

A PROBLEM-SOLVING APPROACH TO THE TEACHING OF EVOLUTION

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Introduction

Evolution is undoubtedly the most important theoretical framework in biology. Unfortunately evolution is rarely accorded a place in the biology curriculum commensurate with its importance within the discipline. Evolution is often equated with natural selection and is taught from a primarily functional perspective while comparative and historical approaches, that are critical for developing an appreciation of the power of evolutionary theory, are often neglected. The result is that evolution is poorly understood and widely disparaged among both teachers and American society at large.

A problem-based approach to the teaching and learning of evolution may offer a number of benefits to students. Stewart (1988) has outlined four classes of potential learning outcomes from the use of problem-solving in genetics:

- (a) the conceptual structure (laws, theories, and their organization) of a particular discipline;
- (b) problem-solving heuristics that are not specific to a particular discipline;
- (c) content-specific problem-solving procedures (domain-specific instantiations of general heuristics and problem-solving algorithms specific to the domain); and
- (d) insight into the nature of science as an intellectual activity (Stewart, 1988).

A problem-based approach to the teaching and learning of evolution could be facilitated through the use of a problem-solving environment.

A Model of Desired Performance

One of the fundamental goals of my research (Brewer, 1996) was to generate a model of desired student performance that could guide curriculum development and instruction. In my review of literature, I was able to identify seven significant questions necessary for constructing good phylogenies (see Table 1). A model of desired performance was constructed based upon the

most commonly used expert strategy: inclusion/exclusion. The inclusion/exclusion strategy was the only strategy that was successful at finding multiple topologies across all problem types. In addition, the inclusion/exclusion strategy was applied successfully both in my computer program, *Phylogenetic Investigator* and on paper. The revised version of *Phylogenetic Investigator* (2.0), Brewer and Hefner (1996a) permits the reordering of both taxa and characters in the data matrix. This ability may facilitate display-based methods for constructing inclusion/exclusion hypotheses which could substantially reduce the need for working memory necessary to implement this strategy (Larkin, 1989). The model of desired performance provides a basis for developing an approach to teaching evolution based on effects-to-causes problems (Table 2).

Problem Solving in Biology

Problem-solving research in biology has focused primarily upon genetics (See Stewart & Hafner, 1994, for a review). Collins (1986), Stewart (1989), and Hafner and Stewart (1995) studied genetics problem solving in the context of a particular problem-solving environment: *Genetics Construction Kit (GCK)* (Jungck and Calley, 1984). Model-based conceptions of problem solving have been particularly fruitful in the domain of genetics as applied to problem solving using GCK. Between genetics and tree construction there are many similarities, but also at least two important differences.

In genetics problems, as studied by Collins (1986), Stewart (1989), and Hafner and Stewart (1995), knowledge production is possible when there is a space of potential experiments in addition to a space of potential models. In phylogenetic tree construction, as presented here, knowledge production is not possible. GCK permits the practically limitless generation of new data whereas in this research, experts were provided with a matrix of data. In practice, it is

Table 1. Methods Necessary for Answering Phylogenetic Questions.

QUESTION	FORM OF DATA	
	PHYLOGENETIC TREE	DATA MATRIX
Is a character a uniquely-apomorphic or a shared-apomorphic character?	Find unique characters between a species that possesses it and its ancestor. Shared-apomorphic characters are found below common ancestors	Perform phylogenetic inference
Has a given species been previously described or is it unknown?	Look at the branches sequentially and consider whether the species has each apomorphy until reaching a taxon or an inconsistency	Compare a row of the matrix with all other rows
Which groups of species represent evolutionarily complete units (clades)?	Identify all taxa descended from postulated ancestor	Perform phylogenetic inference
How closely related are two or more species?	Find the most recent common ancestor and count the number of steps (character transitions) between taxa	Perform phylogenetic inference
Given a species, what other species may have the same or similar characteristics?	Look at sister taxa to estimate shared properties	Perform phylogenetic inference
When did a character change in state (in relative terms)?	Find the transition on the tree	Perform phylogenetic inference
What similarities and differences exist among patterns of evolutionary change?	Follow the links between taxa and ancestors	Perform phylogenetic inference

possible for additional knowledge production to occur in phylogenetic inference: a researcher can look for additional characters or taxa. In fact, researchers attempt to present the most complete data matrix possible before beginning phylogenetic analysis. The goals of phylogenetic methods are to produce those trees that summarize present knowledge. These results are often used to guide subsequent knowledge production, however. In this wider context, the concept of an experimental space may take on greater significance.

