

Darwin's Missing Link—A Novel Paradigm for Evolution Education

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ABSTRACT: Microevolutionary mechanisms are taught almost exclusively in our schools, to the detriment of those mechanisms that allow us to understand the larger picture—macroevolution. The results are demonstrable; as a result of the strong emphasis on micro processes in evolution education, students and teachers still have poor understanding of the processes which operate at the macro level, and virtually no understanding at all of the history of life on our planet. Natural selection has become synonymous with the suite of processes we call evolution. This paper makes the case for a paradigm shift in evolution education, so that both perspectives—micro and macro—are given equal weight. Increasingly, issues of bioethics, human origins, cloning, etc., are being cast in a light that requires an understanding of macroevolution. To deny our students access to this debate is to deny the call for universal science literacy. A methodology from professional practice is proposed that could achieve this goal, and discussed in light of its utility, theoretical underpinnings, and historical legacy. A mandate for research is proposed that focuses on learners' understanding of several challenging macroevolutionary concepts, including species, the formation of higher groups, deep time, and hierarchical thinking. © 2006 Wiley Periodicals, Inc. *Sci Ed* 90:767–783, 2006

INTRODUCTION

A cursory glance at the evolution section of any grade-school biology textbook will reveal the prominence given to Charles Darwin, his voyage on HMS *Beagle*, natural and artificial selection, and a variety of other elements that support the theory he expounded in *The Origin of Species*. However, I have yet to find space devoted to what I consider to be his most important contribution to our understanding of evolution. Arguably, Darwin's most radical claim was that all of life had descended from a common ancestor. Perhaps, to reinforce this contention, the only figure he included in *The Origin of Species* was a branching diagram—a *cladogram*—depicting the origin and fate of species and natural groups of species: the persistence though time of some, and the extinction of others (Figure 1). The resulting hypothesis of relationships traces the history of extant taxa (taxa are any taxonomic group)

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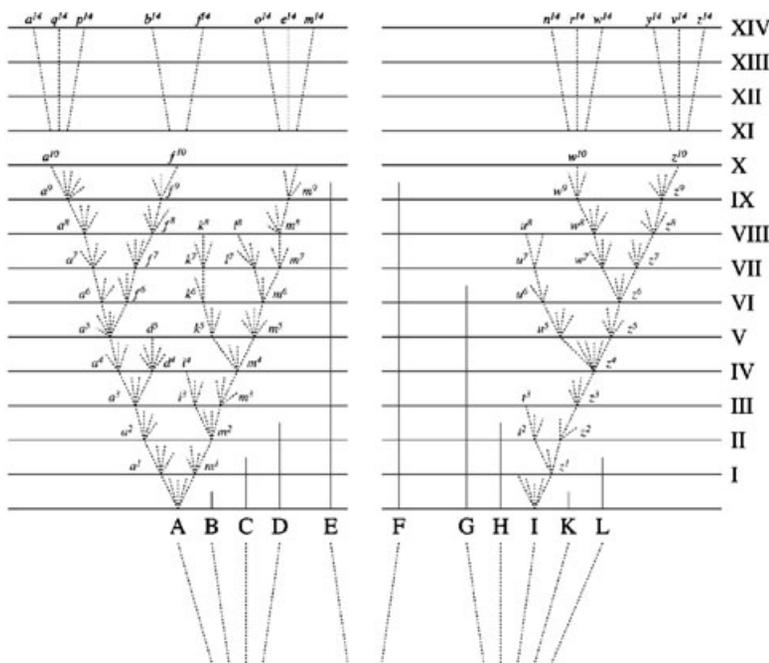


Figure 1. Darwin's attempt to reconstruct a phylogeny of ancestor–descendant species relationships from *The Origin of Species*, 1858.

back through time to their common ancestors. This hypothesis and the theoretical basis that underpins it are the backbone of understanding *macroevolution*—the subdiscipline that synthesizes events of earth history and deep time with the mechanisms that generate and maintain the biodiversity of our planet. Without a clear perspective on macroevolution, an understanding of the full spectrum of evolution is simply not possible. This notwithstanding, microevolutionary mechanisms are taught almost exclusively in our schools, to the detriment of those mechanisms that allow us to understand the larger picture. The effects are demonstrable; as a result of the strong emphasis on micro processes in evolution education, students and teachers have a poor understanding of the processes that operate at the macro level, and virtually no understanding at all of the history of life on our planet (Anderson, Fisher, & Norman, 2002; Anderson, Randle, & Covotsos, 2001; Bishop & Anderson, 1990; Brumby, 1979; Catley, 2001; Clough, 1994; Clough & Wood-Robinson, 1982; Cobern, Gibson, & Underwood, 1999; Demastes, Good, & Peebles, 1995, 1996; Greene, 1990; Halldon, 1988; Jensen & Finley, 1996; Lawson & Thompson, 1988; Lucas, 1971; Passmore & Stewart, 2002; Rutledge & Warden, 2000, 2002; Samarapungavan & Wiers, 1997; Sandoval & Morrison, 2003; Settlege, 1994; Sinatra, Southerland, McConaughy, & Demastes, 2003; Southerland, Abrams, Catherine, & Anzelmo, 2001; Stewart & Rudolph, 2001).

