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Photos to phylogenies: A scavenger hunt to explore the tree of life

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Abstract

The evolutionary biologist Theodosius Dobzhansky famously stated that "nothing makes sense in biology except in the light of evolution" (Dobzhansky 1973). Because phylogenies represent evolutionary relationships, they are critical for biology students to understand; however, phylogenetics can be a dry and difficult subject, and its applicability to everyday life can be unclear. The laboratory activity presented here introduces students to the foundations of phylogenetics, sends them outdoors to document local species, and asks them to build, correct, and map character state changes onto trees of their observed organisms. This activity empowers students to actively engage with phylogenetics and conceptualize its relevance to the world around them.

Keywords: phylogenetics, biodiversity, parsimony

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INTRODUCTION

All organisms on Earth today descended from one last universal common ancestor (LUCA; Glansdorff et al. 2008). Evolutionary divergence has produced the tremendous biological diversity that draws many high school and college students to the life sciences. It has also shape the genetic sequences that underlie biochemical pathways and medically important traits making it a relevant topic for students interested in both the organismal and molecular sides of the biology curriculum. While most students can intuit this process of descent with modification, many struggle with phylogenies that illustrate evolutionary relationships. However, an understanding of evolution is incomplete without proficiency in phylogenetic analysis (O'Hara 1988).

Teaching phylogenetics in high school and undergraduate biology classrooms presents numerous challenges. Baum and Offner (2008) describe struggles that students often encounter when analyzing phylogenetic trees, including confusion about different tree shapes, not knowing how to assess evolutionary relatedness among taxa at tips, and misunderstanding where ancestral populations/species are located. Constructing trees and using parsimony to map character state changes are additional hurdles for students, and while effective activities have been designed to improve mastery of these tasks, misconceptions remain common (Young et al. 2013, Smith et al. 2017). Finally, piquing students' interest in phylogenetics can be difficult, as they may not easily recognize its relevance to their everyday lives.

To address these challenges, I designed and implemented a ~180-minute lesson, which can be divided into multiple shorter periods as necessary. In the first phase (introductory lecture), students receive basic instruction on phylogenetics, which includes a lecture that is broken up by problem-solving activities. In the second phase (outdoor excursion), students go outside to photograph local biodiversity, and use iNaturalist to identify the organisms in their pictures. In addition to giving students a break from the traditional classroom setting, this outdoor excursion can introduce them to campus green spaces, the use of which can improve their perceived quality of life (McFarland et al. 2008). In the third phase (tree-building and analysis), they return to the classroom and work in progressively larger groups to sketch hypothetical trees based on easily observable morphological traits. They also search peer-reviewed literature for published phylogenies, which they use to correct their morphology-based trees. Finally, students apply the principle of parsimony to map character state transitions onto their corrected trees. Through these activities, students discover how to interpret and create phylogenies, reinforce their knowledge through active learning exercises, and see the relevance of phylogenetic analysis as they apply it to species in their everyday environment.

STUDENT OUTLINE

Objectives

Explain the evolutionary relationships indicated by a phylogenetic tree
Explore a local outdoor environment and discover its biodiversity
Use iNaturalist to identify organisms from photographs
Build a phylogeny based on easily observable characters
Add or remove taxa from a phylogeny while maintaining the correct branching pattern
Employ the principle of parsimony to map character state changes onto a phylogeny

