Science as a Way of Knowing—Evolutionary Biology[1]

JOHN A. MOORE

Department of Biology, University of California,
Riverside, California 92521

SYNOPSIS. This essay is part of an educational project of the American Society of Zoologists that will make proposals for improving the first-year biology course in the universities. The detailed suggestions emphasize the importance of the conceptual framework of the biological sciences. The topic for this year is Evolutionary Biology and it is developed largely by the hypothetico-deductive method emphasizing that science, in addition to its store of information, is a way of knowing. Other topics will be considered in future years in the ongoing project.

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WHY A NEW EDUCATIONAL PROJECT?

The problem

The state of education in the United States is widely regarded as a national crisis that severely compromises the present and future. However, members of the American Society of Zoologists, together with other biologists, are in a position to deal with some of the problems of education in a significant manner.

This optimism is based on the fact that the ASZ members, together with other biologists, occupy responsible posts in the major institutions of higher education and, therefore can exert great influence. University faculties set the curriculum for what is taught in the universities and play a major role in educating those who will teach in the schools. This, in turn, determines what is taught as biology in the pre-college years. This central role of the universities places a special obligation upon them. Whereas a generation ago it was thought that educational reform should start at the high school level, it is now widely recognized that it should begin at the university level. So long as our universities train the teachers, any reform in the pre-college courses must be preceded by the reform of the teaching in our universities. (This argument is greatly expanded in Moore, 1981.)

Inadequate biological education is especially serious, since biology is the science most frequently elected at all levels. For many students a biology course will not only introduce them to the world of life but will also be their total experience with the world of science.

One measure of our failure in teaching may be seen in the present conflict between biologists and creationists. Ignorance and misunderstanding of the evolutionary process, and what is science and what is not, would not be so pervasive if we had discharged our professional responsibilities more effectively in recent decades.

The members of the ASZ Education Committee wish to identify the reasons why education in science fails to meet societal requirements and to begin remedial actions. In this endeavor, we seek cooperation of the full membership of the American Society of Zoologists and of our sister societies. Seven of them have already indicated their interest in and support for this project by cosponsoring this first effort. This is a task for all biologists. A few ASZ committee members can do little, but with the involvement of biologists as a whole, we can do a very great deal.

The possible cause

Our preliminary analysis suggests that a major portion of the crisis in science education results from our overemphasizing facts, especially those relating to the exciting discoveries in modern biology, without providing a conceptual framework for the science. We convey more information than understanding. You can test this assumption for yourself by asking your students what is the evidential basis for some of the important concepts in biology. Can your students tell you *why* we think that genes are parts of chromosomes; why we think that the substance of heredity is (nearly always) DNA. Why, in spite of the tremendous variation in structure and function, we recognize a class of objects as "cells"? Why do we assume, beyond a reasonable doubt, that organisms evolve? See if you can find *any* important concept that your students can support with adequate data and argument.

A decade ago Paul Doty and Dorothy Zinberg (1972) had some forceful observations to make on our problems. This is what they had to say:

> The greatest overall threat to a science education that aims to remain viable and useful for a long time is that it will succumb to the temptation of being current. With a great burst of scientific discovery having taken place in the quarter century just behind us, with half of the scientific literature having been written in the last dozen years, with half of the Ph.D.'s granted in the United States awarded in the last nine years, the urge to be current, to be modern, is unavoidable. In proper measure, it is essential for orientation and motivation of the student and for the establishment of the bench marks by which future develop-

ment is measured. In excess, the student drowns in a world of facts and concepts for which he is unable to recognize the precedents and from which he is unable to project the future.

So, how do we solve the dilemma of orienting and motivating the student without drowning him? It may be simpler to reach an accomodation that will be acceptable to the student than to the professor of biology. After all, it is the teacher, not the student, who is aware of all those facts and exciting discoveries. For a student who is still at the stage of being unsure whether or not blood is the physical basis of inheritance, the details of the chemical structure of the genetic materials may not be as exciting, or as meaningful, as the professor might suppose.

Many of our best teachers agree that the essence of education should be to provide students with the conceptual framework of a field. Facts come and go—not necessarily because they are wrong, but because they become uninteresting or irrelevant. A conceptual framework, however, gives meaning to existing data and allows one to integrate new data and thoughts into a meaningful whole. The conceptual framework of a field is constantly adjusted and remodelled but it is never discarded. Once learned, it is not easily forgotten.

It might have been predicted, for example, that the conceptual framework of the field of biological classification would have undergone a revolution once Darwinism became accepted. Darwinism provided an explanatory hypothesis for the resemblances and the differences among organisms—and that is what classification is all about. The new view saw variation among organisms as a reflection of evolutionary processes yet the conceptual framework of systematics remained. Darwinism enriched the conceptual framework but it neither destroyed nor even greatly modified the then existing scheme of classification.

Plans for the Science as a Way of Knowing *project*

Innovation in education is much like innovation in evolution in one important

respect: we can neither predict the success of a new program nor of a new species. Recognizing this, the ASZ Education Committee proposes to begin some experiments—offer suggestions for making the first-year college and university courses in biology more effective. Each year, for as long as this project is useful, we will organize symposia for the Annual Meetings and produce written materials that will offer suggestions for how the major areas of biology might be included in a first-year university course. The sequence might be something like this:

1983. Science as a Way of Knowing—Evolutionary Biology
1984. Science as a Way of Knowing—Genetics
1985. Science as a Way of Knowing—Developmental Biology
1986. Science as a Way of Knowing—Biology and Human Affairs
1987. Science as a Way of Knowing—Cell Biology
1988. Science as a Way of Knowing—Physiology
1989. Science as a Way of Knowing—Animal Kingdom
1990. Science as a Way of Knowing—Ecology

All of this is tentative. The information that we obtain from this first year's experiment will be the basis of future plans. Once the cycle of topics has been completed, it will start over. By that time not only will the fields have changed but so will many of those responsible for the first-year courses. The cycle is long and it might be useful to think of scheduling two topics for a single year. Coverage of rapidly developing fields could be made more frequently than more slowly developing fields. Somewhere in this schedule there must be consideration of the overall organization of the course—how much emphasis can be allowed for each topic. If our project proves useful, hopefully we can elicit the cooperation of botanists. We are after all talking about biology, not just zoology.

The plans for each year will be much the same until experience shows us how to do

things better. There will be two symposia. A General Symposium will involve two or three speakers, each offering a personal suggestion for how the topic for the year might be developed. A Special Symposium will identify those aspects of current research that are so noteworthy that they should be included in a first-year course—and hence will eliminate something else. The dual approach of these two types of symposia may help us to balance what is timeless with what is timely.

The organizer of each year's symposia will prepare a written essay presenting his point of view. This will be distributed at the sessions. The document you are now reading is the essay for the first year.

It goes without saying, but we intend to emphasize it none the less, that we do not accept that there is a single approach to excellence in education. We will offer no single model and each symposium speaker will present what seems to him to be worthy of consideration. All we are asking is that you think about what is proposed and take for your own what you feel is useful and important. Surely there is much fine teaching in first-year university biology courses, yet collectively what we do cannot be accepted as satisfactory since the results do not always meet the requirements of the students or of society. We must seek new and better ways of educating our students in the science of biology.

First, I will ask you to consider some of the rules that one should observe in teaching any part of biology: pedagogical themes, if you will. Following this, the bulk of the essay will be devoted to suggestions for teaching evolutionary biology, the topic for 1983.

The suggested approach: science as a way of knowing

The title of our project summarizes in six words our philosophy of teaching science. This philosophy will be presented briefly now in a series of suggestions and then put into practice in the specific proposals for teaching evolution.

No matter what major area of biology is being considered, we suggest that the following principles should be followed.

First, it should be made abundantly clear to the student *what the problem or question is.* Science is a way of seeking answers to questions about natural phenomena and it will be far easier for the student to understand the answers if he is aware that there is a question. This suggestion may seem too obvious to be mentioned but recall some of the lectures you may have heard recently. Did you always know why the research had been done? Was it clear what problem was being illuminated by the data presented?

Second, *try using the hypothetico-deductive approach in presenting topics* to your students. This approach is not very different from the "common sense" procedures we use in solving everyday problems—a point worth emphasizing to your students. The hypothetico-deductive procedures are among the most important methods that enable us to know things in science. They can be powerful adjuncts to teaching as well.

Scientific knowledge begins with a question—not surprising since there cannot be answers unless there are questions. Some phenomenon of nature is observed, we become curious about it and wish more information. It is nearly impossible to obtain an answer to any important question in science unless we first make a guess about what the answer might be. This guess is our *hypothesis.* The guessing is not a random affair. The guess will be based on various observations, hunches, and clues. This process, in which we combine the specific bits of information and logic to produce a more general statement (a hypothesis) is known as *induction.*

There is an absolute requirement for the hypothesis: *it must be testable.* Thomas Hunt Morgan explains it this way:

> It is the prerogative of science, in contrast with the speculative procedures of philosophy and metaphyscs, to cherish those [hypotheses] that can be given an experimental verification and to disregard the rest, not because they are wrong, but because they are useless.

It is well to emphasize to students that, surprising as it may seem, the most difficult part of scientific procedures is to know what

questions to ask and then be able to formulate useful hypotheses and deductions. F. S. C. Northrop (1947) has this to say:

There are many reasons for believing that perhaps more than anywhere else it is at the beginning of any investigation that the source of genius is to be found. For what characterizes a genius like Galileo, Lavoisier or Einstein is the economy of thought and effort by means of which he achieves his result. Each one of these men found the key factor in the situation and went directly to the heart of the problem which had been baffling to his predecessors. The methods which all three used at later stages in their investigations are well known. It was in finding the key difficulty and in knowing precisely at what points to direct the well-known methods that the genius consists.

The point that Northrop is making is that genius consists of knowing not only what questions to ask but how to seek an answer.

So we have our question and we have formulated one or more hypotheses that represent possible answers. We continue by saying, if the hypothesis is true, the following consequences must follow. These consequences are *deductions*. If the hypothesis is true, as we are assuming, the deductions must also be true. Then we set about *testing the deductions* by making observations or performing experiments. If the data from the observations or experiments show that the deductions are incorrect, then we must either abandon the hypothesis or modify it to conform to what we observed from the tests. If the deduction proves to be true, then we can say that the hypothesis *may* be true—at least it has not been falsified so far. The more deductions that are tested and found to be true, the more likely it is that the hypothesis is true. Should we be able to formulate and test critical and elegant deductions and they continue to be verified, we reach the stage when we can say that *the hypothesis is true beyond reasonable doubt.* The hypothesis then becomes a statement that is part of the conceptual framework of the field.

In summary, then, the idealized view of

scientific methods and the method being proposed to teach science are:

1. Ask a question.
2. Develop an hypothesis by induction.
3. Make deductions from the hypothesis.
4. Test the deductions.
5. Use conclusions from the tests to validate or falsify the hypothesis.

Third, *whatever data are obtained must share this essential characteristic: they must be obtainable by other scientists.* That is, the data must be verifiable. If an important discovery is made, it is never fully accepted by the scientific community until it has been verified by other scientists. If the original discoverer has made an error, the error would likely be corrected when others attempt to verify the original report. *Science tends to be a self-correcting way of knowing.*

These three suggestions: making the question or problem explicit, using the hypothetico-deductive mode in teaching, and emphasizing that science is a self-correcting enterprise, should provide students with understanding as well as information. Here are some additional suggestions that you may wish to consider. They have to do with the specific strategies of teaching.

Teaching strategies

A. Do not introduce data unless they are to be used to answer some question or illuminate some concept. The amount of data that can be presented to students is, for all practical purposes, unlimited. Therefore, selections have to be made. All information has some value but that value increases greatly if the information becomes part of some conceptual construct. Beware of facts for facts' sake. Charles Darwin would have approved of this suggestion. In a letter to his friend, Henry Fawcett, he wrote, "How odd it is that anyone should not see that all observation must be for or against some view if it is to be of any service" (F. Darwin, 1903, vol. 1, p. 195).

B. Do not make the mistake of assuming that, just because something has been known for a long time, it is not worthy of presenting to your students. Many of the basic concepts of biology, especially of evo-

lutionary biology, are quite old. They are still basic and they will not be old to the student who does not know them. More often that not, the questions asked and tentatively answered by biologists long ago are the sorts of questions that will puzzle a student first approaching a field of knowledge. In addition, there are frequently resemblances between a logical analysis of a problem that we might make today and the actual historical steps of discovery.

C. From time to time emphasize that science is a human endeavor—done by human beings to answer questions of human interest or human importance. This may come as an astonishing revelation to your students. Science is closely related to human concerns—intellectual, medical, technological, social, or economic. Science is done by human beings who have the normal range of strengths and limitations of human beings in general. When scientists get up in the morning, the males at least, put their pants on one leg at a time.

D. Although my main emphasis so far has been on the conceptual basis of science, we must always remember that science bases its statements on data. It is as pointless to teach concepts without giving the evidential basis for them as it is to teach facts without giving the conceptual framework that they subtend.

So much for suggestions about teaching science in general. Now follow some suggestions for teaching evolution in the first-year university course.

TEACHING EVOLUTIONARY BIOLOGY

The first suggestion is to treat it seriously and allow sufficient time for its presentation. There is a real gap between what biologists say they want to do and what they do when it comes to teaching evolution. On 28 November 1958, the famous geneticist H. J. Muller addressed the Central Association of Science and Mathematics Teachers, meeting in Indianapolis. His title was "One Hundred Years Without Darwinism are Enough." Muller was concerned that evolution was taught either ineffectually or not at all in the schools. But let him tell it (Muller, 1959):

It ill befits our great people, four generations after Darwin and Wallace published their epochal discovery of evolution by natural selection, to turn our backs on it, to pretend that it is unimportant or uncertain, to adopt euphemistic expressions to hide and soften its impact, to teach it only as one alternative theory, to leave it for advanced courses where the multitudes cannot encounter it, or, if it is dealt with at all in a school or high school biology course, to present it as unobtrusively and near the end of the course as possible, so that the student will fail to appreciate how every other feature and principle found in living things is in reality an outgrowth of its universal operation.

Are we teachers in whose hands lies the responsibility of bringing to the next generation a true and modern view of the nature of things, as gained by the devoted efforts of the world community of critical scientific minds, not deeply ashamed that we have been so remiss in our task of awakening in that developing generation an adequate realization of the most basic forces of life and of how these forces have worked and are still working to give rise to all life's outer manifestations? Why dabble around with the superficialities of our subject and bemuse our young charges with technical terms and baffling complexities if we do not make fully clear to them the deepest known meanings and unifying underlying principles and if we do not show from step to step, in a true perspective, the ways in which these principles have engendered all the other manifold features of living things?

Muller was talking mainly about the biology of the pre-university years where the fundamentalist religions were a powerful force in preventing the teaching of evolution in the schools. But, as Muller wrote,

we have no more right to starve the masses of our people intellectually and emotionally because of the objections of the uninformed than we have a right to allow people to keep their children from

being vaccinated, and thus endanger the whole community physically.

Muller saw the intellectual starvation of our masses as terribly dangerous.

In an equally well known essay, "Nothing in Biology Makes Sense Except in the Light of Evolution," Theodosius Dobzhansky (1973a) summarized his position after surveying the major fields of the biological sciences:

> Seen in the light of evolution, biology is, perhaps, intellectually the most satisfying and inspiring science. Without that light it becomes a pile of sundry facts—some of them interesting or curious but making no meaningful picture as a whole.

These essays of Muller and Dobzhansky made considerable impressions but seemingly little impact on what is actually done in the classrooooms. I do not know of a single biologist who does not regard evolution as the basic concept of the biological sciences. This is true to such a degree that it has become an almost unacknowledged point of view. It *is* the way we think. But our students do not come to us thinking that way.

And therein lies the problem. All too often the professional biologist takes evolution for granted and assumes that his students need not be instructed. This becomes obvious when the sequence of topics for the introductory courses is planned. Quite frequently, evolution is relegated to the very end. The reason usually given is that evolution will have much more meaning if all other topics in biology are treated first: evolution is said to make sense only when there is a firm basis of biological knowledge. But if we really believe, along with Muller and Dobzhansky, that evolution illuminates all the rest, we cannot relegate it to the end of the course.

A possible compromise could be to consider evolution, at different levels of detail, in several places in a course. One might start, for example, with a brief introduction to evolutionary biology near the beginning of the course. A single lecture, or possibly two, could introduce students

to the fundamental notion that the organisms of today are the descendants of very different sorts of organisms that lived in the past. The mechanisms of evolutionary change—natural selection and other ways—would have to be postponed until genetics has been treated.

If this suggestion is followed, it would then be possible to use the concept of evolutionary change to illuminate many of the biological phenomena considered in the course. These phenomena would "make sense" when it was realized that they had a history and what they are today is a consequence of that long history.

One of the more poignant aspects of our brouhaha with the creationists is our insistence that evolution is the unifying theme of the biological sciences while at the same time we use it so uncertainly in our general courses in university biology. Is it really our unifying theme?

Defining some terms

When discussing evolution it is especially important that we indicate to our students how we intend to use terms such as "theory," "hypothesis," "proven," "fact," and "concept." My usage follows.

Theory for a scientist may represent the grandest synthesis of a large and important body of information about some related group of natural phenomena. For non-scientists the term may be pejorative: "evolution is just a theory," meaning that it is a dubious notion. Both of these very different meanings, together with others, are fully countenanced by lexicographers, so it is essential that students know how the term is being used.

I will use "theory" as a term applying to a body of knowledge and explanatory concepts that seek to increase our understanding of ("explain") a major phenomenon of nature. Thus, the Cell Theory would be taken to consist of the many sorts of observations—morphological and physiological—relating to the basic units of structure and function of most living creatures.

Used this way, a theory cannot be disproven. There is no way that the Cell Theory can be falsified. Some of the things we think we know about cells may be shown

to be false but the consequence of this will be that some of the data or concepts included in the Cell Theory will be eliminated or replaced by other data and concepts that are more probable. Theories are never disproved, only improved.

Theories are so important and so nearly coextensive with the fields of knowledge for which they provide the conceptual framework that, quite frequently, the term "theory" is abandoned. Thus, the books appearing today are not entitled "The Cell Theory." More likely the title will be something such as "Cells" or "The Biology of Cells."

One can acknowledge the usefulness of a theory even though the ultimate causes of the phenomena to which it applies are unknown. Thus, one can accept the Theory of Gravitation as a useful synthesis of available knowledge relating to the mutual attraction of bodies—and yet have no adequate understanding of what "pulls" them together.

Hypothesis for me is a tentative explanation of some phenomenon. It is an "educated guess." Many use "theory" and "hypothesis" as synonyms. I will not. In the formative years of a science, hypotheses may grow into theories. Some of the early speculators about the underlying causes of organic diversity and of adaptation adopted an hypothesis of evolutionary change to account for these phenomena. As data and certainty increased, one could begin to recognize a large body of information and verified hypotheses as the "Theory of Evolution."

I will use *concept* to mean the intellectual framework of a theory or a generalized way of looking at a phenomenon. I usually prefer to speak of the "concept of evolution" rather than "theory of evolution" just so the listener will not think I am talking about some dubious hypothesis.

A scientific statement is "true" if all attempts to falsify it have failed. So used, the term means "true beyond all reasonable doubt." In general, I think we overdo this tentativeness of scientific statements. Good form, I know, but it can be carried to foolish extremes. Cannot we accept as "true" that water is composed of hydrogen and oxygen? Then again, some statements are true because they are definitions. An experienced ornithologist, after having a good look at a medium size bird with a grayish back and a reddish breast, does not have to be so precious as to say that the bird is "a robin beyond all reasonable doubt." We have agreed that a bird with certain well-defined features is to be known as a "robin." If the experienced ornithologist has seen a bird with those features it is, by definition, a robin.

We can also accept that historical events that have left adequate records need not be verified by experiment or by observation of a rerun of the event. One can accept the reality ("truth") that dinosaurs once existed without making them evolve through the many steps from primitive amphibians through primitive reptiles to their magnificent selves. There are many things in biology that cannot be repeated experimentally or verified by direct observation. This does not mean that we exclude them from the domain of science—a fact that the philosopher Popper (1976) seemed not to have understood (see Williams, 1973).

For a biological phenomenon to be *proven* means to me that it has been tested extensively and elegantly and has not been falsified. Once again this means, especially for important phenomena, "proven beyond all reasonable doubt."

What are the questions?

The hypothesis of evolutionary change smoldered in the human intellect from the days of the early Greeks. It came into full flame during the 19th century when interest in natural history was intensified. Travelers, scientists, and professional collectors brought back to Western Europe a bewildering variety of new kinds of animals and plants from all parts of the world and even from the depths of the ocean.

As familiarity with living organisms increased, so did questions about them. The sorts of questions that eventually led to the concept of evolutionary change were varied but the main ones seem to have been these three.

1. How could one account for the

extraordinary amount of organic diversity? What was the explanation for all those species, hundreds of thousands and possibly millions of them, and with their amazing differences in structure, behavior, and way of life?

2. How could one explain the remarkable adaptations of living creatures? The more one learned about the structure and behavior of organisms, the more remarkable was their exquisite adjustment to the life they led. The intricate structure of a bird's feather, as revealed by the microscope, showed it to be a contrivance perfected for lightness and strength. Bones are generally thick and heavy but some of the bird's bones are hollow and the walls thin. The lungs of birds extend into air sacs, which both lightens the body and improves respiration. The entire bird seems to be a perfect solution to the problem of flight. No human engineer could duplicate the bird's remarkable achievement. All of man's attempts to fly had ended in death or ridicule.

3. What was the basis of the *scala naturae*, or scale of nature, that saw all species of animals or plants as part of a continuum that, with small gaps, appeared to extend from the simplest to the most complex species? One could start with some fish, such as sharks, and find a sequence of types extending through the dolphins to the great whales. One could pass in small steps from typical lizards, through lizards with ever-shorter legs, to snakes with no legs at all. There seemed to be patterns in organic variety.

How does one seek answers?

It is not obvious. Even with our knowledge today of what the answers proved to be, can we imagine any direct research program that might be expected to provide answers to the three questions just listed? What can your students suggest? What would we want to observe or subject to experiment? Some of your students may see the difficulty: not one of our three questions has been formulated in a manner precise enough to enable us to use the procedures of science to seek an answer. One cannot begin to make observations or con-

duct experiments with a question. One must start with a provisional answer—a testable hypothesis—if there is to be any hope of gaining some understanding of the phenomenon. In science, we might almost say that we seek answers to "answers." We cannot just ask why there is incredible variety in the world of life. We have to make a guess—hypothesis—for what the reason might be and then set about seeing if it is so.

