Novice Instructors and Student-Centered Instruction: Identifying and Addressing Obstacles to Learning in the College Science Laboratory

Dale Winter¹, Paula Lemons², Jack Bookman³ and William Hoese⁴.

ABSTRACT: We identify and analyze some widespread problems with the implementation of student-centered instruction in introductory college science and mathematics laboratory courses. Specifically, we observe potential problems with interactions between the instructor and individual students, interactions between the instructor and small groups of students, and the instructor's ability to monitor the learning environment. We describe our underlying assumptions regarding the purpose and nature of student-centered introductory college laboratory course, and analyze the problems that we identify using these assumptions. We provide practical suggestions for dealing with each category of problems.

KEY WORDS: Laboratory instruction, student-centered instruction, active learning, cooperative learning, questioning techniques, learning theory, instructor-student interactions.

1. Introduction

As Elizabeth Hazel notes in (Hazel, 1993, p.155):

"Laboratory work is the hallmark of education in science and technology based fields. Student laboratories are a costly resource yet their educational potential is often not fully realized in practice. It is timely that their design and delivery and the forms of student assessment used be examined critically for their contribution to high quality learning."

In this article, we focus on the delivery and facilitation of learning experiences in the context of the college science laboratory. Specifically, the purposes of this article are to: (1) identify and analyze problems with the implementation of student-centered instruction (SCI) in introductory college science (by which we mean science and mathematics) courses, and (2) to suggest some solutions. The difficulties that we describe were observed in student laboratories from a variety of fields (biology, mathematics and physics). In particular, we focus on forms of interactions between the instructor and students that may diminish the quality of the learning experience for the

¹ Department of Mathematics, Harvard University, One Oxford Street, Cambridge MA 02138.

² Department of Biology, Box 90338, Duke University, Durham NC 27708.

³ Department of Mathematics, Box 90320, Duke University, Durham NC 27708.

⁴ Department of Biological Science, California State University, Fullerton, P.O. Box 6850, Fullerton CA 92834-6850.

students, specifically those that are ubiquitously observed and correctable. (The specific areas of instructor difficulty are summarized in Appendix A.) We provide a large number of suggestions for ways that instructors can alter their behavior in introductory college science and mathematics laboratories that may alleviate some of the difficulties that we perceive.

Student-centered instruction is as much a collection of assumptions about the purpose and nature of instruction as it is a collection of instructional techniques. Felder and Brent characterize student-centered instruction as follows:

"Student-centered instruction is a broad teaching approach that includes substituting active learning for lectures, holding students responsible for their learning, and using self-paced and/or cooperative (team-based) learning. Other ways to center our teaching on students include assigning open-ended problems and those requiring critical or creative thinking, reflective writing exercises, and involving students in simulations and role-plays." (Felder & Brent, 1996, page 43)

There are many reports of the success of SCI from experienced instructors who are skilled in its use, (Felder & Brent, 1996; McKeachie, 1994; Johnson et. al., 1991; Davidson, 1985; Heller et. al., 1992; Novak, 1993). However, on many college campuses (especially research-oriented universities with large numbers of undergraduates) these experienced individuals are not the ones who lead the introductory level labs. Instead, student learning in the introductory laboratory is often facilitated by inexperienced instructors who often have little or no teaching experience, training, or well-developed ideas about how to conduct their lab (Case, 1989).

As noted elsewhere, (Felder & Brent, 1996; DeLong & Winter, 1998; Prestine & McGreal, 1997), SCI is not an easy philosophy and set of techniques for instructors to effectively use. If used improperly, the positive learning outcomes that have been described in the literature are unlikely to be realized. Indeed, DeLong and Winter document instructional problems encountered by graduate student instructors when attempting to use student-centered methods in pre-calculus and calculus classes (DeLong & Winter, 1998). Similarly, in our observations of math, biology, and physics laboratories, we note that as laboratory instructors attempt to use student-centered methods to facilitate learning in laboratory courses, they also act in ways that may not accomplish the goals that they are trying to implement. Our observations and the suggestions we make provide a guide for teachers who want to improve their skills in SCI and for those who are preparing future faculty to use SCI.

2. METHODOLOGY

2.1 Data Collection and Analysis

This study was initiated in January 1999, and represents a body of data collected throughout 1999. Qualitative methods allow us to develop sufficiently detailed information about college science laboratories. Our methods are best described as *clinical observations* (Romberg, 1992). Our analytical method is a grounded research method (Glaser & Strauss, 1967) with the sorting of observations and creation of analytical categories conducted by the entire group of investigators. In total, we collected data from 40 laboratory sections. Our team of observers included two biologists and two mathematicians, with occasional assistance from faculty in other disciplines.

The main source of data was the notes made by observers during visits to laboratory sections. About 30 of the 40 observations were made by pairs or trios of observers. The presence of multiple observers for each laboratory session was an important feature of our approach. An obvious benefit is that with more observers, there is the opportunity to "triangulate" observations and interpretations (Asiala et. al., 1996).

The observers notes were coded in a preliminary fashion by sorting episodes of classroom activity into the categories of "effective" and "problematic." The main criteria for sorting classroom episodes in this preliminary analysis was whether the methods or outcomes of the episode were consistent with the observers' assumptions about the nature and objectives of the introductory college science laboratory (see Section 3).

The episodes in the problematic category were then grouped according to the nature of the classroom activity described in each episode. For example, interactions between the instructor and small groups of students were grouped together. Within each of these new groupings, the episodes were examined to identify the problems that occurred in many different classrooms with many different instructors, and in different disciplines. The groupings and recurring problems were then ranked according to perceived importance. The main assumptions that underlie these rankings are recorded in Section 3.

During the first phase of data collection (Spring 1999), no follow-up interviews of instructors were held. During the second phase of data collection (Fall 1999), we conducted follow-up interviews with instructors to discuss the observations. As part of the preparation for these meetings, we prepared suggestions for each instructor. We grouped these suggestions to correspond with the persistent problems that we had identified.

The narrative vignette presented in this article were created directly from the notes compiled by one of the observers. This vignette was reviewed by the other team members who observed the laboratory session described to ensure that it was an accurate portrayal of the laboratory session. We composed several vignettes to illustrate the laboratory environments that we observed. In the interests of space, we have selected one vignette to include in this article. While this vignette is broadly illustrative of many of the difficulties that we observed, it does not represent every single problem.

2.2 The Nature of the Classes Observed

We observed introductory math, physics and biology laboratories and biology sessions devoted to problem-based inquiry (referred to hereafter as seminar). Generally, the classes consisted of some kind of introductory lecture together with individual, pair, or group-based activities. The introductory lectures were usually no longer than ten minutes in duration, and were sometimes extemporaneous in nature. Some instructors also concluded the session with a lecture in which they attempted to either complete the lab for the students or summarize major points from the lab. This was only common in the introductory biology labs and seminars. Generally the mathematics and physics labs did not have any definite conclusion. Students usually just trickled out of these labs when they thought that they had completed all of the tasks for the lab session.

The activities for each lab or seminar were all designed by experienced faculty (usually faculty who had taught some component of the course). The activities were designed to deepen students' comprehension of the subject matter discussed in the lecture component of the course, or to guide students in the discovery of scientific or mathematical knowledge. In both the biology and mathematics courses, the lab TAs were introduced to the activities in a preparatory meeting the previous week.

During laboratory group work, students normally were divided into groups of three or four. While the students worked, instructors would circulate and try to clarify specific issues. Ideally, the instructors would provide guidance and hints, try to correct misconceptions, and ensure that the pace of the class and treatment of the subject matter were appropriate for the course. The biology labs and seminars visited were led by a single instructor and typically included about twelve students. The physics labs visited were also led by a single instructor and typically included between twenty and thirty students. The mathematics labs visited were the largest, including approximately thirty students each and led by an instructor, sometimes with an assistant.

2.3 The Subjects

The majority of the laboratory and seminar classes visited were led by graduate student instructors with little or no teaching experience. Several classes visited were led by more experienced graduate student instructors. In several of the mathematics laboratory sections visited, the lab was led by an advanced undergraduate (usually a senior) who had several semesters of experience as a lab assistant. Three of the mathematics laboratories visited were led by mathematics faculty members.

