ICONS OF EVOLUTION? WHY MUCH OF WHAT JONATHAN WELLS WRITES ABOUT EVOLUTION IS WRONG

ALAN D. GISHLICK
NATIONAL CENTER FOR SCIENCE EDUCATION

INTRODUCTION

THE PARADIGM OF EVOLUTION

Evolution is the unifying paradigm, the organizing principle of biology. Paradigms are accepted for their overall explanatory power, their "best fit" with all the available data in their fields. A paradigm functions as the glue that holds an entire discipline together, connecting disparate subfields and relating them to one another. A paradigm is also important because it fosters a research program, creating a series of questions that give researchers new directions to explore in order to better understand the phenomena being studied. For example, the unifying paradigm of geology is plate tectonics; although not all geologists work on it, it connects the entire field and organizes the various disciplines of geology, providing them with their research programs. A paradigm does not stand or fall on a single piece of evidence; rather, it is justified by its success in overall explanatory power and the fostering of research questions. A paradigm is important for the questions it leads to, rather than the answers it gives. Therefore, the health of a scientific field is based on how well its central theory explains all the available data and how many new research directions it is spawning. By these criteria, evolution is a very healthy paradigm for the field of biology.

In his book *Icons of Evolution* (2000), Jonathan Wells attempts to overthrow the paradigm of evolution by attacking how we teach it. In this book, Wells identifies ten examples that are commonly used to help to teach evolution. Wells calls these the "icons," and brands them as false, out of date, and misleading. Wells then evaluates ten "widely used" high school and college biology textbooks for seven of these "icons" with a grading scheme that he constructed. Based on this, he claims that their treatments of these icons are so rife with inaccuracies, out-of-date information, and downright falsehoods that their discussions of the icons should be discarded, supplemented, or amended with "warning labels" (which he provides).

According to Wells, the "icons" are the Miller-Urey experiment, Darwin's tree of life, the homology of the vertebrate limbs, Haeckel's embryos, *Archaeopteryx*, the peppered moths, and "Darwin's" finches. (Although he discusses three other "icons" — four-winged fruit flies, horse evolution, and human evolution — he does not evaluate textbooks' treatments of them.) Wells is right about at least one thing: these seven examples do appear in nearly all biology textbooks. Yet no textbook presents the "icons" as a list of our "best evidence" for evolution, as Wells implies. The "icons" that Wells singles out are discussed in different parts of the textbooks for different pedagogical reasons. The Miller-Urey experiment isn't considered "evidence for evolution"; it is considered part of the experimental research about the origin of life and is discussed in chapters and sections on the "history of life." Likewise, Darwin's finches are used as examples of an evolutionary process (natural selection), not as evidence for evolution. *Archaeopteryx* is frequently presented in discussions of the origin of birds, not as evidence for evolution itself. Finally, textbooks do not present a single "tree of life"; rather, they present numerous topic-specific phylogenetic trees to show how relevant organisms are related. Wells's entire discussion assumes that the evidence for evolution is a list of facts stored somewhere, rather than the predictive value of the theory in explaining the patterns of the past and present biological world.

TEXTBOOK "ICONS": WHY DO WE HAVE THEM?

Paradigms and all their components are not necessarily simple. To understand the depth of any scientific field fully requires many years of study. It is the goal of elementary and secondary education to give students a basic understanding of the "world as we know it," which includes teaching students the paradigms of a number of fields of science. In order to do this, teaching examples must be found. It is this need to find simple, easy-to-explain, dynamic, and visual examples to introduce a complex topic to students that has led to the common use of a few examples — the "icons." Yet, with our knowledge of the natural world expanding at near-exponential rates, the volume of new information facing a textbook writer is daunting. The aim of a textbook is not necessarily to report the "state of the art" as much as it is to offer an introduction to the basic principles and ideas of a certain field. Therefore, it should not be surprising that introductory textbooks are frequently simplified and may be somewhat out-of-date. In *Icons of Evolution*, however, Wells makes an even stronger accusation. Wells says: "Students and the public are being systematically misinformed about the evidence for evolution" through biology textbooks (Wells, 2000: xii). This is a serious charge; to support it demands the highest level of scholarship on the part of the author.

Does Wells display this level of scholarship? Is Wells right? Are the "icons" out-of-date and in need of removal? And more importantly, is there something wrong with the theory of evolution?

In the following sections, each textbook "icon" is reexamined in light of Wells's criticism. The textbooks covered by Wells are examined as well, along with the grading criteria (given in the appendix of *Icons* [Wells, 2000] and on the Discovery Institute's website) that he used to assess their accuracy. What was found is that although the textbooks could always benefit from improvement, they do not mislead, much less "systematically misinform," students about the theory of biological evolution or the evidence for it. Further, the grading criteria Wells applied are vague and at times appear to have been manipulated to give poor grades. Many of the grades given are not in agreement with the stated criteria or an accurate reading of the evaluated text. Beyond that, *Icons of Evolution* offers little in the way of suggestions for improvement of, or changes in, the standard biology curriculum. When Wells says that textbooks are in need of correction, he apparently means the removal of the subject of evolution entirely or the teaching of "evidence against" evolution, rather than the fixing of some minor errors in the presentation of the putative "icons." This makes *Icons of Evolution* useful at most for those with a certain political and religious agenda, but of little value to educators.

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THE MILLER-UREY EXPERIMENT

THE EXPERIMENT ITSELF

The understanding of the origin of life was largely speculative until the 1920s, when Oparin and Haldane, working independently, proposed a theoretical model for "chemical evolution." The Oparin–Haldane model suggested that under the strongly reducing conditions theorized to have been present in the atmosphere of the early earth (between 4.0 and 3.5 billion years ago), inorganic molecules would spontaneously form organic molecules (simple sugars and amino acids). In 1953, Stanley Miller, along with his graduate advisor Harold Urey, tested this hypothesis by constructing an apparatus that simulated the Oparin-Haldane "early earth." When a gas mixture based on predictions of the early atmosphere was heated and given an electrical charge, organic compounds were formed (Miller, 1953; Miller and Urey, 1959). Thus, the Miller-Urey experiment demonstrated how some biological molecules, such as simple amino acids, could have arisen abiotically, that is through non-biological processes, under conditions thought to be similar to those of the early earth. This experiment provided the structure for later research into the origin of life. Despite many revisions and additions, the Oparin–Haldane scenario remains part of the model in use today. The Miller–Urey experiment is simply a part of the experimental program produced by this paradigm.

WELLS BOILS OFF

Wells says that the Miller–Urey experiment should not be taught because the experiment used an atmospheric composition that is now known to be incorrect. Wells contends that textbooks don't discuss how the early atmosphere was probably different from the atmosphere hypothesized in the original experiment. Wells then claims that the actual atmosphere of the early earth makes the Miller–Urey type of chemical synthesis impossible, and asserts that the experiment does not work when an updated atmosphere is used. Therefore, textbooks should either discuss the experiment as an historically interesting yet flawed exercise, or not discuss it at all. Wells concludes by saying that textbooks should replace their discussions of the Miller–Urey experiment with an "extensive discussion" of all the problems facing research into the origin of life.

These allegations might seem serious; however, Wells's knowledge of prebiotic chemistry is seriously flawed. First, Wells's claim that researchers are ignoring the new atmospheric data, and that experiments like the Miller–Urey experiment fail when the atmospheric composition reflects current theories, is simply false. The current literature shows that scientists working on the origin and early evolution of life are well aware of the current theories of the earth's early atmosphere and have found that the revisions have little effect on the results of various experiments in biochemical synthesis. Despite Wells's claims to the contrary, new experiments since the Miller–Urey ones have achieved similar results using various corrected atmospheric compositions (Figure 1; Rode, 1999; Hanic et al., 2000). Further, although some authors have argued that electrical energy might not have efficiently produced organic molecules in the earth's early atmosphere, other energy sources such as cosmic radiation (e.g., Kobayashi et al., 1998), high temperature impact events (e.g., Miyakawa et al., 2000), and even the action of waves on a beach (Commeyras et al., 2002) would have been quite effective.

Even if Wells had been correct about the

Researcher(s)	Year	Reactants	Energy source	Results	Probability
Miller	1953	CH_4, NH_3, H_2O, H_2	Electric discharge	Simple amino acids, organic compounds	unlikely
Abelson	1956	CO, CO_2, N_2, NH_3, H_2, H2O	Electric discharge	Simple amino acids, HCN	unlikely
Groth and Weyssenhoff	1957	CH_4, NH_3, H_2O	Ultraviolet light (1470–1294 ?)	Simple amino acids (low yields)	under special conditions
Bahadur, et al.	1958	Formaldehyde, molybdenum oxide	Sunlight (photosynthesis)	Simple amino acids	possible
Pavolvskaya and Pasynskii	1959	Formaldehyde, nitrates	High pressure Hg lamp (photolysis)	Simple amino acids	possible
Palm and Calvin	1962	CH_4, NH_3, H_2O	Electron irradiation	Glycine, alanine, aspartic acid	under special conditions
Harada and Fox	1964	CH_4, NH_3, H_2O	Thermal energy (900–1200º C)	14 of the "essential" amino acids of proteins	under special conditions
Oró	1968	CH_4, NH_3, H_2O	Plasma jet	Simple amino acids	unlikely
Bar-Nun et al.	1970	CH_4, NH_3, H_2O	Shock wave	Simple amino acids	under special conditions
Sagan and Khare	1971	CH_4, C_2H_6, NH_3, H_2O, H2S	Ultraviolet light (>2000 ?)	Simple amino acids (low yields)	under special conditions
Yoshino et al.	1971	H_2, CO, NH_3, montmorillonite	Temperature of 700°C	Glycine, alanine, glutamic acid, serine, aspartic acid, leucine, lysine, arginine	unlikely
Lawless and Boynton	1973	CH_4, NH_3, H_2O	Thermal energy	Glycine, alanine, aspartic acid, ?-alanine, N-methyl-?-alanine, ?-amino-n-butyric acid.	under special conditions
Yanagawa et al.	1980	Various sugars, hydroxylamine, inorganic salts,	Temperature of 105°C	Glycine, alanine, serine, aspartic acid, glutamic acid	under special conditions
Kobayashi et al.	1992	CO, N_2, H_2O	Proton irradiation	Glycine, alanine, aspartic acid, ?-alanine, glutamic acid, threonine, ?-aminobutyric acid, serine	possible
Hanic, et al.	1998	CO_2, N_2, H_2O	Electric discharge	Several amino acids	possible

Figure 1. *A table of some amino acid synthesis experiments since Miller–Urey. The "probability" column reflects the likelihood of the environmental conditions used in the experiment. Modified from Rode, 1999.*

Miller–Urey experiment, he does not explain that our theories about the origin of organic "building blocks" do not depend on that experiment alone (Orgel, 1998a). There are other sources for organic "building blocks," such as meteorites, comets, and hydrothermal vents. All of these alternate sources for organic materials and their synthesis are extensively discussed in the literature about the origin of life, a literature that Wells does not acknowledge. In fact, what is most striking about Wells's extensive reference list is the literature that he has left out. Wells does not mention extraterrestrial sources of organic molecules, which have been widely discussed in the literature since 1961 (see Oró, 1961; Whittet, 1997; Irvine, 1998). Wells apparently missed the vast body of literature on organic compounds in comets (e.g. Oró, 1961; Anders, 1989; Irvine, 1998), carbonaceous meteorites (e.g., Kaplan et al., 1963; Hayes, 1967; Chang, 1994; Maurette, 1998; Cooper et al., 2001), and conditions conducive to the formation of organic compounds that exist in interstellar dust clouds (Whittet, 1997).

Wells also fails to cite the scientific literature on other terrestrial conditions under which organic compounds could have formed. These non-atmospheric sources include the synthesis of organic compounds in a reducing ocean (e.g., Chang, 1994), at hydrothermal vents (e.g., Andersson, 1999; Ogata et al., 2000), and in volcanic aquifers (Washington, 2000). A cursory review of the literature finds more than 40 papers on terrestrial prebiotic chemical synthesis published since 1997 in the journal *Origins of life and the evolution of the biosphere* alone. Contrary to Wells's presentation, there appears to be no shortage of potential sources for organic "building blocks" on the early earth.

Instead of discussing this literature, Wells raises a false "controversy" about the low amount of free oxygen in the early atmosphere. Claiming that this precludes the spontaneous origin of life, he concludes that "[d]ogma had taken the place of empirical science" (Wells, 2000:18). In truth, nearly *all* researchers who work on the early atmosphere hold that oxygen was essentially absent during the period in which life originated (Copley, 2001) and therefore oxygen could not have played a role in preventing chemical synthesis. This conclusion is based on many sources of *data*, not "dogma." Sources of data include fluvial uraninite sand deposits (Rasmussen and Buick, 1999) and banded iron formations (Nunn, 1998; Copley, 2001), which could not have been deposited under oxidizing conditions. Wells also neglects the data from paleosols (ancient soils) which, because they form at the atmosphere–ground interface, are an excellent source to determine atmospheric composition (Holland, 1994). Reduced paleosols suggest that oxygen levels were very low before 2.1 billion years ago (Rye and Holland, 1998). There are also data from mantle chemistry that suggest that oxygen was essentially absent from the earliest atmosphere (Kump et al., 2001). Wells misrepresents the debate as over whether oxygen levels were 5/100 of 1%, which Wells calls "low," or 45/100 of 1%, which Wells calls "significant." But the controversy is really over why it took so long for oxygen levels to start to rise. Current data show that oxygen levels did not start to rise significantly until nearly 1.5 billion years after life originated (Rye and Holland, 1998; Copley, 2001). Wells strategically fails to clarify what he means by "early" when he discusses the amount of oxygen in the "early" atmosphere. In his discussion, he cites research about the chemistry of the atmosphere without distinguishing whether the authors are referring to times before, during, or after the period when life is thought to have originated. Nearly all of the papers he cites deal with oxygen levels after 3.0 billion years ago. They are irrelevant, as chemical data suggest that life arose 3.8 billion years ago (Chang, 1994; Orgel, 1998b), well before there was enough free oxygen in the earth's atmosphere to prevent Miller–Urey-type chemical synthesis.

Finally, the Miller–Urey experiment tells us nothing about the other stages in the origin of life, including the formation of a simple genetic code (PNA or "peptide"-based codes and RNA-based codes) or the origin of cellular membranes (liposomes), some of which are discussed in all the textbooks that Wells reviewed. The Miller–Urey experiment only showed one possible route by which the basic components necessary for the origin of life could have been created, not how life came to be. Other theories have been proposed to bridge the gap between the organic "building blocks" and life. The "liposome" theory deals with the origin of cellular membranes, the RNA-world hypothesis deals with the origin of a simple genetic code, and the PNA (peptide-based genetics) theory proposes an even simpler potential genetic code (Rode, 1999). Wells doesn't really mention any of this except to suggest that the "RNA world" hypothesis was proposed to "rescue" the Miller–Urey experiment. No one familiar with the field or the evidence could make such a fatuous and inaccurate statement. The Miller–Urey experiment is not relevant to the RNA world, because RNA was constructed from organic "building blocks" irrespective of how those compounds came into existence (Zubay and Mui, 2001). The evolution of RNA is a wholly different chapter in the story of the origin of life, one to which the validity of the Miller–Urey experiment is irrelevant.

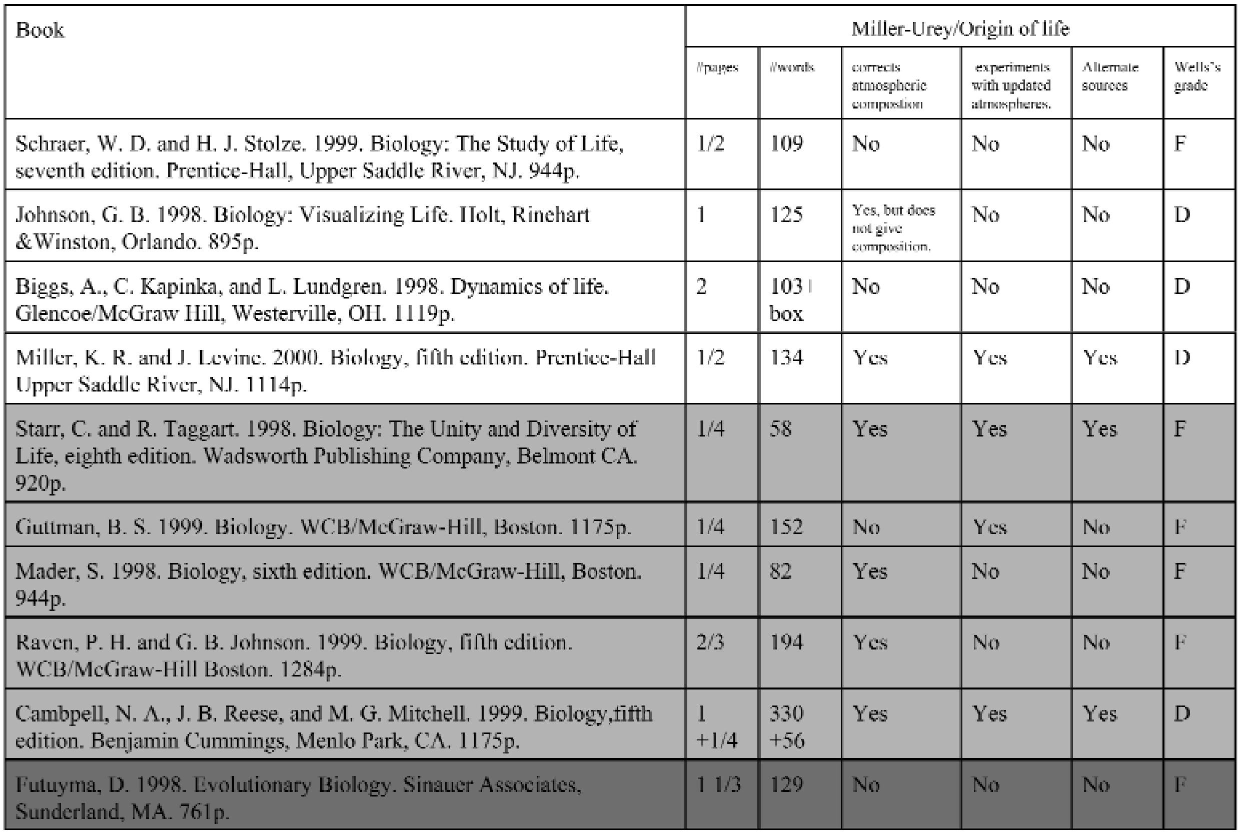
WHAT THE TEXTBOOKS SAY

All of the textbooks reviewed contain a section on the Miller–Urey experiment. This is not surprising given the experiment's historic role in the understanding of the origin of life. The experiment is usually discussed over a couple of paragraphs (see Figure 2), a small proportion (roughly 20%) of the total discussion of the origin and early evolution of life. Commonly, the first paragraph discusses the Oparin-Haldane scenario, and then a second outlines the Miller–Urey test of that scenario. All textbooks contain either a drawing or a picture of the experimental apparatus and state that it was used to demonstrate that some complex organic molecules (e.g., simple sugars and amino acids, frequently called "building blocks") could have formed spontaneously in the atmosphere of the early earth. Textbooks vary in their descriptions of the atmospheric composition of the early earth. Five books present the strongly reducing atmosphere of the Miller–Urey experiment, whereas the other five mention that the current geochemical evidence points to a slightly reducing atmosphere. All textbooks state that oxygen was essentially absent during the period in which life arose. Four textbooks mention that the experiment has been repeated successfully under updated conditions. Three textbooks also mention the possibility of organic molecules arriving from space or forming at deep-sea hydrothermal vents (Figure 2). No textbook claims that these experiments conclusively show how life originated; and all textbooks state that the results of these experiments are tentative.

It is true that some textbooks do not mention that our knowledge of the composition of the atmosphere has changed. However, this does not mean that textbooks are "misleading" students, because there is more to the origin of life than just the Miller–Urey experiment. Most textbooks already discuss this fact. The textbooks reviewed treat the origin of life with varying levels of detail and length in "Origin of life" or "History of life" chapters. These chapters are from 6 to 24 pages in length. In this relatively short space, it is hard for a textbook, particularly for an introductory class like high school biology, to address all of the details and intricacies of origin-of-life research that Wells seems to demand. Nearly all texts begin their origin of life sections with a brief description of the origin of the universe and the solar system; a couple of books use a discussion of Pasteur and spontaneous generation instead (and one discusses both). Two textbooks discuss how life might be defined. Nearly all textbooks open their discussion of the origin of life with qualifications about how the study of the origin of life is largely hypothetical and that there is much about it that we do not know.

WELLS'S EVALUATION

As we will see in his treatment of the other "icons," Wells's criteria for judging textbooks stack the deck against them, ensuring failure. No textbook receives better than a D for this "icon" in Wells's evaluation, and 6 of the 10 receive an F. This is largely a result of the construction of the grading criteria. Under Wells's criteria (Wells, 2000:251–252), any textbook containing a pic-



Book	Miller-Urey/Origin of life					
	#pages	#words	corrects atmospheric composition	experiments with updated atmospheres.	Alternate sources	Wells's grade
Schraer, W. D. and H. J. Stolze. 1999. Biology: The Study of Life, seventh edition. Prentice-Hall, Upper Saddle River, NJ. 944p.	1/2	109	No	No	No	F
Johnson, G. B. 1998. Biology: Visualizing Life. Holt, Rinehart &Winston, Orlando. 895p.	1	125	Yes, but does not give composition.	No	No	D
Biggs, A., C. Kapinka, and L. Lundgren. 1998. Dynamics of life. Glencoe/McGraw Hill, Westerville, OH. 1119p.	2	103 + box	No	No	No	D
Miller, K. R. and J. Levine. 2000. Biology, fifth edition. Prentice-Hall Upper Saddle River, NJ. 1114p.	1/2	134	Yes	Yes	Yes	D
Starr, C. and R. Taggart. 1998. Biology: The Unity and Diversity of Life, eighth edition. Wadsworth Publishing Company, Belmont CA. 920p.	1/4	58	Yes	Yes	Yes	F
Guttman, B. S. 1999. Biology. WCB/McGraw-Hill, Boston. 1175p.	1/4	152	No	Yes	No	F
Mader, S. 1998. Biology, sixth edition. WCB/McGraw-Hill, Boston. 944p.	1/4	82	Yes	No	No	F
Raven, P. H. and G. B. Johnson. 1999. Biology, fifth edition. WCB/McGraw-Hill Boston. 1284p.	2/3	194	Yes	No	No	F
Cambpell, N. A., J. B. Reese, and M. G. Mitchell. 1999. Biology,fifth edition. Benjamin Cummings, Menlo Park, CA. 1175p.	1 +1/4	330 +56	Yes	Yes	Yes	D
Futuyma, D. 1998. Evolutionary Biology. Sinauer Associates, Sunderland, MA. 761p.	1 1/3	129	No	No	No	F

***Figure 2.** Textbook treatments of the Miller–Urey experiment. Textbooks are listed in order of increasing detail (AP/College textbooks highlighted; note that Futuyma is an upper-level college/graduate textbook).*

ture of the Miller–Urey apparatus could receive no better than a C, unless the caption of the picture explicitly says that the experiment is irrelevant, in which case the book would receive a B. Therefore, the use of a picture is the major deciding factor on which Wells evaluated the books, for it decides the grade *irrespective of the information contained in the text*! A grade of D is given even if the text explicitly points out that the experiment used an incorrect atmosphere, as long as it shows a picture. Wells pillories Miller and Levine for exactly that, complaining that they bury the correction in the text. This is absurd: almost all textbooks contain pictures of experimental apparatus for any experiment they discuss. It is the text that is important pedagogically, not the pictures. Wells's criteria would require that even the intelligent design "textbook" *Of Pandas and People* would receive a C for its treatment of the Miller–Urey experiment.

In order to receive an A, a textbook must first omit the picture of the Miller–Urey apparatus (or state explicitly in the caption that it was a failure), discuss the experiment, but then state that it is irrelevant to the origin of life. This type of textbook would be not only scientifically inaccurate but pedagogically deficient.

WHY WE SHOULD STILL TEACH MILLER–UREY

The Miller–Urey experiment represents one of the research programs spawned by the Oparin-Haldane hypothesis. Even though details of the model for the origin of life have changed, this has not affected the basic scenario of Oparin–Haldane. The first stage in the origin of life was chemical evolution. This involves the formation of organic compounds from inorganic molecules already present in the atmosphere and in the water of the early earth. This spontaneous organization of chemicals was spawned by some external energy source. Lightning (as Oparin and Haldane thought), proton radiation, ultraviolet radiation, and geothermal or impact-generated heat are all possibilities.

