Seeing the Wood for the Trees: An Analysis of Evolutionary Diagrams in Biology Textbooks

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This study presents the findings of an analysis of evolutionary diagrams found in 31 biology textbooks for students ranging from middle school to the undergraduate level. Since the early 1990s, cladograms have found their way into high school biology textbooks, yet we know little about their effectiveness as interpretive and instructional tools in biology education. In this article we document the frequency and types of cladograms found in 31 textbooks, and classify and survey the other types of evolutionary diagrams used in the texts. Although cladograms comprised approximately 72 percent of the diagrams overall, we found virtually no attempt to explain their structure and theoretical underpinnings. Various other noncladogenic evolutionary diagrams, comprising 28 percent of the total, were distributed throughout all textbooks studied. On the basis of our analysis, we conclude that many of these evolutionary diagrams are confusing and may reinforce alternative conceptions of macroevolution. Biology educators should therefore recognize these problems and take measures to ameliorate their effects.

Keywords: evolutionary diagrams, biology textbooks, cladograms, alternative conceptions, macroevolution

Graphical representations of evolutionary relationships among taxa have a long history in biology. The pervasive effect of two particularly influential representations, the "Chain of Being," rooted in the ideas of Plato and Aristotle, and the "Tree of Life," epitomized by Haeckel's trees of the late 1800s, can still be seen in contemporary representations. The Chain of Being encompasses the physical and metaphysical world in an unbroken chain that stretches from nonliving matter all the way to "supernatural" beings. It is possible to trace a connection from the Great Chain of Being depicted in Didacus Valades's 1579 *Rhetorica Christiana* (Lovejoy 1936), through Bonnet's (1745) *scala naturae* (scale of being) and Lamarck's (1809) extension of the "chain" in *Philosophie Zoologique,* to Haeckel's trees of the late 1800s. The Chain of Being and Tree of Life are founded on the concept of a linear evolutionary progression from simple to complex, with a distinctively teleological perspective. Although many other forms—both hierarchical and otherwise—have also appeared in the scientific press over the past 300 or so years, many current representations of evolution mirror the great chain as a process of orderly progression (Nee 2005).

This study documents the type, frequency, and distribution of evolutionary diagrams in 31 contemporary textbooks aimed at a wide array of readers from middle school to the undergraduate level. Today, practicing biologists use phylogenetic trees in the form of cladograms and phylograms to hypothesize and study phylogenies. Some would argue that phylograms are a subset of cladograms, but they are based on quite different methodologies and underlying philosophies. The topologies, however, can be identical, except for nonequal branch lengths. These attempt to convey the inferred degree of relatedness based on, for example, the number of nucleotide substitutions between taxa.

We found that cladograms (*sensu stricto*) were well represented ($n = 505$) in textbooks. Phylograms, in contrast, were very rare ($n = 6$). We also found a large number of other types of diagrams ($n = 192$) that at best are open to multiple interpretations and, at worst, are ambiguous or based on long discredited evolutionary mechanisms. Because there were so few phylograms (four examples in two introductory biology textbooks for majors and two examples in two botany textbooks), we excluded those diagrams from our analyses.

Although cladograms began to appear in high-school textbooks in the early 1990s, there has been virtually no research examining the functionality of these or other types of evolutionary diagrams in life science pedagogy. How well do evolutionary diagrams in textbooks reflect current thinking in evolutionary biology? More important, do they reinforce or reduce common misconceptions of evolutionary processes? Such information is vital to understanding how best to

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incorporate macroevolution into biology education and to facilitate the "tree thinking" called for by a number of researchers (O'Hara 1988, Gilbert 2003, Goldsmith 2003, Baum et al. 2005, Catley et al. 2005, Catley 2006, Staub et al. 2006, Sandvik 2008). Tree thinking is a habit of mind that uses the history of life on Earth as its first line of evidence while providing students with a hierarchical view of the natural world.

Implementing tree thinking in the evolution curriculum is consistent with the National Science Education Standards, which specify that students should learn to use the methodologies and tools from professional practice (NRC 1996, AAAS 2001). However, if students also encounter in their textbooks a large number of diagrams that fail to meet the criteria of being a cladogram (by violating structural rules or their theoretical underpinnings), they may be at a severe disadvantage in understanding macroevolution. The data we present here demonstrate that many evolutionary diagrams in textbooks are confusing and open to multiple interpretations, and reinforce alternative conceptions of macroevolution. Our ongoing empirical research on university students' interpretations of such diagrams supports this conceptual analysis. Consequently, biology educators should recognize this and be ready to take ameliorative action. Ultimately, we hope to influence textbook designers and producers to exclude poor diagrams from their materials in future editions and to provide clear explanations for the diagrams that are included.

Textbooks and diagrams surveyed

The textbooks we analyzed represent a sample of convenience. Nevertheless, we made a concerted effort to select texts that were currently being used by a variety of different schools in classes taught at a variety of different levels. The books are well established and have been in use for many years at schools across the country.

Approximately half of the middle- and high-school textbooks were being used by public and private schools in Nashville, Tennessee. Nashville is a large city with an urban school system that serves approximately 74,000 students (35 percent white, 48 percent black, 13 percent Hispanic), 70 percent of whom receive free or reduced-price lunches. The private schools are largely nonsectarian, college-preparatory schools. One school is affiliated with the Catholic Church. Other texts were being used by public school systems in smaller towns and cities in other parts of the United States. Textbooks from online and independent study courses are also represented. The college texts were being used by a number of public and private universities and colleges (including one community college) across the United States and Canada. They fall into three categories, which are equally represented in our sample: introductory biology textbooks for nonmajors, introductory textbooks for majors, and textbooks for zoology and botany courses.

Table 1 lists the textbooks surveyed and the schools that we know were using them at the time of our survey. Books were examined in their entirety, and we evaluated every diagram that represented a set of evolutionary relationships. Repetitions of a diagram within a textbook were ignored. The resulting 697 diagrams were first categorized as cladograms ($n = 505$) or other evolutionary diagrams ($n = 192$). These categories were then subdivided as discussed in the following sections. As noted earlier, the six phylograms were excluded from our analyses.

Criteria for inclusion as a valid cladogram

In this article we use the term "cladogram" to refer to branching diagrams that are constructed using cladistic principles of most recent common ancestry. We have avoided the generic label "phylogenetic tree" because of the even greater confusion that would arise, at least with respect to the diagrams studied in our sample, where the following terms are used for a variety of diagrams comprising many topologies: "family tree" (which seldom contain any families but show mostly classes or phyla), "evolutionary tree," "phylogenetic diagram," "phylogenetic tree," "diagram," "tree of life," "phylogeny," and "evolutionary diagram."