3. ASSUMPTIONS ABOUT THE COLLEGE SCIENCE LABORATORY

Observational data of the sort that we have collected will admit multiple interpretations, according to the assumptions on teaching and learning that researchers employ, (Geertz, 1973). Our assumptions about learning have profoundly shaped our selection of areas of difficulty and the suggestions that we have offered. We agree (Asiala et. al., 1996) that it is important for researchers to make these assumptions explicit.

3.1 Assumptions on Learning in College Science Laboratories

In regards to the purpose of the college science laboratory, we assert that students should: (1) learn content in a meaningful, non-arbitrary, non-verbatim way; (2) spend as much time as possible involved in activities that focus on higher order thinking skills (Bloom et. al., 1956); (3) develop and practice a repertoire of non-routine problem-solving skills; (4) learn technical skills and the use of equipment, (Hazel, 1998); (5) appreciate the application of scientific knowledge and methods, (Hazel, 1998); (6) learn to work cooperatively with colleagues, developing teamwork skills, (Hazel, 1998); and (7) foster student autonomy and self-direction.

Assumptions about these purposes should be consistent with assumptions about the nature of student learning in laboratories. Our assumptions about learning include that: (1) students should be motivated to learn the content in ways that are meaningful (i.e. so that the learner is able to modify his or her existing conceptual framework to accommodate the new material (Winter et. al., 2000; Ausubel, 1963); (2) students can learn from each other, and through interactions with their peers students may construct meaningful understandings of the subject matter (Novak, 1977); (3) students tend to be able to understand material when new material is related to old material; (4) learners' efforts to place new material in relation to existing conceptions may be facilitated by the intervention of a suitably knowledgeable and properly prepared instructor (Novak, 1977); and (5) learning is an active process (often, but not necessarily, physically active).

3.2 Assumptions about the Desired Characteristics of Laboratory Instructors

We contend that ideal laboratory instructors should: (1) prior to intervening, have some idea of what the learner is thinking and what the learner is trying to do; (2) have his or her own conceptual framework that accommodates both the material that students have already learned and the material that the students are currently trying to learn; and (3) be able to facilitate interactions not only between themselves and students but also among students to encourage students so that they may work to construct meaningful understandings of the laboratory subject matter.

4. INTERACTIONS BETWEEN INSTRUCTOR AND STUDENTS

We present our data in the form of a vignette that provides a context in which to discuss the problem areas we identified. We selected this vignette to *illustrate* these problem areas, but these problems were not isolated incidents but widely observed in each discipline. We then provide potential solutions at the end of each section.

The events described in the vignette below represent a significant portion of an introductory biology seminar on dating phylogenetic hypotheses using fossil, biogeographic, and molecular clock data (see Appendix). The episodes described took place after the instructor had attempted to conduct a class-wide discussion of phylogenetic hypotheses and the kinds of data that can be used to build these diagrams.

Seminar ended with a short discussion that took place immediately after the events described. We have assigned the fictitious names 'Alice,' 'Ann,' 'Alan' and 'Anthony' to the students from group A, and the names 'Ben' and 'Brad' to students from group B. While there were four students in group B, the vantage point of the observers was such that the conversation of two of the students could not be recorded.

The instructor erased the board as the students began to work, and then began walking between the two groups. The students [group A] asked each other if the material on the handout was correct or not, and finally Alice asked the instructor, "Is this 350 million supposed to be 350 million or 150 million?" The instructor walked over and confirmed that the date was 350 million. Alice then turned to the last page of the handout and said, "See, these don't make any sense."

"Shouldn't the one beginning with 'a' come after the one beginning with 'p'?" asked Ann.

"They're missing the intermediate." suggested Alan.

These questions and comments were directed to the other members of group A. The instructor hung around in the space between the two groups, and waited for students to ask him a question directly.

The instructor walked over to group B, and looked at what the students were doing. The students were not discussing their work with each other. The instructor looked at the work that the students had written down and asked one of them:

Instructor: Therefore, which node should have branched off before

that time?

Ben: Did this mean that they found the fossil?

Instructor: Yeah, they found that fossil. If you find a fossil within

this clade, when did they branch off?

Ben: . . . (only has a second or two to answer)

Instructor: In terms of the nodes.

Ben: ... (only has a second or two to answer)

Instructor: You found a fossil that looked like this ancestor, so

what does that mean?

Ben: The fossil came after the ancestor?

Instructor: Yeah.

The instructor returned to group A and asked, "How's it going?" Alice responded that they were confused by the units - groups or species. The instructor answered and then returned to group B. The instructor noticed that one of the students in group B had finished with the fossils, and was now working with the biogeographical data. The instructor asked:

Instructor: Was that guy on one big island?

Brad: ... (no reply)

Instructor: Here's the thing, there was one common ancestor.

Did it arise on just one island or did it arise on two different islands? Does that help it to make sense?

Some of the students in group B were ready to begin their molecular clock calculations, and they asked the instructor how to do this. The instructor told them to calibrate the clock by looking for the node that they knew the best, and then to look for a place where

the two families have been separated. The students began calculations while the instructor watched. As the calculations progressed, the instructor asked the students in group B a string of questions, to which the students really seemed to be trying to respond. The instructor looked at the results of the students' calculations and remarked, "I think your 100 is good, but there's more data that you need to take into account. Hold on a minute I'll just need to check on these other guys."

In the meantime, group A had been struggling with the molecular clock data. Alice and Ann tried to talk it through to make sense of the data, while Alan listened to the conversation and occasionally said something. The fourth student, Anthony, did not appear to be participating in the conversation at all. Typical contributions to the conversation were along the lines of, "I think you take five percent of this . . . I don't know," or, "I got ninety but I don't know if it's right or not." The instructor glanced briefly at the table, and then went back to group B. Seeing that group B was struggling with the molecular clock data, the instructor stopped the class and began an explanation of the molecular clock calculation on the chalk board.

After the explanation, group A appeared to be at exactly the same point as they had been for the last ten minutes. The instructor returned to work with group B. After five minutes, the instructor walked over to group A and began to walk back to group B when Alice said:

Alice: We've been using 95 million for this clade.

Instructor: (Didn't recognize student was addressing him.) Hmm?

Alice: We've been using 95 million for this clade.

The instructor looked at the calculations that Alice had written, and explained a point about one of the calculations.

This vignette illustrates several persistent areas of difficulties that arise from interactions between the instructor and the students when the students are principally occupied with their learning activities. We group these difficulties into two categories, according to whether the 'unit' that the instructor is attempting to interact with is a small group of students or an individual student.

4.1 Interacting with small groups of students.

Cooperative learning is a well-described form of SCI. As noted by many authors (Felder & Brent, 1994; Johnson et. al., 1991), cooperative learning is not simply students working on activities while sitting together in groups. Instead, cooperative learning involves a number of important ingredients including interdependence, individual accountability, face-to-face interactions, use of collaborative skills, and group processing (Felder & Brent, 1994). As the vignette illustrates, instances of cooperative learning were not commonly observed.

Felder and Brent (Felder & Brent, 1994) suggest benefits from cooperative learning that are consistent with the assumptions about the nature of the introductory science laboratory that we described in Section 3. For example, working together may encourage students to actively work at constructing meaningful understandings. Additionally,

students may benefit from the explanations given by others and may persevere longer with learning activities if they have access to the thought processes of other students. In order for these benefits to be realized, it is important that the instructor carefully observe both the students' work on learning activities and his or her own forms of behavior as a participant in the learning environment (DeLong & Winter, 1998). For example, instructors who hope that having students work together will enable some students to learn from other students undermine this objective if they are constantly interfering with students.

We perceived two major categories of difficulties with instructors interactions with groups of students: (a) instructors failed to encourage student-student interaction when this was appropriate and (b) instructors' ways of involving themselves in students' work could discourage students from interacting with each other.

