Chapter 9

Missing Links: How Cladograms Reify Common Evolutionary Misconceptions

Andrew Shtulman

Abstract

Cladograms are tree-like structures devised by evolutionary biologists for conveying patterns of shared ancestry among biological kinds. These representations have become highly popular in science textbooks and science museums, yet most non-biologists have difficulty reading them. This chapter discusses how those difficulties stem from common misconceptions about evolution—misconceptions reinforced not only by what is included in cladograms but also by what is not included. Cladograms routinely omit information about extinction (depicting only the extant species within a taxonomic grouping), biodiversity (depicting only a subset of those species) and variation (depicting species with a single label), and these omissions, while irrelevant to how biologists understand cladograms, likely have cognitive consequences for how non-biologists understand them. The chapter concludes by considering other types of diagrams—circle diagrams, spiral diagrams, and bush diagrams—that depict patterns of shared ancestry with different graphing conventions and may thus be more appropriate than cladograms when their intended audience is non-biologists and their intended purpose is education.

A fundamental principle of modern biology is that all life is interconnected. Every organism on the planet is related to every other organism through common

ancestry. This principle has implications for our understanding of all biological phenomena and is one that most biology educators hope to teach their students. Visual representations are a common means of teaching this principle, as visual representations can capture the depth and breadth of phylogenetic information more succinctly than words can. But the translation of phylogenetic information into visual representations has its challenges (Pennisi). One could design representations that highlight any number of phenomena: patterns of speciation and extinction across time, patterns of speciation and extinction across geography, changes in the complexity of existing lifeforms, or changes in the frequency of different anatomical plans. Historically, biologists have experimented with representations that highlight each of these phenomena (Gould, "Redrafting"), but one representation, in particular, has come to dominate modern biological science: the cladogram.

Cladograms highlight a single property of life—common ancestry—and they do so through a series of branching relations. Given a collection of *taxa,* or taxonomic groupings (e.g., species, genus, family, or order), the pair of taxa that share a common ancestor more recently than any other pair are connected with lines that converge at a node. This node represents their common ancestor. The pair is then connected to every other taxa via the same logic: taxa that share more recent ancestors are connected prior to those that share more distant ancestors until all taxa are interconnected. Each new connection yields a new node, with deeper nodes signifying ancestors that are more distant (time-wise) and more widespread (descent-wise). As an illustration, consider the cladogram displayed in figure 9.1, which depicts the ancestral relations among apes. This cladogram indicates that humans and chimpanzees share a more recent ancestor than do any other pair of apes. Humans and chimpanzees, in turn, share a more recent ancestor with gorillas than they do with orangutans, and humans, chimpanzees, and gorillas share a more recent ancestor with orangutans than they do with gibbons.

Within the scientific community, cladograms have become a mainstay of phylogenetic analysis for a number of reasons, the foremost being that technological advances in gene sequencing have made it possible to discern shared ancestry at a molecular level. But one need know nothing about the genetic basis of cladograms to glean profound insights from them. Cladograms can greatly alter commonsense notions of when and how different types of lifeforms emerged. By appearance alone, we might assume that manatees are closely related to dolphins and that elephants are closely related to cows, but a cladogram that includes all four would tell us that manatees are actually more closely related to elephants and that dolphins are more closely related to cows. Likewise, we might assume
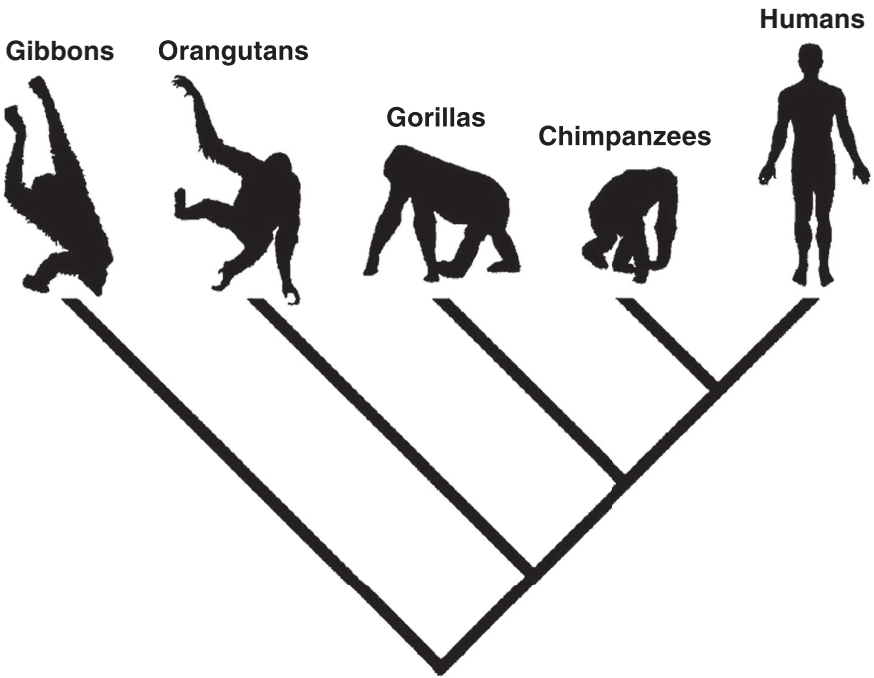
Figure 9.1 Cladogram (in the form of a ladder diagram) depicting the ancestral relations among five modern primates, adapted from Gregory, "Understanding Evolutionary Trees."

that two creatures with eyes are more closely related to one another than either is to a creature without eyes, yet a cladogram that includes both eyed and non-eyed creatures would tell us that eyes emerged independently across several lineages and that having eyes is not as reliable an indicator of shared ancestry as certain other traits, like having lungs or having a spine.