The traditional answer: Divine Creation

We will start by briefly considering how people attempted to answer our three questions about two centuries ago. One available answer, the age-old notion of evolution, had been revived by several writers—Lamarck (1809) and Chambers (1844). Neither made a convincing argument. The main reason for this was that science and society already had an explanation for adaptation, the diversity of organisms, and related matters. This explanation, itself thousands of years old, was well established in Western thought. It was Divine Creation, as described in Genesis. God had created everything, animals, plants, the earth, and the cosmos at some remote time in the past—some said as long ago as 4004 B.C. The many sorts of animals and plants of today were each a consequence of an act of Divine Creation. The remarkable adaptations were an example of the care exercised by the Creator. That the species could be arranged in an almost continuous scale of variation meant only that they were created that way. Whatever one observed in nature was the consequence of the specific events of creation. There were no real problems. Every question relating to cause had the same answer—that is the way God did it.

One might have supposed that the belief that what organisms were and did depended directly on Divine Creation would have stopped all serious study. Far from it. It was reasoned that one might learn about the Creator from studying what He had created. This approach, which was known as *Natural Theology*, had its beginnings in England with the Rev. John Ray (1627–1705; see Raven, 1950). Ray's philosophy

is given by the title of his most famous book (1691): *The Wisdom of God Manifested in the Works of the Creation.* The title, he explains, means "the Works of God at first, and by him conserv'd to this Day in the Same State and Condition in which they were first made." No change; no evolution.

And Ray could accept no other explanation than Divine Creation:

> every Pile of Grass or Ear of Corn sufficiently proves [that God exists] for, they say all the Men of the World cannot make such a Thing as one of these; and if they cannot do it, who can or did make it but God? To tell them that it made itself, or sprung up by Chance, would be as ridiculous as to tell the greatest Philosopher so.

In answer to our question why there are so many species, Ray wrote that an example of God's "infinite Power and Wisdom [is] the vast Multitude of Creatures, and those not only small, but immensely great [which] are Effects and Proofs of his Almighty Power."

Our question about adaptation has the same explanation. "The admirable Contrivance of all and each of them, the adapting all the Parts of Animals to their several Uses, the Provision that is made for their Sustenance" is all the work of the Creator.

An example of "adapting the Parts of the same Animal one to Another . . . is the proportioning the Length of the Neck to that of the Legs." That is, if animals are to have legs upon which to stand, they must have a neck of appropriate length, otherwise they "could not conveniently gather their Food or Drink if they wanted a Neck." All species that need a neck of appropriate length have one except the elephant. The problem for the elephant is that its head is so massive and heavy that it could not be suported by a neck of sufficient length to allow the head to reach the ground. The solution was to create an elephant with a trunk on the front of its head to enable it to secure food and water.

Natural Theology continued to flourish and remained the most conceptually developed part of biology almost to the time of Darwin. Darwin and Huxley were thor-

oughly familiar with a widely read book of William Paley (1743–1805), Archdeacon of Carlisle, *Natural Theology; or, Evidences of the Existence and Attributes of the Deity, collected from the appearances of nature* (1802). Most of Paley's appearances were collected not from nature but from John Ray, without giving credit. In any event it is a well written summary of Natural Theology.

Natural Theology reached a remarkable peak with the publication of the *Bridgewater Treatises* between 1833 and 1836. The Right Honourable and Reverend Francis Henry, Earl of Bridgewater, left a sum of 8,000 pounds sterling to be invested and the interest used to have a series of books written:

> On the Power, Wisdom, and Goodness of God, as manifested in the Creation; illustrating such work by all reasonable arguments, as for instance the variety and formation of God's creatures in the animal, vegetable, and mineral kingdoms; the effect of digestion, and thereby of conversion; the construction of the hand of man, and an infinite variety of other arguments; as also by discoveries ancient and modern, in arts, sciences, and the whole extent of literature.

In all there were eight treatises covering subjects in biology, geology, mineralogy, meteorology, chemistry, physics, and astronomy. They provide a synthesis of science for the early years of the 19th century. Those in biology were especially successful in covering the field. They included many observations of the sort that Charles Darwin was to use in support of his hypothesis of evolution by natural selection. In fact, one cannot read the *Bridgewater Treatises* devoted to biology without being struck by how slight a change in emphasis would be required to switch from the hypothesis of Divine Creation of species to an hypothesis of creation of species by evolution. So far as obtaining the data are concerned, Darwin need not have made that Voyage of the Beagle—he could have stayed home and obtained enough facts for his theory from the *Bridgewater Treatises.*

Within three decades after publication of the *Bridgewater Treatises,* the Divine Cre-

ation hypothesis began to be replaced in the minds of most scientists by the hypothesis of evolution. Kuhn (1970) employs the term "paradigm" to mean a generally accepted way of explaining a scientific phenomenon of first magnitude. Divine Creation was one paradigm for explaining the phenomenon of organic variation, adaptation, the scala naturae, and much more. The paradigm of evolution was a different way of explaining the same phenomena. Kuhn observes that one paradigm may replace another in what he calls a "scientific revolution." A scientific revolution will occur when the old paradigm ceases to be a useful and acceptable way of explaining the phenomena to which it applies. Your students may find Kuhn's analysis of interest. His scientific revolution represents one way of knowing being replaced by another way of knowing.

Some useful references to the topics considered so far are Mayr (1982), J. C. Greene (1959), Gillispie (1951), Eiseley (1958), Glass (1959), Wells (1963), Hooykass (1972), McPherson (1972), Adams (1938), Osborn (1894), Knight (1972), and Geikie (1905).

The Darwinian answer: evolution

In the autumn of 1859 one of the most influential books of all times was published: *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life.* The author was Charles Robert Darwin (1809–1882), an English gentleman naturalist whose writings on coral reefs, geology of South America, barnacles, and a voyage of the exploring ship *Beagle* had been well received.

Darwin was interested in answering the three sorts of questions that have been our concern. He was rather successful in doing so but, of greater importance, he started lines of investigation and thought that have continued to be highly productive to this day. He succeeded where others had failed because of his insistence that only naturalistic data and concepts be employed. All before him had invoked to some extent supernatural explanations, mainly—what we find today is a consequence of Divine

Creation. The 19th century scientists were becoming increasingly reluctant to accept supernatural explanations. For some the fact that supernatural forces could explain anything and everything meant that they could explain nothing. In all fields science was advancing rapidly and what had seemed impervious to analysis a generation before was succumbing to careful observation and experiment.

One of the great advantages of having Charles Darwin introduce the modern version of the subject of evolution to students is that he explicitly uses the procedures that scientists are supposed to use—mainly the hypothetico-deductive method. He tells us what made him consider the hypothesis of evolution at a time when it was held in low esteem. Then he tells us what he did: "The line of argument often pursued throughout my theory is to establish a point as a probability by deduction and to apply it as hypotheses to other points to see whether it will solve them" (quoted by Ghiselin, 1969, p. 4).

Antecedents to the hypothesis of evolution by natural selection. The stage of induction

First, what observations suggested that the hypothesis of evolution might be worth considering? What were the clues that suggested to Darwin that some explanation other than Divine Creation might be possible? This putting of clues and observations together to form a hypothesis is known as *induction*. Induction is a logical step from specific statements to more general statements, in contrast with deduction where one begins with a general statement (the hypothesis) and moves to the more specific deductions. There were three clues, according to Darwin, all dating from the years he spent on H. M. S. Beagle and becoming clearer after he had returned to England and discussed them with other naturalists. These three observations are casually referred to in the first sentence of the Introduction to the *Origin* and in more detail in his *Autobiography* (see Barlow, 1958, p. 118; also see Sulloway, 1982a and 1982b for a different interpretation).

1. While the Beagle was engaged in

charting the coasts of Argentina, Darwin conducted considerable field work on land, stimulated in part by his susceptibility to *mal de mer*. He observed many species that were new to him. Some were very strange, such as the armadillo. Darwin was also collecting fossils and among these he found the remains of some extinct armadillos— the glyptodonts. The clue is this: two very strange animals of the same general sort, one living and one extinct, were observed in the same part of the world.

What hypotheses can your students give for this observation?

2. Darwin visited many localities on the east coast of South America from Brazil to southern Argentina. He noted that some of the species that he encountered in one locality might be present at other places yet the individuals in the various localities might not be exactly the same. Thus, the clue is that what appeared to be the same species was made up of local populations that varied with the locality. Individuals from populations close to one another might differ almost imperceptibly, while populations more distantly separated might be almost as different as two species. This phenomenon is known as *geographic variation*. It was not the sort of thing Darwin had observed in England. There all of the individuals of a species were very much alike. But England is small and the climate does not vary greatly from place to place.

Can your students suggest a hypothesis for this observation?

3. A similar phenomenon was encountered in the Galapagos, a group of volcanic islands off the coast of Ecuador. One of the most striking kinds of animals there are the giant tortoises. It was pointed out to Darwin by one of the residents that each island had its own variety of tortoise. The differences were such that an experienced person could tell the island from which any individual originated. Here was geographic variation occurring on islands within sight of one another. He noted similar examples in some species of plants and birds. The Galapagos finches remain to this day a notable example (Lack, 1947).

Had you been with Darwin, would this last observation have suggested evolution to you, especially in view of the almost universal rejection of that hypothesis by authorities in biology and geology?

Formulating the hypothesis of evolution

Darwin convinced himself that the three observations just listed could be explained on the basis of evolutionary change. The standard explanation in the 1830s would have been that both the extinct armadillo-like creature and the living species had been separately created. If so, Darwin asked, isn't it surprising that both the fossil form and the living form are found in precisely the same part of the earth? The living animals were scampering over the land that held the entombed fossils. Wouldn't it be simpler to assume that the extinct form evolved into the living form?

With respect to the phenomenon of geographic variation, Darwin wondered just how precise Divine Creation had to be. John Ray had said that living species are exactly the same as the day they were created. That would seem to mean that each local population of a species, no matter how slightly it differed from the neighboring populations, represents a distinct act of Creation. Did a slightly different sort of tortoise have to be created for each little island in the Galapagos?

On the other hand the phenomenon of geographic variation could be explained on the basis of evolution. The hypothesis would go something like this. A widespread species on the South American mainland would find its local populations in a variety of environmental situations. Possibly the local populations would respond in some manner to the local conditions and evolve into distinctive populations. The Galapagos finches could have had a similar history. Long ago a few birds might have been accidently carried by winds or storms from the west coast of South America, where their closest relatives live today, to the Galapagos. There they spread slowly from island to island. This may have been a rare event since at the present time there seems to be little or no inter-island movement. Thus, each

island would have an almost completely isolated population and possibly it would slowly evolve so that each island would come to have its own variant—as with the tortoises. But how could they change?

Darwin was offering speculation and, for that period, rather wild speculation. He was saying that if evolution could occur it could account for the armadillos, tortoises, and finches.

A skeptical biologist would have observed that neither the hypothesis of creation nor of evolution could be validated. Both might seem reasonable—or wrong. There is, however, a fundamental difference between the two hypotheses: creationism is based on supernatural events that could never be studied by the methods of science; evolution is assumed to be based on natural phenomena that could, in theory at least, be studied by scientists. For those individuals deeply interested in answers to our original three questions, the research program seemed clear: study what can be studied with the procedures of science; reject creationism, not because it is wrong, but because it cannot be studied.

Darwin remained uncertain. A hypothesis of evolution was certainly plausible but the statements of science must be based on probability not plausibility. He was fully aware that the writings of Lamarck and Chambers on evolution were thoroughly discounted. Lyell was the foremost authority in geology and he had much to say on species as well. He had rejected evolution. The influences of fellow scientists were indeed powerful when essentially all rejected the notion of evolution. But more important than that, Darwin could not imagine what could be the mechanism of evolutionary change. How could one species possibly change into another? One practically had to enter the realm of supernatural phenomena to propose a way. Nearly all experience suggested what was called the *fixity of species*, that is, species do not change.

If one suspects that species are not fixed, proof must be given that one species can change into another. No one had ever observed such a thing and Darwin believed that the reason was that evolution is an

exceedingly slow process. Yet if one was to consider seriously the hypothesis of evolution, a way to test it must be found. Remember the Morgan quote: "cherish those [hypotheses] that can be given an experimental verification and to disregard the rest, not because they are wrong, but because they are useless." With this point of view the notion of evolution was useless—but so was creationism.

A mechanism for evolutionary change: the hypothesis of evolution by natural selection

We have been discussing the Darwin of the late 1830s—two decades before he published the *Origin*. He was unable to make much progress in understanding the basis of variation or adaptation simply because he could not think of a reasonable mechanism. But eventually he did and one of the most interesting things about his proposed mechanism is that the basic idea came not from fellow biologists or geologists but from a sociologist.

The Rev. Thomas Robert Malthus (1766–1834) published his important study, *An Essay on Population*, in 1798. Malthus was greatly distressed by the prevalence of human misery and poverty that he saw in England during those years of the Industrial Revolution. Why was there such misery? He suggested that the answer was to be found in the relation between the rate of human population growth and the rate of increase of the human food supply. He suspected that people were outbreeding the crops and the inevitable consequence would be not enough food for all. Thus, misery and hunger are inexorable consequences of being human. There has always been starvation and probably always would be unless human beings changed their reproductive behavior. Malthus suggested that all life has the same problem:

> Through the animal and vegetable kingdoms, nature has scattered the seeds of life abroad with the most profuse and liberal hand. She has been comparatively sparing in the room, and the nourishment necessary to rear them. The germs of existence contained in this spot of earth, with ample food, and ample room

to expand in, would fill millions of worlds in the course of a few thousand years. Necessity, that imperious all-pervading law of nature, restrains them within the prescribed bounds. The race of plants, and the race of animals shrink under this great restrictive law. And the race of man cannot, by any efforts of reason, escape from it. Among plants and animals its effects are waste of seed, sickness, and premature death. Among mankind, misery and vice.

Darwin tells us that this suggestion of Malthus was the key that he sought—a mechanism for evolutionary change. He was well aware of variation among the individuals of a species—in minor ways to be sure. Some might be large, others small; some with one color pattern, others with a different pattern; some with long hair, others with short hair. So far as he could tell, there is no reason to suspect that every character might not vary. If some of the variant characters better adapt the individual to surviving and leaving offspring, wouldn't it be reasonable to suppose that, over the course of time, individuals of the better adapted type will make up most and eventually all of the population? They would simply outbreed the less adapted types of individuals.

Thus the normal variation that all naturalists agreed characterized species in nature would allow nature to select the "better" variants and slowly the species would change. Darwin referred to this phenomenon as *natural selection* and hypothesized that it could be the long sought mechanism of evolutionary change. Evolution was an ancient idea; natural selection was a new idea. Darwin realized that he had to make a case for natural selection, and if he could, the hypothesis of evolution would become more likely. The title of his book contained a statement of his hypothesis: *On the Origin of Species by Means of Natural Selection, or the Preservation of the Favoured Races in the Struggle for Life.*

This hypothesis is testable, hence useful. We will now formulate a series of deductions and seek to test them.

Deduction 1: *If the hypothesis of evolution by*

natural selection is true, there must be variation among organisms

This deduction can be tested by finding out whether or not there is variation among the individuals of a species. The first two chapters of the *Origin* provide the evidence known to Darwin concerned with this deduction.

It comes as a surprise to many to learn that the *Origin* begins not with the phenomenon of variation of organisms in nature but under domestication. There was a good reason for this. The first sentence of Chapter 1 reads:

When we look to the individuals of the same variety or subvariety of our older cultivated plants and animals, one of the first points which strikes us, is, that they generally differ much more from each other, than do the individuals of any one species or variety in a state of nature (*Origin*, p. 7; unless otherwise noted all references are to the first edition).

Darwin could be confident that most of his readers would be familiar with the dramatic variation shown by most cultivated plants and domesticated animals. In the 19th century there was a great deal of interest in England in selecting new varieties of domesticated plants and animals. The results could be striking. Notice how Darwin emphasized that the selected varieties "generally differ much more from each other, than do the individuals of any one species or variety in a state of nature." Darwin was planting the notion that selection could be both quick and powerful in producing variations. His readers might not be aware that there was variation, albeit less, in wild populations. Thus he was wise to begin his argument with the familiar.

Darwin was also planting the idea that all differences need not be the consequence of Divine Creation. He could be sure that no reader would believe that Creation was the reason for the new breed of sheep or for a better beet. It would be accepted that the cultivated varieties were the product of *artificial selection.*

The great power of this principle of selection is not hypothetical. It is certain

that several of our eminent breeders have, even within a single lifetime, modified to a large extent some breeds of cattle and sheep (*Origin*, pp. 30–31).

Darwin felt that artificial selection was a model for natural selection, the difference being in the agent responsible. In one case nature selected what was "better" for survival and the production of offspring. In the other, man selected what was "better" for his purposes: cows that produced more milk, hens that had more breast meat or laid more eggs, roses that were more beautiful.

Darwin studied the various breeds of domestic pigeons and used them as an example of the amazing amount of variation that is possible.

There was no doubt that variation under domestication is a fact. This is so certain that to qualify it with the phrase "beyond a reasonable doubt" would be just plain silly. What about variation in nature? After all, Darwin was interested mainly in the possibility of evolution in nature, not in the barnyard. But he came to see the two as but aspects of the same forces.

There is a tremendous amount of variation in nature. Darwin had been impressed by this while on the Beagle expedition. Later he combed the publications of fellow scientists for additional facts. He found variation not only in superficial external features but in internal structures as well.

I am convinced that the most experienced naturalist would be surprised at the number of the cases of variability, even in important parts of structure, which he could collect on good authority, as I have collected, during a course of years (*Origin*, p. 45).

The most important point about variation in nature for Darwin was the fact that there seemed to be a continuous array of cases: from two populations being essentially identical; to two being slightly different, but sufficiently so for naturalists to classify them as two varieties; with greater differences they would be recognized as different subspecies; and finally so distinctive that each population would be classified as a "good" species.

Certainly no clear line of demarcation has as yet been drawn between species and sub-species—that is, the forms which in the opinion of some naturalists come very near to, but do not quite arrive at the rank of species; or again, between sub-species and well-marked varieties, or between lesser varieties and individual differences. *These differences blend into each other in an insensible series; and a series impresses the mind with the idea of an actual passage* (*Origin*, p. 51; italics mine).

Thus, Darwin found ample and convincing evidence of variation in populations of organisms, both in nature and in domestication. Therefore the deduction is correct and the hypothesis of evolution by natural selection becomes somewhat probable—at least it has not been falsified.

Deduction 2: *Natural selection can be operative only if more offspring are born that survive*

The idea that only a few of the many offspring of animals, or of the many seeds of plants, survive, was again something that Darwin's readers would know or suspect. They might also have observed that the population size of organisms seems to remain about the same year after year. A single oyster produces millions of egg each year yet the sea does not fill with oysters. A single oak tree can produce thousands of seeds each year yet, in natural areas, the number of oak trees remains about the same.

There is no exception to the rule that every organic being naturally increases at so high a rate, that if not destroyed, the earth would soon be covered by the progeny of a single pair. Even slow-breeding man has doubled in twenty-five years, and at this rate, in a few thousand years, there would literally not be standing room for his progeny .... The elephant is reckoned to be the slowest breeder of all known animals, and I have taken some pains to estimate its probable minimum rate of increase: it will be under the mark to assume that it breeds when thirty years old, and goes on breeding till ninety years old, bringing forth three

pair of young in this interval; if this be so, at the end of the fifth century there would be alive fifteen million elephants, descended from the first pair (*Origin*, p. 64).

Yet, in the likelihood, an average original pair would have only two surviving offspring—14,999,998 would not have made it. Thus, the *Struggle for Existence* is a tremendously impressive fact of nature.

It is the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms; for in this case there can be no artificial increase of food, and no prudential restraint from marriage (*Origin*, p. 63).

Thus, the deduction that more offspring are produced than can survive can be accepted as true. The hypothesis of evolution by natural selection is not falsified by this test and, hence, becomes more probable.

Deduction 3: *If the hypothesis of evolution by natural selection is true, there must be differences between the offspring that survive and reproduce and those which do not*

"Selection" implies that some individuals are chosen and others are discarded. An animal breeder can not develop a new variety of sheep, with heavier fleece for example, if he lets all the individuals in his flock reproduce. Success could only be assured if he kept the lambs of parents with the better fleece and sent all the other little lambs to market.

Similarly in nature if it is a matter of chance or luck which perish and which survive there would be no selection. What evidence did Darwin have to offer on this important deduction, which is the very heart of the concept of natural selection? He could make an effective case for the reality of artificial selection and suggested that the same general principle could hold in nature as well. But was there any evidence?

It may be said that natural selection is daily and hourly scrutinizing, throughout the world, every variation, even the slightest; rejecting that which is bad, pre-

serving and adding up all that is good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life. We see nothing of these slow changes in progress, until the hand of time has marked the long lapse of ages, and then so imperfect is our view into the long past geological ages, that we see only that the forms of life are now different from what they formerly were (*Origin*, p. 84).

Darwin rested his case on this logical argument, not data. There was no critical evidence that demonstrated a difference between the offspring that survived and those that perished. Compelling as the logical argument might be, the hypothesis of evolution by natural selection would be iffy until evidence for the reality of natural selection could be offered. Nevertheless, the inherent logic of the argument was sufficient for many 19th century naturalists.

Even to this day, the demonstration of natural selection remains difficult except in certain special situations. Darwin himself realized that demonstration would be most difficult for he believed that "we see nothing of these slow changes in progress, until the hand of time has marked the long lapse of the ages . . . ." And he felt sure that those ages were considerably greater than the life span of any human observer. So it would never be possible for a scientist to observe one species evolving into another.

Today this is how we view the situation. Since natural selection has been operating on natural populations continually, any genetic variant that could be classed as "good" would surely have appeared at some time in the past and have been screened by selection. Thus, the populations that we see today are the best that selection has been able to accomplish with the genetic variants that have appeared to date. The chance of any observer being lucky enough to detect a truly new genetic variant in a natural population under natural conditions that would be "better" is extraordinarily slight.

The deduction was eventually tested by

other means and shown to be correct. The most dramatic evidence comes from situations in which a population is presented with an environmental challenge never before encountered and, hence, never before selected for. Examples are insects sprayed with pesticides and microorganisms exposed to antibiotics. When the population encounters this new environment, for which they are clearly not adapted, there may be a rapid evolution of resistance.

