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CURRICULUM ARTICLE

Characters Are Key: The Effect of Synapomorphies on Cladogram Comprehension

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Abstract Cladograms, phylogenetic trees that depict evolutionary relationships among a set of taxa, are one of the most powerful predictive tools in modern biology. They are usually depicted in one of two formats—tree or ladder. Previous research (Novick and Catley 2007) has found that college students have much greater difficulty understanding a cladogram's hierarchical structure when it is depicted in the ladder format. Such understanding would seem to be a prerequisite for successful tree thinking. The present research examined the effect of a theoretically guided manipulation—adding a synapomorphy on each branch that supports two or more taxa—on students' understanding of the hierarchical structure of ladder cladograms. Synapomorphies are characters shared by a group of taxa due to inheritance from a common ancestor. Thus, their depiction on a cladogram may facilitate the understanding of evolutionary relationships. Students' comprehension was assessed in terms of success at translating relationships depicted in the ladder format to the tree format. The results indicated that adding synapomorphies provided powerful conceptual scaffolding that improved comprehension for students with both weaker and stronger backgrounds in biology. For stronger background students, the benefit of adding synapomorphies to the ladders was comparable to that of approximately two hours of instruction in phylogenetics that emphasized the ladder format.

Keywords Cladograms · Synapomorphies · Evolution education · Phylogenetics · Evolutionary relationships

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Cladograms are phylogenetic trees that depict evolutionary relationships among a set of taxa in terms of nested levels of common ancestry. Synapomorphies are (morphological, molecular, or behavioral) characters shared by a group of taxa due to their inheritance from a common ancestor. Synapomorphies thus constitute evidence for historical relationships and their associated hierarchical structure. For example, the cladogram in Fig. 1a shows the evolutionary relationships, supported by synapomorphies, among genera of *Mollusca*. Cladograms are one of the most powerful predictive tools in modern biology. Using monophyly—groupings comprising all descendent taxa and their most recent common ancestor (a.k.a. clades)—to organize and make sense of the 3.5 billion year history of life on Earth, they provide a conceptual framework for basic and applied biology in fields as disparate as conservation, ecology, behavior, molecular biology, epidemiology, and pharmacology (e.g., Futuyma 2004; Hillis 2004; Nickels and Nelson 2005; Yates et al. 2004). Given the importance of cladograms in biology, it is not surprising that a number of researchers and educators have called for the inclusion of tree thinking in biology curricula for both biology majors and nonmajors, as well as at the high school level (e.g., Baum et al. 2005; Catley 2006; Catley et al. 2005; Goldsmith 2003; O'Hara 1988).