For their simplicity, cladograms are surprisingly powerful tools for decoding the mysteries of diverse morphology, and, as such, they have spread beyond the scientific domain into the public domain, becoming a stock representation in science textbooks (Catley and Novick) and science museums (MacDonald and Wiley). Recent research, however, suggests that most non-biologists have difficulty understanding cladograms (Gregory, "Understanding Evolutionary Trees"). In this chapter, I argue that those difficulties stem from common misconceptions about evolution (Shtulman; Shtulman and Calabi, "Cognitive Constraints") and that individuals who hold such misconceptions are not simply confused by cladograms but actively misinterpret them. In particular, I argue that misconceptions about evolution influence not only our understanding of the elements contained

within a cladogram—its lines, nodes, branches, and tips—but also our under-standing of the elements missing from a cladogram. Three such elements, routinely omitted from cladograms, are those that pertain to extinction (cladograms typ-ically depict only the extant species within a *clade,* or group of organisms united by a particular common ancestor), biodiversity (cladograms typically depict only a subset of extant species within a clade), and variation (cladograms depict spe-cies as unitary entities and provide no representation of the variation within a species). Information about extinction, biodiversity, and variation is irrelevant to how biologists use cladograms—to depict a hypothesized sequence of speciation events among a predefined set of species—but omitting that information may paint a skewed picture of evolution for non-biologists.

In short, I argue that, when viewing cladograms, non-biologists interpret an absence of evidence—evidence regarding extinction, biodiversity, and varia-tion—as evidence of absence. Further, I argue that cladograms may need to be replaced with other types of representations, such as circle diagrams (Novick and Catley), spiral diagrams (Ricou and Pollock), or bush diagrams (Gould, "Bushes"), when their intended audience is non-biologists and their intended purpose is education.

Common Misconceptions about Evolution

The eighteenth-century biologist Jean-Baptiste Lamarck proposed a theory of evolution in which organisms acquire adaptive traits throughout their lives and then pass those traits to their offspring. Students in today's biology classrooms are easily dissuaded of the idea that acquired traits are inherited (Springer and Keil); amputees do not, after all, give birth to limbless babies. But they are less easily dissuaded of the broader idea, implicit in Lamarck's theory, that individ-uals evolve rather than populations. In other words, non-biologists tend to view evolution as the uniform transformation of all individuals within a species rather than the selective survival and reproduction of just a few.

At least two factors are responsible for this misconception. One factor is our tendency to essentialize species or assume that species possess an underlying nature (or "essence"), which determines their outwardly observable appearance and behavior (Gelman; Medin and Atran; Solomon and Zaitchik). This bias serves us well when reasoning about the development of individual organisms, but serves us poorly when reasoning about the evolution of entire species, because it causes us to undervalue the variation within a species. And without variation, there can be no selection. Another factor is our tendency to perceive nature as

a caring and benevolent place—a peaceable kingdom rather than a Malthusian struggle (Ozkan et al.; Zimmerman and Cuddington). We underestimate the extent to which organisms compete for resources, especially within the same species. Consequently, we fail to appreciate the transformative power of selection, that is, the transformative power of dying without leaving any offspring. We gravitate instead towards the more optimistic belief that organisms will somehow acquire the traits they need to acquire in order to survive, with selection playing no role in this process (for a review, see Gregory, "Understanding Natural Selection"). These misconceptions are highly coherent (Shtulman and Calabi, "Cognitive Constraints") and highly robust (Shtulman and Calabi, "Tuition vs. Intuition"). In fact, they resemble theories of evolution proposed prior to Darwin in the history of science (Shtulman).

Misconceptions about the mechanisms of evolution give rise to misconceptions about the outcomes of evolution, that is, misconceptions about the origin of new species (speciation) and the demise of old species (extinction). With respect to speciation, those who hold an essentialist view of evolution have difficulty conceiving of speciation as the splitting of one population into two, because all members of the original population are assumed to be united by a common and enduring essence. Consequently, they prefer to view speciation as the holistic metamorphosis of one population into another. This preference for linear evolution ("anagensis") over branching evolution ("cladogenesis") leads to the misconception that morphologically similar species are related through direct descent rather than common descent—for example, that chimpanzees are the ancestors of humans rather than their cousins (Catley et al.). Furthermore, most non-biologists deny that morphologically dissimilar species, like salamanders and sparrows or bees and brontosauruses, are related at all (Poling and Evans, "Religious Belief"; Shtulman).

With respect to extinction, the belief that organisms acquire the traits they need to acquire gives rise to the misconception that extinction is rare, occurring at the hands of catastrophic disasters, like earthquakes or floods, but not at the hands of more mundane forces, like predation or disease. Extinction, from a selection-based view of evolution, is just selection writ large, but it cannot be such from an essentialist view because essentialist views make no room for selection. Whatever process is responsible for adapting a species to its environment should also ensure that the species will not go extinct. Consequently, those who hold essentialist views of evolution greatly underestimate the frequency of extinction over time (Shtulman) and the ubiquity of extinction across species (Poling and Evans, "Are Dinosaurs the Rule").

Common Misinterpretations of Cladograms

The fact that most non-biologists hold deep-seated misconceptions about speciation and extinction does not bode well for their interpretation of cladograms, which depict patterns of speciation and extinction across clades. Indeed, several studies have found that non-biologists have difficulty reading cladograms (Catley et al.; Gregory, "Understanding Evolutionary Trees"; Halverson et al.; Novick et al., "Linear Versus Branching"; Phillips et al.; Shtulman and Checa) and constructing cladograms (Meir et al.; Novick and Catley,; Novick et al., "Characters are Key"). These difficulties cluster into two general categories.