More will be presented later on the modern evidence for the reality of natural selection. That evidence came a century after Darwin and hence was not available for him to answer his critics.

Deduction 4: *If the hypothesis of evolution by natural selection is true, only those variations that are inherited will be important*

In Darwin's time the relation between the characteristics of individuals and their inheritance was poorly understood. It was obvious, of course, that much was inherited: the offspring of chickens were chickens, not pigeons. On the other hand some of the minor differences among a flock of chickens might be passed to the offspring and some not. Some of these minor characteristics might then reappear after several generations. If that was the case, was the variant new or had it been transmitted but in a dormant state—whatever that might mean.

> Our ignorance of the laws of variation is profound. Not in one case out of a hundred can we pretend to assign any reason why this or that part differs, more or less, from the same parts in the parents (*Origin*, p. 167).

These confusing aspects of inheritance were especially notable, and noticed, in human families. At times twins would be of the same sex and be remarkably alike in appearance and in personality. At other times twins might differ in sex and characteristics or be of the same sex and still differ in appearance and personality— being no more alike than brothers and sisters born one at a time.

In 1859 there was simply not enough information about inheritance to provide the necessary foundation for the hypothesis of natural selection. Darwin realized that this was a critical lack and nine years later, in 1868, published a two volume work on inheritance: *The Variation of Animals and Plants under Domestication.* Most of the data were extracted from the literature and they varied from reliable to totally unreliable observations and it was not possible to tell which was which.

Neither Darwin nor or anyone else was able to account for the origin, or apparent origin, of new variations. Darwin assumed that new variations were related in some way to the environment but not in a Lamarckian sense—that is, he did not believe that the environment induced specific adaptations (long hair in cold climates, etc.). The best that Darwin could do was to conclude:

> Whatever the cause may be of each slight difference in the offspring from their parents—and a cause for each must exist—it is the steady accumulation, through natural selection, of such differences, when beneficial to the individual, that gives to all the more important modifications of structure, by which the innumerable beings on the face of this earth are enabled to struggle with each other, and the best adapted survive (*Origin*, p. 170).

Although Darwin accepted that there could be new variations appearing in populations, there was great uncertainty on the part of many scientists that these variations could be of sufficient magnitude to enable one species to evolve into another. All sorts of bizarre traits had been selected to produce a bewildering variety of breeds of pigeons—*but they were all pigeons.* Even the most extreme breeds could be crossed and produce fertile offspring. Ability to cross and produce fertile offspring was the generally accepted test for good species at that time. Darwin had emphasized earlier that some of the breeds of dogs, for example, are as different in structure and behavior as different wild canine species, but they still could be crossed. Nevertheless, no arti-

ficial selection had produced a "new species."

One of Darwin's critics, Fleeming Jenkin (1867), suggested that new variants could never produce any lasting effect. His was a most telling argument. If a new variant arose in a population, according to Jenkin, it would of necessity have to cross with the other members of the population. When different varieties were crossed it was accepted that *blended inheritance* was the rule. That is, the offspring would be intermediate. So, the offspring of the variant and a regular individual would be intermediate. Their offspring would, most likely, breed with the regular forms again so the next generation would be even more like the regular individuals. Thus, any new variations would be expected to be diluted and disappear. That would be the consequence if blended inheritance was the rule—and in Darwin's time that was accepted as one of the few sure things that could be said about inheritance. Thus, Jenkin's argument was a telling blow to the Darwinian hypothesis. It was telling, however, because it was thought to be valid. Now we know better. Inheritance is not a matter of blending the differences of the parents—but Mendel was still a half-century in the future.

Thus Darwin was not able to confirm the validity of Deduction 4 that the variations which are important in evolution are inherited. (But the deduction did seem highly probable and eventually convincing data were accumulated.) This, coupled with the fact that Deduction 3—the attempt to demonstrate natural selection in nature—could likewise not be confirmed, led many scientists to have serious doubts about the hypothesis that natural selection is the mechanism for evolutionary change.

At the same time the number of scientists and others who came to accept evolution increased. To them Mr. Darwin had made his point about the possibility of evolution, he just did not know what made it happen. But in retrospect, Huxley (1888, p. 197) maintained "the *Origin* provided us with the working hypothesis we sought."

What, then, was the basis for the accep-

tance of the hypothesis of evolution as the answer to our questions about organic variety and adaptation? The answer lay hidden in the rocks.

The critical information required for proving the hypothesis of evolution is data on the conversion of one species into another. Evolution means descent with change, so it would be necessary to show that ancestors and descendants are in fact, different. On the face of it, that sounds like a nearly impossible task. Remote ancestors are remote and hence not available for direct study. Nevertheless, the hypothesis of evolution, no matter how logical it might seem, would remain in doubt unless some means of reconstructing the past history of life exists. So one of our most critical deductions will be:

Deduction 5: *If the hypothesis of evolution is to be established as true, we must be able to obtain information on organisms that lived in the past*

The data for this deduction were already available to Darwin. The rocks of the earth's crust held the secrets of many events that occurred in the past. Long-cooled lava flows told of ancient volcanic eruptions. Limestone told of ancient sea bottoms where the sediments were slowly changed to rocks. Smooth horizontal rocks, with parallel grooves, told of ancient glaciers that had ground across them. The depths of canyons gave some idea of the length of time that it must have taken rivers to cut them.

Evidences of past life were to be found in one of the two basic kinds of rocks. The granites and lavas are formed by the cooling of molten rock from the interior of the earth. These are the *igneous rocks*. The horizontal layers of rock that form such a conspicuous feature of cliff faces in many parts of the world are the *sedimentary rocks*. These layers, or strata, of sedimentary rocks start as material settling at the bottom of a lake, inland sea, or ocean; or are deposited on land by wind or eroding waters. Gradually these deposits are covered and the buried ones slowly change to stone. This method of formation means that the topmost deposits of sediments are the most recent

and the lowest layer the oldest. If these deposits happen to include the remains of animals or plants, these may be fossilized—changed to stone. Thus the sedimentary rocks are time capsules of earth history. Each stratum contains information about events occurring at the time of its formation.

The possibility of the remains of a dying organism being fossilized is exceedingly remote. Most dead organisms are quickly consumed by other organisms. Organic compounds and the energy they contain are too valuable to be wasted in nature. If the organism has hard parts: shells, teeth, bones, or an exoskeleton, there is a better chance of these structures surviving rapid destruction—and hence the chance of their fossilization increases.

But fossils do occur so we have the possibility of learning something about life in the past that could throw light on whether or not evolution has occurred. Thus, we can become somewhat bolder in formulating our deductions since the past is not closed to study.

Deduction 6a: *If the hypothesis of evolution is true, the species that lived in the remote past must be different from the species alive today*

The basic idea in evolution is that natural populations slowly change over long stretches of time and, therefore, ancestors and descendants will, of necessity, be different from one another.

Once again, the data to evaluate the deduction were available to Darwin and other naturalists: fossils had been known for a very long time. A few fossil species proved to be very similar, or even identical, with living species but the vast majority were very different from life today. Especially striking and interesting were the remains of some of the vertebrates, whose bony skeletons increased their chances of being fossilized. There were huge elephant-like creatures that had lived on land and monstrous reptiles that had lived in the sea. There were spectacular plant remains such as the giant tree ferns and many other species entirely different from any alive today.

Thus it was true beyond a reasonable

doubt that few of the species alive today occur also as fossils in the remote past. The vast majority of the fossil species are no longer with us. The deduction is shown to be true so the hypothesis of evolution is made more probable.

We can continue with a similar but more sophisticated deduction.

Deduction 6b: *If the hypothesis of evolution is true, the older the sedimentary strata, the less the chance of finding fossils of contemporary species*

Testing of this deduction will involve not only finding fossils but knowing something about the time they lived. In the middle of the 19th century there were no accurate methods for determining the ages of the strata of sedimentary rocks. Nevertheless, it was possible to obtain data that allowed a test of Deduction 6b. If we are looking at the face of a cliff of sedimentary rocks, the layers will generally be more or less horizontal and we have seen that the bottommost layer will be the oldest and the topmost the youngest. For Deduction 6b we need not know whether the oldest layer is a million, ten million, or a hundred million years old. Such data would be fine to have but all we need to know is relative age and this can be determined by the position of the layer relative to other layers. If the deduction is correct and if the layers are relatively young (geologically speaking), we should find more fossils of still-living species in the topmost layer and fewer in successively lower layers.

This hypotheses was first tested by the famous English geologist and friend of Charles Darwin, Sir Charles Lyell (1797–1875), and by a French geologist, Gérard Paul Deshayes (1797–1875). They collected fossil shells from different strata that had been formed in a geological era known as the Tertiary. The oldest strata had been given the name Eocene and the most recent Pliocene. These divisions of the Tertiary are shown in Figure 1, which is the modern geological time scale. Table 1 gives the data. Nearly all of the Recent Pliocene fossils belong to species still alive whereas almost none of the Eocene fossils do. The deduction has been tested and found to be true,

so we can say that the hypothesis of evolution becomes even more probable.

The finding that progressively older strata have progressively fewer species that are alive today is not what one would expect from the hypothesis of Divine Creation. If all species of animals and plants had been created within four days, as a literal interpretation of Genesis I demands, all strata might be expected to have the same array of fossils. That is most definitely not what the geological record shows. Nevertheless, Lyell's data do not prove that Divine Creation did not occur—if supernatural forces are invoked, anything can be explained. What one could say, however, is that if we accept as valid evidence only what we can observe and employ only the naturalistic methods of science, the hypothesis of evolution is more probable than the hypothesis of Divine Creation. Science as a way of knowing was proving to be a powerful method of gaining an understanding of the natural world.

Deduction 7: *If the hypothesis of evolution is true, we would expect to find only the simplest organisms in the very oldest fossiliferous strata and the more complex ones to appear in more recent strata.*

Some cautionary remarks must be made about this deduction. Evolution means change—not necessarily becoming more complex. Some species alive today, many parasites for example, may be simpler structurally than their ancestors. Nevertheless, Darwin and other evolutionists assumed, as we do today, that the very earliest forms of life must have been small and simple and that slowly, very slowly, more complicated species evolved.

During the first half of the 19th century, geologists developed a time scale that forms a framework for discussing the past. The basic data consisted of measuring the thickness of the sedimentary strata and arranging them in a sequence from the oldest to more recent. This is the *geological column*. Even on the basis of the strata known at the time, the geological column turned out to be dozens of miles thick. Of course, this huge pile of rocks was not observed in any one locality. Sedimentary rocks are not

Table 1. *Percentages of Tertiary species still living. Data from Lyell (1854, pages 389-395).*

	Fossil species	Alive today	Percent of fossil species still alive
Recent Pliocene	226	216	96
Older Pliocene	569	238	42
Miocene	1,021	176	17
Eocene	1,238	42	3

formed as a uniform layer across the earth's crust but, at any specific period of time, deposition will occur in one restricted region; later it will occur elsewhere. By examining all the available cliffs and railroad cuts, it was eventually possible to put the pieces of the puzzle in place and be able to arrange all of the strata in a composite column of rocks.

The early work on accumulating the data for the geological column was done in England at the time of the Industrial Revolution. One of the important activities then was the linking of all parts of England, Wales, and Scotland by railroads. The railroad builders frequently had to cut deep pathways through hills. This afforded the geologists a wonderful opportunity to observe strata in places where, otherwise, they would have been covered.

When first devised the geological column measured only relative time. That is, the lower the stratum, the older it was. Absolute geological time became known only after the radioactive methods for dating became available in the early years of the 20th century. A modern version of the geological column is shown as Figure 1.

Even in the early years of the 19th century, geologists realized that the oldest strata contained simpler forms—invertebrates alone were found. Only later did higher vertebrates—reptiles, birds, and mammals—appear. The same was true for the plant kingdom. Algae, mosses, ferns and similar plants were very old; the angiosperms were more recent. In 1824 Lyell (1826, p. 513) had this to say:

An opinion was entertained soon after the commencement of the study of organic remains, that in ascending from the lowest to the more recent strata, a

TIME FROM BEGINNING	ERA	PERIOD / Epoch
		QUARTERNARY
0.01		Recent
1.8		Pleistocene
		TERTIARY
6	CENOZOIC	Pliocene
25		Miocene
38		Oligocene
55		Eocene
65		Paleocene
140		CRETACEOUS
180	MESOZOIC	JURASSIC
230		TRIASSIC
280		PERMIAN
350		CARBONIFEROUS
400		DEVONIAN
430	PALEOZOIC	SILURIAN
500		ORDOVICIAN
550		CAMBRIAN
670		EDIACARIAN
2,500	PROTEROZOIC	
4,600	ARCHEAN	

Fig. 1. A modern version of the geological time scale. Time in million years.

TABLE 2.   *Time and life. The data for 1852.*

Cambrian	No reliable evidence of life; "a few obscure traces of fossils have been detected."
Silurian	No land plants. Oldest fossil fish. Many invertebrates: trilobites, graptolites, brachiopods.
Devonian	No reptiles. Many fish, some with armored plates (the ostracoderms).
Carboniferous	Many invertebrates. Oldest known reptiles.
Permian	More reptiles.
Triassic	Reptiles and batrachians. Horsetails.
Jurassic	Large reptiles such as pterodactyls, plesiosaurs. Cycads, conifers, ferns. A few palms. First mammals.
Cretaceous	Mostly marine fossils. Reptiles, many invertebrates.
Eocene	Mediterranean-type plants. Many mammals but all are of extinct species. Nearly all shells are of extinct species.
Miocene	All the mammals and about two-thirds of the shells are of extinct species.
Pliocene	About the same.
Recent	All of the shells and many of the mammals are of living species. First human remains.

gradual and progressive scale could be traced from the simplest forms of organization to those more complicated, ending at length in the class of animals most related to man [i.e. the mammals].

In the 1820s one had to be cautious—after all, very little paleontological work had been done. Much more was known in the 1830s when Lyell's *Principles of Geology* was first published. His *Manual*, which contained the data on paleontology that had been removed from later editions of the *Principles*, appeared in its fourth edition in 1852—a few years before the *Origin*. By then the data were much more convincing. Some of them are shown in Table 2.

Darwin and others at mid-century spoke of the inadequacy of the geological record. In many ways it was inadequate since relatively few geologists had explored the

strata in only a small part of the world. Nevertheless, the record was sufficiently adequate to test Deduction 7. It was true beyond a reasonable doubt that there had been a progression of forms of life, with the less complex species appearing before the more complex. The various kinds of invertebrates were well represented at the very beginning of the fossil record in the Silurian; the mammals were first encountered in the much younger Jurassic strata. Thus the hypothesis of evolution becomes more probable.

Essentially all of the prominent geologists in the pre-*Origin* years were creationists. One was Lyell who made the first grand synthesis of geological data and he saw the progression of life. He fully realized that each major group of strata had its own distinctive life forms—many not known in either younger or older strata. How could a creationist explain such facts? The great French anatomist and geologist Cuvier (1769–1832) had suggested that there had been a series of creations and extinctions. His hypothesis explained the data of the early 1800s as well as did the hypothesis of evolution.

Darwin's hypothesis was radically different from Cuvier's. For Darwin the species at any one period of earth history were the progenitors of the species of all subsequent periods. There was no break in the lineage of life. Presumably all forms alive today are the remote descendants of the first sorts of life that appeared on earth. Thus the most critical deduction of all will be:

Deduction 8: *If the hypothesis of evolution is true, it must be possible to demonstrate the slow change of one species into another*

Darwin failed. There were no critical data in the 1850s that showed the evolution of one species into another. Darwin thought that this was but a reflection of the inadequacy of the fossil record. In a sense he was correct but today, when we know so much more about speciation, we realize why it is exceedingly difficult to obtain convincing fossil evidence of the evolution of one species into another.

Darwin and others at the time were more interested in a related question: were there fossils that were intermediate between major groups of animals? Were there *missing links*, which if discovered, could document the evolution of life? This leads to another deduction.

Deduction 9: *If the hypothesis of evolution, which assumes that all of today's species are the descendants of a few original forms, is true, there should have been connecting forms between the major groups (phyla, classes, orders)*

Why then is not every geological formation and every stratum full of such intermediate links? Geology assuredly does not reveal any such finely graduated organic chain; and this, perhaps is the most obvious and gravest objection that can be urged against my theory. The explanation lies, as I believe, in the extreme imperfection of the geological record (*Origin*, p. 280).

If that explanation was correct, one must assume that greater efforts by collectors of fossils would eventually supply the data. It was also possible to predict what sorts of fossils might be the most promising. The answer is the vertebrates. There are two main reasons for this. First, the bones and teeth of vertebrates are excellent candidates for fossilization. Second, the vertebrates—or rather the Phylum Chordata of which they are the principal representatives—are the most recently evolved of the major phyla. Many of the invertebrate phyla were already present in the then oldest known strata from which fossils had been collected—the Silurian rocks. What may have happened during earlier times could not be determined without fossil remains. This means that the common ancestors of any two of the phyla already present in the Silurian would have lived at an earlier time when no fossil record was then available. On the other hand, one could work with the bony chordates—the vertebrates. Of the major groups—fishes, amphibians, reptiles, birds and mammals—only the most primitive, the fishes, were present in earliest fossil-bearing strata. If, as Darwin imagined, all the other ver-

tebrates were evolved from fishes, there would be a chance of documenting his belief.

The first dramatic proof for the existence of fossils intermediate between major groups came in 1861—two years after the publication of the *Origin*. In a quarry near Solenhofen in Bavaria, a feather was discovered in strata of Jurassic age. Shortly thereafter a well-preserved specimen of a strange fossil was discovered and named *Archaeopteryx*. It was a confusing mixture of structural features of modern birds and primitive reptiles known as archosaurians. The skull was somewhat bird-like but the jaws contained teeth, characteristic of reptiles but absent in all modern birds. There was a long reptilian-like bony tail, in contrast with the modern birds which have the tail vertebrae fused in a short projection—the "tail" being feathers only. In fact, the skeleton was more similar to that of the archosaurians than to modern birds. Nevertheless, *Archaeopteryx* had wings and the entire body was covered with true feathers. It could be debated whether *Archaeopteryx* should be classed as a reptile or bird but, using the presence or absence of feathers as the main diagnostic feature, paleontologists classified it as a bird.

Of course this is exactly what would be hoped for in a "missing link"—a species so perfectly intermediate between two major groups that one could debate to which group it should be assigned. Darwin had assumed that birds must have evolved from primitive reptiles and here was the evidence that should have convinced many scientists that they had. *Archaeopteryx* remains today as one of the best examples of a link no longer missing. "Here was a truly intermediate form between the reptiles and the birds" (Colbert, 1980, p. 183). Another modern paleontologist (Ostrom, 1974) offers this opinion:

> *Archaeopteryx* represents a "main-line" or transitional organism between an archosaurian ancestor and all subsequent birds. Some critics may attack this premise on the grounds of improbability, but my response to that is a challenge for them to identify *any positive* anatomical evi-

dence (in *Archaeopteryx* or any later bird) that precludes either archosaurian ancestry or the main-line position ancestral to later birds.

Here then was the "smoking gun" that Darwin and the other evolutionists required—a fossilized link between two major groups of vertebrates. This gave strong credibility to the hypothesis of evolution. One would have assumed, therefore, that intense enthusiasm would follow such a discovery. Surprisingly, this was not the case.

The specimen discovered in 1861 was sent the the British Museum (Natural History) in 1862 and was studied immediately by the famous English anatomist Richard Owen (1863). It was restudied by Huxley (1868). Neither saw in *Archaeopteryx* the importance we ascribe to it today. In the fourth edition and later editions of the *Origin*, Darwin gave a single entry in the index for *Archaeopteryx*. There we read only that a

> strange bird, the Archaeopteryx, with a long lizard-like tail, bearing a pair of feathers on each joint, and with its wings furnished with two free claws, has been discovered in the [Jurassic] slates of Solenhofen (*Origin*, 1892, p. 266).

There is another mention however that first appeared on page 284 of the fifth edition:

> Even the wide interval between birds and reptiles has been shown by [Huxley] to be partially bridged over in the most unexpected manner, on one hand by the ostrich and extinct Archaeopteryx, and on the other hand by [one of the dinosaurs].

Archaeopteryx is not listed in the index of the five volumes of Darwin's letters (F. Darwin, 1888, 1903). In a lecture given in 1880, Huxley (1895a, pp. 234–235) saw and emphasized its importance. This was in his essay, "The coming of age of 'The Origin of Species'." He quoted Darwin's belief that there must have been links between birds and reptiles but that such a belief was not supported by evidence in 1859. Huxley continues.

But the progress of knowledge has justified Mr. Darwin to an extent which could hardly have been anticipated. In 1862, the specimen of Archaeopteryx, which, until the last two or three years, has remained unique, was discovered; and it is an animal which, in its feathers and the greater part of its organization, is a veritable bird, while, in other parts, it is distinctly reptilian.

Slowness in recognizing the importance of a new discovery in science is far from being unusual. In science, as in other fields of knowledge, it is exceedingly difficult to put two and two together unless one already knows that the answer is four.

Thus the critical deduction that there must be forms intermediate between major groups of organisms could be satisfied in this one case. Is one enough? Only one was available to Darwin in his lifetime. Subsequently, and especially in the 20th century, other dramatic and more complete examples have been discovered. Some of these will be mentioned later. Nevertheless, the "missing links" tend to remain missing, but today we realize that there are compelling arguments for why this is so.

One final deduction will have to do with time. Darwin's *Origin* appeared during a period of history when most educated people assumed that the earth was not very old. Bishop Ussher's date of Creation as 4004 B.C. was so widely accepted that it was included in the King James Version of the Bible then printed. Nevertheless, geologists were coming more and more to the opinion that the earth was very old. Hutton (1788, p. 304) concluded his famous study, the *Theory of the Earth*, with this statement: "The result, therefore, of our present inquiry is, that we find no vestige of a beginning—no prospect of an end." Irrespective of Hutton's very considerable firsthand knowledge of geology, his statement was hypothesis, not fact.

Darwin knew that he needed vast ages if his hypothesis of evolution was to be accepted.

Deduction 10: *If the hypothesis of evolution is true, the age of the earth must be very great, possibly many millions of years old*

How could one possibly measure the age of the earth? Neither Hutton nor anyone since him has been able to look at the surface of the earth and find any evidence that at some period of time there was no earth and then, later, the earth came into existence. Even if one found such evidence, was there any way of saying when that origin of the earth had occurred? No. The answer had to be sought by indirect means.