This paper makes the case for a paradigm shift in evolution education, so that both perspectives—micro and macro—are given equal weight, and perhaps even more importantly, that each is presented in such a way as to inform the other. Such a shift would result in students who possess a holistic view of evolution, one that captures the full grandeur of Darwin's theory. This vision would encapsulate the entire range of evolutionary biology, from variation in the genome of individuals, through natural selection, to speciation, extinction, and the formation of higher groups (cladogenesis), including their history throughout

time. In the process, students would come to understand the mechanisms that create and maintain the biodiversity of the planet. They would appreciate its history, fragility, and the plight of much of it—and as a result would be better-informed citizens of the Earth.

As currently construed, evolution education misses much of the picture above the level of the organism. Far from taking center stage, species—the very units of evolution—are relegated to the role of confusing, amorphous entities that appear to be little better understood by the general public than by Aristotle himself (Catley, 2001, 2002; Evans, 2000; Samarapungavan & Wiers, 1997). Explorations of species radiations, based on novel evolutionary characters (*cladogenesis*, leading to the formation of higher taxa), are not part of the school biology mandate (Catley, 2002; Catley, Lehrer, & Reiser, 2005). An appreciation of deep time and extinction—both inextricably linked to earth processes—is seldom seen as of more than passing interest. And ecology, so difficult yet vital a topic for society to understand, is rarely approached from the perspective of being a product of evolution.

Ecology, if presented in any coherent form at all in school, is mostly as a one-dimensional array of causal relationships among organisms and their environment. The science education literature is replete with documentation of common misunderstandings and alternative concepts of ecological processes. However, despite this recognition, little has been done to examine innovative ways to engage students in this subject. We continue to teach ecology in ways that fail to integrate the multiple hierarchic levels that many studies have shown to be the hallmark of deep understanding. One innovative notion is that classification is best understood in an ecological context, such that the sets of inter-relationships are presented as manifestations of natural selection over very long periods of time. Adaptations, rather than seen in isolation as “needs of an organism,” are best introduced as characters or behaviors that have been selected by the environment over time to be those best suited to a particular habitat. This way of classification (in the form of cladograms) becomes a powerful predictive tool simply because it is based on observable characters that reflect the history of events that led to the patterns of both evolutionary and ecological relationships among taxa.

Such visualizations would provide students a sense of the historical processes that underpin both sets of relationships and act as a starting point for developing new questions. Students will begin to see kinds (taxa) as collections of attributes (characters) with a history that largely determines how they operate within the ecological systems they study. Consequently, they will appreciate the fragility of these systems such that abrupt changes which result from man-made perturbations cannot be withstood. These systems, selected for stability over eons, are simply unable to change in the time frames of human life times.

Both autecology (the study of single species) and synecology (the study of community systems) are disadvantaged when not considered from a historical viewpoint. Research has shown that students without a sufficient understanding of macroevolution take little account of the specialist and generalist adaptations that are the products of millions of years of selection. They assume, for example, that when the prey of a particular predator is removed from a predator/prey system, the predator simply switches to another prey species without any long-term effects on the ecosystem (Eilam, 2002). Students believe that an organism’s “needs” are fulfilled by simply feeding on something else, unaware that as products of selection sets of trophic relationships experience complex and mostly unpredictable cascade effects when disturbed.

As this piece is being written, early in 2005, there have been a spate of articles in the popular media decrying the fact that despite the obvious need and the mandated requirements of the National Science Education Standards, teachers—for a variety of reasons—are not engaging in the teaching of evolution. Typical of such articles is one from the *New York*

Times, “Evolution Takes a Back Seat in U.S. Classes”: <http://www.commondreams.org/headlines05/0202-12.htm>. A National Science Teachers Association survey (April 2005) found that 30% of teachers felt “pushed to de-emphasize or omit evolution or evolution-related topics from their curriculum.” A major recommendation of this paper is that specific tools, those that scientists use to understand evolutionary processes, should be made available to teachers as aids to instruction in the classroom.

A HISTORICAL PERSPECTIVE

How did the imbalance between our understanding of micro- and macroevolution come to be? For a large part of the 20th century, the evolutionary model born of the “New Synthesis” of the 1930s–1940s has held sway. Seminal figures like Fisher, Ernst Mayr, Haldane, Sewall Wright, Dobzhansky, Julian Huxley, and Gaylord Simpson forged a synthesis between Darwin’s theory and genetics, paleontology, population genetics, systematics, and advances in mathematical modeling. While this endeavor represented a quantum leap in our approach to and understanding of evolution, modern systematic theory had yet to emerge. The collection of papers edited by Huxley as the book *The New Systematics* in 1940 clearly shows that the systematics of the day, while still struggling for a unifying theory, was resolutely bringing genetic and ecological perspectives to bear on the study of species. In the introduction to this publication, Huxley writes:

It is safe to prophesy that such micro evolutionary studies will become increasingly important in the near future. As such work proceeds, *The New Systematics* will gradually come into being. It will in some ways doubtless help classical taxonomy in its pigeon-holing functions; it will give a much more detailed picture of the actual facts of organic nature and its distribution in groups and in character-gradients over the globe; it will reveal many facts and principles of great importance to general biology; and through it taxonomy will become the field of major interest for all those concerned with the study of evolution at work.

The legacy of the “New Synthesis” has been a focus on population-level research throughout much of the 20th century. In particular, it has been driven by the quest to better understand genetics as it operates over real-time generations. By studying such taxa as *Drosophila* and yeast, we have accumulated vast amounts of knowledge on the molecular basis of inheritance, variation, and selection. By comparison, our knowledge of macroevolutionary processes such as speciation and the formation of higher groups has lagged far behind. By themselves, the products of the “New Synthesis” do not adequately account for the history of life or for its diversity.