First, most non-biologists misinterpret the ordering of the taxa along the tips of the cladogram, reading information into the ordering that is not supported by the cladogram's branching relations. The ordering of taxa in a cladogram is, to a large extent, arbitrary. While taxa that share a most recent common ancestor must be adjacent (e.g., chimpanzees and humans in figure 9.1), their ordering relative to one another can be changed (e.g., chimpanzees can appear either to the left of humans or to their right), as can the ordering of entire clades (e.g., gorillas can appear either to the left of the human/chimpanzee clade or to its right). Any two clades can be rotated around the node that connects them, resulting in 2^n possible orders for every node in the graph. The five species depicted in figure 9.1, for example, could be presented in 16 (or 2^4) possible orders, including the following three:

Gibbons, (Orangutans, ((Chimpanzees, Humans), Gorillas))
Gibbons, (((Humans, Chimpanzees), Gorillas), Orangutans)
(((Chimpanzees, Humans), Gorillas), Orangutans), Gibbons

These rotations are possible because a branch between two taxa indicates only that those taxa share a more immediate ancestor with each other than they do with any other taxa, in the same way that two siblings share a more immediate ancestor with each other than they do with any of their cousins. Nevertheless, most non-biologists assume that taxa on the left are more ancient or more primitive than those on the right—or, in a vertically arrayed cladogram, that taxa at the bottom are more ancient or more primitive than those at the top. A corollary of this assumption is that the further apart two taxa appear along a cladogram's tips, the more distantly they are related. Figure 9.1, for instance, would be commonly misinterpreted as indicating that gibbons are the most ancient/primitive of the five taxa and that gibbons are more closely related to orangutans than they

are to humans. In reality, this cladogram indicates that gibbons have evolved independently from other apes for as long as other apes have evolved independently from gibbons, and gibbons are no more closely related to orangutans than they are to humans.

Second, most non-biologists misinterpret the linear elements of a cladogram, assuming that the length of the line connecting a taxon to its nearest node conveys information about that taxon's evolutionary history when, in fact, it does not. The lengths of a cladogram's lines are essentially arbitrary, as are their orientation and their curvature. Moreover, the number of nodes contained on any given line provides no information about how closely the taxon at its tip is related to any other taxon. Gibbons and humans, for instance, are as closely related to one another as gibbons and gorillas despite the fact that, in figure 9.1, there are four nodes on the path from gibbons to humans but only three on the path from gibbons to gorillas. The number of nodes is merely a byproduct of the number of taxa included in the cladogram. Drop chimpanzees from the cladogram and the number of nodes between gibbons and humans drops from four to three. Nevertheless, most non-biologists read meaning into how long a line is (the longer the line, the older the taxon) and how many nodes appear on its surface (the more nodes, the more distantly the taxon is related to other taxa in the clade). These misinterpretations are not unreasonable; how long a line is and how many nodes appear on its surface bear meaningful information in other types of diagrams (e.g., road maps, line graphs, flow charts, blueprints).

Further complicating matters, many depictions of shared ancestry designed for public consumption include scientifically questionable elements. Cladograms, by definition, are a representation of cladogenesis, or branching evolution, yet most cladograms in textbooks and science museums include representations of anagenesis, or linear evolution as well (Catley and Novick; MacDonald and Wiley; MacFadden et al.). That is, the nodes in these diagrams are labeled with extinct species, implying that those species gave rise to the extant species along the diagrams' tips. Empirically, such representations are suspect because biologists cannot ascertain whether an extinct species is the ancestor of an extant species or its cousin, and the latter inference is several times more likely (given the ubiquity of extinction). Other problematic features common to cladograms in science textbooks and science museums include varying the thickness of its branches without explanation, varying the endpoints of its branches without explanation, segregating "higher" taxa from "lower" taxa, and placing humans on the top-most branch of a vertically arrayed cladogram or the right-most branch of a horizontally arrayed cladogram (Catley and Novick; MacDonald and Wiley; Torrens and Barahona).

Potential Misinterpretation of Information Missing from Cladograms

To summarize thus far, most non-biologists hold essentialist views of evolution that make branching speciation a conceptual quandary, so they ignore the branching relations in a cladogram and attend primarily to its non-informative elements: the ordering of its tips, the lengths of its lines, and the frequency of its nodes. Ignoring the branching relations in a cladogram is highly problematic, but it is not the only problem that may arise from an essentialist view. Cladograms omit several types of information that, from a biologist's point of view, are innocuous forms of simplification but, from a non-biologist's point of view, may be seen as veridical representations of evolutionary change. Below I discuss three such omissions, noting how those omissions may reify and reinforce the essentialist misconceptions reviewed above.

The Omission of Extinction
Cladograms have come to dominate the biological sciences mainly because they can be constructed using highly objective information: similarities in genetic structure (Pennisi). It is possible to build cladograms from morphological information, but such information is less reliable, as it is rarely clear from visual inspection alone whether a trait observed in two taxa was inherited from a common ancestor (a *homologous* trait) or was derived separately in response to similar selection pressures on organisms whose common ancestor did not possess that trait (an *analogous* trait). This situation poses problems for including extinct taxa in modern cladograms because our knowledge of extinct taxa is primarily morphological in nature; fossils contain no living tissue for genetic analysis. As a result, when extinct taxa are included in textbook diagrams or museum diagrams, they tend to be placed in the branches of the diagram rather than at its tips (Catley and Novick; MacFadden et al.). Among genuinely cladistic representations of shared ancestry in textbooks and museums, extinct taxa are rare (MacDonald and Wiley).

   This absence of extinct taxa potentially reinforces the misconception, noted above, that extinction is uncommon and that extinction affects only certain types of species (Jarnefelt, this volume; Poling and Evans, "Are Dinosaurs the Rule"; Shtulman). The reality is that over 99.9% of the species that once existed are now extinct (Mayr), and cladograms, by representing the 0.1% of species that happen to have survived to the present (and a small subset of the 0.1% at that), present a skewed picture of the outcome of evolutionary change. Perhaps more problematic, the blind and messy process of mutation-plus-selection is

represented as a series of straight and orderly lines. The historical record is wiped clean of all false starts and blind paths, leaving only the "successful" lineages still present today. While cladograms are certainly an improvement over anagenetic representations of evolutionary change, they still vastly underrepresent the frequency of cladogenesis in that every instance of cladogenesis represented in the tree was likely accompanied by dozens of instances not represented.