The first crude estimates were based on the thickness of the strata. Geologists had become convinced that sedimentary rocks came from material that had been deposited, generally under water. If one knew the rate of deposition and the thickness of a group of sedimentary rocks, one could compute how long it had taken them to form. Then, if one knew the total thickness of all the sedimentary rocks, it would be possible to give a figure for how long it took for all sedimentary rocks to form. That would give a minimum estimate of the age of the earth but would not, of course, tell us whether the earth had an origin or had always been in existence.

None of these estimates could be made with any exactness. The rate of deposition of materials would depend on the rainfall, slope of the land, and the nature of the material being eroded—all of which might vary over long periods of time. A given stratum of rocks might be very thick in one place and thin in another. One could never be sure that all strata were known.

Nevertheless, geologists came to believe that the earth must be very old.

A man must for years examine for himself great piles of superimposed strata, and watch the sea at work grinding down old rocks and making fresh sediment, before he can hope to comprehend anything of the lapse of time, the monuments of which we see around us" (*Origin*, p. 282).

The then known strata in Great Britain alone totalled 72,584 feet, or 14 miles thick. Darwin knew of an estimate for deposition by the Mississippi River: 600 feet in 100,000 years. Thus, each foot would represent 166.67 years. That would mean that the

known sedimentary rocks in Great Britain would have taken 12 million years to form. Yet an even longer time might have elapsed, as one might imagine that the great Mississippi River, draining much of the continent, would have a very high rate of deposition.

Various other ingenious methods were used to determine the age of the earth. The salinity of rivers flowing into the ocean was measured. Knowing that and the total amount of salt in the ocean, one could estimate how long it had taken the ocean to receive its salt. Another method consisted of making an assumption about the temperature of the earth at the time it was formed and then estimating how long it would take for it to cool to its present temperature. Whatever the method employed, it turned out that the earth must be very old. No method, however, was capable of giving a reliable answer.

In was not until the 20th century, and especially since 1940, that reliable methods for determining the age of rocks have been perfected. All of these depend on the rate of radioactive decay of materials in the rocks. One can now estimate the age of rocks with an error of only several percent. These are the data used in Figure 1.

Although an acceptably accurate method for dating rocks was not available to Darwin, it seemed true beyond all reasonable doubt that an almost inconceivable length of time had elapsed since the organisms that lay buried in the oldest fossiliferous rocks had lived, and the present.

Was Darwin right?

What is one to conclude? Was the hypothesis of evolution, as advanced in 1859, true beyond all reasonable doubt? Different minds answered this question in different ways. Darwin's data and arguments were so reasonable for some scientists that they assumed that he must be right. Huxley was one of these: "My reflection, when I first made myself master of the central idea of the 'Origin' was, 'How extremely stupid not to have thought of that!'" (Huxley, 1888, p. 197). Other scientists were unconvinced. Some were

deeply antagonistic. The same varied reactions came from men of the church and men of state. Yet Huxley was able to write in the late 1880s that "even the theologians have almost ceased to pit the plain meaning of Genesis against the no less plain meaning of Nature."

Darwinism was the great revolution in biology in the 19th century. That evolution was the explanation of organic diversity, adaptation, and the scala naturae was accepted by essentially all biologists and geologists. There was more doubt, however, about natural selection being the primary mechanism of evolutionary change.

One of the great achievements of evolutionary theory was that after 1859 it began to "make sense" of an otherwise bewildering mass of data. That will be our next major topic but, first, some references to the subjects so far covered will be given.

A Darwinism bibliography

The literature pertaining to Darwin and his life and times is enormous. Some of the key references will be cited.

Freeman (1977) provides an invaluable listing of all Darwin's publications, including most of the reprintings.

Darwin first published his views on the origin of species in a joint paper with A. R. Wallace in 1858. This famous paper is reprinted in J. Moore (1957) and de Beer (1958).

The *Origin* was first published, on 26 November 1859, with a press run of 1,250 copies, by John Murray. The second edition appeared on 26 December of the same year. The third edition appeared in 1861, the fourth in 1866, the fifth in 1869, and the sixth in 1872. A few corrections were made thereafter. The one-volume Murray editions from 1878 through 1891 give the final text.

Peckham (1959) provides a variorum of all editions. This makes it possible to see how Darwin changed the wording in the five editions after the first. The index to the *Origin* is brief and inadequate for many purposes, but recent printings of the Harvard University Press facsimile of the first edition have an expanded index containing references to modern concepts. In addi-

tion, Barrett, Weinshank, and Gottleber (1981) have published a computer-generated concordance of the first edition. Information about most of the individuals and items mentioned by Darwin, usually without citations, can be found in Freeman (1978).

Darwin's first and in many ways his most popular book is an account of the voyage of the Beagle (1839). It has been reprinted innumerable times. Some references dealing with the book and voyage are: Moorehead (1969), Marshall (1970), Barlow (1933 and 1954), Mellersh (1968), and Thomson (1975).

Many of Darwin's shorter papers have been made available in convenient form by Barrett (1977).

In recent years many of Darwin's notebooks and draft manuscripts, never intended for publication, have been issued: the essays of 1842 and 1844 (F. Darwin, 1909a; de Beer, 1958a); the Beagle diary (Barlow, 1933); the Red Notebook from the last year of the Beagle (Herbert, 1980); the manuscript on natural selection, intended to be part of a very large work of which the *Origin* was an abstract (Stauffer, 1975); the journal (de Beer, 1959a); notebooks on the transmutation of species (de Beer, 1960a–1967); ornithological notes (Barlow, 1963), notes and letters (Simpson, 1950).

General accounts of Darwin and his theory are Mayr (1982), Eiseley (1958), Ghiselin (1969), J. C. Greene (1959), J. Huxley and Kettlewell (1965), de Beer (1964), Ruse (1981), Irvine (1955), Allan (1977), Lanham (1968), Stone (1980—an historical novel but accurate), S. A. Bell (1959), C. D. Darlington (1959) and Appleman (1970).

Some of the 19th century accounts of Darwinism are Wallace (1870, 1889), Romanes (1892–1897), Poulton (1896), Jordan (1898), Gray (1876), LeConte (1891), Tyndall (1874), C. Darwin (1868, 1870), Schmidt (1873), Winchell (1871), Depéret (1909), Joly (1891), Vernon (1903), and T. H. Huxley (all citations except 1868).

Most of Darwin's fascinating letters seem to have been published. Often he expressed himself more openly in them than he cared to do in print. The more important of them, together with much general information, were published by his son, Francis Darwin (1888, 1903). Others have been published by Barlow (1967), Carroll (1976), F. Darwin (1909b), de Beer (1959b, 1960b, 1968), Litchfield (1915), Lowenberg (1939), Stecher (1961, 1969).

Some of the more personal insights are provided by Ashworth (1935), Atkins (1976), British Museum (1909), Raverat (1952), Irvine (1955), Eiseley (1958), Stone (1980), Osborn (1928), Gruber (1981) and by his autobiography (F. Darwin, 1888, vol. 1, ch. 2; Barlow, 1958, the complete version; Simpson, 1950).

For Darwin's close friend Charles Lyell see L. G. Wilson (1970, 1972), Bailey (1963), and Mrs. Lyell (1881). For Alfred Russel Wallace see Marchant (1916), F. Darwin (1909b), McKinney (1972), George (1964), Osborn (1928), and Williams-Ellis (1966). For Thomas Henry Huxley see Bibby (1959), Irvine (1955, 1960), L. Huxley (1900), and Osborn (1928). In the United States one of the most effective supporters of Darwin was Asa Gray. See Dupree (1959). His most outspoken opponent in the United States was Louis Agassiz. See Lurie (1960).

For the 19th century geological background, Lyell's books are fundamental. The three volumes of the *Principles* were published from 1830 to 1833. In 1838 he removed most of the historical geology from the *Principles* and published it separately as *The Elements of Geology*. In 1851 this was revised as the *Manual of Elementary Geology*. By 1853 the *Principles* was in its ninth edition and it ended with the twelfth of 1875.

Other sources for information on 19th century geology are: Playfair (1802), Buckland (1836), Dana (1863), Miller (1851–1860), Reingold (1964), Osborn (1931), Mather and Mason (1970), Schuchert and LeVene (1940), Merrill (1924), Lanham (1973), Adams (1938), Bailey (1963), Geikie (1905), Gillispie (1951), J. C. Greene (1959), M. T. Greene (1982), Ostrom and McIntosh (1966), and L. G. Wilson (1972).

For students who are not science majors

useful references are J. C. Greene (1959), Barlow (1958), Irvine (1955), Stone (1980), Eiseley (1958), Moorehead (1969), Raverat (1952), Gillispie (1951), and especially Gould (1977, 1980, 1983).

For general criticisms, including the religious reactions in the 19th century (the 20th century creationist controversy will be discussed later), see Glick (1972), Hooykaas (1972), T. H. Huxley (1888, 1895a–f), Kogan (1960), Mivart (1871), Irvine (1955), Mayr (1982), Rogers (1973), Russett (1976), R. J. Wilson (1967), Draper (1894), Hofstadter (1955, 1963), Hull (1973), Turner (1974), Ellegård (1958) and A. D. White (1896).

Some human interest episodes. Darwin's theory of evolution raised fundamental intellectual and emotional problems for many people. Some of the episodes may prove interesting for your students to explore. Here are some suggestions:

The famous debate between Huxley and Bishop Wilberforce at the Oxford meeting of the British Association on June 30, 1860 is described in F. Darwin (1888, vol. 2, pp. 320–322).

Lyell, the master of time and life, was slow to accept Darwin's hypothesis. A comparison of the different editions of his *Principles* and *Manual* would prove of interest. See also L. G. Wilson (1970, 1972), Bailey (1963), and Mrs. Lyell (1881).

Huxley and Prime Minister Gladstone had numerous debates in the press. One of the more fascinating was about the biblical story of the Gadarene swine (Matthew 8: 28–33; Mark 5: 2–13; Luke 8: 26–39). See T. H. Huxley (1895b, essay V and 1895f, essays X and XI).

The two American biologists, Asa Gray and Louis Agassiz, were pro and con on the issue of Darwinism. Dupree (1959) and Lurie (1960) can be consulted to see why.

A. R. Wallace independently came to the same conclusion about natural selection as had Darwin—before Darwin had published. For the solution of this problem—who should receive credit for the discovery—see F. Darwin (1888, vol. 2, ch. IV), Barlow (1958, pp. 121–122) and Moore (1957, pp. 342–344).

Darwin was ill for much of his life after he returned from the Beagle voyage. Winslow (1971) and Colp (1977) have speculated on the causes.

And, of course, there has been much speculation on Darwin's religious views. See F. Darwin (1888, vol. 1, pp. 304–317) and Gillespie (1979).

Now back to the main line of the argument.

"Nothing in biology makes sense except in the light of evolution"

The next five deductions will be grouped under the title of Dobzhansky's paper of 1973a. The great appeal of the theory of evolution for scientists in the last part of the 19th century was that it made so much sense out of an otherwise bewildering mass of data in biology and geology. By the last quarter of the 19th century, it was accepted by the majority of biologists and geologists that evolution was true beyond all reasonable doubt. It is proper, therefore, that we change its designation from "hypothesis" to "theory."

Apart from explaining the existing data, the theory of evolution proved of great value in directing the course of research. All important theories in science have this dual role—to explain the data already on hand and to suggest ways of acquiring additional information. Science is not only a way of knowing; it is also a way of discovering.

Dobzhansky's statement is likely to be accepted by scientists familiar with biology, yet we must admit that it does not make too much sense in and of itself. By implication, no other concept except evolution provides a satisfying explanation of biological phenomena. But surely the biology of Ray, Paley and the authors of the *Bridgewater Treatises* made perfect sense to them. For them "Nothing in biology made sense except in the light of Divine Creation." Natural theology can account for all of the phenomena of life to a degree of completeness that the Theory of Evolution can never achieve.

Nevertheless, natural theology came to be viewed as a sterile enterprise. The answer was always the same: "What is, is what was created." Supernatural powers

and processes, far beyond the ken of scientists to detect or study, explained all. After 1859 the more intellectually satisfying answer became: "What is, is what evolved." Nothing in evolutionary theory was beyond the power of scientists to try to study directly or indirectly. Some problems might be very difficult to study—for example, the history of life. For such information one had to be content mainly with fossils, fortuitously formed and fortuitously found. An additional glimpse of the past was possible when it was recognized that the species alive today have built into their gross and molecular structure evidences of their past history.

The modern mind, even of a fervent creationist, has the notion of biological relatedness so firmly embedded that we must remind ourselves of a fundamental difference between species that have been created and species that have evolved.

If each species had been created and remained in essentially the same form until the present, there could be no biological, or as we would now say genetic, relatedness among different species. Even the untutored mind recognizes a relatedness among dogs, wolves, foxes, and coyotes. Yet if each had been separately created they can be no more related to one another than any one of them is to a hippopotamus, dogfish, dodo, or oak tree. The biological, and usual, meaning of "related" is "connected by common ancestry." The separately created, constant through time, canine species could not have shared a common ancestry. Each species could have only creatures of its own kind for ancestors.

The new view that evolution brought was that canine species must have shared a common ancestor at some time in the remote past, and that over the ages, the ancestral population had split into separate lineages that led to the species as we know them today. On a larger scale, an evolutionist could suggest that all members of the Phylum Chordata are related in the sense that all share a common ancestor—some long extinct prochordate. If we accept this notion as worthy of analysis, we can view it as an hypothesis to be tested and formulate the following deduction.

Deduction 11: *If the members of a taxonomic unit, such as the Phylum Chordata, share a common ancestry, that should be reflected in their structure*

This notion—that the structure of all descendants from a common ancestor would show evidences of this descent—is based on the belief that modifications of the original structure would evolve very slowly. Hence, some of the original characters, or obvious modifications of them, must be present in the descendants. And of course if we put the putative descendants in the same taxonomic group, that means we recognize certain structural characteristics that they share.

Comparative anatomy was the discipline that first recorded the common characteristics of organisms in a systematic manner. This is not surprising since, at an earlier time, knowledge of physiology was rudimentary and cellular structure was unknown.

The Flemish anatomist Vesalius (1514–1564) put human anatomy on a firm footing in his *De Humani Corporis Fabrica* of 1543. Twelve years later a French naturalist Pierre Belon (1517–1564) published a book on birds. In it he showed, side by side, the skeletons of a bird and of a human being. The dramatic thing he did was to give the same names to the bones of the bird that had human counterparts. There was no difficulty, for example, in showing that two such apparently different structures—the bird's wing and the human arm—had corresponding bones.

Comparative anatomy was a major activity for biologists from the 16th to well into the 19th century. Skeletons received special attention. Not only were they more permanent than the soft tissues but, when the study of fossils became an active enterprise in the 18th century, the only possible comparisons of living and fossil species were of their bones.

The recognition of similar parts in different organisms is the concept of *homology*. For Belon in the 16th century and for later workers, the proximal bone of the human arm and of the bird wing are modifications of the "same thing." A skeptic could ask,
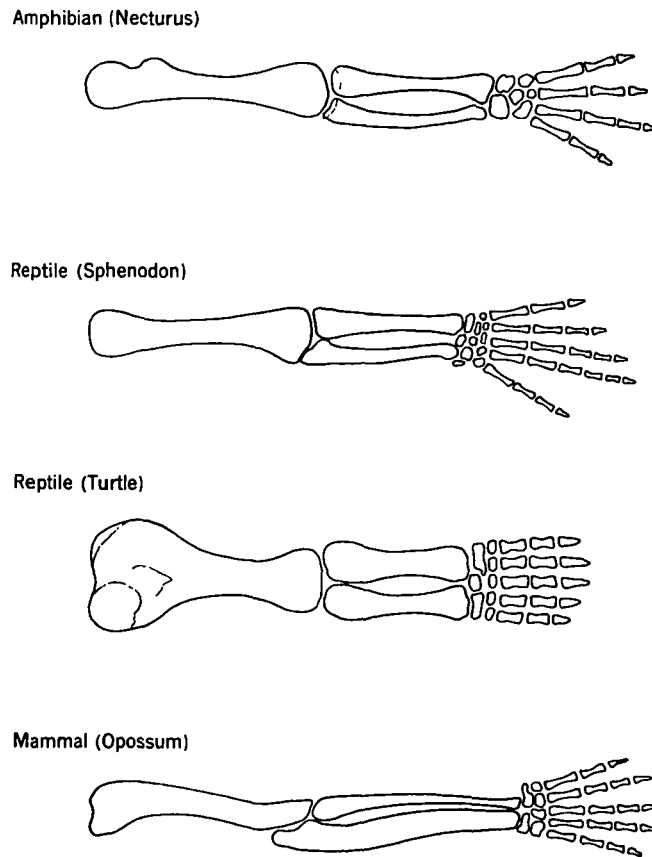
Amphibian (Necturus)

Reptile (Sphenodon)

Reptile (Turtle)

Mammal (Opossum)

Fig. 2.   The front limbs of four kinds of tetrapods.

"How could they be the same thing when they are parts of structures that differ so greatly in appearance and function?" The answer could only have been vague and unsatisfactory. But the concept of evolution made it obvious how the parts of birds and mammals could resemble one another: it would be held that the arm and wing are derived, through evolutionary modifications, from the anterior paired appendage of a common ancestor. Homology, then, is similarity based on common descent.

This explanation could be extended to suggest that the anterior paired appendages of all vertebrates—the pectoral fins of fishes, whales, and dolphins; the wings of birds, bats, and pterodactyls; the digging foreleg of a mole; the hoofed foreleg of horses and cattle; the prehensile arm of a

sloth; and the tool-using hand of man—are examples of the same ancestral structure modified in different ways in different animals (Fig. 2). The driving force, according to the hypothesis, is natural selection acting on variation.

The Phylum Chordata has numerous splendid examples of how the concept of evolution made sense of the details of comparative anatomy. The data of comparative anatomy suggest that the living chordates can be arranged in ten subphyla and classes that indicate, in a very general way, increasing complexity: Hemichorda, Urochorda, Cephalochorda, Agnatha, Chondrichthyes, Osteichthyes, Amphibia, Reptilia, Aves, Mammalia. The first three are marine protochordates; the last seven are vertebrates. The Agnatha, Chondrich-

TIME

PROTOCHORDATES

AGNATHANS

CHONDRICHTHYES

BONY FISH

AMPHIBIANS

BIRDS

REPTILES

MAMMALS

STEM REPTILES

BONY FISH

AGNATHANS

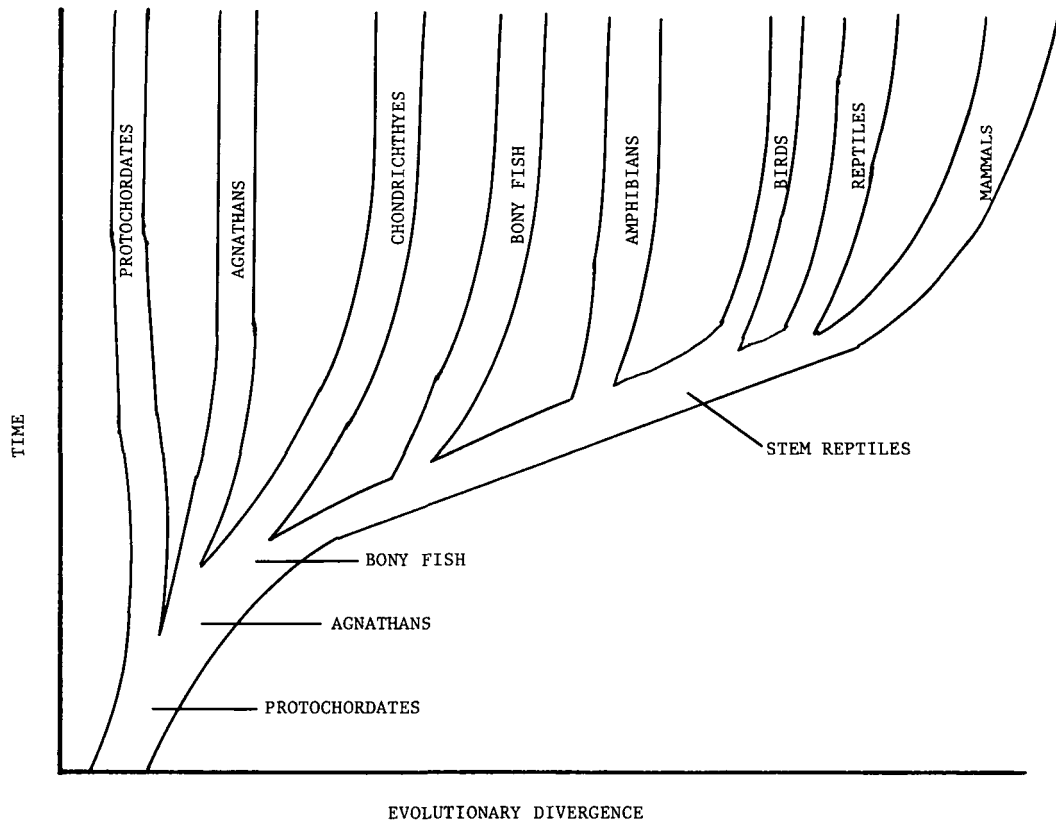PROTOCHORDATES

EVOLUTIONARY DIVERGENCE

FIG. 3. The evolutionary relationships of the major chordate groups.

thyes, and Osteichthyes are fishes. The Amphibia, Reptilia, Aves, and Mammalia are tetrapods.

When the concept of evolution was applied, the data remained the same—only the interpretation changed. Biologists began to think of chordate evolution as a progression from very simple protochordates to the more complex birds and mammals. It seemed clear that different groups had split off the main line (the "main line" being that leading to us, naturally!) and to varying degrees had retained some of the characteristics of their ancestors at the time of the split. Thus the famous cephalochordate, Amphioxus, was looked upon as a relic of a pre-vertebrate stage of chordate evolution. The lamprey and hagfish of today, which differ so much in superficial appearances from the earliest known ver-

tebrates, the ostracoderms, are so like them in fundamental ways that all are placed in the same class—the Agnatha. One can study living Agnatha, therefore, to learn something of a remote agnathan period of vertebrate evolution.

Slowly the paleontological data were obtained to show the broad outlines of vertebrate evolution. To a gratifying degree, the sequence that had been suggested by the data of comparative anatomy turned out to be the sequence of evolution. Figure 3 shows the broad outlines of vertebrate history.

