

Comparisons, Phylogeny, and Teaching Evolution

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Introduction

Comparisons are central to research and teaching in biology and are ubiquitous in both. Furthermore, biological comparisons generally take for granted some baseline knowledge of phylogenetic relationships. The main point of my paper is that the teaching of biology—and of evolutionary biology in particular—would benefit greatly from making more explicit use of phylogenetic trees in formulating comparisons. In addition to providing far richer comparisons, this would have the ancillary benefit of making “tree thinking” (O’Hara, 1997) second nature to biology students. Success in this endeavor requires that we pay more attention to teaching the basics of phylogenetic biology and overcoming the preconceptions that students have about phylogeny. Educators also need more ready access to phylogenetic knowledge and will need to pay more attention to the variety of evolutionary messages that phylogenetic comparisons can support.

Many people bring to bear some level of subliminal knowledge of phylogenetic relationships in making biological comparisons. Consider, for example, how we make generalizations relevant to humans from observations of other organisms. Which of the following organisms would you want to know the most about in predicting how humans might respond to a particular disease treatment: a mushroom, a chimp, a corn plant, or a fruit fly? Most people will quickly pick the chimp out of this lineup. But why? Of course, the chimp looks the most like us. But why is this? It’s because we share a much more recent common ancestor with the chimp than we do with the others—we have had much less time to diverge from one another and we therefore share many attributes retained from our common ancestor. Of course, we also share common ancestors with the mushroom, the fruit fly, and the corn plant, but these existed in the much more distant past, and we have obviously all diverged very considerably since then. When it comes down to it, it is only this phylogenetic reasoning

that leads us to trust predictions about all sorts of attributes that we can’t immediately observe, such as responses to particular medicines. Yet phylogenetic knowledge is rarely directly acknowledged as the basis for so many of the comparisons that we make on a daily basis.

Why might it help to make phylogenetic reasoning more explicit? Consider a family visiting an aquarium and observing a tunafish and a dolphin. Most parents seem to appreciate that tunas and dolphins are superficially similar but not very closely related to one another, and they commonly “explain” to their children that the tuna is a true fish while the dolphin is really a mammal. They are intending to express something about relationships but are doing so in a way that provides little real understanding. Noting that these organisms have been classified in different named groups amounts to just rephrasing that they differ from one another. It helps a bit, as parents often will, to list some differences between these organisms: fish have scales whereas mammals have hair, and so on. But this still is nowhere near as revealing as bringing phylogenetic relationships explicitly into the discussion (figure 1). For example, it might then be noted that dolphins are more closely related to mice, elephants, and bats, not to mention to lizards, turtles, birds, and frogs, than they are to tunafish. Among other things, this perspective provides the basis for concluding that dolphins descended from ancestors that lived on the land and had regular limbs, which means that the dolphin lineage must have moved into the water where limbs were lost (or greatly modified). Tunafish, on the other hand, never had terrestrial organisms in their ancestry—they are ancestrally aquatic and have fins, not limbs.

Notice that explicitly adding phylogeny into the discussion serves to highlight evolutionary change through time, as opposed to static differences (O’Hara, 1988). In this case, it implies that there was once a shift from living in the water to living on land, which, among other things, entailed the evolution