This speculation—that non-biologists are unclear on how extinction is (and is not) represented in cladograms—is supported by a study of how visitors to the Los Angeles Natural History Museum interpret one of the museum's cladograms (Shtulman and Checa). Participants completed a series activities using a cladogram that depicted all 19 orders of mammals. In one activity, participants decided whether an extinct, pig-like creature—an "entelodont"—could be placed within the cladogram and, if so, where. Virtually all participants (96%) agreed that the entelodont could be placed within the cladogram, but only a minority (39%) discerned that it should be located on a branch within the ungulate clade. Most participants thought the entelodont should be located either at the bottom of the cladogram, near its root (45%), or on a separate branch altogether (12%). Thus, the modal response was to treat the entelodont either as an ancestor to all mammals or as an isolated lineage related to no mammals.

The Omission of Biodiversity

Just as extinct taxa tend to be omitted from cladograms, so are many extant species within the depicted clades. Such omissions date back to one of the very first depictions of the interconnectedness of life: Ernst Haeckel's (1866) "tree of life," covering everything from insects to mammals. While Haeckel devoted an entire layer of branches to the four thousand species of mammals—conspicuously depicted at the top of the tree, with humans in the center—he devoted only a single branch to the million species of insects (Gould, "Redrafting the Tree of Life"). Another example of the omission of extant species can be seen in figure 9.1. Only one tip in this cladogram represents a unitary species: the tip labeled "humans." The tips labeled "orangutans," "gorillas," and "chimpanzees" represent two species each—Bornean and Sumatran orangutans, eastern and western gorillas, common and pygmy chimpanzees—and the tip labeled "gibbons" represents 15 different species. These examples, among others (see Gould, "Redrafting the Tree of Life"), suggest that the less salient a taxon is in our folkbiology, the fewer tips we devote to that taxon in our cladograms.

Obviously, not all species can be represented in a single cladogram; a cladogram containing 3000 species, designed by David Hillis and his colleagues at the University of Texas at Austin, is legible only when enlarged to a size of 1.5

meters or more (Pennisi), and 3000 species is less than 0.1% of the total number of known species. But all species within a clade can be represented if the clade chosen for depiction is sufficiently small. For instance, figure 9.1 could be redesigned such that gibbons are dropped from the cladogram and the remaining clades could be expanded to include all known species. Doing so would not only highlight the diversity among the great apes but would also lessen the impression that those species are ordered from least complex to most complex, as is implied by the current ordering.

An additional problem created by compressing a diverse clade into a single tip is that the particular species chosen to label the clade, as a whole, likely influences our interpretation of its relation to other clades in the diagram. Consider, for instance, the fact that the genus *Pan* is almost always represented by *Pan troglodytes,* the common chimpanzee, rather than *Pan paniscus,* the pygmy chimpanzee or "bonobo." These two species, while roughly similar in morphology, differ widely in behavior. Whereas common chimpanzees are hostile, patriarchal, and meat eating, pygmy chimpanzees are docile, matriarchal, and vegetarian. We humans are as closely related to pygmy chimpanzees as we are to common chimpanzees, yet our relation to common chimpanzees undoubtedly looms larger in our minds given how frequently that relation is depicted in primate cladograms.

There is no research, to my knowledge, supporting the speculation that the type of biodiversity represented in a cladogram influences how we interpret that cladogram. There is, however, ample research demonstrating that non-biologists underestimate biodiversity in general. For instance, US undergraduates conceptualize trees and fish as basic-level categories—categories that are optimally cohesive in terms of the number of features shared by all category members—even though, from a biological point of view, "tree" and "fish" should function as superordinate categories given the great diversity of organisms they cover (Rosch et al.). Likewise, in a survey of US undergraduates' tree knowledge, over 90% reported familiarity with Cedar, Hickory, Maple, and Spruce trees, but fewer than half reported any familiarity with Alder, Buckeye, Hawthorn, or Sweetgum trees, even though many had encountered those trees daily on their campus (Coley et al.). And use of tree terms, flower terms, bird terms, and fish terms in English-language documents has dropped precipitously from the nineteenth century to the twentieth, concurrent with a precipitous increase in artifact terms (Wolff et al.). These data suggest that we systematically underestimate the biodiversity around us and are therefore unlikely to infer the biodiversity missing from a cladogram.

The Omission of Variation

As noted above, non-biologists tend to view variation between species as pervasive and adaptive but variation within species as minimal and nonadaptive—a byproduct of essentialism. Such notions influence a variety of cognitive processes, including memory (Legare et al.), categorization (Nettle), induction (Shtulman and Schulz), and explanation (Opfer et al.). Cladograms do not help dissuade these notions. If anything, they reinforce them by representing diverse populations with a single image or a single label. The only variation depicted in a cladogram is variation across species, which, depending on the species chosen for inclusion, can be quite dramatic.

Admittedly, the unit of analysis in a cladogram is some form of higher-order taxon (e.g., species, genus, family, order) and any attempt to depict variation within a population would detract from the information cladograms are designed to display (i.e., the ancestral relations among those populations). Nevertheless, the omissions described above—omission of extinct taxa and omission of several extant taxa within the same clade—likely exacerbate essentialist interpretations of biological kinds in that taxa are regularly isolated from the continuum of variation from which they came.

Figure 9.1, for instance, portrays only five taxa when, in reality, those taxa cover 22 different species. Humans' place among the apes would appear much less distinct if all 22 species were explicitly represented (and if the branches of the cladogram were rotated so that humans appeared somewhere in the middle of that continuum). Humans' place among the apes would also appear less distinct if extinct apes were intermixed with the extant ones. Indeed, cladograms depicting humans among a sea of extinct hominids, like the cladogram on display in the Hall of Human Origins at the American Museum of Natural History (Novick et al., "Depicting the Tree of Life"), likely engender less essentialist views of humankind than those that depict humans among organisms with minimal resemblance to humans (e.g., fish, turtles, birds, flowers), though future research is needed to verify this speculation.