In its purest form, a cladogram (figure 1) is a hierarchical diagram depicting the distribution of characters among taxa. Although historically there has been some controversy concerning the interpretation of such cladograms as phylogenetic trees (transformed cladistics), for the purposes of this analysis, we define them as synonymous with testable phylogenetic trees. "A cladistic hypothesis is a cladogram specifying a pattern of nested sets of relationships among taxa that is a consequence of a nested pattern of synapomorphy" (Eldredge and Cracraft 1980, p. 50). At the core of the cladogram is the three-taxon statement, which specifies that taxon A is more closely related to taxon B than either is to taxon C, thus supporting the concept of monophyly as defined by Hennig (1966). Cladograms do not make statements about ancestor or descendent polarity. In this regard, they are very different from classical "evolutionary trees" that routinely include ancestors, even when little evidence for them exists.

Importantly, in cladograms, taxa are depicted at the same level at the terminal points of branches, but never on a branch. The latter depiction would violate the constraint that cladograms make no statements about ancestor or descendent polarity. The only inscriptions allowed on branches are characters (synapomorphies that support sets of relationships) or the nodes that define branching events.

Cladograms in professional journals are generally depicted in two topologies, which we refer to (in keeping with our prior published work) as tree and ladder (figure 1a and 1b, respectively); occasionally other formats are also seen (e.g., figure 1c). Novick and Catley (2007) reported that of the 190 figures containing tree or ladder depictions of cladograms that were published in the 2005 issues of *Systematic Biology* (across 57 articles), 83 percent contain trees and 17 percent contain ladders. Clearly, the "tree" topology is the format of choice in professional systematic journals.

The trees and ladders in textbooks do not always follow the standard formats shown in figure 1. We classified cladograms as trees if they clearly depicted distinct nested levels (e.g.,

Table 1. Biology textbooks used by selected middle schools, high schools, and colleges and universities.

Textbook level and bibliographic information	Where textbook was in use when the survey was conducted
Middle-school life science (grades 6–7)	
Glencoe Life Science. 2002. New York: McGraw-Hill.	
Life Science. 2001. Austin (TX): Holt, Rinehart and Winston.	Metropolitan Nashville (TN) Public Schools (a large, urban school district in the Bible Belt with approximately 74,000 students)
Life Science. 2005. Orlando (FL): Holt, Rinehart and Winston.	University School of Nashville (an independent K–12 school in Nashville); Ensworth (an independent K–12 school in Nashville); Harding Academy (an independent K–8 school in Nashville)
Texas Science. 2002. New York: Glencoe McGraw-Hill.	
High-school biology (grades 9–12, excluding advanced-placement biology)	
BSCS Biology: An Ecological Approach. 9th ed. 2002. Dubuque (IA): Kendall/Hunt.	Montgomery Bell Academy (an independent, all-boys school in Nashville for grades 7–12)
Campbell NA, Williamson B, Heyden R. 2004. Biology: Exploring Life. Needham (MA): Pearson.	Apex Learning (provider of textbooks for online high school courses)
Johnson GB. 1998. Biology: Visualizing Life. Austin (TX): Holt, Rinehart and Winston.	University of Nebraska (Lincoln) Independent Study High School
Johnson GB, Raven PH. 2001. Biology: Principles and Explorations. Austin (TX): Holt, Rinehart and Winston.	Ann Arbor (MI) public schools (a small, suburban school district in a Midwestern college town; approximately 17,000 students)
Kaskel A, Hummer PJ Jr, Daniel L. 2003. Biology: An Everyday Experience. New York: Glencoe/McGraw-Hill.	
Mader SS. 2007a. Biology. 9th ed. Boston: McGraw-Hill.	Harpeth Hall (an independent, all-girls school in Nashville for grades 5–12); Father Ryan (a Catholic high school in Nashville)
Miller KR, Levine J. 2002. Biology. Upper Saddle River (NJ): Prentice Hall.	University School of Nashville; Ensworth; Iowa City (IA) Community School District (a small, suburban school district in a Midwestern college town; approximately 11,000 students)
Modern Biology. 2002. Austin (TX): Holt, Rinehart and Winston.	Metropolitan Nashville Public Schools; Father Ryan
Postlethwait JH, Hopson JL. 2006. Modern Biology. Orlando (FL): Holt, Rinehart and Winston.	Harpeth Hall
College introductory biology	
Audesirk T, Audesirk G, Byers BE. 2005. Biology: Life on Earth. 7th ed. Upper Saddle River (NJ): Prentice Hall.	Southern Oregon University (a public university in Ashland)
Campbell NA, Reece JB. 2005. Biology. 7th ed. San Francisco: Pearson.	Metropolitan Nashville Public Schools; University School of Nashville; Ensworth; Montgomery Bell Academy; Harpeth Hall; Father Ryan; Iowa City Community School District; Palo Alto (CA) Unified School District (a small, suburban school district in Silicon Valley; approximately 10,000 students); Rose-Hulman Institute of Technology (a private science and engineering school in Terre Haute, IN)
Campbell NA, Reece JB, Simon EJ. 2004. Essential Biology. 2nd ed. San Francisco: Pearson.	Ohio State University (a public university in Columbus); Vanderbilt University (a private university in Nashville); University of Montana (a public university in Missoula)
Campbell NA, Reece JB, Taylor MR, Simon EJ. 2006. Biology: Concepts and Connections. 5th ed. San Francisco: Pearson.	Colby College (a small liberal arts college in Waterville, ME); Western Carolina University (a public university in Cullowhee, NC)
Freeman S. 2005. Biological Science. 2nd ed. Upper Saddle River (NJ): Prentice Hall.	Ohio State University; Kenyon College (a small liberal arts college in Gambier, OH); Michigan State University (a public university in East Lansing); University of California, Los Angeles (a public university); Western Kentucky University (a public university in Bowling Green)
Lewis R, Parker B, Gaffin D, Hoefnagel M. 2007. Life. 6th ed. Boston: McGraw-Hill.	Indiana University (a public university in Bloomington)
Mader SS. 2003. Inquiry into Life. 10th ed. Boston: McGraw-Hill.	Casper College (a community college in Casper, WY)
Mader SS. 2007b. Essentials of Biology. Boston: McGraw-Hill.	Ohio State University
Purves WK, Sadava D, Orians GH, Heller HC. 2004. Life: The Science of Biology. 7th ed. Sunderland (MA): Sinauer.	Vanderbilt University; Western Carolina University; University of California, Los Angeles; Casper College; Davidson College (a small liberal arts college in Davidson, NC); Reed College (a small liberal arts college in Portland, OR); University of Arizona (a public university in Tucson)
Raven PH, Johnson GB, Losos JB, Singer SR. 2005. Biology. 7th ed. Boston: McGraw-Hill.	Indiana University
Solomon EP, Berg LR, Martin DW. 2006. Biology. 7th ed. Belmont (CA): Brooks/Cole.	University of Tennessee, Knoxville (a public university)
Starr C, Taggart R. 2006. Biology: The Unity and Diversity of Life. 11th ed. Belmont (CA): Thomson Brooks/Cole.	Michigan State University

