Comments on Evolutionary Biology[1]

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Major Issues in Evolutionary Biology

Put simply, evolutionary biology is the scientific study of *the history of life on planet Earth*. It is a multifarious enterprise, to say the least. The phrase "biological evolution" is used in a number of different contexts. Distinction of three fundamentally different components of contemporary biological understanding of evolution is central to keeping the issues in perspective and for disentangling much of the misunderstanding that accompanies debates about evolution. For want of better names, these three contexts can be titled:

1. The Principle of Biological Evolution.
2. Theories of Evolutionary Processes.
3. Historical Scenarios of Evolutionary Change.

Each of these three categories makes a separate contribution to the overall fabric of evolutionary biology.

The Principle of Biological Evolution. In broad terms, the "principle of biological evolution" is a statement about the phylogenetic relatedness of species and about modification of characters through time. At its irreducible core it is recognition that genealogical connections exist among all living organisms on earth. The elementary step in a genealogy is the biological relationship of parent and offspring. A genealogy is commonly represented by a family tree, which is nothing more than a branching network of varying degrees of relationship built upon repeated linkages of parents with offspring. The principle of biological evolution states that the history of organic life is the history of single family tree of immense scale and complexity. The principle of biological evolution is, therefore, an assertion that living organisms have a specific property: universal genealogical relatedness. Establishing the truth of this assertion is an empirical matter. When biologists insist that evolution is a *fact* they are simply saying that there is convincing evidence that the world does indeed have the property that the principle of biological evolution asserts.

The fact of genealogical relatedness has an immediate corollary when it is coupled with the observations that (1) a vast diversity of organisms, differing greatly in form and function, inhabit the earth and that (2) the current array of species differs greatly from the constellations of species that existed in previous times. Clearly, species have changed through time. The principle of biological evolution, therefore, has two components: genealogical relatedness and transmutation of species.

Modern biology is clear on the fact of evolution. The genealogical relatedness of organisms is attested to by an enormous body of data drawn from diverse, independent lines of evidence--comparative anatomy, paleontology, comparative physiology, biosystematics, comparative ethology, embryology, genetics and

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molecular biology. The multiplicity, diversity, and independence of the lines of evidence cannot be emphasized too much. The copious evidence that Darwin assembled constitutes a miniscule fraction of the data that now exist. In every area of biology are found tell-tale signs of genealogical relatedness. To say that everything in biology attests to the principle of evolution is, at worst, a mild exaggeration. A century and a quarter after the publication of the *Origin of Species*, biologists can say with confidence that universal genealogical relatedness is a conclusion of science that is as firmly established as the revolution of the earth about the sun. Anyone can, of course, deny this conclusion. To do so, however, is possible only by denying the collective professional judgment of a large segment of the scientific community. (This statement does not refer to facile assertions from a few overly enthusiastic popularizers of evolution or to biased opinions of some hypothetical group of atheistic biologists. It refers to the studied consensus of hundreds of conscientious biologists who are intimately familiar with the organisms, the phenomena, and the data that constitute the evidence upon which the principle of evolution is supported.)

Theories of Evolutionary Processes. Recognition of the fact of biological evolution is one thing. Explanation of the processes by which the events occurred is another. Darwin recognized this distinction, and his greatness lies in the fact that his work encompassed both elements. Not only did he build a strong case for establishing the fact of evolution, he also concieved the theory of natural selection as the mechanism responsible for giving direction to the transformation of species. The idea of evolution was not new with Darwin. Earlier writers such as Buffon, Erasmus Darwin, Lamarck, and Robert Chambers, whose popular *Vestiges of the Natural History of Creation* was published in 1844, recognized the possibilities of transmutation and relatedness of species. Without a mechanism that could account for the origin of adaptations, however, their ideas failed to arouse strong interest from the scientific community. The exquisite adaptations of organisms to their various roles in the economy of nature were obvious to naturalists and were the basis for the prevalent "argument for design," which interpreted the apparent design in nature as direct evidence of God's active role as designer. By providing a mechanism to account for adaptive change, Darwin's theory of natural selection has the joint distinction of being the primary factor responsible for convincing the scientific community of the fact of evolution and, at the same time, being the primary cause for the negative reaction by the religious community who saw in the theory of natural selection a denial of God's role as the designer of creation.