The tasks of genetics and phylogenetic tree construction are not parallel and genetics heuristics that relate to knowledge production and experimental spaces are not necessarily applicable to phylogenetic tree construction. The

differences in the construction of problems in these two areas reflect that the study of genetics has primarily taken place within the experimental/functional tradition in biology whereas the study of phylogeny is situated within the comparative/ evolutionary tradition.

A second important difference relates to the different complex of relationships among and between models, data, and activities in the two domains. Stewart and Hafner (1991) suggested that, in the context of Mendelian genetics, problem solving could be seen as using, elaborating, or revising models. Model-using problem solving encompasses the inquiry involved in the testing and justification of well structured problems that are primarily empirical in nature. Research into model-elaborating and

model-revising problem solving seeks to describe how scientific inquiry addresses problems of conceptual depth and reasoning in the context of discovery.

Phylogenetic tree construction is, at one level of organization, a model-building activity. The tree that is being constructed can be considered a model that helps to explain the data in the matrix. This model does undergo elaboration and revision during its construction and at these levels model-elaborating and model-revising problem solving can offer insight into the nature of the processes being used. Hafner and Stewart (1995) described heuristics from genetics model-revising problem solving. Some of these heuristics match phenomena observed in phylogenetic tree construction (Table 3).

At another level, phylogenetic tree construction is a form of model-using problem solving. Experts use a model of phylogenetic inference, supported by models and assumptions, that reflects beliefs about evolutionary process. These models of phylogenetic inference result in a well-structured conception of the nature of correspondence between a data matrix and a finished tree. Problems of phylogenetic tree construction are probably incapable of presenting anomalous data that would lead to a reevaluation of the model that underlies phylogenetic inference. In this sense, the process of tree construction seems to fit the model-using problem solving category closely.

Stewart and Hafner (1991) described several observations regarding model elaborating problem solving which appear to parallel phenomena in phylogenetic tree construction. Their statement that model-elaborating problem solving may result in "Developing within model conceptual insights" appears similar to expert observations that a particular node will be true in any most parsimonious tree. Their statement that model-elaborating problem

solving may result in "Linking models because they share objects, processes, or states" parallels one method of tree construction based on linking subtrees together based on shared taxa. Also, some participants recognized that families of potential solutions could be identified and evaluated based on common criteria. One participant said, while solving a problem:

This is the one. This only adds one extra step. All the other ones add 2, that the nice thing recognizing these are basically just permutations of the same thing means that basically if one of these tries adds more

Table 2. A Model of Desired Performance for Phylogenetic Tree Construction.

- (1) Organize the characters, mentally, in the matrix, or on paper, to find the largest inclusion/exclusion character group hypothesis or hypotheses. (Consider the order of the taxa in the matrix as a mechanism of enhancing inclusion/exclusion patterns).
- (2) Translate a hypothesis into taxa by organizing the taxa in the drawing field.
- (3) Postulate an ancestor for each character or group of identical characters in the inclusion/exclusion hypothesis.
- (4) Link the most inclusive ancestors, to the next less inclusive ancestors, and continue until reaching the terminal taxa.
- (5) Distribute homoplasious characters.
- (6) Considering each homoplasious character, starting with the character that requires the most steps:
 - 6a) Evaluate whether options that improve its distribution always result in matching losses in other characters.
 - 6b) Evaluate whether other homoplasious characters have similar distributions that reinforce each other.
- (7) Construct other topologies based on additional inclusion/exclusion hypotheses from (1) or parsimony hypotheses from (6a) or (6b)
- (8) For each topology consider alternate optimizations for each homoplasious character.

Table 3. Model-Revising Heuristics With Instantiations in Phylogenetic Tree Construction.