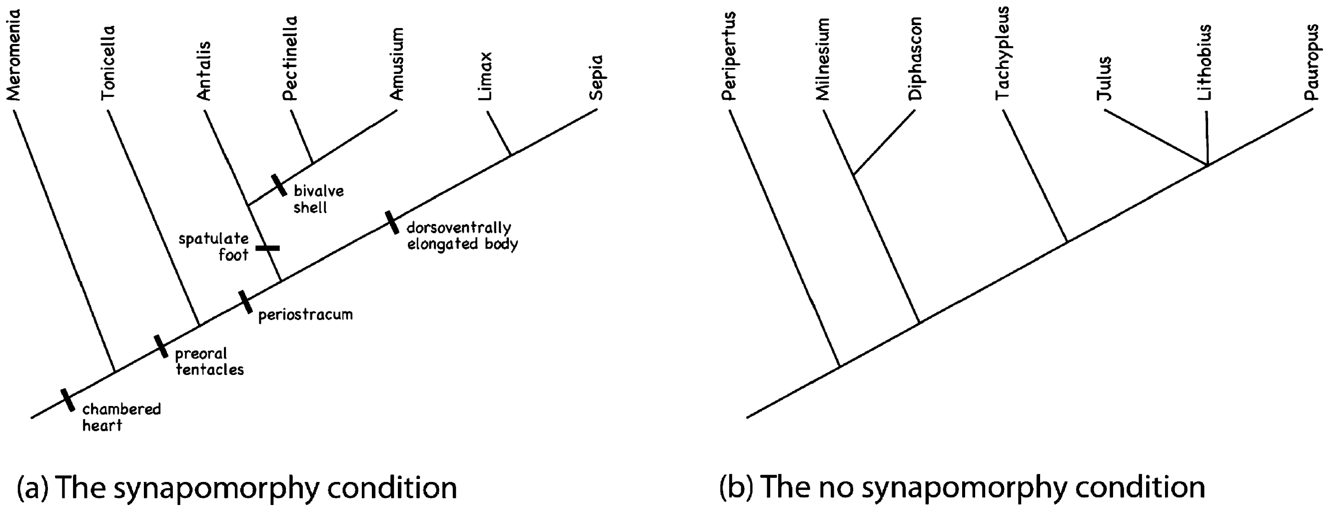


Fig. 1 Two of the ladder cladograms used in the translation task, with **a** and **b** showing, respectively, the synapomorphy and no synapomorphy conditions

Although cladograms can be depicted in a variety of different formats, they are most often drawn in one of two formats, which we have referred to in our earlier research as ladders and trees (see Fig. 2).[1] For example, in Catley and Novick's (2008) analysis of the evolutionary diagrams in 21 high school and college introductory biology textbooks and six college zoology and botany textbooks, 94% of the 498 cladograms were depicted in one of these two formats. Although the tree format is much more common in the professional systematics literature (see Novick and Catley 2007), the ladder format is somewhat more common in high school and college biology texts (for both nonmajors and majors at the college level; Catley and Novick 2008). This disconnect between professional and educational practice is unfortunate. Even though the tree and ladder formats are structurally equivalent (i.e., isomorphic), they are not psychologically equivalent: college students, both biology majors and nonmajors, find it much more difficult to understand the hierarchical structure of, extract relevant information from, and reason appropriately from the ladder than the tree format (Novick and Catley, 2007, 2010).

In the present article, we are concerned with students' ability to understand the hierarchical structure of the ladder format, which would seem to be a prerequisite for successful tree thinking. We review evidence on this issue, propose a theoretically guided method for overcoming students' difficulties, and report the results of an experiment testing our hypothesis. Finally, in light of our results, we discuss implications for teaching tree thinking.

Novick and Catley (2007, Exp. 2) asked college students with varying backgrounds in biology to translate the evolutionary relationships depicted in one format to an alternate format. Success at translating structures between alternative formats is a good indicator of diagram comprehension because it requires an understanding of the structure of the relationships depicted (e.g., Jones and Schkade 1995; Kozma and Russell 1997; Novick 2004). We consider here Novick and Catley's two conditions in

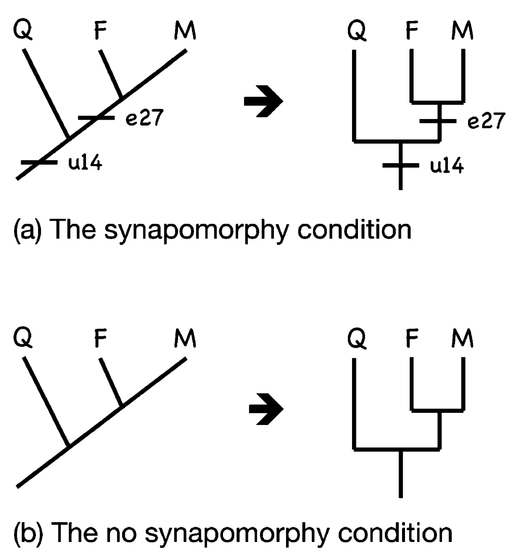


Fig. 2 The three-taxon statements printed at the top of each translation page, with **a** and **b** showing, respectively, the synapomorphy and no synapomorphy conditions. In each case, the cladogram on the *left* illustrates the ladder format, and the cladogram on the *right* illustrates the tree format

[1] Cladogram formats have been referred to using a variety of different terms (e.g., tree, ladder, comb, pectinate). From a graph-theoretic perspective (Chartrand 1985), both formats illustrated in Fig. 2 are trees. Thus, appropriate modifiers for that term could be used to refer to both formats, such as diagonal tree and rectangular tree. However, this more complex nomenclature becomes unwieldy in a long article. Given the absence of widely accepted labels for the different formats, for simplicity and for consistency with the precedent established via our use of these terms in other papers, we refer to the two formats in this article as *ladders* and *trees*.