The difference between the theory of natural selection and recognition of the evolutionary relatedness of organisms is made apparent by the distinct histories of the two concepts over the century following publication of *The Origin of Species*. General acceptance by the scientific community of the principle of evolution came relatively quickly, and, once established, acceptance continued to grow as more and more independent lines of evidence attesting to its reality were provided by ever expanding biological research. The theory of natural selection, on the other hand, experienced far less congenial treatment. Although the theory of natural selection has proved to be extremely seaworthy, it has sailed on rough seas and at times was thought to be on the verge of floundering. A major theme in the history of evolutionary biology over the last 125 years is debate over the role of natural selection as a mechanism of evolutionary change.

A synopsis of this history will be given later. The key point for now is that biologists are now increasingly aware that evolutionary processes are pluralistic. Darwin's theory of natural selection, Sewall Wright's shifting-balance theory, Kimura's neutral allele theory, Gould's punctuated equilibria, and a variety of models of speciation are all examples of theories concerning the mechanisms of evolutionary change. All of these theories, which are properly regarded as complementary rather than all-or-none mutally exclusive alternatives, are concerned with mode and tempo of evolutionary change. The principle of genealogical relatedness is common to all. Contemporary debates are over the relative importance and relevance of these different theories as explanations of the evolutionary processes that have actually occurred. When geologists discovered plate tectonics, they did not cease to regard erosion as a mechanism of geologic change. So too, few, if any, biologists doubt the central role of natural selection in the events of biological evolution, but they will argue heatedly over whether the *role* of natural selection, relative to other mechanisms, should be awarded a mere plurality, a simple majority, a landslide victory in the American sense, or the unanimous victory of a totalitarian election.

Historical Scenarios of Evolutionary Change. A third component of evolutionary biology is the component concerned with reconstructions of specific genealogies and elucidation of specific changes that led to transformation of specific traits and characters found in individual species. This component, which is the broadest and most diverse of the three, is the area of evolutionary biology most directly of concern to taxonomists, systematists, and morphologists, who deal with establishing natural relationships among different kinds of organisms and their structures. Not surprisingly, it is also the area that laypersons most often have in mind when they think of evolution. People like stories, especially detective stories, and detective stories are what this category is all about. Like cosmology, geology, and forensic science, evolutionary biology is a science of history. Unlike experimental sciences in which data are generated by experiments designed to test some process of nature, the data of the sciences of history are the preserved results of past processes that are hidden in the current universe. Whereas the potential data of experimental sciences are limited only by the abilities of investigators to devise critical experiments, the data base of historical sciences is limited to the finite evidence that history has left. In both cases, however, the conclusions and theories of the field are always open to the possibility of revision (or even falsification) in the light of new empirical evidence.

The problem of reconstructing specific scenarios is distinct both from the principle of evolution and from theories about the processes of evolutionary change. Genealogical patterns of branching can be studied independently of whatever processes were responsible for their creation. In fact, a group of taxonomists known as cladists, whose goal is construction of a system of classification that is based exclusively upon genealogical relationships, have developed a productive methodology that rigorously excludes any consideration of process. Because of the latter, cladists have been cited by critics of evolutionary biology as having made the very concept of evolution questionable. The criticism is ironic. To accuse cladism, which is rooted on the principle of evolution, of casting doubt upon the existence of evolution demonstrates a colossal failure to distinguish the principle of evolution from processes of evolutionary change.[2]

Reconstruction of specific scenarios utilizes the same kinds of evidence that forms the basis for the principle of evolution. The principle of evolution, however, rests upon widespread evidence of genealogical relatedness throughout all the living kingdoms. Historical scenarios, on the other hand, require clues that reveal the nitty-gritty details of particular branching points in an individual genealogical tree. The reconstruction of specific scenarios is the area in which individual pieces are most subject to debate and revision as new information comes to light. Some scenarios have been worked out in considerable detail with support from substantial amounts of evidence. Others, for which data are sparse,

[2] See Gould (l987) for a brief, clear discussion of this mistaken criticism of the cladists.

are highly speculative. Little general importance, however, rides on the rise or fall of any one scenario. The principle of evolution does not hinge upon the accuracy with which any one scenario is known.