General Heuristic

Phylogenetic Instantiation

1. Conduct a systematic search of the initial experimental space (initial because the experimental space is reconceptualized as a result of model revision).
2. Use existing models as templates to interpret features of the cross space search that: conform to the expectations of the model; do not conform to model expectations (anomaly recognition).
3. Use existing models as templates to postulate additional causal factors (changes in objects, states and processes) operating in a new problem type.
4. Utilize/build upon model revisions that have worked in the past. A model that can accommodate a large number of problem types, and thus which provides for explanatory unification within a discipline, is valued.
5. Bracket the case of interest with cases on either side (interpolation).
6. Break problems of increased complexity into independent subproblems, applying existing models to each. Subsequently focus upon the nature of the possible dependence between the subproblems.
7. Use limiting/defining relations within existing models to: postulate additional causal factors; explore the implications of a change in one component of a model for other components of that model.
8. Generally match a revised model to data prior to making specific mappings.
9. Use model revisions to determine the structure of the revised experiment space, and systematically explore previously unsearched portions of that space.
10. Use external memory aids to represent search through both model and experimental spaces.

- Not applicable to tree construction. (The construction of the hypothesis being revised represents a systematic evaluation of the data prior to revision).
- Construct homoplasious characters in parallel and look for matched duplicated characters at the tips of branches in order to find possible alternate topologies
- Optimize new characters and taxa onto existing trees.
- Not applicable to tree construction. (Phylogenetic trees (i.e., the models being revised) are different from one problem to the next.)
- Not applicable to tree construction. (A phenomenon similar to bracketing is described in the context of model-elaborating problem-solving below). Remove problematic taxon, solve the problem without taxon, and then map taxon back onto finished tree.
- Find all topologies for a problem and construct a consensus tree.
- Consider parsimony, e.g., compare the savings of fixing one character with the cost of breaking other affected characters.
- Map new data onto old tree to provide a baseline before constructing different topologies.
- Not applicable to tree construction. (The concept of an experimental space does not correspond directly between genetics and tree construction.)
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than that does then they're all out the window.

Regarding the nature of model-revising problem solving, Stewart and Hafner (1991) posed a series of questions. Among these they asked:

Do solvers use initial over-simplified models as starting points to develop a series of models of increasing complexity and realism? (Stewart and Hafner, 1991, p. 115)

This statement closely characterizes the nature of considering inclusion/exclusion. The solver begins by finding the largest group of completely inclusive/exclusive characters. This hypothesis is used to construct the initial hypothesis. Subsequently, homoplasious characters are mapped onto the tree and the finished hypothesis is then evaluated for parsimony. Using inclusion/exclusion results in generating an over-simplified model which is then revised, using parsimony, to create a finished tree or trees.

What anomalous data is overlooked by solvers, and is it possible to account for differences in the oversights in terms of different models that different solvers use? (Stewart and Hafner, 1991, p. 115-116)

The concept of anomalous data does not correspond exactly between genetics and phylogenetic tree construction. In genetics, anomalous data refer to differences between observed phenotypic ratios and those predicted by a model. Phylogenetic tree construction represents model construction *de novo* in response to available data. In genetics, problem solving revolves around model-using, elaborating, and revising problem solving. In phylogenetic tree construction, the primary activity can be seen as either model-using (with respect to a model of tree construction) or model-building (with respect to any particular tree being constructed). Phylogenetic data can only be anomalous in the second conception of tree construction. In this context, anomalous data can be characters or taxa that do not appear to "fit" with the others. In general, participants overlooked incompatible characters until an initial model had been constructed and then the incompatible characters were added and their effect on the structure of the tree was evaluated. Several participants noted taxa that appeared incompatible with the others

and one participant removed this taxon, constructed a solution, and then evaluated how the taxon could be placed back into the solution. See the strategy "Seeking the culprit:" in Brewer (1996a) for more detail.