The Miller–Urey experiment represents a major advance in the study of the origin of life. In fact, it marks the beginning of *experimental* research into the origin of life. Before Miller–Urey, the study of the origin of life was merely theoretical. With the advent of "spark experiments" such as Miller conducted, our understanding of the origin of life gained its first experimental program. Therefore, the Miller–Urey experiment is important from an historical perspective alone. Presenting history is good pedagogy because students understand scientific theories better through narratives. The importance of the experiment is more than just historical, however. The apparatus Miller and Urey designed became the basis for many subsequent "spark experiments" and laid a groundwork that is still in use today. Thus it is also a good teaching example because it shows how experimental science works. It teaches students how scientists use experiments to test ideas about prehistoric, unobserved events such as the origin of life. It is also an interesting experiment that is simple enough for most students to grasp. It tested a hypothesis, was reproduced by other researchers, and provided new information that led to the advancement of scientific understanding of the origin of life. This is the kind of "good science" that we want to teach students.

Finally, the Miller–Urey experiment should still be taught because the basic results are still valid. The experiments show that organic molecules can form under abiotic conditions. Later experiments have used more accurate atmospheric compositions and achieved similar results. Even though origin-of-life research has moved beyond Miller and Urey, their experiments should be taught. We still teach Newton even though we have moved beyond his work in our knowledge of planetary mechanics. Regardless of whether any of our current theories about the origin of life turn out to be completely accurate, we currently have models for the processes and a research program that works at testing the models.

HOW TEXTBOOKS COULD IMPROVE THEIR PRESENTATIONS OF THE ORIGIN OF LIFE

Textbooks can always improve discussions of their topics with more up-to-date information. Textbooks that have not already done so should explicitly correct the estimate of atmospheric composition, and accompany the Miller–Urey experiment with a clarification of the fact that the corrected atmospheres yield similar results. Further, the wealth of new data on extraterrestrial and hydrothermal sources of biological material should be discussed. Finally, textbooks ideally should expand their discussions of other stages in the origin of life to include PNA and some of the newer research on self-replicating proteins. Wells, however, does not suggest that textbooks should correct the presentation of the origin of life. Rather, he wants textbooks to present this "icon" and then denigrate it, in order to reduce the confidence of students in the possibility that scientific research can ever establish a plausible explanation for the origin of life or anything else for that matter. If Wells's recommendations are followed, students will be taught that because one experiment is not completely accurate (albeit in hindsight), everything else is wrong as well. This is not good science or science teaching.

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DARWIN'S "TREE OF LIFE"

PHYLOGENETIC TREES

In biology, a phylogenetic tree, or phylogeny, is used to show the genealogic relationships of living things. A phylogeny is not so much evidence *for* evolution as much as it is a codification of data about evolutionary history. According to biological evolution, organisms share common ancestors; a phylogeny shows how organisms are related. The tree of life shows the path evolution took to get to the current diversity of life. It also shows that we can ascertain the genealogy of disparate living organisms. This is evidence for evolution only in that we can construct such trees at all. If evolution had not happened or common ancestry were false, we would not be able to discover hierarchical branching genealogies for organisms (although textbooks do not generally explain this well). Referring to any phylogenetic tree as "Darwin's tree of life" is somewhat of a misnomer. Darwin graphically presented no phylogenies in the *Origin of Species*; the only figure there depicts differential rates of speciation. If anyone deserves credit for giving us "trees of life," it is Ernst Haeckel, who drew phylogenies for many of the living groups of animals literally as trees, as well as coining the term itself.

WELLS'S SHELL GAME

Wells uses phylogenetic trees to attack the very core of evolution — common descent. Wells claims that textbooks mislead students about common descent in three ways. First, Wells claims that textbooks do not cover the "Cambrian Explosion" and fail to point out how this "top-down" pattern poses a serious challenge to common descent and evolution. Second, he asserts that the occasional disparity between morphological and molecular phylogenies disproves common descent. Finally, he demands that textbooks treat *universal* common ancestry as unproven and refrain from illustrating that "theory" with misleading phylogenies. Therefore, according to Wells, textbooks should state that there is no evidence for common descent and that the most recent research refutes the concept entirely. Wells is completely wrong on all counts, and his argument is entirely based on misdirection and confusion. He mixes up these various topics in order to confuse the reader into thinking that when combined, they show an endemic failure of evolutionary theory. In effect, Wells plays the equivalent of an intellectual shell game, putting so many topics into play that the "ball" of evolution gets lost.

THE CAMBRIAN EXPLOSION

Wells claims that the Cambrian Explosion "presents a serious challenge to Darwinian evolution" (Wells, 2000:41) and the validity of phylogenetic trees. The gist of Wells's argument is that the Cambrian Explosion happened too fast to allow large-scale morphological evolution to occur by natural selection ("Darwinism"), and that the Cambrian Explosion shows "top-down" origination of taxa ("major" "phyla" level differences appear early in the fossil record rather than develop gradually), which he claims is the opposite of what evolution predicts. He asserts that phylogenetic trees predict a different pattern for evolution than what we see in the Cambrian Explosion. These arguments are spurious and show his lack of understanding of basic aspects of both paleontology and evolution.

Wells mistakenly presents the Cambrian Explosion as if it were a *single* event. The Cambrian Explosion is, rather, the preservation of a series of faunas that occur over a 15–20 million year period starting around 535 million years ago (MA). A fauna is a group of organisms that live together and interact as an ecosystem; in paleontology, "fauna" refers to a group of organisms that are fossilized together because they lived together. The first fauna that shows extensive body plan diversity is the Sirius Passet fauna of Greenland, which is dated at around 535 MA (Conway Morris, 2000). The organisms preserved become more diverse by around 530 MA, as the Chenjiang fauna of China illustrates (Conway Morris, 2000). Wells erroneously claims that the Chenjiang fauna predates the Sirius Passet (Wells, 2000:39). The diversification continues through the Burgess shale fauna of Canada at around 520 MA, when the Cambrian faunas are at their peak (Conway Morris, 2000). Wells makes an even more important paleontological error when he does not explain that the "explosion" of the late Early and Middle Cambrian is preceded by the less diverse "small shelly" metazoan faunas, which appear at the *beginning* of the Cambrian (545 MA). These faunas are dated to the early Cambrian, not the Precambrian as stated by Wells (Wells, 2000:38). This enables Wells to omit the steady rise in fossil diversity over the ten million years between the beginning of the Cambrian and the Cambrian Explosion (Knoll and Carroll, 1999).

In his attempt to make the Cambrian Explosion seem instantaneous, Wells also grossly mischaracterizes the Precambrian fossil record. In order to argue that there was not enough time for the necessary evolution to occur, Wells implies that there are no fossils in the Precambrian record that suggest the coming diversity or provide evidence of more primitive multicellular animals than those seen in the Cambrian Explosion (Wells, 2000:42–45). He does this not by producing original research, but by selectively quoting paleontological literature on the fossil record and claiming that this proves that the fossil record is complete enough to show that there were no precursors for the Cambrian Explosion animals. This claim is false. His evidence for this "well documented" Precambrian fossil record is a selective quote from the final sentence in an article by Benton et al. (2000). While the paper's final sentence does literally say that the "early" parts of the fossil record are adequate for studying the patterns of life, Wells leaves out a critical detail: the sentence refers not to the Precambrian, but to the *Cambrian and later times*. Even more ironic is the fact that the conclusion of the paper directly refutes Wells's claim that the fossil record does not support the "tree of life." Benton et al. (2000) assessed the completeness of the fossil record using both molecular and morphological analyses of phylogeny. They showed that the *sequence of appearance* of major taxa in the fossil record is consistent with the pattern of *phylogenetic relationships* of the same taxa. Thus they concluded that the fossil record is consistent with the tree of life, entirely opposite to how Wells uses their paper.

Wells further asserts that there is no evidence for metazoan life until "just before" the Cambrian explosion, thereby denying the necessary time for evolution to occur. Yet Wells is evasive about what counts as "just before" the Cambrian. Cnidarian and possible arthropod embryos are present 30 million years "just before" the Cambrian (Xiao et al., 1998). There is also a mollusc, *Kimberella*, from the White Sea of Russia (Fedonkin and Waggoner, 1997) dated approximately 555 million years ago, or 10 million years "just before" the Cambrian (Martin et al., 2000). This primitive animal has an uncalcified "shell," a muscular foot (Fedonkin and Waggoner, 1997), and a radula inferred from "mat-scratching" feeding patterns surrounding fossilized individuals (personal observation; Seilacher, pers.

comm.). These features enable us to recognize it as a primitive relative of molluscs, even though it lacks a calcified shell. There are also Precambrian sponges (Gehling and Rigby, 1996) as well as numerous trace fossils indicating burrowing by wormlike metazoans beneath the surface of the ocean's floor (Seilacher, 1994; Fedonkin, 1994). Trace fossils demonstrate the presence of at least one ancestral lineage of bilateral animals nearly 60 million years "just" before the Cambrian (Valentine et al., 1999). Sixty million years is approximately the same amount of time that has elapsed since the extinction of non-avian dinosaurs, providing plenty of time for evolution. In treating the Cambrian Explosion as a single event preceded by nothing, Wells misrepresents fact — the Cambrian explosion is *not* a single event, *nor* is it instantaneous and lacking in any precursors.

Continuing to move the shells, Wells invokes a semantic sleight of hand in resurrecting a "top-down" explanation for the diversity of the Cambrian faunas, implying that phyla appear first in the fossil record, before lower categories. However, his argument is an artifact of taxonomic practice, not real morphology. In traditional taxonomy, the recognition of a species implies a phylum. This is due to the rules of the taxonomy, which state that if you find a new organism, you have to assign it to all the necessary taxonomic ranks. Thus when a new organism is found, either it has to be placed into an existing phylum or a new one has to be erected for it. Cambrian organisms are either assigned to existing "phyla" or new ones are erected for them, thereby creating the effect of a "top-down" emergence of taxa.

Another reason why the "higher" taxonomic groups appear at the Cambrian Explosion is because the Cambrian Explosion organisms are often the first to show features that allow us to relate them to living groups. The Cambrian Explosion, for example, is the first time we are able to distinguish a chordate from an arthropod. This does not mean that the chordate or arthropod lineages evolved then, only that they then became recognizable as such. For a simple example, consider the turtle. How do you know a turtle is a turtle? By the shell. How would you recognize the ancestors of the living turtle, before they evolved the shell? That is more complicated. Because its ancestors would have lacked the diagnostic feature of a shell, ancestral turtles may be hard to recognize (Lee, 1993). In order to locate the remote ancestors of turtles, other, more subtle, features must be found.

Similarly, before the Cambrian Explosion, there were lots of "worms," now preserved as trace fossils (i.e., there is evidence of burrowing in the sediments). However, we cannot distinguish the chordate "worms" from the mollusc "worms" from the arthropod "worms" from the worm "worms." Evolution predicts that the ancestor of all these groups was wormlike, but which worm evolved the notochord, and which the jointed appendages? In his argument, Wells confuses the identity of the individual with how we diagnose that identity, a failure of logic that dogs his discussion of homology in the following chapter. If the animal does not have the typical diagnostic features of a known phylum, then we would be unable to place it and (by the rules of taxonomy) we would probably have to erect a new phylum for it. When paleontologists talk about the "sudden" origin of major animal "body plans," what is "sudden" is not the appearance of animals with a particular body plan, but the appearance of animals that *we can recognize* as having a particular body plan. Overall, however, the fossil record fits the pattern of evolution: we see evidence for worm-like bodies first, followed by variations on the worm theme. Wells seems to ignore a growing body

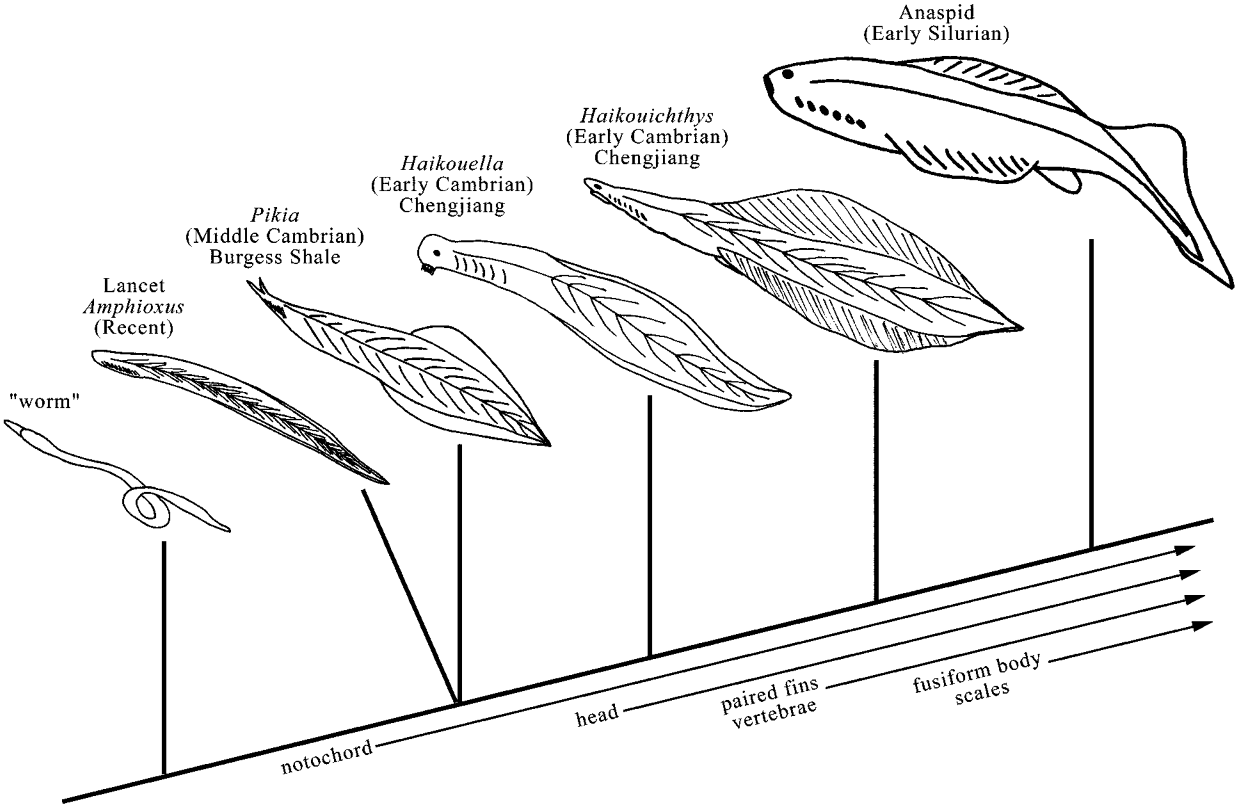


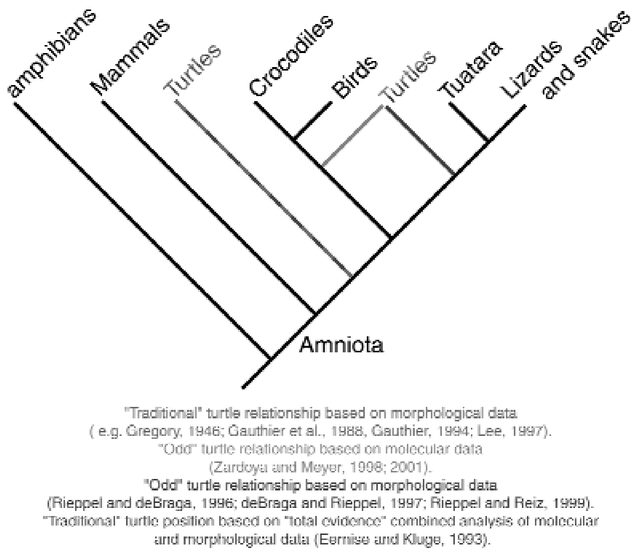
Figure 3. *Stepwise evolution of vertebrate features as illustrated by living and fossil animals.*

of literature showing that there are indeed organisms of intermediate morphology present in the Cambrian record and that the classic “phyla” distinctions are becoming blurred by fossil evidence (Budd, 1998, 1999; Budd and Jensen, 2000).

Finally, the “top-down” appearance of body-plans is, contrary to Wells, compatible with the predictions of evolution. The issue to be considered is the practical one that “large-scale” body-plan change would of course evolve before minor ones. (How can you vary the lengths of the beaks before you have a head?) The difference is that, many of the “major changes” in the Cambrian were initially minor ones. Through time they became highly significant and the basis for “body-plans.” For example, the most primitive living chordate *Amphioxus* is very similar to the Cambrian fossil chordate *Pikia*. Both are basically worms with a stiff rod (the notochord) in them. The amount of change between a worm and a worm with a stiff rod is relatively small, but the presence of a notochord is a major “body-plan” distinction of a chordate. Further, it is just another small step from a worm with a stiff rod to a worm with a stiff rod and a head (e.g., *Haikouella*; Chen et al., 1999) or a worm with a *segmented* stiff rod (vertebrae), a head, and fin folds (e.g., *Haikouichthyes*; Shu et al., 1999). Finally add a fusiform body, fin differentiation, and scales: the result is something resembling a “fish” (Figure 3). But, as soon as the stiff rod evolved, the animal was suddenly no longer just a worm but a chordate — representative of a whole new phylum! Thus these “major” changes are really minor in the beginning, which is the Precambrian–Cambrian period with which we are concerned.

CONGRUENCE OF PHYLOGENIES BASED ON DIFFERENT SOURCES OF DATA

Wells also points to the occasional lack of congruence between molecular- and morphology-based phylogenies as evidence against common descent. (Molecular phylogenies are based on comparisons of the genes of organisms.) Wells omits the fact that the discrepancies are frequently small, and their causes are largely understood (Patterson et al., 1993; Novacek, 1994). Although not all of these discrepancies can yet be corrected for, most genetic and morphological phylogenies are congruent for 90% of the taxa included. For example, all phylogenies, whether morphological or molecular, consider all animals bearing amniotic eggs to be more closely related to one another than to amphibians. Within this group, all reptiles and birds are more closely related to each other than they are to mammals. Finally, birds and crocodiles are more closely related to each other than to lizards, snakes, and the tuatara (Gauthier et al., 1988; Gauthier, 1994). The only group whose placement varies for both molecular and morphology data sets is turtles. This is due to a phenomenon called “long branch attraction” or the “Felsenstein Zone” (Huelsenbeck and Hillis, 1993). Long branch attraction is caused when a organism has had so much evolutionary change that it cannot be easily compared to other organisms, and due to the nature of the methodology used to evaluate phylogeny, it can appear to be related to many possible organisms (Felsenstein, 1978; Huelsenbeck and Hillis, 1993). This is the case for turtles. Turtles are so morphologically and genetically different from the rest of the reptiles that they are hard to place phylogenetically (Zardoya and Meyer, 2001). Still, researchers have narrowed down the possible turtle relationships to a few possibilities (Rieppel and deBraga, 1996; Lee, 1997; deBraga and Rieppel, 1997; Zardoya and Meyer, 1998; Rieppel and Reiz, 1999; Rieppel, 2000; Figure 4), and none of these claim turtles are mammals. The uncertainty over the precise placement of turtles with respect to other groups, however, does not mean that they did not evolve. Unfortunately, genes can never be totally compared to morphology since genetic trees cannot take fossil taxa into account: genes don’t fossilize. No diagnostic tool of science is perfect. The imperfections in phylogenetic reconstruction do not make common ancestry false. Besides, are these extremely technical topics really appropriate for introductory textbooks?



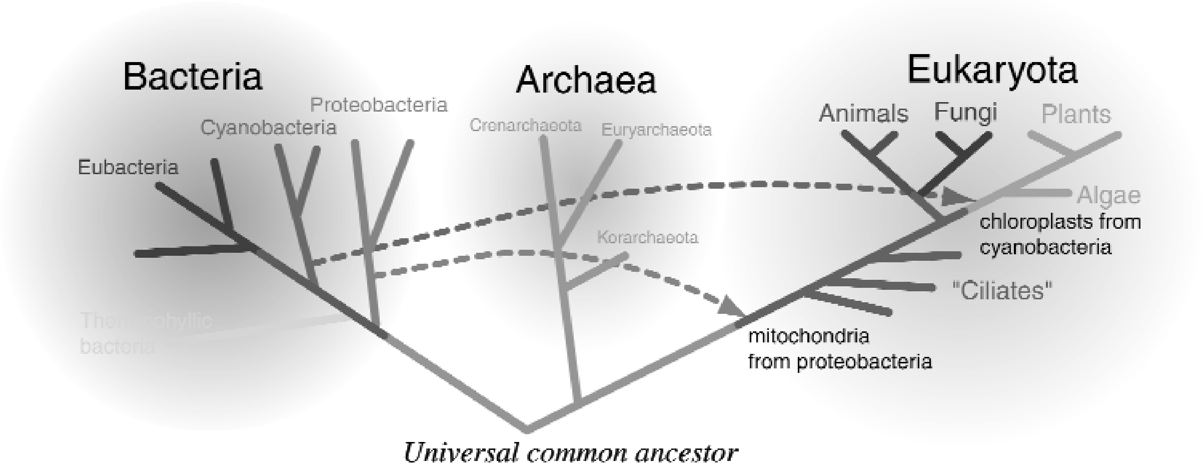
"Traditional" turtle relationship based on morphological data (e.g. Gregory, 1946; Gauthier et al., 1988, Gauthier, 1994; Lee, 1997).
"Odd" turtle relationship based on molecular data (Zardoya and Meyer, 1998; 2001).
"Odd" turtle relationship based on morphological data (Rieppel and deBraga, 1996; deBraga and Rieppel, 1997; Rieppel and Reiz, 1999).
"Traditional" turtle position based on "total evidence" combined analysis of molecular and morphological data (Eernise and Kluge, 1993).

Figure 4. *Amniote relationships based on different sources of data. Note that the only group whose position varies is turtles.*

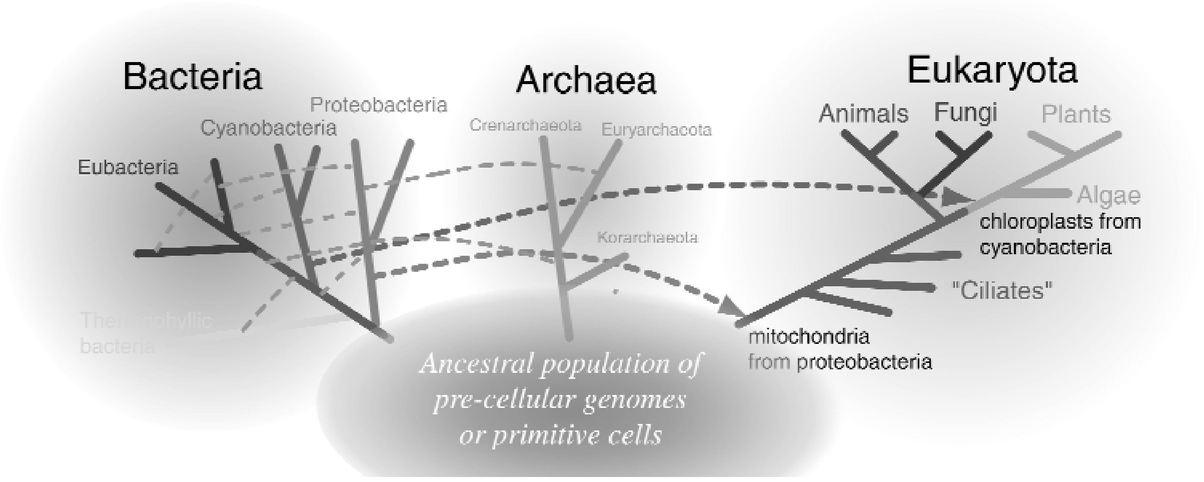
Instead of clearly discussing these actual phylogenetic issues, Wells invents one that isn’t even real. He cites a 1998 paper that placed cows phylogenetically closer to whales than to horses, calling that finding “bizarre” (Wells, 2000:51). Yet this is not “bizarre” at all; it was *expected*. All the paleontological *and* molecular evidence points to a whale orgin within artiodactyls, and further to the fact that artiodactyls (cows, deer, antelopes, pigs, etc.) are not more closely related to perissodactyls (horses, rhinos, and the tapir) than they are to whales (Novacek, 1992, 2001). Wells makes this statement smugly, as if to suggest that everyone should think that this sounds silly. Unfortunately, it is Wells's criticism that is silly.