Consider, for example, the case of the species *Homo sapiens*. The conclusion that humans and chimps are close cousins is supported beyond any reasonable doubt by a variety of independent lines of evidence from sources as disparate as biochemistry, anatomy, behavior, paleontology and archeology. The increasingly refined evidence from the fossil record is only one part. Popular attention has be given to debates about whether the recently discovered fossil specimen named "Lucy" proves to have belonged to a directly ancestral group or to a group that is more equivalent to a great-great-aunt. There is a implication in the popular view that if Lucy is not a direct ancestor then the relatedness of humans and chimps is still in doubt. The inference is clearly mistaken--aunts and nieces, too, are relatives. The debates may raise valid questions about details in the genealogy but not about the existence of a common genealogy.[3]

A Synoptic History of Evolutionary Theory Since Darwin

Darwin's view of evolution has proved to have been surprisingly accurate in its main features (in spite of his gross ingorance of some important details such as the mechanism of inheritance); nevertheless, there have been major developments in evolutionary theory since his time. A synopsis of the history of evolutionary theory will help clarify our current understanding of the processes of evolutionary change. The teatment presented here will necessarily be cursory.[4] To do a full job is a task worthy of an entire career![5]

Biological evolution has three component processes: phyletic evolution, diversification, and extinction. Phyletic evolution refers to changes in the genetic composition and characteristics of individual lineages through time. Typically (but not exclusively) it involves the cumulative development of adaptations. Diversification, formally known as speciation, entails the splitting of lineages, with different parts of an individual lineage diverging along different paths of phyletic evolution. Extinction is the disappearance of a lineage through failure to reproduce itself from generation to generation. Darwin saw the natural selection of individuals within variable populations as being the mechanism that provides direction to phyletic evolution. He saw the diversification of species as being the result of situations in which a part of a species finds itself in changed conditions under which natural selection takes it on a new and different path of phyletic evolution.

The cornerstone upon which Darwin founded his theory of natural selection is the existence of inheritable variations among individuals within a species. From biogeography and natural history Darwin was aware of the widespread existence of minor differences among individuals as an empirical fact, but he lacked

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[3] For recent, moderately detailed, but readable, discussions of human evolution see Brace (1983) and Isaac (1983).

[4] The historical statements in the following narrative draw heavily upon the treatments found in Mayr (1980) and Provine (1971). Provine (1986, Chapter 7) contains additional material relevant to this discussion. These books give extensive and quite readable treatments of the major issues. Maynard Smith (1982, pp 1-6) also gives a short synopsis of the recent history of evolution.

[5] The historian William Provine is, in fact, presently in the middle of what promises to be an illustrious career devoted primarily to the history of evolutionary biology in the 20th century.

any theory to account for the production of variation. Likewise, he recognized the fact of heredity but was encumbered with the theory of blending inheritance (which proved, nearly half a century later, to be grossly incorrect) that was inadequate, on theoretical grounds, to support the variation required by the theory of natural selection. Under blending inheritance, occasional rare variants with distinct effects (known as "sports" in Darwin's time) would have their effects quickly diluted by sexual reproduction. Darwin, therefore, viewed minor variations as the stuff upon which natural selection acts, and he emphasized gradual and continuous change as the primary mode of phyletic evolution, with natural selection as a process (not a force) analogous to the geological process of erosion.