which students were asked to redraw presented relationships in the tree format. For two problems, the relationships were depicted in a nested circles format (similar to a Venn diagram); for two other problems, the relationships were depicted in the ladder format. One problem of each type involved five taxa and the other involved six. Students' translations were scored as correct or incorrect. Students were much more successful when the relationships were initially depicted in the circle rather than the ladder format, with mean accuracy scores of 0.77 and 0.50, respectively. Type of translation problem interacted with biology background: the difference in translation accuracy between students with stronger versus weaker backgrounds in biology was smaller for the circle to tree translation problems (means of 0.87 and 0.70, respectively) than for the ladder to tree translation problems (means of 0.71 and 0.33, respectively).

Novick and Catley (2007) showed through a perceptual segmentation experiment and error analyses of students' translations that an important source of students' difficulty in understanding the hierarchical structure of the ladder format is that it is obscured by the Gestalt principle of good continuation (e.g., Kellman 2000). This perceptual principle states that a continuous (straight or curved) line is interpreted as a single entity. This natural interpretation of continuous lines, which people apply to all figures containing such lines (e.g., Shimaya 1997; van Tuijl 1980), conflicts with the correct interpretation of such lines when presented in ladder format cladograms. In a ladder, most continuous lines belong to multiple monophyletic groups. Thus, different segments of a line depict different hierarchical levels of relationship rather than the entire line depicting a single hierarchical level. This means that correct interpretation of a ladder's hierarchical structure requires attending to segments of continuous lines (referred to in the phylogenetic literature as internal or external branches), ignoring the full line itself. For example, in both ladders shown in Fig. 1, the "main" line running from the bottom left to the top right of the cladogram looks like a single entity but actually represents five hierarchical levels.

In the present research, we tested an implication of Novick and Catley's (2007) finding that understanding the hierarchical structure of the ladder format is impaired because it is difficult to mentally break good continuation to recognize distinct line segments (phylogenetic branches representing lineages) as conveying the critical structural information. In particular, if some method can be devised to encourage students to break good continuation at the appropriate places, accuracy at translating from the ladder to the tree format should improve. We hypothesized that one way to accomplish this would be to add a synapomorphy on each line segment to provide a perceptual cue as to where to break the line and start a new hierarchical level (see Fig. 2). Moreover, this manipulation is educationally appropriate. Evolutionarily, a synapomorphy is the marker for the most recent common ancestor of the monophyletic group consisting of the set of taxa above that point in the cladogram. It is the evidence for a speciation event, where an ancestral species split into two new lineages, forming what we will refer to here as a *branching point* on the tree. In experiment 1, we evaluated the effectiveness of adding synapomorphies to ladders. In experiment 2, we compared the effectiveness of this simple manipulation to two days of instruction in the principles of phylogenetics that focused on the ladder format as the primary medium of instruction.

It is important to note that it is by no means a foregone conclusion that adding synapomorphies will facilitate translation. In the ladders used in our research, this manipulation entailed an 84% increase in the amount of information (defined simply as the number of verbal labels) students in the synapomorphy condition had to keep track of to successfully complete the translation task. Thus, a strong argument could be made that our manipulation would impair rather than improve performance.

Experiment 1

Method

Subjects The subjects were 113 undergraduates at Vanderbilt University. Some subjects participated in partial fulfillment of course requirements for their evolution class (23 females, 20 males). The remaining subjects (34 females, 34 males, 2 undisclosed sex) were recruited from the psychology department's paid subject pool. The average year in school for the full sample was 2.82 (2= sophomore, 3=junior).

At the end of the study, subjects indicated whether they had taken any of 13 primarily organismal biology and three historical geology classes at Vanderbilt (or equivalent courses elsewhere). Students were placed in the stronger biology background group if they had taken at least the two-semester introductory biology sequence for biology majors and pre-med students. All remaining students were assigned to the weaker background group. The 53 stronger background students (28 females, 25 males) had taken an average of 3.07 semesters of biology (or historical geology) classes (of those on our list). In contrast, the 60 weaker background students (29 females, 29 males, 2 unknown sex) had taken an average of only 0.40 semesters of such coursework. This is nearly an 8:1 difference in coursework between the groups.