Alternative Representations

The only cladogram we have considered thus far is figure 9.1, which is a particular type of cladogram: a ladder diagram. Cladograms can also be constructed as "trees," as shown in figure 9.2 (Catley and Novick). The omissions described above are not fatal flaws of tree diagrams or ladder diagrams. Both could be redesigned to include the omitted information. Still, tree and ladder diagrams may
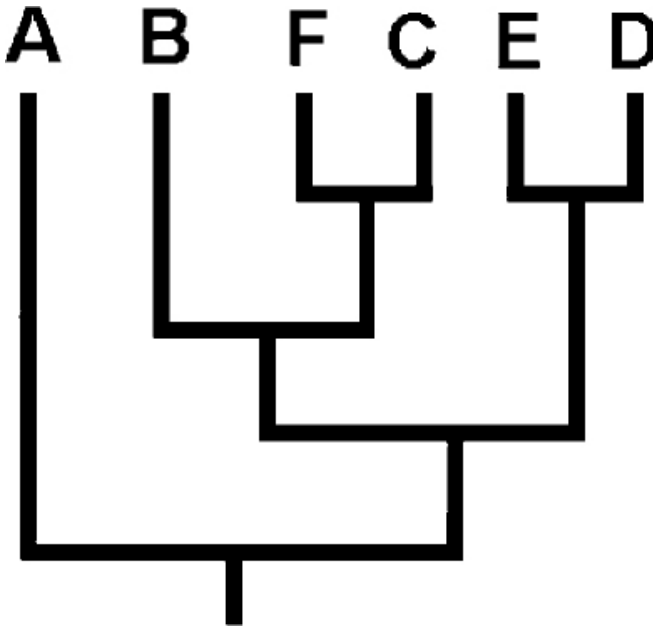
Figure 9.2 Tree diagram depicting the ancestral relations among six hypothetical taxa, adapted from Gregory, "Understanding Evolutionary Trees."

not be the best representation of information about extinction or biodiversity. Other types of representations may be better suited for those purposes. Tree and ladder diagrams may play an essential role in modern biology (Novick and Catley), but their value as a scientific tool does not justify their use in the public domain. It is an empirical question which representations of phylogenetic information are best suited for conveying that information to a lay audience.

Below, I outline three hypotheses relevant to this question: (1) circle diagrams are better suited than tree or ladder diagrams for conveying information about common ancestry but are not well suited for conveying information about extinction or biodiversity; (2) spiral diagrams are better suited than tree or ladder diagrams for conveying information about biodiversity but are not well suited for conveying information about common ancestry or extinction; and (3) bush diagrams are better suited than tree or ladder diagrams for conveying information about extinction but are not well suited for conveying information about common ancestry or biodiversity. The first of these hypotheses has been (partially) tested and supported, but the remaining two have not. All three, however, are motivated by what we currently know about how people understand evolution

and how people read cladograms, outlined above. And they are proposed in the spirit of what other authors in this volume have argued: that intuition can facilitate scientific reasoning, rather than obstruct it, if the right intuitions are accessed and accessed in the right ways (Blancke, Tanghe, and Braeckman, this volume; Evans, this volume).

Circle Diagrams

In an analysis of the visual representations contained in 31 biology textbooks, Catley and Novick, in "Seeing the Wood," found that cladograms are most typically portrayed as ladders (figure 9.1). The second most common format is that of a tree (figure 9.2). Trees and ladders are informationally equivalent, differing only in whether the lines connecting taxa meet at an angle or at a rectilinear juncture, but trees are easier to read because the clades are more visually distinct, which makes the nested relations among those clades easier to discern (Novick and Catley). A third type of diagram—the circle diagram, depicted in figure 9.3—makes the nested relations among clades even more salient. A circle diagram differs from a tree or ladder diagram in that shared ancestry is conveyed with concentric circles rather than nested branches. It is essentially a bird's eye view of a tree or ladder diagram—in this case, a bird's eye view of figure 9.2—in that the branches of such diagrams are collapsed to a single dimension. Doing so is conceptually ideal given that the vertical dimension of a tree or ladder diagram conveys no intrinsic meaning. Moreover, circles are a more natural representation of groups than are branches, as all members of the group can be encapsulated in one spatially continuous figure.
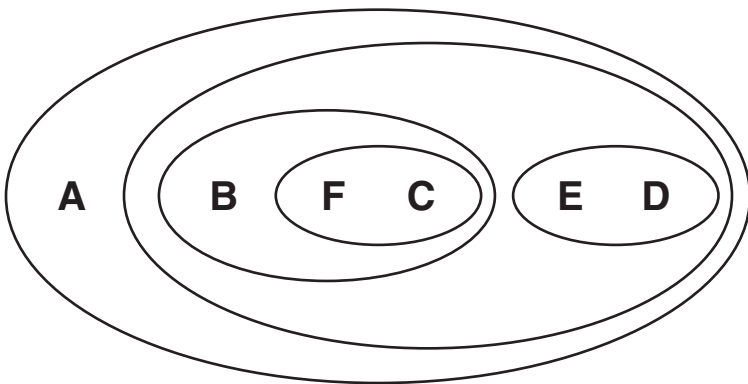

Figure 9.3 Circle diagram of the same taxa displayed in figure 9.2.

Novick and Catley explicitly compared the affordances of ladder, tree, and circle diagrams by asking two groups of college undergraduates—psychology majors and biology majors—to translate the phylogenetic information presented in one format (e.g., a tree diagram) into another (e.g., a ladder diagram) ("Understanding Phylogenies"). They found that participants were most accurate at translating phylogenetic information from circle diagrams. In fact, presenting phylogenetic information in a circle diagram nullified the effect of participants' background knowledge, with psychology majors performing nearly as accurately as biology majors (85% accuracy vs. 95% accuracy, respectively). Presenting the information in a tree or ladder diagram, on the other hand, decreased accuracy relative to the circle-diagram condition, by 15–50% for biology majors and by 50–75% for psychology majors. Circle diagrams allowed participants to glean information about common ancestry that was otherwise opaque in the form of trees or ladders.

