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Is a New Evolutionary Synthesis Necessary?

G. Ledyard Stebbins and Francisco J. Ayala

The current theory of evolution, known as the "modern synthesis" (1), has been challenged by some scientists. Gould, for example, has written that "The modern synthesis, as an exclusive proposition, has broken down on *both of its fundamental claims*: extrapolationism (gradual allelic substitution as a model for all evolutionary change) and nearly exclusive reliance on selection leading to adaptation" (2; emphasis added). Gould goes on to voice the need for a "new and general evolutionary theory [that] will embody [the] notion of hierarchy and stress a variety of themes either ignored or explicitly rejected by the modern synthesis." Similar statements have been made by a few others (3, 4).

Many evolutionists would be surprised to see identified as the two "fundamental claims" of the modern synthesis those listed by Gould and most would not agree that the modern synthesis has "broken down." The impression that a "straw man" has been erected is confirmed when one discovers that the proposed new "themes" (2-4) are part and parcel of the modern synthesis (1, 5-12). However, the critics' appeal to the pluralistic structure of evolutionary theory, to the hierarchical nature of evolutionary processes, and to the distinctive contributions made by the study of macroevolutionary phenomena deserve attention.

Mutation and Selection

Genetic changes underlie the evolution of organisms; mutations are the ultimate source of the genetic variation that makes possible the evolutionary process. "Genetic mutations are changes in the hereditary materials. . . . They can be classified in one of two major categories: *gene* (or point) *mutations*, which affect only one or a few nucleotides within a gene; and *chromosomal mutations* (or aberrations), which affect the number of chromosomes, or the number

or the arrangement of genes in a chromosome" (1, p. 57). Gene mutations are the source of allelic variation; chromosomal mutations make possible the evolution of the amount and organization of the hereditary material (DNA). It is misleading to criticize the modern synthesis on the alleged grounds of its exclusive reliance on "point mutations (micromutations)"

Summary. The current (synthetic) theory of evolution has been criticized on the grounds that it implies that macroevolutionary processes (speciation and morphological diversification) are gradual. The extent to which macroevolution is gradual or punctuational remains to be ascertained. Macroevolutionary processes are underlain by microevolutionary phenomena and are compatible with the synthetic theory of evolution. But microevolutionary principles are compatible with both gradualism and punctualism; therefore, logically they entail neither. Thus, macroevolution and microevolution are decoupled in the important sense that macroevolutionary patterns cannot be deduced from microevolutionary principles.

(2). Chromosomal mutations (traditionally known as chromosomal abnormalities or aberrations) played an essential role in the development of the modern synthesis and remain one of its pivots (6, 9-10).

The frequencies of genes and gene arrangements change through the generations (evolve) owing to four processes: mutation, migration (gene flow), random drift, and natural selection. These four elementary processes of genetic change were already characterized by the early theorists who established the mathematical foundations of the modern synthesis (5, 12, 13). The highly organized character of organisms and their obvious adaptations are largely the result of natural selection operating under a variety of constraints, but responding to the demands of the environment. The constraints include the existing structure of organisms (and, hence, past history), the genetic variation available, as well as the particular circumstances of the physical and biotic components of the environment.

Without natural selection, populations of organisms would disintegrate over the generations because mutation and drift are random with respect to adaptation. But it is not correct that, for the synthet-

ic theory, "All genetic change is adaptive"; or that "genetic drift certainly occurs—but only in populations so small and so near the brink that their rapid extinction will almost certainly ensue" (2, p. 120; 3, pp. 20, 23-25). Controversy concerning the relative importance of random drift vis-à-vis natural selection has existed from the very beginning among the proponents of the modern synthesis. Fisher (12), for example, minimized the importance of random drift, but this is an important and decisive process in Wright's "shifting balance" version of the modern synthesis (5). Some evolutionists have relegated the importance of random drift to restricted—but by no means trivial—circumstances, such as "founder effects," which occur when a population is derived from only a few colonizers (7).