Some of the classic examples of modification of parts that reflect evolution are jaws and ear ossicles, the arteries leaving the heart, the basic structure of all chordates, and the excretory organs. The first two will be described briefly now and the
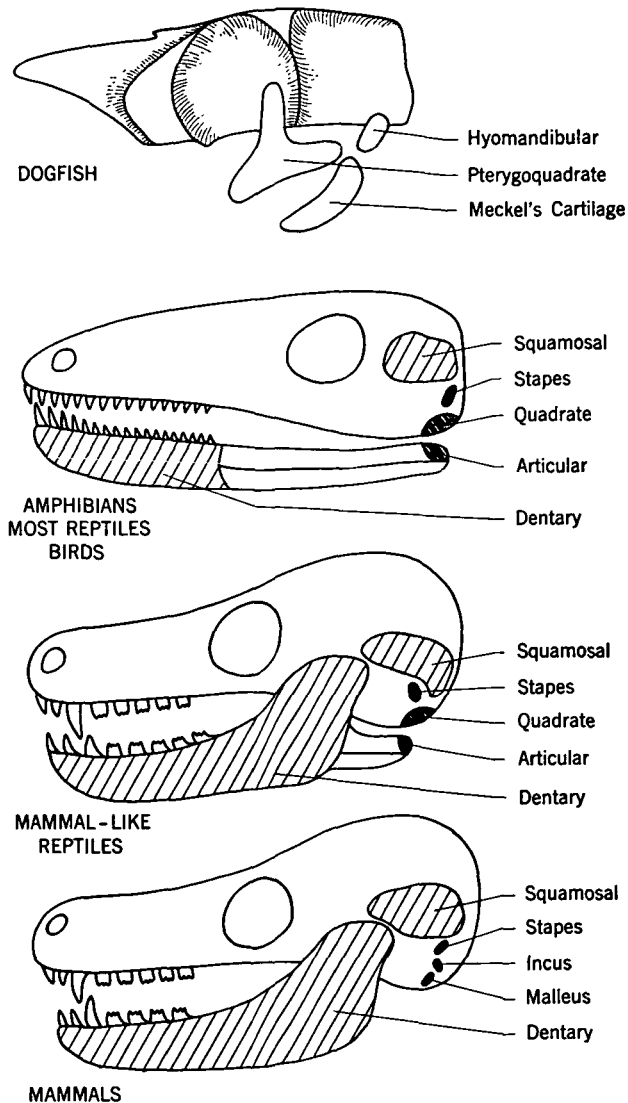
FIG. 4.   The jaw articulation and ear ossicles of four vertebrates.

last two in relation to the next hypothesis, which concerns embryonic development.

Jaw joints and ear bones. The ear has two main functions in the vertebrates. In fishes it is an organ of balance only. In tetrapods the ear retains its function as an organ of balance but adds the detection of vibrations in air. The fishes lack both a tympanic membrane and ear ossicles. The living amphibians have one ear ossicle—the stapes—and, except for the urodeles, a tympanic membrane. Living reptiles and birds have basically the same structure as the amphibians. In mammals, however, there are two additional ear ossicles—the malleus and incus. What could be the origin of these ear bones?

A tentative answer was worked out almost entirely on the embryos of living vertebrates. Figure 4 tells the story briefly. Correlated with the formation of the "new" bone, *i.e.* the stapes in amphibians and the two "new" ones in mammals, there are important changes in the articulation of

FIG. 5. The main arteries of the anterior trunk region of a vertebrate embryo.

the jaws. In the fishes the hyomandibular bone supports the jaws. The amphibian embryo has a hyomandibular but it becomes converted to the stapes of the adult. In a similar manner, the articular of the lower jaw and the quadrate of the upper jaw become reduced in size and move into the ear to form the malleus and incus of the mammals.
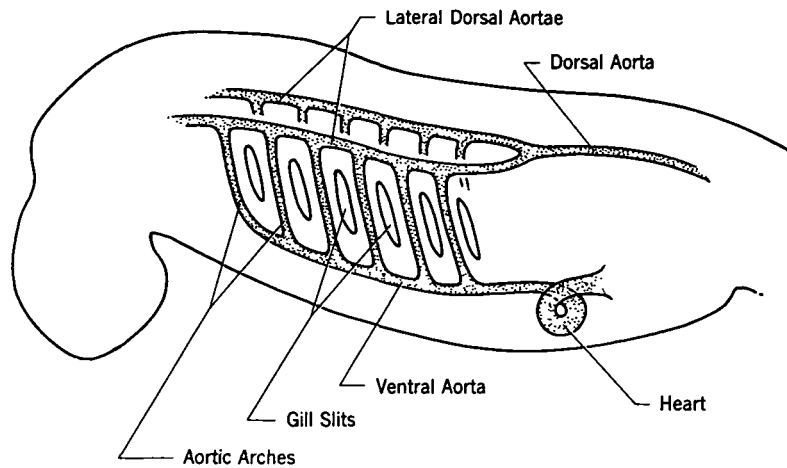
The hypothesis was advanced that these events in development might be a reflection of what had occurred in evolution. One would then deduce that at some stage in the past, presumably when reptiles were evolving into mammals, there would be evidence of the loss of the quadrate and articular as the jaw articulation and the modification of these bones into the incus and malleus. Concurrently, the jaw articulation must have switched to the mammalian pattern—the dentary of the lower jaw moving against the squamosal of the upper jaw. Now this suggests a very interesting and, seemingly, dangerous deduction for a paleontologist to make. Since there must always be some articulation point of the jaws if the animal intends to eat, how could there be a switch from the reptilian type to the mammalian type? It seemed unlikely that parents with the articular-quadrate joint would produce offspring with the dentary-squamosal type. But how else?

The answer was provided by the fossil synapsids, the mammal-like reptiles. As their name suggests, they are intermediate in structure between reptiles and mammals. In recent years a very large number of fossils has been found—mainly in South Africa. The different kinds show all gradations from the characteristic reptilian jaw articulation to that of the mammals. One genus from the Triassic is especially noteworthy. It was given the jaw-breaking name *Diarthrognathus*, which means "two-jointed-jaws," in recognition of the fact that it had two functional jaw articulations—reptilian and mammalian. One could not ask for a better intermediate between reptiles and mammals.

For more details on these dramatic discoveries see Goodrich (1930, ch. 8), Romer and Parsons (1977, pp. 480–483), Colbert (1980, pp. 136–137, 246–251), Hildebrand (1982, pp. 261–263), Young (1971, pp. 411–413; 1975, p. 124; 1981, p. 416), Romer (1969), Berrill (1955) and Luria, Gould, and Singer (1981, pp. 631–633).

The transformation of the aortic arches. The embryos of all vertebrates have a circulatory system of almost diagrammatic simplicity—in contrast to the confusing patterns among the adults. In the anterior part of the body there is a ventral vessel that carries blood anteriorly to the region of the gill slits (Fig. 5). There six pairs of aortic arches branch off and extend through the gill bars to the lateral dorsal aortae. The
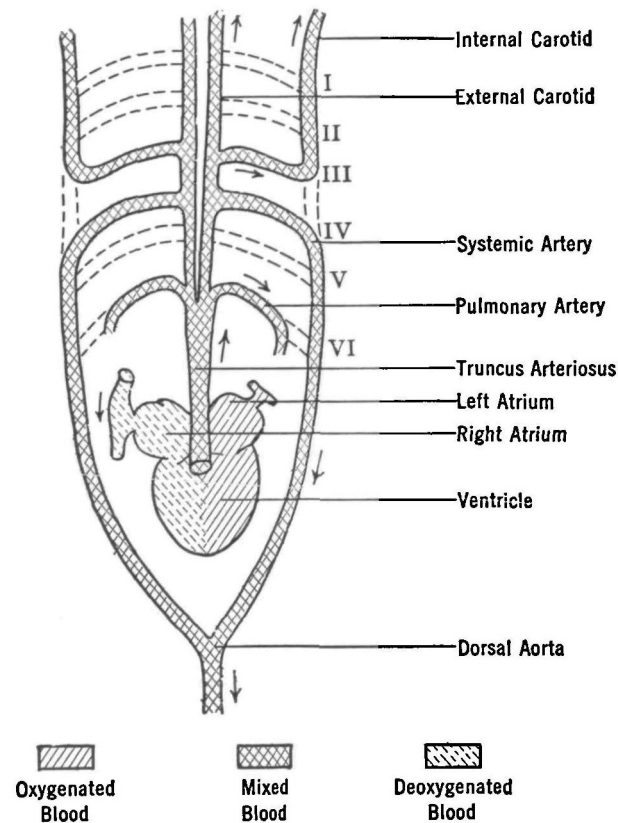
JOHN A. MOORE

FIG. 6.   The transformation of the aortic arches in a frog.

lateral dorsal aortae join posteriorly to form the dorsal aorta, which carries blood to all parts of the body behind the gill region.

This simple pattern of the embryo is transformed in very different ways in different vertebrates to produce the circulatory systems of the adults. Figures 6 and 7 provide two examples. In these two figures the point of view has been changed from that of Figure 5. If we were to look at the embryo of Figure 5 from below and spread the lateral dorsal aortae apart for clarity, we would end with the perspective of Figures 6 and 7.

The frog embryo passes through a stage with the six aortic arches. With further development some are lost or modified until the adult pattern as shown in Figure 6 is formed. The human embryo also has six pairs of aortic arches (never all at one time) and these become transformed (Fig. 7) but

in a manner quite different from that of the frog.

For more details on the transformation of the aortic arches see Goodrich (1930, ch. X), Romer and Parsons (1977, pp. 416–426), Hildebrand (1982, pp. 261–263), Young (1975, pp. 210–212) and de Beer (1928, pp. 327–336).

How can one account for these phenomena? If each species had been created, why would there be this unduly complex way of making a circulatory system? Wouldn't it be simpler to begin with the adult plan? On the other hand, one could account for the data in a satisfactory manner if the concept of evolution was invoked as an explanatory hypothesis. In evolution, what is already in existence is modified. In creation, there is nothing in existence to be modified. Thus, if the early chordates had a a pattern of blood vessels as shown in
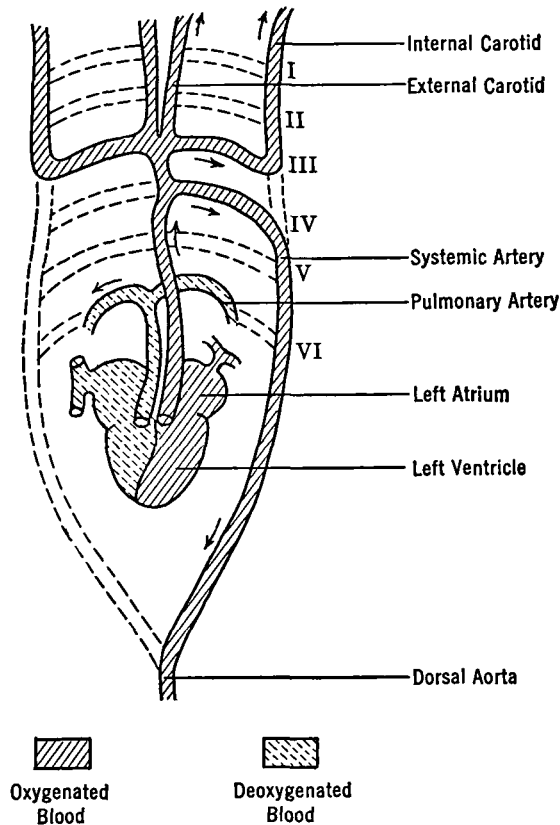
FIG. 7. The transformation of the aortic arches in a mammal.

Figure 5, modifications of that simple arrangement by retaining some of the aortic arches and eliminating others would give the very diverse patterns that characterize the different chordate classes.

There are important differences between the relation of the data on ear ossicles to the concept of evolution and the relation of the data on aortic arches to the concept of evolution. Before there was fossil evidence from the mammal-like reptiles, one could say only that the transformation of the reptilian articular and quadrate into the mammalian malleus and incus could be explained on the basis of evolution. That the concept of evolution could explain the data is *indirect evidence* for the correctness of the hypothesis. It was only later that the fossil record showed that the deduction that the reptilian articular and quadrate evolved into the mammalian malleus and incus was

true beyond all reasonable doubt. The fossils, therefore, provided *direct evidence* for the correctness of the hypothesis of evolution.

In a like manner, the data on the aortic arches can be explained on the basis of the modifications of a fundamental plan to produce the conditions we observe in the classes of vertebrates. The evidence is also indirect. It seems likely that the data on aortic arches will always remain indirect evidence for the correctness of the hypothesis of evolution—hearts and blood vessels are not usually preserved in the fossil record.

Thus the concept of evolution allows us to "make sense" out of the data—and that is the grand purpose of a good theory. This is not an easy point of view to understand—especially for students—as Medawar (1981) points out:

The reasons that have led professionals without exception to accept the hypothesis of evolution are in the main too subtle to be grasped by laymen. The reason is that only the evolutionary hypothesis makes sense of the natural order as it is revealed by taxonomy and the animal relationships revealed by the study of comparative anatomy . . . . In biosystematics and comparative zoology the alternative to thinking in evolutionary terms is not to think at all.

It takes effective teaching and serious thinking by the student for this point to be mastered.

The discussion of these two examples, ear ossicles and aortic arches, emphasizes the close relationship between adult structure and embryology. This is not surprising—the structure of adults is derived directly from an earlier stage in life when they were embryos. The next deduction, therefore, will come as a natural outgrowth of the last.

Deduction 12: *If the members of a major taxonomic unit share a common ancestry, that should be reflected in their embryonic development*

Early in the 19th century embryologists noticed that embryos of different classes of chordates resemble one another much more closely that do the adults. Darwin mentioned that Agassiz had inadvertently failed to label an embryo when he first obtained it and then could not tell "whether it be that of a mammal, bird, or reptile" (*Origin*, p. 439).

After 1859 one of the main preoccupations of embryologists was to study embryos for whatever light they could throw on evolution. In those days when the fossil record was even more inadequate than it is today, the changes in the course of development were thought to reflect what had occurred in phylogeny. There could almost never be any direct evidence for the evolutionary changes in the soft tissues that fail to fossilize.

Embryology rises greatly in interest, when we thus look at the embryo as a picture, more or less obscured, of the

common parent-form of each great class of animals (*Origin*, p. 450).

As more and more vertebrate embryos were studied it seemed that, in some very general way, embryonic development did reflect evolution. This led the German biologist Ernst Haeckel (1834–1919) to propose his famous aphorism: "Ontogeny Recapitulates Phylogeny." Experience has shown that to be an extreme statement. In development we do not pass through stages in which we resemble *adult* fishes, amphibians, reptiles, and lower mammals. Nevertheless, human beings do recapitulate some of the features of the embryos of lower forms.

The basic chordate body plan. There are three diagnostic characteristics of all species that are classified as chordates: the possession of a notochord, gill slits or pouches in the pharynx, and a dorsal nerve tube. The human adult has only one—the dorsal nerve tube, which has become our brain and spinal cord. As embryos we had all three. Our notochord lasted only through the early embryonic stages. The gill pouches also disappear in development but the first becomes the Eustachian tube of our ear.

Figure 8 shows an idealized chordate with little except the three diagnostic characteristics. We now know that all chordate embryos show this same basic pattern early in development.

This discovery finds a ready interpretation if all chordates share a common ancestor. It is reasoned that the very early chordates possessed the features shown in Figure 8 and, as evolution proceeded, the embryos of higher forms continued to reflect the ancestral condition. The intense interest shown in *Amphioxus* is based on the fact that, in many aspects of its morphology, it has the features we predict for the earliest of chordates (Willey, 1894). The ammocoete larva of the lamprey is held in the same high regard—and for the same reason (Moore, 1957, ch. D-4).

The example just given resembles that of the aortic arches. The concept of evolution allows us to understand the data. And, once again, if the theory suggests an intellectually satisfying explanation and
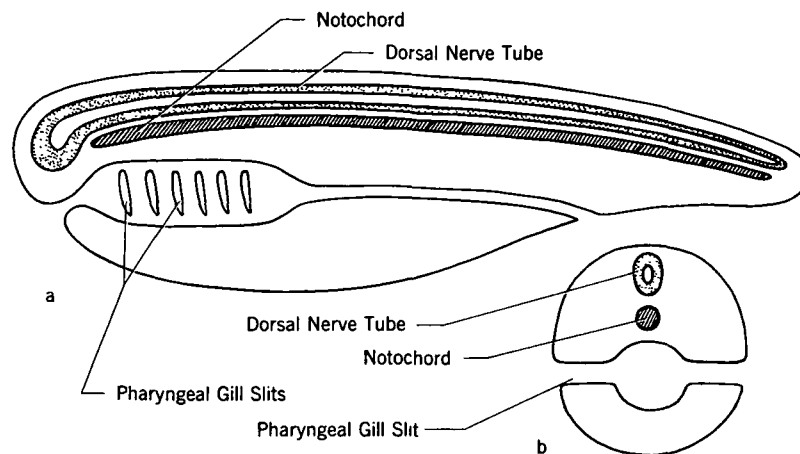
FIG. 8. An idealized chordate showing the three diagnostic characteristics: a. lateral view; b. cross section in the gill region.

does not invoke supernatural forces, it can be accepted.

The vertebrate kidneys. An even more famous case of ontogeny recapitulating phylogeny is the vertebrate kidney. Figure 9 shows the events in a highly schematic manner. The early embryos of reptiles, birds, and mammals have a kidney in the anterior portion of the coelom—the pronephros. Later in development the pronephros degenerates and a second kidney takes over—the mesonephros. It, too, disappears and is replaced by a third kidney—the metanephros, which remains as the kidney of the adult. The embryos of fishes and the agnathan lamprey start with a pronephros in the embryo and replace it with a mesonephros, which is the kidney of the adult. No metanephros develops.

Without the concept of evolution, the recapitulation of pronephros, mesonephros, and metanephros in human embryos would not make much sense. With the concept of evolution, it does.

More details are to be found in Goodrich (1930, ch. 13), de Beer (1958b) and Romer and Parsons (1977, ch. 13).

Deduction 13: *If evolutionary divergence is the basis of organic diversity, that should be reflected in our system of classification*

Classification, often regarded as one of the dullest parts of the biological sciences, is a device of utmost importance in enabling us to deal with everyday life. Classification consists of combining objects and ideas on the basis of some characteristics held in common. Classification is the most powerful method we possess for packaging information. It is so much a part of our lives that we forget how basic it is.

Suppose that someone begins to speak to you about a VW, one that you have never seen. Nevertheless, you automatically recognize "VW" as "automobile." With that recognition you will immediately have a vast amount of available information—about motors, wheels, seats, batteries, gasoline, role in accidents, relation to pollution and the Persian Gulf, and a host of other details.

Classification is the same information-packed and predictive device in biology. Let us suppose that you have carefully dissected and studied one mammal—fetal pig, rabbit, white rat, whatever. You are next presented with a new mammalian species, never before studied by a scientist. Without touching the creature, you would be able to make a host of predictions about its anatomy, physiology, reproduction, and development. When you checked the predictions they would be found to be correct or almost correct in most instances. To paraphrase a well-known dictum: "when you have studied one mammal, you know them all."

Different systems of classification for
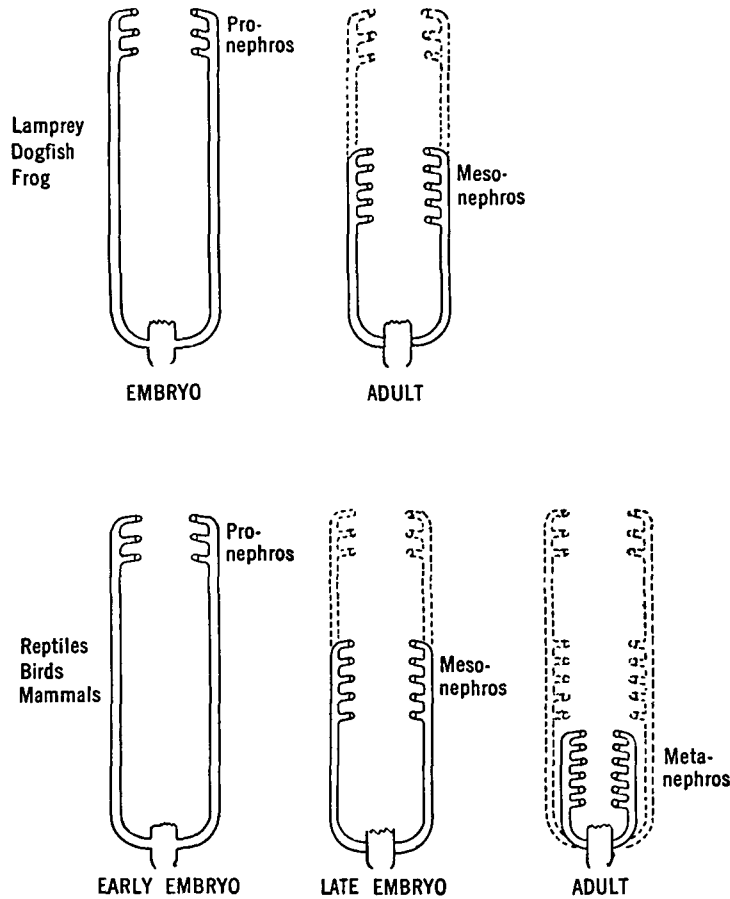
FIG. 9.   Developmental changes in the kidneys of vertebrates.

biological species have been used for different purposes. The ancient Herbrews made an important distinction between animals that were clean *vs.* unclean. The clean could be eaten, the unclean not. For details see chapter 11 of Leviticus and also McKenzie (1965, pp . 141–143).

Aristotle, the father of so many fields in biology, is also acclaimed as the father of the classification of animals. The principal features that he employed were the presence or absence of blood and the mode of reproduction (Thompson, 1910). This results in the main categories shown in Table 3.