(continued)

vertically), even if the corners where the horizontal and vertical lines met were rounded rather than forming a 90-degree angle, and even if the horizontal lines were somewhat curved. We classified cladograms as ladders if they contained a continuous "main" line running from the bottom left to the top right of the diagram (occasionally from the top left to the bottom right). This line could be either straight (as in the standard form in figure 1b) or curved. The choice of some

Table 1. (continued)

Textbook level and bibliographic information	Where textbook was in use when the survey was conducted
College zoology and botany	
Hickman CP Jr, Roberts LS, Larson A, I'Anson H, Eisenhour DJ. 2006. Integrated Principles of Zoology. 13th ed. Boston: McGraw-Hill.	Vanderbilt University
Judd WS, Campbell CS, Kellogg EA, Stevens PF, Donoghue MJ. 2002. Plant Systematics: A Phylogenetic Approach. Sunderland (MA): Sinauer.	College of Wooster (a small liberal arts college in Wooster, OH)
Miller SA, Harley JP. 2005. Zoology. 6th ed. Boston: McGraw-Hill.	Norfolk State University (a public university in Norfolk, VA)
Raven PH, Evert RF, Eichhorn SE. 2005. Biology of Plants. 7th ed. New York: Freeman.	University of Wisconsin–Madison (a public university)
Ruppert EE, Fox RS, Barnes RD. 2004. Invertebrate Zoology: A Functional Evolutionary Approach. 7th ed. Belmont (CA): Brooks/Cole Thomson Learning.	University of Guelph (a public university in Guelph, Ontario, Canada)
Walters DR, Keil DJ, Murrell ZE. 2006. Vascular Plant Taxonomy. 5th ed. Dubuque (IA): Kendall/Hunt.	Western Kentucky University

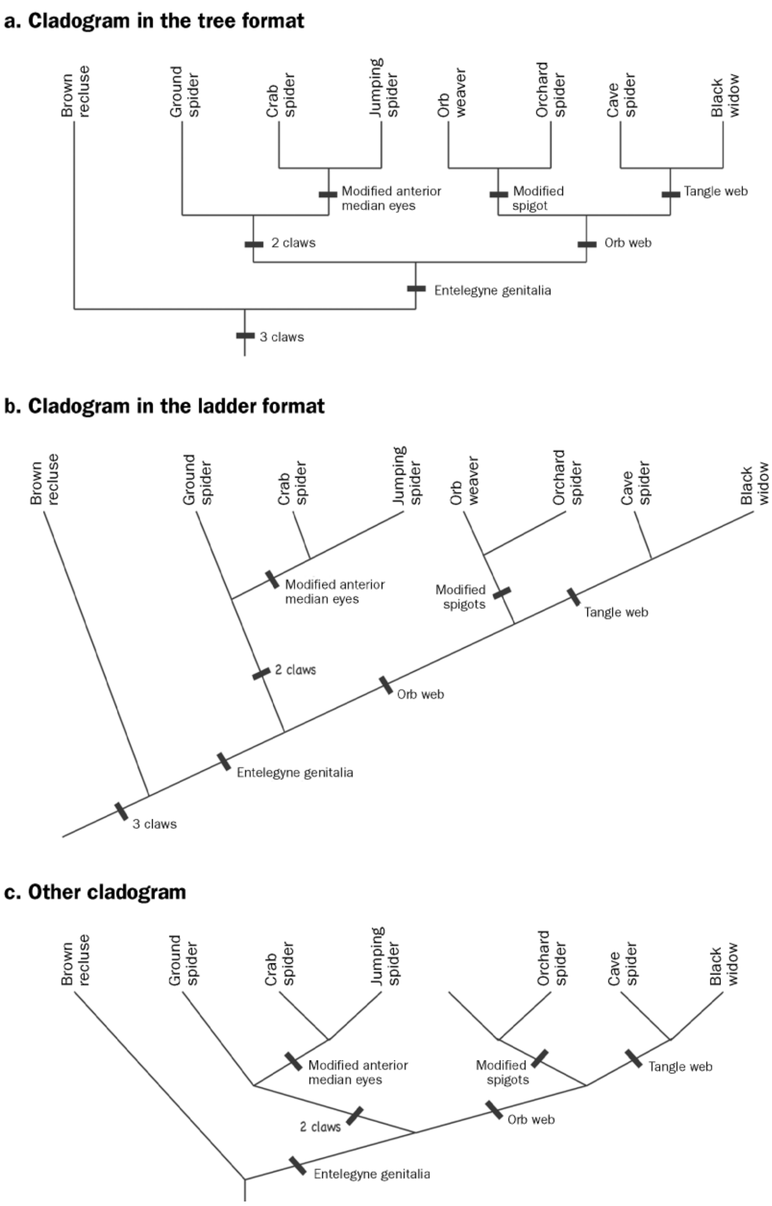

Figure 1. Three formats for depicting cladograms: (a) tree, (b) ladder, and (c) other.

textbook illustrators to make the traditionally straight lines and sharp angles more curved is interesting and may reflect people's preference for objects with curved features over similar objects with pointed features and sharp angles (Bar and Neta 2006). In a small number of cases (about 5.5 percent), the cladograms followed neither the tree nor the ladder format; these were assigned to the "other cladogram" category. In all cases, diagrams of the appropriate form were assigned to these categories whether they included character evidence (synapomorphies) or not (most did not).

Coding categories for other evolutionary diagrams

The remaining evolutionary diagrams were coded with respect to whether they fell into each of 15 categories. The first five categories were mutually exclusive; each diagram could be placed into only one of the following categories:

- *Almost-a-tree cladogram.* A diagram that appears largely like a tree but has some irregularities or violations (e.g., side branches or terminal nodes ending at more than one level) that preclude its classification as a valid tree.
- *Almost-a-ladder cladogram.* A diagram that looks like a ladder but has irregularities or violations precluding its classification as a valid ladder (figure 2a).
- *Tree of life.* A modern-day, Haeckel-like diagram showing a progression from "simpler" to more "complex" taxa as one moves from lower to higher on the diagram, or a diagram having the topology of an actual tree (figure 2b; compare with Haeckel's tree in figure 3); the diagram may show the whole tree of life starting with "protists," or it may show just a portion of the tree.
- *Anagenesis.* A diagram showing a clear linked, linear progression of taxa along a single branch, suggesting that one taxon "turned into" the next (figure 2c).