A second question asked by Stewart and Hafner was:

Do solvers use two models to define the extremes of a continuum of cases in which the real case is presumed to lie? (Stewart and Hafner, 1991, p. 116)

Solutions in phylogenetic tree construction are not generally organized along a continuum, although one such continuum is used to consider character optimizations: the ACCTRAN optimization constructs homoplasy as the earliest possible gain with subsequent losses and the DELTRAN optimization results in latest possible acquisition of apomorphic character states. Using these two extremes becomes important during interpretation of phylogenetic trees. Solutions related to multiple topologies are not easily conceptualized as existing along a continuum. A phenomenon similar to bracketing exists, however, in which the initial inspection does not seem to lead to a single likely solution to the problem. One way to proceed is to follow what seems to be the best path then optimize that topology to seek others. In this example, a participant has found what appears to be the best inclusion/exclusion hypothesis, but is concerned that there may be another less obvious path to a solution: while solving a problem s/he said:

I can tell with these that [...] this break is going to be at least one of the options. ... if you take a situation like this and you push all these putative homoplasies way down the tree, that's the easiest way to tell if membership in these is going to collapse and you're going to have to consider moving things around, if you push them way, way down, then you're going to remove as much support above as possible and if you've made a mistake in that initial allocation, you'll see it much more quickly ... when I see something like that, I always want to consider two possibilities: one is that these are not right and the other is the possibility that you can move all that mess way down

Another way is to identify all of the likely paths

toward solutions and construct each *de novo*: In this example, another participant found out that there are two paths that seem equally likely of producing a solution:

So here it's hard to pick a sort of a set of characters that you think you ought to just go with because there are actually sort of 2 sets and it's basically 1 and 2 vs. 4 and 5 and so what I might actually do is draw trees based on those two sets initially and see what they say about each other.

In both these examples, the solvers are using a process that is analogous to bracketing in order to estimate where solutions are and how best to ensure that all of the best solutions are found.

A third question asked by Stewart and Hafner was:

Do solvers use incomplete models as templates to capture larger or more obvious effects which can then be "factored out" to detect phenomena which would otherwise be masked or be too small to be seen. (Stewart and Hafner, 1991, p. 116)

This question closely characterizes the overall aims of phylogenetic inference. Scientists construct phylogenetic trees for the purpose of recognizing which characters can be explained most easily as the result of descent and which require some other explanation. Phylogenetic tree construction identifies those characters which closely fit a larger pattern and allows the scientist to focus research effort on the more problematic characters. Solving another problem a different participant said:

What cladograms do is give you a very efficient way to curtail the range of appropriate questions in investigations. Cladograms keep you from running off and asking questions that you shouldn't be worrying about. ... the cladogram doesn't ... use the data to test the initial hypothesis, but everything that you postulate as a homoplasy on that cladogram, you've actually done a test against evidence, you say, this doesn't fit, and there are obviously two reasons for that, one is that its real homoplasy, in which case you've got all these really interesting evolutionary things to

research, or you made a mistake in which case, so what?

This aspect of model-revising, however, does not take place during phylogenetic tree construction. It is a higher level phenomenon by which phylogenetic trees are used to revise biological models in general.

Phylogenetic Investigator

This research has implications for the on-going development of Phylogenetic Investigator. PI was originally designed to allow someone to pose and solve phylogenetic problems, and draw representations for peer persuasion. This study examined its capability to facilitate posing realistic problems of tree construction, solving problems, and drawing phylogenetic trees. There was no disagreement that it was capable of presenting realistic problems. Although some experts had reservations about the biological significance of the contentless problems presented in this research, everyone agreed that these problems as represented in PI, were consistent with practices in phylogenetic biology. In terms of solving problems, PI permitted, but did not facilitate expert problem solving and most experts felt the need to supplement the environment by using paper and pencil. Below I discuss how the results of this research inform modifications to the interface for PI in terms of matrix modification and tree drawing.

Reordering data in the matrix appeared to facilitate pattern recognition and display-based reasoning. Participants (1, 3, 5, 6, 8, 9) used PI's ability to reorder rows in the data matrix and participants (1, 4, 6, 8, 9) said that the ability to move columns in the matrix would be useful as well. In addition, S7 said that she had previously engaged in this activity, although it was no longer a feature of her problem solving. One problem that was observed in moving rows was that the row selected to be moved was not highlighted. This sometimes caused confusion about which row had been selected and whether it was actually moved to the correct new location. These insights were used to improve the data matrix in a subsequent version of PI. In the new version, both rows and columns can be moved. When they are selected, the row or column of data is outlined with a box. After a new location is selected, the column and box are moved to the new location and the box flashes to indicate the new location of the data.