(a) Instructors failed to encourage student-student interaction

In many of the seminars and laboratories that we observed, instructors missed opportunities to encourage interactions within groups. In the vignette, for example, the attention that the instructor pays to group A is simply to respond to Alice's questions. At all other times, the instructor is either busy with group B or else is simply waiting for a student to ask a question. While the instructor is responding to Alice's questions about molecular clocks and checking her calculations, Anthony has been silent and has not contributed anything to the group's effort for some time. The instructor does not seem to notice.

We note that student participation in a group's efforts may take many different forms, with physically active forms of participation being the easiest to detect (e.g. speaking, operating experimental equipment, analyzing results). We also recognize that there are a variety of learning styles, and that some students simply may not do well in a highly participatory interactive learning environment, legitimately preferring to work on their own, (Felder, 1993). We saw little evidence to suggest that many instructors were sufficiently well acquainted with their students to recognize that this was the case. Some quiet students withdrew from participation in the group (and presumably stopped learning), perhaps due to the pressure not to reveal that they had fallen behind, or else due to the pressure not to slow the other students down (for example, Anthony's withdrawal from the group in the vignette). Because a silent, withdrawn student is often a student who either needs some help to work through the material or needs help to find ways to participate fully in the group's work, we feel that it is important for instructors to look for such students and to find ways to include them in what the group is doing.

Related to this is the point that many of the instructors we observed may not actually know what cooperative learning is (c.f. Johnson et. al., 1991; Felder & Brent, 1996; Reynolds et. al., 1995), and may feel that simply having students working and sitting together represents a cooperative learning situation. For example, the instructor in the illustrative vignette may actually think that all is well with group A, because someone (Alice) in group A seems to be producing answers at approximately the rate that the

instructor expects. However, our observations (e.g. Alice and Ann cannot find a way to do their calculations that both agree is "right," Alan can't make any suggestions about how to proceed at all, and Anthony is completely withdrawn from what the other students are doing) reveals that very little cooperative learning is taking place.

When we have observed classes whose instructors seemed not to encourage studentstudent interactions, we have suggested:

- When possible, encourage students to position their desks so that they are facing each other, and so that all members of each group are in the "inner circle."
- Try to notice whether or not students are participating in discussion and questions to prompt group discussion.
 - ♦ Think of ways to engage disinterested students who may have been excluded from the group due to dominating members. One method might be to ask directed questions to the disengaged students that will require a response, not to you but to the group. For instance, "<Student 1's name>, share with the group two ways that <Student 2's name> might test his hypothesis."
 - ♦ When you interact with a group, try to draw quiet people into the discussion by specifically asking them a question.

(b) Instructors ways of involving themselves in student work could discourage students from interacting with each other

In most of the classes that we observed, the instructors were somewhat self-conscious, but not really conscious of themselves. That is, instructors tried to project a professional and helpful image, and were certainly aware of the presence of observers in the classroom (self-conscious), but instructors often seemed not to be aware of conspicuous patterns in their conduct in the classroom (conscious of self), especially when these patterns had an arguably deleterious effect or seemed unfair to some of the students in the class. Our observations suggest that this "consciousness of self" can impact student learning.

(b)(i) Instructor spends conspicuously more time with some groups, even when other groups are clearly struggling

One aspect of a lack of consciousness of self that we observed repeatedly was the tendency of instructors to spend more time with some groups of students than with others. For example, in the illustrative vignette, the instructor spends considerably more time with the students in group B, rather than the students in group A, and interacts with the students in group B on different terms. The instructor engages the students in group B in extended conversations about the results that they are obtaining from their work on the learning activities (see the conversations that the instructor has with Ben and Brad). On the other hand, the instructor asks group A only if everything is "okay." Towards the

end of the vignette, the instructor does not realize that one of the students (Alice) actually intends to be speaking with him when she asks about her calculations. When the instructor is working closely with the students in group B on interpreting and using the data from molecular clocks to date the nodes on a phylogenetic hypothesis, the students in group A have clearly reached a situation where they have not made any appreciable progress for some time. Students in this situation can benefit from careful and judicious guidance from the instructor to help them examine the work that they have done and identify the avenues that are still open to them.

These were not isolated instances; we observed similar scenarios in many of our laboratory and seminar visits. In response, we suggested the following to instructors:

- Keep making some kind of contact with each of the groups when you come around to visit them. Many times that you ask the students anything even if it is just, "Is everything okay?" students have questions.
- Intentionally balance your time among groups. Obviously sometimes one group will require more attention than another, but often multiple groups need extensive help. Even if you can't get to another group immediately, acknowledge that they are struggling and confirm to that group that you will be with them as soon as possible.
- Try not to get "bottled up" with one group for a really long time.
 - ♦ Get students going, and then check back with them a few minutes later.
 - ♦ Ask the students to pool their thoughts and let you know when they have done this you'll be back then.

(b)(ii) Instructor emphasizes instructor-student interactions rather than encouraging student-student interactions

In the vignette, the instructor seems to be quite conscious of the need to facilitate a learning process within a group of students. For example, in the conversations noted with Ben and Brad, the instructor seems to be making a genuine effort to help these students deepen their understanding of interpreting and dating phylogenetic hypotheses by asking them probing questions. Unfortunately, this instructional behavior was not replicated in all seminars and labs. On the contrary, in many cases, the instructor seemed to feel that the best approach was to try to explain everything over and over again to students, sometimes altering the explanation. One of the fundamental problems with this method is that it places the focus on the instructor talking at students rather than on students discussing with each other.

As we stated earlier in this article, we have assumed that students learn by constructing their own understanding. According to such a paradigm, students' poorly formed conceptions of the subject matter are not simple misunderstandings to be corrected by thorough explanations on the part of the instructor. Rather they are the products of the

students' constructive learning processes (Finkel & Monk, 1983). The instructor needs to recognize the attempts of groups of students to make sense of the material as important steps in constructing meaningful understandings, rather than assume that the students have misunderstood (DeLong & Winter, 1998). Instead of repeating previous explanations, or perhaps rewording previous explanations, the appropriate course of action in the constructivist paradigm is for the teacher to use his or her expertise to guide the students' learning process (Mintzes et. al., 1998; Smith, 1994; Connell, 1998; Chickering & Gamson, 1991).

When we have observed instructors who have shown a persistent tendency to supplant groups' efforts to make sense of the material for themselves, we have suggested:

- Try to encourage students to speak to each other, as well as supplying you with explanations.
 - ♦ When a student has asked you a question, you could respond with a question like, "Did anybody else make any progress on this?" "Was anyone else able to work this out?"
 - ♦ When you see a group of students who are working individually, ask one of them to summarize the progress that the group has made for you.
 - ♦ If students are asking you if they have the "right answers," first of all ask the other students in the group what they got for an answer.

(b)(iii) Group has a "spokesperson," and instructor just tends to interact with spokesperson

A persistent pattern that we noticed in many different classes was that interactions between the instructor and groups of students are always with the same student from each group. For example, in the account of the biology seminar given here, the instructor's interactions with group A are always interactions with Alice. Note that it is not by the instructor's design that this is the case. Most of the interactions between the instructor and group A are initiated by Alice, so it is somewhat understandable that the instructor would respond to her questions. While we are not advocating that instructors ignore students' questions or requests for clarifications or asserting that the fact that students ask questions is problematic, we have observed potential problems with this "spokesperson effect" when it leads to the exclusion of some group members from full participation in learning.

Our impression is that the main goal of many students that we observed was to complete the activities (i.e. to obtain "answers" acceptable to the instructor) as quickly and easily as possible. With this imperative, it is easy for students who do not think or read as quickly to get left behind by the faster members of the group. We suggest that individual students are often reluctant to speak out when they feel themselves falling behind, and may prefer to remain silent even though they are well aware of the fact that they do not

understand what the other members of the group are talking about. When the overriding goal of the group is completion of activities as quickly and with as little fuss as possible, there is an additional pressure not to speak out, as this might slow the other students down and "waste" their time. We believe that this may be what is going on in the vignette while group A is struggling to complete the activities on molecular clocks. Alice and Ann are trying to get answers that "look right," Alan listens, trying to understand what they are doing, and Anthony says nothing, clearly having fallen behind the others.