During the last decade no other issue

has been more actively debated among evolutionists than the role of random drift. Molecular studies have shown that protein polymorphisms are pervasive in natural populations and that protein changes accompany the evolution of species (14). The neutrality theory of protein evolution proposes that evolution at the molecular level is largely due to random drift rather than being impelled by natural selection (15). But many evolutionists maintain that natural selection plays an essential role even at the molecular level (14). The "selectionist" and "neutralist" views of molecular evolution are competing hypotheses within the framework of the synthetic theory of evolution (16).

The Origin of Species

Living beings do not represent a continuum of all possible gene combinations generated at random, but are rather naturally grouped into species: arrays of populations between which intermediates are rare or absent. The distinctness of species is preserved by reproductive isolating mechanisms, that is, by biologically determined impediments to gene exchange, such as ethological or ecological

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differentiation and hybrid sterility. In sexually reproducing organisms, species may be defined as "groups of interbreeding natural populations that are reproductively isolated from other such groups" (6, 7).

Interest in the process of speciation has recently burgeoned among paleontologists who sponsor the punctuated equilibria model (3, 4, 17), which is contrasted with the gradualistic model of macroevolution. Proponents of the punctualist model argue that, according to paleontological evidence, "species have tended to last for such long intervals of geological time that, once formed, they must have evolved very slowly. . . . This condition, when compared to the rapid pace of large-scale evolution, implies that most sizable evolutionary steps in the history of life must have occurred cryptically from a paleontological vantage point, during the rapid origination of certain species from small, localized populations of pre-existing species" (3, p. 3).

Whether macroevolution occurs according to the punctualist or the gradual model is something to be decided empirically. Certainly both modes have occurred in evolution, and the question then is their relative importance and the identification of factors that determine one or the other mode. Our primary concern here is, however, not this issue but rather whether any inconsistencies exist between the punctualist mode of evolutionary change and the synthetic theory's understanding of the speciation process.

We note, first, that the alleged relevance of punctuational evolution to speciation is based, at least in part, on two misunderstandings. The first one is a definitional artifact: paleontologists recognize species by their different morphologies as preserved in the fossil record (18). Thus, speciation events yielding little or no morphologically different products go totally unrecognized. Sibling (that is, morphologically indistinguishable) species are common in many groups of insects, in rodents, and in other well-studied organisms (6, 7). Speciation as seen by the paleontologist always involves substantial morphological change *because only when such change has occurred is the paleontologist able to recognize the presence of a new species*. The second misunderstanding concerns the time scale. When punctualists argue that paleontological evidence indicates that speciation is a rapid process (3, 4, 17), they are using a geological time scale. Instantaneous events in the paleontological scale, as in the transition

between different geological strata, may involve thousands, at times many thousands, of years. In the microevolutionary scale of the population biologist, a thousand years is a long time, not an instant.

A more fundamental point is that rapid speciation, even in the microevolutionary scale, is not inconsistent with, and has been postulated by, the synthetic theory. Lewis's model of "saltational" speciation (19) and White's "stasi-patric" speciation (20) are speciation models proposing that new species can arise in a few generations, as a result of the reproductive isolation produced by translocations and other chromosomal mutations. Polyploidy is the limiting case of rapid speciation—requiring only one or two generations—through chromosomal change (6, 10). Rapid speciation without chromosomal reorganization has not only been postulated by the proponents of the modern synthesis (6, 7, 11) but has been studied experimentally. A notable example—an incipient neospecies that arose in a *Drosophila paulistorum* culture, sometime between 1958 and 1963—was the subject of investigation by Dobzhansky for many years (21). In brief, the synthetic theory recognizes that there are a number of modes of speciation and that some of them, variously grouped under such terms as "saltational," "rapid," or "quantum" modes, require only a few generations and are effectively instantaneous in the geological time scale (22).

According to Gould, "The most exciting entry among punctuational models for speciation in ecological time is the emphasis, now coming from several quarters, on chromosomal alterations as isolating mechanisms" (2, p. 123). The role of chromosomal mutations in speciation is, like other important empirical questions, a subject of continued investigation and increased understanding. But the works to which Gould refers represent only the most recent accomplishments of a continuum that extends back to the 1930's (6, 9, 10, 23). Summarizing in 1950 the earlier work, Stebbins (10) concluded that (i) the most effective chromosome barriers of reproductive isolation come from the accumulation of small chromosomal changes; (ii) these changes may accumulate in a short time, such as 50 to 100 generations, to the point of resulting in reproductive isolation; (iii) these small changes occur largely independently of changes in the genes affecting external morphology; and, therefore, (iv) morphologically undifferentiated species may exhibit substantial chromosomal differences.