During the last half-century, diagrams like those made by Darwin have been supplanted by a methodology that honors his ideas about species, relationships among them, and the genesis and extinction of groups of species. It was not until the late 1960s and early 1970s that a new theory emerged for inferring phylogeny and reconstructing the history of life. With the publication in 1966 of Willi Hennig’s *Phylogenetic Systematics* (Hennig, 1966), biologists at last had a tangible methodology rooted in empirical data and testable theory. The 1980s saw phylogenetics (a method that considers only shared, derived characters to be relevant when reconstructing phylogenies) undergo a bloody war with phenetics (a method that considers all characters to be of equal importance), with both methodologies vying to don the cloak of scientific respectability.

Only comparatively recently has phylogenetics been welcomed into the fold. Today, it is seen not only as an indispensable tool for elucidating hypotheses in all fields of comparative

biology, but, if reconstructing the history of life on our planet is seen by humanity as a worthwhile goal, as the only subdiscipline capable of achieving it. The last 20 years have seen the ascendancy of phylogenetics as one of the most important and influential areas of contemporary biology. Driven by the search for monophyletic groups (those comprising the most recent common ancestor and all descendants) based on synapomorphies (shared, derived characters), this methodology is at the same time a powerful predictive tool and a rigorous information retrieval system. Apart from providing natural classifications and testable hypotheses of evolutionary relationships, a conceptual model for understanding evolution and biodiversity, and a predictive roadmap for bioprospecting medicines, genes, etc., phylogenetics can also serve as the basis for rational conservation policies. One has only to flip through the pages of *Science* or *Nature* to find ample evidence for this claim.

The methodology I am proposing will allow students and teachers to use evidence gathered from extant taxa to construct cladograms in order to facilitate an understanding of evolution. I am also calling for research into understanding how best to introduce these ideas to students. These diagrams allow visualization of many evolutionary processes, which can be very difficult to comprehend due to the temporal and spatial dimensions involved. Cladograms are most simply understood as line diagrams that depict the distribution of characters among taxa (Figure 2). As such, they can be interpreted as a hypothesized and testable record of the history of the relationships among taxa over time. Cladograms are extremely powerful predictive tools in modern biology. They can be used to test hypotheses as disparate as the origin of the orb web in spiders and the sequence and timing of ocean inundations and drying of the continental United States during the Cenozoic (Catley, 1993, 1994; Coddington, 1989). However, they have yet to be utilized to any degree in life science education. While beginning to make an appearance in biology textbooks, they do so as disembodied entities with little or no explanation of the principles underlying them—and thus invite gross misinterpretation by both students and teachers alike. Catley and Novick (2006) have shown that undergraduates—both those with strong and those with weak biology backgrounds—have

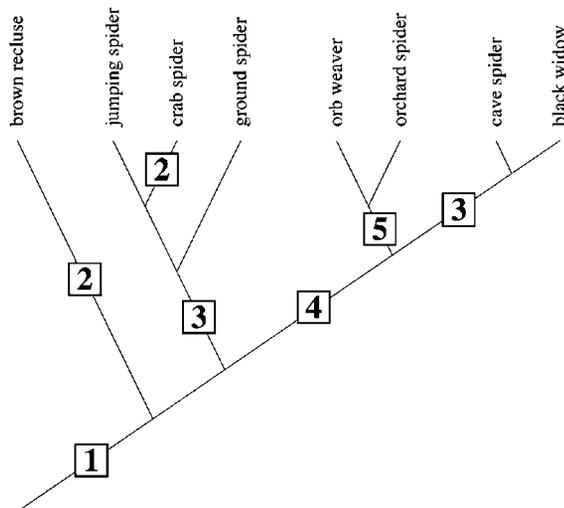


Figure 2. Cladogram showing relationships among spider taxa. Characters 2 and 3 occur more than once on the tree (i.e., they are homoplasious).

difficulty interpreting these diagrams, particularly when the same sets of relationships are displayed as different hierarchical diagrams. It seems reasonable to assume that bringing cladistic methodology into the classroom, by providing teachers with a powerful tool to help interpret and present complex evolutionary processes to their students, should also provide greater motivation to become engaged in evolution education.

UNDERSTANDING THE SCIENCE

Fully appreciating this thesis requires some understanding of three elements: *systematics*, *phylogenetics*, and *cladistics*. As biological subdisciplines and methodologies, all three tend to be used concurrently and as a result inform each other. The science of systematics is the study of species and the evolutionary relationships among them. The elements of study are species or groups of species. Unlike population geneticists, who study genetic variation among individuals, systematists discover and describe new species; then, using cladistic methodology, they reconstruct relationships among groups of species (or clades) based on special characters called *synapomorphies* (shared, derived characters). It is important to understand that species, are in fact, hypotheses. Organisms (individuals) have both traits and characters. Traits are variable among organisms (they are polymorphic), whereas characters are fixed (every member of a species exhibits the character). Such characters are thought to be the markers of the speciation event itself and are known as *autapomorphies*. Often, when species have been erected on small sample sizes of organisms, characters are subsequently shown to be traits when more specimens are examined. Consequently, the species hypothesis, at least based on that particular character, is falsified. There are countless examples in the taxonomic literature of descriptions of new species that have, at a later date, been synonymized with previously described species.

