Evolving the Concept of Homology

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Abstract: Understanding homology is fundamental to learning about evolution. The present study shows an exercise that can be varied in complexity, for which students compile research illustrating the fate of homologous fish skull elements, and assemble a mural to serve as a learning aid. The skull of the most primitive living Actinopterygian (bony fish), the bowfin, *Amia calva,* is the starting point for tracing the evolutionary fate of homologous bones in other living and extinct vertebrates. By tracing bone fates through time and across lineages, students learn both their names and association patterns. Emphasizing bone group associations, structures and functions replaces memorization of names, while facilitating understanding of evolutionary processes that shaped complexes and the vertebrates in which they occur. Working in groups, students learn cranial ossification patterns from fish to amphibians, reptiles, mammals and birds that might otherwise seem unpredictable or unrelated to natural selection. Goals of this project include clarifying evolutionary processes, relating complex structures to functions, and assisting students in gaining a deeper understanding of features that define vertebrate anatomical relationships.

Keywords: Homology, evolution, vertebrates, fossils, comparative anatomy

Introduction

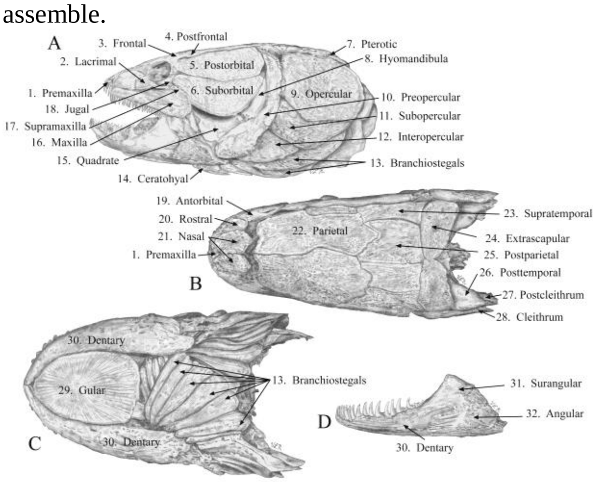
One of the most fundamental concepts underlying student understanding of the theory of evolution is homology, a term coined by Sir Richard Owen in 1848, which discusses the structure of the skeleton in vertebrates (Owen, 1848). Homology may be defined simply as organs or body parts that arose from a common origin, but may have diverged in appearance, function or both over time. Yet students often have difficulty in grasping the implications of this idea. An excellent means of illustrating complex concepts is to show examples that reveal their meaning. Such examples are even more instructive when students identify them using their own resources, by developing their own ideas while doing research on topics they have chosen.

In teaching organismal components of courses ranging from introductory biology and zoology and those for which the main focus is exposition of evolutionary processes, such as comparative vertebrate anatomy, evolution, vertebrate paleontology and natural history, it is essential to convey the role the theory of evolution plays in allowing scientists to predict and interpret the relationships between living and extinct taxa. Evolution serves as a way of explaining relationships of living organisms as they change through time (succinctly defined as descent with modification). It is essential for those engaged in teaching science, especially evolution, to ensure that students learn both the precise language of evolutionary theory, and how to interpret correctly the complexities inherent in the understanding of concepts such as homology, natural selection and phylogeny. Moreover, a true understanding of these important biological concepts requires a person to be able to apply them to examples from the fossil record and living organisms. This is one definition of critical thinking, a skill all students must master to enable them to evaluate the quality of information from all sources, and a main goal of education across all subjects and at all levels.

Therefore, this study proposes an innovative method of teaching homology, a fundamental concept inherent to an understanding of evolution. The exercises described here allow students to interact among their own groups to discover how patterns change through time, using a study of the skull bones of fishes. Many courses in organismal biology require students to learn about the skeletons of animals. This is often one of the first exercises that require students to learn a large amount of detailed anatomical information. This endeavor is often intimidating, and one of the reasons many students avoid progressing further into the study of science. If learning anatomical details can be combined with obtaining a deeper understanding of important concepts, students can gain a clearer perspective of evolution. The project described herein is designed to be flexible in the level of detail it requires as well as the number of participants that can be involved. It is aimed toward advanced placement biology classes in high schools, community college students or those taking a sophomore or junior level university course. The plan can be simplified for use at lower grade levels, or more complexity of research and presentation of information could be added to increase the level of effort required for more advanced class work.

The purpose of this project is to choose one of the 28 numbered ossification centers identified on the skull of *Amia calva* (Figure 1), and to trace its evolutionary fate from Actinopterygian fishes to other vertebrate groups. This fish has been chosen as the organism central to this project because the skulls of bony fishes have more bones represented as individual elements than do the skulls of other organisms. *A. calva* is the most primitive of the living forms, with the earliest fossils of related species found as early as the Devonian, over 400 million years ago, and therefore, shows one of the most primitive skull bone patterns that demonstrate skull element relationships.