From Microevolution to Macroevolution

We come now to what has been called "the central question" posed by the proponents of punctualism, namely, "whether the mechanisms underlying microevolution can be extrapolated to explain macroevolution" (24). The argument has been succinctly expressed as follows: "if species originate in geological instants and then do not alter in major ways, then evolutionary trends cannot represent a simple extrapolation of allelic substitution within a population" (2, p. 125).

The question raised is the general issue of reduction as it applies to the different levels of the evolutionary process. Evolutionary trends are high-level phenomena predicated from events that encompass different species, as well as genera and higher taxa, and that extend over long periods of time. Microevolutionary studies are, on the contrary, concerned with evolutionary changes in populations that occur within "instants" of geological time. But, as so often happens with questions of reductionism, the issue of "whether the mechanisms underlying microevolution can be extrapolated" to macroevolution involves separate issues that must be distinguished in order to arrive at a satisfactory resolution.

Three separate questions, at least, are involved: (i) whether microevolutionary processes *operate* (and have operated in the past) throughout the different taxa in which macroevolutionary phenomena are observed; (ii) whether the microevolutionary processes identified by population geneticists (mutation, chromosomal change, random drift, natural selection) can account for the morphological changes and other macroevolutionary phenomena observed in higher taxa or, rather, whether additional kinds of genetic processes need to be postulated; and (iii) whether evolutionary trends and other macroevolutionary patterns can be predicted from knowledge of microevolutionary processes.

These distinctions may perhaps become clearer if we state them as they might be formulated by a biologist concerned with the question whether the laws of physics and chemistry can be extrapolated to biology. The first question would be whether the laws of physics and chemistry apply to the atoms and molecules present in living organisms. The second question would be whether biological phenomena can be accounted for as the result of interactions between atoms and molecules according to the laws known to physics and chemistry or

whether the workings of organisms require additional kinds of interactions between atoms and molecules. The third question would be whether living phenomena can be predicted from the laws of physics and chemistry.

As to the first question, it is unlikely that any paleontologist would claim that mutation, chromosome change, drift, natural selection, and other microevolutionary processes do not apply to each of the populations of the higher taxa that are considered in macroevolution. There is, of course, an added dimension—macroevolutionists are largely concerned with phenomena of the past. Direct observation of microevolutionary processes in populations of long-extinct organisms is not possible. But there is no reason to believe that the processes of mutation, random drift, and natural selection, or the nature of the interactions between organisms and the environment would have been different in nature for, say, Paleozoic brachiopods and ostracoderms than for modern molluscs and fishes. Extinct and living populations—like different living populations—may have experienced quantitative differences in the relative importance of one or another process, but the processes could hardly have been different in kind.

The Origin of Differences Between Higher Taxa

The second question raised above has more substantive implications than the first. Can the microevolutionary processes studied by population geneticists account for macroevolutionary phenomena or do we need to postulate new kinds of genetic processes? The large morphological (phenotypic) changes observed in evolutionary history, and the rapidity with which they appear in the geological record, is one major matter of concern. Another issue is stasis—the apparent persistence of species, with little or no morphological change, for hundreds of thousands or millions of years. The apparent dilemma is that microevolutionary processes apparently yield small but continuous changes, while macroevolution as seen by punctualists occurs by large and rapid bursts of change followed by long periods without change.

Forty years ago Goldschmidt argued that the incompatibility is real: “The decisive step in evolution, the first step towards macroevolution, the step from one species to another, requires another evolutionary method than that of sheer accumulation of micromutations” (25). The specific solution postulated by

Goldschmidt, that is, the occurrence of systemic mutations, yielding hopeful monsters, can be excluded in view of current genetic knowledge, but the issue raised by him deserves attention.

