EVOLUTION

The Tree-Thinking Challenge

David A. Baum, Stacey DeWitt Smith, Samuel S. S. Donovan

The central claim of the theory of evolution as laid out in 1859 by Charles Darwin in *The Origin of Species* is that living species, despite their diversity in form and way of life, are the products of descent (with modification) from common ancestors. To communicate this idea, Darwin developed the metaphor of the "tree of life." In this comparison, living species trace backward in time to common ancestors in the same way that separate twigs on a tree trace back to the same major branches. Coincident with improved methods for uncovering evolutionary relationships, evolutionary trees, or phylogenies, have become an essential element of modern biology (*1*). Consider the case of HIV/AIDS, where phylogenies have been used to identify the source of the virus, to date the onset of the epidemic, to detect viral recombination, to track viral evolution within a patient, and to identify modes of potential transmission (*2*). Phylogenetic analysis was even used to solve a murder case involving HIV (*3*). Yet "tree thinking" remains widely practiced only by professional evolutionary biologists. This is a particular cause for concern at a time when the teaching of evolution is being challenged, because evolutionary trees serve not only as tools for biological researchers across disciplines but also as the main framework within which evidence for evolution is evaluated (*4*, *5*).

At the outset, it is important to clarify that tree thinking does not necessarily entail knowing how phylogenies are inferred by practicing systematists. Anyone who has looked into phylogenetics from outside the field of evolutionary biology knows that it is complex and rapidly changing, replete with a dense statistical literature, impassioned philosophical debates, and an abundance of highly technical computer programs. Fortunately, one can interpret trees and use them for organizing knowledge of biodiversity without knowing the details of phylogenetic inference. The reverse is, however, not true. One cannot really understand phylogenetics if one is not clear what an evolutionary tree is.

The preferred interpretation of a phylogenetic tree is as a depiction of lines of descent. That is, trees communicate the evolutionary relationships among elements, such as genes or species, that connect a sample of branch tips. Under this interpretation, the nodes (branching points)
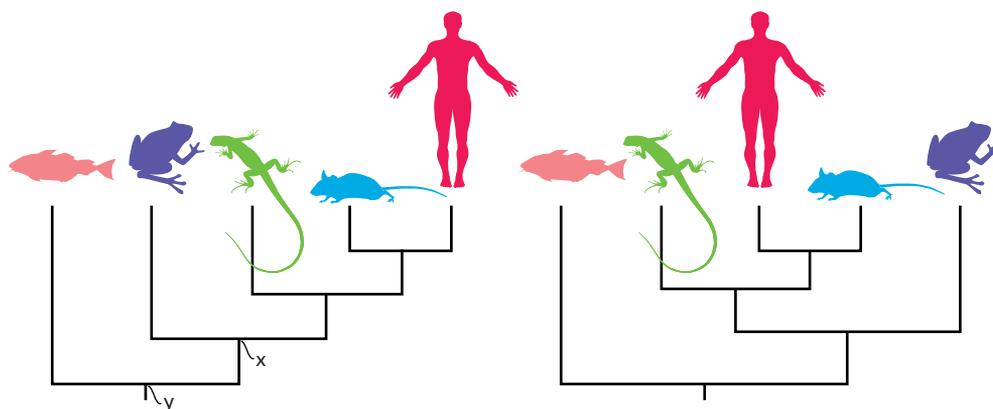
Which phylogenetic tree is accurate? On the basis of the tree on the left, is the frog more closely related to the fish or the human? Does the tree on the right change your mind? See the text for how the common ancestors (x and y) indicate relatedness.

on a tree are taken to correspond to actual biological entities that existed in the past: ancestral populations or ancestral genes. However, tree diagrams are also used in many nonevolutionary contexts, which can cause confusion. For example, trees can depict the clustering of genes on the basis of their expression profiles from microarrays, or the clustering of ecological communities by species composition. The prevalence of such cluster diagrams may explain why phylogenetic trees are often misinterpreted as depictions of the similarity among the branch tips. Phylogenetic trees show historical relationships, not similarities. Although closely related species tend to be similar to one another, this is not necessarily the case if the rate of evolution is not uniform: Crocodiles are more closely related to birds than they are to lizards, even though crocodiles are indisputably more similar in external appearance to lizards.

But what does it mean to be "more closely related"? Relatedness should be understood in terms of common ancestry—the more recently species share a common ancestor, the more closely related they are. This can be seen by reference to pedigrees: You are more closely related to your first cousin than to your second cousin because your last common ancestor with your first cousin lived two generations ago (grandparents), whereas your last common ancestor with your second cousin lived three generations ago (great-grandparents). Nonetheless, many introductory students and even professionals do not find it easy to read a tree diagram as a depiction of evolutionary relationships. For example, when presented with a particular phylogenetic tree (see the figure, left), people often erroneously conclude that a frog is more closely related to a fish than to a human. A frog is actually more closely related to a human than to a fish because the last common ancestor of a frog and a human (see the figure, label x) is a descendant of the last common ancestor of a frog and a fish (see the figure, label y), and thus lived more recently. [To evaluate your tree-thinking skills, take the quizzes (*6*)].