- *Other links.* A diagram showing taxa that are connected in some way not covered by any of the previous four categories (e.g., figure 2d).

The next three categories were not mutually exclusive, but there were restrictions on whether these codes could be given, depending on which of the five codes in the previous set was assigned:

- *Tree cladogram with side branches.* A diagram that looks like a valid dichotomous cladogram but contains one or more branches originating off to the side of a branch, thus violating consistent di- or polychotomy (figure 2e; only diagrams coded as "almost a tree" could receive this code).

- *Terminal branches with different end points.* A diagram in which the terminal branches end at different levels (figure 2f; only diagrams coded as "almost a tree," "almost a ladder," or "tree of life" could receive this code).

- *Nonterminal branches labeled with taxa.* A diagram in which one or more of the nonterminal branches is labeled with some kind of taxonomic or categorical label (only diagrams coded as "almost a tree," "almost a ladder," or "tree of life" could receive this code).

The final seven coding categories were not mutually exclusive, and there were no restrictions on when these codes could be given:

- *Lateral transfer.* A diagram depicting lateral transfer of genetic material or hybridization.

- *Bar graph representation.* A diagram in which at least some taxa are represented by a rectangular bar (potentially of varying length) rather than by a line (figure 2g).

- *Branches vary in thickness.* A diagram in which the branches have varying thickness rather than being drawn simply as lines (figure 2h).

- *Root node labeled as ancestor.* Any linked diagram in which the root is labeled as representing an ancestral species.

- *Time.* A diagram that includes an indication of time.

- *Instructional.* A diagram that attempts to instruct readers about some aspect of interpreting evolutionary diagrams.

- *Hominid evolution.* A diagram containing either a set of hominid species or *Homo sapiens* in the context of other primates (and no other taxa).

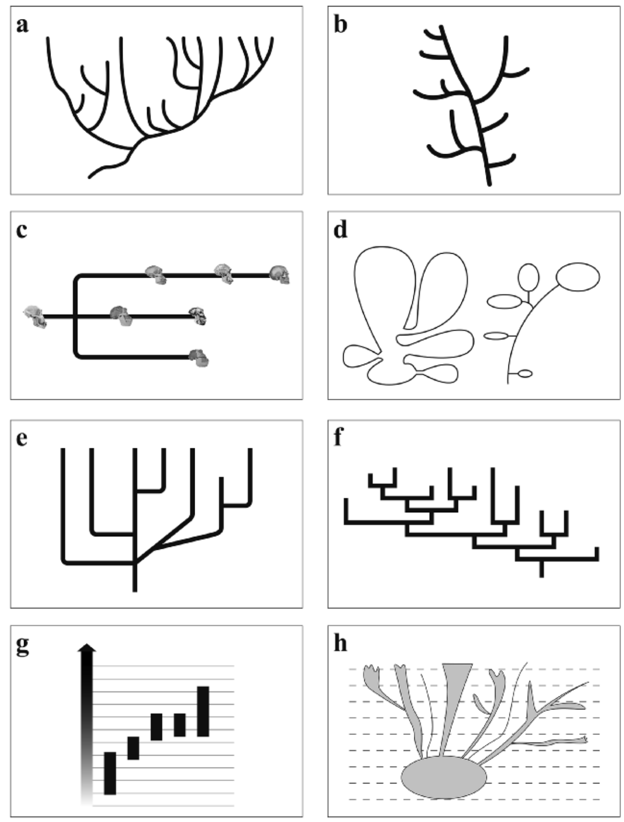

Figure 2. Topologies of some noncladogram evolutionary diagrams: (a) almost a ladder, (b) tree of life, (c) anagenesis, (d) other links, (e) tree with side branches, (f) terminal taxa with different end points, (g) bar graph, and (h) branches vary in thickness.

The two investigators coded each of the other evolutionary diagrams independently with respect to whether each of the possible codes was applicable, and reliability was computed before discrepancies were resolved through discussion. The mean proportion agreement across all codes was 0.92. The mean number of discrepancies per diagram was 1.01.

Cladogram analyses

Table 2 shows the distribution and (relative) frequency of cladograms (in tree, ladder, and other formats) and other evolutionary diagrams encountered in the 31 textbooks. The results are presented separately for each textbook category. Immediately apparent is the fact that a large majority of the diagrams (72 percent) are cladograms. There are striking differences across grade levels, however. In middle-school texts, there are few cladograms ($n = 7$), with almost twice as many noncladograms ($n = 13$). In high-school texts, the ratio of cladograms to noncladograms is approximately equal (53 percent versus 47 percent, respectively). During this formative period when students should be systematically introduced to tree thinking, the high proportion of other evolutionary diagrams in these textbooks is disturbing.

As might be predicted, the proportion of cladograms in college textbooks increases substantially. In introductory texts for nonmajors, introductory texts for majors, and zoology/botany texts, 65 percent, 83 percent, and 78 percent of the diagrams, respectively, are cladograms. However, it is a matter of concern that in the 18 college texts surveyed, more than 20 percent of the diagrams that depict evolutionary relationships are other evolutionary diagrams. Looking at the data another way, the mean number of other evolutionary diagrams per textbook *increases* from middle school, through high-school and college introductory biology, to college zoology and botany (3.25, 5.78, 6.00, 5.83, 9.33). Other evolutionary diagrams, far from being isolated phenomena, are distributed across textbooks that cater to all age levels. We examine these diagrams in more detail in the next section.

Returning to the cladograms, our analysis indicates that ladders comprise more than half of these diagrams. Considering only the tree and ladder formats, which account for 94 percent of the examples and are the predominant formats seen in the scientific literature, 55 percent of cladograms are represented as ladders. This preference for the ladder over the tree format is consistent across the five textbook samples: middle school (86 percent ladders, 14 percent trees), high school (59 percent ladders), college introductory biology for nonmajors (53 percent ladders), college introductory biology for majors (54 percent ladders), and college zoology and botany (55 percent ladders). Looking at the data another way, of the 28 textbooks that contain tree or ladder cladograms, 18 have more ladders than trees, and 10 have more trees than ladders.