Introduction

The Structure and Interpretation of Phylogenies

All life on Earth today can trace its ancestry back to a last universal common ancestor, which existed billions of years ago and is otherwise difficult to characterize (e.g. Glansdorff et al. 2008). With millions of species alive today, disentangling their evolutionary relationships can be difficult; however, analyzing evolutionary relatedness and diversification is critical for understanding biodiversity, adaptation, biochemical processes, and physiology. **Phylogenies** are tree-like structures that illustrate the evolutionary relationships among **taxa** (groups of organisms) and their diversification from common ancestors. Therefore, phylogenies also indicate the passage of evolutionary time (Figure 1A). In rooted phylogenies, the **root** (oldest part) of the tree is a single **branch** (or line representing an evolving taxonomic group) leading to a **node** (or point of divergence) from which all other branches diverge. The first branch to diverge from the earliest node in the tree leads to the **outgroup** to all other taxa in the phylogeny. Throughout the rest of the tree, branches split at nodes; this represents the divergence of two groups from a common ancestor. At the ends of **terminal branches** (the last branches in the tree) are **tips**, which represent the taxa whose relationships are being shown (Figure 1B). Two or more taxa belong to a **monophyletic clade** if their common ancestor and all of its descendants are also considered. In contrast, a **paraphyletic clade** includes an ancestor and some (but not all) of its descendants, while a **polyphyletic clade** includes some taxa but does not include their common ancestor or other of its descendants (Figure 1C). While trees may have different shapes or orientations, their basic structure is the same.

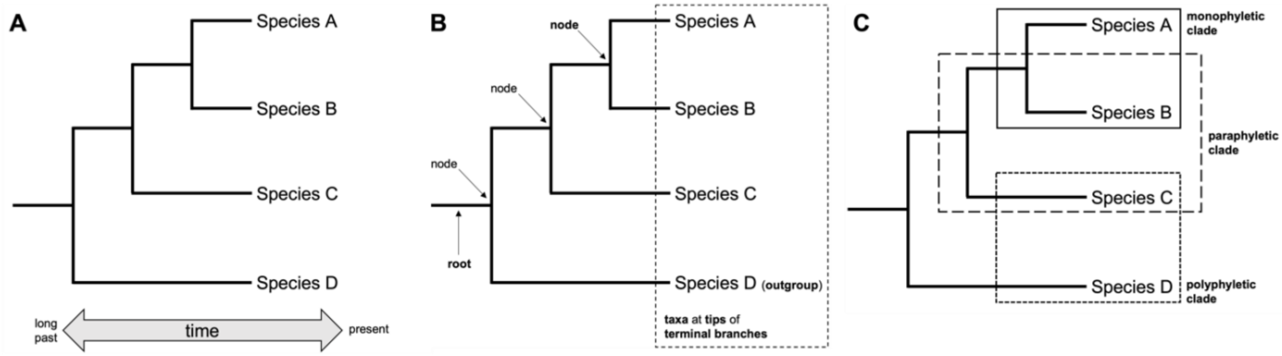

Figure 1. The fundamental structure and components of a phylogenetic tree. A phylogeny illustrates the evolutionary relationships among organisms by showing divergences from common ancestors over time (A). The oldest branch in the tree is the root; it leads to a node representing the common ancestor of all the organisms, or taxa, whose relationships are illustrated. The first taxon to diverge is the outgroup; along with it, an internal branch splits from the oldest node in the tree and later diverges further and gives rise to the remaining taxa. The names of taxa are indicated at the tips of the tree (B). A monophyletic clade, or an ancestor and all its descendants, is shown in a solid box. A paraphyletic clade, which includes an ancestor and some of its descendants, is indicated in a dashed box. A polyphyletic clade, or taxa without their common ancestor or other of its descendants, is shown in a dotted box (C).

When an ancestral branch diverges into two (or more) at a node, the placement of one descendent branch relative to the other(s) is arbitrary. For example, consider a phylogeny with a root on the left, horizontal branches, and tips on the right. To the right of each node, either descendent branch can be placed above the other; their relative vertical order does not change the relationship indicated. Rather, only the pattern of divergence from common ancestors illustrates relatedness. Two taxa are more closely related if they share a younger most recent common ancestor (MRCA), meaning that their MRCA is further away from the root of the tree. Similarly, two taxa are more distantly related if their MRCA is older, or closer to the root of the tree (Figure 2).