In this scenario, by responding exclusively to the spokesperson when interacting with the group, the instructor may be actually exacerbating the situation of other students in the group who have fallen behind, and who are no longer able to learn in that situation. By speaking only with the group's "spokesperson," the instructor misses opportunities to focus the group's activity on learning, rather than on just completing the activities as quickly as possible, and also misses opportunities to include all of the students in this learning process.

We note, however, that we have also observed classes where the "spokespeople" were careful to spend time communicating their ideas to the other students in the group. That is, after conferring one-on-one with the instructor and developing an understanding of the point they were stuck on, the spokesperson then taught the other students in his or her group the lessons learnt. Although this is certainly preferable to the situation described above, we suggest that all students should be encouraged to work to develop their own understandings of new material and to contribute to the understanding of other group members, rather than relying exclusively on their peers to sort everything out for them.

In classes where we have observed deleterious effects of group "spokespeople," we have suggested that instructors:

- Try to vary the directions that you approach groups from, so that you can get beside (and more easily interact with) all students in a group.
- Intentionally attempt to draw all members of the group into interaction
- When answering questions from individuals within a group, include the entire group in your answer. One way to do this is by actually posing the same question or a rephrased version of the question to another group member.

4.2 Interacting with individual students.

A persistent theme in the difficulties that we perceived involving instructor-student interactions was the predilection of many of the instructors to simply tell students what tasks to carry out in order to produce answers or even to tell students what answers to record in their work. We feel that this kind of instructor-student interaction (especially when it is the only or predominant form of instructor-student interaction) potentially diminishes the value of the laboratory for students.

For example, in many of the classes that we visited, we noted that both instructors and students focus on getting "right answers" and this overshadowed many of the interactions between instructor and students. One of the major implications of the constructivist framework is that students are unlikely to create meaningful understandings if they are always simply provided with "right answers." Instead, students need to engage in a process of inquiry in which they attempt to formulate theories to explain the phenomena they encounter, and then test their theories, (Dubinsky, 1998; Smith, 1998). Instructors would recognize this form of student behavior as a necessary part of a learning process, and encourage students as they work. Just as the students should be expected to spend quite a lot of their time constructing meaningful understandings of the subject matter, instructors should expect to spend quite a lot of their time recognizing and supporting students' efforts to learn. This conception of what the instructor should be doing in the laboratory can have quite different implications from the view that the instructor's primary role is to dispense bits of knowledge in the form of answers to questions that students are not able to immediately formulate an answer for themselves.

The main categories that we perceived here were that: (a) instructors and students tend to de-emphasize conceptual learning in favor of "getting the work done," (b) instructors lack the experience in using questions to guide students and to promote conceptual learning, and (c) instructors do not develop a clear picture of what students understand.

(a) De-emphasizing conceptual learning in favor of "getting the work done"

The vignette shows an episode where the students may be engaged in a constructive learning process. In the first part of the seminar, where the students in group A are trying to make sense of a phylogenetic tree, the instructor waits for the students to ask questions directly. Whether or not the instructor interprets the students' activity as an important part of a learning process or not, we feel that his actions at this point were appropriate, as we feel that it is important for the students to engage in a process of inquiry, rather than to simply receive "right answers" from the instructor. Likewise, later in the vignette, Alice and Ann are trying to make sense of some data about molecular clocks, with little (or no) involvement of the other members of their group. When Alice goes on to ask the instructor about their calculations, the instructor looks at the calculations and then tries to explain something that he feels will clarify the calculation for the students.

As we have noted, inquiry-based learning is often a new and somewhat uncomfortable activity for many students, (Bookman & Blake, 1996; Bookman & Friedman, 1994ab, Schoenfeld, 1985). It forces them to engage in a tentative, speculative, and somewhat open-ended activity rather than the more prescribed, rule-bound activities to which they may be accustomed. For example, the dialog that Alice and Anne conduct in the vignette contains as many statements of uncertainty ("I don't know") as it does statements about using molecular clocks. Clearly, these students are engaged in an activity where they are attempting to obtain an answer that seems "right" to them, but they are also engaging in an activity where they need to construct understandings of how molecular data is used to

date biological events. When the instructor does interact with the students, he focuses simply on the final product of these interactions. The instructor does not, for example, ask the students to recreate their thought processes and relate these. Furthermore, as seen in the vignette, this is a process that two (of the four) students from group A are engaged in, while the other two students do not seem to be very fully engaged in this learning process, perhaps simply waiting for the other students to figure it out, or perhaps for the instructor to provide the class with a method for performing these calculations.

According to our observations, although the instructor realized that when the students seemed to be discussing the content among themselves, it might be best for him not to interfere too much, he did nothing to recognize the potential value of the process that the students had engaged in, and did nothing to encourage students as they worked. Recognizing that Alice and Ann were both involved in a potentially valuable attempt to make sense of the molecular clock data - and telling the students that their activity was valuable - may have helped these students to persist with their attempts to make sense of molecular clock dating, and may also have helped to draw the other two students (Alan and Anthony) back into the discussion.

In order to recognize and value students' genuine efforts to engage in inquiry-based learning, we have suggested the following to instructors:

- Instead of just telling a student whether the answers obtained are right or wrong, try to get her to tell you how she obtained her answers. This will give you an opportunity to examine the student's thought processes and understandings, and can help you to see exactly where the student may have gone wrong.
- Regularly check on the progress of each student in the class.
- Recognize when a student has done something significant, or has improved over time, and communicate this recognition to him or her.
- When a student gives an incorrect answer, try to first point out something that was right about it before prompting him or her in a new direction.

(b) Lacking the experience to use questions to guide students and to promote conceptual learning

The formulation and use of guiding questions as a method of facilitating inquiry-based learning has been advocated by many authors (Schoenfeld, 1990; Krantz, 1993; Skemp, 1975; Mintzes et. al., 1998; Case, 1991) The difficulties that many instructors have in formulating "good" questions has also been recognized by several authors (DeLong & Winter, 1998; Napell, 1976). We observed several difficulties with the ways instructors used questions.

(b)(i) Tending to tell the students what to do, rather than attempting to guide them

In typical college instructional situations, time is usually an important factor. When coupled with the fact that students will usually be examined (at least indirectly) on much of the factual content and techniques developed during lab and seminar times, both students and instructors feel pressure to ensure that all of the information that they will be "responsible for" come exam time has been covered. In such scenarios, the instructor arguably does have an obligation to make all relevant information readily available to students, and simply telling students this information may be the most expedient way to discharge this responsibility.

This tension to make all information available to students before the end of class is apparent in the vignette. Sensing that students are unable to work with the molecular clock, both instructors turn to whole class discussions in the last few minutes of class to explain the methodology and to provide an example for students to follow.

Although this is not always inappropriate, sometimes it is. In an effort to give instructors some guidance about when to explain and when to use guiding questions, we have made the following suggestions:

- Ask students to describe the intellectual content instead of having to explain everything yourself. This is not to say that you should never explain anything, just to let the students explain the things that they are capable of explaining and save your efforts to think up really clear explanations for the really hard stuff.
- When you interact with a student, try to help the student work out the problems for himself, rather than just telling students what procedure to follow. For example, (1) ask the student what parts of the lab he has been able to figure out and which parts he is stuck on or (2) formulate questions which will help the student to recognize what information she needs to solve a problem, find the information she needs, and then recognize how to use that information to understand the part of the lab she is working on.

(b)(ii) Formulating questions to ask students and waiting for responses

Many instructors that we observed instinctively recognized that they could focus students' attention and learning by asking questions that stimulated students to think about the content in a new or novel way, or to make connections between the material that they were working with, and other concepts that had been introduced into the course. However, many of the instructors that we observed, while fully intending to stimulate students' thinking in productive ways, had difficulty formulating and using questions effectively.