The modern period of biological classification begins with Karl von Linné (1707–1778) who regularized the system of giving

Latin names to all plants and animals (including himself—"Linnaeus"; for biographies see Blunt, 1971 and Larson, 1971). His *Systema Naturae* of 1758 is the starting point for our taxonomy. Linnaeus, following Aristotle, employed a very few characteristics for classifying organisms: nature of the heart, type of reproduction, warm or cold blooded, etc. This procedure of using a only a few characteristics is called an *artificial system.*

As more and more was learned about the anatomy and embryology of animals, the artificial system proved to be inadequate: it appeared to unite species that differed in fundamental ways. It was suggested that a *natural system* of classification would better reflect the state of nature. The natural

TABLE 3. *Aristotle's basic classification of animals.*

Animals without blood	
without shells	worms
with a soft shell	crabs
with a calcareous shell	snails
with an articulate body	insects
Animals with blood	
Oviparous	
with fins	fishes
without feet	serpents
with feet	reptiles
with feet and wings	birds
Viviparous	mammals

TABLE 4. *A typical mid 19th century classification. From Baird (1851).*

Division I. Radiata

   Class 1. Infusoria (protozoans)
   Class 2. Zoophyta (hydroids and sponges)
   Class 3. Acalephae (medusae and ctenophores)
   Class 4. Echinoderms (starfish, sea urchins)
   Class 5. Intestina (flatworms, nematodes)

Division II. Mollusca

   Class 1. Acephala (tunicates and bivalve mollusks)
   Class 2. Gastropoda (snails)
   Class 3. Pteropoda (pteropods)
   Class 4. Cephalopoda (octopus, squid)

Division III. Articulata

   Class 1. Annelida (annelid worms)
   Class 2. Cirrhopoda (barnacles)
   Class 3. Crustacea (crustaceans)
   Class 4. Arachnida (spiders, mites, scorpions)
   Class 5. Insecta (insects)

Division IV. Vertebrata

   Class 1. Pisces (agnathans, sharks, bony fish)
   Class 2. Reptilia (amphibians and reptiles)
   Class 3. Aves (birds)
   Class 4. Mammalia (mammals, including man)

system differed only from the artificial system in employing many more characteristics, including those of internal anatomy and development. Although the details of a natural system of classification could not be agreed upon by all, a representative one from the middle of the last century is shown in Table 4 (modified from Baird, 1851, vol. 2, pp. 213-219). The basic four divisions are those of Cuvier.

The way the natural system worked in practice can be understood by seeing how two of the "errors" of the scheme shown in Table 4 were corrected. In Division I, the Radiata, the hydroids are placed in one class and the medusae in another. That is a reasonable step if one uses only external morphology. The hydroids are plant-like species that are usually sessile. The medusae, or jellyfish, are free swimming cup or plate shaped animals—with no apparent similarities to the hydroids. Eventually it was discovered that most species of hydroids reproduce by asexual budding and the buds are medusae. Furthermore, many of the medusae reproduce sexually and the offspring are hydroids. Before this was known, there were cases where two very different forms were placed in separate classes when they were none other than parent and offspring of the same species.

A similar example is the Class Acephala of the Mollusca, which combines the tunicates and the bivalve mollusks. A bivalve mollusk without its shell is a rather amorphous creature—recall the last oyster on a half shell that you ate. The tunicates are,

likewise, usually rather featureless lumps growing on wharf pilings. So bivalve mollusks and tunicates were put in the Acephala because they lacked well-marked heads and did not seem to have much in the way of positive characteristics. The story changed when the embryos of tunicates were discovered. They proved to be tiny tadpole-like larvae with a notochord, dorsal nerve tube, and pharyngeal gill slits. The adult retains only the gill slits. Thus it seemed more natural to include the tunicates with the other kinds of animals that have those three characteristics—the chordates.

One of the most vigorous supporters of the natural system was Asa Gray. He notes that the purpose of the artifical system of Linnaeus "is merely to furnish an easy mode of ascertaining the names of plants; their relationships being left out of view" (Gray, 1842, p. 185). The artificial system is still used today for one purpose—keys for identifying plants and animals. Can you consider, for example, having to check the life cycle of a putative chordate to see whether or not it ever had a notochord or pharyn-

geal gill slits or whether a plant in hand had developed from a seed with one or two cotyledons?

The purpose of the natural system is to ascertain relationships.

The object proposed by the natural system of botany, is to bring together into groups those plants which most nearly resemble each other, not in a single and perhaps unimportant point (as in an artificial classification), but in all essential particulars; and to combine the subordinate groups into larger natural assemblages, and these into still more comprehensive divisions, so as to embrace the whole vegetable kingdom in a methodical arrangement. All the characters which plants present, that is, all the points of agreement or difference, are employed in their classification; those which are common to the greatest number of plants being used for the primary grand divisions; those less comprehensive for subordinate groups &c.; so that the *character*, or description of each group, when fully given, actually expresses all the known particulars in which the plants it embraces agree among themselves, and differ from other groups of the same rank. This complete analysis being carried through the system, from the primary divisions down to the species, it is evident that the study of a single plant of each group will give a correct (as far as it goes), and often a sufficient idea of the structure, habits, and even the sensible properties of the whole (Gray, 1842, p. 191).

But what can possibly be the basis of there being groups of related species? We noted before that if species are separately created they cannot be related in any biological manner whatsoever. Yet there are groups of organisms: groups of individuals make up a species; related species are united in a genus; related genera in a family; related families in orders, orders in classes, and so on.

It was difficult to provide a naturalistic explanation for how there could be natural groups. Some saw no need to. Agassiz rec-

ognized the problem and offered a personal answer.

The divisions of animals according to branch, class, order, family, genus, and species . . . constitute the primary questions respecting any system of Zoology, [and] seem to me to deserve the consideration of all thoughtful minds . . . . To me it appears indisputable, that this order and arrangement . . . [are] in truth but translations into human language of the thoughts of the Creator (Agassiz, 1859, pp. 8–9).

By 1859 the major groups had been delimited in a manner that, for the most part, are the natural groups we recognize today. This had been accomplished by detailed studies of the anatomy of the adults and the beginnings of information on development. When the hypothesis of evolution was suggested there was no change in the system of classification. What had changed was, for the first time, there was a naturalistic explanation for how there could be natural groups: the data could be explained by the hypothesis that all the members of any taxonomic group—from species to phyla—shared a common ancestor.

The deduction has proved to be true.

Deduction 14: *If there is a unity of life based on descent from a common ancestor, this should be reflected in the structure of cells*

And it is—to an astonishing degree. Common ancestry demands a unity of life and nowhere is this more obvious than in the fact that the bodies of nearly all organisms are built of the same units of structure—cells.

By the time of the *Origin* it was becoming increasingly obvious that cells are important structural units in plants and animals. Plant cells, or more properly their walls, had been known for generations and often illustrated beautifully (Grew, 1682; Moore, 1972*b*, pp. 28–35). In 1839 Theodor Schwann had made a cogent case for cells being a fundamental unit of structure in animals (see Moore, 1972*a*, ch. 2) but to him cells were not permanent structures;

they were formed by the body in a process thought to resemble crystalization. In 1855 Virchow suggested the hypothesis *omnis cellula e cellula* (all cells from cells) which, when proved to be true, suggested that every cell is the current expression of a lineage of life extending back in time to the origin of life itself.

During the last half of the 19th century, considerable knowledge of cells at the level of resolution of the light microscope was obtained. Cells were found to exist in great variety but all shared a basic structure consisting of an outer limiting membrane, a nucleus, and associated cytoplasm. *Omnis cellula e cellula* was accomplished by mitosis except in the formation of gametes—then meiosis was the mechanism. There were questions about the microorganisms—were bacteria really cells and did they have a nucleus? These debates lasted until the availability of the electron microscope (EM) and improved techniques settled many issues of fine structure.

For us today the most exciting information about cell structure is coming from EM studies. This new knowledge has even resulted in a fundamentally different scheme of classification. The old system, up to about 1950, recognized three main kingdoms: microorganisms, plants, and animals. Today more and more biologists prefer a scheme that recognizes five kingdoms, with a fundamental distinction between organisms with nucleated cells and those with non-nucleated cells (Whittaker and Margulis, 1978; Luria, Gould, and Singer, 1981, pp. 754–757). Those without nuclei are known as Prokaryota ("before nucleus") and those with nuclei as Eukaryota ("true nucleus"). This is the scheme:

Prokaryota
Kingdom 1. Monera: bacteria, mycoplasms, spirochaetes, blue-green algae.
Eukaryota
Kingdom 2. Protista: protozoans, green algae.
Kingdom 3. Fungi: yeasts, molds, mushrooms.

Kingdom 4. Animalia: multicellular animals.
Kingdom 5. Plantae: red and brown algae, bryophytes, vascular plants.

Evolutionists in the 19th century more or less accepted the hypothesis that life must have started with organisms at least as simple as a bacterium yet few of them would have dared to be so optimistic as to believe that a useful fossil record existed for such tiny and fragile creatures.

In recent years, however, new methods of collecting and preparing specimens are providing us with information about organisms that lived more than three billion years ago. The oldest so far discovered are from Western Australia and South Africa. The Australian material comes from a site with the improbable name North Pole (Groves, Dunlop, and Buick, 1981). There, in the Warrawoona Group rocks, specimens identified as blue-green algae with a probable age of 3.5 billion years have been discovered. The Fig Tree Chert of South Africa has yielded what seem to be bacteria (*Eobacterium*) and blue-green algae (*Archaeospheroides*). Thus the first evidences of life are of prokaryotes that are much like the prokaryotes living today.

Living prokaryotes are all small—usually less than 10 micrometers and some only 0.2 micrometers. In common with all cells, there is an outer limiting membrane or plasmalemma. The contents of the cell are not compartmentalized. There are ribosomes but no mitochondria, Golgi, chloroplasts, or lysosomes. There is no nucleus, that is, a membrane-bound vesicle containing chromosomes. There is, of course, DNA. This is in the form of a double helix, which is not associated with proteins, and is free in the cell. The DNA may form a tangled mass visible with the EM as a nucleoid.

The characteristic features of the prokaryotic cell, therefore, are a plasmalemma, RNA-containing ribosomes, and naked DNA. We are now realizing that this

was the limit of evolutionary complexity for most of life's span on earth. The generally accepted date for the formation of the earth is 4.5 billion years ago. The oldest known prokaryotic organisms date to 3.5 billion years ago. There is considerable debate about the earliest eukaryotic organisms—paleocytology is a difficult field—but a date of 1 billion years ago seems the best we can do for the present. Thus for the first 70 percent of the time life is known to have existed, only prokaryotic organisms were present. This level of organization permitted only tiny cells that existed singly or formed simple filaments. But masses of filaments can form large structures. For example, the stromatolites that occur on some coasts may form large biscuit shaped structures. Fossil stromatolites, dating back about 1.8 billion years, are known from the Great Slave Lake region of Canada and about 3.5 billion years ago from Western Australia (Walter, Buick, and Dunlop, 1980). Nevertheless, no prokaryotic cells show the complexity of eukaryotic cells and they have not been able to form complex multicellular organisms with many kinds of differentiated cells.

Then about a billion years ago, life took a momentous step—the eukaryotic cell came into existence. The important difference between a prokaryotic and eukaryotic cell is that the latter has some of its contents compartmentalized. That is, related sets of molecules concerned with the same function are surrounded by membranes that provide some isolation and regulate the passage of materials in and out of the compartments. The DNA, now associated with protein, is surrounded by a nuclear membrane with pores. The energy-yielding reactions are compartmentalized in mitochondria. The photosynthetic reactions of green plants are isolated in chloroplasts. Some of the secretory processes are restricted to the Golgi. Other membrane systems, such as the endoplasmic reticulum and the associated ribosomes, provide the protein synthesizing machinery of the cell.

In recent years an interesting hypothesis for the origin of certain organelles of eukaryotic cells has gained increasing support. The suggestion is that structures such as mitochondria and chloroplasts began as prokaryotic cells. These entered other cells where they became symbionts. The result was the eukaryotic cell. Margulis (1981) provides a summary of the evidence. Examples of symbiosis have long been known: algae and fungi cooperate to form lichens; algae live in the cells of several kinds of animals, including the giant clam, to which they supply food; and the nematocysts of coelenterates survive digestion by nudibranchs and are moved to the nudibranch's dorsal surface where they function in defense of the host.

Once the functions of cells became compartmentalized, as at the eukaryotic level of organization, there can be a true division of labor. With time this permitted the evolution of multicellular organisms with some cells different from others. Groups of specialized cells then took over the separate physiological functions. Yet even in the largest and most complex organisms the fundamental unit of structure and function remains the cell. The cells of eukaryotic organisms form an integrated whole. The functioning of the individual cells of the complex eukaryotic organisms can be seen as necessary for the life of the organism just as the functioning of the organism seems to be concerned mainly with the life of its individual cells. The cell is the organism's way of doing things just as the organism is the cell's way of doing things.

Most of the details of structure and function in the cells make sense because what cells are and what they do are reflections of their evolutionary history.

Some useful references to this rapidly changing field are Bernal (1967), Margulis (1970a, 1970b), Orgel (1973), Ponnamperuma (1972), Knoll and Barghoorn (1977), Hanson (1977), Dickerson (1978), J. W. Schopf (1978), Woese (1981), Cloud (1978), Folsome (1979), Scientific American (1979a), Walter, Buick, and Dunlop (1980), Groves, Dunlop, and Buick (1981), Barghoorn (1971), Cloud and Glaessner (1982), Avers (1976), and Freifelder (1983).

Deduction 15: *If there is a unity of life based on evolution, that should be reflected in the molecular processes of organisms*

There is a tremendous diversity in structure, physiology, and behavior among the species of the five kingdoms of life. There is far less diversity in the cells of which their bodies are composed. There is still less diversity in the basic molecular processes that occur in all cells. This has become clear only in recent years with the wealth of new techniques available for the study of molecular events in cells.

The fact that the basic metabolic reactions in the cells of all organisms are so much alike can be interpreted to mean that they developed in the first stages of life and have been retained, with relatively little modification, in the descendants. It is difficult to find another naturalistic explanation. We cannot study the molecular reactions of those ancient blue-green algae and bacteria from the North Pole deposits of Australia or the Fig Tree Cherts of South Africa. Nevertheless, these ancient progenitors have closely similar living counterparts and, by studying them, we can make reasonable inferences about what happened in the past.

Some of the more striking of these molecular uniformities are:

1. All cells consist of the same classes of organic compounds: nucleotides, proteins, lipids, and carbohydrates.

2. Reactions involving these organic compounds are controlled in all cells by the same class of proteins—the enzymes.

3. In all cells, DNA contains the coded information that regulates the life of the cell and transmits the information to the next generation. (In a few types of viruses the closely similar RNA performs the same functions.)

4. In all organisms, DNA is composed almost entirely of combinations of six kinds of molecules: 2 pyrimidines (thymine and cytosine), 2 purines (adenine and guanine), a sugar (deoxyribose), and phosphate. The purine and pyrimidine bases are sometimes chemically modified.

5. In all organisms, RNA is composed of combinations of six kinds of molecules: 2 pyrimidines (uracil and cytosine), 2 purines (adenine and guanine), a sugar (ribose), and phosphate. Again, the bases are sometimes chemically modified.

6. The DNA code, which transmits hereditary information from generation to generation, and provides the information for intracellular synthesis and control, consists of the sequence in which the purines and pyrimidine bases are arranged. Each specific triplet of bases is related to a specific amino acid. The code is universal for all forms of life—a simply astonishing fact, except within the context of evolution.

7. In all organisms the specific information encoded in DNA serves as a template for the synthesis of specific messenger RNA. Enzymes organized by specific messenger RNA molecules, in cooperation with transfer RNA, join amino acids to form specific proteins.

8. In all cells, proteins are synthesized from about 20 kinds of amino acids. Except for the 5 carbon sugars of DNA, RNA, ATP and other specialized molecules including some co-enzymes, the major carbohydrates of cells consist of 6 carbon sugars, such as glucose, and polymers of 6 carbon sugars, such as starch and cellulose. Important lipids in all cells consist of glycerol plus 3 molecules of fatty acids or 2 molecules of fatty acid and 1 molecule of a phosphorus-containing compound. Nucleic acids, proteins, carbohydrates, and lipids account for nearly all of the organic compounds of life, of which there are enormous numbers of kinds. Nevertheless, this great diversity is based on relatively few building blocks—much as the rich English language combines only a few of the 26 letters to fill an unabridged dictionary.

9. All cells obtain energy by oxidizing reduced compounds, as in glycolysis—the anaerobic fermentation of glucose to pyruvic acid. In glycolysis, chemical energy is transferred to convert ADP to ATP. ATP is the immediate energy source for cells. Some prokaryotes and most eukaryotes use oxygen as a major electron acceptor, as in the aerobic breakdown of pyruvic acid to carbon dioxide and water. In these aerobic

processes, as compared with anaerobic reactions, much more energy is transferred to convert ADP to ATP. These are striking examples of the fact that many of the basic metabolic pathways are the same or similar in all cells.

Most of the energy for life is the energy of sunlight captured by green plants in the reactions of photosynthesis and stored in carbohydrates. Chemosynthetic bacteria carry out processes very similar to those of other organisms, even though they power their reactions from reduced compounds such as methane, rather than from sunlight.

10. Nowhere is the biochemical unity of life shown more dramatically than in experiments where genes of higher organisms, such as human beings, can be incorporated into the DNA of bacteria. There, using the bacterial synthetic machinery, the human gene can direct a human-type protein to be synthesized.

Although the sorts of data just listed are not proof of evolution, there is no other naturalistic explanation that can make as much sense of them. Similarly, there are no molecular data that falsify the concept of evolution. More than anything else, the molecular data point to a unity of life based on common descent.

Many more examples of the biochemical unity of life could be given and there is an almost irresistable urge to do so—mainly because so much of it is recent and hence of great interest to us (the teachers). Students may be content with a more modest dose, especially if it means that they will be introduced to other equally important ideas—new to them but old for us.

For more details see Purves and Orians (1983), Dustin (1980), Avers (1976), Luria, Gould, and Singer (1981), Dickerson (1972, 1978), Folsome (1979), Margulis (1970*b*), Orgel (1973), Ayala (1976), J. W. Schopf (1978), Scientific American (1979*a*), Nei and Koehn (1983), and Freifelder (1983).

A summing up

This ends our formal analysis of Darwinism, which was accomplished mainly in a series of deductions stemming from the proposition, "If the hypothesis of evolu-

tion is true . . . ." The first 10 deductions sought a direct test of the hypothesis. The last 5 emphasized the role of the hypothesis in bringing rational order to the data of biology and geology.

It is this second function of the concept of evolution that has so impressed scientists. To a considerable degree the two statements quoted earlier—Dobzhansky's that "Nothing in biology makes sense except in the light of evolution" and Medewar's that "the alternative to thinking in evolutionary terms is not to think at all"— are fully accepted by scientists familiar with the data of biology and geology.

In the last half of the 19 century the concept of evolution guided the research programs in comparative anatomy, cytology, inheritance, paleontology and, to a lesser degree, in systematics and animal behavior.

By 1900 Darwin and other scientists had made it possible to accept as true beyond all reasonable doubt that evolution had occurred. The most direct evidence had come from paleontology but all major disciplines of biology made a contribution. The more original portion of Darwin's thesis, namely that the mechanism of evolutionary change is primarily natural selection acting on variations, was not so generally accepted. Fleeming Jenkin continued to be the monkey on Darwin's back—and would remain so until routed by Mendelian genetics.

Evolution after Darwin

The last edition of the *Origin* was published in 1872 and Darwin was interred in Westminister Abbey April 26, 1882 a few feet from another of England's illustrious sons—Sir Isaac Newton. Together they had revolutionized the biological and physical sciences.

The amount of research performed in the last hundred years that relates directly or indirectly to evolutionary biology is enormous in quantity but more modest in conceptual advances. For the most part the work has been "normal science" as Kuhn (1970) designates the mopping-up activities that follow a scientific revolution.

The problem for those teaching first-year

college and university courses in general biology is to select among the many topics that might be considered a few that can be given meaningful consideration in the ever tight schedule. My suggestions will follow. They tend to be those topics that have been well documented and are of obvious importance to evolutionary theory. Some of the more active fields in evolutionary biology today do not meet these two criteria and I cannot see that they should be included to the exclusion of the other suggested topics. I prefer to include what is important and probable in a first-year course and leave the more questionable areas of research to advanced courses.

After a period of intense activity and interest in the years following the *Origin*, evolutionary biology underwent an eclipse. Then, in the 1930s, there was renewed activity that saw the then isolated fields of genetics, systematics, and paleontology addressing in unison the problems of evolution. This was the "Modern Synthesis" that set the course for research and speculation that lasts to this day (Mayr and Provine, 1980).

The seminal works of the Modern Synthesis were Dobzhansky (1937), Mayr (1942), and Simpson (1944), to which we should add Fisher (1930), Wright (1931), and Haldane (1932) who provided a mathematical framework for the analysis of natural populations and evolutionary change. Most of these founding fathers revised their initial contributions: Dobzhansky (1970), Mayr (1963, 1970), Simpson (1953), and Wright (1968-1978).

Other useful sources of information and analysis, appearing in this century but mainly since the Modern Synthesis, are: Headley (1900), Morgan (1903), Weismann (1904), Lock (1906), Butler (1911), Crampton (1911), Geddes and Thomson (1911), Dendy (1912), Delage and Goldsmith (1913), Lloyd (1914), Morgan (1916), Lull (1917), Morgan (1925), Kerr (1926), Morgan (1935), Robson and Richards (1936), de Beer (1938), Goldschmidt (1940), Cott (1940), J. Huxley (1940, 1942), Lack (1947), Clausen, Keck, and Hiesey (1948), Jepsen, Mayr, and Simpson (1949), Simpson (1949), Schmalhausen (1949), Stebbins (1950), Simpson (1953), J. Hux-

ley, Hardy, and Ford (1954), Dobzhansky (1955), Mayr (1957), Maynard Smith (1958), Rensch (1959), Tax (1960), Blair (1961), Dobzhansky (1962), Rhodes (1962), Grant (1963), Mayr (1963), G. C. Williams (1966), Jukes (1966), Dobzhansky, Hecht, and Steere (1967-), Wright (1968-1978), Ehrlich, Holm, and Raven (1969), Mayr (1970), Grant (1971), Dobzhansky (1970), Salthe (1972), Ehrlich, Holm, and Parnell (1974), Lewontin (1974), Nei (1975), Frazzetta (1975), Mayr (1976), Ayala (1976), Stebbins (1977), Volpe (1977), Grant (1977), Dobzhansky, Ayala, and Valentine (1977), M. J. D. White (1978), Futuyma (1979), Solbrig and Solbrig (1979), Ayala and Valentine (1979), Stanley (1979), P. J. Darlington (1980), Mayr and Provine (1980), B. Wallace (1981), Atchley and Woodruff (1981), Mayr (1982), Maynard Smith (1982), Stebbins (1982), Milkman (1982), and Ayala (1982). These references are in chronological order to enable one to trace the evolution of our thinking about evolution—there was a great change in what was said after the Modern Synthesis of the 1930s and 1940s.