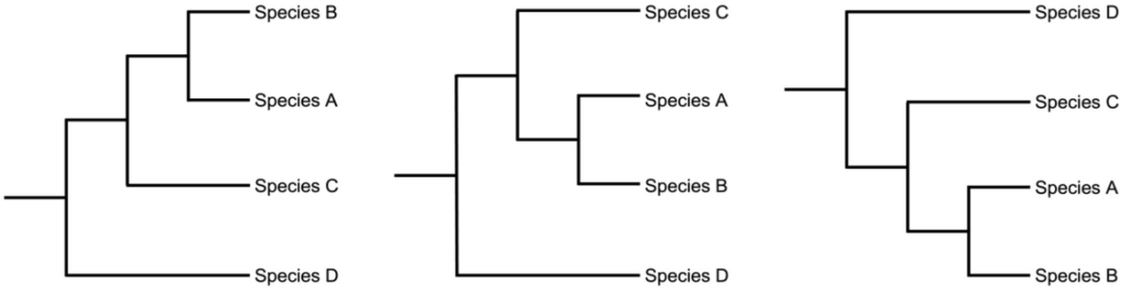

Figure 2. Despite different vertical orientations of the branches, these three phylogenies illustrate the same evolutionary relationships as the trees in Figure 1. Species A and B share the most recent common ancestor, meaning they are closest relatives. Species D diverges earliest, so it is the outgroup to the other taxa. Note that the node from which species A and B diverge is the furthest in time from the root, and the node from which species D diverges is closest to the root.

How Do We Know Who is Closely Related to Whom?

Several types of evidence can be used to reconstruct evolutionary history and depict it in a phylogeny. However, different types of evidence may suggest different relationships, so not all phylogenies are completely correct. Phylogenies may be based on morphological, developmental, physiological, and/or molecular (DNA and/or protein sequence) characters, or a combination of these. Accurate phylogenies are usually constructed with the use of many different characters (Larson 1998). This is because processes such as **convergent evolution** - by which similarities evolve independently in separate taxa rather than being passed down from a common ancestor - can cause one or a few characters to indicate incorrect relationships.

While molecular data are now much more widely used than morphological data, for the sake of simplicity, consider an example dataset of three species and three morphological characters. Without knowing any further information about the three species, we can construct three different trees that represent their possible relationships. Species 1 and 2 could be closest relatives with species 3 as outgroup, species 1 and 3 could be closest relatives with species 2 as outgroup, or species 2 and 3 could be closest relatives with species 1 as outgroup. To evaluate these three possible trees, we need to consider characters. For this example, consider the ancestral state - or the state of all three characters in the MRCA of all three species - to be the absence of all three traits. Species 1 has no endothermy, wings, and no hair. Species 2 has endothermy, no wings, and hair. Species 3 has endothermy, wings, and hair. To summarize these data, we need to construct a **character matrix**, in which taxa are represented as rows, and characters are represented as columns. In this character matrix, a 0 indicates the absence of a trait, while a 1 indicates the presence of that trait (Table 1).

Table 1. Character matrix for three species.

Taxon	**Endothermy**	**Wings**	**Hair**
Species 1	0	1	0
Species 2	1	0	1
Species 3	1	1	1

To evaluate our three competing trees (Figure 3A), we can apply the principle of **parsimony**, which tells us to choose the tree that necessitates the fewest **character state transitions**. In our example, this means the gain of a trait, since the ancestral state is the absence of all three traits; however, losses can also be considered character state transitions. For the tree in which species 1 and species 2 are closest relatives, and for the tree in which species 1 and 3 are closest relatives, we need a minimum of two independent gains of endothermy, each in a terminal branch. If species 2 and 3 are closest relatives, we just need one gain of endothermy in the internal branch leading to the common ancestor of these two species. Thus, for endothermy, the tree in which species 2 and 3 are closest relatives is the most parsimonious. This tree is also the most parsimonious when we consider hair. However, when we consider wings, the tree in which species 1 and 3 are closest relatives is the most parsimonious (Figure 3B). To determine the most parsimonious tree overall, we add the number of state changes necessary for each character and in each tree. The tree in which species 2 and 3 are closest relatives is the most parsimonious overall, because it only requires four total character gains (Figure 3C).