While it is encouraging that the textbooks analyzed contain many valid cladograms, the large number of ladders compared with trees is discouraging. Not only is this not representative of what is seen in the scientific literature, as indicated earlier, but the results of our experimental research show conclusively that ladders are much more difficult than trees for university students to understand and interpret. For example, Novick and Catley (2007, experiment 2) found that students were much more successful at translating the relationships depicted in a circle diagram to a tree diagram than to a ladder diagram (mean proportions correct of 0.78 and 0.35, respectively). Novick and Catley (2008) asked interpretation questions such as whether taxon A or taxon C is the closer evolutionary relation to taxon B. The mean proportion correct for this question was 0.70 when the relationships were depicted on a tree, compared with only 0.42 when they were depicted on a ladder. Presumably the same patterns would be found for 7th–12th graders.

An analysis of the other evolutionary diagrams

In this section, we turn to the in-depth analysis of the other evolutionary diagrams, which comprised 28 percent of the evolutionary diagrams catalogued here. These diagrams exhibit large variability of format and are widely distributed across the whole spectrum of examined textbooks. Figure 4 shows the percentage of these diagrams that received each code, and table 3 shows the percentage of textbooks at each level that included at least one diagram that received each code. We focus our comments primarily on the high school and college textbooks because we surveyed so few middle school textbooks. Beginning at the high school level, in 41 of the 60 cases (4 levels times 15 codes), at least half of the textbooks included a diagram receiving one of the indicated codes. For example, diagrams depicting the tree of life and anagenesis are pervasive in both high-school and college biology textbooks, occurring in 16 to 17 of the 27 such texts we surveyed.

We found that most evolutionary diagrams in textbooks are not annotated, nor are their theoretical underpinnings explained. They seem to appear under the assumption that students are already familiar with their structure and interpretation. Supporting this conclusion, we documented only 18 diagrams spread across just nine textbooks (only six diagrams in three textbooks at the middle-school and high-school levels) that were dedicated to some type of instruction on structure and interpretation. Consequently, students and teachers have little basis or prior knowledge on which to evaluate and differentiate among diagrams. It is perhaps not surprising, therefore, that undergraduates, even those with stronger backgrounds in biology, encounter difficulties with tasks involving the interpretation of cladograms (Novick and Catley 2007, 2008, Sandvik 2008).

Diagrams that are almost a tree or ladder. Those diagrams in the "almost a tree" and "almost a ladder" categories comprised 26 percent and 21 percent of the other evolutionary diagrams, respectively. In general, most of the textbooks at the high-school level and above had such diagrams. These diagrams are especially insidious because they give students the impression that they are indeed real trees or ladders but instead violate certain rules (e.g., curved branches, branches of unequal length, nonterminal taxa). Because such diagrams often differ from true cladograms by only one or two criteria, students very likely are not aware they are invalid. They simply add to the confusion when presented alongside nonviolating diagrams. Such diagrams would not be found in professional journals.

Of the diagrams that almost met the criteria for being a valid tree, 62 percent had side branches not supported by any branching event (figure 2e). Side-branch diagrams were found in a little more than half of the high-school and college introductory biology textbooks. Such diagrams violate the rule that cladograms only depict dichotomous and polytomous branching events. A basic tenet of monophyly is that two taxa share a most recent common ancestor (MRCA) that is not shared with a third taxon. It would be impossible to teach this critical principle using a diagram with side branches.

Perhaps more important is that such topologies support the idea of paraphyly—that is, taxa arising from within a group such that the new group does not contain the MRCA and all of its descendants (e.g., *Aves*). Such paraphyletic groups are antithetical to the philosophical tenets of cladistics, which recognize only monophyletic groups (Hennig 1966)—those

Table 2. Type, frequency, and distribution of evolutionary diagrams from 31 biology textbooks from middle school through college-level zoology and botany.

Texbook	Cladogram Trees	Cladogram Ladders	Cladogram Other	Other evolutionary diagrams
Middle school (6th and 7th grades)				
Glencoe Life Science (2002)	0	0	0	4
Life Science (2001)	0	3	0	5
Life Science (2005)	1	3	0	1
Texas Science (2002)	0	0	0	3
Total middle school	1	6	0	13
Mean number of diagrams per book	0.25	1.50	0	3.25
Proportion of diagrams in book	0.05	0.30	0	0.65
High school (9th–12th grades)				
BSCS Biology (2002)	0	1	2	4
Campbell, Williamson, Heyden (2004)	1	5	3	5
Johnson (1998)	1	2	0	4
Johnson, Raven (2001)	0	3	2	10
Kaskel et al. (2003)	0	0	1	0
Mader (2007a)	11	3	1	5
Miller and Levine (2002)	1	11	0	4
Modern Biology (2002)	0	3	1	7
Postlethwait and Hopson (2006)	6	1	0	13
Total high school	20	29	10	52
Mean number of diagrams per book	2.22	3.22	1.11	5.78
Proportion of diagrams in book	0.18	0.26	0.09	0.47
College-level introductory biology: Nonmajors				
Audesirk et al. (2004)	6	0	0	5
Campbell, Reece, Simon (2004)	0	12	2	5
Campbell et al. (2006)	15	2	0	2
Mader (2003)	1	4	1	3
Mader (2007b)	5	4	1	5
Starr and Taggart (2006)	1	10	2	16
Total college (nonmajors)	28	32	6	36
Mean number of diagrams per book	4.67	5.33	1.00	6.00
Proportion of diagrams in book	0.27	0.31	0.06	0.35
College-level introductory biology: Majors				
Campbell and Reece (2005)	27	1	1	6
Freeman (2005)	0	43	2	2
Lewis et al. (2007)	7	5	3	9
Purves et al. (2004)	30	0	0	3
Raven, Johnson, et al. (2005)	15	10	0	14
Solomon et al. (2006)	0	32	0	1
Total college (majors)	79	91	6	35
Mean number of diagrams per book	13.17	15.17	1.00	5.83
Proportion of diagrams in book	0.38	0.43	0.03	0.17
College-level zoology and botany				
Hickman et al. (2006)	1	26	1	13
Judd et al. (2002)	34	44	3	20
Miller and Harley (2005)	1	14	2	6
Raven, Evert, Eichhorn (2005)	0	6	0	6
Ruppert et al. (2004)	50	0	0	3
Walters et al. (2006)	0	15	0	8
Total college (zoology and botany)	86	105	6	56
Mean number of diagrams per book	14.33	17.50	1.00	9.33
Proportion of diagrams in book	0.34	0.41	0.02	0.22
Total number of diagrams	214	263	28	192
Mean number of diagrams per book	6.90	8.48	0.90	6.19
Proportion of all diagrams	0.31	0.38	0.04	0.28

Note: Complete bibliographic information for the textbooks is given in table 1.

that contain the MRCA and all of its descendants. Sandvik (2008) also noted that many biology textbooks contain evolutionary trees illustrating paraphyly. It is only by seeking to discover natural, monophyletic groups (or clades)—those that reflect the actual evolutionary processes that created them—that science will make progress toward discovering the tree of life and all of the invaluable knowledge such an endeavor will provide (AMNH 1994a, 1994b, 1999).