Design and materials There were two independent variables, both of which varied between subjects. One was biology background (weaker versus stronger). The other was whether a synapomorphy marked each branching point in the cladograms (see Fig. 1). There were 27 weaker and 29 stronger background students in the no synapomorphy condition and 33 weaker and 24 stronger background students in the synapomorphy condition.

Subjects received eight cladograms drawn in the ladder format, each showing evolutionary relationships among seven taxa. We constructed cladograms involving seven rather than only five to six taxa as in Novick and Catley's (2007) experiments because those authors reported that the median number of taxa in both the trees and ladders depicted in 12 undergraduate introductory biology textbooks evaluated by Catley and Novick (2008) was 7. Thus, our cladograms were similar in complexity to those that college students must interpret in their textbooks, thereby increasing the validity of our research. Seven of the eight cladograms were completely resolved (e.g., Fig. 1a), meaning that there were six branching points, each of which split into two lineages. One cladogram (Fig. 1b) had only five branching points because the final split led to a polytomy—a situation in which three or more lineages emerge from the same branching point because the relationships among them cannot be determined. In the synapomorphy condition, each branching point was marked by a synapomorphy.

As shown in Fig. 1, all taxon names were written in Latin. This was done so that students would have to rely on their understanding of the hierarchical structure depicted in each ladder to guide their translation to the tree format rather than on their potentially faulty prior knowledge of the taxa in question. The synapomorphies were written in English. Although nearly all the synapomorphies were morphological characters, we attach no theoretical significance to this aspect of our materials. Each ladder was printed at the top of an 8.5×11-in. piece of paper.

Procedure The eight ladders were collated into a booklet in two different orders. Approximately half of the subjects in each condition received each order.[2] The translation pages were preceded by an instruction page that began as follows: "Each problem presents a diagram depicting evolutionary relationships among seven taxa. Your task is to translate these evolutionary relationships from the format in which they are presented to an alternative format that nevertheless represents exactly the same set of relationships." Subjects were then shown a three-taxon ladder with the terminal branches labeled *Q*, *F*, and *M*, followed by the correct translation of that ladder into the tree format. In the synapomorphy condition, the two branching points in each cladogram were labeled with synapomorphies (*u14* and *e27*). Subjects were then told that their task for each problem in the booklet was to "take the evolutionary relationships shown in the first format and redraw them in the second format. The new diagram you draw (in the bottom format) should show *exactly the same set of evolutionary relationships* as depicted in the original diagram (in the top format), just like the two diagrams on this page show the same set of evolutionary relationships in the two different formats. For example, two taxa that are closely related in the original diagram should be shown as similarly closely related in the new diagram."