Phylogenetics is the branch of biology that constructs and tests phylogenies, but does not necessarily require the discovery and description of new species. The name of the game is to construe testable monophyletic groups of species that reflect their actual history. Armed with such phylogenies, biologists are able to test all sorts of hypotheses in biochemistry, behavior, biogeography, ecology, etc. Cladistics (explained in some detail later) is the methodology used to construct phylogenies using the criteria of parsimony. Parsimony was first purposed by William of Occam (1285–1349) and is known as “Occam’s Razor.” It is the logical principle that underpins all of western science and states that given two equally predictive theories, choose the simpler. In phylogenetic terms, the tree (or trees) that minimizes the number of evolutionary steps of the characters used to construct it is accepted as the most well supported. In other words, if two trees (topologies) constructed from the same data set are competing, the tree that minimizes the number of extra steps required to account for the data (i.e., has less characters that reverse or occur in parallel) is to be preferred. This is the most parsimonious tree, because it contains less ad hoc hypotheses and is therefore more easily falsifiable. Consequently, it is accepted as the best hypotheses of the “real” relationships.

From Aristotle through Linnaeus and even as recently as some 40 years ago, observed similarity (shared characters) has been the basis for grouping taxa together. “Similarity was similarity” and there was no way to determine whether it was as a result of convergent or parallel evolution (i.e., had no basis in most recent shared ancestry and therefore was not informative). To a large extent, such synthetic classifications were simply “just so stories” with no way to test their assertions. While Darwin was able to construct a diagram hypothesizing such relationships (Figure 1) and clearly understood the implications of such a powerful idea, he proposed no methodology to detect such patterns, nor a theoretical basis that might account for them. It took 108 years following publication of *The Origin of Species*

for Willi Hennig (1966) to propose a rationale that enabled biologists to construct and test the phylogenies Darwin proposed. Hennig, a German fly systematist, was the first to formally propose the idea of defining groups not on simple similarity, but rather on a special type of similarity he called a *synapomorphy*, a shared, derived character. Here the critical difference is the concept of a character not only being shared, but also derived—an evolutionary novelty restricted to the group in question that would not be shared by all members of the larger group. For example, the presence of vertebrae in chordates would be the opposite of a synapomorphy—a *synplesiomorphy*—because it is shared by all members of the group. However, within chordates we could identify a smaller subset, for example, only those taxa producing amniotic eggs, which would be defined by the synapomorphy “producing eggs with inner membranes” and comprising reptiles (including birds) and mammals. Hennig defined such groups as being monophyletic (supported by a synapomorphy and containing the ancestor of the group and all descendants). Modern systematics is largely the search for synapomorphies that support such groups, proposed in the testable framework of cladistics.

On the assumption that life evolved only once on this planet (and there is no evidence to the contrary), then all taxa both extant and extinct form one huge and potentially retrievable “tree of life.” By breaking apart this impossibly complex set of relationships into manageable monophyletic groups (clades), biologists then try to piece well-supported groups back together into a synthesis that reflects the history of life on the Earth. The knowledge that such an undertaking could produce is truly unimaginable. A summary of the work of the scientific community in progress can be found at <http://tolweb.org/tree/phylogeny.html>.

Seeing the natural world as a series of hierarchically nested sets of taxa supported by synapomorphies is a powerful tool when it comes to understanding the patterns and processes of evolution. However, it is important to understand that any proposed synapomorphy is only informative in relation to the group in question. In the context of hierarchy, one person’s synapomorphy is another person’s synplesiomorphy. Depending on the level of hierarchy being investigated and the question being proposed, a synapomorphy can flip-flop to become a synplesiomorphy. For example, body hair in mammals is a synplesiomorphy (shared by all members of the group—it is an ancestral character and noninformative within this group). However, in relation to reptiles, body hair, believed to be derived from scales, is therefore a synapomorphy, providing evidence of most recent common ancestry. Initially, this might seem confusing, but careful consideration will reveal this paradigm to be a powerful tool for reconstructing and understanding history.

Comparison of the two groups Vertebrata (Chordata) and “Invertebrata” illustrates this principle. The synapomorphy of a backbone unequivocally supports Chordata. Outgroup comparison reveals this character to be restricted and therefore more likely to be derived. The paradigm of outgroup comparison allows inferences to be made about events that happened in the past without the need to refer to fossils. Knowledge of the polarity of a character (derived or plesiomorphic) is very important when constructing phylogenies. Parsimony dictates that if the character in question is also found in a closely related group, it is more likely to be plesiomorphic (more generally distributed) and not derived (restricted). While not infallible, this method has held up very well as a way of determining character polarity.

The vast majority of animal taxa (>98%) do not exhibit this condition. It is also more parsimonious to assume it arose only once, at the base of the clade Chordata, than to assume it arose separately on multiple occasions in each taxon that has a backbone. Within Chordata we discover even more restricted characters, each of which support a nested clade of species: lungs, four limbs, amniotic eggs, body hair, etc. (Figure 3). In short, Chordata is a “good” valid group based on the synapomorphy of a backbone. It is monophyletic. However, consideration of the group “Invertebrata” reveals no such evidence of shared

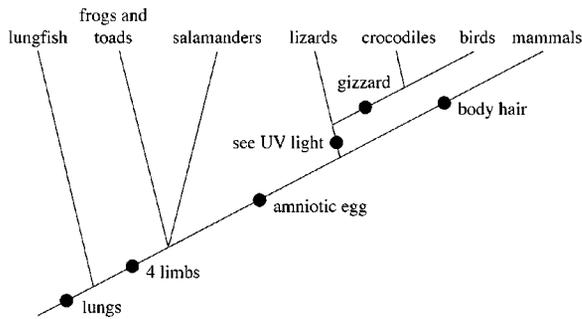


Figure 3. Cladogram depicting hierarchically nested sets of taxa (clades) based on synapomorphies (derived characters restricted only to the groups they support).

ancestry. Indeed, despite recent advances in molecular systematics, we still have little idea of the relationships among this huge assemblage of lineages. There are no synapomorphies that support this group. It is not monophyletic. Erecting a group based on the absence of a character, such as “backbone,” is misleading and completely noninformative.