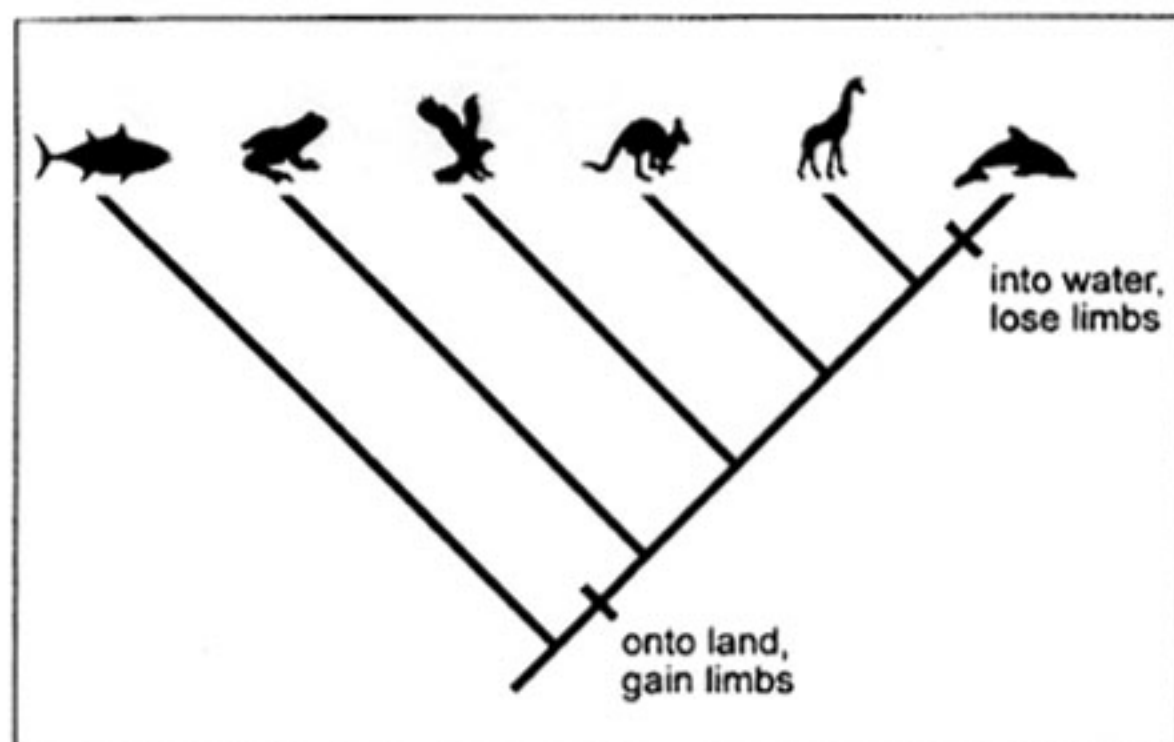


Figure 1. A greatly simplified phylogeny of the vertebrate animals showing that tunafish and dolphins are very distantly related, despite their similarity in body form. Evolutionary shifts in habitat (from water to land and back again) and in characters (the gain and loss of limbs) are highlighted by making the phylogeny explicit.

of limbs, and later a shift from the land back into the water and the loss of limbs (figure 1). The phylogeny provides us with a historical narrative about the direction of evolutionary change, and in this case it highlights convergence in the dolphin lineage on a fishlike solution to living in the water. From this perspective, many observations fall into place. For example, it makes sense that dolphins have hair, mammary glands, and lungs, all of which were retained from their terrestrial mammalian ancestors. Many new questions also open up. For example, the observation of convergent evolution properly frames the question, What's so great about being shaped like a torpedo when you move through the water? In short, phylogenies make biological comparisons more productive. In the process, making explicit use of phylogenetic trees raises consciousness about evolutionary change, making it easier for students to absorb evolutionary thinking and incorporate it naturally into their learning.

Reading Trees

A critical first step in making use of phylogenetic information is becoming comfortable with what phylogenetic trees are; that is, what they are meant to represent, how they should (and should not) be read, and how we converse about them. Perhaps the best way to get started is simply by drawing (growing) a phylogenetic tree from the bottom up. Start with a single ancestral species moving through time, have it branch in two at some point, have one or both of the descendant species branch again later on, perhaps have some species go extinct along the way, and so forth, on up to a set of species that exist in the present.

Now think about the meaning of "phylogenetic relationship." We say that two (or more) species are more closely related to one another than either one is to a third species, if and only if they share a more recent common ancestor (figure 2). And, to refer to a complete branch of a phylogenetic tree—one that includes an ancestor and all its descendants—we use the words "monophyletic group" or "clade." It is critical to appreciate that the definitions of phylogenetic relationship and of monophyly that I have just given never refer to organismal similarity. Closely related species (members of a clade) may often, in fact, be more similar to one another than they are to more distant relatives (in the example above, for instance, humans and chimps are more similar to one another than either one is to a corn plant), but phylogenetic relationship is ultimately measured only in terms of the recency of common ancestry and not by the similarity of organisms to one another. The importance of this distinction will become clear in the following, when we explore in a little more detail divergence and convergence along the branches of a phylogenetic tree.

