For decades, the traditional approach to the teaching of evolutionary biology in American high schools and colleges has emphasized evolutionary patterns (especially those evident from the vertebrate fossil record), with only secondary consideration given to the many evolutionary processes that have molded those patterns. As our understanding of these evolutionary processes has become increasingly more refined, there has been a gradual pedagogical shift in many classrooms toward a process-oriented approach to the teaching of evolution, placing less emphasis on the conventional "evidence-for-evolution" theme. It is now widely recognized that a full understanding of evolutionary biology requires not only knowledge of the evidence for evolution, but also comprehension of many basic evolutionary processes. Understanding of these processes, in turn, demands mastery of a daunting set of abstract concepts including panmixia, vicariance, natural selection, and genetic drift. Because an understanding of these concepts will rarely be gained by simple exposure to historical facts (such as the fossil record), today's teacher of evolution must become increasingly process-oriented in approach and is challenged, therefore, to develop effective strategies for teaching complex evolutionary processes and concepts.

In the U.S., widespread scientific illiteracy in the area of evolution suggests that our current methods for teaching evolution are falling far short of their intended goal. Research has shown that even those students who perform well (in terms of final grade) in a traditional evolution course often fail to grasp the most basic evolutionary concepts (Bishop and Anderson, 1990). After a semester in a traditional evolution course, most students can define natural selection, genetic drift, and other basic
evolutionary concepts, but few understand the causes and consequences of evolutionary processes, and even fewer understand the interrelationships among them. Clearly, our current approach to teaching evolution needs to be reexamined.

We find it curious that most evolution courses in the U.S. are taught in lecture-only format with no laboratories or discussion sessions. Widespread absence of laboratories is usually the result of pedagogical inertia combined with the common feeling that abstract concepts, such as many in evolution, are not readily amenable to laboratory instruction. Considering that: (1) laboratories have been an effective teaching tool in the sciences for decades, and (2) evolution is the most fundamental of all biological concepts, it would be ironic, indeed, if a course in evolution could not benefit from use of laboratories. In contrast to lectures, laboratories provide the student with tangible and intimate contact with the subject matter. Perhaps more important, laboratory sessions encourage students to think and talk about concepts, ideas, and issues, rather than act as passive observers (as in the traditional lecture format).

For the past several years, the authors have taught evolutionary biology to undergraduate students at their respective institutions, one a small, private college on the west coast (Occidental College), the other a large, state university in the southeast (Louisiana State University). At both institutions, the course in evolution was taught for decades in the orthodox, lecture-only format. In 1982, the first author (JCH) began experimenting with brief, hands-on simulations of various evolutionary concepts, such as natural selection and genetic drift. The response from the students was so tremendously positive and encouraging that additional laboratories were developed and a weekly, 3-hour laboratory was added to the course in its third year. These laboratories continue to be a very popular component of the evolution course at Occidental College. When the second author (MSH) learned of the positive reception the laboratories received at Occidental College, he soon developed a course at Louisiana State University called Evolution Laboratory to serve as an adjunct to his lecture course in evolution. This laboratory also has been well received and is now the subject of on-going research in the field of science education.
The evolution laboratories we have developed are described in detail in a 70-page manual that accompanies the course. Although the laboratories are deceptively simple in design, it must be remembered that they focus on complex, abstract concepts that beginning students of evolution usually fail to grasp. Thus, the apparent simplicity of the laboratories is intentional, as is the avoidance of sophisticated experiments and computer simulations that tend to mystify, rather than clarify. The laboratory format varies widely from week to week depending on the nature of the material being covered; several of the laboratories involve simulations or hands-on exercises, whereas others are demonstrations or discussions. Above all, the laboratories are designed to reinforce the students' understanding of the evolutionary terms and concepts introduced in lecture and assigned readings. To this end, the students are challenged each week to find meaningful connections among the various evolutionary terms and concepts introduced that week, and they are taught to use concept maps (Ausubel et al., 1978) to assist them in their search for linkages among evolutionary concepts.

In addition to the inclusion of hands-on laboratory exercises, we also challenge more conventional pedagogy in evolution by the addition of discussion sessions to our courses. Discussion sessions are designed to promote critical thinking about controversial, often emotionally charged issues relevant to evolutionary biology (e.g., genetic engineering, adaptation, creation science, etc.). We have found that discussion sessions are easily fit into the weekly lab period (as done by MSH) or they can be scheduled as separate, weekly one-hour class meetings (as done by JCH). In either setting, the discussion sessions provide a fun, alternative instructional tool that facilitates comprehension of sophisticated issues. To ensure that students are prepared for these discussions, each student is required to compose (in advance of the meeting) a brief argumentative essay on the topic. These essays and discussions are critical components of the course because they tend to expose misconceptions that obstruct the students' understanding of basic evolutionary concepts.

