals their evolutionary relationships.

This week in lab we will also compare the characteristics of modern reptile and modern mammal skulls. As you will see, there are quite major, fundamental differences that are so striking that you'll be able to pick up any skull from these two groups of animals that you'd never seen before, and then be able to unambiguously tell whether it belonged to a reptile or mammal. The profound morphological differences between these two modern groups may appear at first to be incompatible with the Darwinian ideas that these two groups of animals shared a common ancestor and that they gradually diverged from this ancestor by incremental changes caused at least in part by natural selection. After thinking about how this major evolutionary transition might have occurred, next week we will examine casts of fossil skulls and detailed line drawings of fossils from long extinct species (from up to 350-400 million years ago!) that nonetheless exhibit both similarities and differences to modern reptiles or mammals. Working in groups, we will try to figure out what these fossils reveal about how the evolutionary transition from mammals to reptiles might have occurred, and whether it seems to have occurred according to basic Darwinian ideas.

This lab focuses on skulls for many reasons. First, skulls are highly complex, with lots of bones, teeth, and other structures and traits to examine and compare between species. Second, skulls contain many different functional systems, including features used for feeding and sensory perception, including visual, hearing, olfactory, and tactile (whiskers!) sensing, so that the overall skull anatomy may reflect many different adaptations. Third, because of the many potentially adaptive functional systems, skulls can often provide many clues about an animal's ecology, life history, and even behavior! Fourth, skulls and teeth are often very common and well preserved in the fossil record, so we can reconstruct evolutionary transitions. Skulls are just very cool, in and of themselves, and we hope that by the end of this lab you'll be an enthusiastic and skilled skull reader!!!

Exercise 1: Observation and comparison of modern mammal skulls

When you sit down you will find a number of mammal skulls at your table. Some of these skulls are natural bone, while others are casts, or plastic "bone clones." Ignore the differences in color, texture, material, etc. that are irrelevant for our purposes and just focus on the structural features of the skulls. **In all cases please be very careful when handling the skulls, as they are delicate and even the casts are very expensive.** Please always support the skulls carefully with your hands and do not hold them far above the table surface in case they fall!

Choose one skull and look at it. Take about 10-15 minutes to carefully observe and describe the critical features of the skull. For most of you this will be a new experience, and you may feel at a complete loss! Refer to the figure of a primitive mammal skull for the names of the major processes (projections of a bone that protrude from the rest of the bone) and skull features and to the list of "key questions in analysis of mammalian skull" from the last two pages of this handout (you may want to detach them for easier reference). The point is not to identify each of the elements, but instead to use this terminology as an aid to communication. It is easier to say "the coronoid process is small and pointed" than "the piece of the bone that seems to be sticking up from the back of the jaw bone is small and pointed." Don't worry about memorizing these names - - there will be plenty of time for that if you take Biology 330L or go to med or vet school!

While you should look at all aspects of the skull, please focus especially on the parts of the skull involved in feeding - - look especially closely at the **dentition** (diversity of teeth), **jaw joint** (how mobile is the jaw, and is the joint in line with the lower teeth, so the jaws close like scissors, or is the joint off set from the line of the teeth, so the from and back teeth come together at about the same time?), **shape of lower jaw**, including its processes, and the parts of the skull where the two major **jaw muscles** attach (the temporalis muscle attaches to the lower jaw along the coronoid process and to the brain case along the sagittal crest, whereas the masseter muscle attaches to the angular process on the lower jaw and the zygomatic arch of the skull - -

look at your skull figure to see where these features of the skull are, and don't try to memorize these technical names). Your main goal is to think about how the features of the skull reflect adaptations, especially to particular diets. Mammals are endothermic ("warm blooded") and need lots of food that can be digested rapidly - - **try to figure out how the structure of the skull affects its function, by enabling the animal to efficiently acquire (kill?!) and process particular types of food! What kind of food does your animal eat? Questions at the end of the lab handout will help you!**

Make descriptive notes on the skull specimen in this space:

After about 10-15 minutes, discuss the other skulls on your table with the other students at your table. First compare the skulls each of you have examined in detail, then look at the other skulls on the table. Finally, go to the other tables and look at the other skulls in the lab. Think about what these differences might mean in terms of the functional basis of the diversity that you see. Try to guess what each animal might eat based on its skull morphology and group together the ones on your table that you think eat the same things.

Finally, the entire lab will have a discussion about the skulls and how their structures relate to their function, especially in terms of feeding.

Exercise 2: Patterns of evolution of modern mammal skulls

Your instructor will give you cards that identity the species of the skulls and will hang a phylogeny of the mammals on the board. Any reconstructed phylogeny is a hypothesis of evolutionary relations, since of course we have not actually observed the full set of speciation events! Although phylogenies of many groups of organisms, including mammals, are rapidly improving with the increasing data from DNA sequencing projects, there is often some controversy about some of the relationships. This phylogeny is an approximation of several previously published phylogenies based on multiple gene sequence data sets, and it seems to be reasonably accurate.

Spend some time with the cards and the phylogeny. Identify the animals that you and your tablemates have looked at - - did you guess right? Does your knowledge of the identities of the skulls change your interpretation of the function of the various structures, especially those related to feeding? Discuss these issues with your tablemates!

Now that you have familiarized yourself with the skulls, add your cards to the giant phylogeny on the board using the colored tape provided by your TA. Now you should have two different arrangements of the skulls - - one grouping (of the actual skulls) is based on your criteria of similarity, while the other is based on the evolutionary relationships of the species.

These two arrangements should be different!!

