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ON THE NATURE OF CONTROVERSIES IN EVOLUTIONARY BIOLOGY

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While en route to a scientific meeting recently, I chanced on an article entitled "Life after Darwin" [1] in one of the airline magazines. The conclusion ventured that "even acknowledging that no scientific theory can fully measure up to Popperian standards, it would still seem that some theories are better than others. Darwinism is probably one of the others" [1, p. 50]. The author refers to the proposition made by Sir Karl Popper in 1919 that a major criterion for a scientific hypothesis is its "falsifiability." Although recently challenged [2], this "Popperian standard" has permeated all aspects of biology. The importance of falsifiability and problems with its definition aside, this doctrine has been used as a banner against classic views of selection and adaptation.

In "Life after Darwin," the hypothesis of "punctuated equilibrium" was portrayed as being more falsifiable than that of Darwinian selection and as being its antithesis. Punctuated equilibrium proposes that species undergo little or no evolutionary change over long periods of time punctuated by brief periods of speciation and rapid evolutionary change [3]. Most biologists agree that the rates of evolutionary change vary over time and also between taxa and at different levels of biologic organization, although they would not question Darwin's principal theory of evolution through natural selection operating at the level of the individ-

This essay received honorable mention in the 1988 Dwight J. Ingle Memorial Writing Award competition for young authors. The author acknowledges numerous discussions with colleagues and mentors who helped shape the ideas in philosophy and biology expressed in this paper—even though these colleagues may not agree with some of the conclusions. Special thanks are extended to K. John Morrow, Ray C. Jackson, Robert J. Baker, Fred B. Stangl, Jr., Craig S. Hood, Linda Daniels, Christy Wright, and Mike Kennedy.

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0031-5982/90/3303-0681$1.00

ual. Thus, punctuated equilibrium should certainly not be viewed as incompatible with the modern synthesis of views on evolution [4, 5].

Such characterizations have become common in popular literature. This is but one of the many recent controversies in evolutionary biology in which attacks and counterattacks rage and subside in mysterious ways. Some evolutionary controversies have drifted from intellectual exchanges to political diatribes. The scientific debates regarding the mechanisms of evolution are portrayed by religious fundamentalists as indicating a bankruptcy of the whole idea of evolution. Battles over "creation science" in the public school curricula exemplify the results of this perception. Clearly, understanding controversies about evolution that result in heated exchanges is vital not only to basic science but also to the health of evolutionary science as an enterprise and its perception by the general public.

The scientific approach invariably involves choices between opposing methodologies and hypotheses. At any one time, scientists have—as they should—divergent views on issues for which there is a dearth of data and ample room for speculation. Issues such as the degree of divergence in DNA sequences of two populations, the relationships of a group of species, or Mendelian versus blending inheritance are intrinsically more amenable to new evidence and resolution than are concepts regarding the tempo and mode of evolution. The question thus remains, Are controversies over mechanism and level in evolution ever resolved and, if so, how? Do opposing parties reach a level of compromise and synthesis of ideas? Does an evolutionary theory advance when a new generation arrives that is more receptive to it? Or does the new generation devise its own ideas and arguments, ignoring the old controversies? It is not my intention to critically evaluate any of the currently debated evolutionary hypotheses. Rather, my aim is to present a view of evolutionary controversies using three examples in the areas of systematic philosophy, subspecies designation, and sociobiology.

Systematic Philosophies

Since the time of Linnaeus, the founder of modern classification, the procedures and methods of classification have undergone marked changes aimed at creating a better ordering of living organisms. The best classification, it has been argued, should be a natural one, reflecting true evolutionary relationships. But what is a natural classification and, more important, how does one determine "true relationships"? These questions are highly controversial and have given rise to at least two divergent schools of thought: cladistics and phenetics. Cladistics, first proposed by Hennig [6], is a philosophy of systematics that proposes a set of rules for constructing evolutionary trees on the basis of postulated character changes in the taxa under study. This approach emphasizes the importance of assigning derived versus primitive conditions for each character (called character states) and using only shared derived character states in defining groups of species. Phenetics is a philosophy of systematics that originated when computer technology allowed analyses of many morphological characters for large samples of organisms to determine the degrees of similarities and differences. Proponents of this approach argue that the only way of objectively arriving at relationships is to use overall similarity between organisms [7].

A somewhat less ardent and more equivocal group, led by Mayr and other "traditional evolutionists," speaks of the "adaptive component of evolution" in classification. They stress the importance of genetic studies over periods of time in permitting inferences about degrees of divergence and affinity [8]. The primary difference between this school and the cladistic school is that the latter wants classification to reflect cladistic affinities and insists that taxa must be strictly holophyletic (i.e., must include all descendants from a common ancestor, as defined by derived character states [9]), whereas the former thinks that classification should also reflect such factors as the degree or amount of divergence [10].