Below we offer a brief synopsis of each of the evolution laboratories we currently use in our courses. The labs are listed roughly in the sequence presented during the semester. We encourage others to use labs
and discussion sessions in their evolution courses, and we welcome specific comments and inquiries about our course design.

**SYNOPSIS OF EVOLUTION LABORATORIES**

Laboratory: *Introduction to Concept Mapping.*-- This laboratory begins with a general introduction to the course followed by a short video on the evidence for evolution. The remainder of the lab concentrates on use of concept maps as learning tools. Students practice constructing concept maps based on everyday objects and experiences.

Laboratory: *What is Biodiversity?*-- This lab exposes students to the concept of biodiversity and its role in biological conservation. Students conduct biological inventories of four simulated communities (all of which are in immediate danger of destruction), and they calculate several estimates of biodiversity for each. They then compare the communities to see which is "most diverse" and, presumably, most deserving of protection. They soon realize that the concept of biodiversity is not easily defined and, in fact, has multiple meanings.

Laboratory: *Discussion Session: The Meaning of "Adaptation."*-- Despite its widespread use in biological lexicon, the word "adaptation" is among the most misused and misunderstood of all terms. Prior to lab, students read two articles (assigned in lecture), one attacking the "adaptationist program," the other defending it. Each student brings to lab a short argumentative essay (maximum 3 pages, double spaced) that takes a firm stance in this controversy. In lab, the instructor presents a series of questions to be discussed by advocates of the two positions. Among the questions to be addressed is: "Is adaptation a process or a product?" The grade received on the written essay is influenced by the student's willingness and ability to verbalize his/her position in lab.

Laboratory: *The Concept of Geological Time.*-- An appreciation of the geological time scale is important in evolutionary biology, but because of the vast amounts of time involved, it is extremely difficult for the student to comprehend. A time-line mural can provide an effective means for visualizing and understanding this temporal scale. The time-line mural is a class project, with each student constructing a segment of the temporal
scale. Temporal segments are assigned during the first week of class, and the mural is assembled during this lab. The student is responsible for researching his/her portion of the time scale and for depicting major biological and geological events that occurred during that time. Each student also provides a short, oral synopsis of his/her section of the mural.

Laboratory: *Exercises in Taxonomy and Classification.* Following a brief video on taxonomy, students work through a series of nine exercises designed to illustrate basic problems that face systematists who study organismal relationships using morphological data. The exercises focus on several sets of museum specimens (birds, mammals, reptiles, and plants) that each student must classify into basic taxonomic categories (species, genera, families, and orders). Students are forced to consider the confounding factors of individual variation, age variation, geographic variation, sexual dimorphism (in size, shape, and color), and adaptive convergence.

Laboratory: *The Science of Biometry (Biostatistics).* Students are introduced to the basics of mensuration and the methods of summarizing descriptive statistics for natural populations. Students work in teams to record morphometric data from fruits of *Persea americana* (the avocado). They then calculate populational statistics with the aid of a computer. Descriptive statistics will include mean, range, standard error, standard deviation, and variance. The allometric relationship between seed mass and fruit mass is explored using bivariate plots of log-log transformations. Students consider the potential functional relationship between seed and fruit size in avocados.

Laboratory: *Protein Electrophoresis and Population Genetics.* This is an in-depth examination of the methods and application of protein electrophoresis to studies in population genetics. Students are taught the basic rationale for the technique, followed by a brief demonstration of electrophoretic procedures. Students are then presented with mock gels that show allelic variation at four genetic loci in two hypothetical populations. Students use the gels to calculate allelism, heterozygosity, and polymorphism. They then conduct computer-assisted analyses to detect departure from Hardy-Weinberg equilibrium, and to calculate F-statistics and estimates of genetic distance.
Laboratory: **Exercises in Genetic Drift.**-- This lab emphasizes the importance of finite population size and genetic drift in natural populations. Students simulate genetic drift beginning with 11 bottles of black (B) and white (W) beans (representing alternate alleles at a single genetic locus, with B dominant over W); each bottle has a known beginning allele frequency. Students sample "genotypes" (pairs of beans) blindly from the bottles to simulate founder events. They then calculate allele frequencies in the new population and repeat this exercise until fixation of one of the two alleles occurs. They compare their results (number of generations to fixation) with theoretical expectations for time to genetic fixation. Students also calculate genetic heterozygosity and Wright's F-statistics for populations of different size to see the effects of genetic drift in natural populations.

Laboratory: **Natural Selection Simulation.**-- Students act as predators in an artificial environment to simulate the effects of natural selection on the phenetic and genetic constitution of a prey population. The basic idea of the simulation is taken from Stebbins and Allen (1975), but includes advanced concepts such as evolution in changing environments, the effects of asexual versus sexual reproduction, calculation of allele frequencies following bouts of reproduction, and average fitness of populations. Students use their understanding of population genetics to predict gene frequencies and fitness values for future generations, then they test their predictions by experimentation.