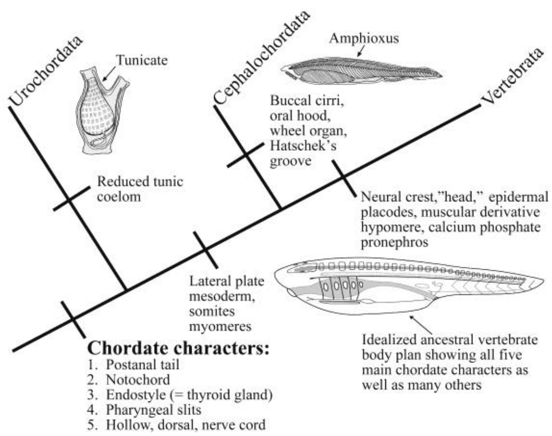
Figure 1. The skull and mandible of *Amia calva* are shown in lateral view (A) and ventral view (C). The skull only is shown in dorsal view (B). The mandible alone is shown in D. All bones are labeled and numbered in each view. This figure serves as the template around which students will assemble the collective table of bone homologies. Bone numbers correspond to spaces on the table students will assemble.



Background

Vertebrates differ from other living organisms, particularly in their degree of cephalization (i. e., evolution of a head), or the specializations of the anterior part of their bodies to concentrate and protect the organs of special sense, including the visual, olfactory and auditory systems. One early specialization prior to the evolution of vertebrates is the expansion of the anterior end of the hollow, dorsal nerve cord into a brain. The anterior aspect of the bodies of early protovertebrates also acquired specializations for feeding, such as ingesting and processing foods (Figure 2). Most of the early animals belonging to this lineage went extinct without leaving fossils for study; therefore, the characters that illustrate the evolutionary pathway leading to chordate and vertebrate origins have been reconstructed using comparisons to living organisms that show some of these traits. As living species are not necessarily adapted to the same ecological niches as ancestral protovertebrates, they may show only some of the chordate or early vertebrate characters, or in only a part of their life stages. For example, the Urochordata are represented by a group of organisms called tunicates, animals that exemplify some of the characters that were present in the lineage that evolved into the chordates and vertebrates. Because these characters are present in only the larval forms, these animals are not merely earlier versions of chordates or vertebrates. Another group, the Cephalochordata, show a greater number of characters of the Vertebrata, and are exemplified by *Amphioxus*, the lancet, a small, aquatic filter-feeding organism that shows the five main chordate characters as well as others that occur in vertebrates. However, *Amphioxus* also shows unique derived characters not present in vertebrates, indicating they are closely related, but not directly ancestral to this group. No fossil has yet been found that shows all of the characters that must have been present in early vertebrates, and none that preclude it from being the ancestor; therefore the "idealized" ancestral vertebrate body form is shown in the lower right side of Figure 2.

Figure 2. Cladogram of protovertebrates, chordates and early vertebrates that depict examples of a species of each group, or an idealized hypothetical ancestral body form. The cladogram nodes show where the diagnostic vertebrate characters appear for the first time.



The skull and mandible of *Amia calva* are shown in lateral view (A) and ventral view (C). The skull only is shown in dorsal view (B). The mandible alone is shown in D. All bones are labeled and numbered in each view. This figure serves as the template around which students will assemble the collective table of bone homologies. Bone numbers correspond to spaces on the table students will assemble.

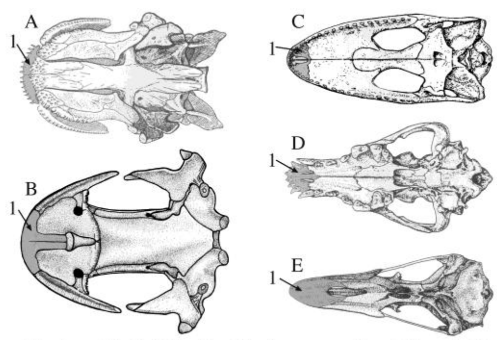
Only under unusual circumstances does the fossil record preserve impressions of soft tissue of long dead animals; more commonly skeletal and dental elements, i. e., the "hard parts" are the only evidence that an individual animal existed. Therefore, skeletal structures are foremost among those that must be studied by students of vertebrate biology. As early as the Cambrian, nearly 600 million years ago, organisms had skeletons to support and protect delicate internal structures, but also to serve as levers for muscles to pull against in performing locomotor and other life functions. Some animals had cartilaginous skeletons; ossified cartilage skeletal elements may be preserved, but most of the bones that make up bodies of fossils are bone, i. e., calcium carbonate ($CaCO_4$). Bony skeletal elements arise from two sources, dermal bones from layers of the skin, and endochondral bones from mesoderm that also gives rise to the skeletal or voluntary muscles. Both of these types of bony elements occur in the skull, although they often cannot be distinguished based on appearance of the adult bone. Nevertheless, the developmental history of these bones can provide clues as to their location and function in the skull. Bones arise at ossification centers, and the number of these determine how many bones form the skull of a vertebrate. Through time, and as cranial structures and functions evolve, ossification centers may change, which results in the loss or fusion of bones.