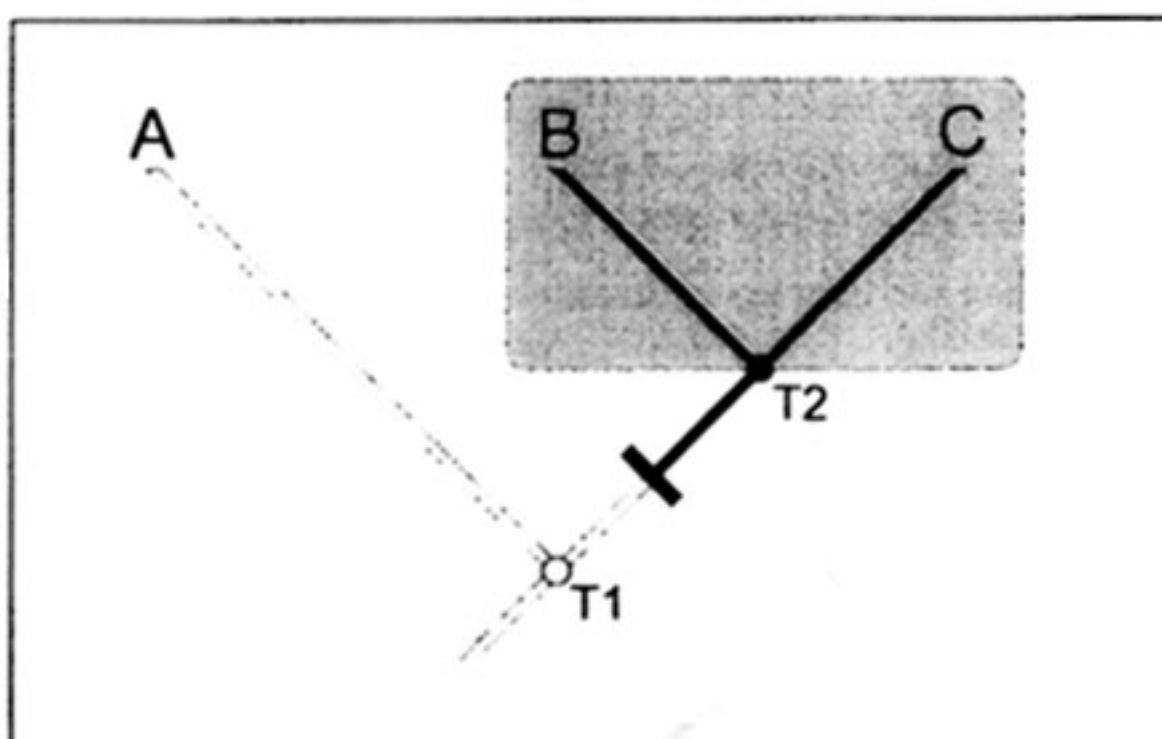


Figure 2. "Phylogenetic relationship" refers to sharing common ancestors, not to similarity. B and C are more closely related to one another than either one is to A because B and C share a more recent common ancestor (at T2 as opposed to T1). The shaded area marks a monophyletic group (or clade), which contains an ancestor and all of its descendants. Note that this is not the only clade that could be shown on this tree; for example, everything descended from the ancestor (at time T1) of A, B, and C forms a clade. The change in branch color from white to black (which is also marked by a bar across the branch) signifies an evolutionary change in a character from one state to another.

Two other points are worth noting about reading phylogenetic trees, since they often seem to confuse beginners. First, a phylogenetic tree is like an Alexander Calder mobile in the sense that the branches can be swiveled around any particular node in every which way, but the relationships remain the same. Second, there is no favored side or tip of the tree toward which everything is heading. There is a tendency for novices to read trees from left to right, and therefore

to consider the branches on the left to be “primitive” and the one farthest to the right to be the most “advanced.” Another common mistake is to interpret a less diverse “basal” clade as possessing the ancestral state of a character as compared with its more diverse but, of course, equally basal sister clade (Crisp & Cook, 2005). Often, it seems that the authors of published trees even cater to these preconceptions, for example, by placing the branches that they happen to be most interested in as far to the right as possible. This is especially true whenever *Homo sapiens* is included in a tree, and in general it seems difficult for people to resist reading phylogenetic trees as though everything leads up to humans. This is a holdover from the much earlier, pre-Darwinian image of life as a ladder leading from pond scum on a bottom rung to humans at the very top. But, as Robert O’Hara (1992) has stressed, phylogenetic trees are ramifying structures and can be read from the base toward any tip one wishes to focus on. The story of evolution, in other words, can be “told” from the standpoint of a mushroom (with everything viewed as leading up to it) just as much as from the vantage point of a human. There is no one natural perspective—it depends only on what one is interested in and wishes to highlight at the moment.

It is also critical to appreciate how phylogenetic trees are used to infer the conditions present in ancestors (internal segments in the tree) and thereby the direction and sequence of evolutionary change (figure 2). Every characteristic present in any organism evolved at some point along the branches of the tree of life. Each one originated (via mutation) in some population and then (owing to natural selection or genetic drift) rose in frequency, eventually to fixation. Knowledge of phylogenetic relationships, combined with information on the features of known organisms, can be used to infer where in the tree (along which branches) particular features of interest most likely arose, and therefore what ancestors were like.

There are a variety of methods for inferring both phylogenetic relationships and ancestral conditions (employing different optimality criteria, such as maximum parsimony or maximum likelihood; reviewed in Felsenstein, 2003; Holder & Lewis, 2003), but the details of these methods are perhaps not so critical from the standpoint of teaching biology at the K–12 level. A few simple examples tend to provide students with enough of an intuition to move forward in using trees. For instance, all other things being equal,

if the members of two sister lineages all possess a certain characteristic, say the presence of limbs, and this condition is absent in all more distant relatives, then the condition was most likely present in the common ancestor of the two lineages and retained by the descendants (figure 2). Of course, there are circumstances where this conclusion might not be justified. For example, if the rate of evolution is high in the trait of interest and a long time has passed since the lineages diverged, then it may be more likely that the shared trait actually evolved independently. When possible, it also helps to have students play with interactive computer programs such as MacClade (Maddison & Maddison, 2000; see also Mesquite, www.mesquiteproject.org), which quickly drive home the connection between hypothesized phylogenetic relationships and inferred ancestral character states.

Using Trees in Making Comparisons

The use of phylogenetic trees in comparative biology has expanded dramatically over the past few decades, to the point that hardly an area of biology remains untouched. To provide a flavor of the possibilities, I will touch briefly here on several uses of phylogenies by referring to projects that I have recently been involved in. This, of course, is a highly biased sample, if for no other reason than the emphasis is on plants (and fungi). Also, my examples concern evolutionary biology and ecology, as opposed to the many uses of phylogeny in medicine, agriculture, conservation, and so on (for which see Yates, Salazar-Bravo, & Dragoo, 2004). In any case, I hope that the examples mentioned here will help interested readers locate the scores of other studies that have explored similar territory (see also Futuyma, 2004).