Some of these difficulties can be seen in the illustrative vignette. For example, the instructor has observed Ben's work on dating a node on the phylogenetic tree, and seen a problem. He attempts to guide Ben's thinking by raising the point that there is another node that should have already branched off, but Ben has not taken this into account. Instead of simply telling Ben this, the instructor asks a question, "Therefore, which node should have branched off before that time?" Ben does not answer immediately (he asks a

question about the nature of the evidence which the instructor answers). The instructor then followed up by asking his initial question again. We find the instructor's actions up to this point to be excellent, and very supportive of a process of student inquiry. However, as he attempts to follow up, the instructor asks questions that Ben will likely have to think seriously about, with hardly a pause to allow Ben to think. Likewise, the instructor quickly rewords his questions, presumably to try to help Ben make sense of the question more easily. However, the instructor may actually be making things more difficult for Ben, because by rapidly asking a string of questions, Ben does not have a chance to think carefully about the first question he was asked, let alone the subsequent string of questions. In the end, the instructor asks Ben a much simpler question ("You found a fossil that looked like this ancestor, so what does that mean?") that is much more immediately related to facts that the student can recall with little or no thought.

In most instances that we observed, the questions that the instructors were attempting to formulate were very intimately associated with the actual content that the students were studying at the point in time. Because good questions depend upon the precise nature of the subject matter of the lab, the intentions of the instructor and the cognition of the learner, we are unable to produce a recipe for generating good questions under any circumstances. Some of the specific suggestions that we have made to instructors who have struggled with the formulation and use of questions are:

- As part of your preparation for class, spend some time anticipating areas where students may get stuck and formulating some probing questions to guide them through these parts of the exercise.
- Try to use some questions that ask the students about the intellectual content they are supposed to understand, instead of explaining the intellectual content and asking, "Does that make sense?"
 - ♦ Observe and listen to the students for a little while to see what they are working on. Compose a question that goes a little beyond what the students appear to have explicitly worked out. If they can answer that question quickly and correctly, then it is a good bet that they have a clear picture of what they have been studying.
 - ♦ Suggest a modification of the data or model that the students have been using, and ask the students how their conclusions or answers would change.
- When you ask a probing question, students will probably have to think about their answers. Give them plenty of time to do this before rephrasing, repeating or answering the question yourself.

(c) Not developing a clear picture of what students understand

Constructivist theories of learning generally agree that the most important information that an instructor can have before attempting to help a student learn is an accurate picture

of what the students know (Novak, 1993; Mintzes et. al., 1998; Skemp, 1975). While thorough knowledge of the learners' thoughts, (Schulman, 1986; Thompson, 1992), is an ideal, the practicalities of a college classroom make this ideal difficult to attain. In the course of our observations, however, we noted that sometimes instructors paid close attention to what the students were trying to do, whereas other times, the instructors seemed to take little notice of the students' work, focusing instead on the answers that the students developed, or on other tasks such as arranging the physical environment of the classroom. All of the instructors that we observed seemed to want to help students learn. However, when instructors attempted to assist or guide students with little or no idea of how the students were thinking about the content, the instructor's efforts often helped students very little.

An example that occurs in the illustrative vignette is the conversation between the instructor and Ben. By asking a question, Ben has clearly indicated to the instructor that he was not in a position to respond meaningfully to the instructor's question. Instead of recognizing this, and trying to build a picture of what Ben understands about using fossil evidence to date the nodes on phylogenetic trees, the instructor simply repeats his previous question. The strategy that the instructor eventually settles on is to "dumb down" the question to a level that requires only the most basic understanding on the part of the student. We suggest that by taking a little time to develop a more accurate picture of what Ben understood and how he understood it, the instructor would have been in a position to help Ben answer the original question, rather than resorting to low-level questions to produce the illusion that the student is actually making a connection. Here, the instructor is doing the intellectual work; all that the student is doing is voicing some of the words in the place of the instructor.

When we have observed instructors who do not realize the important role of determining what the learners think is going on, we have suggested that the instructor make a conscious effort to watch and listen to the students. We have found it helpful to suggest particular areas of student-student interaction that instructors might pay close attention to:

- When you are observing a group of students try to notice what the students are doing in terms of:
 - ♦ Are the students interacting with each other?
 - ♦ Where are the students in their work on the lab? Are they on schedule to complete their work?
 - ♦ Are the students getting near (or at) points of the lab that you can reasonably expect them to have trouble?
 - ♦ Is the "product" that students are completing appropriate given the goals of the particular lab session, the wider goals of the course, and up to the standards of intellectual or mathematical rigor expected in this course?

5. MONITORING AND THINKING ABOUT THE TEACHING AND LEARNING ENVIRONMENT

In addition to difficulties that arise from interactions between instructors and students, we also regularly observed difficulties in instructors' abilities to monitor and think about the teaching and learning environment. In an activity based classroom, two types of goals exist - practical goals (management goals such as completing activities in the time available) and learning goals (such as students being able to use their knowledge in new situations or being able to clearly communicate what they've learned) (see appendix). While instructors are expected to achieve both, the time constraints of a lab session require them to make trade-offs. For example, with only 15 minutes remaining, an instructor must decide whether to rush students to complete the exercise or to allow them to continue struggling to understand a difficult concept. Thus, instructors must manage time appropriately, monitor intellectual activity, and adjust their plan to meet as many of the practical and learning goals as possible.

Our idea of monitoring and thinking about the teaching and learning environment is perhaps better understood using analogies from soccer or basketball. When dribbling, the player must know where the ball is and she must also know where all the other players are so that she can pass the ball. Likewise, while paying attention to the practical goals, an instructor must know if students or groups of students are achieving the larger learning goals and, if not, adjust so that these goals will be achieved. While it is difficult to do both of these at once, this is, nonetheless, a skill needed by SCI instructors.

Since most of the instructors we observed were inexperienced, they were often at a loss for how they should occupy their time. They tended to recognize that they should be doing something but their choices of what to do were frequently inappropriate. For example, several instructors invested their energy in organizational tasks, sorting through student papers, organizing overhead transparencies, or taping posters from group work onto the wall. While it is necessary to give small groups time to begin working together, it is difficult at best for an instructor to monitor and alter the teaching and learning environment if he is distracted from important cues by organizational tasks.

Based on our observations, components of this category include (a) not paying attention to students' intellectual activity and (b) making inappropriate use of time available in the lab.

(a) Not paying attention to students' intellectual activity

(a)(i) Instructors do not recognize that they should monitor students' intellectual progress.

Many instructors who fail in this category simply do not recognize that they should monitor the intellectual progress of the class as a whole. For instance, in the vignette, the instructor did not notice Anthony's non-participatory body language. Anthony sat away from the table and at times even put his head down. Thus he achieved neither practical nor learning goals. In other labs, the instructor invested up to one third of the time in the presentation of background information. In addition, instructors often made no attempts to include students in discussion or to ask them questions to test how they were progressing in their learning. We have observed instructors who have prepared extensive notes about what they will present to the entire class but who have apparently not attempted to predict what interactions within small groups may take place or points within the exercise where students will struggle. After lecturing, these instructors seem to breathe a sigh of relief as if to say, "My job is now done."

Similarly, instructors often hover around small groups of students, waiting to be asked a question. This happened in the vignette, where the instructor hung around in the space between the two groups and waited for students to ask him a question directly. We have witnessed this on other occasions as well where instructors stand several feet away from groups, don't say anything, don't look at what students are writing down, and stare into space. It seems possible that they are behaving this way out of hesitancy to disrupt group activity. However, without getting close enough to the group to gain information from what students are saying, what the students are writing, and how the students are sitting, it's unclear that the instructor could really know what's going on.

When we have observed instructors who fail to recognize that they should monitor the intellectual progress of students, we have made the following suggestion (note that portions of this suggestion were also mentioned in section 4.2(c)):

- When you are observing a group of students try to notice what the groups of students are doing in terms of :
 - ♦ Are any of the students struggling or lagging behind others?
 - ♦ Is each student in the group contributing to the discussion?
 - ♦ Are any students in the group off-task?

(Note: for additional suggestions see section 4.2 (c))

(a)(ii) Instructors tend to use only the most able students in the class as an indicator of how students are doing.

Another common mistake made by instructors who do not monitor and think about the teaching and learning environment sufficiently is that they receive their information about how students are doing primarily from the star students. The root of this problem is similar to that of the "spokesperson effect" described in Section 4.1(b)(iii). Whether by design or by circumstances (such as the physical layout of the room), many instructors that we observed tended to approach a group of students by walking towards the group's "spokesperson." Other students in the group may lack the confidence necessary to ask the instructor a question about the material. Since they don't say anything, the instructor

may overlook these students and fail to receive important information about how they're progressing through the practical and learning goals.