Single-gene or chromosome mutations may have large effects on the genotype because they act early in the embryo and their effects become magnified through development. Single-gene “macromutations” have been carefully analyzed, for example, in *Drosophila melanogaster*—mutations such as “bithorax” and the homeotic mutants that transform one body structure, for example, antennae, into another, such as legs. These large-effect mutations are not incompatible with the synthetic theory. Whether the kinds of morphological differences that characterize different taxa are due to such “macromutations” or to the accumulation of several mutations with small effect has been examined particularly in plants where fertile interspecific, and even intergeneric, hybrids can be obtained. The results of numerous studies do not support the hypothesis that the establishment of macromutations is necessary for divergence at the macroevolutionary level (10, 23). In animals, even a familial character, the presence of three ocelli in drosophilids, can be changed by artificial selection, demonstrating that a family-distinctive trait can be produced by the accumulation of small mutations present in natural populations (26). Moreover, Lande has convincingly shown that major morphological changes, such as in the number of digits or limbs, can occur in a geologically rapid fashion through the accumulation of mutations each with a small effect (27). In general, the evidence from plants as well as from animals supports Fisher’s (12) theoretical argument that the probability of incorporation of a mutation in a population is inversely proportional to the magnitude of the mutation’s effect on the phenotype.

Nevertheless, rapid phenotypic evolution may be caused by relatively slight genetic changes that affect critical stages of development. Alberch (28) has described differences in the number and position of tarsal bones in salamanders of the genus *Plethodon*. It is not known at present whether only one mutation, or several with additive effects, is involved. But the important point is that only a few of the possible genetic changes can, in interaction with the rest of the genome, yield a functional phenotype; and, therefore, the organ can change in only one or very few directions. Phenotypic evolution is thus directed along certain channels that may be followed by separate

lineages. To what extent canalization of development restricts the possible directions of morphological evolution is a question as yet unsolved.

How often mutations with large phenotypic effects are involved in the origin of new taxa is also an unsolved question. The punctualists’ thesis that such mutations may have been largely responsible for macroevolutionary change is based on the rapidity with which morphological discontinuities appear in the fossil record (2, 3). But the alleged evidence they present does not necessarily support the proposition. Microevolutionists and macroevolutionists use different time scales. The “geological instants” during which speciation and morphological shifts occur may involve intervals of the order of 50,000 years. There is little doubt that the gradual accumulation of small-effect mutations may yield sizable morphological changes during periods of that length. Anderson’s study of body size in *Drosophila pseudoobscura* may serve as an example (29). Large populations, derived from a single set of parents, were set up at different temperatures and allowed to evolve on their own. A gradual, genetically determined, change in body size ensued, with flies kept at lower temperature becoming larger than those kept at higher temperatures. After 12 years, the mean size of the flies from the population kept at 16°C had become, when tested under standard conditions, approximately 10 percent greater than the size of the flies from the populations at 27°C; the change of mean value being greater than the standard deviation in size at the time when the tests were made. Assuming ten generations per year, the populations diverged at an average rate of 8×10^{-4} of the mean value per generation.

Paleontologists have emphasized the “extraordinary high net rate of evolution that is the hallmark of human phylogeny” (3). Interpreted in terms of the punctualist hypothesis, human phylogeny would have occurred as a succession of jumps, or geologically instantaneous saltations, interspersed by long periods without morphological change. Could these bursts of phenotypic evolution be due to the gradual accumulation of small changes? Consider cranial capacity, the character undergoing the greatest relative amount of change. The fastest rate of net change occurred between 500,000 years ago, when our ancestors were represented by *Homo erectus*, and 75,000 years ago, when Neanderthal man had acquired a cranial capacity similar to that of modern humans. In the intervening 425,000 years, cranial capacity evolved

from about 900 cubic centimeters in Peking man to about 1400 cubic centimeters in Neanderthal people. Let us assume that the increase in brain size occurred in a single burst at the rate observed in *Drosophila pseudoobscura* of 8×10^{-4} of the mean value per generation. The change from 900 to 1400 cubic centimeters could have taken place in 540 generations or, if we assume 25 years per generation, in 13,500 years. Thirteen thousand years are, of course, a geological instant. Yet, this evolutionary "burst" could have taken place by gradual accumulation of small-effect mutations at rates compatible with those observed in microevolutionary studies (30).