Now, identify patterns that you think are examples of convergence. With your tablemates, look for skulls that seem to be similar based on some aspect(s) of skull morphology but are from species that are highly divergent (distantly related) according to the phylogeny. **Each table should come up with at least two examples of convergent evolution, and be prepared to explain these examples to the rest of the class. What are your reasons for feeling that the similarities of particular traits are due to convergence, as opposed to a recent shared evolutionary history? Think about the cases of convergence you've observed**

in lab today - - what kinds of adaptations might they illuminate? You and your tablemates will present your ideas to the rest of the class. You may also want to discuss how our approach to studying convergence this week (using phylogeny) compares to the more casual approach used in last week's lab with the greenhouse plants (where we didn't give you the phylogenies).

Exercise 3: Comparison of modern mammal and reptile skulls

Now that you have a good sense of the structure and function of the mammalian skull, its time to step back a bit and begin to think about how they evolved from non-mammalian ancestors. As a first step in grappling with these issues we will compare modern reptile skulls to the modern mammal skulls you've been studying. You will observe lots of differences in the skulls of the two groups, and while we have a somewhat limited group of reptilian skulls, you will notice quite a bit of variation among the different reptiles in terms the structural elements.

Each table will have at least one reptile skull. Working together as a table, examine the reptile skull and try to orient yourself. Try to answer each of the following questions, and jot down your answers. Feel free to make sketches if that will help you.

1. Start by trying to find the **brain case**! Where is it?!? Is it large or small, compared to the mammalian skulls? Are all of the bones in the rear of the skull encasing the brain? If not, what do you think their function is?

2. Now look at the mouth. Do you notice any **teeth**? If so, think about how they differ (if at all) from the mammalian teeth. Think about tooth structure, complexity, the closeness with which the teeth come together when the jaw closes, etc.

3.

Look at the lower jaw, and try to figure out if there is just one bone, as in the mammals, or more, that might be fused together, with a suture joining them together? How many **lower jaw bones** (per side) are there in your reptile skulls? Are they all fairly substantial in size, or are some larger than others (if you think there are multiple bones).

4. Look carefully at the **jaw joint**, and try to compare it to the mammalian jaw joints. Try to imagine how these jaws open and close. Try to figure out where the **jaw muscles** attach to the lower jaw and to the skull itself. Are there the sorts of processes or arches or ridges of bone that mammals have for their jaw muscles? Do you think these reptiles can manipulate their jaws from side to side, or front and back? Thinking about all of these features, do you think they can they chew their food?

5. Now look at the **nostrils** - - are there one or two openings in the skull?

6. Looking carefully at the **nostrils**, try to trace the passage that air might take as the reptile breathes. Does the air enter the underside of the skull into the front of the mouth, or towards the back of the mouth near the throat (and windpipe)?

7.

Now look at a mammal skull and compare its nostrils and air passage to that of the reptiles. Does either type of skull have a **secondary palate** in the roof of the mouth that separates the main part of the mouth from the air passage? Think about whether the reptile or mammal would be able to breath (safely) while it is eating. Under what circumstances do you think a secondary palate would be favored by natural selection? Finally, try to get a chance to examine the roof of an **alligator or crocodile's** mouth - - is it more similar to the other reptiles or to the mammals? Why do you think it is or is not similar? What might be the adaptive significance of the structure of its roof of its mouth? (this is cool!)

You and your lab mates will share your ideas in a brief discussion. First discuss how the reptiles and mammals skulls differ in **structure**, then discuss the potential adaptive or **functional** significance of these differences.

As part of the discussion, try to speculate on which aspects of the mammal and reptile skulls are **ancestral** (appear similar to the traits in the common ancestor of the reptiles and mammals) and which appear to be **derived** (evolved more recently than the divergence of reptiles and mammals from their common ancestor). Are you basing these speculations on anything, or is it just a guess (ok, you probably remember from lecture!).

KEY QUESTIONS IN ANALYSIS OF MAMMALIAN SKULL

Describe the dentition.

- How many teeth of each tooth class (incisor, canine, premolar molar) are there? Are there major modifications from the primitive condition?
- Are major sets of teeth lost, or modified?
- Is there a diastema (a large gap between sets of teeth)?
- Examine the morphology of the molars. What kind of molars do you see – crushing, blade-like or multi-sheer surface or, is molar morphology unlike any of these three major types?
- What kinds of jaw movements are necessary to properly occlude the teeth (straight up and down, side to side, or anterior and posterior?).
- Is there a very tight occlusion or do movements between the upper and lower teeth seem to be important?
- Can the molars be occluded (brought together as the jaw closes) at the same time as the incisors? Do both sides of the jaw occlude simultaneously?
- Look at the jaw joint. What kind of movement does it allow?
- What kind of food/material would you think the molar would be particularly well-adapted to process? Look at other teeth.
- Can you identify any particular specializations of the incisors? Is the canine big? Are the premolars molarized?

Look at the skull as a whole.

- How heavy is it?
- Does it have any big bulges or processes? Is there a big sagittal or nuchal crest?
- How big are the orbits for the eyes? Are they oriented towards the front or the side?
- How big does the nasal cavity seem?
- How big is the brain?

Reconstruct the origin and insertion of the masseter and temporalis.

- Look for hints on the skull that can provide you with clues to the anatomy such as muscle scars, enlarged crests or processes.
- Examine the general shape of the jaw – does it have a big angle, a high coronoid process?
- Where is the bite point? What is the functional effect of having a bite point that is far back on the jaw vs. one that is further forward?
- Which of these two muscles, the masseter or the temporalis, do you think is the most important? Are they equal? Are they both reduced?

The illustrations below are of a skull that is probably fairly similar to the primitive condition for therian mammals. Don't worry about memorizing any of this terminology now, however, you can use these terms as you describe your study skulls. The drawings are from Wible, J. R. (2003) Annals of the Carnegie Museum (vol 72, no. 3, pp. 137-202)