Ignorance of the nature and origin of variation and the mechanisms of inheritance plagued evolutionary biology until the 1920's. In the later part of the 19th century these difficulties led to Darwin's theory of evolution by natural selection falling into disfavor within large segments of the scientific community, which, nevetheless, had come by that time to recognize the validity of the principle of evolution. A large number of theories were proposed to explain transmutation of species. Two major anti-Darwinian themes were prevalent in the popular theories and debates. First, the inheritance of acquired characters--variously attributed to use and disuse, or to direct induction by enviromental conditions (Geoffroyism), or to innate tendencies within the individual towards perfection (Orthogenesis)--was widely held to be the primary mechanism responsible for producing new adaptations. It remained the dominant alternative to natural selection as the direction giving mechanism of evolution in the minds of many biologists until well into the 20th centuray. Second, Darwin's emphasis upon gradual, continuous change was criticized by many naturalists who felt that discontinuous variations, termed "saltations" by Huxley, were the typical raw material from which new species were created. For example, Darwin's cousin Francis Galton, creator of the statistical concept of regression on the mean, was, in general, a strong supporter of Darwin, yet he argued against gradualism by drawing an analogy between supposedly discontinous jumps of evolution and the pushing of a roughly hewn stone from resting upon one facet into a new resting position upon an adjacent facet. Even Huxley chastised Darwin for burdening himself unnecessarily with the view that *Natura non facit saltum*.

The tide first turned against the notion of inheritance of acquired characters with the work of the German embryologist August Weismann who observed that (in animals, at least) the cell lineage that leads to an individual's germ cells (eggs or sperm) from which the next generation is formed is independent from the cell lineages that differentiate into the structures of the body (the soma). Weismann could see no possibility for a mechanism that would translate changes acquired by somatic structures into changes in the hereditary material in the germ cells. He is reputed to have argued that inheritance of an acquired character would be as if one were to send a telegram to China and it arrived translated into Chinese.[6]

The advent of modern genetics came with the rediscovery of Mendel's laws at the turn of the century. The initial reaction precipitated a stormy and bitter debate that lasted for almost two decades. Mendel's success was due to his use of variants that have discrete effects--green versus yellow seeds, red versus white flowers, etc.--which enabled him to recognize the particulate nature of the genetic material. Recessive variants (i.e. those whose effects cannot be seen in the traits of offspring of crosses between two pure bred lines) do not blend with the alternative (dominant) variants in such crosses. Instead, the recessive variants maintain their integrity, even though their effects are hidden in the immediate offspring, and can reappear in their original form in predicatable proportions in later generations. This was a new

[6] Recounted by Maynard Smith (1982, p.2).

insight of major significance: the genetic variation required for the theory of natural selection is not destroyed by sexual reproduction; the difficulties imposed by the theory of blending inheritance are irrelevant.

Early Mendelian geneticists, led by William Bateson in England, focused their attention exclusively upon variants with discrete effects and eschewed any work with traits, such as body shape or size, that show a continuous spectrum of variations in populations of organisms. The later were regarded by the Mendelians as mere random fluctuations about the norm, having neither genetic basis nor evolutionary significance. The Mendelians held to a view of evolution proceding through discontinuous jumps. They viewed the role of natural selection as being that of maintaining the norm for a species, and they generally favored the theory, proposed by Hugo de Vries in 1900, of evolution through mutation as the basis for the creation of new species.[7]

On the other side of the debate was a group known as the biometricians. Led by Karl Pearson they subscribed to Darwin's views of continuous variation and gradual evolution through natural selection. They gathered voluminous data on continuous variations and developed statistical methods for analyzing the degree to which offspring resemble their parents. For the biometricians evolutionary change was primarily a statistical problem; they dismissed Mendelian genetics and the discrete variants with which the Mendelians worked as irrelevant to natural populations. In short, the biometricians were onto the important kind of variation but had no genetics, whereas the Mendelians had begun to get genetics straight but could not yet deal with continuous variation.