THE UNIVERSAL COMMON ANCESTOR

Finally, Wells cites the "failure" of molecular phylogeny to clarify the position of the Universal Common Ancestor as proof that there is no common ancestry for any of life. Here, Wells mixes up the different scales of descent in order to tangle the reader in a thicket of phylogenetic branches. He is



"Traditional" view



Woese's view

Figure 5. *The traditional view of phylogenetic relationships for the three "domains" of life compared to Woese's view. Note that the only difference lies in whether there is a single "root" at the base of the tree. Regardless, eukaryotes, archaeans, and bacteria all share a common ancestor on both, although Woese does posit a greater degree of lateral trasfer for single-celled organisms.*

attacking the notion that life originated with one population, and that all life can trace its ancestry back to that population, the Universal Common Ancestor (UCA). The problem has been that it is hard to determine relationships when there is nothing to compare to. How do you compare "not life" to "life"? We have no fossils of the earliest forms of life, and the high degree of genetic change that has occurred in the 3.8 billion years since the early stages of life make it nearly impossible to reconstruct the "original" genetic code. This does not invalidate the concept of common ancestry; it just makes it difficult and potentially impossible to untangle the lineages. And this does not mean that there is not one real lineage: the inability to determine the actual arrangement of "domains" at the base of the tree or to characterize the UCA does not make the UCA any less real than the inability to characterize light unambiguously as either a wave or a particle makes light unreal.

Some authors (e.g., Woese, 1998) go further and suggest that there is no "UCA"; rather, they suggest, life arose in a soup of competing genomes. These genomes were constantly exchanging and mixing, and thus cellular life may have arisen multiple times. Wells misrepresents the statements of those scientists to make it look as if they are questioning the entirety of common ancestry, when what they question is just the idea of a *single* common ancestor at the base of life. Further, when some suggest that we should abandon the search for the UCA, they do not mean that they don't think it existed. They mean only that it may be a waste of time to try to find it given the current technology and methods at our disposal. Regardless of the status of a UCA, which is at the base of the tree of life, the entire debate has nothing to do with the branches of the tree — the shared descent of eukaryotes, of animals, or common descent among vertebrates, arthropods, or angiosperms (Figure 5). That is still *a lot* of evolution that Wells's inaccurate attack on the idea of a UCA does nothing to dispel.

WHAT THE TEXTBOOKS SAY

The concept of common ancestry is at the core of evolution. The very idea that different species arise from previous forms via descent implies that all living things share a common ancestral population at some point in their history. This concept is supported by the fossil record, which shows a history of lineages changing through time. Because evolution is the basis for biology, it would be surprising if any textbook teaching contemporary biology would portray common descent other than matter-of-factly.

Textbooks treat the concept of common descent in basically the same way as do scientists; they accept common ancestry of living things as a starting point, and proceed from there. Phylogenies thus appear in many places in a text, which makes it very hard to evaluate exactly how textbooks "misrepresent" biological evolution using trees. Most texts show a phylogeny in chapters discussing systematics and taxonomy. In this section there is usually a tree of "kingdom" or "domain" relationships, which may be what Wells considers a tree showing "universal" common ancestry; unfortunately, his discussion is too vague for a reader to be sure whether that is what he is referring to. Many textbooks show additional, more detailed trees in their discussions of different taxonomic groups. In terms of textbook presentations, then, there is no single "Darwin's tree of life" presented in some iconic state, but many various phylogenies shown in the appropriate sections of most books. Textbooks also present trees in the chapters on processes and mechanisms of evolution, in the "Origin of life" or "History of life" chapters, and in chapters dealing with individual taxonomic groups.

Book	Darwin's "Tree of Life"			
	//pages	//words	mentions Cambrian	Wells's grade
Schraer, W. D. and H. J. Stolze. 1999. Biology: The Study of Life, seventh edition. Prentice-Hall, Upper Saddle River, NJ. 944p.	3/4 (1)	148	No	F
Johnson, G. B. 1998. Biology: Visualizing Life. Holt, Rinehart &Winston, Orlando. 895p.	(8)	NA[1]	Yes	F[2]
Biggs, A., C. Kapinka, and L. Lundgren. 1998. Dynamics of life. Glencoe/McGraw Hill, Westerville, OH. 1119p.	1 (15)	105	Yes	F[3]
Miller, K. R. and J. Levine. 2000. Biology, fifth edition. Prentice-Hall Upper Saddle River, NJ. 1114p.	1(10)	302	Yes*	F[4]
Starr, C. and R. Taggart. 1998. Biology: The Unity and Diversity of Life, eighth edition. Wadsworth Publishing Company, Belmont CA. 920p.	(31)	NA[5]	Yes	F[6]
Guttman, B. S. 1999. Biology. WCB/McGraw-Hill, Boston. 1175p.	1 (24)	111+[7]	No	F
Mader, S. 1998. Biology, sixth edition. WCB/McGraw-Hill, Boston. 944p.	(15)	NA[8]	Yes	F[9]
Raven, P. H. and G. B. Johnson. 1999. Biology, fifth edition. WCB/McGraw-Hill Boston. 1284p.	(19)	NA	No	F
Cambpell, N. A., J. B. Reese, and M. G. Mitchell. 1999. Biology,fifth edition. Benjamin Cummings, Menlo Park, CA. 1175p.	NA[10]	NA[10]	Yes	D
Futuyma, D. 1998. Evolutionary Biology. Sinauer Associates, Sunderland, MA. 761p.	1+[11]	>200	Yes	D

1. Johnson contains no specific section for a "tree of life"; some phylogenies appear in the text.
2. Johnson discusses the rapid origin of major animal body plans in the Cambrian, though he does not call it an "explosion." A "D" would be a more appropriate grade.
3. Wells grade is an "F"; however, the book discusses the Cambrian in the "History of life" section (p. 406), although it does not explicitly call it "explosion." A "D" may be a more appropriate grade on Wells's scale.
4. The text explicitly discusses the "Cambrian Explosion" by name on p. 601; it also discusses problems with rooting the universal tree on p. 326. A "D" would be a more appropriate grade, perhaps even a "D+."
5. Much like Campbell et al., Starr and Taggart integrate phylogenies throughout the text and use them to structure the diversity of life section.
6. The text discusses the Cambrian, although it does not refer explicitly to an "explosion." A "D" would be a more appropriate grade.
7. Guttman devotes one paragraph to describing what phylogenetic trees are. Trees appear throughout the book when discussing evolutionary relationships of different organisms.
8. There is no single "tree of life" section in the text. Phylogenetic method is discussed in detail in the "Classification" chapter (chapter 28; p. 491–506) and phylogenetic trees appear throughout the text.
9. The Cambrian is discussed in the "History of life" section (chapter 20; p. 333) but is not called an "explosion". A "D" may be a more appropriate grade.
10. Phylogenetic trees are integrated throughout Unit 5 (p. 490–665) , and there is no single treatment of the "tree" in the evolution chapter.
11. Futuyma has a section titled "Tree of life" in the "History of life" chapter; however, phylogenetic trees appear throughout the book.

Figure 6. *Evaluation of Wells's grading of Textbook Icon #2, "Darwin's Tree of Life." Parenthetical notations indicate the number of phylogenetic trees shown in the book.*

This is because phylogenetic trees are not part of the "evidence for evolution," but rather graphical representations of the history, genealogy, and taxonomy of life. No textbook misrepresents the methods that are used to construct trees or the trees themselves, although some trees contain out-of-date relationships and occasionally incorrect identifications of organisms pictured in them. When textbooks cover the Cambrian period, the rapid appearance of many body plans is discussed not as a "paradox" for evolutionary theory, but as an interesting event in the history of life — which is how paleontologists and evolutionary biologists consider it.

WELLS'S EVALUATION

Overall, Wells's grading system for this "icon" is so nebulous that it is hard to figure out exactly how he evaluated the textbooks at all. The "Universal Common Ancestor" is far different from the "Cambrian Explosion." These deal with very different places in the "tree of life" as well as very different issues in evolution. Wells's grades seem largely based on presentations of "common ancestry." For example, according to Wells, if the textbook treats common ancestry as "fact," then it can do no better than a D. In order to get a C or better, a book must also discuss the "top-down" nature of the Cambrian explosion as a "problem" for evolution; if a book only mentions the Cambrian Explosion, it gets a D. Here Wells does not even apply his grading scheme consistently (Figure 6). For example, Wells chastises textbooks (Miller and Levine's in particular) for not discussing the Cambrian Explosion, yet most of the textbooks he reviews actually mention it (Figure 6) and Miller and Levine devote an entire page (p. 601) to it. Many of the reviewed textbooks discuss the Cambrian period in the history of life sections, but do not specifically call it an "explosion." These discussions usually mention that it was a "rapid" origin of animal groups. Does Wells actually require that the book *explicitly* mention the "Cambrian Explosion" by name? If so, it should have been specified in the criteria. Or is it that it he only looked for "Cambrian Explosion" in the notoriously spotty indexes of the textbooks? A reevaluation suggests that five of the books to which he gives an F should receive, even by his criteria, a D. Finally, one text (Miller and Levine's) even mentions the confusing nature of the basal divergence of life caused by lateral transfer, yet this discussion can receive no credit in the grading. This is because although Wells considers the "phylogenetic thicket" to be extremely important to reject universal common ancestry, he apparently does not consider it important enough to account for it in his grading scheme. All of this calls into question how well Wells actually reviewed the texts he graded as well as whether his grades have any utility at all.

WHY WE SHOULD CONTINUE TO TEACH COMMON DESCENT

There is no reason for textbooks to significantly alter their presentations of common descent or phylogenetic trees. As long as biological evolution is the paradigm of biology, common descent should be taught. All living organisms that reproduce have offspring that appear similar to, but not exactly like, their parents. We can observe descent with modification every day, and like Darwin, we can confidently extrapolate that it has gone on throughout the history of life. Through this process, small differences would accumulate to larger differences and result in the evolution of diversity that we see today and throughout the history of life.

The concept of descent allows us to make testable predictions about the fossil record and the genetics of organisms. For example, we predict that all animals sharing a common ancestor would have a similar genetic code, use the same cellular processes, and so on; these predictions are confirmed by biochemistry and genetics. In terms of fossils, we would expect to see animals with transitional morphologies in the past, as well as animals that appear similar, but not identical, to those living today. We also predict that these organisms, both past and present, can be arranged into a branching hierarchy of forms, which appears much like a genealogy. This is what the biological community considers science; this is what we should teach.

HOW TEXTBOOKS COULD IMPROVE THEIR PRESENTATIONS OF PHYLOGENY

There is always room for improvement in the presentations of the concept of common descent. Textbooks could improve by updating the phylogenies, many of which are now out-of-date. They should also remove discussions of "phenetics" (an outdated form of phylogenetic reconstruction and classification) from the phylogenetic reconstruction sections, and expand discussions of cladistics and more modern descent-based taxonomies. Finally, textbooks should make a clear distinction between molecular clocks and genetic phylogenies, something many fail to do clearly. However, to make textbooks conform to Wells's criteria would be to misrepresent the entire life sciences and to deprive students of pedagogically useful visual representations of the unity of life.

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HOMOLOGY

HOMOLOGY

Homology is a specific explanation of similarity of form seen in the biological world. Similarities can often be explained by common descent; features are considered homologous if they are shown to be inherited from a common ancestor. For example, although the arms of four-limbed vertebrates externally appear quite different, all have the same basic underlying skeletal and muscular pattern. Such shared patterns are best explained by the inference that they were inherited from a common ancestor that also had this pattern. Proposed homologies are evaluated using comparative anatomy, genetics, development, and behavior.

WELLS RIDES THE HOMOLOGY MERRY-GO-ROUND...

Wells claims that homology is used in a circular fashion by biologists because textbooks define homology as similarity inherited from a common ancestor, and then state that homology is evidence for common ancestry. Wells is correct: this simplified reading of homology is indeed circular. But Wells oversimplifies a complex system into absurdity instead of trying to explain it properly. Wells, like a few biologists and many textbooks, makes the classic error of confusing the definition of homology with the diagnosis of a homologous structure, the biological basis of homology with a procedure for discovering homology. In his discussion, he confuses not only the nature of the concept but also its history; the result is a discussion that would confuse anyone. What is truly important here is not whether textbooks describe homology circularly, but whether homology is used circularly in biology. When homology is properly understood and applied, it is not circular at all.

...BACK TO THE FUTURE

Before 1859, the year Darwin published the *Origin of Species*, homology was defined as similarity of structure and position, and distinguished (although inconsistently) from "analogy," which was defined as similarity of function but not necessarily of structure and position. An example of homology and analogy are the wings of birds and bats. The arms of birds and bats would be considered homologs because they have the same structure and position in both animals. Their wings, however, are analogs. Both wings have the same function (flight), yet the bird's wing is made of feathers, and the bat's is made of skin. They are different structures.

The pre-Darwinian basis for similarity was the idea of an "archetype." The archetype, however, was never clearly defined. The idea belongs to a morphological theory that came from the German transcendentalist philosophers of the late 1700s and early 1800s. It was largely out of fashion by the 1840s, but Richard Owen, who codified this distinction, was dedicated to a philosophy of transcendental causes, as many historians of science have noted (e.g. Russell, 1916; Desmond, 1982; Rupke, 1993; Padian, 1995a, 1997).

Yet the pattern of the biological world more resembles a genealogy than a gallery of cookie-cutter "archetypes." Darwin accounted for the similarities in structure and position among very different animals as being the result of natural selection working on shared ancestral patterns. The concept of homology shifted from reflecting a vague "archetype" to reflecting descent with modification.

Today, biologists still diagnose homologous structures by first searching for structures of similar form and position, just as pre-Darwinian biologists did. (They also search for genetic, histological, developmental, and behavioral similarities.) However, in our post-Darwin period, biologists *define* a homologous structure as an anatomical, developmental, behavioral, or genetic feature shared between two different organisms because they inherited it from a common ancestor. Because not all features that are similar in two organisms are necessarily inherited from a common ancestor, and not all features inherited from a common ancestor are similar, it is necessary to *test* structures before they can be declared homologous. To answer the question, "could this feature in these groups be inherited from a common ancestor?" scientists compare the feature across many groups, looking for patterns of form, function, development, biochemistry, and presence and absence. Many features are tested simultaneously against genealogy through a process that Kluge (1997; see also Kluge, 1998, 1999 for discussions of independent homology tests) termed testing "multiple ad hoc hypotheses of homology."

If, considering all the available evidence, the distribution of characteristics across many different groups resembles a genealogical pattern, it is very likely that the feature reflects common ancestry. Future tests based on more features and more groups could change those assessments, however — which is normal in the building of scientific understanding. Nevertheless, when a very large amount of information from several different areas (anatomy, biochemistry, genetics, etc.) indicates that a set of organisms is genealogically related, then scientists feel confident in declaring the features that they share are homologous. Finally, while judgments of homology are in principle revisable, there are many cases in which there is no realistic expectation that they will be overturned.

So Wells is wrong when he says that homology assumes common ancestry. Whether a feature reflects common ancestry of two or more animal groups is *tested* against the *pattern* it makes with these as well as other groups. Sometimes, though not always, the pattern reflects a genealogical relationship among the organisms — at which point the inference of common ancestry is made. Today, the testing process is carried out by a method called "phylogenetic systematics" or "cladistics," which can be done without assuming an evolutionary relationship among the groups — but descent with modification is the best explanation for the patterns the comparisons of features it reveals.

Evolution and homology are closely related concepts but they are not circular: homology of a structure is *diagnosed* and *tested* by outside elements: structure, position, etc., and whether or not the pattern of distribution of the trait is genealogical. If the pattern of relationships looks like a genealogy, it would be perverse to deny that the trait reflects common ancestry or that an evolutionary relationship exists between the groups. Similarly, the *closeness* of the relationship between two groups of organisms is determined by the extent of homologous features; the more homologous features two organisms share, the more recent their common ancestor. Contrary to Wells's contention, neither the definition nor the application of homology to biology is circular.

As mentioned, new evidence from various fields of biology has expanded our understanding of homology beyond just anatomical structures. Anatomical homologies, behavioral homologies, developmental homologies, and genetic homologies can be independently diagnosed and tested.

Behavioral homology recognizes features of animal behavior that can be traced to common ancestry. For example, consider the nesting practices of birds and crocodilians. Both of these groups share the behaviors of nest-building, parental care of young, and "singing" to defend territory and attract mates. Most people know birds do these things, but fewer know that their cousins the alligators and crocodiles do these things as well. They inherited these behaviors from a shared ancestor. Because of homology, we infer these behaviors for their extinct ancestors as well; thus it came as no surprise when fossils of many non-avian dinosaurs were found nesting with their young (Horner and Makela, 1979; Horner, 1982; Clark et al., 1999).

Developmental homologies are features in the developmental programs of organisms. An example of this is the "pharyngeal pouches" that nearly all vertebrates acquire to some degree during their development, but which become very different structures in the adults. For example, the embryological pharyngeal pouches of jawless chordates (e.g., *Amphioxus*, hagfishes, and lampreys) develop into pharyngeal arches and slits, which support the gill structure and allow water to exit the pharynx after passing over the gills. In jawed vertebrates, such as sharks and fish, the pharyngeal pouches develop into gill supports and portions of the jaw skeleton. In land vertebrates (tetrapods), these arches and pouches develop into jaw skeleton and musculature, but other pouches/arches, which in gill bearing vertebrates developed into gill structure, now develop into ear bones and cavities, and thyroid and tracheal cartilages (Gilbert, 2000). The evolution of the different adult pharyngeal morphologies of vertebrates are the results of alterations of these embryonic structures and their components through the developmental program (Graham, 2001).

Today we also recognize genetic homologies. There are similar genes that control the development of non-homologous features. For example, there is a gene, named "*Pax6*," possessed by fruit flies, mice, and many other organisms, which influences the development of the eye. Biologists hypothesize that the gene is inherited from a common ancestor not only because of its biochemical similarity but also because of its distribution in numerous taxa. However, the actual eyes that the gene forms are not a result of common ancestry — their shared ancestor most likely lacked eyes, although it may have had light-sensing ability. The eyes of flies, mice, and many other creatures are of different structure and position and are not historically continuous, yet the *Pax6* gene is historically continuous and responsible for them all. This homologous gene functions as a "switch" that triggers the development of light-sensing organs (Gilbert, 2000), but the "downstream" genes that they trigger are no longer the same: they govern different developmental programs and thus build structurally different eyes in flies, mice, and other organisms. The relatively new field of evolutionary developmental biology (evo-devo for short) deals with these processes. The discoveries made in just the last 10 years in this field have greatly increased our understanding of homology, and have made the picture more complex. Wells nearly ignores this important new field in his discussion, a surprising omission for one whose background includes a degree in biology.

HOMOLOGY, EVOLUTION, AND THE NATURE OF SCIENCE

Some formulations of the concept of homology appear to be circular, but as discussed above, because there is an external referent (the *pattern* that characteristics take across groups) that serves as an independent test, the concept, properly defined and understood, is not. Wells's claim that homology is circular reveals a mistaken idea of how science works. In science, ideas frequently are formulated by moving back and forth between data and theory, and scientists regularly distinguish between the definition of a concept and the evidence used to diagnose and test it.

Homology is in fact no more circular than the methods used in geology to determine paleogeography and plate tectonics. For example, in the 1920s, Alfred Wegener used the shape of the continents, the correlation of rock strata, the correlation of fossil organisms, and the position of glacial striations as evidence for his proposal that the continents were once joined in one supercontinent and have subsequently "drifted" to their current locations. Today, geologists can estimate where a certain section of a continent used to be by looking at polar wander, paleomagnetism, glacial striations, correlation of strata and fossils, and shape. Is this any more circular than the reasoning for homology? No. Evidence was used to infer that continents had moved, and then the concept of plate tectonics was applied to *different* data to determine the positions of continents at different times. The analogy to plate tectonics is also relevant to Wells's implication (Wells, 2000:77) that we don't fully understand the mechanisms of homology: the mechanism of sea floor spreading may not yet be fully understood, but the continents still move.

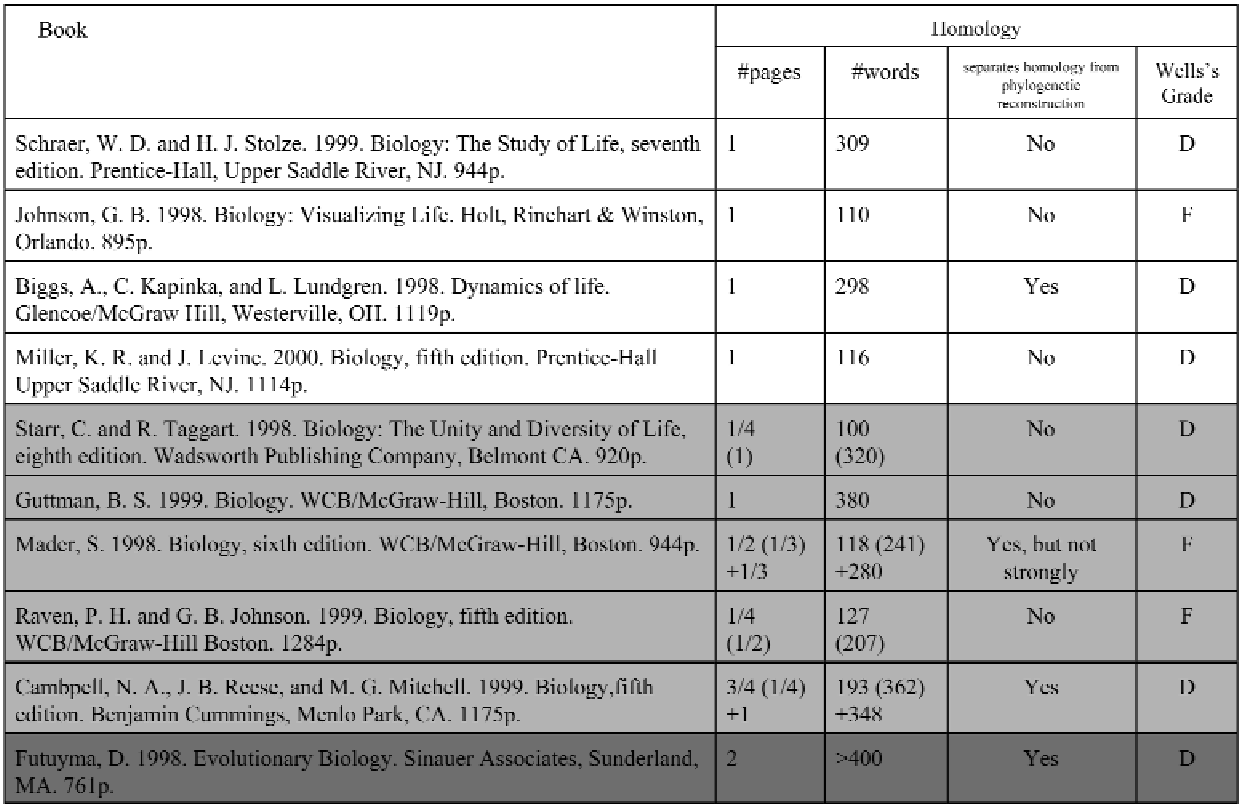
WHAT THE TEXTBOOKS SAY

The presentations of homology in the textbooks reviewed by Wells differ only in the lengths of their discussions. Overall, textbooks give homology (usually including discussions of analogy and vestigial features) 2–10 paragraphs (Figure 7). Because the shorter introductory textbooks have little space to devote to the complexities of how homology is defined, diagnosed, and applied, their explanations verge on the circular. The longer upper-level textbooks make a clearer distinction between the explanation for homology (common ancestry) and using sets of homologies to reconstruct relationships (Figure 7). All textbooks include diagrams of the forelimbs of various vertebrates, and all but one color-code homologous elements for easy identification. Guttman includes a second figure showing homologous bones in a number of tetrapods and one fish skull, clearly illustrating how skulls have been reshaped. Futuyma, Guttman, and Campbell, et al. include the best discussions and illustrations of homology, but nevertheless earn a D from Wells.

Most textbooks include discussions of analogy and vestigial structures along with discussions of homology. Analogous features are features with similar functions (but not necessarily similar structures) that are not inherited from a common ancestor but evolved convergently, whereas vestigial features are remnant structures that have been retained from previous forms. Wells notably leaves out any mention of analogous features or vestigial structures from his evaluation (such as the limb girdles of snakes or the limb girdles of whales cited by most textbooks).