The ability to infer where and when character changes occurred during the course of phylogeny opens up many exciting opportunities for understanding the patterns and processes of evolution. For example, there are a variety of methods to assess whether the evolution of a particular trait of interest was correlated with the evolution of other traits, in which case there may be a causal connection between them (e.g., one trait may have promoted the evolution of the other). In one such study (Hibbett & Donoghue, 2000), we documented subtle evolutionary connections between the type of wood decay mechanism and the genetic mating systems of basidiomycete fungi (mushrooms and relatives). It might also be that a particular trait change was historically correlated

with certain environmental or biogeographic changes (e.g., movements from the tropics into the temperate zone, or movements from North America into South America). Phylogenies can also be used to infer whether particular directions of character change have been favored in evolution. For example, using a maximum likelihood approach, we argued that bilateral flower symmetry may have been lost more often than gained (Ree & Donoghue, 1999).

By examining whole suites of character changes at once, it may even be possible to reconstruct what a particular ancestor looked like or how it probably functioned. In one such study (Chang, Jonsson, Kazmi, Donoghue, & Sakmar, 2002), we inferred the DNA sequence of the rhodopsin visual pigment gene for the Triassic ancestor of the archosaurs (the clade that includes alligators, dinosaurs, and birds). It was even possible to synthesize the hypothesized ancestral protein in the lab and measure the wavelengths of light that it absorbed, and therefore (by inference) the visual capacity of these organisms.

It is also possible to make inferences about the geographic ranges of ancestors and hence the direction of movement of lineages in the past. For example, using a method that minimizes dispersal and extinction events (dispersal-vicariance analysis: Ronquist, 1997), we recently hypothesized that many plant groups in eastern North America had ancestors that once lived in Asia and that these lineages may have entered North America at several times during the Tertiary, perhaps mainly through the Bering land bridge (Donoghue & Smith, 2004). Likewise, by inferring the physiological and anatomical attributes of ancestors, it is possible to hypothesize the habitats that they once occupied. On this basis, we have suggested that the first flowering plants probably lived in shady, disturbed habitats—what we're calling the "dark and disturbed" hypothesis (Field, Arens, Doyle, Dawson, & Donoghue, 2004). Finally, by combining inferred ancestral habitats with age estimates for key lineages, we have concluded that tropical rain forests probably originated in the mid-Cretaceous, quite a bit earlier than postulated by previous researchers (Davis, Webb, Wurdack, Jaramillo, & Donoghue, 2005).

There are a variety of other uses of trees that don't rely on inferring ancestral conditions (of characters, ranges, habitats, and so on). It is now common, for instance, to compare phylogenetic trees obtained from different groups of organisms to test the degree to which these correspond, either in terms of their

shapes and/or in terms of the estimated ages of various events (Page, 2002). One obvious use of such comparisons is in asking about the degree to which the diversification of a group of parasites has been driven by the diversification of their hosts. Trees are also often compared in studies of historical biogeography, where the idea is to discover the extent to which the relationships of organisms occupying particular geologic and biotic regions correspond to one another (e.g., are species from New Zealand and South America more closely related to one another than they are to species from Australia?). It is also worth noting that there are a variety of methods—using tree shape with or without information on the absolute ages of clades—for inferring where in a phylogenetic tree there may have been significant shifts in the rate of diversification (e.g., Nee, 2001; Moore, Chan, & Donoghue, 2004). Used in concert with methods for inferring ancestral character states, these approaches can be used to test whether particular character changes ("key innovations") may have stimulated an increase in speciation rate, a decrease in extinction rate, or both. Finally, it should be mentioned that phylogenetic trees are beginning to be used in studies of community ecology (e.g., Webb, Ackerly, McPeck, & Donoghue, 2002) and in measuring and elucidating global patterns of biodiversity (e.g., Wiens and Donoghue, 2004).

Sometimes it is of great interest to compare trees obtained from different sorts of data. For example, in studies of plant evolution, it has become routine to compare a gene tree obtained from an analysis of one or more nuclear genes with one derived from the (typically) maternally inherited chloroplast genome. Discordance in this case might be attributable to hybridization in the past. Similarly, microbiologists compare trees from different genes to infer the occurrence of lateral gene transfer events.

Finally, it is important to draw attention to what is probably the most obvious and common use of trees, namely, to make generalizations that extend the knowledge obtained from organisms that have been studied in detail to those that have not. Much of our detailed knowledge of biology has been obtained from only a handful of model organisms, such as the fruit fly, *Drosophila melanogaster*; the nematode worm, *Caenorhabditis elegans*; and the corn plant, *Zea mays*. Generalizing this knowledge to other organisms that have not been studied in such detail, or perhaps not at all, relies directly upon phylogeny.

In plants, for example, much of our knowledge of development comes from studies of corn; the tiny mustard plant, *Arabidopsis thaliana*; and the snapdragon, *Antirrhinum majus*. Finding shared genes underlying particular developmental processes (and functions) in *Arabidopsis* and *Antirrhinum*, but not in corn, allows us to predict that these were inherited from their shared ancestor and that all other plants derived from that ancestor also possess these genes/functions. In this case, predictions can be made about well over 120,000 species that have not been examined in detail. Of course, such predictions may prove to be incorrect as we examine additional species in detail, but knowledge of phylogeny permits us to at least formulate working hypotheses about the distribution of genes and functions.