When we have observed instructors who use only the most able students as indicators of progress being made, we have made the following suggestion:

• Look at how the "regular" students are doing as well as the "stars" of the class. Talk with all students from time to time. Don't just take the stars assurances "everything's fine" at face value all the time.

(a)(iii) Instructors miss students' requests for help

A prime example of missed requests for help can be taken from the vignette. Near the end of this vignette, Alice asks the instructor a question as he is leaving the group. The instructor does not realize that Alice has asked him a question, and Alice is forced to repeat herself. The instructor seems surprised that Alice has a question. We suggest that such problems may be related to those discussed in (a)(i) above. Instructors who hover at a distance from groups also tend to make this mistake. Again, this prohibits instructors from receiving cues about intellectual progress - verbal cues such as students sitting silently rather than discussing or whispering to each other "I have no idea what this means!" and non-verbal cues like students making eye contact with the instructor or sitting back from the table in frustration.

When we have observed instructors who miss students' request for help, we have made the following suggestions:

- Observe someone else's lab and concentrate on what students are doing.
- Look for signs of groups telling you that they want you to interact with them:
 - ♦ Obvious: raised hands.
 - ♦ Not so obvious: three or four students all reading silently, sitting back from table or desk.
 - ♦ Eye contact from individuals.
 - ♦ Little evidence of written work or accomplishment of experimental tasks.

(b) Making inappropriate use of time available in the lab

In planning and executing a successful collaborative learning lesson, instructors must also consider the role of time, the limiting factor in achieving both practical and learning goals. A common observation that we made is that time runs out before all of the goals of the laboratory are met. We have observed two different scenarios that lead to this same result.

We have observed that poor planning or execution in the way time is used at the beginning of class makes it almost inevitable that time will run out at the end. If an

exercise is designed to involve students for 40 minutes and 20 of those minutes are used by the instructor, then students will not have time to complete the practical goals, and the learning goals will likely suffer as well. Time is often consumed at the beginning of class for other reasons as well, such as instructors tending to logistical details (e.g. what assignments are due and when). In contrast, instructors who effectively manage time at the beginning of class often do two things:

- (1) They list assignments and due dates on the board at the front of the classroom and remind students to read the board and be aware of upcoming deadlines; and
- (2) They skip lengthy introductions, provide a few concise comments about the goals and purpose of the day's activities, and immediately get students to work on the exercise.

Secondly, some instructors tend to get bogged down with groups that are stuck on a concept they don't understand and end up spending an inordinate amount of time helping them. A variety of factors may contribute to this problem. Certainly, the nature of the material being covered may be difficult for students to grasp within a limited amount of time. Although the curriculum used in the settings we observed is designed with time constraints in mind, there is no perfect curriculum. Inevitably, some student or group of students will struggle to achieve the learning goals. It also seems to us that running out of time at the end is confounded by poor interactions with groups of students or individual students (discussed at length in Section 4.1 and 4.2).

Sometimes it is the best choice for instructors to reassemble the entire class and explore a concept together instead of allowing the students to keep working in small groups. Often the instructors we observed did not recognize when they had arrived at this point. We are not saying that instructors should turn to class-wide discussions and mini-lectures at the first signs of struggle on the part of groups. Rather we are advocating that they be aware of the point at which students have done all that they can in groups and need the instructor to intervene with the entire class to help make sense of an idea.

When we have observed some of the problems that have just been described, we have made the following suggestions:

- When introducing a topic, consider directing your introduction specifically to what students will need to know to work with the exercise. Determine the time that should be allotted for this introduction, then practice to ensure that it will fit within this time slot.
- Be prepared to adapt the exercise to accomplish the most important goals as time begins to run out. For instance, if all of the groups seem to be struggling with the same part of the exercise, perhaps group work could end 10 minutes earlier than you planned in order to work through the problem as a class.
- Leave some time at the end of class for a final wrap-up discussion. This may help the students to synthesize the information that they have been working with.

• When appropriate, reconvene the entire class earlier to discuss problems as an entire group.

7. CONCLUSIONS

In this study, we have observed certain widespread difficulties encountered by novice instructors in their interactions with groups of students, interactions with individual students, and monitoring the teaching and learning environment. These difficulties are summarized in Appendix A (following the references). The difficulties we have described are difficulties that we have observed in a number of active learning environments in biology, mathematics and physics and may be more closely connected with the form of learning environment, rather than any particular area of subject matter. With this understanding, we suggest that the origin of the kinds of difficulties that we have described lie not only with the difficulty of the subject matter, but in large part with the instructor's ability to create and sustain a learning environment that encourages and supports students' efforts to learn.

During the second phase of observations, we conducted follow-up interviews with many of the instructors. Based on our observations, our assumptions about the college science laboratory (see section 3) and the follow-up interviews, we suggest that three related limitations may be at the root of many of the classroom difficulties that we have reported. These are:

- (1) the instructors lack of knowledge of pedagogical techniques (such as what cooperative learning entails) or lack of practical experience of how to implement these techniques;
- (2) the instructors lack of knowledge of how students learn; and
- (3) the following underlying assumptions held by many science instructors and students:
 - (a) Dissemination of information and creation of understanding amount to the same thing.
 - (b) All of the information must be conveyed to students during the limited amount of time that is available. The conveyance of this information is the responsibility of the class instructor during class time.
 - (c) If students have not been specifically alerted to items of information then they are not under any obligation to examine that content. Conversely, exam writers are under the obligation not to include any questions on the exam that address issues that students have not been specifically alerted to.

These assumptions exert a powerful influence over the kinds of activities that occur in college classrooms. Through the follow-up interviews that we conducted with instructors, we feel that these assumptions may be responsible, at least in part, for the reluctance to facilitate student learning, and instead to simply convey answers to students. The instructors tended to view themselves as lecturers, task managers, or authorities of the knowledge of their discipline rather than facilitators of student learning processes. If this is true, it helps to explain some of the choices that instructors make regarding how they use their time during lab. Because the instructors we observed have succeeded within the

educational system, they may fail to recognize the steps that less successful learners must go through to gain a working knowledge of new material.

We feel that instructors need to:

- (1) be aware that inquiry-based learning activities are often quite disconcerting for students, especially if those students view the main reason for their attendance at the lab or seminar as the collection of important facts that they will be asked to recall (Bookman & Friedman, 1994a),
- (2) encourage students to spend a lot of time engaged in the construction of their own understandings of the subject matter, and
- (3) recognize when students are engaged in processes that may lead to meaningful learning, and encourage them as they work

Because the categories of difficulties we discussed were based on the empirical data gathered in our observations, we do not claim to have produced an exhaustive list of difficulties faced by inexperienced instructors using SCI. For instance, we have deliberately not addressed issues that arise when the instructor chooses to adopt a more traditional role of lecturer or discussion leader, as these problems have been identified and extensively discussed elsewhere (Krantz, 1993; McKeachie, 1994; Morganroth-Gullette, 1982; Lambert et. al., 1996; Resnick, 1989; Christensen et. al., 1991). We note that even in student-centered laboratories, occasions exist when it is appropriate to deliver short lectures- for example to bring closure to a session by summarizing key concepts. In the situations that we observed, the difficulties were typical of the problems experienced by inexperienced lecturers (Krantz, 1993).

A natural next step in this program of study might be to construct a preliminary model of how the laboratory instructors think science should be taught. This model could be refined and tested through a program of structured or semi-structured interviews of laboratory instructors. Possible questions that seem natural to include are as follows: How do instructors characterize cooperative learning? What do they view as the learning goals of the laboratory? What types of pedagogical models have they experienced? Such a tool would allow us to develop and analyze the underlying causes behind particular instructor behaviors and would inform us of how we might better train laboratory instructors.