That said, it's not clear that circle diagrams are an ideal format for presenting information about extinction or biodiversity for the simple reason that they do not expand well. With each new clade comes a new circle, and each circle must surround, or be surrounded by, other circles. The net effect can be an overwhelming number of boundaries. These boundaries direct attention effectively when few in number but may attract attention, as focal objects themselves, when more numerous. To represent the predominance of extinct taxa or the diversity of extant taxa within a clade, an alternate format is probably desirable.

Spiral Diagrams

Figure 9.4 depicts the same information as depicted by figure 9.2 (and figure 9.3) but in a qualitatively different format: a spiral. Spiral diagrams are most frequently used to illustrate the interconnectedness of all life on earth, from bacteria to fungi to animals to plants (Ricou and Pollock), but they could just as easily be used to represent a more select group of taxa, like the primates depicted in figure 9.1.

Spiral diagrams may be an ideal format for depicting the ancestral relations among a single family or order for several reasons. First, spiral diagrams are more efficient in their allocation of tips to branches. More species can be packed into a spiral diagram than into a similarly sized tree or ladder diagram because the tips are arrayed in a circle, thereby making use of both horizontal and vertical dimensions of the space. Second, spiral diagrams lack the directionality or polarity inherent in tree and ladder diagrams. There is no top-most branch or right-most branch that might be construed as the "pinnacle" taxon (as many non-biologists
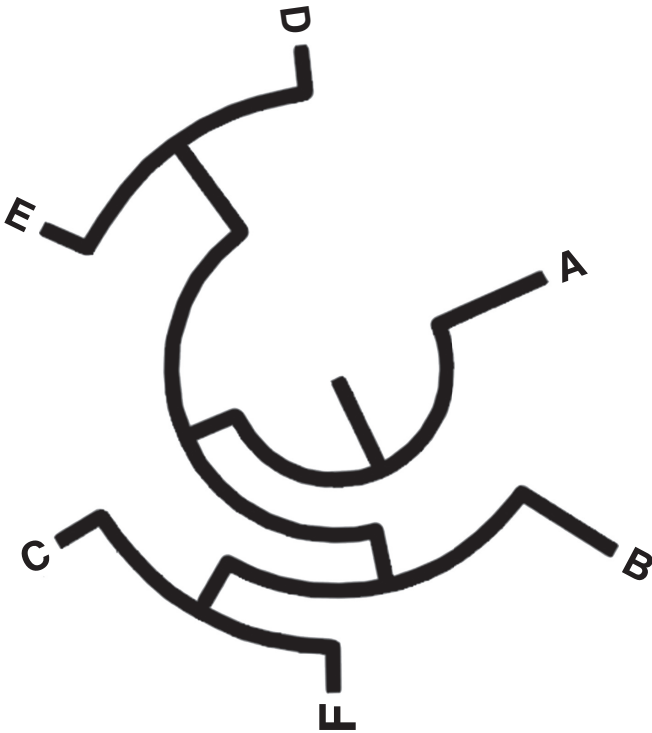
Figure 9.4 Spiral diagram of the same taxa displayed in figure 9.2, adapted from Gregory, "Understanding Evolutionary Trees."

are prone to construe humans; see Guillo, this volume). Third, spiral diagrams convey an intrinsic sense of proportionality by virtue of their pie-like structure. The proportion of space occupied by one clade (e.g., the great apes) relative to another clade (e.g., the lesser apes) is more apparent in a spiral diagram than in a tree or ladder diagram and might thus convey a more veridical representation of diversity within and across clades.

The main drawback to using a spiral diagram is that precise information about common ancestry is difficult to discern from a spiral diagram, particularly for spirals that contain hundreds—or thousands—of species (Novick et al., "Depicting the Tree of Life"). Spiral diagrams are also ill-suited for depicting extinct taxa for the same reasons that tree and ladder diagrams are: all taxa are displayed along a single line (or curve, in this case), and it is thus difficult to differentiate extinct taxa from extant taxa unless they are denoted with different fonts or different colors. While one could potentially vary the placement

of the tips in a tree diagram to indicate which taxa are extant and which are extinct, this strategy would be difficult to implement in a spiral diagram without breaking the continuity of the spiral. Spiral diagrams may thus be best suited for representing information about the density of taxonomically similar lifeforms or the interconnectedness of different types of life.

Bush Diagrams

None of the diagrams reviewed thus far are ideal for representing extinct taxa because they feature all taxa along a single line (or curve) with no inherent markers for distinguishing extant taxa from extinct taxa. One way to circumvent this problem, in a tree diagram or ladder diagram, would be to place extinct taxa within its branches rather than at its tips, but doing so would render the diagram non-cladistic and potentially misleading, as noted above. An alternative solution would be to relax the constraint that all branches need to terminate along a single line or the constraint that all branches need to be oriented in the same direction (Gould, "Bushes"). The result is a bush diagram of the kind displayed in figure 9.5. Figure 9.5 conveys the same information as that conveyed by figures 9.2, 9.3, and 9.4, but in a less orderly manner, consistent with the less-than-orderly nature of evolutionary change itself. Indeed, what is most salient in a bush diagram is not the ordering of the taxa but the branches connecting taxa to nodes. Its nodes take visual precedence over its tips. And in such a diagram, there is no expectation that the tips represent only extant taxa because the tips are not arrayed along a line implicitly interpreted as "present day."

The bush diagram in figure 9.5 was co-opted from one the most iconic sketches of evolutionary change drawn by Darwin in 1837. This sketch, appearing in his *Notebook B,* was annotated with the conjecture, "to have many species in same genus . . . requires extinction." Darwin underlined "requires" to emphasize the necessity of extinction to speciation. He recognized that species do not just metamorphosize from lesser-adapted forms to better-adapted forms. They fractionate, splitting into a diversity of forms, and that diversity is then selectively winnowed. Every modern species represents a small fraction of the innumerable lifeforms that once existed—lifeforms whose fate was extinction rather than propagation.