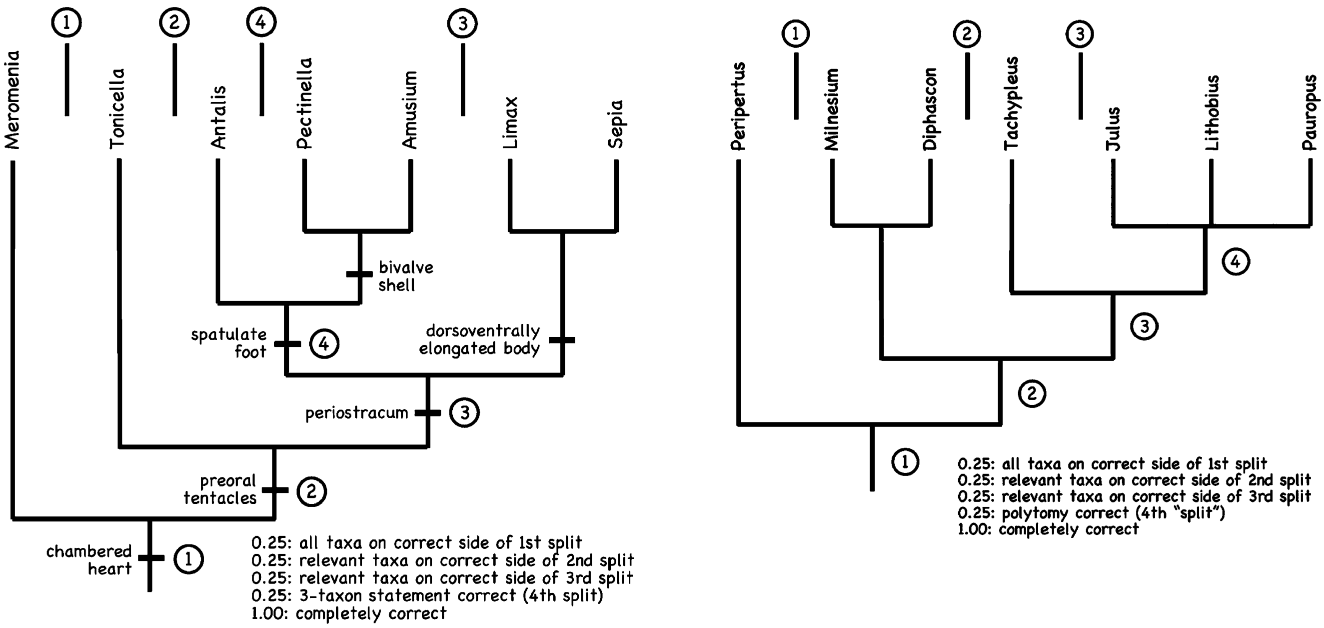
To help students complete the diagram translations, the example three-taxon ladder and tree from the instruction page (with synapomorphies in that condition) were reprinted at the top of each translation page (see Fig. 2). The inclusion of a correctly translated three-taxon statement in the instructions and on each translation page is a departure from Novick and Catley's (2007) procedure, which did not include this information. We added the example translation because it is pedagogically appropriate and clearly illustrates the required task.

The booklet for this experiment was one of several booklets that subjects completed at their own pace in a single session lasting approximately 50–75 min. Each booklet was a separate experiment. The results of the other experiments will be presented elsewhere. At the end of the session, subjects completed a questionnaire that asked for background information such as year in school and biology courses taken. Subjects participated individually or in groups in a classroom-like lab room or classroom on campus. They were not allowed to consult outside resources to complete the tasks.

Results and Discussion

Each ladder had either three or four "major" branching points, each of which yielded a clade of three or more terminal taxa (i.e., those named at the tips of the cladogram). Subjects received partial credit for each such branching point for which they correctly assigned taxa in their translation to the two groups indicated by the split. Each correct assignment was worth 0.25 points for cladograms with four branching points (n=5) and 0.33 points for cladograms with three branching points (n=3). Figure 3 shows the scoring keys and correct answers for the ladders depicted in Fig. 1. To receive the maximum score of 1, subjects had to draw the branching structure of the tree completely correctly (e.g., as shown in Fig. 3, or valid rotations around the branching points of those trees). Although subjects in the synapomorphy condition were required to include the synapomorphies in their translations,

[2] There were no differences in translation accuracy due to the ordering of the eight problems.



(a) Correct answer and scoring key for the ladder in Fig. 1a

(b) Correct answer and scoring key for the ladder in Fig. 1b

Fig. 3 Tree format translations for the ladders shown in Figs. 1a, b, along with the associated scoring key for each translation. The *vertical lines* at the top of each cladogram and the *circled numbers* located above those lines and at the branching points indicate the splits referred to in the accompanying scoring key

these were ignored when coding translation accuracy with respect to branching structure (for consistency across the two conditions).[3]

We conducted a 2 (biology background)×2 (presence versus absence of synapomorphies) between-subjects analysis of variance (ANOVA) on the mean accuracy scores across the eight translation problems. The means for each cell of the design are shown in Fig. 4. As expected, there was a significant main effect of biology background, $F(1, 109)=15.05$, MSE=0.09, $p<0.001$, with stronger background students doing better than weaker background students. More critically, the main effect of synapomorphy condition was significant, $F(1, 109)=10.33$, $p < 0.01$. Students were more successful at translating from the ladder to the tree format when synapomorphies were provided than when they were not. This effect appeared to be equally strong for both biology background groups as the interaction was not significant, $F(1, 109)=0.01$, $p > 0.90$. As shown in Fig. 4, weaker background students improved by 0.19 with the addition of the synapomorphies, and stronger background students improved by 0.17. The better performance in the no synapomorphy condition compared to that found by Novick and Catley (2007, Exp. 2) is largely due to having given partial credit for some incorrect translations in this experiment, whereas Novick and Catley used a 0/1 scoring scheme.