We now raise the question of "stasis," the long-term persistence of species without morphological change. According to the model of punctuated equilibria, most phenotypic macroevolutionary change occurs in rapid bursts followed by long periods of stasis, during which little if any morphological change takes place. Phenotypic stability is compatible with microevolutionary processes; it ensues from stabilizing selection (1, 6, 8). Stebbins (10) in 1950 pointed out the morphological similarity, in forest trees and some herbs, between populations that have been separated from each other for millions of years. According to Dobzhansky (31), a successful morphology may persist unchanged for extremely long periods of time, even through speciation events. Some sibling species in *Drosophila* diverged from each other millions of years ago, yet their morphologies have remained identical to each other and to their ancestral species (32). Dobzhansky postulated that evolution in such cases continues, however, at the physiological or biochemical level; a prediction confirmed by recent molecular studies (33, p. 587).

Whether the phenomenon of paleontological stasis is as common as claimed by the punctualists needs to be carefully examined (34). As indicated by Levinton and Simon (18), paleontological taxonomy at the species level "requires the identification of species-specific characters which are invariant with time." Stasis may often be only apparent, as another artifact of the definition of species used.

Reduction, Hierarchy, and Macroevolution

We have just argued that the macroevolutionary patterns proposed by the model of punctuated equilibria—short periods of rapid phenotypic change fol-

lowed by long spans of morphological stasis—are compatible with the theory of population genetics concerning microevolutionary processes. But does the theory predict that macroevolution will be punctuational? This is the third question formulated above, and the answer can only be no. The theory of population genetics is compatible with both punctualism and gradualism. Logically, therefore, it does not entail either. Whether macroevolution occurs predominantly according to the model of punctuated equilibria or to the model of phyletic gradualism is a question to be decided by studying macroevolutionary patterns, not by inference from our knowledge of microevolutionary processes (35).

Levinton and Simon (18) have written that "the implications of [the species-selection model proposed by the punctualists] should be of immediate concern to population biologists studying microevolutionary phenomena because it claims to negate the importance of population level phenomena in long term evolution," and they have gone on to "question the [punctualists'] belief that microevolution is decoupled from macroevolution." Statements of this kind need to be clarified. We have established above that at least three different issues are at stake, and have stated our solution to the first two issues. We may reiterate our points paraphrasing the terminology used by Levinton and Simon. Population level phenomena are important to long-term evolution because the populations in which macroevolutionary patterns are observed are the same populations that evolve at the microevolutionary level. Moreover, the study of microevolutionary phenomena is important to macroevolution because any theory of macroevolution that is correct must be compatible with well-established microevolutionary principles and theories; and indeed we have argued that the model of punctuated equilibria is compatible with the theory of population genetics. In these two senses—identity at the level of events and compatibility of theories—macroevolution cannot be decoupled from microevolution. But there is one sense (which epistemologically is most important) in which macroevolution and microevolution are decoupled, namely, in the sense that macroevolution is an autonomous field of study that must develop and test its own theories. In other words, macroevolutionary theories are not reducible (at least at the present state of knowledge and probably in principle) to microevolutionary theories.

Gould (2, p. 121) has pointed out that

the study of evolution embodies "a concept of hierarchy—a world constructed not as a smooth and seamless continuum, permitting simple extrapolation from the lowest level to the highest, but as a series of ascending levels, each bound to the one below it in some ways and independent in others . . . 'emergent' features not implicit in the operation of processes at lower levels, may control events at higher levels."

The world of life is hierarchically structured. There is a hierarchy of levels: from atoms, through molecules, organelles, cells, tissues, organs, multicellular individuals and populations, to communities. Time adds another dimension of the hierarchy, with the interesting consequence that transitions from one level to another occur such that as time proceeds the descendants of a single species may include several species, genera, families, and so forth. Hierarchical organization often is such that the phenomena at a given level cannot be inferred from knowledge of the phenomena at a lower level of the hierarchy. Statements about "emergent" features imply this inability to predict from one level of organization to another. Consider, for example, the question whether water has emergent properties relative to its components, hydrogen and oxygen. One could argue that among the properties of hydrogen and oxygen one must include their ability to combine according to the formula H_2O and to exhibit the properties attributed to water. Proceeding accordingly, one could claim that the properties of oxygen and hydrogen include those of hemoglobin and other proteins as well as human speech and abstract thought, because oxygen and hydrogen have these properties when combined with other given atoms in certain ways. But this is a definitional maneuver that contributes little to the understanding of the relationships between complex systems and their constituent parts.