The fossil record

Today very much more can be said about the history of life than was possible in Darwin's time. Generations of paleontologists have explored most of the earth's crust and filled the museums with fossils. The data of paleontology that were supportive of the concept of evolution a century ago have now reached the state where all with an open mind will regard them as complete proof. Nevertheless there is much more to be learned. As is true with all science, each discovery provides more questions than answers.

Darwin spoke of "the imperfection of the geological record." It is still imperfect but this is a consequence of the fact that we are asking more difficult questions. In Darwin's day the principal information desired was whether or not organisms intermediate between major groups had ever existed as the hypothesis of evolution demanded. *Archaeopteryx*, the fossil, said "yes." But once that question was answered it was only natural that scientists would wish

to know about links between the archosaurian reptiles and *Archaeopteryx* and between *Archaeopteryx* and more modern birds. Thus for each missing link discovered there were two missing links to be sought.

The ultimate goal of paleontology is to document, to the greatest extent possible, the lineages of life. This has been accomplished but only in a very elementary manner—even for the chordates, which provide us with the best data. For some of the very important questions, for example the antecedents of the phyla, there is almost no solid information (House, 1979).

One problem relating to the interpretation of the data should be mentioned. Some paleontologists are reluctant, and wisely so, to say whether or not a specific fossil is on the *direct* ancestral line to a later fossil species or to a surviving species. To offer such an opinion with any high degree of confidence would require a huge sample of fossils from rocks of slightly differing ages covering the entire span from the putative ancestor to the putative descendant. Such a complete record has never been available but, for the basic question, it is not essential. What is required is fossils that are intermediate in structure and occurring in strata of intermediate age.

These are some of the important points, in my opinion, that are appropriate to discuss with first-year students.

1. Does the fossil record, broadly considered, present a consistent pattern? That is, do the fossils of successive strata show trends or is their distribution in time random? Do the prokaryotes appear first and the more complex forms in some reasonable sequence? The answer to all of these questions is "yes." One does not find jaw bones of apes and leg bones of horses in the oldest known rocks. There is a sequence that makes sense—as was already known to Buckland (1836) and Lyell (1826) (Table 2). The work of the last century has made this conclusion even more certain. Any good modern textbook of geology such as Raup and Stanley (1978), Dott and Batten (1976), and Seyfert and Serkin (1979) may be consulted for details.

2. Is there good evidence for intraphy-

lum evolution among the chordates? Yes, rather good and getting better. The broad picture can be extracted from Colbert (1980), Romer (1966), and Romer and Parsons (1977, ch. 2). The following is a synopsis of the main lineage from the earliest chordates to human beings.

The earliest known chordate is the agnathan, *Anatolepsis*, from the Upper Cambrian of Wyoming. The first jawed fishes, the acanthodians, date from the Silurian and were followed by an extensive radiation of fishes in the Paleozoic. Crossopterygian fishes such as *Eusthenopteron*, which were ancestral to the amphibians, appear in the Devonian. *Ichthyostega* of the Upper Devonian is clearly intermediate between crossopterygian fishes and labyrinthodont amphibians.

The amphibians radiated extensively in the Paleozoic. In the late Carboniferous the labyrinthodont amphibians gave rise to primitive reptiles and again the fossil data are convincing. One genus, *Seymouria*, is such a blend of amphibian and reptilian features that it is arbitrary whether it should be classed as one or the other. The earliest reptiles, the cotylosaurs, date from the Carboniferous. All other reptiles evolved from them, including the late Carboniferous synapsids, which are on the line to mammals. In the Permian the theriodont reptiles, such as *Cynognathus*, show some of the morphological features characteristic of the primitive mammals. The first mammals appear in the Triassic. The transition from mammal-like reptile to mammal has been especially well documented. In addition to Colbert (1980) and Romer (1966), see Sloan (1983), Kemp (1982), and Broom (1932).

Earlier this year an exciting new intermediate type was discovered. The cetaceans—whales, porpoises, and dolphins—were already known to occur in the early Cenozoic by which time they were fully formed for aquatic life. Their origin was a mystery but on anatomical grounds their ancestors were suspected. Colbert (1980, p. 326) made this prediction:

Cetaceans are certainly the most atypi-

cal, and in many ways the most highly specialized [mammals] in the extent to which they have diverged from their primitive eutherian ancestors. [They] probably arose in early Cenozoic times from primitive carnivore-like ungulates known as mesonychids.

That may appear as a bold, though improbable, prediction since the carnivores are dog-like and the ungulates include horses and related species. Whales might not appear to have much resemblance to either. But Colbert was correct. Gingerich, Wells, Russell, and Shah (1983) and Gingerich (1983) have reported the discovery of *Pakicetus* in early Eocene strata in Pakistan. It is intermediate in structure between the mesonychid land mammals and the middle Eocene whales. The authors conclude: "Evidence suggests that *Pakicetus* and other early Eocene cetaceans represent an amphibious stage in the gradual evolutionary transition of primitive whales from land to sea."

This discovery is important for adding another bit of information about the evolutionary radiation of the mammals. It is of even greater importance for students in showing the accuracy of predictions in evolutionary biology. Not only was a predicted intermediate type discovered but it was found in strata of the predicted age. The geological record may be inadequate in providing a detailed account of the radiation of mammals yet it is complete enough so that new discoveries provide few real surprises. Had *Pakicetus* never been discovered, already existing evidence would have made it highly likely that the cetaceans had evolved from the mesonychid land mammals and done so in the early Cenozoic. QED.

3. Does the fossil record provide more detailed lineages? Not very many, but there are notable examples. Some of the better are of invertebrate groups, which tend not to be so meaningful to students. One of the best among the vertebrates is still the venerable story of horse evolution. In addition to Colbert (1980) and Romer (1966), see Simpson (1961), Woodburne (1982) and

MacFadden (1977, especially for the reproduction of Huxley's delightful drawin< of "Eohippus + Eohomo"). See Gingerich (1983) for other examples.

As an interesting sidelight, the American West proved to be a rich source of fossil vertebrates and the discoveries were of worldwide importance in the last part of the 19th century. The United States government supported four major expeditions to the West: those of King, Hayden, Wheeler, and Powell (Stegner, 1954; Bartlett, 1962; Goetzmann, 1966). Two of the more important paleontologists who worked the West were Cope and Marsh. Their colorful relationship is described in the three references just given plus Osborn (1931), Schuchert and LeVene (1940), and Ostrom and McIntosh (1966).

4. What is the rate of evolution? Simpson (1944, ch. 1 and 1953, chs. 1–2) and T. J. M. Schopf (1982) provide estimates.

Most living species of mammals go back 100,000 years, Almost none go back 1,000,000 years. The mean may be about 200,000 years between the appearance of one species and the next.

The evolution of different genera in horses required about 5.5 million years. About 20 million years were required for genera of ammonites. Some genera seem to last forever—the brachiopod genus, *Lingula*, has spanned 400 million years.

Evolution is, as Darwin suspected, a very slow process.

5. Can geological time be measured accurately? There are now numerous independent radiometric methods for measuring the time when rocks were formed—and hence the age of fossils within them. The most important fact to be noted is that different methods give the same answers. This ability to confirm was never possible with earlier methods, such as salt in the ocean, that later proved to be inaccurate. There have been many reviews: Eicher (1976), Brush (1982), Harland *et al.* (1983), Hurley (1959), and Berry (1968).

6. What can be said about the origin of life? A great deal has been said but this reflects the degree of interest in the question more than the amount of information

available. The data that can be accepted are that the geologically oldest organisms are similar to the simplest organisms known today—bacteria and blue-green algae—and that it is possible to simulate what are thought to be the chemical and physical conditions of the early earth and observe the spontaneous formation of some of the key molecules that characterize life.

Oparin (1938, 1968) and Haldane (1929) proposed the hypothesis that is generally accepted today as a working model. There was a prebiotic chemical evolution that resulted in the oceans containing a large variety of organic molecules—the thin hot soup stage. Other possibilities have been suggested such as the origin of life in association with the sort of conditions now being observed near the hot steam vents of the ocean floor. Eventually, and with great improbability, a molecule capable of self-replication, such as a nucleic acid, was formed. There must have followed an assemblage of molecules that could promote the self-replication of nucleic acid—perhaps in microspheres as Sidney Fox (1965, 1981) suggests. Then in some wholly unknown manner the cellular level of organization was reached. To this day cells remain the fundamental units of structure and function. Except for *in vitro* laboratory experiments, it takes the biochemical machinery of a cell to synthesize new DNA—and only a cell can produce another cell.

In 1863 Darwin wrote "It is mere rubbish, thinking at present of the origin of life" (F. Darwin, 1888, vol. 3, p. 18). We can do much better a century later but still we have no more than some probabilities and some possibilities to test and contemplate. The important point today is that the problem is approachable. See Bernal (1967), Ponnamperuma (1972), Scientific American (1979a), Folsome (1979), Fox (1965, 1981), Margulis (1970a), Dickerson (1978), Eigen *et al.* (1981), Nei and Koehn (1983), and the other references given earlier when cells and biochemical similarities were discussed.

The genetic basis of evolution

The lack of reliable information about inheritance prevented careful thinkers

from accepting Darwin's explanation for the *mechanisms* of evolution. Darwin could neither account for the origins of new variations nor their persistence. He assumed that the environment, or conditions of life, must somehow be associated with the origin of variation. Darwin was reluctant to accept the Lamarckian view that the environment induces specific variations. Somehow new variations must arise by chance. But once they had appeared, he could not counter Fleeming Jenkin's argument that they would be quickly diluted in blended inheritance.

The rapid increase in our understanding of the mechanisms of inheritance after 1900, when Mendel's work became generally available, put evolutionary theory on a sounder basis. The essential points to be emphasized in a first-year course should include these:

1. The variation that is of importance in evolution is a consequence of the action of genes.

2. There is no blending of genes in inheritance. In heterozygous cells the different alleles are not modified by their association. Their reappearance in subsequent generations, in unmodified form, demonstrates this basic fact. The old notion of blended inheritance was based on perfectly valid observations: if two quite different individuals are crossed, their offspring are usually more or less intermediate. It was only when Mendel and his followers concentrated on individual characters, not the sum total of all characters, that it became obvious that blending does not occur.

3. New variations arise by changes in DNA: mutations at various loci, changes in chromosome structure, etc.

4. Although the rate of mutation is very low for any one locus, given the very large number of loci, new variations are appearing constantly. Although the individuals of most species resemble one another very closely, there is nevertheless a huge amount of hidden genetic variability. It has been estimated that as many as a third of all loci may be polymorphic.

5. This huge amount of heterozygosity means that crossing over in meiosis will result in an even greater variety of genetically different gametes.

6. Thus mutation plus genetic recombination result in highly diverse offspring. It has been suggested, for example, that every human being (apart from identical twins) has a unique genetic endowment that probably never existed before or will recur in the human population. There is ample variation on which natural selection can act.

7. Mutation consists of changes in the structure of DNA. In many instances this appears to be a consequence of an error during the replication of DNA or defects in the DNA repair mechanisms. The replication and repair systems can be adversely affected by some radiations, chemicals, temperature, etc. and, thus, they increase the frequency of mutations.

8. To the best of our knowledge mutation is random with respect to the locus involved and in the specific alteration of DNA structure that occurs. The neo-Lamarckian view that the type of mutation is directly related to the environmental stimulus is without foundation. The neo-Darwinian view that mutation is random and that natural selection is responsible for selecting some mutants and eliminating others accords with available data.

9. In the absence of selection the allelic frequencies remain the same as described by the Hardy-Weinberg population formula where, given alleles p and q, their equilibrium frequencies will be $p^2 + 2pq + q^2 = 1$. Thus evolution will occur when conditions alter the Hardy-Weinberg equilibrium and change the frequencies of genes.

Changing gene frequencies

Evolution is a sustained and appreciable change in gene frequencies in a population. These changes can be the result of natural selection, genetic drift, or both.

Natural selection, assumed be an ubiquitous force in evolution, has not been easy to demonstrate. There are, however, many situations where it seems highly probable that existing differences among populations are the consequences of natural selection.

Since Darwin's day it has become obvious why selection is difficult to observe, as we have noted earlier. Any natural population will have been subjected to natural selection throughout its history. At any one time the genetics of the population will be the best that mutation and natural selection have accomplished, not what *might* be accomplished had selection been more rigorous. The likelihood is remote for an investigator being able to observe a population at a time when there are significant genetic differences between the individuals that survive and those that do not.

On the other hand, if a population faces a new environmental challenge—one for which it has not been selected in the immediate past—there is the possibility of an observer documenting changes in gene frequencies. This has proved possible in three sorts of situations: industrial melanism in moths and the development of resistance to pesticides in arthropods and to drugs in microorganisms.

The peppered moth (*Biston betularia*) of England and many other species of moths living in the more heavily industrialized regions of the world have evolved melanic forms in the years since the Industrial Revolution. This can be documented in many cases because naturalists have collected moths for many years and deposited the specimens in museums. Therefore the recent history of the population is known. The genetics of melanism can be determined by crossing the original and the melanic forms.

This problem has been worked out beautifully by Kettlewell (1959, 1973). In non-industrialized regions of England the tree trunks have heavy growths of pale-colored lichens. The moths in such places are also pale. In industrialized regions gases kill the lichens and expose the dark tree trunks. In the last century melanic forms of the moths have become common in these areas. Mutations to the melanic form seem to occur throughout the range of the species. If they happen to appear in the non-polluted areas, they are conspicuous on the pale trunks and thus more easily seen and captured by birds. If they appear in an industrial area, they will be protectively colored and have a better chance of surviving. Laborious field observations have shown that this actually occurs. Natural selection, in this case predation by birds,

causes notable changes in the frequencies of the alleles that control the moth's pigmentation.

It may be necessary to emphasize to students that this is *not* an example of Lamarckian evolution—common sense might suggest that the polluted environment is somehow directly causing the change in pigmentation. The data seem conclusive that melanic mutations occur at random throughout the range of *Biston*. The polluted environment is not the cause of the mutation to melanism but if such a change occurs it will be favored by natural selection.

A very large number of insects and other arthropods have become resistant to pesticides. Many kinds of microorganisms have become resistant to antibiotics and other drugs. In those cases that have been carefully analyzed, the explanation is the same as for industrial melanism. Mutations appear by chance. If they happen to increase the survival of the individuals in their new environment—one with pesticides or drugs—they increase in frequency.

Brown (1971), Georghiou (1972), and Georghiou and Taylor (1976) have provided reviews of selection by pesticides and Richardson (1978) for the evolution of resistance to biological control. For microorganisms see Elliott (1973). All of the recent books on evolutionary biology provide general discussions of natural selection.

Genetic drift. An accidental change in gene frequencies can occur when a few individuals of a population become isolated from the rest. The few indivuduals will have only a sampling of the alleles of the entire population so any new population that develops from these "founders," as Mayr calls them, will differ from the original population.

It may be unwise to discuss genetic drift in a first-year course. There is so much that might be discussed that a selection of topics is a necessity. Genetic drift has interested evolutionists for decades but its importance relative to natural selection is probably slight. In any event it is but part of the more general phenomenon of genetic change. Once a portion of a population becomes isolated from the bulk of the population, or a population is greatly reduced in size and so comes to have a different gene pool, it will continue to be molded by natural selection. Natural selection is continuous; genetic drift is rare and episodic.

Patterns of evolution

Given the reality of inherited variability in populations and the efficacy of natural selection, one can by logical induction predict the slow change of a population over time. Thus one can begin some three billion years ago with an ancient prokaryote population and understand how we became its descendants. Here we have the evolution of a single lineage and, at any one time, only a single species of that lineage is present.

The interaction of variation and natural selection alone, however, cannot explain the presence of the millions of species on the earth today or the vastly greater numbers that occurred throughout the past. That was Darwin's main problem—what is the origin of species?

Darwin and the naturalists who followed him were much impressed with the frequent difficulty in deciding whether two populations should be considered a single species or two. The two populations might run the gamut from seeming identity, to differing in slight ways, to differing enough to be regarded as subspecies, or to being so different that they could be considered specifically distinct. The answer was clear to Darwin—the gamut reflected different degrees of evolutionary divergence.

It was noted frequently that the extent of the differentiation was associated with barriers to dispersal: two subpopulations might be separated by a mountain range or other condition inhospitable to the organisms. This seemed to be a clue. It was not possible to understand how a single population in which all individuals had the opportunity to interbreed freely could split into two species, *i.e.* speciate. On the other hand if the population was physically divided by some barrier to free dispersal, one could imagine how the isolated subpopulations might slowly evolve differences from one another.

The evidence now seems overwhelming

GEOGRAPHIC SPECIATION

Increasing Dryness

Increasing Coldness

Time 1. Single Species.
The population is restricted to Zone A.

Time 2. Single Species.
Some individuals have migrated to Zone B and others to Zone C. Selection will promote the development of a population adapted to a cold, dry environment in B and to a warm, dry environment in C.

Time 3. Three Subspecies.
Evolution through the selection of spontaneous mutations in the three isolated populations has reached the point where each zone has its own adapted population. These populations, though slightly different from one another, could still interchange genes, consequently they are subspecies.

Time 4. Three Species.
The three isolated populations have diverged to the point where isolating mechanisms prevent the interchange of genes. If individuals from either Zone B or Zone C migrate back to Zone A, they can occupy this zone together with the Zone A species without the danger of losing their specific identity.
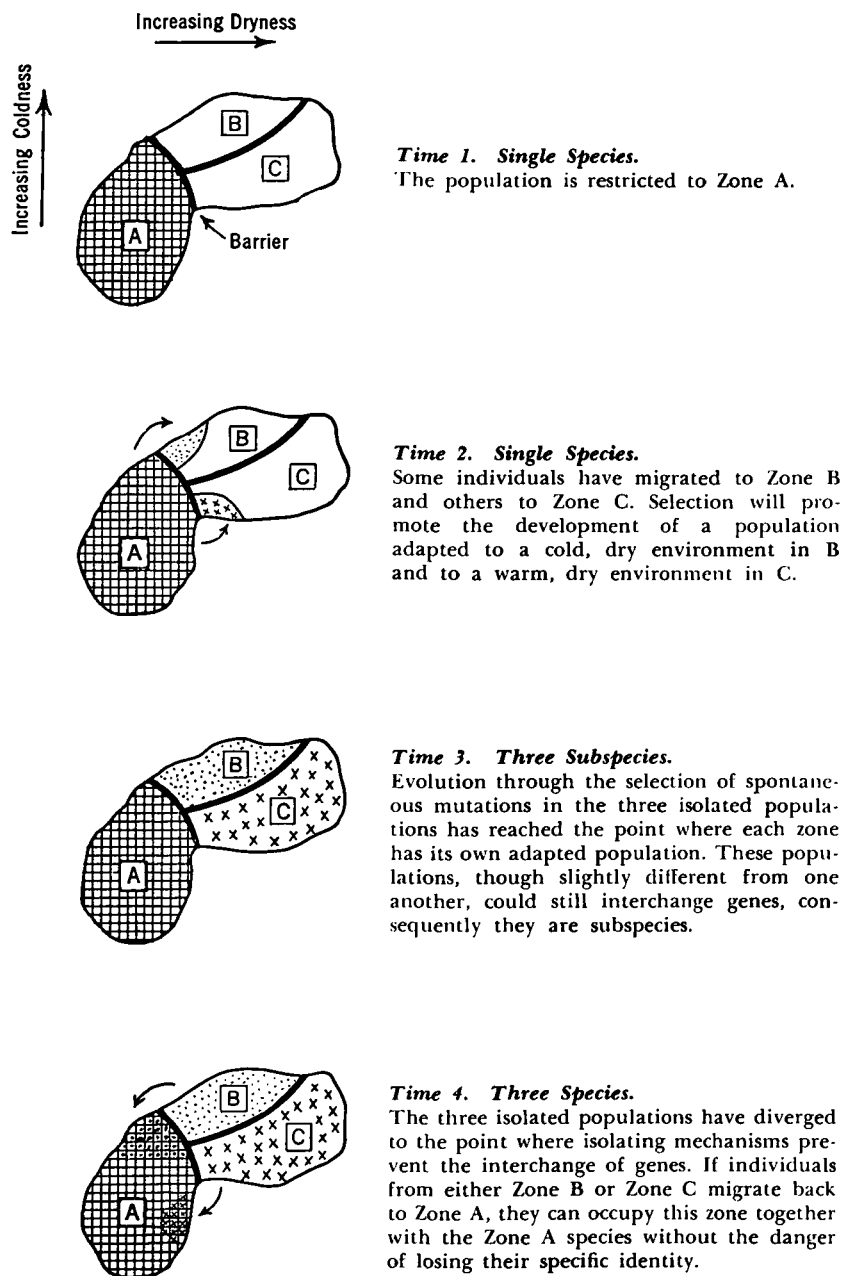
FIG. 10.   A model for geographic speciation.

that this pattern, *geographic speciation*, is the principal mechanism for the origin of new species. Figure 10 shows the events in highly schematic form.

The importance of geographic speciation in evolution had long been recognized by naturalists but it was largely due to Mayr's book in 1942 that this information came to the attention of geneticists. That interdisciplinary communication was one of the more notable events in the "Modern Synthesis" of evolutionary thought. For

more recent discussions of geographic speciation see Mayr (1963, 1970, and 1982, pp. 411–417).

Chromosomal changes and speciation. Not infrequently students ask whether or not scientists have ever observed the origin of a new species. The answer is "no" for geographic speciation—the time required is in the thousands of years. There are a few special cases in plants where the origin of new species has been observed. Whether or not it is practical to explain these cases to students will depend on their background in genetics and cytology and the time available.

A pattern that is relatively easy to understand involves the hybridization of two species followed by an accidental doubling of the chromosomes in the hybrid. The hybrid plant will possess one haploid set of chromosomes from one species and another set from the other species. This quite often gives an individual that is robust and excellent in all ways—until the time of reproduction arrives. Normal ova and pollen can be produced only if there is normal pairing of chromosomes in meiosis. Normal pairing can occur only between homologous chromosomes and the hybrid will possess different chromosomes from the two parent species. The result is meiotic chaos and generally abnormal gametes (this is the mule's problem).

If, however, there was an accidental doubling of the chromosomes, the hybrid would have all of its chromosomes in homologous pairs and meiosis could be normal. It would have the tetraploid number of chromosomes, which would make it difficult to be crossed back to the parent species.