The largest category (43 percent) of other evolutionary diagrams was terminal branches with different end points, which described 83 diagrams across 25 texts (figure 2f). Such diagrams were found in all of the zoology and botany textbooks and in nearly all of the high school and college introductory biology textbooks. Fifty-two percent of the diagrams that almost met the criteria for being a tree and 55 percent of the diagrams that almost met the criteria for being a ladder received this code. In a cladogram, taxa are depicted terminally and all at the same level because they are considered of equal rank. When taxa are shown at different levels, the assumption is that these taxa are in some way more "primitive" because they evolved earlier in the fossil record. There is seldom any evidence to support such assumptions, so this depiction only adds another potential layer of confusion to student interpretations.

For the almost-a-tree and almost-a-ladder diagrams that had terminal branches at different levels, we examined whether the lower branches were explicitly labeled as depicting extinct taxa. This is a reasonable notation, which, if appropriately applied, should promote understanding rather than confusion. We found that for the 27 such tree-like diagrams, 13 were explicitly labeled, 1 was not labeled but the shorter line ended at dinosaurs (which students presumably know are extinct), and 13 were unlabeled. For the 22 such ladder-like diagrams, 3 were labeled, 2 ended at dinosaurs, and 17 were unlabeled.

"Tree of life" representations. Diagrams based on Haeckel's (1874) famous tree of life (figure 3; a spreading, branching tree that resembles the biological entity), or a modern interpretation thereof (figure 2b), comprise 34 diagrams (18 percent) in 16 textbooks. Sixteen of the 27 textbooks at the high-school level and above had 1 to 7 diagrams each in this category (mean = 2.13). Such diagrams depict life as an ordered progression from "simpler," "lower," or less "evolved" (e.g., Monera) at the base of the tree to more "complex," "higher," or more "evolved" (e.g., mammals, hominids, "man") at the crown. These diagrams are the epitome of a teleological view of evolution; they overtly suggest the notion of direction and progress.

As discussed earlier, such notions are firmly rooted in the 18th-century depiction of the *scala naturae* (Bonnet 1745).

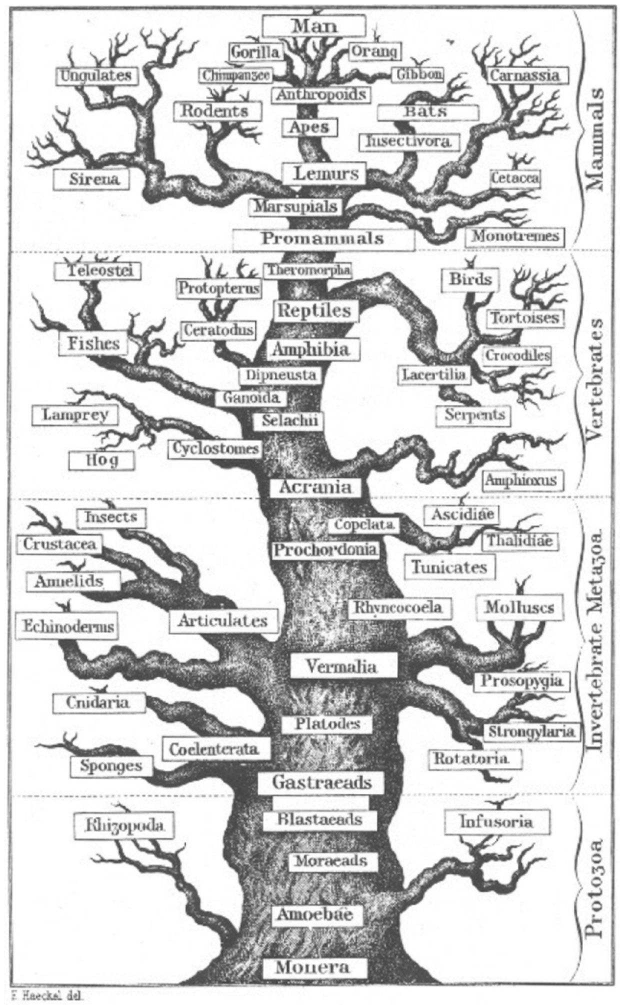

Figure 3. Haeckel's tree of life. Source: Haeckel (1874).

Table 3. Percentage of textbooks at each educational level with at least one noncladogram evolutionary diagram that received each of the 15 codes in the present study, and the total number of textbooks (out of 31) that had at least one diagram that received each of these codes.

	Educational level					
Code	Middle school (percentage)	High school (percentage)	Introductory college: Nonmajors (percentage)	Introductory college: Majors (percentage)	Zoology, botany (percentage)	Total number of textbooks
Almost a tree	25	67	67	67	67	19
Almost a ladder	50	56	50	17	83	16
Tree of life	0	56	67	33	83	16
Anagenesis	25	67	50	83	33	17
Other links	75	11	33	33	67	12
Tree with side branches	25	56	67	50	33	15
Different end points	25	89	83	83	100	25
Nonterminal taxa	0	56	50	67	100	18
Branches vary in thickness	0	22	50	33	83	12
Lateral transfer	0	0	33	17	17	4
Bar graph	0	33	50	50	0	9
Root = ancestor	50	78	67	67	50	20
Time	50	78	100	100	83	26
Instructional	25	22	33	17	50	9
Hominid evolution	50	67	83	67	17	18