Why are trees liable to misinterpretation? Some evolutionary biologists have proposed that nonspecialists are prone to read trees along the tips (*1*, *7*), which in this case yields an ordered sequence from fish to frogs and ultimately to humans. This incorrect way to read a phylogeny may explain the widely held but erroneous view that evolution is a linear progression from primitive to advanced species (*8*), even though a moment's reflection will reveal that a living frog cannot be the ancestor of

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a living human. The correct way to read a tree is as a set of hierarchically nested groups, known as clades. In this example, there are three meaningful clades: human-mouse, human-mouse-lizard, and human-mouse-lizard-frog. The difference between reading branch tips and reading clades becomes apparent if the branches are rotated so that the tip order is changed (see the figure, right). Although the order across the branch tips is different, the branching pattern of evolutionary descent and clade composition is identical. A focus on clade structure helps to emphasize that there is no single, linear narrative of evolutionary progress (*1, 7*).

There are other problems in reading relationships from trees (*9*). For example, there is a common assumption that trait evolution happens only at nodes. But nodes simply represent places where populations became genetically isolated, permitting them to accumulate differences in their subsequent evolution. Similarly, living species may be mistakenly projected backward to occupy internal nodes of a tree. But it is incorrect to read a tree as saying that humans descended from mice when all that is implied is that

humans and mice shared a common ancestor. Thus, for all its importance, tree thinking is fraught with challenges.

Tree thinking belongs alongside natural selection as a major theme in evolution training. Further, trees could be used throughout biological training as an efficient way to present information on the distribution of traits among species. To this end, what is needed are more resources: computer programs (*10*), educational strategies (*11, 12*), and accessible presentations of current phylogenetic knowledge (*13–15*).

Phylogenetic trees are the most direct representation of the principle of common ancestry—the very core of evolutionary theory—and thus they must find a more prominent place in the general public's understanding of evolution. As philosopher of science Robert O'Hara (*16*) stated, "just as beginning students in geography need to be taught how to read maps, so beginning students in biology should be taught how to read trees and to understand what trees communicate." Among other benefits, as the concept of tree thinking becomes better understood by those in the sciences, we can hope that a wider

segment of society will come to appreciate the overwhelming evidence for common ancestry and the scientific rigor of evolutionary biology.

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CHEMISTRY

Following the Flow of Energy in Biomolecules

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Some biological molecules, such as those in visual or photosynthetic systems, have evolved to efficiently convert energy from one form to another. How do these molecules channel energy rapidly and efficiently so that useful work can be performed without this energy being dissipated ineffectively into the surroundings? Dissipation of molecular vibrational excitation energy typically takes place on picosecond time scales, so biological molecules must be able to channel energy rapidly and efficiently if they are to be able to direct it in a useful manner. In biological systems excited by light, the nonradiative electronic transitions can occur on time scales ($<< 10^{-12}$ ps) that are even faster than vibrational energy dissipation (*1–3*), hinting at how nature solves the problem of directing energy flow. On page 1006 of this issue, Kukura *et al.* (*4*) take an important step forward in defining the process of directed energy flow in the visual pigment rhodopsin.

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Photoexcited biological molecules offer a unique opportunity to monitor the evolution of excitation energy as it transforms a reactant molecule into its final products. With the advent of appropriate femtosecond laser techniques (*5*), it has become possible to examine the underlying dynamics of the elementary vibrational and electronic excitations that guide the structural changes and, ultimately, the function of a variety of biomolecules (*6–8*). The work presented by Kukura *et al.* enhances our ability to monitor rapid structural changes in such molecules by introducing the technique of femtosecond stimulated Raman spectroscopy (FSRS). In their report, Kukura *et al.* follow the evolution of the retinal chromophore as it is excited to photorhodopsin and decays into bathorhodopsin, all within the first picosecond of the visual process. They do this by taking advantage of the broad spectral bandwidth of their probe pulse to obtain very high quality time-resolved stimulated Raman spectra over the range of 600 to 2000 cm^{-1}.

How does this experiment generate ultrafast time resolution, as well as the high

spectral resolution associated with Raman spectra, without violating the uncertainty principle? Although not emphasized in the report by Kukura *et al.*, these authors are fully aware (*9*) that the underlying time scale for the generation of the Raman photon is dictated by the dephasing time of the coherence between the initial and final vibrational levels of the material undergoing the Raman process. A typical time scale for the vibrational dephasing time is on the order of 10^{-12} s, which translates to a 10 cm^{-1} Raman bandwidth. This means that the FSRS experiment reads out Raman radiation from the sample that is averaged over its vibrational dephasing time window (that is, the stimulated Raman signals continue to appear at the detector, even after the probe pulse has passed through the sample). Thus, there is no violation of the uncertainty principle. However, being able to control the "gating" of the Raman coherence by changing the time delay between the photochemical pump and the broadband probe allows the dephasing time window to be moved so that rapid structural dynamics can be monitored. Changes in the vibrational frequencies that take place within the dephasing time window affect the FSRS lineshape, and the authors have done a convincing job of simulating these lineshape changes as shown in the supporting online material of their paper.

A key conclusion of the work on rhodopsin is that low-symmetry hydrogen out-of-plane (HOOP) wagging motions

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