Laboratory: **Discussion Session: The Units of Selection.**-- Recently, biologists have begun to question the neo-Darwinian focus on the individual as the sole unit of natural selection. This controversy is explored in this discussion session. Prior to lab, students read two articles (assigned in lecture), one arguing that "genes" are the principal units of selection, the other arguing that the "group" is the primary unit of selection. Each student brings to lab a short argumentative essay that takes a firm stand in this controversy. The discussion will focus on the questions: "What is the evidence for genic and group selection?" and, "Is there a clear distinction between units of selection and units of evolution?"

Laboratory: **Principles of Biogeography.**-- Students are introduced to the field of biogeography by investigating several factors that determine...
the geographic distribution of organisms. The laboratory is divided into
two exercises, one of which focuses on the role of dispersal, the other on
the role of vicariance in biogeography. Working in lab teams, students
monitor the deployment of three hypothetical species throughout a
simulated environment that contains considerable topographic (hence
climatic and ecologic) variation. As the species spread throughout the
environment, students will witness the complex interactions between the
processes of dispersal, vicariance, extirpation, extinction, and speciation.

Laboratory: Discussion Session: The Neutralist-Selectionist
Controversy.-- In this lab, students explore the question, "How much
variation in nature is the result of natural selection?" Prior to lab, students
read two articles (assigned in lecture) stating the viewpoint of the
"selectionist" school versus the "neutralist" school. As before, each student
brings to lab a short argumentative essay supporting one of the two
positions. The discussion focuses on the questions: "What is the evidence
for selective neutrality?" and, "What is a molecular clock?"

Laboratory: The Study of Chromosomes (Cytogenetics).-- Students
prepare and analyze the karyotypes of several local animals and plants.
They examine the chromosomal preparations under the microscope and
determine the organism's diploid number and fundamental number.
Students learn how comparative cytogenetics is used to detect chromosomal
abnormalities and to infer relationships among organisms.

Laboratory: Principles of Phylogeny Reconstruction.-- This lab
focuses on the use of phenetic and cladistic methods to ascertain
relationships among organisms. Students work in teams to develop
dendrograms (trees of relationships) for a set of six simulated organisms
(complex wooden objects). Under the phenetic approach, students use the
morphometric procedures they learned in the Biometry lab to develop a
morphological distance matrix for the six objects. The matrix is then
converted into a dendrogram using the UPGMA procedure (explained in
lecture). Under the cladistic approach, students are challenged to find
shared-derived character states (synapomorphies) to define various clades.
Near the end of lab, we compare and contrast the dendrograms generated
by each group.
Laboratory: Discussion Session: Genetic Engineering and Eugenics.
- Prior to lab, students complete assigned readings on the pros and cons of genetic engineering and eugenics. As before, each student brings to lab a short argumentative essay arguing for or against the use of genetic engineering in modern medicine. The lab begins with a short video on genetic engineering, followed by a brief overview of relevant techniques. Once it is clear that the students understand the concept of genetic engineering, the class discusses the many scientific and moral issues involved in the controversy surrounding use of this modern molecular technique.

Laboratory: Discussion Session: Evolution and Creation Science.--
Prior to lab, students read several short articles supporting or refuting creation science. Each student brings to lab a short argumentative essay supporting one of the two sides in this emotionally charged and highly controversial issue (so that students will feel more secure, they are encouraged to defend a position that is not necessarily their own personal view). The discussion focuses on questions such as: What is science? What is a scientific theory? What is "fact"? What is the scientific method? etc.

Laboratory: Discussion Session: Macroevolution versus Microevolution.-- Is macroevolution a simple extrapolation of microevolutionary events, or are the two concepts phenomenologically distinct? Each student brings to lab a short argumentative essay supporting one of the two sides in this issue. The discussion focuses on the question: What is macroevolution, and how can the neo-Darwinian paradigm explain it?

Laboratory: Discussion Session: The Evolution of Homo sapiens.--
This lab begins with a brief video on human evolution. Students are then given a series of skulls (without identification tags) including fossil hominids, modern apes, and modern man. The students attempt to arrange the skulls in correct phylogenetic sequence using cranial characters known to be useful in primate systematics. The currently accepted primate phylogeny is then revealed and the class discusses the "missing link" controversy, paedomorphosis in human evolution, the biological concept of "race," and other related topics.
Laboratory: Field Trip to View Fossils. During his voyage around the world, Darwin's examination of fossils of extinct South American mammals had profound influence on his nascent theory of evolution by means of natural selection. In the same vein, we feel strongly that today's student of evolution should have a similar opportunity for direct exposure to the strongest evidence for evolution. Examination of fossilized remains of extinct organisms gives students a first-hand appreciation of how fossils provide scientists with a window into the history of life. Most U.S. high schools, colleges, and universities are reasonably close to a park, museum, or research site that can provide students with a view of fossilized remains of life on earth.

LITERATURE CITED