While the focus of this work has been on the difficulties encountered by instructors, it is important to point out that we have observed many successes within math and science laboratories. We observed instructors who recognize the need to use questioning as a teaching tool, students who take on the responsibility of teaching other members within their group, and instructors who are keenly aware of students' intellectual processes. While not the subject of this manuscript, these observations and similar ones have been used to develop a series of principles to guide instructors in a collaborative learning environment (Winter et al., 2000). Our experience suggests very strongly that all laboratory instructors have the potential to facilitate student learning in the college-level science or mathematics laboratory.

Based on both the research literature and our observations of well-implemented SCI we believe that the potential of this approach to enhance student learning in college science and mathematics laboratories is clear. However, existing references and training programs (Case, 1989; Caroll, 1980; Lambert & Tice, 1993; Nyquist et. al., 1989) appear to do little to prepare inexperienced instructors to function as facilitators of learning in a SCI setting. We hope that the results reported here will not only serve to inform the efforts of individual laboratory instruction, but also to help create training programs that will enable all instructors to build the skills and notions of teaching and learning needed to adeptly facilitate student learning in a laboratory setting.

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Appendix A: Summary of Potential Problems with Student-Centered Laboratory Instruction.

INTERACTIONS BETWEEN INSTRUCTOR AND STUDENTS

- 1. Interacting with small groups of students.
- (a) Instructors failed to encourage student-student interaction
- (b) Instructors ways of involving themselves in student work could discourage students from interacting with each other
 - (i) Instructor spends conspicuously more time with some groups, even when other groups are clearly struggling
 - (ii) Instructor emphasizes instructor-student interactions rather than encouraging student-student interactions
 - (iii) Group has a "spokesperson," and instructor just tends to interact with spokesperson
- 2. Interacting with individual students.
- (a) De-emphasizing conceptual learning in favor of "getting the work done"
- (b) Lacking the experience to use questions to guide students and to promote conceptual learning
 - (i) Tending to tell the students what to do, rather than attempting to guide them
 - (ii) Formulating questions to ask students and waiting for responses
- (c) Not developing a clear picture of what students understand

MONITORING AND THINKING ABOUT THE TEACHING AND LEARNING ENVIRONMENT

- (a) Not paying attention to students' intellectual activity
 - (i) Instructors do not recognize that they should monitor students' intellectual progress

- (ii) Instructors tend to use only the most able students in the class as an indicator of how students are doing
- (iii) Instructors miss students' requests for help
- (b) Making inappropriate use of time available in the lab

Appendix B: Introductory Biology Seminar Curriculum "The Rate of Evolution"

The items contained within this appendix made up the packet that was given to Introductory Biology seminar instructors several weeks prior to the day they were to teach this seminar in the fall of 1999. The packet included a mind map that details goals for the seminar and a possible format for teaching it, mentor (teaching assistant) notes that provides background on the methodology addressed in seminar as well as an answer key, and the actual in-class exercise that students received.

Seminar 6: PBI #3 The Rate of Evolution Mind Map Fall 1999

Learning Goals:

- Build on lab to understand that phylogenetic trees provide relative relationships between taxa
- Introduce three techniques that are used to place dates on lineages
- Apply hypothetical data to date a given phylogeny

Practical Goals:

Discuss methods of dating

Format:

- The mentor may begin this seminar by having a brief discussion about the questions that were at the end of the lab exercise and talk about the trees the students developed both using morphological and chromosome banding patterns.
- The discussion can then turn to the idea that once a phylogeny has been established, how do we go about placing dates on that phylogeny.
- After introducing the three techniques used for dating lineages the students then turn to applying these techniques to place dates on a hypothetical lineage using various forms of data. Probably because the concept of the molecular clock is less familiar than contental drift or fossils, students last year tended to struggle more with these data, unsure how they were useful in determining dates. It might be worth weighting this technique a bit more in the introduction.
- You may divide the section in to small groups to discuss the data. Each group goes through the fossils, biogeographic information, and molecular clock data to establish ranges of ages for the nodes on the phylogeny. Last year some mentors found this especially useful because groups tended to use the data slightly differently, especially from the molecular clock, leading easily into a discussion of the strengths and weaknesses of each method.
- One key point to make with this data-set is that specific dates for each node cannot be established. Instead, what we can do is narrow the time window for when each of these events must have occurred.
- The mentor then re-groups the section for a general discussion on what the students have found. This discussion offers the opportunity to talk about the underlying assumptions for each technique (e.g. there is a degree of uncertainty in dating fossils using radioisotopes that will then translate into uncertainty in calculating dates at different nodes).

Seminar 6: PBI #3 The Rate of Evolution Mentor Notes Fall 1999

NOTE: The students should determine the upper and lower bounds for the age of each node

Fossil Dating:

The most common method for dating fossils and rocks uses the rate of decay of radioisotopes. The basic idea is that radioactive isotopes (uranium, thorium, rubidium and others) are incorporated into rocks as they form in proportion to their presence in the environment. Each type of radioactive isotope then begins to decay at its own constant rate, becoming, by this process, a stable isotope. These decay rates can serve as "radiometric clocks" because the absolute ages of rocks can be calculated from the proportions of radioactive and stable isotopes present. For example, uranium-238 spontaneously decays into lead at a slow but precisely known rate. By knowing this constant rate and by comparing the amount of ²³⁸U still present in a rock with the amount of lead derived from its decay, the age of the rock can be estimated with less than a 5 percent error.

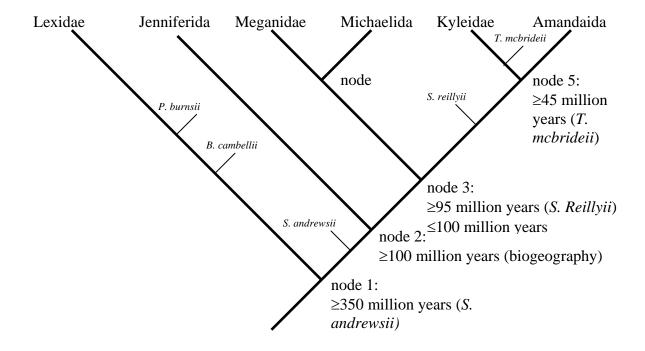
Vicariance Biogeography:

Disjunct distributions of organisms can occur when widespread ancestral forms are separated by some geological event, like the separation of continents. Vicariance biogeography uses the study of plate tectonics and other dynamic geological processes as a tool to explain the distribution of taxa. Under strict vicariance hypotheses, the cladistic relationships among related disjunct taxa should mirror faithfully the historical relationships among the geographic regions occupied.

In this exercise the taxa of Meganidae, Michaelidae, Kyleidae, and Amandaidae are all part of a single clade. This means that there must be derived characters that unite this group that originated between **node 2** and **node 3**. Because there are members of this clade on each land mass, the land masses must have split after this clade originated (after node 2). Because there are not members of Meganidae and Michaelidae on the rectangle land mass (or Kyleidae and Amandaidae on the oval land mass) the land masses must have split before these two terminal clades originated (before node 3). Although once the landmasses split the lineages evolve independently, we cannot necessarily place the splitting of the land masses at a node because there may have not been any divergence between the clades until sometime later.

Molecular Clocks:

The substitution of one nucleotide for another may take thousands or millions of years (with the exception of viral genes). The number of nucleotide substitutions between two sequences is important to molecular evolution because it is used to compute the rate of evolution, to estimate divergence time, and to reconstruct phylogenetic trees. The process of measuring nucleotide substitutions in DNA sequences is much more complex than what we present to the students. To compare sequences, one must first align the sequences, determine if multiple substitutions have occurred at any site, and determine whether changes have occurred in coding or non-coding sequences. Protein-coding and noncoding sequences are usually treated separately because they usually evolve at different rates.



Molecular clock data:

The narrowest window of time that we can use to calibrate the molecular clock data is for node 3. There are a number of ways to calibrate the molecular clock. 1. Use each set of data to calculate ages (0.1 and 0.09 for K and 100 million years and 95 million years). 2. Average K values and the range for the node. We have 2 estimates of K for this node (0.1 and 0.09) and these can be averaged to 0.095. We have a range of time for this node that is between 95 and 100 million years and these can be averaged to 97.5 million years. From this we calculate a rate of change that is 0.095 substitutions per site/97.5 million years. We can then use this to calculate the time since divergence for

Kyleidae and Amandaidae:

(0.05 substitutions per site) * (97.5 million years/0.095 substitutions per site) = 51 million years

Using molecular clock data we now date node 5 at 51 million years.