In sum, these results clearly show that adding synapomorphies to the ladders caused a large improvement in students' ability to correctly extract the hierarchical structure depicted, despite the need to keep track of 84% more information (verbal labels). This improvement was equally powerful regardless of the biology background of the students. It is important to note that this improvement is not simply due to subjects receiving partial credit for incorrect translations that included components of the correct response. The effect holds if a more draconian scoring criterion is used in which all imperfect translations receive a score of 0. Recoding the data this way, the proportion of correct translations increased from $M=0.44$ to $M=0.66$ for weaker background students with the addition of the synapomorphies and from $M=0.66$ to $M=0.97$ for stronger background students.

[3] The mean number of synapomorphies correctly placed (defined as appearing beneath all and only the taxa whose grouping the synapomorphy supports) was 5.77 for stronger background students and 5.10 for weaker background students. Perfect translation of the synapomorphies would yield a mean across problems of 5.875. Recall that translation accuracy was scored based solely on structural accuracy of the tree, without regard to whether the synapomorphies (in that condition) were placed in their correct locations. Thus, it is worth noting that every synapomorphy included in a completely correct translation of the branching structure was placed in the correct location.

Experiment 2

In experiment 2, we compared the effectiveness of the synapomorphy manipulation to two days of instruction in

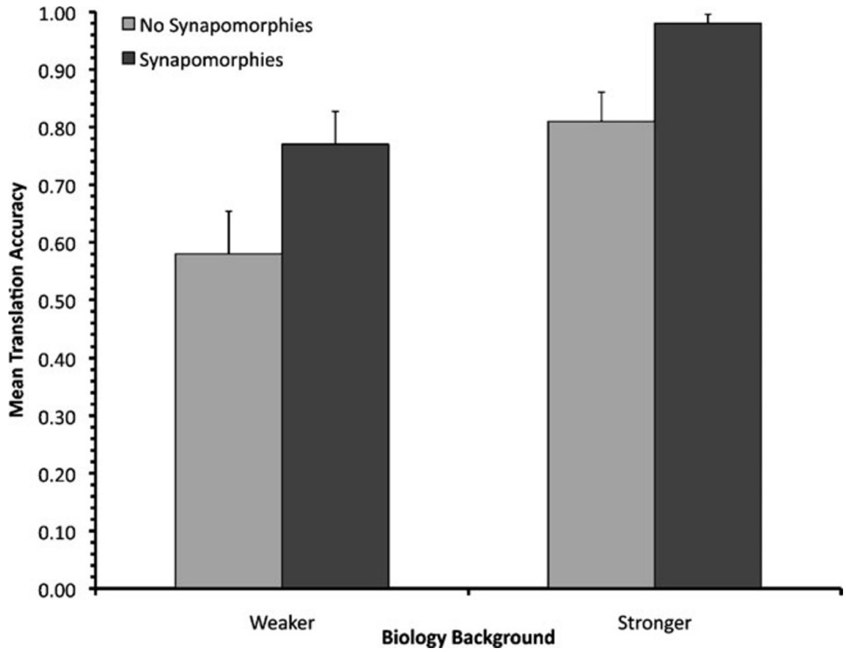


Fig. 4 Mean translation accuracy scores (+SE) as a function of biology background and synapomorphy condition

phylogenetics in an evolution class. This is a strong test of the effect of adding synapomorphies because the phylogenetics instruction was conducted primarily using the ladder format as the instructional medium.