The study of genome evolution falls in this same general category. At present, only a handful of eukaryotic genomes have been sequenced in their entirety, and when these are placed in a phylogenetic context we can begin to make generalizations about genome size, structure, and function. One important area of research concerns the diversification of gene families, especially those that underlie development. As it turns out, many important regulators of development are members of large gene families, the members of which have diversified to play a variety of different roles. By inferring relationships among the multiple members of a gene family from a variety of organisms, we can begin to piece together where and when in the tree of life various major gene duplication events (and losses) occurred.

Phylogenetic Surprises

Some of the most effective uses of phylogenetic trees in teaching biology and evolution are those that highlight counterintuitive results. Students often appear to assume that evolution proceeds at a more or less even pace, in terms of the evolution of characters and the differentiation of lineages through time, but also with respect to rates of speciation and extinction. If this were the case, then closely related species would always be more similar to one another than they are to distant relatives (see above), and the number of species belonging to different clades would correspond to the ages of those clades. These expectations are not infrequently upheld in real life, enough so that the dramatic exceptions stand out as surprises. Catching students off guard with a surprise can provide an excellent opportunity to drive home general mes-

sages about evolution that might otherwise seem too abstract to be of interest.

Some phylogenetic surprises relate to the pace of speciation and extinction. Our ability to infer with increasing confidence the absolute times of divergence points within trees has resulted in some extraordinary insights into the generation of diversity and the maintenance of lineages. At one end of the spectrum are cases of extremely rapid radiation, in which hundreds of species are produced within a very short time. Some of the best known cases are the so-called "species flocks" of cichlid fishes in the rift lakes of East Africa (e.g., Salzburger & Meyer, 2004). In Lake Victoria, for example, it is estimated that literally hundreds of species (perhaps as many as 500) have originated within the last 100,000 years, which raises fascinating questions about the roles of geography, ecological factors, and sexual selection in driving speciation in this system. At the other end of the spectrum are so-called living fossils—lineages that appear to have existed for very long periods of time, apparently without much morphological change and without spinning off many other species. Well-known examples include the maidenhair tree, *Ginkgo biloba*, and the coelacanth, *Latimeria chalumnae*, both of which have probably existed in much the same form at least since the Mesozoic.

Other surprises arise from extreme and sometimes very unequal amounts of change along particular branches of a tree, such that close relatives end up looking very different from one another, or from convergence on very similar structures in distantly related lineages. Some examples involve both phenomena (figure 3). One of my favorite cases in plants concerns convergence on the water-lily life-form. Previous classification systems placed the water lotus (*Nelumbo*) close to the true water lilies (Nymphaeales), but it now appears, based on studies of both morphology and DNA sequence data, that the two groups are only very distantly related to one another (their most recent common ancestor probably existed over 130 million years ago). The water lilies now appear to be a very early branching lineage within the flowering plants, whereas the water lotus belongs within the large "eudicot" clade, where it seems to be most closely related to the sycamore trees (*Platanus*) and the proteas (Proteaceae) of the Southern Hemisphere (Soltis, Soltis, Chase, Endress, & Crane, 2004). Even for botanists this is a startling result, both in view of the similarities of the leaves (lily

pads) and flowers of water lilies and the lotus, but also in terms of the vast differences in appearance between the lotus and its close relatives, which are mostly large trees, many living in dry areas. I've found that this remarkable discovery consistently stimulates excellent discussions on the power of natural selection, the nature of plant development, paleobiogeography, and any number of other evolutionary topics.