Many synapomorphies have indeed proved to be powerful novelties that have resulted in large and evolutionarily “successful” radiations. A few examples are flight and metamorphosis in insects, silk production in spiders, calcified bone and amniotic eggs in vertebrates, and ovules enclosed within a carpel in flowering plants. As we explore the natural hierarchy in greater detail, searching for clades within clades, biologists detect often less dramatic and sometimes more obscure synapomorphies. For example, enlarged anterior median eyes in jumping spiders, the elytra (hard wing cases) of beetles, and the ability to dislocate the lower jaws in snakes and extinct mososaurs. Characters are not confined to morphological markers; the same methodology is used for behavioral as well as molecular characters. Phylogenetic thinking as a “way of looking at the world” is a habit of mind that uses history as its first line of hypotheses testing, and one I contend we should be teaching our students in grade school.

PHYLOGENETICS AT WORK

Especially, when reporting on recent discoveries in human evolution, the popular press often publishes cladograms to illustrate a story. Papers in leading scientific journals (such as *Nature* or *Science*) that make claims about relationships among taxa—whether based on molecular, morphological, or behavioral data—use cladograms as their hypotheses. Recent widely reported discoveries illustrating this point include those that elucidate the unexpected similarity of mouse and *Drosophila* DNA to human DNA. Other papers examine the debate over the large amounts of junk DNA observed in humans and other species and why it has been conserved over time. Such research can be understood and its implications fully appreciated only through the lens of macroevolution. When did *Homo sapiens* and rodents or *H. sapiens* and *Drosophila* last share a most recent common ancestor (MRCA)? What events might have selected for the conservation of large amounts of so-called “junk” DNA? Such knowledge should lead biologists to ask more probing questions about the function of these areas of the genome. Understanding certain biochemical pathways that appear to have been so critical to both arthropods and mammals that they have been maintained for

hundreds of millions of years could lead to significant discoveries in medical science. The recent discovery of fossils of a new species of *Homo*, *Homo floresiensis*, introduces the question, Where would this species fit on a cladogram of hominid relationships? Perhaps, more importantly, knowing that this species was extant only some 12,000 years ago, What implications does this have for our own history?

A scientifically literate high-school student should be able to evaluate such claims in light of the data presented. Increasingly, issues of bioethics, human origins, cloning, conservation, bioengineered food stuffs, etc. are being cast in a light that requires an understanding of macroevolutionary events and the history of life on the planet. To deny our students access to this debate is to deny the call for universal science literacy. It is widely accepted that biology will be the “science of the 21st century.” Whether they are producers or consumers of this knowledge, our students will not be able to participate fully in society without an understanding of the mechanisms that underpin and explain all of biology.

For example, it is not possible to fully appreciate biodiversity solely by understanding population-level processes. Knowledge of natural selection, while vitally important, explains little about the incredible diversity of species on the planet. As currently taught, natural selection stops short of fostering an understanding of its effects over time on species themselves, or on cladogenesis. It concentrates almost exclusively on processes that occur within individuals and populations. Knowing that variation in beak lengths is a naturally occurring phenomenon in populations tells us nothing about the 10,000 or so extant species of birds or how they came to be, and nothing about their unique history or the processes and contingency of their impressive radiation.

The justifiably popular book *The Beak of the Finch* (Weiner, 1994) and the recent work by the Grants on Darwin’s finches (Grant, 1999) document measurable morphological change over comprehensible time periods. These books make significant contributions to our understanding of natural selection at work. However, despite their excellent treatment of these processes, speciation and the formation of higher taxa are at best peripheral to their theses. These works do little to promote an understanding of the role of species, and nothing at all to help understand the origin of higher taxa. In a nutshell, natural selection has become synonymous with the suite of processes we call evolution.

DARWIN'S MISSING LINK

Despite its relatively recent emergence as a recognized methodology, the phylogenetic perspective is hardly new. Indeed, Darwin can rightly be cited as the first cladist to publish a cladogram in *The Origin of Species* (Figure 1). While his assertion that all life had descended from a common ancestor was heretical in 1858, we now have irrefutable evidence to support this argument. Species, speciation, and the formation of higher groups (clades) are central not only to Darwin’s theory of natural selection, but also to an explanation of the diversity on earth.

However, the units of evolution—species—and the process of speciation are referred to as peripheral concepts, not appropriate until grades 9–12 (American Association for the Advancement of Science, 2001). I maintain that species, as a concept, can and should be introduced in the early grades together with the concept of variation, and that this fundamental understanding should be reinforced and revisited throughout the middle- and high-school curriculum. Species exist in both space and time, and in addition to being the fundamental elements of Linnaean classification, they are also the units of evolution and biodiversity. Despite their central and fundamental importance in life science, data shows that students and many of their teachers have especially poor understanding of these concepts (Catley, 2001, 2002). Ideas about new species genesis as “arising when one species changes

into a different species over time” abound, as do spurious notions of species definitions themselves—in particular, the juxtaposition of individuals and the species they comprise (Catley & Novick, 2006).