While we would need more information to draw conclusions about wings, it is possible that convergent evolution explains their presence in species 1 and 3. This discrepancy in parsimony between endothermy/hair and wings highlights the importance of using multiple characters to build phylogenies. Furthermore, molecular data are prioritized over morphological data for building accurate phylogenies because they provide vast amounts of information; a sequence alignment is a matrix in which each nucleotide or amino acid is an individual character. Furthermore, DNA sequences are directly transmitted from parents to offspring, and molecular sequences are less affected by convergent evolution than morphological characters are (Zou and Zhang 2016). Later in this lesson, you will compare morphology-based trees against sequence-based trees.

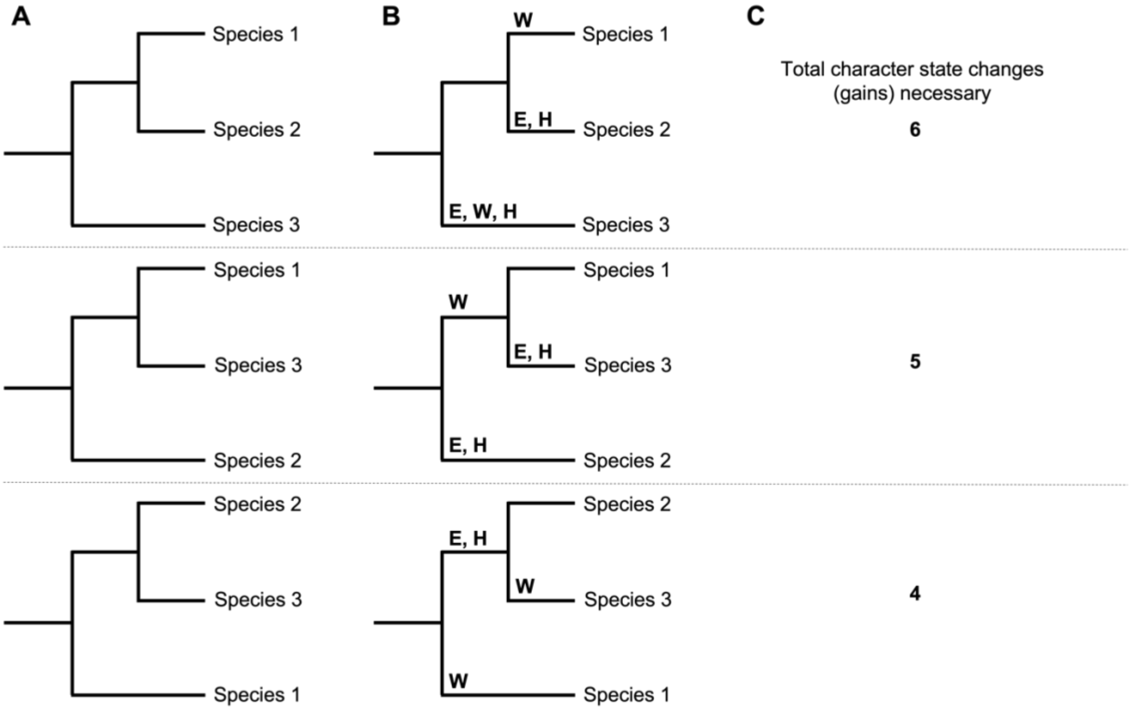

Figure 3. The relationships among any three species can be represented by one of the trees shown in A. If we consider the character matrix in Table 1 and apply the principle of parsimony, character state changes must be mapped onto each tree as indicated; E = endothermy, W = wings, H = hair (B). To select the most parsimonious tree overall, all necessary character state changes are added together; the tree with the fewest is the most parsimonious (C).