Method

Of the 53 stronger background students in experiment 1, 42 participated as a requirement for their evolution class. These students completed the translation booklet twice—immediately prior to the lectures on phylogenetics (shortly after the middle of the semester; these data were included in experiment 1) and again at the end of the semester (4.5–5 weeks later). The phylogenetics unit and subsequent units on speciation and macroevolution were taught by the third author. Subjects participated in the same condition at both times ($n=25$ and $n=17$ without and with synapomorphies, respectively). The materials and procedure were the same as in experiment 1.

The instruction in phylogenetics consisted of approximately 2.5 hours of lecture spread across two days. Students were introduced to the nature of phylogeny as it relates to speciation, including relevant terminology concerning cladogram structure and characters. Students were shown the equivalence between a three-taxon ladder and tree approximately halfway through the two-day unit. That presentation was similar to that shown to subjects on the instruction page and at the top of each translation page in the no synapomorphy condition (see Fig. 2b). Nearly all of the instruction on the principles of phylogenetics and the structure of cladograms used the ladder format. For example, the critical notion of the nesting of monophyletic groups (clades), which provides the hierarchical structure in a cladogram, was illustrated using a ladder.

Results and Discussion

Our intention was to examine whether the effect on translation accuracy of adding synapomorphies to the ladders was similar before versus after instruction in phylogenetics. This was not possible because the subjects in the synapomorphy condition before instruction performed at ceiling, with a mean accuracy of 0.97 (using the partial-credit scoring scheme described in experiment 1). Therefore, we restricted our analyses to an examination of (a) the effect of adding synapomorphies to the ladders prior to instruction and (b) the effect of phylogenetics instruction on translation accuracy for the 25 subjects in the no synapomorphy condition. With respect to the first question, a one-factor between-subjects ANOVA yielded a significant effect of synapomorphy condition, $F(1, 40)=4.97$, MSE=0.05, $p < 0.04$, with mean accuracy scores with and without synapomorphies of 0.97 and 0.82, respectively. This test confirms that this subset of the experiment 1 stronger background group performed comparably to that group as a whole. With respect to the second question, a one-factor within-subjects ANOVA yielded a significant effect of time relative to instruction, $F(1, 24)=12.23$, MSE=0.02, $p < 0.01$. The mean accuracy before instruction was 0.82; after instruction it improved to 0.96.

These results indicate that for students with stronger backgrounds in biology, the effect on translation accuracy of adding synapomorphies to the ladders is comparable to the effect of two days of instruction in phylogenetics. This result is important because correct translation of the ladders to the tree format provides strong evidence that the students understood the hierarchical structure of the ladders. Presumably, the instructional manipulation would be more effective than simply adding synapomorphies with respect to performance on more complex tasks. It is noteworthy, however, that for this difficult translation task, the two manipulations led to comparable improvements in performance.

General Discussion

The Utility of a Cognitive Psychological Approach to Investigating Tree Thinking

Understanding the hierarchical structure of the ladder cladogram format is difficult because the Gestalt principle of good continuation (e.g., Kellman 2000) leads students to interpret multiple hierarchical levels as representing only a single level (Novick and Catley 2007). We hypothesized that adding a synapomorphy to support each branching point in a ladder would facilitate students' ability to extract the correct hierarchical structure because the synapomorphies break good continuation where the hierarchical level changes. The results of experiment 1 found that adding synapomorphies dramatically improved translation accuracy for students with both stronger and weaker biology backgrounds, and similarly so for both: $\Delta=0.17$ for stronger background, $\Delta=0.19$ for weaker background. This represents a 21% improvement for stronger background students and a 33% improvement for weaker background students. The results of experiment 2, with stronger background students, showed that this simple manipulation was as effective as two days of instruction on phylogenetics with respect to translation accuracy.

These results illustrate the power of combining cognitive/perceptual psychology and evolutionary biology. From a cognitive perspective, synapomorphies are important because they identify the points along continuous lines at which a new hierarchical level occurs, thereby breaking good continuation. From a macroevolutionary perspective, synapomorphies are important because they constitute the evidence for common ancestry, associated monophyletic groupings, and thus the historical relationships depicted in cladograms. Both perspectives converge in advocating that if the ladder format must be used, it is critically important to include a synapomorphy at each branching point.