Amandaidae and Jenniferidae; Kyledae and Jenniferidae; Meganidae and Jenniferidae:

(0.296 substitutions per site) * (97.5 million years/0.095 substitutions per site) = 304 million years

Using molecular clock data we now date node 2 at 304 million years.

NOTE: These numbers are estimates that depend on how accurate the different measurements that contribute to the calculation are (e.g. the range for the dates of the fossils is $\pm 5\%$ which means that the "date" of the fossil is not exact).

NOTE: The calculations that the students make will be different if they decide to use the clock data for node 5 based on the fossil dates that limit this node to between 95-45 million years old!!

For example:

1. Using 0.05 substitutions per base/45 million years gives a date for node 3 of 81-90 million years.

Meganidae: Amandaidae=

(0.1 substitutions per base) * (45 million years/0.05substitutions per base)= 90 million years

Meganidae:Kyleidae=

(0.09 substitutions per base) * (45 million years/0.05 substitutions per base)= 81million years

2. Using 0.05 substitutions per base/95 million years gives a date for node 3 of 171-190 million years.

Meganidae: Amandaidae=

(0.1 substitutions per base) * (95 million years/0.05 substitutions per base)=190 million years

Meganidae:Kyleidae=

(0.09 substitutions per base) * (95 million years/0.05 substitutions per base)= 171 million years

Resources:

Avise, J. C. 1994. Molecular Markers, Natural History and Evolution. Chapman & Hall. NY, NY.

Futuyma, D. J. 1986. Evolutionary Biology 2^{nd} ed. Sinauer Associates, Inc. Sunderland, MA.

Li, W.-H. 1997. Molecular Evolution. Sinauer Associates, Inc. Sunderland, MA.

Seminar 6: PBI #3 The Rate of Evolution In-Class Exercise Fall 1999

In lab this week, you learned how to reconstruct the pattern of relationships among different organisms based on the unique mixture of primitive and derived characters each species possesses. By systematically comparing shared derived characters, you constructed monophyletic groups and determined which species are more closely related to one another and which are more distantly related. The diagrams you developed tell you the overall pattern of relatedness, but they do not contain any information about when the evolutionary events they represent occurred in absolute time. Ideally, we want to know not only which species share a common ancestor, but exactly how long ago that ancestor was alive.

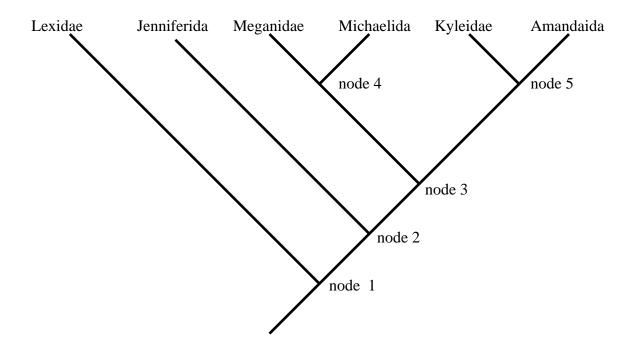
How do you determine when an ancestral species lived or when a particular lineage arose? This is not a trivial problem, and a number of different techniques have been developed to address these questions. In today's seminar we will consider three techniques and use them to date one hypothetical phylogeny.

Fossils often are used to date lineages. Fossils are rare, but many of those that do exist can be dated accurately using radioactive isotopes present in the environment that decay at known rates. Rates of decay can serve as a metric because the absolute ages of rocks can be calculated by measuring the proportions of radioactive and stable isotopes present in a particular sample. Once dated, fossils can be used as evidence for how long ago the group to which they belonged was alive. In this way, we can assign a minimum age to a lineage and therefore establish a minimum age on the position of certain branch points in a cladogram. For example, the hominid fossil, Lucy (*Australopithecus afarensis*) has been determined to be 3.5 million years old. This means that the hominid lineage that gave rise to Lucy must be at least 3.5 million years old.

A second technique uses the history of the earth and the biogeographical distribution of organisms to help determine dates on a phylogeny. For example, one group of freshwater fishes, the cichlids, live in lakes in South America, Africa, and India, but nowhere else in the world. How is it that this group spans these three locations, when South America, Africa, and India are separated by thousands of miles of ocean? It turns out that through a process called continental drift, continents move across the earth's surface over a time course of millions of years. South America, Africa, and India once were joined together in a supercontinent called Gondwanaland. South America, Africa, and India split apart from one another approximately 85 million years ago. Because the cichlid lineage exists today on South America, Africa, and India, we can infer that this group must have existed before the split of these land masses. This means that the cichlid lineage arose at least 65 million years ago.

A third technique that can be used to determine the timing of when lineages in a phylogeny branch takes advantage of the observation that point mutations (single DNA base-pair changes) are presumed to occur randomly. Over the long term, therefore, the number of mutations that occur is proportional to the time since divergence. If we determine the base sequence of the same stretch of DNA shared by many species, we can determine the total number of bases that have changed between two lineages, and use this number to estimate the time since they have diverged. Furthermore, if we can "calibrate" the rate at which mutations occur, we can use this information as a "molecular clock" to establish the real time since the lineages diverged. The correlation between molecular distance and paleontological times of divergence can then be used as a calibration to estimate the time of divergence between other lineages. For example, species that diverged 1 million years ago will have half as many differences in their DNA as species that diverged 2 million years ago.

Imagine you have generated the hypothetical phylogeny presented below of the phylum Melrosa. Consider the terminal taxa to represent the <u>family level</u> of a taxonomic hierarchy (e.g. Ursidae= all bears; Felidae= all cats).



Your job is to use the fossil, biogeographic, and DNA sequence data available to you to determine, as best you can, the absolute dates for each of the nodes in this cladogram.

For each node:

- 1. Determine when this divergence occurred.
- 2. What evidence or combination of different kinds of evidence led you to your answer?

Where in the phylogeny is additional information needed to improve your time resolution? What kind of information do you think would be the most useful?

Each of the methods for dating lineages has underlying assumptions.

After you have gotten as far as you can in dating these lineages based on available evidence, try to identify some of the assumptions associated with using each kind of evidence.

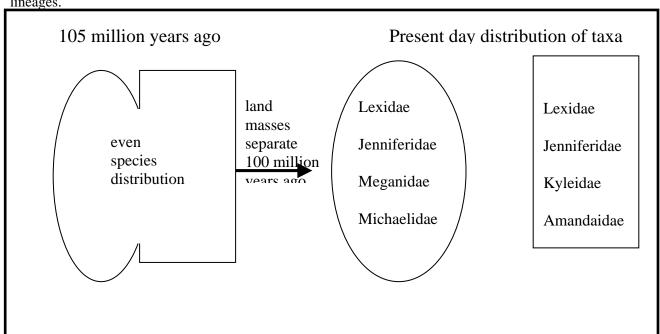
Fossil data:

You identify the following fossils with respect to the group to which each belongs.

Fossil	Age	Group to which this belongs
Billyosus cambellii	200 million years	Lexidae
Peterensus burnsii	180 million years	Lexidae
Sydneyosus andrewsii	350 million years	clade including Jenniferidae→Amandaidae
Samanthaus reillyii	95 million years	clade including Kyleidae→Amandaidae
Taylorotus mcbrideii	45 million years	Kyleidae

Biogeographic data:

The following diagram presents the relative positions of two land masses and the distribution of lineages on each at the present time. You have reason to assume there is no extinction of lineages.



Molecular clock data:

The number of nucleotide substitutions between two sequences is usually expressed in terms of the number (K) of substitutions *per nucleotide site* rather than as the *total number* (N) of substitutions between the two sequences. The K value is also commonly referred to as the evolutionary distance between two sequences. Higher K values represent more mutations. Below are K values calculated from 4 individuals from the following groups:

.05
.10
.09
.30
.28
.31