While biologists themselves are in healthy disagreement concerning the utility of competing species concepts, average students and their teachers are less than comfortable with “species” as a concept at all (Catley, 2001). “In general,” reports the National Research Council, “students recognize the idea of species as a basis for classifying organisms, but few students will refer to the genetic basis of species” (NRC, 1996). Indeed, most contemporary high-school biology texts define speciation as “the evolution of new species” or something similar, and are not particularly informative. It is important to understand species as the least inclusive unit of biological classification, but it is significantly more important to understand species as the unit of evolutionary change itself.

Although epistemological arguments about species concepts are fascinating in themselves, they are not relevant to this discussion. Of central importance is the recognition that species (however defined) are entities that actually exist in the real world. They are the units of evolutionary change and form groups derived from an MRCA (clades) that have a recoverable and informative history. Of central importance is the realization that speciation is the process that links micro- and macroevolution. To understand how this occurs, one needs a basic understanding of speciation.

Genetic variation in a population of organisms is a result of random mutation and recombination (in sexually reproducing taxa). This variation is the engine that drives all processes of change over time. Speciation occurs as the result of the interactions between natural selection, genetic drift and migration (Figure 4). When a population is divided (often by geological processes), selection continues separately in each group, driven by the “requirements” of the local environment. The resultant traits (gene frequencies), when fixed in each population, become the characters that are the markers of the speciation event itself. Groups of species arising from an MRCA become clades, which either persist or become extinct over time. In this fashion, the micro mechanisms that operate on the individual and the population are inextricably linked and melded across time to become the historical pattern of extinction and cladogenesis among species we observe at the macro level. Searching for derived characters shared by two or more species, and studying the distribution of such

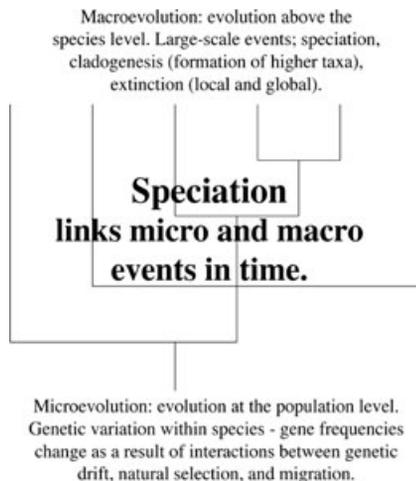


Figure 4. Speciation—the mechanism that links micro- and macroevolution.

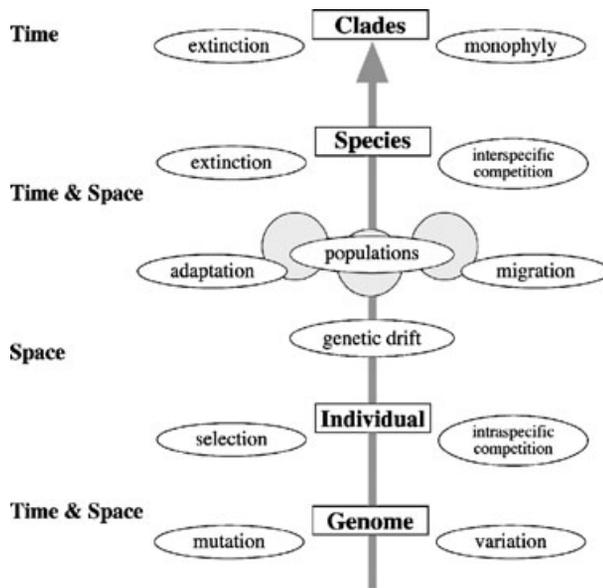


Figure 5. The evolutionary hierarchy.

characters among taxa, allows evolutionary biologists to reconstruct the history of life. These are the perspectives and tools for thinking about and visualizing evolutionary processes at both the micro and macro levels that we need to make available to our students.

However, despite its demonstrable utility, the concept of clades—the top level of the evolutionary hierarchy (Figure 5) which comprises genome, individual, and species—is missing in current educational constructs of what it is to understand evolution (American Association for the Advancement of Science, 2001; Catley et al., 2005). As we have seen, a clade is a naturally occurring group that includes the MRCA and all descendants of that ancestor. An example of a commonly accepted group that is not a clade, because it contains all the descendants but not the MRCA, is birds (Aves). To construe this taxon as a clade (which would reflect the actual events that lead to its formation) would require inclusion of the MRCA, a group of theropod dinosaurs. This is not simply semantics. If we are to ever discover the history of life on our planet together with the wealth of knowledge such a discovery would generate, then the evidence supporting such relationships—indeed, several synapomorphies in this case—cannot be ignored. Irrefutably, birds are indeed reptiles and rather than evolving from dinosaurs are themselves extant flying dinosaurs.

EVOLUTION EDUCATION

How might supporting and encouraging such understanding play out in our educational system? Imagine for a moment a group of high-school students having lunch at KFC. One wipes his fingers and points to the curved nature of the thighbone he just chewed the meat off.

Arturo: “Hey man, here’s one character that puts birds into a group with therapod dinosaurs. Both have thighbones with this twist.”

Jack: “Yeah, and look at this wishbone, we saw the same bone in pictures of a Velociraptor skeleton.”

Jenna: “Whoa, were those the scary carnivores in *Jurassic Park*?”

Arturo: “Yeah.”

Jack: “Do you know, they brooded their eggs by sitting on them until they hatched, just like modern birds? Scientists found the neatest fossils in the Gobi Desert of them doing just that.”

Jenna: “But look, this really clinches it. It’s a hole that goes all the way through the pelvis. Only birds and theropod dinosaurs share this character, it’s unique. What’s the probability of that occurring by chance alone?”