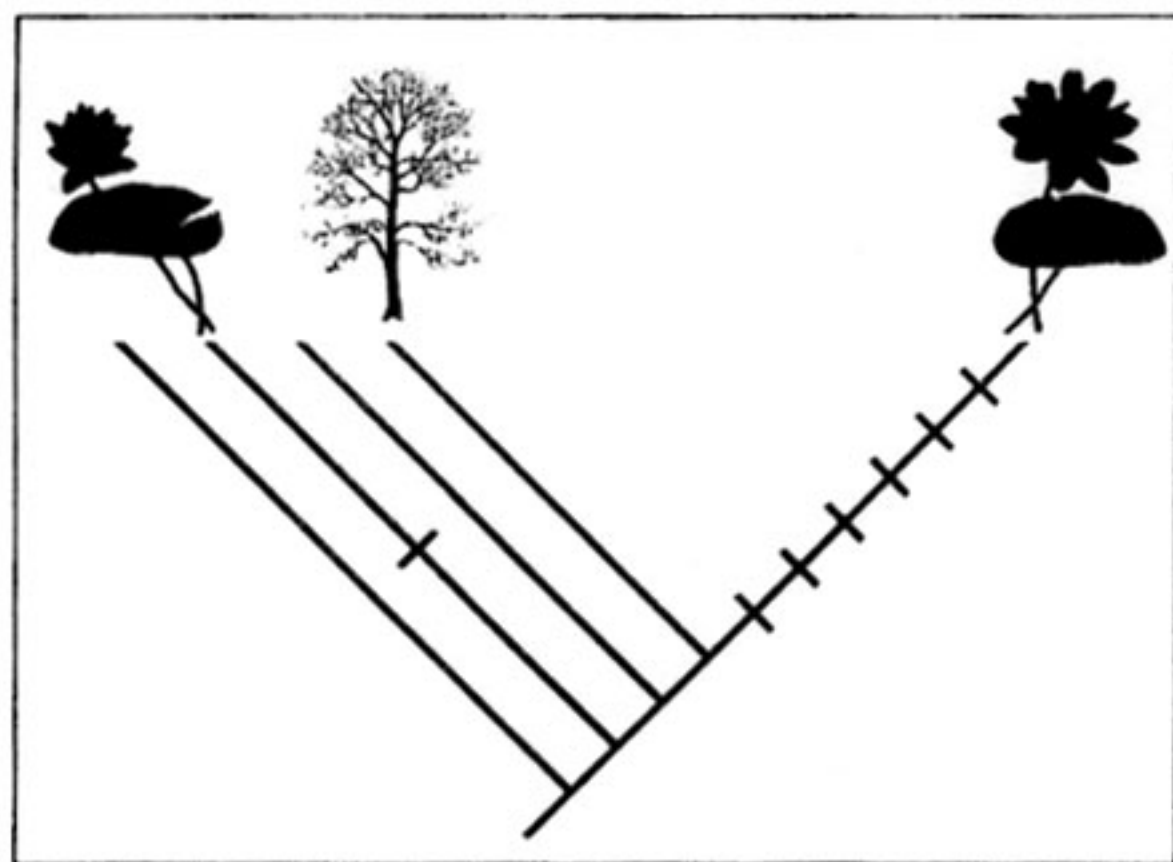


Figure 3. A phylogenetic tree showing that more change has occurred along the branch on the right than along the other branches. In this case, the water lotus (symbolized at the far right) has diverged a great deal from its common ancestor with the sycamore tree. In the process, the water lotus and the water lilies (on the left) have converged in the morphology of their leaves and flowers.

Other wonderful and handy examples of convergence include the evolution of the stem-succulent cactus lifestyle in the true Cactaceae of the New World, in the spurges (Euphorbiaceae) of arid Africa, and in a wide variety of other lineages. Mistletoe-like parasitic plants, with greatly reduced photosynthetic capabilities, have also evolved many times independently, as have insectivorous plants. In the case of the insectivores, it is especially remarkable that pitcher plants have evolved independently in distantly related clades: the New World pitchers (Sarraceniaceae) belong within the Ericales (with blueberries, brazil nuts, and the like), phylogenetically very distant from the Old World pitchers (Nepenthaceae), which are more closely related to some other well-known insectivores (including sundews and the Venus flytrap) and in turn to the Polygonales (rhubarb and relatives) and the Caryophyllales (carnations and relatives). Being a botanist, I've mentioned examples of convergence in plants, but there are many spectacular examples in animals, including the independent origin (and loss) of eyes and of elaborate social systems (e.g., see Conway Morris, 2003).

I often use examples of convergence to highlight aspects of the evolution of organismal design and function. One of my favorite cases concerns the evolution of the tree habit in vascular plants (see Donoghue, 2005, and references therein). On the basis of our much-improved knowledge of vascular plant phylogeny (e.g., see Pryer, Schneider, & Magallon, 2004), it appears that large trees (plants with a single trunk, branched well aboveground) evolved independently within several distantly related lineages (figure 4). Virtually all the familiar trees (maples, oaks, pines, and so on) belong to just one of these lineages, which is the clade that includes all of the seed-bearing plants. Seed plants were trees ancestrally, but this condition has been lost repeatedly (giving rise to other woody forms and to herbaceous plants) and has been regained in some cases (e.g., palm trees evolved within the ancestrally herbaceous monocotyledon lineage of flowering plants). Outside of the seed plants, trees evolved within the lycophyte lineage (which contains the modern club mosses), within the equisetophyte lineage (containing modern horsetails), and in two of the major "fern" lineages (Marattiales and Polypodiales).

Concentrating just on the comparison of extinct lycophyte trees of the Carboniferous with the more familiar seed plant trees of today, it turns out that there are several significant differences in the details of their construction and function (figure 4). In standard seed plants, a cylinder of meristematic cells in the stem known as the cambium produces secondary xylem (wood, for water movement) toward the inside of the stem, secondary phloem (for transport of nutrients) toward the outside, and additional cambial cells. In contrast to this so-called bifacial cambium, in the lycophyte trees the vascular cambium appears to have been unifacial—it produced only secondary xylem, no secondary phloem, and no other cambial cells. Evolution of the unifacial cambium had several major consequences. The cambial cylinder in these plants remained small owing to the inability to add new cambial initials, and therefore they produced rather little wood on the inside of the stem; strength was provided instead by a specialized periderm tissue situated outside of the cambium. But even more important, in the absence of phloem to transport carbohydrates from the usual sites of photosynthesis (leaves) down to the growing roots, these plants needed to maintain photosynthetic activity in the vicinity of any living tissue. Amazingly, it is thought