WELLS'S TEXTBOOK EVALUATION

According to Wells, textbooks should explain that homologies are similarities of structure and function due not to common ancestry but to a common "archetype" or basic plan on which all forms were based (Wells is remarkably cagey as to what he means by "archetype"). When Wells proposes that textbooks revert to a pre-Darwinian view of homology, he doesn't explain what that would mean for biology or biology teaching. He doesn't explain that it would replace a testable model (descent) with a non-existent, untestable, transcendentalist construct. Wells is vague because he merely wants to advance his position and the archetype is consistent with some notion of special creation, as



Book	Homology			
	#pages	#words	separates homology from phylogenetic reconstruction	Wells's Grade
Schraer, W. D. and H. J. Stolze. 1999. Biology: The Study of Life, seventh edition. Prentice-Hall, Upper Saddle River, NJ. 944p.	1	309	No	D
Johnson, G. B. 1998. Biology: Visualizing Life. Holt, Rinehart & Winston, Orlando. 895p.	1	110	No	F
Biggs, A., C. Kapinka, and L. Lundgren. 1998. Dynamics of life. Glencoe/McGraw Hill, Westerville, OH. 1119p.	1	298	Yes	D
Miller, K. R. and J. Levine. 2000. Biology, fifth edition. Prentice-Hall Upper Saddle River, NJ. 1114p.	1	116	No	D
Starr, C. and R. Taggart. 1998. Biology: The Unity and Diversity of Life, eighth edition. Wadsworth Publishing Company, Belmont CA. 920p.	1/4 (1)	100 (320)	No	D
Guttman, B. S. 1999. Biology. WCB/McGraw-Hill, Boston. 1175p.	1	380	No	D
Mader, S. 1998. Biology, sixth edition. WCB/McGraw-Hill, Boston. 944p.	1/2 (1/3) +1/3	118 (241) +280	Yes, but not strongly	F
Raven, P. H. and G. B. Johnson. 1999. Biology, fifth edition. WCB/McGraw-Hill Boston. 1284p.	1/4 (1/2)	127 (207)	No	F
Cambpell, N. A., J. B. Reese, and M. G. Mitchell. 1999. Biology,fifth edition. Benjamin Cummings, Menlo Park, CA. 1175p.	3/4 (1/4) +1	193 (362) +348	Yes	D
Futuyma, D. 1998. Evolutionary Biology. Sinauer Associates, Sunderland, MA. 761p.	2	>400	Yes	D

Figure 7. *Examination of grades applied by Wells for Icon #3. Parentheticals refer to additional coverage. Plus (+) numbers reflect secondary treatments of homology and convergence in phylogenetic recontstruction sections of the text.*

favored by proponents of "intelligent design" creationism and their allies.

Wells's grades (he gives only Ds and Fs) appear to correlate with the length of the textbook's coverage (Figure 7). For example, all books given Ds devote well over 200 words to the discussion of homology, whereas the three books given an F devote fewer than 200 words. This is because the difference between a D and an F for Wells is whether the book defines homology "circularly." Therefore, the ability to treat homology "well" (meaning a D) depends largely on how much space is devoted to the discussion of it. Wells does, however, allow the book to have a picture. In order to receive a B or better, textbooks must define homology as similarity of structure and position and state that homology is based on the concept of an "archetype." Further, they should state that an "archetype" could mean many things, not just common ancestry. He also wants textbooks to state — inaccurately — that mechanisms such as genetics and developmental programs do not account for homology. Finally, he wants textbooks to state that the concept of homology is "controversial." This scheme is rigged for failure because contemporary biology does not consider homology to be either controversial or based on archetypes. There is certainly no reason to accept these grading criteria.

WHY WE SHOULD STILL TEACH THAT HOMOLOGY IS A RESULT OF COMMON ANCESTRY

As our current knowledge of biology suggests, there is no reason to doubt the fact that the patterns of structures, behavior, genes, and developmental programs fit best with the hypothesis that all organisms share common ancestors. Many of the similarities among these widely divergent groups are a result of that ancestry. The questions currently being debated in biology are not whether homology is real, but rather what structures are homologous and how we may best determine homology (because our diagnostic approaches are fallible). This type of discussion of reliability of methodology is typical for science in all fields, not just biology. Descent is the basis for homology; similar genes, acting through development, convey homology between generations. Genes build structures through their interactions in the developmental program. Therefore genes, development, and similarity of structure and position are discovery procedures for homology; they help biologists to determine evolutionary relationships. This fits the patterns and processes we observe in the natural world; this is what we should teach.

HOW TEXTBOOKS COULD IMPROVE THEIR DISCUSSIONS OF HOMOLOGY

The biggest flaw in textbook descriptions of homology is that they, like Wells, tend to confuse the definition of homology with the diagnosis of homologous features. Textbooks need to state explicitly that homologies are similarities seen in the biological world that are best explained as being due to common descent. They should then explain how homologous structures are diagnosed by their similar structure and position, biochemical basis, developmental path, and so on. A more detailed and lengthened discussion would help to remove the appearance of circularity caused by oversimplified descriptions. Describing how homology is used as a tool to discover evolutionary relationships would make it a much more pedagogically useful concept for students because it would show them how evolutionary biologists use anatomical observations to discover evolutionary relationships. Finally, adding the notions of multiple layers of homology from genetics and developmental biology would better show students just how different lines of evidence converge to support homologies and phylogenies. Textbooks should not follow Wells's suggestion to say that homology is merely similarity in structure and position, nor should they state that there are "other" reasons for homologies beyond inheritance from a common ancestor. To revert to Wells's 19th-century notion of homology would leave students unprepared to participate in 21st-century science.

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HAECKEL'S EMBRYOS

ERNST HAECKEL AND COMPARATIVE EMBRYOLOGY

Ernst Haeckel (1834–1919) is both a hero and a villain in the biological community. He was a prominent figure in the late nineteenth-century comparative anatomy community and is famous for his phylogenetic trees, anatomical illustrations, support for evolution, and strong personality. He is perhaps as well known, and considerably misunderstood, for his studies in embryology and his dictum that "ontogeny recapitulates phylogeny," called the Biogenetic Law. Haeckel espoused the view that evolution generally proceeds by placing each innovation on top of a previous one, like adding layers on a cake. Therefore, the embryo of an "advanced" organism should pass through ("recapitulate") the *adult* stages of more "primitive" forms as it develops. However, repeated observations of development by other workers (e.g., Wilhelm His, Walter Garstang, Wilhelm Roux, Adam Sedgwick, Gavin de Beer, and others; see Gilbert, 1991, or Gould, 1977 for a detailed history) clearly showed that embryos do not go through adult stages of lower forms; rather, they share many common features in development. No biologist has accepted the biogenetic law for many decades and it may have been a caricature of Haeckel's actual views anyway. Much of Haeckel's developmental work is now considered invalid, and some historians of science have provided reasonable evidence to suggest that he manipulated his drawings to fit his preconceived views about development and evolution. Haeckel's views about the progressive nature of evolution are no longer accepted.

Regardless of Haeckel's accuracy or preconceptions, comparative embryology continues to be central to our understanding of evolution. Comparative embryology shows how different adult structures of many animals have the same embryonic precursors. These shared developmental features suggest that many animals have ancestors in common. Further comparative embryology shows that closely related animals show a unity of developmental pattern, particularly in earlier stages, and have more developmental features in common than do more distantly related organisms. The fact that certain incipient structures such as pharyngeal pouches or arches exist in all vertebrate embryos yet develop into very different adult structures suggests that they all share a common ancestor whose embryo had pharyngeal pouches (at least at some stage in development). In this way, developmental similarities that are inherited from a common ancestor are homologous, just like the patterns of bones in adult limbs.

DEVELOPING AN ARGUMENT

Wells's entire chapter on embryology amounts to little more than a misreading of Darwin, Haeckel, and others, combined with a general failure to acknowledge recent work on Haeckel and his embryos by Gould, Richardson, and others. In it, he conflates ideas in history of developmental biology with ideas of contemporary developmental biology. He also fails to recognize close to 60 years of work in developmental biology and thus completely omits any discussion of the real developmental evidence for evolution. It almost seems that Wells's goal is to discredit the entire field of comparative embryology by proxy, employing a bait-and-switch between Haeckel and Darwin. Wells's ploy is reminiscent of a child's false logic proof. It goes like this: Darwin relied on Haeckel, Haeckel was a fraud, therefore Darwin is a fraud.

The charge that Ernst Haeckel intentionally "faked" his drawings is irrelevant. Regardless of his intent, the drawings that Haeckel made are incorrect, especially in what he labeled as the "first stage." But it really does not matter what Haeckel thought or whether his drawings are accurate: modern comparative embryology does not stand or fall on the accuracy of Haeckel any more than modern physics stands or falls on the accuracy of Kepler or Newton. Historically, Wells actively ignores the accurate work of many of Haeckel's predecessors and contemporaries (such as William and Jeffrey Parker, Hans Gadow, Hans Selenka, Heinrich Rathke, Virgil Leighton, Hugo Schauinsland, and Alfred Voeltzkow, to name a few). Haeckel and von Baer were not the only embryologists in nineteenth-century science, but you wouldn't know that from reading Wells. Worse, Wells speciously extends his critique of Haeckel to the present day. Wells implies that textbooks misrepresent the study of developmental programs as evidence for evolution by accusing them of using Haeckel's inaccurate drawings, in effect accusing textbooks that show any embryos of "mindlessly repeating" Haeckel. The important question is whether textbooks, and more importantly developmental biologists, still rely on Haeckel's work. The answer is no, but that doesn't stop Wells from acting as if they do.

Wells sets up a straw man in his bait-and-switch, starting with Darwin's famous assertion that embryology represented the "single strongest class of facts" in favor of his theory. Here Wells misrepresents both early embryology and Darwin's own words. When quoting both Darwin and other historical figures, he quotes them out of context, leaves out important parts of quotes, and even changes the order of their appearance, all to misrepresent their real meaning and intent. Wells also conflates "recapitulation" — that is, that embryos go through the adult stages of their ancestors — with the idea that shared features of embryos give insight into their phylogenetic relationships. Failing to distinguish these allows Wells to avoid dealing with the actual evidence for shared developmental features in various embryos and to dismiss the entire field as based on an outdated and outright refuted claim, one that embryologists know to be false but cling to anyway because of an ideological commitment to evolution. Wells should know better, as the holder of a Ph.D. in cell and developmental biology.

REWRITING HISTORY FOR THE GREATER GLORY OF THE REV. MOON

In the introduction to *Icons*, Wells states that he first became aware of the problems in evolutionary theory when he was "finishing his Ph.D. in cell and developmental biology" (Wells, 2000:xi). He claims that he knew that the drawings of embryos presented in textbooks were false because he was a developmental biologist. Shortly thereafter, he claims, his observation was confirmed by other scientists. Before that seminal event, he says, "I believed almost everything I read in my textbooks" (Wells, 2000:xi). This statement is inconsistent with other claims of Wells's. According to statements made by Wells in a sermon on a Unification Church website (http://www.tparents.org/library/unification/talks/wells/DARWIN.htm), he went to graduate school with the specific intent of attacking evolution: "Father's words, my studies, and my prayers convinced me that I should devote my life to destroying Darwinism" and he believed that its weakest point was developmental biology. "I was convinced that embryology is the Achilles' heel of Darwinism; one cannot understand how organisms evolve unless one understands how they develop. In 1989, I entered a second Ph.D. program, this time in biology, at the University of California at Berkeley. While there, I studied embryology and evolution." So it was not so much a "revelation" as it was a plan. If Wells is so revisionist about his own history, how can we trust him with the history of science?

DEVELOPMENTAL ANATOMY, DARWIN, AND EVOLUTION

Wells opens the chapter by telling us what Darwin thought about development and evolution. Wells uses about 5 different quotes from the *Origin* in an attempt to show that Darwin was advocating recapitulation in spite of what the data showed. To do this, he distorts the history. Wells tries to connect Darwin to Haeckel so that he can use that to dismiss Darwin. Wells says that Darwin was not an embyrologist and thus he relied on Haeckel (Wells, 2000:81). Anyone familiar with the history of biology knows that this is impossible. Haeckel did not publish his *Anthropogenie* until 1874 (where the much-maligned embryo drawings first appear), *15 years* after the publication of the *Origin*. (It should also be noted that the drawings referred to by Wells [2000] are not from Haeckel but redrawn from the first edition of *Anthropogenie* in a textbook by Romanes [1892; see figure 10a]. In later editions of *Anthropogenie,* Haeckel corrected some of the errors of the first edition drawings [Richardson and Keuck, 2002; personal observation].) Wells quotes Darwin's praise of Haeckel in his sixth and final edition of the *Origin* in such a way as to obscure the fact that Darwin lauds Haeckel for his phylogenies, not his embryology. The quote is not even from the embryology section of the book; rather it comes from the classification section, in the final sentence of which Darwin praises Haeckel for using homologous features (including but not limited to developmental ones) to generate classifications for organisms. Darwin is praising the application of *his* theory by Haeckel.

Although Darwin did not use Haeckel on embryology, he did use von Baer. Recognizing Darwin's use of von Baer, Wells then accuses Darwin of "misusing" von Baer's work, twisting the data to fit his views. But Darwin does not. Wells claims that von Baer's embryological laws are incompatible with Darwin's conclusions, but they are not. Von Baer may have disagreed with Darwin about his conclusions, but his laws do not prohibit development elucidating common ancestry. Darwin came to a different conclusion from the same body of evidence — this is not "distorting" the evidence. Darwin was making a general inductive argument and searched for data that could test the general proposition of common descent; he argued that von Baer's data could be reinterpreted in terms of common ancestry. This was no more a "misuse" of von Baer than was Alfred Wegener's reinterpretations of the data of geology in light of mobile continents. New scientific theories always use previous data. Is Wells implying that evolutionary biology cannot cite any research that predates 1859? Is Wells implying that developmental sequences such as those illustrated by von Baer and others are not data?

That Darwin and all modern evolutionists advocate some form of the "Biogenetic Law" is the central falsehood of this chapter; in fact the entire "resurrecting recapitulation" section does nothing but assert this. But Wells fails to explain fully what recapitulation means. There are a number of meanings for "recapitulation" that Wells conflates in order to tar the entire field of embryology with a biogenetic brush. As he says in a footnote, a "plain reading" of Darwin shows that Darwin was advocating recapitulation — but just what kind? (1) An embryo of an "advanced" form goes through all the adult stages of all its ancestors. This is a caricature of Haeckelian recapitulation, which is false, and few scientists ever believed it anyway. (2) Evolution proceeds as an "add-on" process so that there is a general progression of embryological stages from "primitive" to "advanced" forms. This more traditional reading of recapitulation is also false and has not been accepted for nearly a century. (3) All closely related organisms go through all the same stages of development and always look similar. This is vague: how closely related is closely related? How are the stages individuated? But however these questions are answered, this reading of recapitulation would generally be agreed to make too sweeping a claim. (4) Some parts of developmental sequences (and some specific characters of them) in closely related animals share more specific similarities (in pattern, sequence, position, etc. of developmental features) with each other than with those of more distantly related animals. That's basically true. All modern biologists recognize that all stages of development are open to modification. This is generally the type of "recapitulation" accepted by the post-Haeckelian embryologists (such as Frank Lillie) cited by Wells, as well as by current embryologists, but Wells treats it derisively as if it were exactly what Haeckel thought. Finally, a "plain reading" of Darwin shows that he was suggesting something between (2) and (3); even though he was not an embryologist, he had a more sophisticated notion of embryology and development than does Wells.

Wells chides Darwin and nineteenth-century embryologists for saying that the "earliest" stages of development are similar when in fact they are not. However, "earliest" is Wells's word, not Darwin's. It does not appear in any of the quotes that Wells uses. Indeed, in the entire section on embryology in the *Origin*, the word "earliest" only appears once, in a quotation from von Baer. Does "earliest" reflect Darwin's belief, or is he merely reporting von Baer's? This is important because numerous scholars have made the mistake of confusing Darwin's reporting of what others thought with his expression of his own views (Padian, 1999). So apparently has Wells. But it really does not matter what Darwin thought: just as modern embryology does not rely on Haeckel, neither does modern evolutionary biology slavishly follow Darwin's beliefs.

It is also important to understand what nineteenth-century scientific workers may have meant by the use of "embryo" and "early stage." For many workers in the nineteenth century, developing organisms weren't called embryos until they reached the tailbud (phylotypic) stage. During earlier stages, they were called "developing ovum" or "developing egg" (see Barry, 1839, or just about any embryology work from 1820 to 1900). What this means is that Haeckel, von Baer, and others, have a different meaning for "early embryo." Yet Wells interprets them using modern definitions.

Wells also criticizes the field of comparative embryology for the way it chooses its data and for its names for embryonic structures. First, Wells emphasizes the disparity of "earliest" developmental stages, accusing biologists of "choosing" taxa (animals) that look most similar for illustrations in textbooks and elsewhere. He criticizes Haeckel for not using animals such as monotremes in his work. But developmental sequences for monotremes were not available in 1874. Monotreme developmental sequences were not known or described until 1884 (Caldwell, 1887; Hughes and Hall, 1998), and it was the developmental features monotremes shared with marsupials that led Caldwell to conclude that monotremes were indeed mammals (Caldwell, 1887). Was the sample of organisms available to Haeckel

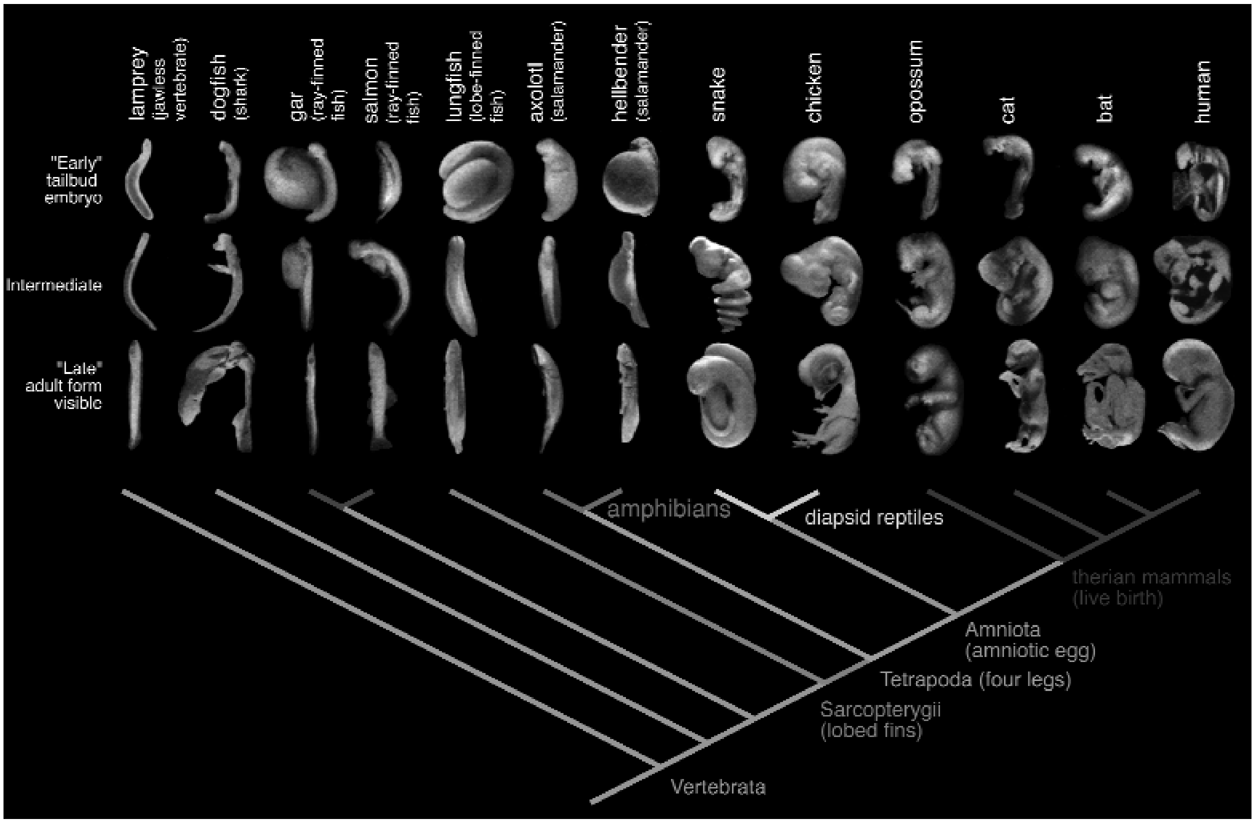


Figure 8. *Developmental sequences of various vertebrates shown in phylogenetic context. Note the shared similarities of some closely related taxa, particularly the amniotes (modified from Richardson et al. 1998).*

biased? Yes, but only in the sense that early embryologists worked with the animals that were available to them. Most specimens of “exotic” animals were shipped to researchers by explorers and received in varying states of decay (Caldwell, 1887). Most nineteenth-century embryologists loved to describe the development of any animal they could. And Haeckel was continually updating and adding new organisms to his embryonic series as they came available. Contrary to what Wells implies, there was no attempt to limit the data, and the sample was not “chosen” for any particular reason.

Today, embryologists work mainly with “model organisms,” which were largely chosen for practical reasons such as ready availability, small body size, large litter size, rapid sexual maturity, rapid reproduction, ability for development to occur in the laboratory, and ability to live indoors for several generations (Bolker, 1995). They were not chosen to “support evolution” as Wells implies. In fact, the model organism that is the subject of Wells’s own dissertation, *Xenopus*, was not the original “model” amphibian. The discovery that *Xenopus* does not need a breeding season was a boon to embryologists and led to its serendipitous adoption as a model organism (Gurdon and Hopwood, 2000). How Wells knows that “model organisms” were chosen to mislead is unclear, especially given his own use of model organisms later in his chapter. Wells doesn’t show developmental sequences for any of the organisms he complains others don’t show. Why not? Because there is no evidence for his insinuation that developmental biologists treat their data selectively in order to hide something. The fact that embryologists tend to present, at least in textbooks, developmental sequences for which there is good data does not refute the idea that closely related taxa, should, and do, have more shared similarities in developmental programs than more distantly related taxa (Figures 8, 9). Wells tries to support his claim by using a quote by Darwin in which he states that embryos of the *same* "class" are most similar in their earliest stages. Wells then says that the quote is false, and cites how the *different* "classes" of vertebrates are very different in their "earliest" stages. This is merely a semantic sleight-of-hand, a bait-and-switch. Darwin is not talking about different "classes." Wells leaves out important information, as usual.

In the figures of embryos (Wells, 2000:95, especially stage 4, "gastrulation"), Wells's illustrator resorts to a number of graphic tricks in order to make the embryos appear more different than they are. First, the embryos are not shown from the same rotational angles. The chicken is shown in a different position than the other "Haeckel's first stage" embryos. Second, they are not all scaled the same. In the figure showing the neural crest infolding, the turtle and chicken are shown at a large scale, neglecting the large yolk they sit on, while the human is shown as part of the whole developing ovum, so that the germinal disc and primitive streak formation are shown differently, even though it is shared by all amniotes (Schaunislaund, 1903; Nelson, 1953; Cruz, 1997; Schoenwolf, 1997; Figure 9). Also pictured is a frog embryo, despite its indirect development, which is very different from that of the other vertebrates pictured. Many of the general "differences" in early embryo development that Wells mentions are a result of organization due to the yolk size rather than being specific differences in the basic body-plan of the embryo (Arendt and Nübler-Jung, 1999).