iNaturalist and Getting Outdoors

In this learning activity, you will download the iNaturalist or Seek app to your phone. (Seek performs similarly to iNaturalist but allows for greater privacy/anonymity by users; iNaturalist allows users to share their observations quickly and easily with a worldwide community.) You will then be assigned a taxonomic group and sent outdoors with a small team to find and photograph members of it. After a predetermined amount of time, you will return to the classroom for tree-building exercises.

Methods and Data Collection

Note: Before following the methods listed here, you should complete phylogenetics practice problems on an assigned worksheet to reinforce your understanding of tree-building and interpretation.

Part A: Documenting Local Biodiversity

After you have been assigned a team and a taxonomic group, go outdoors, and start looking for organisms! When you find a member of your assigned taxonomic group, photograph it, and use iNaturalist or Seek to identify it, at least to the family level. (Seek identifies organisms from live views, but you will be required to submit photos of the organisms you find, so be sure to take pictures regardless of what app you use.) While you may be tempted to collect photos outdoors and use an identification app after returning to the classroom, it is important to complete your identifications in the field, as these apps will likely be unable to identify organisms in some photos/views. You should ensure that you have the required number of identifiable photos before returning to the classroom.

Part B: Building and Analyzing Trees

When you return to the classroom, find a spot on the whiteboard to list all of the species (or families) your team observed from your assigned taxonomic group. You may need to refer to your photos throughout the rest of this activity, so be sure to have them handy on your phones. You will also need to record your responses to the following prompts on a team worksheet.

Part B1: Creating a Character Matrix and Building a Morphology-Based Tree

Identify at least three easily observable characters in the organisms in your photos. Create a matrix to record the state of these characters for all of your identified species/families. If you cannot determine the state of these characters in each photograph, you may use the internet to fill in the gaps. For this exercise, you may move beyond the presence or absence of morphological features and include more variable traits like color, diet, behavioral characteristics, etc. Record your character matrix on your team worksheet.

Now, choose one of your three characters, and use it to sketch a hypothetical parsimonious phylogeny on the whiteboard. You do not have to fully resolve the phylogeny at this point. In other words, the character you choose should give you some clues about the relatedness of your species, but you may show more than two branches diverging from a node if you cannot fully determine the relationships of the descendants. After you have sketched your tree, map changes in the state of your chosen character onto the phylogeny. Sketch your tree and its mapped character state changes on your team worksheet or include a photo of your work from the whiteboard.

Part B2: Interpreting Published Phylogenies and Applying Them to Selected Species

Most phylogenies published today are based on molecular data and include many more taxa than the exercises in this lesson have. And because different sequences can evolve in different ways, not all published phylogenies agree with one another. In this section of the activity, you will search a database of peer-reviewed papers for published phylogenies that include your photographed organisms. Then, you will use the information from these published phylogenies to reconstruct the tree that includes just the organisms you observed. While these published phylogenies may not use the exact taxonomic terms you have assigned to your photographs, your objective is to find one or more that provide enough information for you to redraw a fully resolved tree of the organisms you have observed.

First, select a database (Google Scholar works well for this activity), and search for published phylogenies. If you have trouble finding what you are looking for, try different search terms (e.g. “insects phylogeny,” “evolutionary relationships of insects,” “tree of insects + molecular data,” etc.). Cite any sources that give you useful information on your team worksheet. Now, based on the sources you have chosen to cite, redraw your tree from part B1 such that it is based solely on published sequence-based phylogenies. Be sure to sketch the redrawn tree on the whiteboard (this will be important for part B3) and include the redrawn tree (or a photo of it) on your team worksheet. Note any differences between it and your morphology-based tree from part B1.