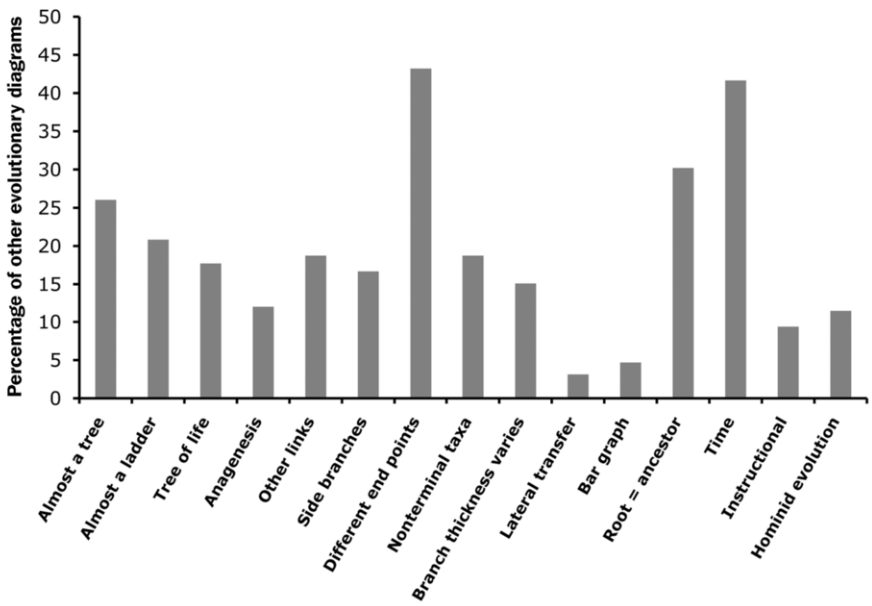

Figure 4. Percentage of other evolutionary diagrams receiving each of the 15 codes given in this study.

Unfortunately, such thinking is also prevalent in today's society (AMNH 1994a, NAS 1998) despite all the evidence to the contrary that supports the contention that evolution is simply adaptation to local circumstances—there is no general pattern of gradual, directed progress. Our analysis of diagrams in modern textbooks indicates that, far more than an historical artifact, diagrams that reflect the same ideas as Haeckel's tree are still widely used. Although in a small number of cases such diagrams are presented in an appropriate historical context, in the large majority of cases they are presented as an appropriate representation of current knowledge. One of biggest obstacles we need to overcome in evolution education is the teleological mindset that evolution is in some way a purposeful and directed process (e.g., Demastes et al. 1995, 1996, Evans 2001, Kelemen and DiYanni 2005, Catley 2006, Sandvik 2008). The tree-of-life depictions in textbooks instead reinforce this inappropriate mindset.

Nonterminal branches labeled. The 36 diagrams (19 percent) in this category were subsumed into almost a tree, almost a ladder, and tree of life categories across 18 texts. Two label categories were encountered—categorical and specific taxa. Twenty-six diagrams (20 almost a tree, 4 almost a ladder, 2 tree of life) have categorical labels on internal branches (e.g., origin of vascular plants, seed eaters, ground finches). In the remaining 10 cases (5 almost a ladder and 5 tree of life), these labels are taxa (e.g., Rosales, Archaeobacteria). Both of these cases (categorical and taxonomic) violate the cladistic tenets of depicting taxa only on terminal branches. In particular, the almost a ladder and tree of life topologies that include taxa on internal branches are easily interpreted as ancestor or descendant scenarios or as anagenesis, where the terminal taxon is assumed to have evolved "out of" the taxon that precedes it on the branch. We suggest avoiding all internal labels on diagrams. Drawing attention to subgroups within the diagram is best achieved by bracketing nested sets of terminal taxa.

Anagenesis. Diagrams that depict speciation as anagenesis (i.e., one taxon turning into another over time) as opposed to branching events (i.e., cladogenesis) accounted for 23 diagrams (12 percent) in 17 textbooks (figure 2c). Such diagrams were most common at the high school and college introductory biology level, with 50 to 83 percent of those texts having at least one such diagram. These diagrams depict two or more taxa placed successively on a single branch such that one taxon leads directly to the next. It is difficult to see how, other than by one taxon changing into the next over time, such a representation could be interpreted. In fact, we found that college students who have progressed no further than introductory biology for nonmajors often interpret such diagrams in this way. Modern evolutionary thinking, in contrast, understands that evolution involves cladogenesis, a process whereby one species splits into two, with the two new taxa sharing a MRCA.

A robust, informative evolutionary diagram is one that leaves no doubt that cladogenesis, not anagenesis, is the process that produces the patterns (relationships) we observe in nature. Diversification and radiation of species within clades can be achieved only by branching or cladogenic events. If new species only arose by anagenesis, then there would never be a net increase in the total number of species; and while change within a single species is well documented, one species changing into another species is not.

Five of the anagenesis diagrams were a version of the classic horse evolution diagram, first presented by Simpson in the 1960s. An additional such diagram was coded as tree of life. This iconic diagram has adorned textbooks for generations, is particularly difficult to interpret, and contains elements of anagenesis, teleology, and the tree of life. Taxa are arranged sequentially alongside a time scale to show the gradual increase in size from *Eohippus* to *Equus* more than 50 million years or so (figure 5). Although the inclusion of time on any diagram may be a useful learning tool, designating the direction of ancestor or descendant relationships when they cannot ever be known with certainty seems more likely to add to than to alleviate confusion. We contend that these and similar diagrams reinforce anagenesis, teleology, and a progressive tree of life and do nothing to present relationships in terms of MRCAs, synapomorphies, and branching events, which reflect modern understanding.

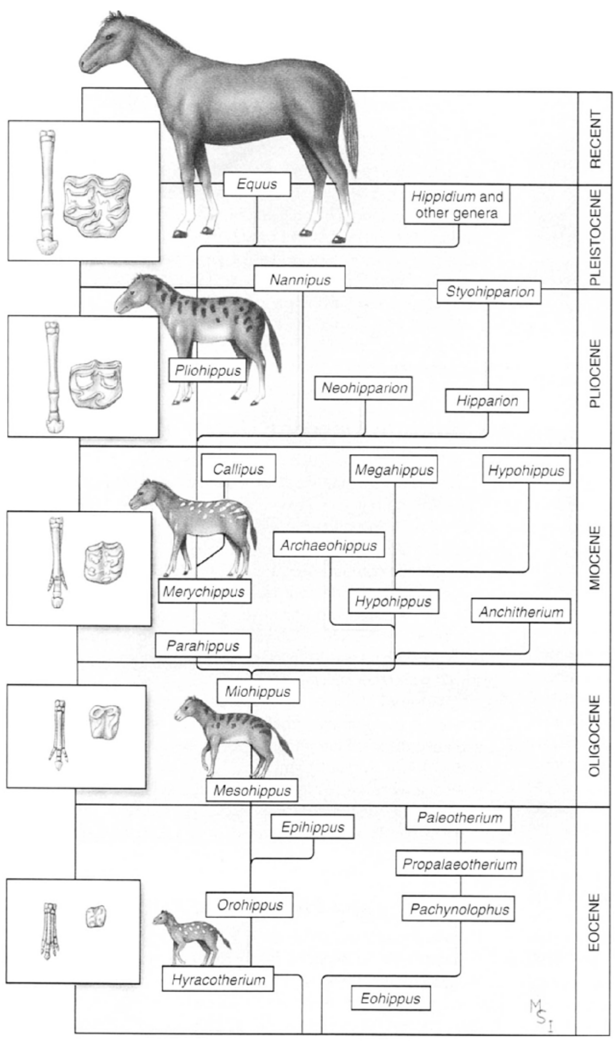

Figure 5. Diagram representing evolutionary relationships among horse taxa. Source: Figure 6–11 in Hickman and colleagues (2006).