Jack: “Very small, I guess.”

Arturo: “You know, it’s one of those special characters that scientists use to reconstruct the history of life. What we learned in biology today about feathers was the coolest thing. Because feathers were found on a fossil nonbird theropod dinosaur in 2001, it seems very unlikely they were used to fly. Maybe these dinosaurs were warm blooded after all, and feathers were selected because they retained body heat? Then only later did they confer an advantage in flight.”

Jenna: “Wow, all that knowledge from a piece of crispy fried chicken?”

Jack: “So all dinosaurs did not become extinct, only some of them. Right?”

Arturo: “Maybe they should call it Kentucky Fried Dino!”

What’s going on here? Students are constructing knowledge? Evaluating evidence? Understanding the big picture? In the real world of 2006, there is probably not a high-school student in America who thinks this way. How might we as science education researchers investigate what students need to think about in order to understand these types of representations?

Three major issues that remain largely unaddressed in the current evolution education paradigm have emerged as central to learners’ understanding of evolution: species, phylogenetics, and deep time. Of these, only learners’ understanding of deep time (Dodick & Orion, 2003a; Trend, 2001)—and to a lesser extent, species—have resulted in a small body of research literature. Education researchers have understandably focused on population-level processes, especially natural selection, as models to understand how people internalize and think about evolution. In particular, there is a significant body of work relating to alternative conceptions, Lamarckian thinking, teleology, and anthropomorphism. By comparison, the literature on learners’ understanding of species is extremely limited (Evans, 2000; Halldon, 1988; Kargbo, Hobbs, & Erickson, 1980; Samarapungavan & Wiers, 1997), and the literature on the use of phylogenetics in education is virtually nonexistent. Given that species are the units of evolution—the entities that undergo evolutionary change and extinction—this is a surprising and disturbing finding.

Curricula developers have produced some excellent examples that help learners deal with alternative conceptions and enhance understanding of natural selection, often using real-world data sets (Sandoval & Reiser, 2003). With their emphasis on approaching evolution by inquiry, recent work by Stewart and Rudolph (2001), Anderson et al. (2002), and John Jungck’s “BioQuest” (www.BioQUEST.org) are significant steps forward that should be applauded.

Passmore and Stewart (2002) suggest that instruction about evolution be rooted in the models scientists use in their field to test and evaluate various types of data. (Alas, phylogenetics, while indispensable to professional practice, is not reflected in our schools.) They also suggest that the model of natural selection be used to engage students in inquiry-type projects where they use the model itself to construct an understanding of natural phenomena. They advocate a curriculum that allows students to “understand how natural selection can be used as a framework to think about evolutionary change” and “participate in inquiry that mirrors the practice of evolutionary biology in important ways”—both

very laudable goals. Their three key design principles for curricula in evolutionary biology are

1. There should be a commitment to designing instruction around *key models in the discipline* under study.
2. There should be recognition that scientific practice is discipline specific. The development of curriculum should therefore take into account *the ways in which scientists operate within their fields*.
3. There should be a commitment to providing opportunities for students to develop, revise, and *use models in ways that are true to the discipline*.

(emphasis added by author)

Interestingly, Sober (1988)—as quoted in Passmore and Stewart (2002)—states that “organisms are related through a common ancestry that has a multimillion-year history. Therefore, the primary activities of evolutionary biologists are making inferences about past speciation events in order to establish phylogenetic relationships and to create explanatory models that can help to account for patterns observed in the historical reconstructions.” This elucidation—that the whole is greater than the sum of its parts—is as valid today as it was in 1988. It is not sufficient that students learn the nuts and bolts of genetics and natural selection in a vacuum and be expected to “understand evolution” in its entirety. Without a framework that melds micro processes with speciation, geologic time, earth processes, and the formation of higher taxa, it is impossible to construct such an understanding.

A section of Passmore and Stewart’s (2002) excellent instructional unit does indeed comprise a data matrix and cladogram that depicts relationships among bird families. Even without an explanation of or an explicit rationale for phylogenetic reconstruction, the authors report, students were able to make logical inferences about character evolution in pheasants from this phylogenetic data set. How much more powerful would this methodological tool be if introduced and reinforced from earlier grades as a way of understanding the natural world?

How might such a phylogenetic perspective—which is so important in providing a full understanding of evolution—be achieved in our schools? A golden opportunity is lost when most students, early in their schooling, are exposed to the life cycle of the monarch butterfly. Persisting into adulthood, we all remember the schematic depicting egg, larva, pupa, and adult. But how many of us are aware that this evolutionary novelty, this synapomorphy—the holometabolic life cycle or “metamorphosis” shared among others by butterflies, beetles, bees and wasps, and flies—resulted in the largest and most important radiation the planet has ever seen? Questions arise about when such thinking is appropriate but one could imagine that if it were introduced from a “tree thinking” perspective (see Figure 6), students might have a conceptual tool to help answer questions such as, “What were the selective advantages to the shared, derived character ‘metamorphosis’?” Alternately, students might explore the evolutionary innovation of the hard front wing cases (elytra) in beetles (the adults of the mealworms so often kept in classrooms) that fueled the greatest species radiation of all time.