Such was the state of affairs half a century after publication of *The Origin of Species*. In the following decade things began to change dramatically. Modern genetics had been born and proceeded to grow on its own. Speculative theories of inheritance were replaced by hard facts and sound understanding. It was inevitable that sooner or later the results of genetics would be incorporated into evolutionary biology. Within the Mendelian camp, discovery of traits that are conditioned by multiple, independent, Mendelian factors and breeding experiments that showed the effectiveness of selection for producing permanent change in a character led many geneticists such as William Castle and Thomas Hunt Morgan, who initially had been openly hostile to Darwinism, to recognize Mendelian inheritance and Darwinian selection as complementary elements of the evolutionary process. In 1918, Ronald A. Fisher, who came out of the biometricians' school, published a theoretical mathematical model with which he showed that the correlations between relatives studied by the biometricians could be derived from Mendelian genetics. (Pearson dismissed the paper without reading it because it dealt with Mendelism! The Royal Society declined to publish the paper.)

Fisher's introduction of mathematical theory into evolutionary biology marks the birth of theoretical population genetics, which ultimately clinched the synthesis of Mendelism, Darwinism, and biometry and ushered in a new era in the history of evolutionary biology. The development of theoretical population genetics is synonymous with the work of R. A. Fisher, Sewall Wright, and J. B. S. Haldane. Landmark publications, published relatively early in their respective careers, were Fisher's *The Genetical Theory of Natural Selection* in 1930, Wright's 62 page paper on "Evolution in Mendelian Populations" in the journal *Genetics* in 1931, and Haldane's *The Causes of Evolution* in 1932. If there were a Nobel Prize in

[7] De Vries supported his mutation theory with his experimental work with the plant *Oenothera*. It is one of the odd quicks in the history of science that *Oenothera* has a highly unusual genetic system. Two decades later, de Vries's "mutants" were shown to the result of this atypical genetic system and not mutants at all in the normal sense.

evolutionary biology, each of these men would surely have received it. Between the three of them they constructed--often in mutual antagonism over some fine point--a remarkable body of quantitative theory that combined Mendelian genetics, natural selection, population structure, mating systems, and stochastic effects due to population size to describe the genetical basis of evolutionary change. Among other achievements, their work provided a firm theoretical foundation for the theory of natural selection and secured its permanent place within evolutionary biology.[8]

The synthesis of Mendelism and Darwinism achieved by the theoretical population geneticists was the first stage in a larger synthesis that came to fruition in the 1940's and is commonly referred to as "neo-Darwinism" or "The New Synthesis". Theoretical population genetics grew out of laboratory and agricultural genetics and deals almost exclusively with fundamental processes of phyletic evolution. Its incorporation into the larger fabric of evolutionary biology as a whole was accomplished by an equally remarkable body of field work and qualitative theory produced by a group of biologists with diverse interests in natural populations and natural history. The history of the synthesis and its impact upon modern biology are documented in the essays in Mayr and Provine (1980). Three key figures (all of Nobel Prize caliber) stand out among an illustrious crowd: geneticist Theodosus Dobzhanksy, ornithologist and biosystematist Ernst Mayr, and paleontologist George Gaylord Simpson.[9] Their seminal works from which the synthesis grew were Dobzhansky's *Genetics and the Origin of Species* (1937), Mayr's *Systematics and the Origin of Species* (1942), and Simpson's *Tempo and Mode in Evolution* (1944).

In broadest terms, the new synthesis created a single coherent view of evolution in which patterns of variation at all levels of biological organization are seen to be consistent with processes of change centered upon Mendelian genetics and Darwinian selection. Alternative explanations such as Lamarkianism, orthogenesis, and de Vries's mutation theory were put to rest. The synthesis--especially in the works of Dobzhansky and Mayr on the processes of speciation--completed the revolution Darwin had begun in thinking about biological species. In Mayr's words, typological thinking had been replaced by populational thinking. Prior to Darwin, species were viewed as fixed, unbridgable types within which individual variations were regarded as aberrant deviations from the Platonic essence of the type. In contrast, the biological species concept of the new synthesis recognizes species as populations of variable individuals for which the variations, rather than the type, are the reality of fundamental importance.[10]