The drawing environment offered several difficulties to experts. The primary complaint was that it was too cumbersome and slow. Several steps were taken to streamline its interface and improve performance. In the revised version, postulated nodes can be placed directly in desired locations rather than needing to be moved. Nodes and links can be removed using the delete key, rather than a special purpose command. Link reassignments can now be invoked more easily, either through a keystroke or by selecting a link and a node, and operate through a menu system, rather than requiring the user to enter node designations. The issue of speed was addressed by redesigning some sections of the program and by restructuring some activities and data structures. This improved the response of the program during performance critical activities, like selecting and moving items, and drawing links.

Some difficulties with the interface represent inherent differences between approaches used by experts and the environment as constructed in PI. The duplicated taxa strategy used by one participant requires multiple copies of nodes to construct single character trees. This conceptualization of the problem and its representation is simply different than that presented by PI. Experts methods and strategies

are adapted to a pre-existing series of tools and representational media. Although the PI drawing environment did not facilitate expert performance on the part of most experts who used it, several participants used it successfully. Further study is required to evaluate whether it can be used successfully to teach fundamental phylogenetic tree construction to novices.

Conclusions

The research program described here has provided insights into the nature of phylogenetic problems and problem-solving methods and how these might be applied to teaching evolution. This report includes a new description of the nature of phylogenetic problems and factors contributing to their difficulty that can inform the construction of problems for educational use that encompass the full range of phylogenetic phenomena. The procedural model of phylogenetic tree construction adds to the knowledge of problem-solving research and can inform desired performance for students. The results of this research contribute to the creation of a knowledge base that can inform curricula that address the teaching of evolution and provide a foundation for subsequent research in the problem solving of phylogenetic inference.

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Courses Taught:

General Botany, Advanced Plant Taxonomy, Identification of Aquatic Vascular Plants; Plant Morphology, Plant Taxonomy, Identification of Woody Plants, Identification of Ferns & Fern Allies

Research and Scholarly Interests:

Flora of Missouri, Atlas Project on Missouri Flora Distribution, Biosystematics of *Silphium asteriscus* complex, Ecophysiology of *Geocarpon minimum*, ongoing project of manual writing for use in local flora courses ("Missouri's Spring Flora" and "Woody Plants of Missouri"), the floristics of Camps Clark, Crowder, and Macon in Missouri

Memberships:

Society of Sigma Xi, Tri-Beta Biological Society, Botanical Society of America, American Society of Plant Taxonomists, International Society for Plant Taxonomy, American Institute of Biological Science, Southern Appalachian Botanical Club, Missouri Prairie Foundation, Missouri Native Plant Society, Ozark Society, Nature Conservancy, National Audubon Society, Sierra Club, The Wilderness Society, The Union of Concerned Scientists, Carrying Capacity Network, Zero Population Growth, National Association of Biology Teachers, Association of Midwestern College Biology Teachers

Summary of AMCBT Involvement:

Member of Steering Committee, Association of Midwest College Biology Teachers, 1989-1991
Panel Discussion Participant with M. Levin, N. Jensen, R. Wilson, & Sr. Jeannene Yackey, "Perspectives on Teaching: Ecology & Field Biology," Oct. 1992, St. Xavier University, Chicago, IL.
Presented workshop with Barbara Newman, "Teaching About Human Population Growth in Introductory Biology Courses," Oct. 1992, St. Xavier University, Chicago, IL.

Selected Educational Activities:

Presented workshop with Barbara Newman, "Overpopulation-The root of our Environmental Problems," to public school teachers at state education meeting, Feb., 1992, Tan-Tara-a Resort, Lake of the Ozarks, MO.
Presented workshop with Dr. Albert Gordon on Population to Association for Biology Education (ABLE), at annual meeting, June, 1990, Springfield, MO.
Organized field trip, "Natural History of Arizona," for Springfield, MO, science teachers during spring break, 1990.
Organized workshop for elementary and secondary science teachers on "The Prairie--A Classroom;" Co-sponsored by SMSU Continuing Education and the Missouri Prairie Foundation, 1987 & 1988.

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