Thus, the purpose of Darwin's best-known visual representation of evolutionary change was to make salient the relation between extant species and extinct species. Darwin's diagram is well suited for this purpose because the "stubbiness" of its terminal branches is consistent with the brevity of the lineages they represent. Indeed, those branches need not be labeled, though they certainly could be
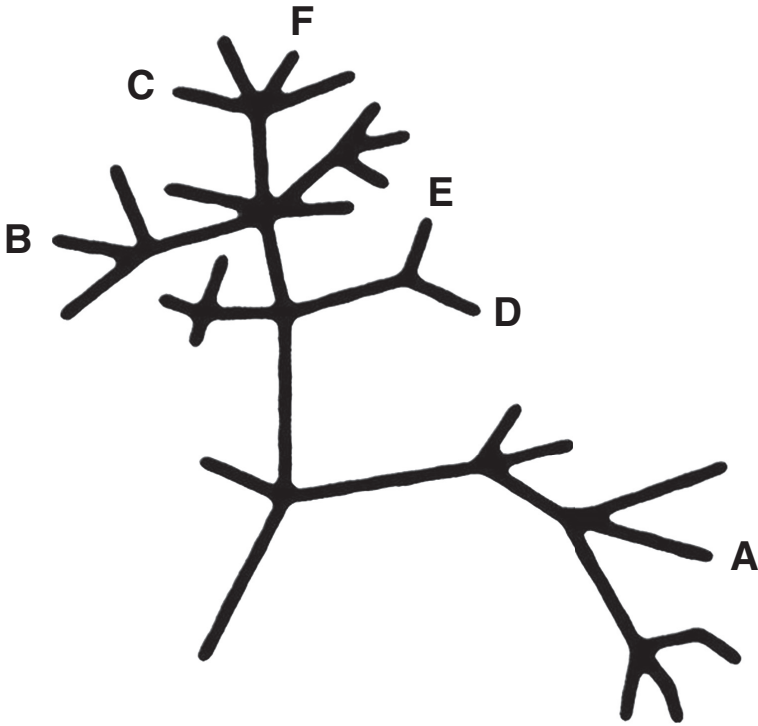
Figure 9.5 Bush diagram of the same taxa displayed in figure 9.2, adapted from Darwin, *Notebook B.*

in cases where biologists know a fair amount about the extinct taxa of interest (e.g., extinct horses or extinct hominids). Of course, a diagram that emphasizes nodes over tips is not an ideal diagram for reading the relations among tips (i.e., for reading information about common ancestry), nor is it ideal for representing the biodiversity among extant taxa insofar that the stubbiness of its tips establishes the expectation that those lineages have been pruned from the tree.

Conclusion

Misconceptions about evolution can lead people to misinterpret cladograms. To date, much research has been done on misinterpretations of a cladogram's core elements—its lines, tips, nodes, and branches—but little research has been done on misinterpretations of the elements missing from a cladogram. Here, I have argued that omission of extinct taxa from cladograms reifies the common misconception that extinction is an atypical outcome of evolutionary change, that

omission of within-clade biodiversity reifies the common misconception that extant species are largely unrelated to one another, and omission of variation (in general) reifies the common misconception that between-group variation is more common than within-group variation, but these hypotheses need empirical verification. I have also argued that circle diagrams, spiral diagrams, and bush diagrams do a better job of representing common ancestry, biodiversity, and extinction, respectively, than do ladder diagrams and tree diagrams, but these hypotheses need verification as well.

Regardless of whether the specific claims sketched above will survive empirical scrutiny, the more general claim that no one graph fits all instructional purposes has been born out in decades of research on graph comprehension and graph construction (for a review, see Anderson et al.). Different graphing conventions have proven effective for representing different types of information, and this conclusion will likely hold for evolutionary diagrams as well. Thus, graphic designers charged with illustrating phylogenetic information in science textbooks or science museums may need to reconsider whether a tree diagram or a ladder diagram is the best diagram for the job. While these diagrams are powerful tools in the hands of biologists, they may be downright misleading to non-biologists. Circle diagrams, spiral diagrams, and bush diagrams, on the other hand, may have the necessary affordances to block the misconceptions reified by traditional representations of phylogenetic information.

Acknowledgment

Works Cited

Anderson, Michael, et al., editors. *Theory and Application of Diagrams.* Springer, 2003.

Catley, Kefyn M., and Laura R. Novick. "Seeing the Wood for the Trees: An Analysis of Evolutionary Diagrams in Biology Textbooks." *BioScience,* vol. 58, no. 10, 2008, pp. 976–87.

Catley, Kefyn M., et al. "Interpreting Evolutionary Diagrams: When Topology and Process Conflict." *Journal of Research in Science Teaching,* vol. 47, no. 7, 2010, pp. 861–82.

Coley, John D., et al. "Inductive Reasoning in Folkbiological Thought." *Folkbiology,* edited by Douglas L. Medin and Scott Atran, MIT Press, 1999, pp. 205–32.

Darwin, Charles. *Notebook B.* 1837, *Darwin Online,* darwin-online.org.uk.

Gelman, Susan A. *The Essential Child.* Oxford UP, 2003.

Gould, Stephen J. "Bushes All the Way Down." *Natural History,* vol. 96, no. 6, 1987, pp. 12–19.

———. "Redrafting the Tree of Life." *Proceedings of the American Philosophical Society,* vol. 141, no. 1, 1997, pp. 30–54.

Gregory, T. Ryan. "Understanding Evolutionary Trees." *Evolution: Education and Outreach,* vol. 1, no. 2, 2008, pp. 121–37.

———. "Understanding Natural Selection: Essential Concepts and Common Misconceptions." *Evolution: Education and Outreach,* vol. 2, no. 2, 2009, pp. 156–75.

Halverson, Kristy L., et al. "Exploring the Complexity of Tree Thinking Expertise in an Undergraduate Systematics Course." *Science Education,* vol. 95, no. 5, 2011, pp. 794–823.

Legare, Cristine H., et al. "Anthropomorphizing Science: How Does it Affect the Development of Evolutionary Concepts?" *Merrill-Palmer Quarterly,* vol. 59, no. 2, 2013, pp. 168–97.