Embryos do reveal phylogenetic information in terms of specific shared features, shared early developmental features such as the formation of a germinal disc and primitive streak in all amniotes or the neural crest cells of all vertebrates. The presence, and sequence of development, of eyes, ears, somites, limbs, guts, nerve cords, tails, organs, etc. are individual features that no one would deny are

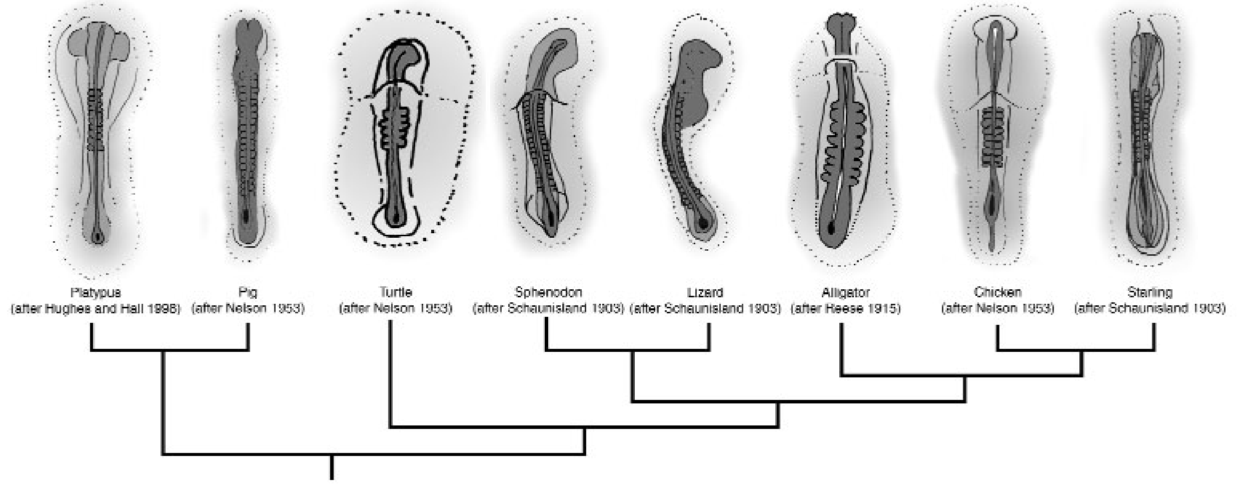


Figure 9. *Embryos of various amniotes shown during somite stage. All amniotes go through the same sequence of development: primitive streak–neural tube–somite formation.*

present in vertebrates and not present in the same way in other animals. These are individual characters whose developmental features are treated as shared features in reconstructing vertebrate evolution; these features do not always have to be in agreement, and some animals can show unusual derived features early in development, such as the snake's tail (Figure 8).

Wells's treatment of comparative embryology is remarkably limited; for example, he never discusses invertebrate development. Yet there are plenty of shared developmental patterns there as well. Despite the very different appearance of echinoderm, hemichordate, and chordate embryos, they all share the deuterostome condition, in which the first cell opening becomes the anus, before they diverge to their adult body plans. Or what about the trochophore larvae of most protostomes and spiral cleavage shared by annelids, arthropods, mollusks (Nielsen, 1995; Fell, 1997)? The nauplius larvae of crustaceans (Gilbert, 1997) or the verliger larvae and development of gastropods, which go through flexure, torsion, and degeneration of muscles on one side of the body, suggestive of their evolutionary history (Nielsen, 1995; Collier, 1997)? These are just a few of the specific similarities of the kind that Wells implies do not exist. Similarities in embryonic sequences are *data* — characters by which we can discover shared similarities among organisms that can be used to reconstruct their relationships. Using such data in phylogeny is not the same as using those characters in any "recapitulationist" way.

Finally, Wells concludes by attacking prominent biologists such as Gould and Futuyma for supposedly not knowing the truth about Haeckel, saying that this is "a confession of ignorance not likely to inspire confidence in the quality of our biology textbooks" (Wells, 2000:107). Wells's own misrepresentations of the letter and spirit of the concepts and authors he presents do little to inspire confidence in what he says about Haeckel or embryology in general. Even if Wells were right about Haeckel's work and Darwin's use of it, what Haeckel and Darwin thought doesn't matter; embryology has moved beyond them. Wells needs to show a lack of *specific* similarities to support his case. Is Wells actually claiming that there are *no* shared features in development at all? That a chicken gets a planula while the duck gets a naupius? If so, he needs to show it, but Wells never gets to specifics — apparently because the specifics aren't there. Innuendo and accusations of fraud do not cut it in science.

WHAT TEXTBOOKS SAY

For any textbook to show Haeckel's drawings themselves as unqualified statements of developmental anatomy or to advocate "recapitulation" in a Haeckelian sense would be inexcusable, but none of the textbooks reviewed by Wells appear to do so. Wells gleefully excoriates Futuyma for using Haeckel's drawings (Figure 10a), but apparently in his fit of righteous indignation, he for-

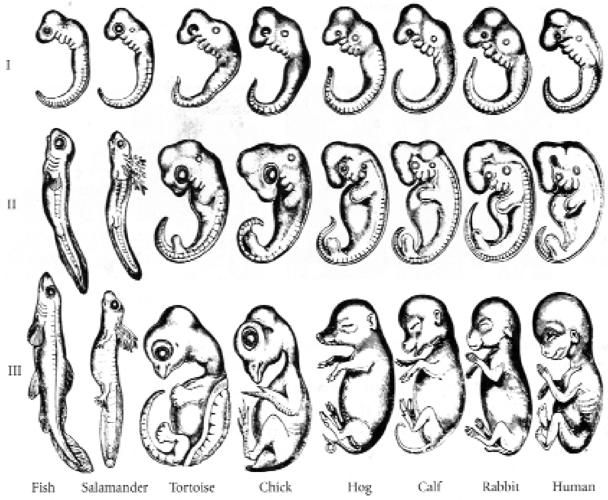


***Figure 10a.** Romanes (1892) embryo drawings reproduced in Futuyma (1998:653).*

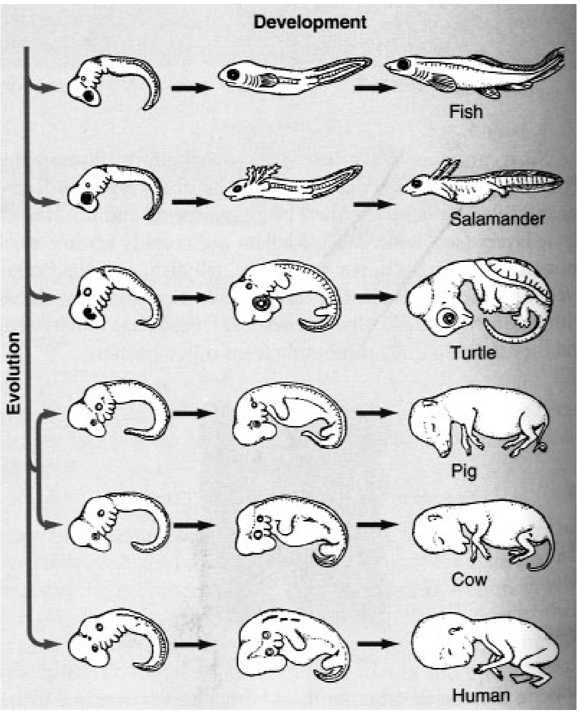


Figure 10b. *Romanes (1892) embryos reproduced and placed in historical context in Guttman (1999:718)*

got to read the text, in which the drawings are discussed in a *historical* context — stating why Haeckel is wrong — and Futuyma has an entire chapter devoted to development and evolution. Guttman (Figure 10b) uses them in an explicitly historical context as well. Wells states that books use "Haeckel's drawings, or redrawn versions of them" (Wells, 2000:255), but this is not true. Figures 10a–j show Haeckel's drawings compared to the drawings in the textbooks reviewed by Wells. It can be clearly seen that a majority of the drawings are not "redrawn." Some textbooks show more accurate drawings (Miller and Levine, Johnson, Biggs, Kapicka and Lundgren; Figures 10f,g,h); some use photos (Campbell, Reese and Mitchell, Mader; Figures 10i,j); only Starr and Taggart (Figure 10c), Raven and Johnson in their development chapter along with accurate drawings and photos; (Figure 10d), and Schraer and Stolze (but redrawn and corrected; Figure 10e) use what could be considered embryos "redrawn" from Haeckel. No textbook discusses embryology in any way

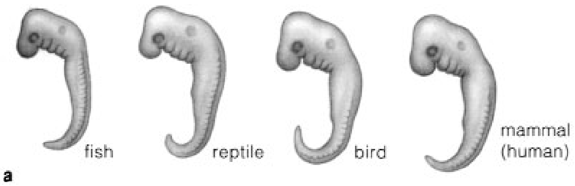


Figure 10c. *Romanes (1892) embryos redrawn in Starr and Taggart (1998:317).*

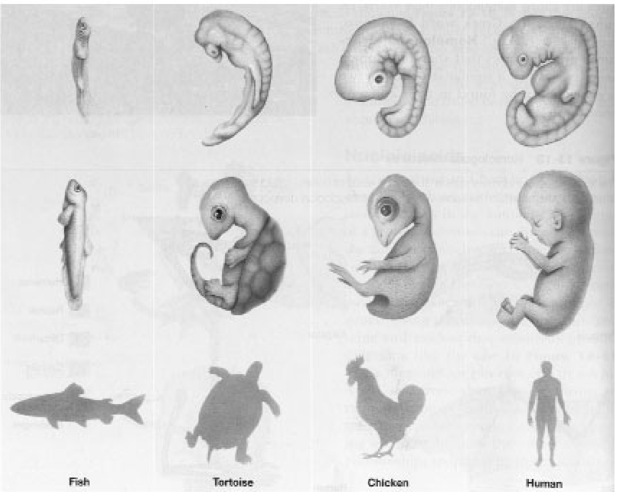


Figure 10d. *Embryos redrawn and somewhat corrected in Raven and Johnson (1999:288).*

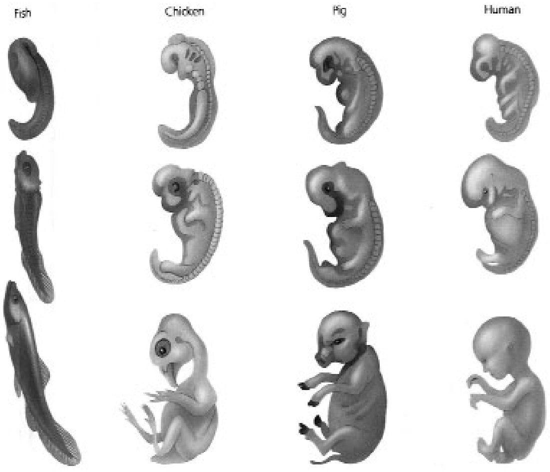


Figure 10e. *Embryos redrawn and corrected in Schraer and Stolze (1999:582)*

that could be considered strongly "recapitulationist." In most textbooks, embryology is presented in just one or two paragraphs, making it hard to discuss all the complexities of development. At a high school level, the aim of the book is to convey some basic concepts of biology, not to confuse students with the complexity of a subject.

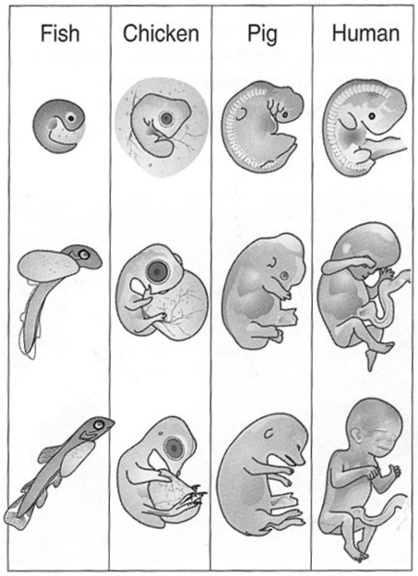


Figure 10f. *Original embryo drawings in Miller and Levine (2000:283).*

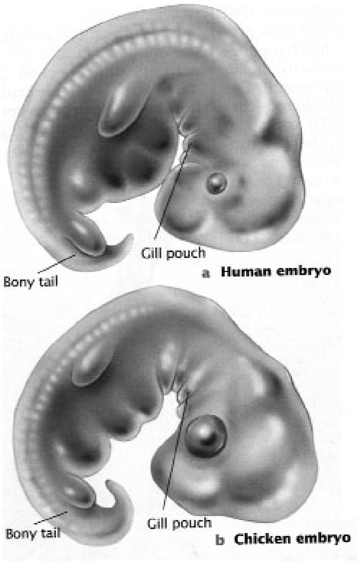


Figure 10g. *Original embryo drawings in Johnson (1998:179).*

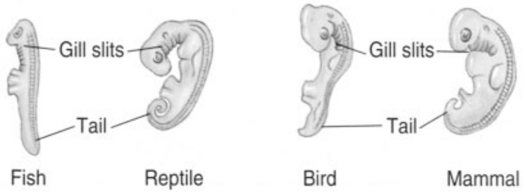


Figure 10h. *Embryo drawings in Biggs et al. (1998:433). Identical drawings appear in the evolution chapter (p.416) of Raven and Johnson (1999).*

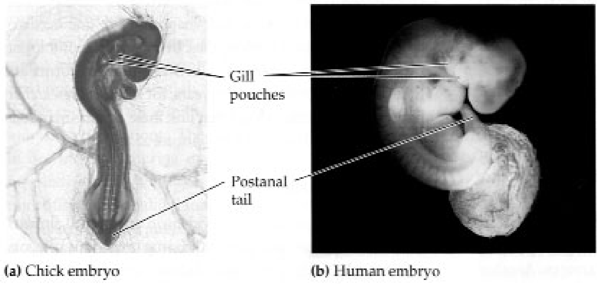


Figure 10i. *Embryo photos in Campbell, Reese, and Mitchell (1999:424).*

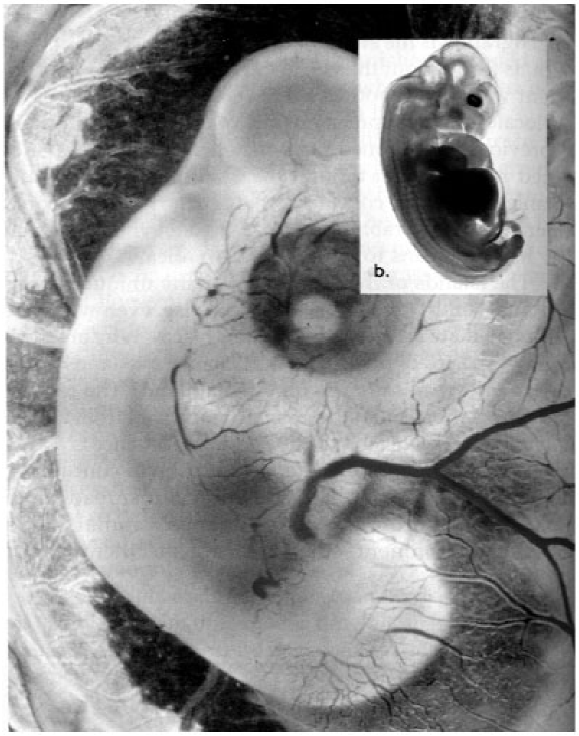
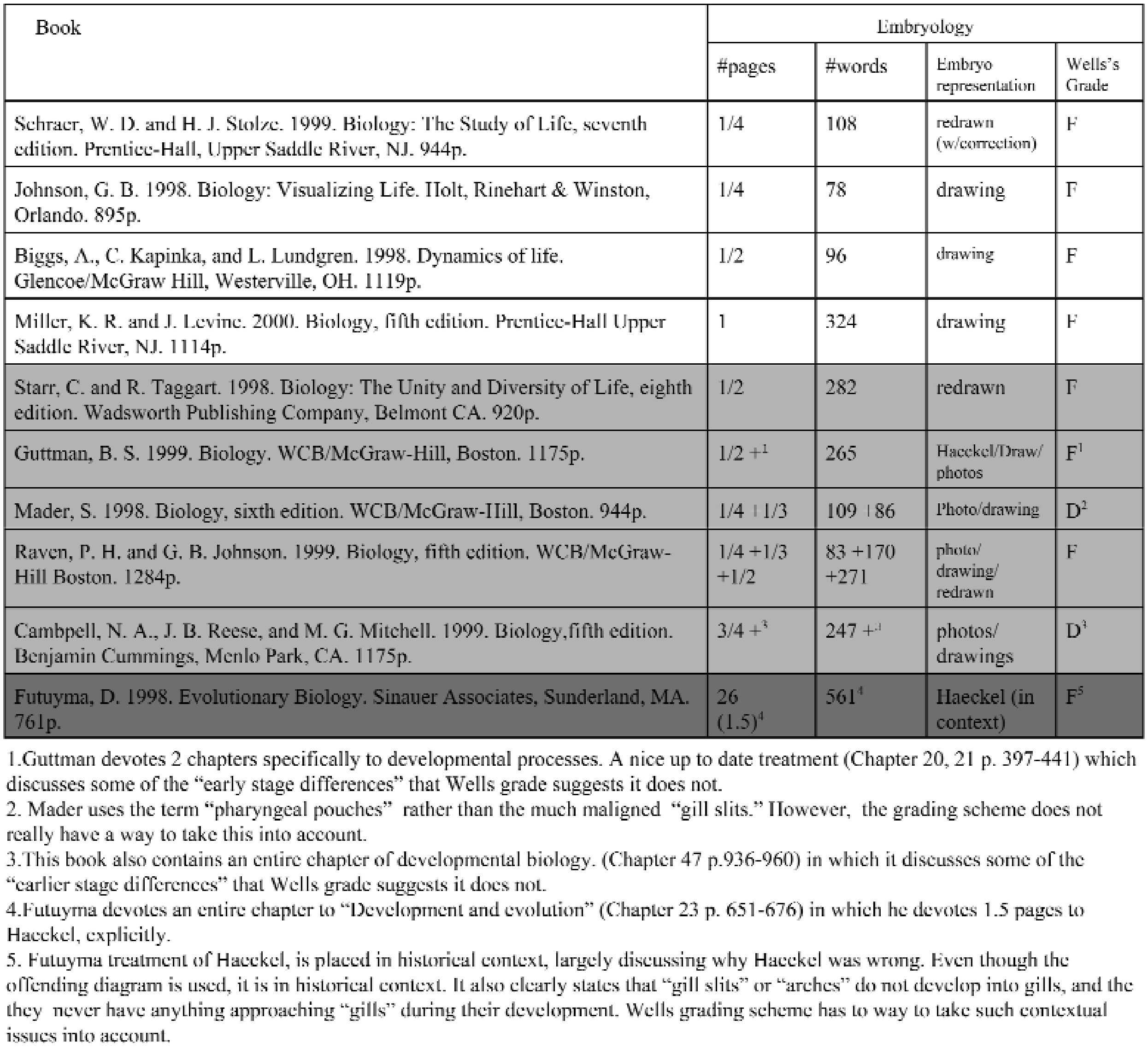


Figure 10j. *Embryo photos in Mader (1998:298).*

WELLS'S "WELL-DEVELOPED" GRADING SCHEME

The grading scheme employed by Wells is designed for failure. This is because Wells assumes all drawings to be "redrawn" from Haeckel and gives *any* book with *a* drawing an F (Figure 11). Wells does not explain how one would determine whether they are simply *redrawn* from Haeckel; in any case none of the books appear to contain mindlessly redrawn figures (Figure 10a–j). Using more accurate pictures only earns a book a D. In order to earn a C or higher, a book must *not use* "misleading drawings or *photos*." This amounts to complaining that textbooks shouldn't allow students to be misled by reality! Wells does not specify what kind of drawings or photos *would not* be misleading. Thus Wells apparently thinks that *all* visual presentations of embryos are misleading, whether they are accurate or not. Wasn't Wells the one complaining about selective use of data? He actu-



Book	Embryology			
	#pages	#words	Embryo representation	Wells's Grade
Schraer, W. D. and H. J. Stolze. 1999. Biology: The Study of Life, seventh edition. Prentice-Hall, Upper Saddle River, NJ. 944p.	1/4	108	redrawn (w/correction)	F
Johnson, G. B. 1998. Biology: Visualizing Life. Holt, Rinehart & Winston, Orlando. 895p.	1/4	78	drawing	F
Biggs, A., C. Kapinka, and L. Lundgren. 1998. Dynamics of life. Glencoe/McGraw Hill, Westerville, OH. 1119p.	1/2	96	drawing	F
Miller, K. R. and J. Levine. 2000. Biology, fifth edition. Prentice-Hall Upper Saddle River, NJ. 1114p.	1	324	drawing	F
Starr, C. and R. Taggart. 1998. Biology: The Unity and Diversity of Life, eighth edition. Wadsworth Publishing Company, Belmont CA. 920p.	1/2	282	redrawn	F
Guttman, B. S. 1999. Biology. WCB/McGraw-Hill, Boston. 1175p.	1/2 +[1]	265	Haeckel/Draw/ photos	F[1]
Mader, S. 1998. Biology, sixth edition. WCB/McGraw-Hill, Boston. 944p.	1/4 +1/3	109 +86	Photo/drawing	D[2]
Raven, P. H. and G. B. Johnson. 1999. Biology, fifth edition. WCB/McGraw-Hill Boston. 1284p.	1/4 +1/3 +1/2	83 +170 +271	photo/ drawing/ redrawn	F
Cambpell, N. A., J. B. Reese, and M. G. Mitchell. 1999. Biology,fifth edition. Benjamin Cummings, Menlo Park, CA. 1175p.	3/4 +[3]	247 +[4]	photos/ drawings	D[3]
Futuyma, D. 1998. Evolutionary Biology. Sinauer Associates, Sunderland, MA. 761p.	26 (1.5)[4]	561[4]	Haeckel (in context)	F[5]

1.Guttman devotes 2 chapters specifically to developmental processes. A nice up to date treatment (Chapter 20, 21 p. 397-441) which discusses some of the "early stage differences" that Wells grade suggests it does not.

2. Mader uses the term "pharyngeal pouches" rather than the much maligned "gill slits." However, the grading scheme does not really have a way to take this into account.

3.This book also contains an entire chapter of developmental biology. (Chapter 47 p.936-960) in which it discusses some of the "earlier stage differences" that Wells grade suggests it does not.

4.Futuyma devotes an entire chapter to "Development and evolution" (Chapter 23 p. 651-676) in which he devotes 1.5 pages to Haeckel, explicitly.

5. Futuyma treatment of Haeckel, is placed in historical context, largely discussing why Haeckel was wrong. Even though the offending diagram is used, it is in historical context. It also clearly states that "gill slits" or "arches" do not develop into gills, and the they never have anything approaching "gills" during their development. Wells grading scheme has to way to take such contextual issues into account.

Figure 11. *Wells's grades for the embryology sections of textbooks.*

ally attacks Mader and Campbell, Reese, and Mitchell, for using "misleading photos" because they show embryos of a chick and a human, which he says "just happen" to have a stronger resemblance than would embryos from any other "classes" of vertebrate. Wells is wrong: a chick embryo at that stage looks much more like an alligator embryo than a mammal embryo (comparisons made from Nelson, 1953, Schaunisland, 1903, and Reese, 1915). This is in accordance with the predictions of evolutionary theory, because an alligator and a chicken share a more recent ancestor with each other than they do with a mammal, and thus should have more similar a developmental program. Wells also chides Mader for saying that embryos "have many features in common" (Wells, 2000:103–104). Does Wells assert that they have *no* features in common? If so, he should document it. Having failed to do this, Wells merely labels anything he does not like "misleading." Wells also takes exception to the colloquial term "gill slits," which is a commonly used non-technical term for pharyngeal pouches. Wells implies that by using this term, biologists and textbooks are saying that all animals' embryos have gills. This is patently false. No textbook reviewed even implies the presence of *gills* in embryos. The question is what these structures are and what they become, not what they are called. Using the terms "gill slits" automatically results in a C even if the textbook contains no images, and regardless of its content. Campbell, Reese, and Mitchell, and Guttman both contain entire chapters devoted to developmental biology in which they *do* discuss some of the "early stage differences" that Wells suggests they do not. They receive no credit for these extensive treatments (Figure 11).

WHY WE SHOULD STILL TEACH COMPARATIVE EMBRYOLOGY

Despite changes in how we view the role of developmental programs as reflections of evolutionary history, we can still see how the same embryonic structures develop into different adult structures. We observe the unity of developmental plan in all vertebrates. This is what we see, and no amount of wishful thinking on the part of evolution detractors can change that. There is no reason to let their baseless complaints and character assassination dissuade biology teachers from presenting the evidence to students.

HOW TEXTBOOKS COULD IMPROVE THEIR PRESENTATIONS OF COMPARATIVE EMBRYOLOGY

Textbooks could largely improve the presentations of embryology by lengthening their discussions of it, and by using photos rather than cartoonish drawings. They could also be more explicit about how embryonic precursors develop into different adult structures. Finally, adding discussions of Hox gene complexes (master developmental control genes) and evolutionary developmental biology would help bring the books up-to-date in their treatment of developmental biology. We are learning more about the evolutionary history and underpinnings of developmental programs every day. We are learning how developmental programs are the source of much of the evolutionary novelty that natural selection shaped. Wells ignores all this. To follow Wells's advice would arrest the development of students' knowledge.