We should note, however, that simply adding synapomorphies to ladder cladograms is not sufficient for promoting successful tree thinking with this format. Novick and Catley (2010) assessed a variety of tree-thinking skills (e.g., identifying the character shared by two taxa, evaluating evolutionary relatedness, determining whether a set of taxa is monophyletic) in college students using both tree- and ladder-formatted cladograms that included synapomorphies. Students' accuracy scores were higher, and they gave more sophisticated justifications for their responses (e.g., based on most recent common ancestry), when evaluating cladograms depicted in the tree rather than the ladder format. Moreover, Catley et al. (2010a) found that this benefit of the tree format over the ladder persisted even after two days of instruction in phylogenetics that focused on the ladder format as the primary means of instruction. Clearly, even with synapomorphies supporting the depicted relationships, the ladder format is challenging for students to understand.

We proposed and found support for one method of breaking good continuation and improving students' understanding of the hierarchical structure of the ladder format. It is reasonable to consider whether there are other means of accomplishing the same goal. For example, one suggestion that has been offered is to add a large round dot to emphasize each place where lines intersect. Whether this manipulation would improve students' comprehension of the hierarchical branching (i.e., cladogenetic) structure of the ladder format is an empirical issue worthy of future study. There is reason to believe, however, that such depictions, especially when dots appear in a series along a continuous line, lead students to focus on anagenetic changes along a lineage, and not the branching evolutionary relationships depicted on cladograms supported by evidence in the form of synapomorphies (Catley et al. 2010b; Novick et al. 2010).

Implications for Evolution Education

Considering the current and earlier (Novick and Catley 2007) translation results along with the reasoning results (Catley et al. 2010a; Novick and Catley 2010), we can make several recommendations for supporting tree thinking in biology education. First, given the difficulties that biology majors have understanding the ladder format even following introductory instruction in phylogenetics, it seems best to teach foundational tree-thinking skills using the tree format at both the college and high school levels. The hierarchical structure of the tree format should be immediately obvious given students' considerable exposure to non-evolutionary hierarchical diagrams that resemble this format (e.g., NCAA basketball tournament brackets) throughout K-12 education and in the popular press (Novick et al. 1999). Moreover, college students have been found to have a good understanding of this type of hierarchical branching structure (e.g., Novick 2006; Novick et al. 1999). More advanced biology classes can build upon the foundation established using the tree format to include additional cladogram formats, like the ladder, whose structure is less transparent.

Second, when the ladder format is used, it is critical that synapomorphies be included to define branching points and associated clades and that the meaning and importance of these characters be clearly conveyed. It is relevant to note here that most of the cladograms (in both formats) printed in high school and college biology textbooks do not include synapomorphies (Catley and Novick 2008). Although the synapomorphies used in the present study were primarily morphological characters, we believe that other types of characters (e.g., behavioral, molecular) could have been used instead. A potential obstacle to implementing the recommendation to include synapomorphies is the difficulty educators may encounter in finding a named character to support each and every monophyletic group of taxa on a cladogram to be presented to students. From the perspective of evolutionary biology, clearly, it is best to include appropriate synapomorphies (i.e., specific named characters as in Fig. 1a) because they constitute the evidence supporting conclusions that two taxa are more closely related to each other than either is to any other taxon on the cladogram. From the cognitive perspective, however, marking branching points with placeholders (e.g., unnamed bars or bars labeled with letters) may be preferable to omitting synapomorphies when they cannot easily be located in the literature. We suspect that such placeholders would serve the cognitive/perceptual purpose of breaking good continuation, thereby facilitating students' ability to accurately interpret the ladders.

Third, given that the best translation performance in Novick and Catley's (2007) research was from the nested circles format to the tree format, it might be productive to introduce the circles format first at younger ages (e.g., middle school; also see Catley et al. 2005). We are not aware of any research examining this issue.

Clearly, these recommendations for supporting tree thinking in biology education barely scratch the surface of what such a curriculum would look like. We encourage others to conduct research on additional challenges to and associated remedies toward meeting the goal of producing high school and college graduates who can effectively interpret cladograms and engage in tree thinking. Such students would be better able to evaluate and support recommendations based on historical evidence concerning a variety of contemporary biologically focused issues (e.g., conservation, biotechnology, novel medicines).

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