FUTURE RESEARCH—A CALL TO ACTION

Far from being one of several competing paradigms currently in use for elucidating and testing evolutionary hypotheses, phylogenetics and its tool, cladistics, is the single methodology used in the subdiscipline. Over time it will, as did the structure of DNA and the molecular theory of inheritance, become a norm of biological literacy. Just as this tool

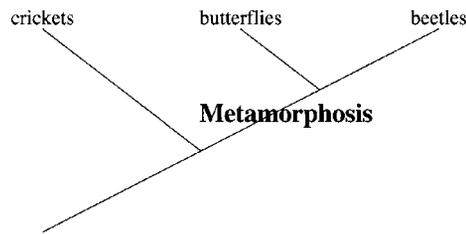


Figure 6. What were the selective advantages of the shared, derived character “metamorphosis”?

is indispensable to scientists, it should also be encouraged in schools, simply because it “does work” in aiding biological understanding. Unfortunately, most science education has not caught up with current practices in the field; in evolution education, in particular, this disconnect is especially acute. Just what do students need to know in order to understand the relationship between a chicken and a theropod dinosaur?

As science education researchers, we face several important questions: Should we allow phylogenetics to diffuse into textbooks and curricula without an understanding of how teachers and students reason with these tools? What elements do students and teachers need to know to effectively understand these types of representations? Specific research questions would need to include the following: What are the difficulties of approaching species as character-based testable hypotheses, as opposed to the static “essences” of Aristotle? While we appreciate that students (Dodick & Orion, 2002, 2003a, 2003b) and many of their teachers (Trend, 2001) encounter significant problems understanding deep time, is this a fundamental cognitive problem, or simply insufficient exposure to the ways of thinking inherent in geology and systematics? The complexities of ecology cannot be understood without a sense of its history and its manifestation as a product of evolution (Eilam, 2002). However, we continue to teach ecology without providing our students this perspective (Hogan & Fisher-Keller, 1998). At which developmental levels are such tools and ways of thinking appropriate? What constitutes a sound trajectory for learning about this way of thinking and incorporating it into biology education?

As one example of such research, the author and a cognitive psychologist collaborator are currently conducting studies with both sixth graders in a diverse urban school and undergraduates at a private university (both in a southern state). Studies with sixth graders explore their understanding of classifications and the graphical representations thereof. A long-term study is being carried out with undergraduates from a wide range of science backgrounds, investigating both their preconceived knowledge of evolution and their ability to reason with diagrams. These diagrams are presented as cladograms and depict sets of hierarchical evolutionary relationships. An instrument that measures such reasoning is currently being tested and refined and will be administered to other populations, including graduate students and middle- and high-school science teachers. Preliminary results provide evidence that all students had greater difficulty interpreting and reasoning with particular types of representations than with others (ladder diagrams compared to tree diagrams), and that this was further impacted by their degree of prior exposure to biology coursework (Catley & Novick, 2006).

Using phylogenetics to pose and test questions about the natural world makes it necessary to appreciate the comparative method, a topic seldom touched on in our K-12 science classes. This particularly powerful methodology takes advantage of millions of years of “natural evolutionary experiments” (Futuyma, 1997) to predict and test hypotheses of adaptation and other evolutionary phenomena. The many tools of the evolutionary biologist include

empirical studies of form and function, experimental studies of the correspondence between fitness and variation within species, and comparison of characters among monophyletic groups of species that establish a correlation with environmental or other features. One of many dichotomies that drive a wedge between science education and the culture of scientific endeavor is a poor understanding of the linear “scientific method.” Wedded as we are to the simplistic notion that science is only science when conducted under the experimental rubric, we miss completely the variety of knowledge-constructing practices used in different scientific communities. As Windschitl (2003) points out, “analyses of practice in various scientific communities have shown that there is no universal method and that science inquiry can take many different forms.” The largely comparative sciences—such as astronomy, geology, anthropology, and evolution—have over hundreds of years yielded valid knowledge without “running experiments.”

As far as life science education is concerned, the time has come for phylogenetics to help span the gap between systematic research and education and become a pedagogical tool for understanding evolution in the classroom (Baum, Dewitt Smith, & Donovan, 2005). With its emphasis on species as the units of evolutionary change, and the cladogram as a visualization of processes acting in time and space, it provides a conceptual framework to explore and test many evolutionary concepts, including hierarchy, natural selection, speciation, variation, evolutionary time frames, co-evolution, adaptation, and convergent evolution. Evolution thus becomes a tool for thinking and learning about biology, rather than simply a collection of facts about life. I hope the case has been made that research is sorely needed on students’ and teachers’ understanding of many challenging macroevolutionary concepts, including species, deep time, natural hierarchy, character evolution, extinction, and evidence of monophyly (synapomorphy). Combining a phylogenetic perspective with the comparative method, these concepts can and must be tackled if we are to ever aspire to a public that truly understands evolution in all its complexity and grandeur.

So, what is going on here? A more pertinent question might be, what should be going on? Creating a pedagogical climate where the sort of discussion and awareness depicted in the KFC scenario is commonplace should be a major goal of life science education. A conceptual framework that facilitates an appreciation of the full array of life that has preceded our own species is a valuable educational and scientific goal. The sense of humility gained through an appreciation of the kinship of all life is a vitally important component in nurturing a stewardship ethic for a planet moving ever deeper toward ecological collapse.

As educators and researchers, we have a responsibility to provide our students with the knowledge, tools, and insight needed to evaluate historical and comparative as well as experimental data. Cultivating an understanding of the place our own species has played in the history and ecology of the planet allows us to make informed decisions on many pressing questions that will have momentous reverberations for future generations.

As Charles Darwin so elegantly stated in *The Origin of Species* (Darwin, 1858), “There is grandeur in this view of life.”

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