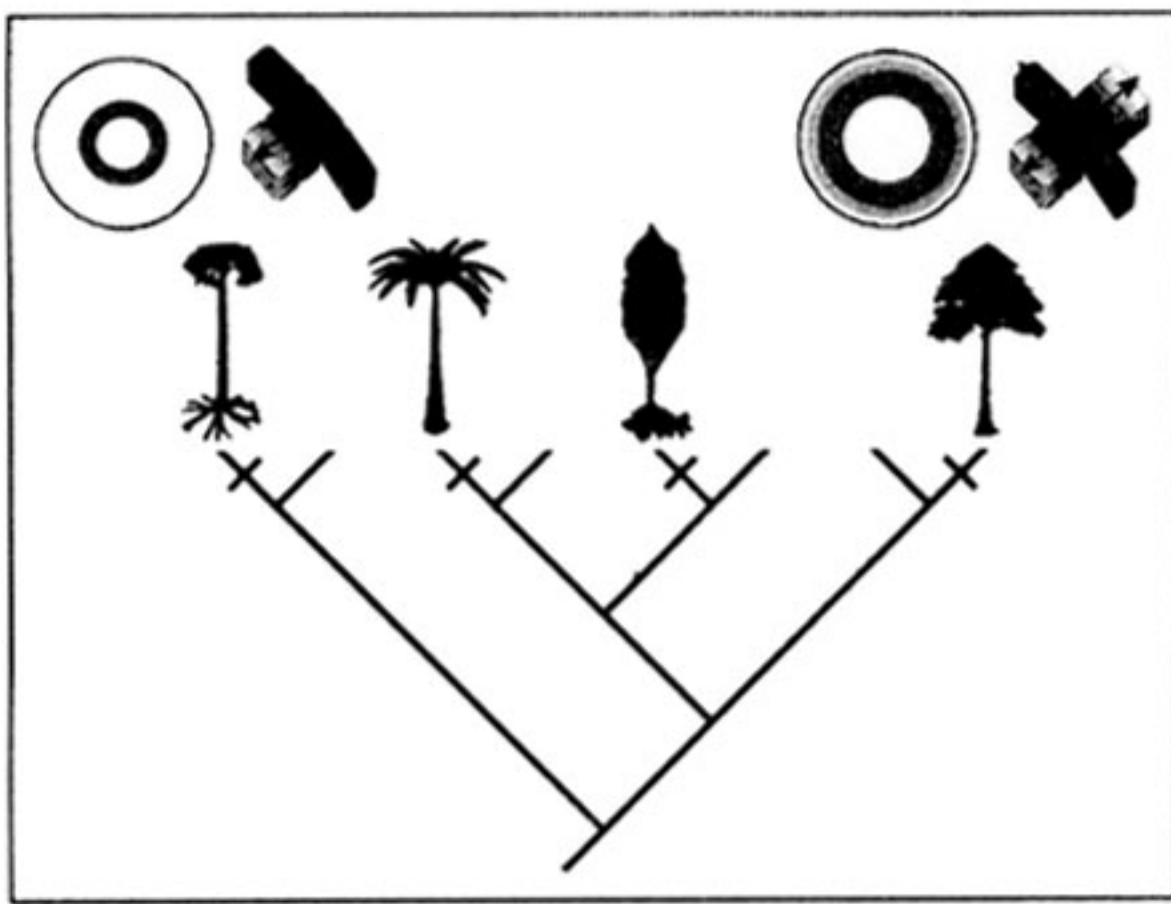


Figure 4. A greatly simplified phylogeny of the vascular plants showing that the tree life-form has evolved a number of times independently. Shown from left to right, it evolved in the lycophyte, marattialean fern, equisetophyte, and seed plant lineages. Lycophyte trees appear to have produced a cylinder of unifacial cambium (dark-colored cells), which produced only a rather small amount of secondary xylem (dark gray) to the inside of the stem. In contrast, in the seed plant lineage a bifacial cambium evolved, producing xylem to the inside (dark gray), phloem to the outside (light gray), and new cambial cells.

that the “rootlets” of these plants could photosynthesize and that they supplied the developing “root” system. Furthermore, the underground stem apparently ramified underground for many years before quickly sending up a tall stem to dispense the spores (often in just one season).

This comparison of modern trees with the extinct lycophyte trees provides a fine opportunity to teach about the ways in which plants grow—how meristems work, where wood comes from, how the phloem functions, and so on. In my experience, students find the evolutionary comparison to be much more fun and more enlightening than studying just the trees found in seed plants today. This comparison also supports a variety of general messages about evolutionary biology. Most important, it provides a concrete example of the way in which the “same” general outcome (the tree habit) can be achieved in different ways in different lineages. In this case, the different solutions also had a significant bearing on subsequent evolution in the two lineages, especially in promoting the bizarre growth habits of the tree lycophytes and perhaps ultimately their demise.

Conclusions and a Proposal

Virtually every lesson in biology involves and benefits from some form of comparison. Fortunately, biological diversity provides us with nearly endless opportunities in this regard. Virtually every feature

that we might be interested in is replicated in some form in other lineages, and variations on a particular theme inform our understanding of biological function as well as of the evolutionary process.