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ARCHAEOPTERYX

ARCHAEOPTERYX: THE FOSSIL

Contrary to Wells's subtitle, *Archaeopteryx* is not a "missing link." The term "missing link" is an outdated term that does not accurately reflect the way biologists and paleontologists think about fossils. We prefer not to talk about "missing links" or "intermediate forms," but rather intermediate *features*. *Archaeopteryx* has features intermediate between those of living birds and ancient reptiles; along with many other fossils, it preserves ancestral features while it shows descendant novelties. *Archaeopteryx* retains the ancestral "reptilian" features of a long bony tail, clawed hands, teeth, and many others. It also has the derived "avian" features of feathers and powered flight. *Archaeopteryx*, along with other dinosaur fossils, shows the evolution of avian features and flight. These fossils show that many features thought of as unique to a certain group of animals were also shared by some of their ancestors; this helps paleontologists to reconstruct the evolutionary history of living animals. When many fossils are looked at in their genealogical context, they blur the lines between the normally recognized taxonomic groups (most of which were based originally only on living forms). *Archaeopteryx* is frequently used for pedagogical purposes because it is easy to recognize its mixture of "bird" and "reptile" features and because it played an historical role in helping to cement Darwin's theory (it was discovered 2 years after publication of the *Origin*). Textbook authors like *Archaeopteryx* for these reasons and often illustrate their discussions with pictures of the Berlin specimen, one of the most beautiful fossils ever discovered, and remarkably complete. Textbooks also use *Archaeopteryx* as an example of how fossils are important for showing transitional features of evolution, and how the fossil record is good evidence that evolution has occurred.

WELLS MISSES MORE THAN THE LINKS

Wells objects to textbook treatments of *Archaeopteryx* as a transitional form or as an "ancestor" of birds. Wells wants textbooks to say that *Archaeopteryx* was not an "ancestor" because modern birds are not descended from it and that its transitional status is "controversial." Wells claims that *Archaeopteryx* has been "quietly shelved" by paleontologists and that the search for a "missing link" between dinosaurs and birds goes hopelessly on "as though *Archaeopteryx* had never been found" (Wells, 2000:138). Paleontologists would find this surprising. By making such claims, Wells exposes the depths of his ignorance of phylogenetic methodology, paleontology, and avian evolution.

Wells is clearly confused by *Archaeopteryx*, "transitional forms," and ancestors. First of all, Wells asserts that *Archaeopteryx* is no longer considered a transitional form or an "ancestor." Wells is correct, but only in a specialized sense, not appropriate in the context of his generalized discussion. We cannot — and do not — say for certain that the animal that we call *Archaeopteryx* was *actually genetically transitional* to living birds, or that it was a *direct genetic ancestor* of living birds. However, in a less strict sense (that appropriate to Wells's discussion), *Archaeopteryx* has a great many transitional *features* between living birds and Mesozoic dinosaurs: if it was not a *direct* ancestor, it was surely a close *collateral* ancestor (see below).

Second, there is no such thing as a "missing link," and paleontologists are not looking for them. Paleontologists collect, survey, and reconstruct past forms of life. Some of these fossil organisms have features that illustrate the path evolution took to reach the forms we see today. We can think of these organisms as showing transitional or ancestral features. Paleontologists are also not looking for ancestors, but rather features of ancestors. Paleontologists distinguish between *lineal* and *collateral* ancestors. Lineal ancestors are those that are directly ancestral to living organisms: your lineal ancestors are your father and mother, grandfathers and grandmothers, and so on. Collateral ancestors are those organisms that share an ancestor with living organisms: your collateral ancestors are your uncles, great-uncles, cousins, second cousins, and so on. Paleontologists do not claim to be able to identify lineal ancestors. Without observational or genetic evidence, how could you ever know that a fossil organism left any offspring? It is not the ancestry that is important to paleontologists, but rather the *ability* to reconstruct the *features* of those ancestors. This is a powerful and important concept, one completely lost on Wells.

To illustrate this powerful approach, let's say you wanted to know something about your own ancestors. If you knew your ancestors came from a certain small village in France in the 1600s, you could return to that village and, even if you can't locate their graves, you might find those of many of their contemporaries in the churchyard. A collection of artifacts from any of those people would give you a perfectly adequate idea of the characteristics, culture, possessions, and daily life of your direct ancestors (Padian and Angielczyk, 1999). Using similar methods for similar reasons, paleontologists try to uncover features of ancestors, not the ancestors themselves.

Even Wells's claim that paleontologists do not think *Archaeopteryx* is "ancestral" is incorrect. *Archaeopteryx* has no features that would actually disbar it from being a direct ancestor of living birds. Whether it was a direct ancestor of today's birds or not is irrelevant: *Archaeopteryx* exhibits unique features of the last ancestor it shared with birds, so, regardless whether it is a *lineal* ancestor, it still preserves features that indicate what the last ancestor of *Archaeopteryx* and birds may have been like. In other words, *Archaeopteryx* has many features intermediate between those of its dinosaurian ancestors and its avian descendants, which is exactly what would be predicted by evolution. No amount of stridency on Wells's part can change that.

When paleontologists reconstruct relationships of living and fossil organisms, they use the features of both living and fossil organisms. This allows them to reconstruct the features of the ancestors and get a pretty good picture of what the ancestors were like. Phylogenetic systematics, commonly called "cladistics," is the method that nearly all biologists use to determine relationships, whether they work on dinosaurs or dinoflagellates, and whether they use molecules or morphology. Its simplicity, objectivity, testability, repeatability, utility, and firm rooting in the principle of descent has led to its near-universal application. Contrary to Wells's characterization, cladistics is not a search for "missing links" or direct ancestors, but for shared evolutionary features. The basic idea behind cladistics is that when novel features arise, they are passed on to descendents. Therefore, these "derived features" should be more informative in reconstructing relationships than those that are present across a larger group. For example, if a population of animals evolve stripes on their backs and all their descendants continue to sport stripes, then all the members of that species that have stripes are probably more closely related to each other than they are to those without stripes. It is that simple, yet Wells's discussion of cladistics reveals that he either does not grasp the method or has no interest in explaining it properly.

In the nearly two pages devoted by Wells to a discussion of cladistics (Wells, 2000:118–119), he states that cladistics is based on overall similarity. Yet as stated above, cladistics is not based on mere similarity, but instead focuses on a special kind of similarity — features that are *derived*, or evolutionary novelties. Evolutionary novelties help to show relationships and thus are "phylogenetically informative." In contrast, similarities that are not evolutionary novelties are "ancestral" features and are not phylogenetically informative. For example, a derived feature of primates is an opposable thumb; this feature is phylogenetically informative because it allows us to group all primates together to the exclusion of other mammals. On the other hand, a five-fingered hand is an ancestral feature and not phylogenetically informative because we would not group all animals possessing a five-fingered hand together to the exclusion of those that do not. For example, we do not propose that all five-fingered mammals are more closely related to each other than they are to three-fingered, two-fingered, or one-fingered mammals. So cladistics *is not* based on mere similarity. Further, paleontologists who apply cladistic methods to the problem of avian evolution do not think that how flight evolved is "irrelevant"; in fact we specifically use cladograms to inform our models of how flight (and other things) evolved. By rooting our explanations in phylogenies, we can move beyond subjective models, and constrain our hypotheses (e.g., Witmer, 1995; Padian, 1995). These explanations can also serve as yet another independent test of our phylogenies (Padian, 2001a, 2001b).

Wells then accuses cladistics of "rearranging" the evidence, stating that the supposed "ancestors" of *Archaeopteryx* are millions of years younger. First of all, none of these more "recent" avian-like dinosaurs thought to be closely related to *Archaeopteryx* (e.g., troodontids and dromaeosaurs) are considered "ancestors"; rather, they retain ancestral features that show us what the ancestors of *Archaeopteryx* were like. Here again Wells mistakes lineal for collateral ancestry. Second, the statement that there are no fossils of these close cousins of *Archaeopteryx* until "millions of years" later is false. Fossils of non-avian maniraptor dinosaurs, which are closely related to the ancestors of *Archaeopteryx*, have been found in rocks dating to the same age as those in which *Archaeopteryx* has been found (Jensen and Padian, 1989); this discovery was reported over 10 years ago. Wells apparently has not done his homework very well.

Despite Wells's claims to the contrary, *Archaeopteryx* is still an important contributor to our knowledge of transitional features, and it clearly shows the dinosaurian ancestry of birds (Figure 12). To confirm this, all one has to do is peruse any piece of literature on the origin of birds. Papers on *Archaeopteryx* and bird evolution appear in many journals each year, and there is even an entire journal (called *Archaeopteryx*) devoted to the study of *Archaeopteryx* and its environment. Rather than consult the vast body of literature on the origin of birds, Wells appears to base much of his discussion on two popular works, one technical — *The Mistaken Extinction* by Lowell Dingus and Tim Rowe (1998) — and the second non-technical — *Taking Wing*, by Pat Shipman (1998). Both are excellent books. However, during the same period when Wells apparently wrote *Icons* (1998–1999), well over 50 papers were published that in some way dealt with *Archaeopteryx* and the dinosaurian origin of birds. A number of these were very

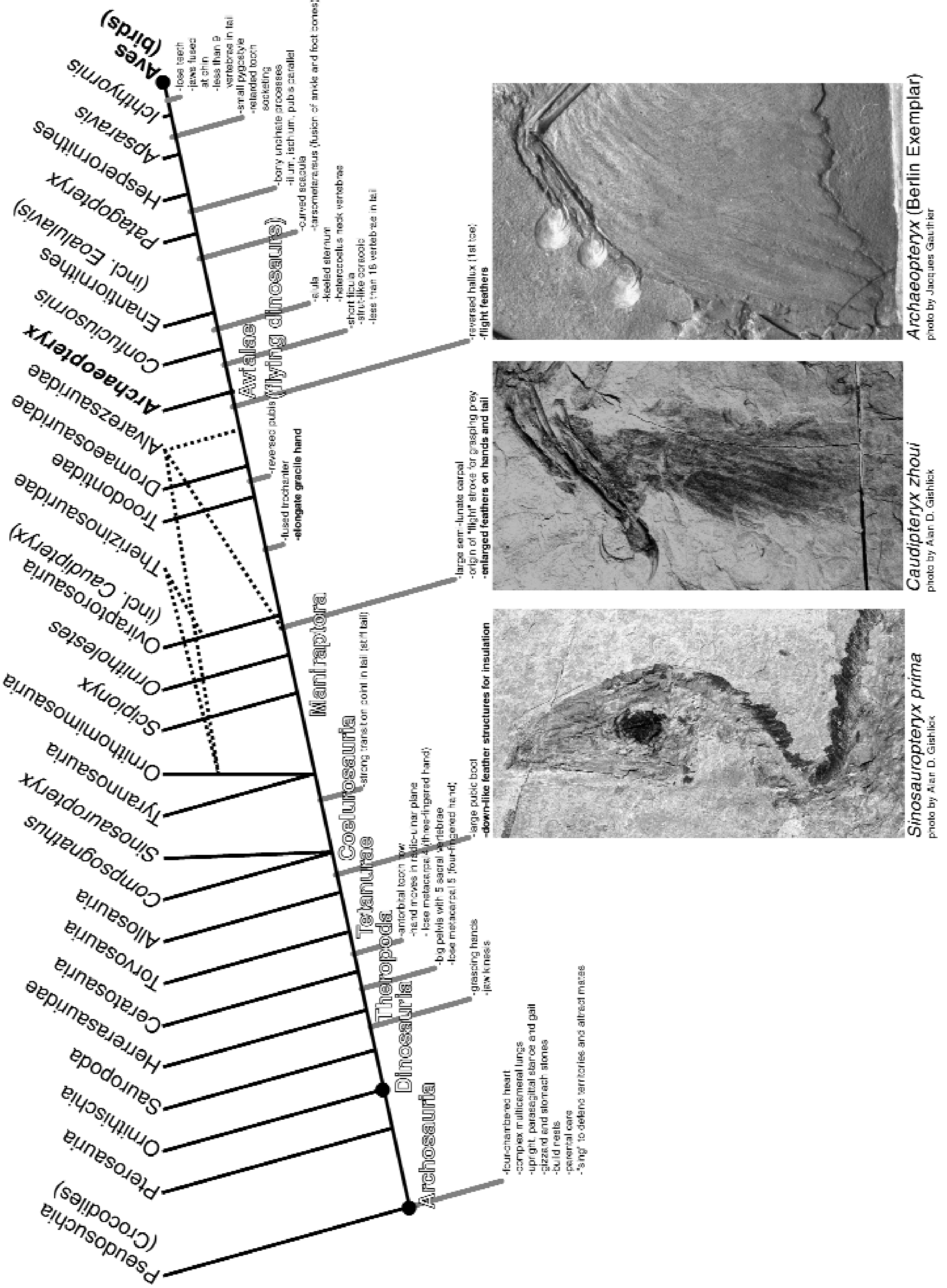


Figure 12. Archaeopteryx *(bold) shown in evolutionary context with respect to crocodilians, non-avian dinosaurs, and birds. Some relevant features plotted.*

important (e.g., Britt et al., 1998; Padian and Chiappe, 1998; Forster et al., 1998; Ji et al., 1998; Burgers and Chiappe 1999; Chiappe et al. 1999; Clark et al., 1999; Garner et al., 1999; Norell and Makovicky, 1999; Ostrom et al., 1999; Wagner and Gauthier, 1999; Xu et al., 1999), yet Wells cites none of them.

Wells also ignores the many fossil discoveries of feathered non-avian dinosaurs from Liaoning, China (see Figure 13), which should play an important role in *any* discussion of avian origins, save for one notable exception. In an attempt to discredit the entire field, Wells brings up "Archaeoraptor," which he regards as a "hoax" and indicative of the sloppy science that paleontologists do. In fact Wells spends the remaining third of the chapter trying to use "Archaeoraptor" in an attempt to slander the field of paleontology. Here too, he gets most of the facts wrong.

"Archaeoraptor" was a fossil bought at the Tucson Gem and Mineral Show for Steve Czerkas, a knowledgeable dinosaur enthusiast and skilled sculptor and artist. Its remains came from the Liaoning area of China, which has produced numerous beautifully preserved fossils of fish, mammals, lizards, and both avian and non-avian dinosaurs. Many of these were preserved with their body coverings, such as fur or feathers, intact. So it was not unexpected to see an allegedly new find from there that combined features of fossil birds and closely related dromaeosaurid dinosaurs, especially given the large body of evidence suggesting that birds evolved from these dinosaurs. The fossils of Liaoning are collected by local villagers and farmers who know that "complete" specimens, particularly those with feathers, are preferred by scientists and collectors. Therefore, a cottage industry has sprung up around using parts to enhance or make "whole" specimens (Chiappe et al., 1999). These constructed specimens are very well done and can fool an untrained eye, which is more or less what happened with "Archaeoraptor." The first paleontologists to see the specimen were immediately suspicious because the prevalence of composite specimens was already known, and its distribution of features were not what would be expected in an avian-like dinosaur. We would not expect it to have the arms of a primitive bird and the legs of a non-avian theropod. Even though a number of paleontologists were skeptical, *National Geographic* went ahead with an article that featured this specimen along with two others. This became an embarrassment for *National Geographic* when, at nearly the same time it ran its article, computerized axial tomography (CAT) scanning of the specimen showed it to be a composite. As it turns out, the legs of the specimen belong to the counterslab of a tiny non-avian theropod called *Microraptor* (Xu et al., 2001); a full description of the composite was published by Rowe et al. (2001). To view the scans of the composite, visit the UT Austin CT lab website (www.ctlab.geo.utexas.edu/pubs/nature2000).

Wells concludes that this sorry episode occurred because of "the cladists' desire to prove their theory. Just as the need for a missing link between apes and humans led to Piltdown man, so the need for a missing link between dinosaurs and birds paved the way for the 'Piltdown bird.'" (Wells, 2000:125). Not so. The people who bought and promoted the specimen weren't cladists, and they never performed a cladistic analysis or attempted to place the specimen in a phylogeny. Piltdown man was an intentional hoax played on scientists, and the hoax was revealed by scientists when the specimen was studied. The forgery of "Archaeoraptor" was discovered by scientific investigation as well, and it was *cladists* Tim Rowe, Xu Xing, and Phil Currie who uncovered it. The name "Archaeoraptor" was never formally published as a scientific name, and has no scientific standing — the animal never existed. This doesn't prevent Wells from italicizing the name as if it *were* a real species. Further, the specimen was never considered important to our understanding of avian evolution. This doesn't stop Wells from pretending otherwise, as if it were somehow important, even crucial, to the idea that birds are descended from dinosaurs.

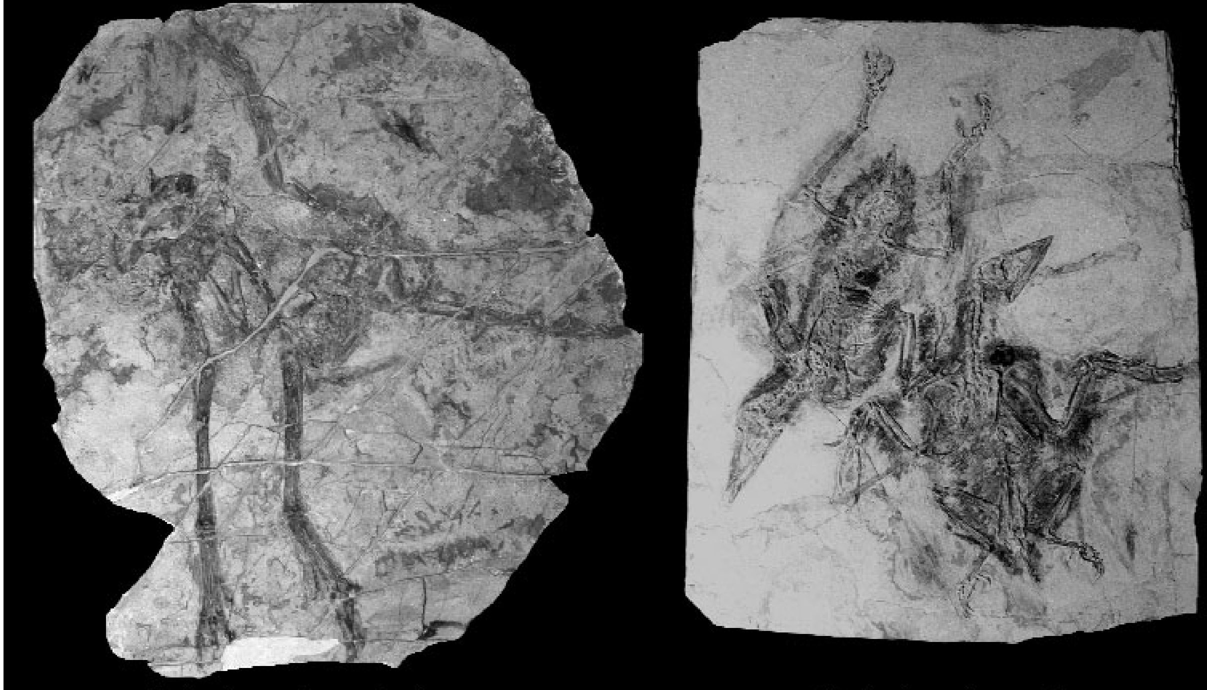
Returning to *Archaeopteryx*, Wells then resorts to a classic creationist taxonomy game. In this game, the creationist says that scientists have to choose whether a fossil belongs to one taxonomic group or another. So, in the case of *Archaeopteryx*, it has to be a bird *or* a reptile. Then the creationist says that because it has feathers it is a bird, and therefore because it is a "bird" it cannot be a transitional form. In effect the transitional features of the fossil are defined out of existence. This is a classic creationist ploy, and nothing new; it is what we have seen for decades from Duane Gish and Henry Morris. Wells uses a slightly different approach, claiming that if *Archaeopteryx* and birds are just dinosaurs, then humans are just fish, which — he implies — is absurd. But this is another case of Wells trying to use semantics to negate the evidence of evolution, just as he did with the Cambrian Explosion.

Here Wells exploits the systematic practice by which all groups of organisms must be "monophyletic," that is, consist of an ancestor and *all* of its descendants. In Wells's rather naïve example, "fish" must be taken to include hagfishes, lampreys, sharks, goldfish and other rayfins, coelocanths, and lungfishes. If "fish" were defined that way, then tetrapods (all animals that have four limbs) would indeed be "fish" and "fish" would become another name for "vertebrate." But "fish" is not a taxonomic name; it is a colloquial term, and as a Ph.D. biologist, Wells should know that. Real systematists don't use the term "fish" except in a restricted sense referring either to a subgroup that is monophyletic such as Actinopterygia or to "rayfins" (things like goldfish, trout, swordfish, etc.) — the vast majority of living "fishes." Humans are vertebrates; so are fishes. Birds, by phylogenetic relationship, are dinosaurs. Just as dogs are canids, and also mammals, and also tetrapods and vertebrates. Consider a mailing address: just because you live on 1010 Main Street does not mean that you don't live in Peoria or in Illinois, or that someone living on 411 South Street *doesn't* live in the same town or state.

Wells's most ridiculous treatment of "science" in this chapter is when he takes childish shots at paleontologists. This is another popular creationist tactic: attacking the character of a prominent scientist or scientific field. In fact, he devotes six pages to making fun of paleontologists at a Florida symposium without appearing to understand what they were saying. Worse yet, Wells completely misrepresents the proceedings. For example, he claims that a "cladistic analysis" showed a specimen presented there, called "*Bambiraptor*," to be an ancestor of *Archaeopteryx*, yet no "cladistic analysis" was mentioned in either the description (Burnham et al., 2000) or the conference proceedings. To my knowledge, no cladistic analysis has ever been performed on that specimen. Wells then claims to be appalled that in the reconstruction, "*Bambiraptor*" was shown covered in feathers even though none were found fossilized with it. But other fossilized dromaeosaurid dinosaurs are found covered in feathers (e.g. Xu et al., 1999; Ji et al., 2001; Norell et al., 2002) and so are the more basal Oviraptorids (Ji et al., 1998). The even more basal Compsognathids are found with down-like feathers as well (Chen et al., 1998; see Figures 12, and 13). So it is conservative to reconstruct "*Bambiraptor*" with a covering of

Sinosauropteryx prima
juvenile with downy body covering

Caudipteryx zhoui
with elongate, veined feathers on hands and tail



Protarchaeopteryx zhoui
with elongate, veined feathers on tail

Confuciusornis sacntus
two small flying dinosaurs

Figure 13. *Some examples of feathered dinosaurs discovered in Laioning, China.*

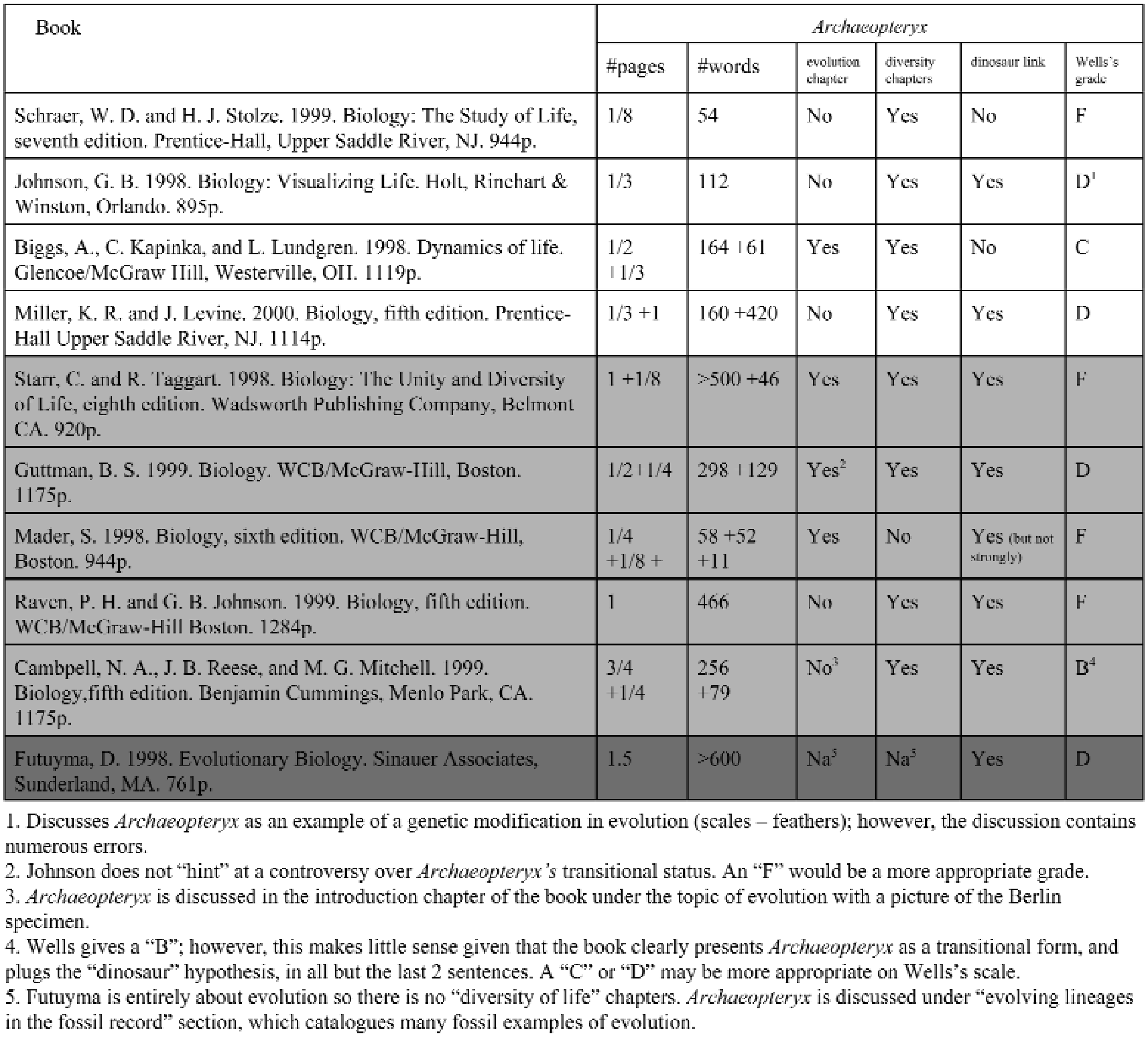
feathers. Besides, the reconstruction is a picture, not scientific evidence — a confusion of Wells's revealed further in the peppered moths chapter. By Wells's logic, we shouldn't accept the likelihood of fur on a fossil sabertooth cat. Is this the kind of "critical thinking" Wells wants us to teach our students?