Procedure

1. For each bone, the student must identify:

A. The main function of the bone itself and those of any group to which it belongs, in *A. calva* as well as its function in representatives of all other vertebrate groups in which it occurs. Those functions must be demonstrated by making a chart or using bullet points for each taxon discussed. An example of the fate of one bone, the premaxilla, is illustrated in Figure 3.

Figure 3. An abbreviated discussion of the evolutionary fate of the premaxilla in (A) the fish *A. calva*, (B) an anuran, *Ambystoma maculatum*, (C) a reptile, *Alligator mississippiensis*, (D) a mammal, *Canis dirus* and (E) a bird, *Anas platyrhynchos*, is shown as an example of the kinds of information students can find and present in their posters. At the bottom is an explanation of the differing forms and functions of this bone in these animals.



The bone labeled 1 in A - E is the premaxilla. Although this bone does not change as drastically in shape and function as do some other bones of the skull, it bears teeth in A (*Amia calva*), C (*Alligator mississippiensis*) and D (*Canis dirus*) but not in B (*Ambystoma maculatum*) and E (*Anas platyrhynchos*).

B. All of the bones that abut the chosen bone, including those that may lie superficial or deep to it. A list of these bones, properly identified and labeled, or an image of the chosen bone and those surrounding it, must be included.

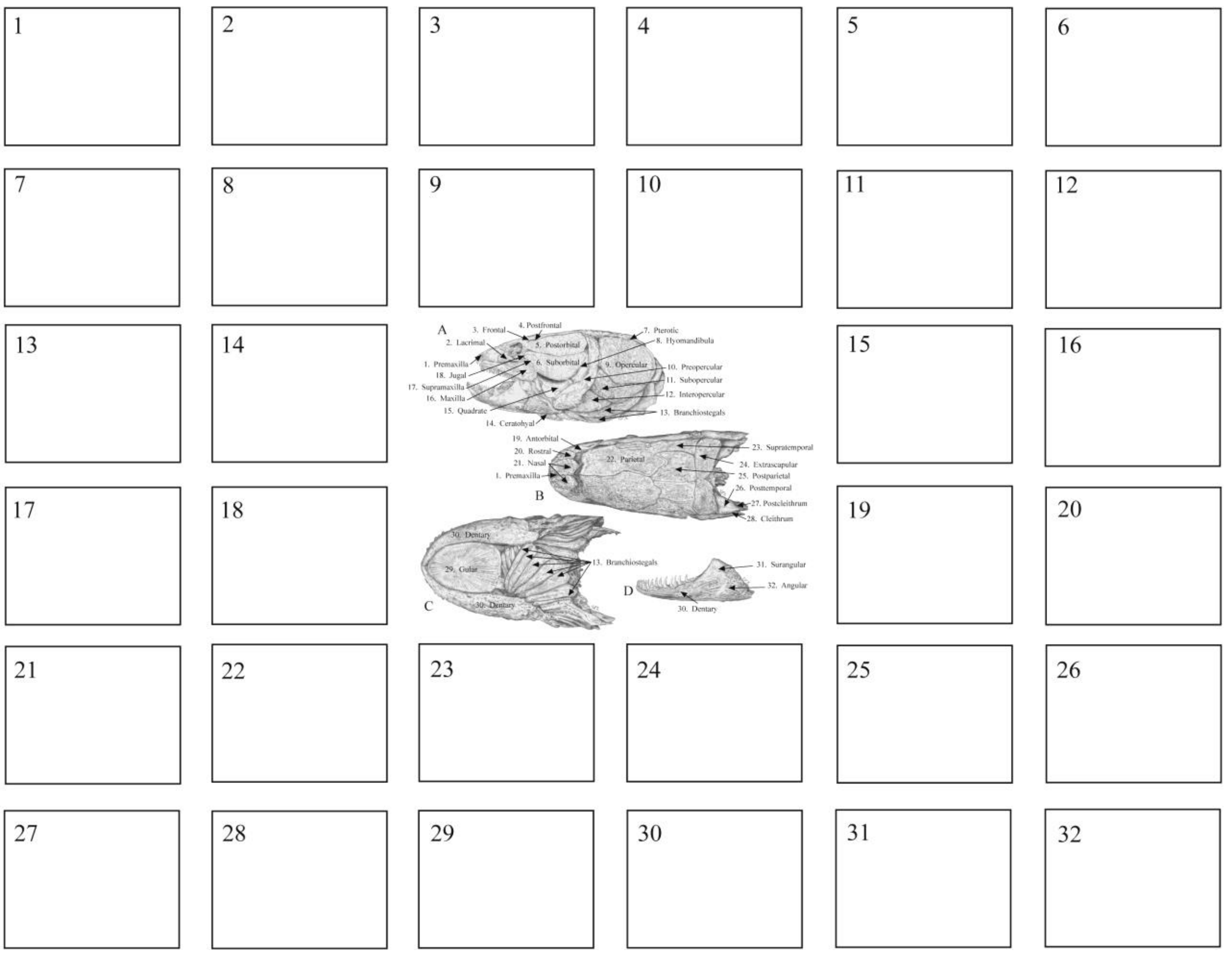
C. The function of the group to which the bone belongs, as well as the other bones that serve the same function within the group. It is important to note here, if the group, or one of the bones that belongs to it, changes function, and if so how that change occurs. In some cases, although a bone may be part of a complex, and to share in that group function, it may take on a unique function in other groups. All of these differences must be documented individually with labeled images and descriptions.