This is more than a hypothetical model. There are many well studied cases of two species crossing, the chromosomes of the hybrid doubling, and the result being a new species—all in a season, instead of 200,000 years. One classic case is *Spartina townsendii* (Huskins, 1931). For other cases see the second edition of Dobzhansky's *Genetics and the Origin of Species* (pp. 231–242), Stebbins (1977, pp. 186–191), and M. J. D. White (1978, ch. 8).

Although geographic speciation appears to be the dominant mode of speciation, there are other less well documented possibilities. Bush (1975) and M. J. D. White (1978) can be consulted for details. It would seem better not to consider these other cases in a first-year course—we must accept that everything cannot be covered so the emphasis must be on the ubiquitous and important and not on the rare and important or ubiquitous and unimportant.

Molecular evolution

Today the study of evolution with the procedures of molecular biology is a very active field of research. The elegance of its probes, the rigor of its methods, and the precision of its answers are making it possible to gain deeper understanding of the processes of evolution. Molecular evolution is also an area where teachers of first-year courses must exert discipline and self-restraint. There will be a desire to open the eyes of students with a heavy dose of molecular evolution but we must face the fact that few students will have the background to understand why the new discoveries are so important and exciting. Neither will there be time to provide an adequate background. Unless there is restraint, it is more likely that the students' minds will become clogged by unappreciated facts than that their eyes will be opened.

Possibly the most practical course to adopt is to attempt to give students an indication of the sorts of questions that the techniques of molecular biology can answer.

The study of evolution at the molecular level is the study of the fundamental molecules of evolutionary change—DNA— and the molecules that represent the immediate products of DNA—the proteins. When one compares the bones of a horse and human being and then their hemoglobin molecules, the methodology is basically the same—comparing structure. The hemoglobin molecules, however, are immediate consequences of gene action whereas the bones are the consequences of complex interactions of cells and their molecules extending over the long period of embryonic development. Proteins are basic; bones are derivative.

Genetic variability. The traditional meth-

ods for detecting the number of alleles of a locus was laborious since it usually depended on genes that produced visible effects and on making a very large number of crosses. Furthermore, if radiations and other mutagenic procedures were used, one could hardly claim that heterozygosity under natural conditions was being studied.

Now we have electrophoretic techniques that enable one to detect differences in proteins—which reflect differences in the genes controlling them. Before these techniques were available, it was assumed that a low level of polymorphism would be normal. Now we know that in human populations about 30 percent of the loci are polymorphic and in any one individual about 7 percent of the loci are heterozygous. The values for other animals are similar.

Relatedness of organisms. The procedures of classical evolutionary biology for estimating relatedness were crude. Hybridization was one. Among similar species, if A and B could be hybridized but neither could be crossed with C, it was assumed that A and B are more closely related to each other than either is to C. If hybridization was impossible, then one had to rely on comparisons of structure—the closer the structural similarity the closer the relatedness and, presumably, the shorter time interval since a common ancestor.

Now it is possible to make detailed comparisons of the base sequences of different DNAs. This does not measure what genes do, merely whether or not their base sequences are similar. When different species of frogs or flies are compared, the sequences are the same for about 81–89 percent of the DNA. Two species of mice may have 95 percent of their sequences the same. A real surprise (shock?) is to learn that the base sequences of human beings and chimpanzees are at the 99 percent level. Whereas the fly species belong to one genus—the same is true for the species of frogs and of mice—we have placed the chimp in a separate family.

Similar experiments, comparing amino acid sequences of many different vertebrates, reveal that human proteins resemble those of other primates closely and, this resemblance of proteins decreases in the following order: rodents, dogs, marsupials, monotremes, birds, and amphibians. This is the same sequence that evolutionists had proposed, on other evidence, before molecular comparisons were possible.

If we take the paleontological estimates for the time when various groups diverged and add the data on molecular differences, we can then make an estimate for the rate of evolution of molecules. One estimate is that there are about 75 amino acid substitutions in protein molecules in 100 million years. In cytochrome c there have been about 25 amino acid substitutions in 500 million years. Human cytochrome c consists of 104 amino acids.

The field of molecular evolution is now in a period of validation. Its discoveries are in accord with what previous methods have established as the major concepts of evolutionary biology—we would be in serious trouble if that had not been the case. The main contributions of molecular evolution to date have been to give more detailed, and often more precise, answers to important questions. This evaluation will surely seem dated in the near future—the possibilities of gaining very much deeper insights into the mechanisms of evolutionary change with the methods of molecular biology seem endless.

For general introductions to the literature, see Nei and Koehn (1983), Rose and Doolittle (1983), Calder (1973), Ayala (1976), Dickerson (1980), Jukes (1966), and Zuckerhandl (1965).

Evolution and human welfare

Compared with the span of human life evolution is generally an exceedingly slow affair and hence might be expected to be of little immediate importance. This is not the case. Evolution impacts our food supply, health, educational system, social interactions, and even plans for our future. Evolution is much more than the study of dry bones—it is an ever present threat and promise for the human species.

Some of the ways that the concept of evolution, or the processes of evolution, are of immediate human concern will be listed briefly and references provided. There will be considerable overlap with

topics that could also be dealt with when genetics is discussed. This is not surprising since genetics is short term inheritance and evolution is long term inheritance. Some topics, such as race, are more appropriately treated as an aspect of genetics and will not be included here.

Few studies of history attempt to deal seriously with the ways evolutionary principles relate to human beings. C. D. Darlington (1969) made such an attempt.

Agriculture

Human life can be sustained only by the death of other lives. Over most of the time span of our species, we depended on wild animals and plants for the substance and energy required to maintain our lives. Civilization became possible after the Agricultural Revolution of Neolithic times when our ancestors began to alter the evolution of a few wild species. Animals and plants were domesticated and selected for those characteristics that would be of immediate benefit to human beings—generally better food and fiber.

Some general references are Angress and Reed (1962), Baker (1970), D. and P. Brothwell (1969), Cohen (1977), de Candolle (1886), Grigg (1974), Heiser (1973), Helbaek (1959), Reed (1959), Sauer (1952, 1969), Singer *et al.* (1954–1958), Ucko and Dimbleby (1969), Vavilov (1951), and Zeuner (1963).

Much is known of the evolutionary history of important crops such as wheat and corn. Some key references are Beadle (1970), Jugenheimer (1976), Poehlman (1979), Peterson (1965), Chandraranta (1964), Higgs (1972), and Scientific American (1970).

Evolutionary principles become apparent when artificial selection is practiced. In natural populations there is tremendous genetic diversity and this is vital in allowing the population to respond to new environmental challenges. When human beings start to select plants and animals they concentrate on greater productivity or some other feature of benefit to man, not the species being domesticated. The inevitable consequence of this selection, which almost always involves close inbreeding, is to elim-

inate a large part of the natural genetic variability. This has two main disadvantages: the domesticated species might not be able to develop resistance to a new disease or to environmental stress and, should one wish to select for some other characteristic, the necessary genetic variability might not be available. Genetic uniformity of domesticated animals and plants might be desirable for the moment but, in the long run, it can be a disaster.

There is a fascinating vignette of evolution in action in the case of wheat and wheat rust. Plant breeders are constantly selecting new strains of wheat that are resistant to the rust. The problem is that the wheat rust is always evolving in ways that will allow it to flourish on wheat. Thus, there is a race between the natural evolution of the rust and the artificially directed evolution of the wheat (Stakman and Christensen, 1946; Stakman and Harrar, 1957, pp. 499–509).

For two good introductions to the evolutionary aspects of domestication see Day (1977) and Horsfall and Cowling (1980). Additional references are Wade (1972), National Research Council (1972), Feldman and Sears (1981), Lewin (1982), Strobel (1975), Hooker and Saxena (1971), Maugh (1982), Holton (1959), Caltagirone (1981), Stevens (1974), van der Plank (1968), and Maxwell and Jennings (1980).

A similar principle of evolution comes into play in human efforts to control insects and other pests of domesticated animals and plants. The pests are usually able to evolve resistant populations. Control, therefore, is a contest of human ingenuity and the ability of the pest population to evolve rapidly and effectively. See Brown (1971) and Georghiou (1972).

Health

Many human health problems are a contest between the speed with which disease organisms can evolve to live on us and we can evolve resistance, a long term affair, or invent ways of controlling the disease organisms.

Long ago, when human populations tended to be isolated, each evolved a degree of resistance to the endemic disease-pro-

ducing organisms, thus permitting survival of the population. The inhabitants of Western Europe had been selected by the organisms causing measles, scarlet fever, smallpox, and a host of other ills. During an epidemic many would die but the survivors tended to be somewhat more resistant and by the 18th century few of the diseases were serious threats to the lives of most members of the population. When Europeans began to colonize other continents they came in contact with native populations that had not evolved immunity to the diseases of Western Europe. The consequences could be devastating. The native Americans were conquered more by European disease than by European arms. See McNeill (1976, 1980), C. D. Darlington (1969), P. T. Baker (1960), Haldane (1957), and Fenner (1970).

The sickle-cell gene is widely distributed in Africa. When homozygous it causes severe anemia and usually early death. When heterozygous it affords considerable protection against malaria but causes a mild anemia (Livingston, 1958; Motulsky, 1960). Thus the human population in malarial regions has been selected for the resistance conferred by the sickle-cell gene.

For the general problems of the evolution of resistance in disease-causing organisms and the human response see Livingston (1960), Motulsky (1960), Friedman and Trager (1981), Elliott (1973), and Black (1975).

The concurrent evolutionary races of man and his prey and predators is what Van Valen (1973) calls the Red Queen Principle. Even as Lewis Carroll's Red Queen had to keep running just to stay in place, interacting natural populations have to keep evolving with respect to one another or become extinct. This is one of the fundamental facts of life. Every population of heterotrophs must continually evolve better ways of preying on other organisms and evolving better ways of avoiding being preyed upon. The pressures may be less for the photosynthetic and chemosynthetic organisms. They need not evolve predatory mechanisms—their main problem seems to be to avoid being eaten. We are only now beginning to realize the huge number of chemicals produced in our food plants that are carcinogens or mutagens (Ames, 1983). Inconvenient for us, perhaps, but these chemicals represent the plant's attempts to avoid being eaten.

Genetic engineering

The French biologist, Jacques Monod, entitled a book *Chance and Necessity* (1971). By this he meant that our evolution to the stage of *Homo sapiens* was based on chance mutations that were selected if they were necessary for the survival of our ancestral populations. Darwin would have approved of this title.

For three and a half billion years the course of life has been guided by chance and necessity. In the last 0.003 percent of this biotic era human beings have purposefully altered the evolution of some species of plants and animals by changing the "necessity." Necessity was no longer defined as "necessary for the organism" but "necessary for mankind." In addition we have inadvertently altered the evolution of many other species by our modifications of the environment. Melanic moths and weeds are examples.

Now we are on the threshold of an era of far greater power that will see us able to mold the genetics of species. We are still unable to control the specificity of mutation—it is still governed by that chance of Darwin and Monod. We are able, however, to transfer a desirable gene from one organism to another in some situations and it is reasonable to predict that the number of situations will increase rapidly. This is the field of genetic engineering.

Less than a decade ago there was a fierce debate involving scientists, political leaders, and the public about the risks of entering this new era. Some of us were terrified by the possibility of a new devastating pathogen, the product of directed genetic recombination, escaping from the laboratory and causing an epidemic that the medical profession would be powerless to control. But it was also realized that this new technique, which could produce disaster, could also produce marvels—bacteria made to synthesize insulin and other human hor-

mones; nitrogen-fixing genes to be intro-
duced into plants. The possibilities for pro-
ducing worthy results seemed endless.
Grobstein (1977) discusses these early fears
and prospects.

As the months went by the dangers
seemed to be far less and the prospects far
better. And there is always that subtle force:
if something can be done, it will be done.
Now genetic engineering is here to stay.
The flow of information in this area has
reached flood proportions. Most issues of
Science and *Nature* have articles dealing with
it. Frequent mention is made in the weekly
news magazines and newspapers, even in
the *Wall Street Journal,* because genetic
engineering is a volatile growth industry.

One can enter the literature of the field
via Cohen and Shapiro (1980), Villa-
Komaroff (1980), Diacumakos (1981), and
the entire 11 February 1983 issue of *Science*
(vol. 219, no. 4585).

My advice for treating this topic in a first-
year biology course will probably not be
taken but here it is.

One cannot overemphasize the impor-
tance of genetic engineering for our future
welfare. Many things are possible now and,
at the current rate of progress, nothing
seems theoretically impossible to accom-
plish. Therefore, we will be in a position
to make decisions about ourselves and other
forms of life never possible before. These
decisions will deeply involve questions of
ethics and the well-being of mankind and
other forms of life. Decisions will be made
and they must be made by informed minds.

It is most unlikely that students in a first-
year course can master the technical aspects
of genetic engineering—the necessary sci-
entific background could not be obtained
in the time that could be allowed for the
subject. But is that background necessary?
I think not. An efficient solution might be
to provide students with information about
the sorts of things that can be done and,
as examples, provide a non-technical
explanation of one or more of the simpler
procedures: an example would be the
transfer of a desirable gene to a plasmid
and then to a bacterial cell where it could
synthesize insulin or some other medically
important substance.

If students become aware of the possi-
bilities in genetic engineering they will be
in a position to consider the implications—
and that is the critical issue. One does not
require an M.D. degree in order to hold a
useful opinion about the delivery of health
care in America.

Human evolution

Our lineage has been evolving for more
than three billion years but for many stu-
dents the main interest is in the last few
geological moments—when our line
became primates and then species of the
genus *Homo.* This has been one of the more
interesting but surely the most contentious
field of biological research. It has involved
international politics (whatever happened
to Peking man? see Shapiro, 1974), intense
rivalry among scientists (Johanson and
Edey, 1981), fraud (Weiner, 1955; Oakley
and Weiner, 1955; Gould, 1983, chs. 16–
17), and has caused severe reactions by the
fundamentalist religious sects (references
shortly).

The subject is surely worthy of a lecture
or so. Some useful references are: Scien-
tific American (1967, 1979b), Pfeiffer
(1969), L. B. S. Leakey and Prost (1971),
Campbell (1972, 1976), Trinkaus and
Howells (1979), Johanson and Edey (1981),
R. E. Leakey and Lewin (1977, 1978),
Howell (1973), LeGros Clark (1978), Pope
(1983), and Rukang and Shenglong (1983).

The *Origin* makes only the most tentative
statement about our evolution: "Light will
be thrown on the origin of man and his
history" (*Origin,* p. 488). Darwin knew of
no fossil remains that threw light on our
origins. Huxley's famous essays of 1863,
Evidence as to Man's Place in Nature, made
explicit the meaning of evolution for our
history. Since there was no adequate fossil
record (the first Neanderthal remains had
been discovered in 1857 but Huxley found
them difficult to interpret) he used the data
of comparative anatomy, especially the
close anatomical resemblances of man and
the anthropoid apes, stone age artifacts,
and observations on the "primitive" races
still living. Some of the earlier attempts to
throw light on our past history are Lyell

(1863), C. Darwin (1870), Lubbock (1869), Haeckel (1905), Joly (1891), Osborn (1916), and Keith (1931).

Students may be interested in the considerable artistic talents of prehistoric man: Breuil (1952), Bataille (1955), Graziosi (1960), Bandi (1961), and Leroi-Gourhan (1967).

Cultural evolution

It is worth emphasizing to first-year students that the human population is learning to circumvent some of the forces of natural selection. Modern medicine and modern agriculture mitigate the selective pressures of disease, malnutrition, and starvation. What we are and what we do are influenced more by cultural than biological factors. To be sure our culture may introduce new selective forces. We have so degraded our environment, adulterated our food, polluted our air and water, been lax in developing safeguards for nuclear technology, and failed to secure peace, to the point where human beings are the main force of selection on human beings. One of our main selective challenges today is to survive the mutagens and carcinogens that we have pumped into the environment.

But cultural evolution could promote a different future—one in which we could overcome the selfish gene (Dawkins, 1976) and emphasize love rather than Love Canals.

Cultural evolution is a vast subject. For a start try Dobzhansky (1962, 1973b), Dubos (1955), Comfort (1966), Campbell (1966), Washburn and McCown (1978), and Ardrey (1976). For more quantative studies see Cavalli-Sforza and Feldman (1981) and Cavalli-Sforza et al. (1982).

The creationist phoenix

Much of the initial opposition to the Darwinian paradigm was due to its obvious conflict with the creationism paradigm. In the middle of the 19th century, most of the Western World accepted as fact the Genesis account of the origin of the earth and its inhabitants. Numerous different stories about creation were to be found in other cultures but these other cultures were not active participants in scientific speculation. The acceptance of the Genesis account had been weakened to some degree during the Age of Reason but, as noted before, most scientists in 1859 were creationists.

In the years immediately after 1859, it was possible legitimately to oppose Darwinism on two counts: inadequate scientific evidence and heresy. Later research supplied the scientific underpinnings but the charge of heresy will always remain—the concept of evolution is in direct conflict with a literal interpretation of Genesis. But this is heresy only in the minds of the fundamentalists. The major religions have accepted evolution and made whatever philosophical adjustments were required.

Huxley was the most notable defender of evolution in Darwin's lifetime and many of his published essays (1893, 1895a–f) are concerned with this subject. The literature of the field is immense. Useful accounts are Eiseley (1958), Glick (1972), J. C. Greene (1959), Hofstadter (1963), Hull (1973), Irvine (1955), Kogan (1960), Moore (1978), Ruse (1981), Russett (1976), Turner (1974), and R. J. Wilson (1967).

The creationist movement waxes and wanes. The current expression of it seems to have peaked last year and is now less in the news. Nevertheless it remains a serious threat to the teaching of science and, by extension, a threat to all freedom of teaching. The creationist challenge to science teaching and its pressures for "equal time" have been dealt with by Nelkin (1977, 1982) and Moore (1975, 1982).

The recent resurgence of creationism is part of a worldwide shift to fundamentalist religions. In the United States there has been a vigorous response by the scientific community. See Futuyma (1983), Newell (1982), Ruse (1982), Kitcher (1982), Zetterberg (1983) and the entire January 1982 and March 1983 issues of the *Journal of Geological Education*.

The problem of evolution vs. creationism does not involve science in any serious manner but it is an important intellectual and social issue. In view of the great confusion that exists in the minds of the majority of Americans it should be considered in first-year university courses. It is,

obviously, a delicate question for some schools and some parts of the nation. The goal of any discussion must not be to persuade religious believers to be non-believers but to show the differences between statements based on scientific information and those based on any of a number of religious belief systems. The claims of some of the more vocal creationists that there are scientific facts that support creationism and falsify the concept of evolution are simply not true—though these claims may gain credence with the general public by constant repetition.

The question of why some people prefer to accept creationism rather than science is interesting but, surely, not of concern to teachers. In the United States people have a right to believe as they wish with or without evidence. They do not have the right, however, to pressure others to conform to whatever sectarian views they may hold. I have tried to analyze this problem (Moore, 1983).

Schedules

Although this long essay forms a unit, it is not intended that evolution be taught as a unit in a first-year biology course. If the concept of evolution is accepted as the grand unifying theme of biology, it should permeate the entire course. My suggestions for scheduling the various topics follow.

Deductions 1–10, plus "Was Darwin right?" form a unit that gives the fundamental concepts of the field and an understanding of the evidential basis for the concepts. This could come early in the course and in association with laboratory exercises designed to illustrate organic diversity.

Deductions 11–15 are intended as examples of the leitmotif that can accompany consideration of all the major subject areas of biology.

The section "Evolution after Darwin" is suggested for late in the course and certainly after cell biology and genetics have been covered.

The topics listed under "Evolution and human welfare" could be treated as a unit or, better, I think, be distributed throughout the course. There are many other topics of this nature that could be developed.

Concluding remarks

I believe that the time has come to accept the fact that the concept of evolution is the unifying theme of the biological sciences and what is taught in the first-year course should reflect this point of view. The main purpose of the ASZ project, however, is to suggest ways for improving biology teaching at the college and university level. There seems to be a gnawing feeling among those concerned with higher education that our problem is not so much what we teach but how we teach. The strategy suggested here is that we should reduce the factual load and give greater attention to the conceptual framework of the field. It is surely true that students can learn far more than they understand, but to what purpose? There are difficulties with the suggested approach. It is far harder to teach concepts than facts and most of our students' prior education will have dealt more with facts than ideas. Concern for ideas does sound elitist but we simply have to accept that higher education is an elitist enterprise. The style of education must be set for those who wish to learn and understand and not by those unable or unwilling to so do. The enjoyment of ideas, like the enjoyment of beer, seems to be an acquired characteristic—and not everyone likes beer.

There are other pressures that make teaching in a conceptual mode more difficult. First-year biology courses are usually very large and for this reason objective-type examinations seem to be the rule. One must accept from the onset, I believe, that it is pointless to attempt to teach concepts and then test for facts—as objective examinations do almost exclusively. Students will not be persuaded when you tell them that the important things they should learn are the "big ideas" when your evaluation of their success in so doing is to ask a question that can be answered by checking a letter A–D.

Another pressure comes from the premeds who tend to dominate many first-year courses. They believe that success for them means learning the maximum number of facts and, in this respect, they have learned to excel. The grades they obtain in science courses will depend on examinations that emphasize facts. The various

national examinations they will take in the screening processes for medical school also stress facts, although attempts to search the higher levels of the students' brains are under way. I have found premeds restive and on occasion hostile when there is a heavy dose of concepts followed by a testing of their understanding with essay-type examinations.

Then it must be admitted that some young instructors, who have just completed a fact-laden, concept-poor science curriculum of some universities, find the conceptual world neither familiar nor comfortable. They have been trained more as technicians than as scientists.

In spite of the difficulties, we must change the ways we do our teaching—for the health of the nation, the welfare of our students, and our own satisfaction. It is terribly important that we make these changes and it will be terribly difficult to do so. Teaching must return to a place of distinction and reward in the universities. This need not result in damage to research programs. Good teaching and good research are not incompatible. Ideally they should be synergistic.

Educational reform, the *sine qua non* for a viable future for our nation and for its citizens, must begin with us. We must help students acquire a deep understanding of the nature of science and its strengths and limitations. This goal is equally important for those who plan a career in science, become teachers of science in the schools, or make the informed decisions of a democracy.

A course in science must be an intellectual adventure. What is known is ephemeral. Science as a way of knowing is forever.

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