The consideration that is important is whether the properties of a complex object or system can be inferred from the study of component parts in isolation. It is for this reason that we do not usually include among the properties of hydrogen those of water, ethyl alcohol, proteins, or human beings (36).

The question of whether macroevolution is an autonomous field of knowledge is more appropriately posed in terms of the relationships between macroevolutionary and microevolutionary theories, rather than in terms of hierarchy of levels or emergent properties (37). The study of macroevolution is auto-

mous with respect to microevolutionary studies if the theories, hypotheses, and models of macroevolution cannot be "reduced" to the microevolutionary theories, hypotheses, or models. Two conditions are jointly necessary and sufficient for the reduction of one branch of science to another: derivability and connectability (38). The condition of derivability requires that the laws and theories of the branch of science to be reduced be derived as logical consequences from the laws and theories of some other branch of science. The condition of connectability requires that the distinctive terms of the secondary branch of science be redefined in the language of the branch of science to which it is reduced—this redefinition of terms is, of course, necessary in order to analyze the logical connections between the theories of the two branches of science.

Microevolutionary processes, as now known, are compatible with the two models of macroevolution—punctualism and gradualism. From microevolutionary knowledge, we cannot infer which one of those two macroevolutionary patterns prevails. Hence, the condition of derivability is not satisfied. Needless to say, the conflict between punctualism and gradualism is not the only macroevolutionary issue that cannot be decided by logical inference from microevolutionary principles. Consider, for example, the question of rates of morphological evolution. Three groups of crossopterygian fishes flourished during the Devonian. The lungfishes (Dipnoi) changed little for hundreds of millions of years and remain as relics. The coelacanths became highly successful in the open ocean until the Cretaceous, then declined and stagnated, leaving only the relictual *Latimeria*. The rhipidistians, in contrast, evolved into the amphibians, reptiles, and, finally, birds and mammals (39). Models to explain divergent rates of morphological evolution must incorporate factors other than microevolutionary principles, including rates of speciation and the environmental and biotic conditions that may account for successions of morphological change in some but not other lineages.

Distinctive macroevolutionary theories and models have been advanced

concerning such issues as rates of morphological evolution, patterns of species extinctions, and historical factors regulating taxonomic diversity. As long as these theories and models are compatible with the theories and laws of population biology, the decision as to which one among alternative hypotheses is correct cannot be reached by recourse to microevolutionary principles. Such a decision must rather be based on appropriate tests with the use of macroevolutionary evidence (3, 4, 18). Thus, macroevolution is an autonomous field of evolutionary study and, in this epistemologically very important sense, macroevolution is decoupled from microevolution (40).

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36. Notice that, under the proposal herein made, whether or not a property is considered emergent depends on the state of knowledge; what appeared at one point as an emergent property might later be predictable from knowledge of the component parts. Notice also that the question of emergent properties is not limited to the world of life.
37. The reason is that the hierarchical differentiation of the subject matter is neither necessary nor sufficient for the autonomy of scientific disciplines. It is not necessary, because entities at a single hierarchical level can be the subject of diversified disciplines: cells are appropriate subject of study for cytology, genetics, immunology, and the like. In fact, identical events can be the subject of concern of different disciplines. The writing of this note can be studied by a physiologist interested in the muscular and nerve processes involved, by a philosopher interested in the epistemological question raised, by a psychologist concerned with thought processes, and so on. Moreover, hierarchical differentiation of subject matter is not a sufficient condition for the autonomy of the concerned disciplines; relativity theory applies all the way from subatomic particles to planetary motions, and genetic laws apply to multicellular organisms as well as to cellular and even subcellular entities.
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41. Supported by NIH grant 1-P01-GM-2221.