In general, the mileage that we get out of biological comparisons depends critically on knowledge of phylogenetic relationships—that the organisms we’re referring to are either quite closely or quite distantly related to one another. Yet this is rarely acknowledged. In the past, this may have been excusable, as knowledge of phylogeny was often quite rudimentary. Today our understanding is vastly improved and increasing at an exponential rate (Hillis, 2004; Cracraft & Donoghue, 2004b), and the time is certainly right to extend the use of phylogenetic information into K–12 classrooms. There appear to be two main impediments to doing this at the moment. First, teachers have generally not been trained in this area and often lack sufficient comfort with this material to leverage new phylogenetic knowledge. Second, the knowledge itself has been accumulating so rapidly that it is hard to keep up with, and it certainly has not yet been digested for classroom uses. Both of these problems will need to be addressed if we are to take proper advantage of this new knowledge base.

With respect to training, it is important to appreciate that in most cases the classroom use of phylogenetic trees does not require a detailed knowledge of phylogenetic methodology. One generally does not need to know precisely how trees are computed under maximum likelihood or other such optimality criteria, although for some purposes it may be useful to direct students to the relevant computational tools (e.g., see Joe Felsenstein’s *Phylogeny Programs*, <http://evolution.gs.washington.edu/phytip/software.html>). What it does take, however, is a solid understanding of the basic principles. Specifically, it is critical to clearly comprehend the basic notion of phylogenetic relationship and how to read trees. In this regard, some Internet resources are already available (e.g., see Douglas Eernisse’s *Introduction to Phylogeny: How to Interpret Cladograms*, http://biology.fullerton.edu/biol402/phytolab_new.html; Steven Nadler’s *Tree Basics, Tree Inference, and Tree Thinking*, http://www.abo.fi/fak/mnf/biol/nni/lec_nadler3.htm; and The *Phylogeny Wing* of the University of California–Berkeley, Museum of Paleontology site, <http://www.ucmp.berkeley.edu/exhibit/phylogeny.html>). Fortunately, Samuel Donovan and others have begun the development of

a Web clearinghouse devoted specifically to tree thinking and the teaching of phylogenetic biology (<http://www.tree-thinking.org/>), and these topics are also now highlighted on the Understanding Evolution Web site (<http://evolution.berkeley.edu/>) and in BioQUEST (<http://www.bioquest.org/>; see Brewer, 1996).

Another key to training in this area is to focus on how best to use phylogenetic information to enrich biological comparisons. My sense is that phylogenetic surprises, such as those I have highlighted above, can provide an excellent stimulus, but the educational value of such exercises depends ultimately on making a clear connection to more general objectives, such as understanding organismal design and basic evolutionary principles. This obviously takes some thought.

Access for educators to up-to-date phylogenetic knowledge is currently quite problematic. In part, of course, the problem is that phylogenetic research is blossoming, and it is difficult to stay on top of all of the major new discoveries (Cracraft & Donoghue, 2004a). Whereas TreeBASE (www.treebase.org) provides some coverage of the primary phylogenetic literature, this is meant to be a research tool and will only rarely be of direct use to K–12 teachers. The Tree of Life Web Project (<http://tolweb.org>), which aims to provide a synthetic account of the entire tree, is much more appropriate for teachers, but this is a work in progress and in any particular case may provide little relevant information. Some segments of the Tree of Life Web Project (<http://tolweb.org/tree/learn/learning.html>) are specifically designed for learning and teaching about phylogeny, but these remain underdeveloped. Several classroom phylogeny exercises are available via the Internet (e.g., see All in the Family, Public Broadcasting Service, <http://www.pbs.org/wgbh/evolution/change/family/index.html>; and What Did T. Rex Taste Like: An Introduction to How Life is Related, University of California–Berkeley, Museum of Paleontology, <http://www.ucmp.berkeley.edu/education/explorations/tours/Trex/guide/index.html>), but these too are quite limited at the moment.

A missing resource, it appears to me, is a Web site devoted to the use of phylogenies in making biological comparisons in the K–12 context. To this end, I believe it would be productive for a collection of interested educators and phylogenetic biologists to collaborate on developing a Web-accessible resource to provide carefully documented case studies in phylogenetic

comparison, including authoritative phylogenetic information, specific lesson plans, and suggestions on materials that might be incorporated in the classroom. One source of examples for such a resource would be teachers who have already developed particular examples to some extent (such as the example above on the independent evolution of large trees); these might simply need to be refined, standardized, and rendered accessible. But I also imagine harvesting the vast number of biological comparisons that are already featured in some way or another in the standards-based curricula that are being implemented across the country. A first phase, of some interest in its own right, would simply aim to identify the sorts of comparisons that are already being used in K–12 classrooms. The goal would then be to flesh these out with the relevant phylogenetic knowledge, and especially to develop the lessons about organisms and evolution that this added information would support. I suspect that the development of such a resource would greatly accelerate the incorporation of phylogeny in teaching at all levels and that this would in turn have a significant impact on the teaching and comprehension of evolutionary biology.

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