Part B3: Combining Trees

Your work in part B2 may have required you to synthesize information from multiple published trees into one that only includes your photographed organisms. If so, you already have practice with the skill you will use here. First, join with one another team in your classroom. Use both of your phylogenies from part B2 to create a single, larger tree that includes all of your photographed organisms. Sketch this tree on the whiteboard and include it (or a photo of it) in your team worksheet. Finally, based on your trees from part B2, create a phylogeny that includes all of the organisms documented by the entire class, and map the origin of at least three morphological traits onto it using the principle of parsimony. You may need to return to peer-reviewed papers for this. For example, if you are combining three trees that show the relationships among seven mammals, seven birds, and seven non-avian reptiles, you may need to consult published literature to determine how the mammals, birds, and other reptiles are related to one another.

Discussion

Throughout this activity, you have gained and practiced important skills in phylogenetic analysis, by which scientists determine and represent the evolutionary relationships among the tremendous diversity of organisms on Earth. First, you identified the parts of a basic phylogeny, and you learned how to interpret evolutionary relationships based on the divergence of branches from ancestral nodes. Next, you developed skills in constructing simple phylogenies. Before the advent of modern sequencing technologies, scientists relied on morphological characters as they estimated evolutionary relationships, and you gained direct experience with this as you created simple character matrices and used them to build trees based on parsimony. You also learned that not all similarities indicate common ancestry; convergent evolution can cause similar traits to evolve independently in different taxa. For this reason, most trees are now based on molecular data, which are also advantageous because DNA/protein sequences provide many characters, and DNA is directly transmitted from one generation to the next.

As you now know, phylogenies show the evolutionary relatedness of the incredible biodiversity in our world. In the second part of this activity, you directly observed, identified, and photographed local biodiversity, and if you used iNaturalist, you contributed to a worldwide repository of organismal observations. Importantly, you explored the outdoor spaces on your campus, the regular use of which may improve your perceived quality of life as a student (McFarland et al. 2008). Finally, you applied phylogenetic analysis to the local species you observed, creating a morphology-based tree on the principle of parsimony. You also searched peer-reviewed papers for published phylogenies that include your observed taxa, and you practiced combining and/or trimming them as you used them to create a corrected tree of your species. You also practiced building progressively larger phylogenies as you combined your tree with another team's and then with the entire class. Through the completion of all these tasks, you have built a solid understanding of the interpretation and creation of phylogenetic trees.

If phylogenetics is particularly interesting to you, there are many research questions you can use it to address. Because modern phylogenetic analysis usually relies on sequence data, the first step in carrying out phylogenetics research is to learn how to select, collect, align, and analyze DNA or protein sequences. Different tree-building methods have been developed, and most are more complex than the parsimony method you employed here. Because of the size of molecular datasets and complexity of tree-building methods, computer programs are usually used for the alignment, analysis, and tree creation steps. Even with molecular sequences and sophisticated computational tree-building programs, uncertainty may remain in the overall structure of the resulting trees. For this reason, tree-building programs often provide support values or probabilities at nodes. For an introduction to molecular phylogenetics, see Yang and Rannala (2012).

In addition to examining the evolutionary relationships among species, you can also use phylogenetics to assess the evolutionary history of single genes, which may not perfectly match the evolutionary history of the species in which those genes were sequenced. Discordance between species trees and gene trees may be especially interesting. For example, although bats and dolphins are not closely related mammals, members of both groups use echolocation to find food and navigate their environments. A phylogeny based on sequences of a protein called Prestin puts bats and some dolphins into a monophyletic clade, and individual amino acid sites within the Prestin protein seem to have independently evolved similarities in bats and dolphins. Although a phylogeny based on Prestin does not reflect true species relationships, it illustrates an amazing case of molecular convergent evolution, which underlies the convergence of echolocation in two very different mammalian taxa (Liu et al. 2010).