Finally, Wells charicatures the conference presentation of Kevin Padian, who not only is a respected paleontologist but also happens to be the president of NCSE. Padian's talk was a critique of the hypothesis that birds evolved from something *other* than dinosaurs. Wells likens Padian's talk to an "old lawyers' joke" about a "cracked kettle." Wells even says that Padian was not trying to be funny, and that it would be unkind to compare his talk to the joke, yet he continues the *ad hominem* attack summarizing Padian's talk as a joke. Wells's summary, however, looks nothing like either the abstract that Padian submitted, which Wells (as a conference attendee) received, or the text of the talk he gave. In particular, Padian never called the *critics* of the dinosaurian origin of birds "unscientific," just their *criticisms*. He never accused them of "selective interpretation" of the evidence; he just said that they did not use accepted methodologies to evaluate the evidence. He never said that scientists reject their methodology regardless of the evidence; he said that we cannot evaluate their methodology because they do not provide one. Finally, Padian's conclusion was not that there was no controversy, but that the controversy over bird origins was journalistic, not scientific (Padian, pers. comm.). If Wells was taking notes at the conference, he didn't do a very good job.

Although Wells smugly chides paleontologists for their supposed views about bird evolution, he has not attended any meetings of the Society of Vertebrate Paleontology or the Ostrom Symposium on the origin of birds. He has no training or expertise in the field. Instead, he relies on caricatures of paleontology and paleontologists, and lampoons the entire field, treating scientists as if they were a bunch of dinosaur-loving buffoons who are easily fooled and misled. This is not science or scholarship; this is tabloid journalism.

WHAT THE TEXTBOOKS SAY

Textbooks cover *Archaeopteryx* with varying degrees of brevity, frequently giving only a paragraph to *Archaeopteryx*, usually in the section on reptiles or birds or in the history of life section. The lengths of the paragraphs vary from 54 words to well over 500 (Figure 14), and the average length falls around 200 words. *Archaeopteryx* is frequently used as an example of a transitional form between reptiles (dinosaurs) and birds. Eight of the books treat it as showing a dinosaurian ancestry for birds, while two state that the ancestry is simply reptilian (Figure 14). Few of these books treat *Archaeopteryx* well and most of these discussions are garbled and contain factual errors about *Archaeopteryx*. For example, Guttman contains numerous errors, even suggesting that it could not fly. Wells apparently does not even know enough about the topic to point this out. Wells only singles out the two books that use the word "link" in their descriptions, Mader and Schraer and Stolze. The most accurate discussions can be found in Raven and Johnson, Campbell et al., and Johnson. *Archaeopteryx* is sometimes used as an example of how fossils can elucidate evolutionary relationships. Few books use *Archaeopteryx* as direct evidence for evolution; some books (e.g., Johnson) instead use the origin of whales as the principal example of a transitional sequence.



Book	*Archaeopteryx*					
	#pages	#words	evolution chapter	diversity chapters	dinosaur link	Wells's grade
Schraer, W. D. and H. J. Stolze. 1999. Biology: The Study of Life, seventh edition. Prentice-Hall, Upper Saddle River, NJ. 944p.	1/8	54	No	Yes	No	F
Johnson, G. B. 1998. Biology: Visualizing Life. Holt, Rinehart & Winston, Orlando. 895p.	1/3	112	No	Yes	Yes	D[1]
Biggs, A., C. Kapinka, and L. Lundgren. 1998. Dynamics of life. Glencoe/McGraw Hill, Westerville, OH. 1119p.	1/2 +1/3	164 +61	Yes	Yes	No	C
Miller, K. R. and J. Levine. 2000. Biology, fifth edition. Prentice-Hall Upper Saddle River, NJ. 1114p.	1/3 +1	160 +420	No	Yes	Yes	D
Starr, C. and R. Taggart. 1998. Biology: The Unity and Diversity of Life, eighth edition. Wadsworth Publishing Company, Belmont CA. 920p.	1 +1/8	>500 +46	Yes	Yes	Yes	F
Guttman, B. S. 1999. Biology. WCB/McGraw-Hill, Boston. 1175p.	1/2 +1/4	298 +129	Yes[2]	Yes	Yes	D
Mader, S. 1998. Biology, sixth edition. WCB/McGraw-Hill, Boston. 944p.	1/4 +1/8 +	58 +52 +11	Yes	No	Yes (but not strongly)	F
Raven, P. H. and G. B. Johnson. 1999. Biology, fifth edition. WCB/McGraw-Hill Boston. 1284p.	1	466	No	Yes	Yes	F
Cambpell, N. A., J. B. Reese, and M. G. Mitchell. 1999. Biology,fifth edition. Benjamin Cummings, Menlo Park, CA. 1175p.	3/4 +1/4	256 +79	No[3]	Yes	Yes	B[4]
Futuyma, D. 1998. Evolutionary Biology. Sinauer Associates, Sunderland, MA. 761p.	1.5	>600	Na[5]	Na[5]	Yes	D

1. Discusses *Archaeopteryx* as an example of a genetic modification in evolution (scales – feathers); however, the discussion contains numerous errors.
2. Johnson does not "hint" at a controversy over *Archaeopteryx's* transitional status. An "F" would be a more appropriate grade.
3. *Archaeopteryx* is discussed in the introduction chapter of the book under the topic of evolution with a picture of the Berlin specimen.
4. Wells gives a "B"; however, this makes little sense given that the book clearly presents *Archaeopteryx* as a transitional form, and plugs the "dinosaur" hypothesis, in all but the last 2 sentences. A "C" or "D" may be more appropriate on Wells's scale.
5. Futuyma is entirely about evolution so there is no "diversity of life" chapters. *Archaeopteryx* is discussed under "evolving lineages in the fossil record" section, which catalogues many fossil examples of evolution.

Figure 14. *Textbooks' treatment of and Wells's grades for* Archaeopteryx.

WELLS'S EVALUATION

In grading textbooks on *Archaeopteryx*, the grading scheme, as usual, seems skewed to fail the books. Any book that does not describe the transitional status of *Archaeopteryx* between *reptiles* and birds as "controversial" gets a D. As mentioned above, there is no controversy about whether it is *transitional*, i.e, possesses structural features both of its reptilian ancestors and of birds. To get better than a D, a book would have to present scientifically incorrect data. What is most puzzling is that some books are given rather high grades compared to those given for other "icons." Close examination of these books suggests that Wells misgraded them (Figure 14). For example, Wells gives Campbell, Reese, and Mitchell a B, yet they clearly state that *Archaeopteryx* is a transitional form between dinosaurs and birds, for which a C or D would have been a more accurate grade given Wells's criteria. This negligent application of his own criteria calls into question the rigor of Wells's evaluation and the value of his grades whether or not one accepts his idiosyncratic criteria.

WHY *ARCHAEOPTERYX* STILL FLIES IN TEXTBOOKS

If anything, the value of *Archaeopteryx* as a pedagogical tool is increasing with all the new discoveries of feathered dinosaurs from China. Literally every new fossil discovery has added to the utility of *Archaeopteryx*. *Archaeopteryx* is still one of our best examples of a fossil that preserves ancestral features while showing descendant novelties. *Archaeopteryx* is but one of many fossils showing a clear genealogical connection between dinosaurs and birds (Figure 12). Much like Mark Twain's, the reports of its death are greatly exaggerated.

HOW TEXTBOOKS COULD IMPROVE THE USE OF *ARCHAEOPTERYX* AND TRANSITIONAL FORMS

Textbooks could improve their explanations of transitions in evolution by focusing on *transitional features* (not forms or individual animals) that are borne by a series of closely related organisms. Further, textbooks should be clear in presenting the idea that in general fossils are not considered to be direct ancestors, but as records of ancestral features. Finally, in discussions of *Archaeopteryx*, textbooks need to tighten up their descriptions and check their facts about the history of both *Archaeopteryx* and the dinosaur–bird relationship. Textbooks should be clear that birds are descendants of dinosaurs and that there are no other credible potential ancestral groups; they should also augment their rather short discussions of avian evolution with some of the new fossil evidence from China where non-avian dinosaurs have been found with feathers (Figure 13). Wells's claims about *Archaeopteryx* are simply inaccurate. To follow his lead would mislead students into thinking that fossils tell us nothing about evolutionary relationships. Considering the fact that Wells doesn't understand ancestry or phylogenetic reconstruction, and he isn't even aware of *Archaeopteryx*'s status in paleontology, should we really be inclined to trust anything he says on these topics?

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PEPPERED MOTHS

THE STORY OF THE PEPPERED MOTH

Industrial melanism in peppered moths is one of the most frequently used examples of natural selection in action. This is largely because of its pedagogical simplicity — it is a straightforward example that is visual and dynamic — and its copious documentation. Industrial melanism refers to the darkening of color that occurred in a number of species of insects following the Industrial Revolution. This change appears to be related to the increase in pollutants in the environment. Before the Industrial Revolution, individuals of the moth species *Biston betularia* (commonly called the "peppered moth") were predominantly white with black speckles. By the end of the 1800s, they were predominantly charcoal grey. This change was well documented and led Tutt (1896) to hypothesize that this change was a result of pollution-stained trees' affecting the camouflage potential of the moths. This change was termed "industrial melanism." In the 1950s, Bernard Kettlewell decided to test the hypothesis that natural selection was working on the differential camouflage of the moths. In order to do this, he released marked light and dark moths into polluted and non-polluted forests. He found that birds appear to prey selectively on light moths in polluted forests and on dark moths in non-polluted forests and so documented the idea of natural selection of these color patterns in moths by birds. After anti-pollution laws took effect and the bark lightened, the moth populations in formerly polluted areas returned to previous color distributions.

HOW MANY MOTHS CAN DANCE ON THE TRUNK OF A TREE? DISTRACTION BY IRRELEVANT DATA

Wells disagrees with the results of the research on industrial melanism in the peppered moth, and manipulates the literature and the data to fit his views. He points out that the "problem" of the peppered moths is far from simple. His discussion centers on three points where he believes textbooks are in error, alleging that (1) the daytime resting places of peppered moths invalidates Kettlewell's experimental results; (2) the photos of the moths are "staged"; and (3) the recovery patterns of populations dominated by light moths after the levels of pollution were reduced do not fit the "model," although he is unclear as to what the "model" is. All three of these objections are spurious. They are distractions from the general accuracy of the story and its value in showing the effects of natural selection on genetic variability in natural populations.

First, Wells argues that the story is seriously flawed because "peppered moths in the wild don't even rest on tree trunks" (Wells, 2000:138). He repeats this point throughout the chapter. However, it is both false and irrelevant, and only serves as a distraction to lead the reader away from the actual story of the moths. Contrary to Wells's assertions, data given by Majerus (1998:123) indicate that the moths do indeed rest on the trunks of trees 25% of the time. The rest of the time moths rest in branches (25%) or at branch-trunk junctions (50%). The facts have been pointed out repeatedly to Wells; his response has been mostly to claim that moths don't rest on "exposed" tree trunks (Wells, 2002 www.discovery.org/viewDB/index.php3?program=CRSC&command=view&id=1144). But this is *not* what he said in the text of *Icons*, which remains flatly wrong. Moths are found all over trees, which is not a surprise (Clarke et al., 1994) and it is mentioned in the references that Wells cites.

To clear up any confusion, no researcher doubts that the peppered moth rests in trees (Clarke et al. 1994; Majerus 1998), which means that the resting substrate is bark. *Entire* trees are stained by pollution — the leaves, twigs, branches, trunks, and the surrounding ground (Kettlewell, 1973) — and so the colors of the moths are relevant no matter where on the tree they rest — trunks, trunk-branch junctions, branches, twigs, and even the leaves. Wells's argument implies that predatory birds can only see moths that are on *exposed trunks*. By making this argument, however, Wells shows an apparent ignorance of the ecology of birds and woodland ecosystems. If you walk into any forest, you can see that the birds fly from tree to tree, branch to branch, and hunt at all levels of the forest. Woodland species of birds that prey on moths and other insects live and hunt *in* the canopy (the leafy part of the trees). These birds are not hunting from outside, soaring above the trees like hawks, as Wells's argument would require.

In the scientific literature, there is extensive discussion of the hunting behavior of birds, including those that hunt peppered moths. Ornithologists have shown the woodland ecosystem to be vertically stratified by competition between different bird species. This zonation means that there are skilled predators patrolling all levels of the forest: the trunks, trunk-branch joints, branches, and higher canopy (Colquhoun and Morley, 1943; Hartley, 1953). Further, birds learn to distinguish their prey against various backgrounds and preferentially hunt prey in locations where they have found it in the past and that birds selectively prey on the more visible moths (Pietrewitz and Kamil, 1977, 1981). In other words, birds hunt the prey they can see and hunt it where it *is*, not where it isn't. Therefore, no matter where the moth rests in the tree, it is visible to predatory birds, and thus its differential camouflage is important.

The purpose of Wells's distraction is to put the actual experiments into question and make it sound as if the textbook authors are either mistaken, or intentionally trying to fool students. The insinuation is that because Kettlewell released the moths during the day, they did not find "normal" resting places. Whether or not this is so, the release and capture experiments took place over a number of days, so the moths were able to take up positions of their choosing, even if the first day was not perfectly "natural" (Kettlewell, 1955, 1956, 1973). Kettlewell's experiments were not perfect — few field experiments are — and they may have magnified the degree of selection, but all serious researchers in the field agree that they were certainly not so flawed as to invalidate his conclusion.

In his second objection, Wells ties the Kettlewell experiments to textbooks by constantly repeating the statement that the illustrative photos were "staged" (Wells, 2000:150); the important issue here is not how the photos were made, but rather their intent. Wells implies that the photos purport to show a "lifelike" condition to prove that moths rest on trunks. This is not the case. The photos are meant to demonstrate the visibility of the different forms of the moth on polluted and unpolluted trees. It is absurd to expect a photographer to just sit around and wait until two differently colored moths happen to alight side by side. Further, how the photos were produced does not change the *actual* data. Birds eat moths and they eat the ones that they see more easily first. The textbook photos never claim to depict a real-life situation, and it is improper to imply otherwise.

The third criticism, and the only scientific one that Wells levels, deals with the recovery of the light form of the moth following the institution of pollution control laws. The main thrust of his argument is that because the recovery of light-colored lichens does not correlate with the recovery of the light form of the moths, the entire story is incorrect. Wells exploits the fact that the original researchers thought that the camouflage of the light moths depended on the presence of lichen. However, the light forms recovered before the lichens did; therefore, Wells concludes, natural selection has nothing to do with the story. Although it is true that the moths are well-camouflaged against lichens, and lichens are destroyed by pollution, nevertheless the camouflage of the moths ultimately depends upon the color of the trees, which reflect the amount of soot staining the trees. Although lichens play a role in camouflage, they are not *necessary*. This is what happened: pollution was reduced, the trees got lighter, then the moths got lighter. Further, in all areas, the light moths have recovered, as predicted by the hypothesis. This is clearly stated in the literature (e.g., Grant et al., 1998), but it does not fit Wells's story, and he just ignores it.

TEXTBOOK TREATMENT OF THE PEPPERED MOTHS

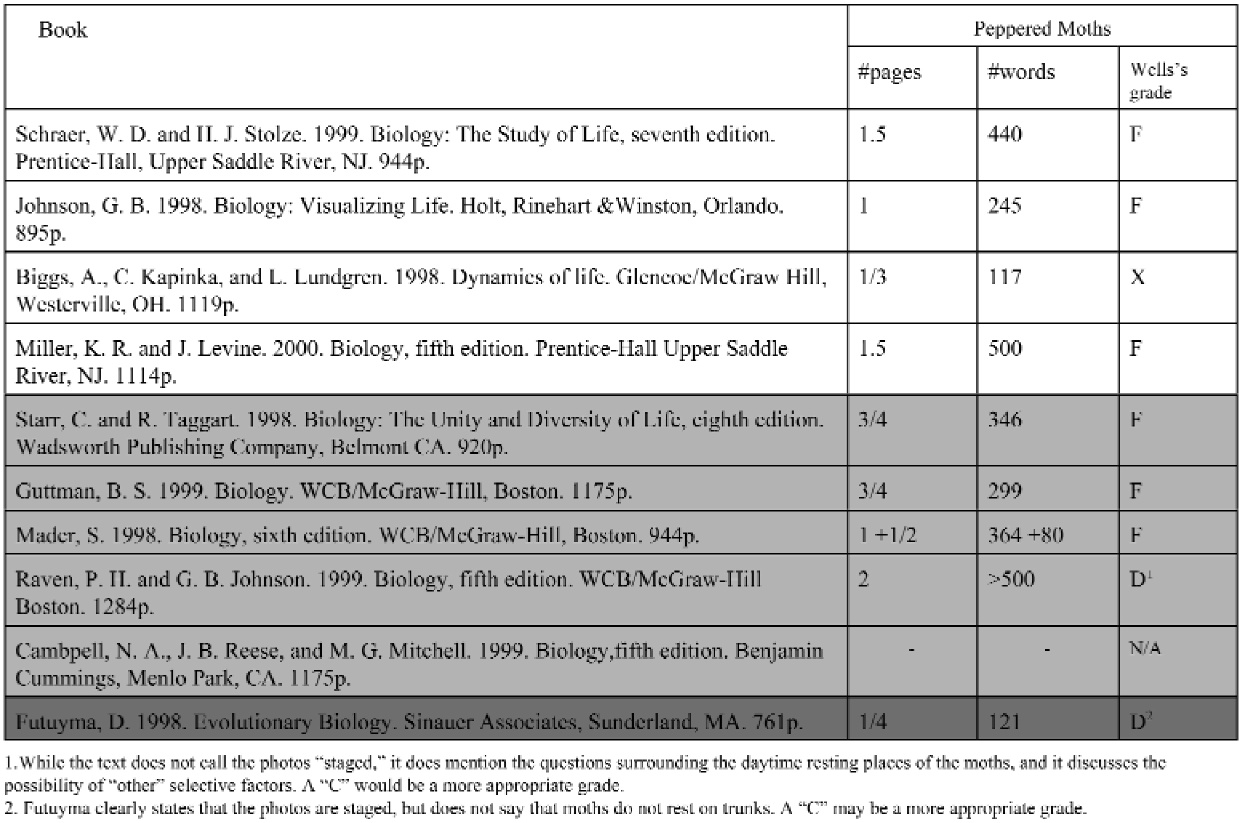
All but one of the textbooks (Campbell, Reese, and Mitchell) reviewed in *Icons* cover the peppered moths and present the basic story correctly. Again, however, the coverage is limited to only a couple of paragraphs (Figure 15), varying from 117 to over 500 words. Miller and Levine devote more than a page to the story, and even discuss some of its complexity, suggesting that the story is not as simple as it seems.

GREY AREA GRADES

Like the grading schemes for the other "icons," this one is stacked against the textbooks as well. Even books that have more extensive discussions of the problems and details (such as Miller and Levine) can at best earn a D. Like the grading schemes for Miller-Urey and Haeckel's embryos, it is based largely on the presence or absence of pictures (Figure 15). Explaining the peppered moth story without photos (as in Biggs et al.), garners a peculiar X grade. In order to get an A or B, a book must contain pictures of moths in "natural" resting places. Given Wells's explanation that these are unknown, presenting those would be impossible. How can textbooks be expected to do that? A C would be awarded to a textbook that (1) used "misleading" pictures, but (2) referred to them as "staged," and (3) stated that the results of the experiment are in doubt. Any standard textbook discussion of the issue, *even if* it mentions that the story is more complicated, is given a D. So as usual, this is a "no win" situation. This falls into Wells's pattern of requiring the books to "criticize" their examples, although the criticisms he insists on are largely fallacious.

WHY WE CAN STILL TEACH PEPPERED MOTHS AS AN EXAMPLE OF NATURAL SELECTION

Although there will always be details of the peppered moth story that we do not fully understand, its status as an example of natural selection is not even remotely in doubt. There is a clear correlation between pollution levels and moth color. Even if bird predation may not be the only factor involved in the selection of one color over another, observations show that bird predation and substrate color play the major roles in natural selection of the color of peppered moths. There are many areas in science where our knowledge is



Book	Peppered Moths		
	#pages	#words	Wells's grade
Schraer, W. D. and H. J. Stolze. 1999. Biology: The Study of Life, seventh edition. Prentice-Hall, Upper Saddle River, NJ. 944p.	1.5	440	F
Johnson, G. B. 1998. Biology: Visualizing Life. Holt, Rinehart &Winston, Orlando. 895p.	1	245	F
Biggs, A., C. Kapinka, and L. Lundgren. 1998. Dynamics of life. Glencoe/McGraw Hill, Westerville, OH. 1119p.	1/3	117	X
Miller, K. R. and J. Levine. 2000. Biology, fifth edition. Prentice-Hall Upper Saddle River, NJ. 1114p.	1.5	500	F
Starr, C. and R. Taggart. 1998. Biology: The Unity and Diversity of Life, eighth edition. Wadsworth Publishing Company, Belmont CA. 920p.	3/4	346	F
Guttman, B. S. 1999. Biology. WCB/McGraw-Hill, Boston. 1175p.	3/4	299	F
Mader, S. 1998. Biology, sixth edition. WCB/McGraw-Hill, Boston. 944p.	1 +1/2	364 +80	F
Raven, P. H. and G. B. Johnson. 1999. Biology, fifth edition. WCB/McGraw-Hill Boston. 1284p.	2	>500	D[1]
Cambpell, N. A., J. B. Reese, and M. G. Mitchell. 1999. Biology,fifth edition. Benjamin Cummings, Menlo Park, CA. 1175p.	-	-	N/A
Futuyma, D. 1998. Evolutionary Biology. Sinauer Associates, Sunderland, MA. 761p.	1/4	121	D[2]

1.While the text does not call the photos "staged," it does mention the questions surrounding the daytime resting places of the moths, and it discusses the possibility of "other" selective factors. A "C" would be a more appropriate grade.

2. Futuyma clearly states that the photos are staged, but does not say that moths do not rest on trunks. A "C" may be a more appropriate grade.

Figure 15. *Wells's grades for textbooks' treatments of peppered moths.*

incomplete, but that does not mean we should not teach about them. There are things we still do not know about gravity, but no one is demanding that examples of gravity in action be removed from textbooks.

HOW TEXTBOOKS COULD IMPROVE THEIR PRESENTATIONS OF PEPPERED MOTHS

For the most part, textbook coverage of the peppered moth story is adequate. As always, expanding the discussion would improve the coverage in the textbooks that cover it briefly. Textbooks could qualify the captions with a statement that the pictures illustrate differential camouflage in order to clear up any misunderstanding (however unlikely) as to the meaning of the photos. A better way for books to improve the topic is by adding other examples of natural selection acting on genetic variation. Some books already cover sickle-cell anemia in humans (Figure 15). Other possible examples include antibiotic resistance in bacteria and myxomatosis virus in rabbits in Australia. The key here is to expand the exposure of students to the many examples of natural selection-driven evolutionary change (e.g., Endler, 1986). What is curious about Wells's criticism of the peppered moth is that he says in *Icons* that he accepts "microevolution." The peppered moths are an example of "microevolution," so why does he have a problem with teaching it?