MacDonald, Teresa, and E. O. Wiley. "Communicating Phylogeny: Evolutionary Tree Diagrams in Museums." *Evolution: Education and Outreach,* vol. 5, no. 1, 2012, pp. 14–28.

MacFadden, Bruce J., et al. "Fossil Horses, Orthogenesis, and Communicating Evolution in Museums." *Evolution: Education and Outreach,* vol. 5, no. 1, 2012, pp. 29–37.

Mayr, Ernst. *This Is Biology: The Science of the Living World.* Harvard UP, 1997.

Medin, Douglas L., and Scott Atran. "The Native Mind: Biological Categorization and Reasoning in Development and Across Cultures." *Psychological Review,* vol. 111, no. 4, 2004, pp. 960–83.

Meir, Eli, et al. "College Students' Misconceptions About Evolutionary Trees." *The American Biology Teacher,* vol. 69, no. 7, 2007, pp. 71–76.

Nettle, Daniel. "Understanding of Evolution May Be Improved by Thinking about People." *Evolutionary Psychology,* vol. 8, no. 2, 2010, pp. 205–28.

Novick, Laura R., and Kefyn M. Catley. "Understanding Phylogenies in Biology: The Influence of a Gestalt Perceptual Principle." *Journal of Experimental Psychology: Applied,* vol. 13, no. 4, 2007, pp. 197–223.

Novick, Laura R., et al. "Characters are Key: The Effect of Synapomorphies on Cladogram Comprehension." *Evolution: Education and Outreach,* vol. 3, no. 4, 2010, pp. 539–47.

Novick, Laura R., et al. "Depicting the Tree of Life in Museums: Guiding Principles

from Psychological Research." *Evolution: Education and Outreach,* vol. 7, no. 1, 2014, pp. 1–13.

Novick, Laura R., et al. "Linear Versus Branching Depictions of Evolutionary History: Implications for Diagram Design." *Topics in Cognitive Science,* vol. 3, no. 3, 2011, pp. 536–59.

Opfer, John E., et al. "Cognitive Foundations for Science Assessment Design: Knowing What Students Know about Evolution." *Journal of Research in Science Teaching,* vol. 49, no. 6, 2012, pp. 744–77.

Ozkan, Ozlem, et al. "Facilitating Conceptual Change in Students' Understanding of Ecological Concepts." *Journal of Science Education and Technology,* vol. 13, no. 1, 2004, pp. 95–105.

Pennisi, Elizabeth. "Modernizing the Tree of Life." *Science,* vol. 300, no. 5626, 2003, pp. 1692–97.

Phillips, Brenda C., et al. "Teaching Tree Thinking to College Students: It's Not as Easy as You Think." *Evolution: Education and Outreach,* vol. 5, no. 4, 2012, pp. 595–602.

Poling, Devereaux A., and E. Margaret Evans. "Are Dinosaurs the Rule or the Exception? Developing Concepts of Death and Extinction." *Cognitive Development,* vol. 19, no. 3, 2004, pp. 363–83.

———. "Religious Belief, Scientific Expertise, and Folk Ecology." *Journal of Cognition and Culture,* vol. 4, no. 3, 2004, pp. 485–524.

Ricou, Joana, and John A. Pollock. "The Tree, the Spiral and the Web of Life: A Visual Exploration of Biological Evolution for Public Murals." *Leonardo,* vol. 45, no. 1, 2012, pp. 18–25.

Rosch, Eleanor, et al. "Basic Objects in Natural Categories." *Cognitive Psychology,* vol. 8, no. 3, 1976, pp. 382–439.

Shtulman, Andrew. "Qualitative Differences Between Naive and Scientific Theories of Evolution." *Cognitive Psychology,* vol. 52, no. 2, 2006, pp. 170–94.

Shtulman, Andrew, and Prassede Calabi. "Cognitive Constraints on the Understanding and Acceptance of Evolution." *Evolution Challenges: Integrating Research and Practice in Teaching and Learning about Evolution,* edited by Karl S. Rosengren et al., Oxford UP, 2012, pp. 47–65.

———. "Tuition vs. Intuition: Effects of Instruction on Naive Theories of Evolution." *Merrill-Palmer Quarterly,* vol. 59, no. 2, 2013, pp. 141–67.

Shtulman, Andrew, and Isabella Checa. "Parent-Child Conversations about Evolution in the Context of an Interactive Museum Display." *International Electronic Journal of Elementary Education,* vol. 5, no. 1, 2012, pp. 27–46.

Shtulman, Andrew, and Laura Schulz. "The Relation between Essentialist Beliefs and Evolutionary Reasoning." *Cognitive Science,* vol. 32, no. 6, 2008, pp. 1049–62.

Solomon, Gregg E. A., and Deborah Zaitchik. "Folkbiology." *Wiley Interdisciplinary Reviews: Cognitive Science,* vol. 3, no. 1, 2012, pp. 105–15.

Springer, Ken, and Frank C. Keil. "On the Development of Biologically Specific Beliefs: The Case of Inheritance." *Child Development,* vol. 60, no. 3, 1989, pp. 637–48.

Torrens, Erica, and Ana Barahona. "Why are Some Evolutionary Trees in Natural History Museums Prone to Being Misinterpreted?" *Evolution: Education and Outreach,* vol. 5, no. 1, 2012, pp. 76–100.

Wolff, Phillip, et al. "Evolution and Devolution of Folkbiological Knowledge." *Cognition,* vol. 73, no. 2, 1999, pp. 177–204.

Zimmerman, Corinne, and Kim Cuddington. "Ambiguous, Circular and Polysemous: Students' Definitions of the 'Balance of Nature' Metaphor." *Public Understanding of Science,* vol. 16, no. 4, 2007, pp. 393–406.

Author Profile

Andrew Shtulman is an Associate Professor in the Departments of Psychology and Cognitive Science at Occidental College. In his research he explores conceptual development and conceptual change, particularly as they relate to science education.