2. Note any bones that have been lost, or have coalesced with those of other ossification centers, and the groups in which this has occurred.

3. Prepare an 11" x 17" poster documenting the chosen bone(s). Specifically, the bone must be depicted in *A. calva* and its function in this organism explained, including the information from items 1-4. In the chart,

images of the other taxa in which the bone has been traced, accompanied by an explanation of the function(s) of each must be included. At the bottom of the poster, must be placed a chart summarizing the bone, any group(s) to which it belongs and the functions it assumes in vertebrate groups represented by *A. calvo* (bony fish), amphibian, reptile, mammal and bird (Figure 4).

Figure 4. A sample template for assembling the table of bone homologies among different vertebrate taxa with numbered spaces that correspond to the bones named in the central illustration of *Amia calva*. The sample entry, for the premaxilla (number 1) to be placed in the upper left was presented in Figure 3.



4. In class each student or group that worked together to determine the fate of a bone will present their results orally, explaining their findings concerning the fate of the bone or bones they have chosen. After each presentation the individual posters will be assembled into a large table with numbered spaces for each bone, which correspond to those on the central image of *A. calva* (Figure 4). The assembled table will serve as a review of skull bones in many vertebrates, as well as a means to illustrate the concept of homology, as a means of promoting student comprehension of the fundamental concepts that explain the theory of evolution.

Modifications of the project for middle school and introductory high school classes.

The project, as described, is aimed toward college level or university students in classes such as comparative vertebrate anatomy, vertebrate paleontology or evolution. To streamline the project for earlier level classes studying the concept of homology, students can be asked to limit the number of taxonomic groups they study in determining the fate of each bone, or the fates of only the more prominent bones in later groups can be traced. Descriptions of the function(s) of bones can be limited in length, and students can give short oral reports or omit this step entirely. To assist introductory students in preparing their posters, teachers can provide images or reference materials to limit the amount of research class members must undertake individually.

Modifications of the project for advanced high school, college or university classes.

Students could be asked to investigate the evolutionary fate of more than one bone or group of bones in the skull of *A. calvo* and other vertebrate groups. Students could also be required to write a paper that describes the changes in the evolutionary fate of the bone or bones among vertebrate taxa, to delve into the history of the development of information about each bone, and to provide the rest of the class with a detailed presentation on their findings. These students could also be asked to discuss the developmental origins of the bones, and structures that may be derived from them, such as the teeth that are rooted in many bones of the skull and mandible.

Conclusions

Regardless of mode, people learn best when they discover information for themselves, and therefore have invested more effort in its acquisition and can thus "claim" the knowledge as their own. This project will allow students to do that, as well as to understand the concept of homology, and to relate it to evolutionary interpretations of cranial bone structures and functions in different vertebrate taxa. This project allows students to work both singly and in groups, and to conduct individual and group research to create a chart collectively, that will serve as a learning tool for their class and subsequent classes. Instead of forcing students to memorize bone names, this project will allow them to make the association between bone structure, position and function within the skull and how each of those bones transforms in shape and function through time in different taxa as a means of meeting the selective pressures on different vertebrate groups.

Suggested Readings

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Acknowledgments

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