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“DARWIN’S FINCHES”

THE STORY OF “DARWIN’S” FINCHES

“Darwin’s finches,” along with Hawaiian honeycreepers and African cichlids, are frequently used as examples of adaptive radiation. In an adaptive radiation, a “founder” species enters a new environment with many unoccupied niches. This species expands (radiates) and evolves adaptations to fit these niches better. The process of becoming adapted to these different niches may lead to, and in these cases has led to, the formation of new species. All the species of finches on the Galápagos Islands appear morphologically very similar, varying mostly in terms of beak size and behavior; they all look very much like a species of finch from the mainland of South America. This suggests that all the finches on the Galápagos are descended from one original colonist species that went through an adaptive radiation. Because of the small, isolated environment of the Galápagos, the finches have become the topic of extensive study into natural selection. The studies that have been conducted on the finches show strong selection for larger beaks during droughts. These data show that climatic changes can have profound effects on the morphology of a species and potentially lead to the formation of new species. When Darwin visited the Galápagos, he observed and collected some of the finch species, believing that they represented a very diverse set of birds that were not closely related. Their significance was not recognized until later, when ornithologist John Gould pointed out that the birds were all closely related finches (Desmond and Moore, 1991). But because Darwin originally collected some of the specimens and because the finches showed so much evidence for evolution and natural selection, they have been dubbed “Darwin’s finches.” This has led many people to conclude (mistakenly) that Darwin’s theory of evolution was specifically inspired by the finches.

A LEGEND IN HIS OWN MIND

Wells apparently feels the need to attack the finches largely because they are an “icon” in need of destruction; the chapter on the finches is perhaps the most poorly conceived section in the book. Wells initially focuses on the “biological urban legend” that the finches inspired Darwin to compose his theory of evolution. Of course this has nothing to do with whether or not the finches are a good example of an adaptive radiation. Therefore, his “requirement” that textbooks specifically mention that the finches “played no role” in Darwin’s formulation of natural selection is irrelevant, only serving Wells’s efforts to portray evolutionary biologists as people who just “make things up.” This is like saying that because Betsy Ross did not really sew the U.S. flag, the flag does not actually exist. Wells even goes so far as to brand the finches a “legend” — what is he trying to imply? Finally, Wells’s assertion that Darwin was not inspired by the finches is not exactly correct. Although Darwin did not realize the significance of the finches until after Gould pointed it out to him in 1837, he then noted that the different species of finches were island-specific like the other Galápagos animals and suggested that they too were descendants of a mainland ancestor. Darwin made extensive notes about the finches in his diaries (Desmond and Moore, 1991). The finches, then, did play a role in the formulation of Darwin’s theory and they became an important part of his evidence for the role of natural selection in evolution; they were not a “speculative afterthought” as Wells claims.

After branding the finches a "legend," Wells switches gears and discusses the finches themselves, acknowledging the strength of the evidence for an adaptive radiation, given the similarities of the different species. Wells almost seems to accept that the finches are descended from a common ancestor; at least, he does not argue explicitly against it. But he demands that there be *direct* evidence for speciation by natural selection; in his attempt to explain how this demand could be met, the remainder of the chapter degenerates into a series of non sequiturs. This is particularly apparent in Wells's discussion of what would constitute "direct" evidence.

Suggesting that the work of Grant and Grant claimed to be that *direct* evidence, he discusses their experimental work on finch beak variation. The most detailed selection work on the finches was done by the husband and wife team of Peter and Rosemary Grant. For over two decades, the Grants and their students have monitored the sizes of the beaks of some of the finches on one small island (Grant, 1999). They have documented that the size of the finch beaks is correlated to the relative rainfall on the island, and thus to the abundance and hardness of the food. During dry years larger beak size is selected for, while during wet years the beak size is more varied. Wells acknowledges that the beaks vary and that this shows natural selection. He seems to accept that the changes in beak shape are caused by natural selection in reaction to drought-caused changes in the food supply. These data are some of the most compelling for natural selection in the wild — something that even Wells has a hard time denying. However, he then contends that because the beak shape returns to a pre-drought size distribution, that no "net" evolution has occurred. But this is a mysterious contention. Natural selection occurred. If the droughts had continued, larger beak sizes would continue to be selected for, but the droughts did not. Evolutionary theory would predict that if climate oscillates, morphology would oscillate as well. The finches fit the predicted pattern. Speciation would require selection to be more constant than a couple of years here or there. It is not unreasonable to extrapolate that if just a couple of years of drought can have that significant an effect on beak size, then extended droughts could cause such variations to become fixed in a population, and lead to speciation. This is no different than extrapolations of unknown orbits. When a new comet is discovered, its orbit is calculated based on a few short-term observations. We assume that the forces acting on the comet are constant and thus we can predict its position in 10, 20, 100, etc. years. If gravity varied, then these extrapolations would be in doubt. In the case of the finches, climate varied and the extrapolations changed. Does Wells not allow scientists to make reasonable extrapolations based on data and observations? If so, physicists must be up next for Wells's scorn. Perhaps what is most interesting about Wells's discussion of this "icon," however, is that in chapter 7 on the peppered moths, he denies natural selection entirely, when he could have made the same argument — that "no net evolution occurred" because the distribution of dark and light forms of the moths returned to pre-industrial levels just as the finch beaks return to predrought levels. For finches he accepts natural selection, but for the peppered moths he does not.

Wells goes on to complain about the extrapolations of speciation rates based on the Grants' data, complaining that the finches aren't an example of natural selection-driven speciation because no new species of finches arose during the duration of the Grants' study. However, no one would expect speciation to occur on that scale, and the Grants never claimed to expect it either. And how would you recognize a new species had formed? More importantly, one wonders how Wells would recognize new species based on his garbled discussion of species concepts (Wells, 2000:172-173), where he claims that one should "expect" "true" species to be separated by more than "just" beak shape and song pattern. This is important because in order to document speciation, you need a model by which to recognize species. Wells provides none, and cannot even manage to explain the currently accepted models properly.

Wells makes much of how the species of finches are freely hybridizing and may in fact be merging. He claims that in order to be "true" species, they should be separated by "more than beak shape and song pattern" (Wells, 2000:172). However, such a separation is a perfectly acceptable definition of species based on Recognition Concept (Paterson, 1985), according to which species are separated by behaviors that lead animals to *recognize* potential mates. This species definition is widely accepted amongst animal workers, which Wells should know, having a Ph.D. in biology. If Wells does not, one would expect him to learn it as minimum required research before critiquing others' diagnosis of species. Whether the species are merging or diverging is unimportant because both divergence and merging *are* forms of long-term evolutionary change. If indeed selection favors hybrids, as Wells appears to think, then the separate species will merge. That's still evolution *and* speciation by *natural selection* because the new hybridized form will be a new species favored by natural selection.

TEXTBOOK COVERAGE OF THE FINCHES

Textbooks use the finches to illustrate a wide variety of concepts, from the history of evolutionary theory to adaptive radiation, natural selection, taxonomy, phylogeny, and niche partitioning. Textbooks that discuss the finches in an historical context generally devote a paragraph or two to the finches, sometimes in the discussion of how Darwin constructed his theory. Finches also frequently appear in sections dealing with patterns of evolution as an example of natural selection and/or adaptive radiation. Only the upper-level books discuss the Grants' work specifically. Space allotted to the finches vary from a few words to a few pages (Figure 16). In terms of the historical discussion, most books discuss the finches in connection with Darwin's visit to the Galápagos Islands. Few books explicitly credit the finches as Darwin's inspiration, however. Most do discuss the fact that they were part of his overall evidence that he collected on his voyage. Many books treat the finches as an example of an adaptive radiation. Some books discuss the finches as examples of natural selection and niche splitting instead; these discussions occur in the chapters on evolutionary processes or patterns. In Raven and Johnson, the finches are treated in detail; the discussion includes an accurate summary of the historical story and the work of the Grants. This book mentions the finches as an example of adaptive radiation along with the African cichlids.

BIRD-BRAINED GRADING

Due to the diversity of treatment of the finches in textbooks, it is hard to evaluate the textbook coverage under Wells's grading scheme. The grading scheme employed for the finch icon is perhaps the strangest of all Wells's schemes. Like others,

Book	Darwin's Finches					
	#pages	#words	Darwin's inspiration	as adaptive radiation	Grant's work mentioned	Well's Grade
Schraer, W. D. and H. J. Stolze. 1999. Biology: The Study of Life, seventh edition. Prentice-Hall, Upper Saddle River, NJ. 944p.	1/2	115	Yes	No	No	F
Johnson, G. B. 1998. Biology: Visualizing Life. Holt, Rinehart &Winston, Orlando. 895p.	3/4	237	Yes/no	No	No	D[1]
Biggs, A., C. Kapinka, and L. Lundgren. 1998. Dynamics of life. Glencoe/McGraw Hill, Westerville, OH. 1119p.	1/8	25	No	Yes	No	F
Miller, K. R. and J. Levine. 2000. Biology, fifth edition. Prentice-Hall Upper Saddle River, NJ. 1114p.	2 1/2	580	No	Yes	No	F
Starr, C. and R. Taggart. 1998. Biology: The Unity and Diversity of Life, eighth edition. Wadsworth Publishing Company, Belmont CA. 920p.	1/2 +1/4	184 +107	No	No	No	F[2]
Guttman, B. S. 1999. Biology. WCB/McGraw-Hill, Boston. 1175p.	1/4	147	Yes	No[3]	Yes	X[4]
Mader, S. 1998. Biology, sixth edition. WCB/McGraw-Hill, Boston. 944p.	3/4 +1/4	213 +116	No	No[5]	No	F
Raven, P. H. and G. B. Johnson. 1999. Biology, fifth edition. WCB/McGraw-Hill Boston. 1284p.	2	>500	No	Yes	Yes	D[6]
Cambpell, N. A., J. B. Reese, and M. G. Mitchell. 1999. Biology,fifth edition. Benjamin Cummings, Menlo Park, CA. 1175p.	1/4 +1/2+1	42 +340 +239	No	Yes	Yes	D[7]
Futuyma, D. 1998. Evolutionary Biology. Sinauer Associates, Sunderland, MA. 761p.	1+[8]	436 +1012	No	Yes	Yes	D[9]

1. Johnson makes no mention of beak shape variation and may hint that the finches were inspirational to Darwin. An "F" would be a more appropriate grade.
2. Starr and Taggart accurately represent the finches role in Darwin's research, a "D" may be a more appropriate grade.
3. Guttman discusses the finches as an example of natural selection in action, along with other examples, in that section it mentions the finches as "influential to Darwin's thinking".Guttman uses Hawaiian honeycreepers as an example of adaptive radiation.
4. Finches are not called an example of adaptive radiation but are considered influential to Darwin. The "X" grade makes litte sense overall, should be an "F."
5. Mader discusses the finches in the context of niche partitioning along with other examples. Mader Uses Hawaiian honeycreepers as an example of adaptive radiation.
6. Raven and Johnson accurately discusses the Darwin-Gould finch connection, and mentions that the beak shape oscillates. A "C" would be a more appropriate grade.
7.Campbell et al. receive a "D" from Wells, however, the text clearly states that beak shape oscillates, and in no way implies that Darwin used the finches as his inspiration. A "C" would be a more appropriate grade.
8. Futuyma discusses the finches in 9 separate sections of the text. One page(436 words) is devoted to the Grants work specifically.
9. Futuyma discusses the the finches are dealt with in great detail and mentions that beak size oscillates. In no way does Futuyma imply that the finches played a role in Darwin's inspiration. Therefore, a "C" may be a more appropriate grade.

Figure 16. *Wells's grades of textbook treatments of Darwin's finches. Plus numbers refer to additional treatments of finches.*

this grading scheme appears constructed specifically for failure. First, Wells objects to textbooks using the finches as an example of adaptive radiation, and he incorrectly equates an "adaptive radiation" with the "origin of species by natural selection" in his grading criteria. Adaptive radiation is a description of a pattern and makes no statement as to the process — which the "origin of speciation by natural selection" does. This is important because one can document an adaptive radiation without knowing the process by which it occurred. He also wants textbooks explicitly to state that the beak shape oscillates. Further, in order for a book to get an A, a B, or even a C, the book must explicitly point out that the finches had nothing to do with Darwin's formulation of the theory of evolution. While books should not suggest that the finches were more important in the formulation than they were, it is interesting that in order to get a good grade, Wells insists that the books *assert the negative*. In his grading scheme, this means that any treatment of the finches that does *not* explicitly say that the finches did *not* inspire Darwin automatically gets a D, even if it mentions the beak size oscillation or evidence of merging. Thus the only criterion for the books' grade is the statement of an unnecessary piece of information — that Darwin was not inspired by finches. This has no pedagogical value and isn't even wholly true; even if it were wholly true, it has no bearing on the theory of evolution one way or the other. This brings up the question of Wells's real intent. His true goals are made apparent by the grades themselves. Wells grades many of the books needlessly low. When reevaluated on Wells's own criteria, many of the books given a D or F should hav been given a C (Figure 16). Is Wells simply looking for any excuse to damage textbooks' reputations?

WHY WE CAN STILL USE THE GALÁPAGOS FINCHES AS A TEACHING EXAMPLE

The finches clearly show adaptive radiation and were important to Darwin's research. Their inclusion in texbooks is perfectly legitimate and should not change. The best way textbooks could improve their presentations of adaptive radiation is to include other examples such as Hawaiian honeycreepers or African cichlids as well. There are numerous examples of adaptive radiation; the more of those that we teach to students, the better they will understand evolution. Comically, Wells never really objects to the finches as an example of natural selection, even concluding that "In this limited sense, the finches provide evidence for Darwin's theory" (Wells, 2000:173). If that is the case, what's the big deal?

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CONCLUSION

ICONS — SHOULD WE KEEP THEM?

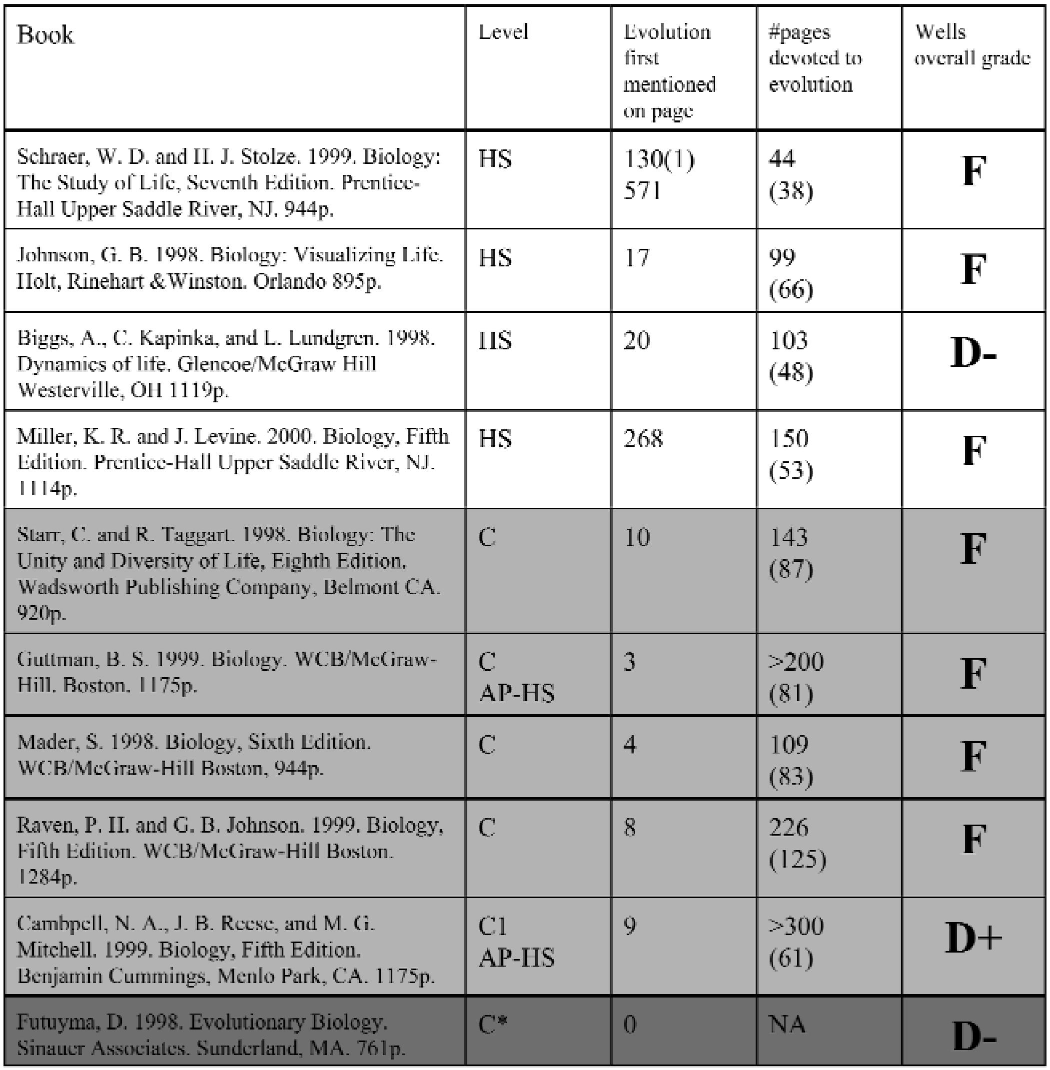
The role of primary and secondary education is to pass on a certain body of accepted knowledge and basic concepts to students in order to prepare them to learn more. The question is whether the criticisms leveled by the author of *Icons* would aid us in that goal; the resounding answer is no. The educational program that would result from implementing the suggestions contained in *Icons* would have just the opposite result: It would seriously hamper science education and leave students unprepared for the future in which science, and biology in particular, will play an increasing role.

Figure 17 shows the grades that Wells gives each textbook, the number of pages each textbook specifically devotes to evolutionary theory compared to the total number of pages that contain evolutionary content (such as phylogenetic relationships), and when evolution is first mentioned in the text. Although the amount of text devoted to evolution varies widely in textbooks, the coverage as a percentage of the total text that evolution is given is very small — usually less than 10% of the total book. Wells evaluates only four high school textbooks in the review, and those have a far smaller treatment of evolution than do the college texts.

It is clear from Wells's treatment of the "icons" and his grading scheme that his interest is not to improve the teaching of evolution, but rather to teach anti-evolutionism. Under Wells's scheme, teachers would be hostile to evolution as part of biology instruction. Wells and his allies hope that this would open the door to alternatives to evolution (such as "intelligent design") without actually having to support them with science.

In order to get a "good" grade from Wells, that is to portray a piece of evidence for evolution "accurately" (in Wells's opinion), one must mention it and then proceed to criticize it. This is not standard pedagogical practice; if an example is that bad, it should be removed from the biology curriculum, rather than introduced and then criticized. What we see is a pattern of grading to create bias rather than accuracy. Rewriting textbooks to criticize evolution serves no teaching purpose (teaching is a positive endeavor, not negative), yet it is clear from the grading that this is the goal of the author. What's worse is that the grading criteria are not even consistently applied. There is no pedagogical or factual basis for these grades, and they should not be taken seriously. To follow Wells's advice would not only result in mis-education about evolution, but about all of biology and other sciences as well. Good teaching may value critical thinking, but it does not value wanton criticism for the sake of criticism.

Finally, in his zeal to attack the textbooks' treatments of evolution, Wells misses a chance to provide a good listing of *actual* errors in textbooks. A study of the textbooks that Wells evaluated uncovered factual errors, inexact wordings, and garbled explanations of biological phenomena that Wells either did not notice or considers unimportant. This lack of documentation of real textbook errors is yet another failure of Wells's effort. Far from being tracts of "evolution propaganda," as Wells implies, many biology textbooks devote too little space to evolution, especially in early chapters. Most of evolution is reserved for the middle of textbooks; it is frequently given less coverage than ATP cycles or photosynthesis. The topics of which Wells is so critical amount to only a small fraction of any given textbook. In fact, evolutionary biologists consider the



Book	Level	Evolution first mentioned on page	#pages devoted to evolution	Wells overall grade
Schraer, W. D. and H. J. Stolze. 1999. Biology: The Study of Life, Seventh Edition. Prentice-Hall Upper Saddle River, NJ. 944p.	HS	130(1) 571	44 (38)	**F**
Johnson, G. B. 1998. Biology: Visualizing Life. Holt, Rinehart &Winston. Orlando 895p.	HS	17	99 (66)	**F**
Biggs, A., C. Kapinka, and L. Lundgren. 1998. Dynamics of life. Glencoe/McGraw Hill Westerville, OH 1119p.	HS	20	103 (48)	**D-**
Miller, K. R. and J. Levine. 2000. Biology, Fifth Edition. Prentice-Hall Upper Saddle River, NJ. 1114p.	HS	268	150 (53)	**F**
Starr, C. and R. Taggart. 1998. Biology: The Unity and Diversity of Life, Eighth Edition. Wadsworth Publishing Company, Belmont CA. 920p.	C	10	143 (87)	**F**
Guttman, B. S. 1999. Biology. WCB/McGraw-Hill. Boston. 1175p.	C AP-HS	3	>200 (81)	**F**
Mader, S. 1998. Biology, Sixth Edition. WCB/McGraw-Hill Boston, 944p.	C	4	109 (83)	**F**
Raven, P. H. and G. B. Johnson. 1999. Biology, Fifth Edition. WCB/McGraw-Hill Boston. 1284p.	C	8	226 (125)	**F**
Cambpell, N. A., J. B. Reese, and M. G. Mitchell. 1999. Biology, Fifth Edition. Benjamin Cummings, Menlo Park, CA. 1175p.	C1 AP-HS	9	>300 (61)	**D+**
Futuyma, D. 1998. Evolutionary Biology. Sinauer Associates. Sunderland, MA. 761p.	C*	0	NA	**D-**

Figure 17. *Grades given to textbooks in comparison to the coverage of evolution given in the text. AP and College level texts shaded. Parenthetical numbers under the heading "number of pages devoted to evolution" refer to the number of pages in the "evolution" chapter.*

lack of coverage of evolution, and the failure to interweave it throughout the entire book, to be the greatest deficit of textbooks.

In conclusion, the scholarship of *Icons* is substandard and the conclusions of the book are unsupported. In fact, despite his touted scientific credentials, Wells doesn't produce a single piece of original research to support his position. Instead, Wells parasitizes on other scientists' legitimate work. He could not have written the "Haeckel's embryos" chapter without the work of Richardson et al. (1997, 1998), or the "peppered moths" chapter without Coyne (1998) and Majerus (1998), or the "*Archaeopteryx*" chapter without Shipman (1998). Even then, Wells's discussions are rife with inaccuracies and out-of-date information. Wells seems to think that scientific theories are supported by certain "keystone" pieces of evidence, removal of which causes the theory to collapse. Paradigms in science work when they provide solutions and further research;

their health is not tied to single examples. The paradigm of evolution is not tied to a single piece of evidence.

If that is the case, why "defend" the "icons" at all? If evolution doesn't need them, why not just replace them? The answer is simple: There is no reason to throw out good teaching examples unless the criticisms leveled against them are valid. We should not just acquiesce to Wells's arguments unless they have merit. Just as no piece of evidence becomes a teaching example without extensive testing, no example should be removed on the basis of one poorly argued, inaccurate, and tendentious book. In each case, it is Wells's arguments that are wanting, not the "icon."

When Alfred Wegener first proposed his theory of continental drift, he was laughed at and ridiculed. What did he do? Did he form a non-profit advocacy group and lobby state school boards and lawmakers to force teaching of "evidence against" geosynclinal theory? Write a book called *Icons of Uniformitarianism*? Evaluate and grade earth science textbooks and demand that they be rewritten to remove examples of "borderlands"? No. He went back and did more *research*. He found like-minded colleagues and they produced *research*. He fought in the peer-reviewed literature. He produced original research, not polemical popular tracts or politics. Eventually his ideas were adopted by the whole of geology — not through politics but because of their overall explanatory power. If Wells and his colleagues want "intelligent design" to succeed, they need to produce that research. Until they do, evolution remains the reigning paradigm and the "icons" are perfectly acceptable teaching aids.

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