The accomplishments of the new synthesis can be viewed in several perspectives. In a narrow sense, the new synthesis embodies a specific model of evolutionary change. The major components of this "neo-Darwinian" model are (1) adaptive change through the natural selection of genetic variations produced by mutation and recombination, (2) allopatric speciation (i.e. speciation in which geographical separation is a necessary prerequisite), and (3) gradual divergence of reproductively isolated populations through successive adaptive changes of small magnitude. In a more general sense the new synthesis established a broad theoretical framework upon which specific biological processes at levels as diverse as genetics, ecology, biosystematics, and paleontology can be fitted into a unified view of evolutionary change. In the explosion of scientific activity that has characterized the past 30 years since Sputnik, the framework

[8] A degree of historical perspective is afforded by realization that these major developments in evolutionary biology occurred several years ***after*** the famous Scopes trial.
[9] Other notable contributors to the synthesis include botanist G. Ledyard Stebbins, German systematist Bernhard Rensch, and, in England, zoologist Julian Huxley (grandson of T. H. and brother of Aldous) and ecological geneticist E. B. Ford.
[10] See Mayr (1978) for a simple, lucid discussion of the significance of populational thinking.

established by the new synthesis has been fleshed out by empirical and theoretical work in all areas of evolutionary biology. Field studies, involving all kinds of organisms, have generated a wealth of information on genetic, cytological, morphological, physiological, and behavioral variability within and among species. Theoretical models have been constructed for a wide variety of specific biological processes to provide mathematical analyses of their expected effects on evolutionary change and speciation.

The most significant new development is the spectacular growth of molecular biology which has brought about new understanding of the underlying molecular mechanisms of inheritance and development. It has also made possible the detection of genetic variation at the molecular level. Early studies of molecular variation revealed two important facts: enormous amounts of small molecular differences exist among individuals of the same species, and many of these molecular variations show patterns of evolutionary changes that appear to have occurred at approximately constant rates. These observations opened a new window for viewing genealogical relationships. The degree to which small chemical differences are found in the structure of particular proteins occurring in different organisms correlates highly with the degree to which the organisms are related.[11] In principle, the molecular data could have been inconsistent with the patterns of genealogical relationships deduced from other lines of evidence such as the fossil record or studies of morphological homologies. Instead, the molecular data have confirmed the previously deduced patterns and provide some of the clearest testimonies to the genealogical relatedness of all organisms.

On the whole, post-synthesis developments have given contemporary evolutionary biology a broad emprical foundation and a robust theoretical structure. This does not mean, however, that our understanding of biological evolution is essentially complete and that all that remains is to fit in a few stray pieces. On the one hand, the principle of genealogical relatedness is supported beyond any reasonable doubt by empirical evidence; historical scenarios for more and more groups have become increasingly refined; and the neo-Darwinian model of the new synthesis is well established as a relevant component in many, if not most, scenarios. On the other hand, there still remain parts of the puzzle that need filling in and fitting together. The heterogeniety of the processes of biological evolution is only beginning to be properly appreciated. Integration of stochastical and historical components of evolutionary change with the neo-Darwinian model of adaptive evolution is only partially complete. Theoretical understanding of the conditions and processes of speciation currently lags behind the large body of empirical data that has been accumulated. Many biologists who are concerned with large scale patterns of evolution beyond the level of species feel that the neo-Darwinian model, while not incorrect, is insufficient to account for large scale macro-evolutionary trends observed by paleontologists and biogeographers and needs to be expanded.[12] In all of these areas, evolutionary biologists are actively searching for an even more comprehensive theory of evolutionary processes.

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[11] For example, cytochrome C is a protein involved in cellular respiration and is found in almost every kind of organism. The cytochrome C found in, say, horses is quite similar in molecular structure to that found in turtles, slightly less similar to that in fish, still less similar to that in insects, and very much less similar to that in bacteria.

[12] See Gould (1982) for a fairly detailed assessment of the modern synthesis from the perspective of a macro-evolutionist.

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