Branches varying in thickness. Some diagrams have branches that vary in thickness (15 percent, comprising 29 diagrams across 12 texts) rather than being drawn simply as lines. Most of these diagrams (22 of the 29) are in five of the six zoology and botany textbooks. Often the branches are drawn as amorphous, elongated blobs with finger-like extensions (figure 2h). Most instances of varying branch thickness (52 percent) occurred with diagrams coded as having "other links." The remaining instances were approximately equally distributed across diagrams coded as almost a ladder (14 percent), tree of life (14 percent), anagenesis (7 percent), and some other, unlinked representation of taxa (14 percent). Because no annotation is typically provided, these branches are very difficult to interpret. We assume they represent the hypothesized population size or number of species varying with time, although they might also represent the geographical distribution of taxa. Cladograms make no assumptions about these parameters that at best can only be vague estimates. We question both the validity and utility of such depictions.

Other types of representations. Diagrams that depict a bar graph type of representation (figure 2g) were rare, representing only 5 percent of the total, but interestingly were almost exclusively confined to those depicting hominid relationships. We discuss representations of hominid evolution in the next section. One of the strangest diagram types encountered was "other links," where taxa were joined in ways not covered by any of our other categories. Such diagrams were not uncommon, comprising 36 (19 percent of the total) in 12 textbooks. Typical of such topologies is figure 2d, which presents taxa as abstract leaf-like structures. These diagrams are particularly difficult to interpret.

As already discussed, cladograms explicitly do not include ancestral taxa and make no a priori assumptions about the direction of evolution. Yet we documented 58 diagrams across 20 texts in which the root was labeled as the ancestral species. At least half of the textbooks at each level included such a diagram. Sandvik (2008) also noted the presence of stem groups in evolutionary trees printed in biology textbooks. Although we recognize the value of teaching the concept of common ancestry, because it is impossible to know which taxon was the common ancestor of any given clade, its inclusion seems disingenuous at best and bad science at worst.

Finally, some representation of time was included on 42 percent of the diagrams, and more than three-quarters of the texts at the high-school level and above included at least one such diagram (mean = 3.17 for these 24 texts). Where temporal data are available, from molecular clock or fossil corroboration, we agree that time should be included on evolutionary diagrams to aid understanding. It is important to note, however, that providing an interval rather than simply an ordinal depiction of time is challenging given the large spans of time covered, yet that may be required to give students a true sense of the time span involved (Catley and Novick, forthcoming).

Hominid evolution. We were especially interested in how human evolution is represented in modern biology textbooks. Clearly, such diagrams would not be expected in botany textbooks, so the data we report are based on the 28 other textbooks. We considered diagrams to portray hominid evolution if they showed *H. sapiens* in the context of other hominoid species (of the genus *Homo* or of the genus *Australopithecus* or both) or of other primates (apes or monkeys or both). Such diagrams (either cladograms or other evolutionary diagrams) were found in 79 percent of textbooks studied. This is encouraging, in terms of situating the evolution of our own species in context; the quality of the diagrams themselves, however, leaves much to be desired. In particular, there is a disturbing association between the context in which *H. sapiens* occurs and how evolution is represented that seems to suggest that humans are special and not subject to the same laws of evolution that other species are. This is unfortunate because it reinforces people's existing misconceptions in this regard (Evans 2001).

Consider first the 27 diagrams depicting *H. sapiens* with other primates but not other hominoid species: 22 are cladograms (11 ladders, 11 trees) and 5 are something else (4 of the 5 are almost a tree or almost a ladder). In contrast, the 18 diagrams depicting *H. sapiens* in the context of other hominid species (*Homo* or *Australopithecus* or both) and possibly also other primates include just 1 cladogram, and it is a ladder, which as noted earlier makes it more difficult to understand. Of the remaining 17 diagrams, 12 show anagenesis (5 in a bar graph format) and 5 show something else (3 bar graphs, 1 tree of life, 1 other). The association between species context and representation type (cladogram versus other) apparent in these data is statistically significant, $\chi^2\,(1) = 24.92, p < 0.001$. Across textbooks, these diagrams suggest that the hominoid lineage split away from the great apes as a branching event (cladogenesis), but subsequently evolution followed a primarily anagenic process, with one hominoid species turning into another until *H. sapiens* arose. More disturbing still, this pattern holds within textbooks, as 11 of the 28 textbooks presented both types of diagrams—primate context as a cladogram and hominoid context as some type of noncladogram.

More than with any other taxa, diagrams of hominoid relationships are rife with multiple and inappropriate topologies. These extremely varied diagrams still persist despite the fact that cladograms depicting hominid evolution were first published 30 years ago (Delson et al. 1977). Spoor and colleagues (2007) recently reported new fossil discoveries of *Homo erectus* and *Homo habilis* that show they were sympatric (coexisted), making anagenesis (*H. habilis* evolving into *H. erectus*) extremely unlikely. As biologists, we need to pay particular attention to the way we depict the evolution of our own species, lest we further reinforce the anthropocentric view so prevalent in today's society. It should seem no more remarkable to students that multiple species of the genus *Homo* coexisted in the past than that multiple species of the genus *Panthera* (lions, jaguars, leopards, and tigers) currently coexist, and no more plausible that *H. erectus* evolved into *H. sapiens* than that lions evolved into tigers.

Concluding remarks

The data presented here are a first step in understanding how to better incorporate macroevolution into biology education, thus facilitating the tree-thinking habit of mind called for by biologists and education researchers (O'Hara 1988, Gilbert 2003, Goldsmith 2003, Baum et al. 2005, Catley et al. 2005, Catley 2006, Staub et al. 2006, Sandvik 2008). Scientifically literate students should be as familiar with the patterns and processes of macroevolution as they are with the mechanisms of change in gene frequencies in populations (Catley 2006). Moreover, the prevalence of inappropriate evolutionary diagrams in life science texts should not remain unchallenged. Consistent exposure during instruction to authentic diagrams that clearly present the current consensus of scientific knowledge should be a major part of biology education.

Acknowledgments

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