Finally, phylogenetics has important real-world implications, including conservation, the study of viral evolution, and even the solving of crimes. For example, when setting conservation priorities, scientists can calculate phylogenetic diversity of taxa and then target those with the greatest diversity for protection (Faith 1992). In the face of infectious disease outbreaks, phylogenetics can be used to show how pathogen populations are spreading and changing over time, as has been done for Ebola and COVID-19 (e.g. Holmes et al. 2016, Gómez-Carballa et al. 2020). Phylogenetic evidence has even been used in court to demonstrate patterns of human immunodeficiency virus (HIV) transmission, showing, for example, that a doctor intentionally injected a nurse with HIV-positive blood (Vogel 1997, Oliveira et al. 2020). These important applications of phylogenetics show that its utility goes far beyond the representation of historical evolutionary relationships. Phylogenetics can be used to protect species and ecosystems more effectively, to provide critical information on rapidly spreading infectious diseases, and even to deliver justice for victims of crime and their families.

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MATERIALS

Students will record answers to practice problems, insert photographs of their organisms, and sketch a character matrix and trees (or include photos of these as drawn on a whiteboard) on a worksheet throughout the activity. A worksheet and partial answer key are included as supplemental files. For the introductory lecture, slides covering the material in the Introduction of the Student Outline are recommended. For documenting local biodiversity, students need a phone with the iNaturalist or Seek app and a camera. For building and analyzing trees based on their photographed organisms, students need internet access, a whiteboard, and dry erase markers.

NOTES FOR THE INSTRUCTOR

The purpose of this lesson is to introduce students to phylogenetics and to green spaces on their college campus. Therefore, the exercises presented here are ideal for first- or second-year college biology students for whom phylogenetics is a relatively new concept and who may not have thoroughly explored their campus yet. The activities can be adapted for high school students, though, and they can also be used as a phylogenetics refresher for upper-level college students before they take a deeper dive into evolutionary biology. Throughout this lesson, instructors may find opportunities to expand upon the concepts and activities presented. For example, as students use peer-reviewed literature to correct their morphology-based trees (part B of the student outline), instructors may want to discuss why different molecular datasets produce different trees, what branch lengths mean, and what distinguishes various tree-building methods (e.g. maximum parsimony, neighbor-joining, maximum likelihood, Bayesian, etc.). Instructors may also wish to have students collect a few DNA sequences from a database and use an online tool to align them (e.g. https://www.ebi.ac.uk/Tools/msa/mafft/) and build a tree (https://www.ebi.ac.uk/Tools/phylogeny/simple_phylogeny/; Madeira et al. 2022).

For the outdoor portion of the lesson, different teams of students will be assigned different taxonomic groups to observe, photograph, and identify. Instructors should visit the campus outdoor space ahead of time to determine what groups of organisms will be easy to find there. Compiling a list of commonly observed species, genera, or families may be useful, especially if teaching assistants help with the activity. Some suggested taxonomic assignments for teams of students include angiosperms, fungi, insects, birds, and mammals, but these can be modified or changed depending on local abundance and instructor preference. Assigning paraphyletic taxonomic groups (e.g. non-insect invertebrates, non-avian reptiles) can add an extra challenge when teams of students combine to form progressively larger trees. I typically instruct each team of students to find, photograph, and identify 6 - 10 members of their assigned taxonomic groups, but this number can be adjusted based on instructor observations of local biodiversity and time constraints.

A worksheet and answer key (for introductory activities only, as the others are much more open-ended) are included as supplemental files. Instructors should feel free to modify any of these as they see fit. In my Evolutionary Biology class, these activities are worth 5% of students' final grade. However, individual instructors should determine the weight of this assignment in terms of students' overall course grade. The attached worksheet assigns each question/problem a percent of the total grade for the activity, but this is also modifiable based on the instructor's preferences.

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Caitlin Conn has been an Instructor at the Berry College since 2019, where she teaches courses in genetics and evolutionary biology.

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