The arguments waxed hot and heavy. Pheneticists defended their system as practical, logical, and universally acceptable, and struck back at cladists for the purportedly arbitrary assignment of derived and primitive character states. Darlington [11] ripped into concepts he believed were representative of cladist philosophy and charged that they "are all oversimplified, in part illogical, inconsistent with real situations that are common in nature and of no practical use in systematics and biogeography." Nelson [12] defended Hennig's views against the arguments of Darlington and Mayr and claimed Darwin as a supporter of his views: "If indeed there is a cladistic school, Darwin was its founder and its chief exponent."

These arguments peaked in articles appearing in the journal *Systematic Zoology* during 1974–1979. The number of articles addressing this controversy decreased during the 1980s, and new journals were established to promote research under particular philosophies (e.g., *Cladistics*). Was all this just so much hoopla? Was any school of thought victorious? The most vocal proponents of each doggedly adhered to their ideas, their zeal fanned occasionally by opponents' publications. Signs of compromise from the less ardent systematists were already evident by the late 1970s, as dissent from strict cladistic or strict phenetic approaches to classification appeared in the literature (e.g., [13, 14]).

Today, practicing systematists would acknowledge that the phenetic approach is desirable in some situations, such as studying intraspecific geographic and sexual variation, in producing efficient taxonomic keys, and in providing easy information retrieval. Similarly, the weighing of characters and empirical determination of primitive versus derived character states are considered appropriate for data sets such as those derived from comparative molecular biology and cytogenetics (e.g., [15, 16]). The practicing systematist decides on the degree to which a particular philosophy of systematics (i.e., strict cladistics, phenetics, or a mixture) should be reflected in the scheme of classification. Thus, it appears that the emphasis shifted (at least among many practicing systematists) from determining the ideal philosophy for building phylogenetic trees and for classifying organisms to more practical considerations in characterizing relationships among organisms.

The Subspecies Controversy

Subspecies and varieties are common features of animal and plant taxonomy. They are considered in both International Codes of Nomenclature (zoological and botanical) and are supposed to describe well-defined units or populations below the species level. Although the zoological literature is replete with subspecific names, the import and even the utility of the subspecies in biological studies have long been the subject of considerable controversy. One school of thought considered the subspecies an important category worthy of taxonomic rank and of great evolutionary significance as the stepping-stone toward complete reproductive isolation and hence speciation. Another view asserted that this is a totally useless concept that confuses the process of evolution with semantics. The peak of this debate occurred during 1954–1956 with several publications in *Systematic Zoology* (see vols. 3–5). Arguments against the subspecies concept usually emphasized the arbitrariness and difficulties inherent in recognizing populations on the basis of geographic variation in morphological characters. Proponents rejected such arguments and concluded that subspecies designations are important for understanding evolution. The two schools failed to resolve their differences, and, after their arguments were exhausted, little was published on this issue.

It is not clear why this problem was not resolved at the time. A new generation of scientists—Lidicker [17] being one of the earliest—shifted the focus from geographic variation per se to studies of evolutionary history and speciation. Understanding the phylogenetic relationships of populations within a species became easier with the advent of modern population-genetic, cytogenetic, and molecular approaches. These new approaches led many systematists to ask more relevant questions about geographic variation and essentially shifted the focus from the description of morphologic variation associated with ecologic variation in different populations and the naming of such populations to a direct study of evolutionary genetic divergence in populations [18, 19]. Such genetically oriented works as Endler's *Geographic Variation, Speciation and Clines* [20] should have provided the necessary impetus and data to resolve the remaining question of designating names for geographically variant populations. However, few geneticists extended the implications of their work to the status of subspecies. Thus, traditional systematists describing "new" subspecies seemed totally unaware of the new genetic research and continued in their comfortable pursuit of new names.

Sociobiology

The most politicized of evolutionary debates is that involving the field of sociobiology. E. O. Wilson and many others developed the field of sociobiology as a way of applying evolutionary principles to human sociology and psychology. They argued that sociobiology is the logical extension of natural selection and of the field of evolutionary genetics into the realm of human culture. One can quickly get the flavor of the controversy aroused by this thesis from the reviews of *Genes, Mind, and Culture* [21]. In this book, Wilson and Lumsden attempted to put sociobiology "on the firm theoretical, quantitative basis" that the critics found lacking in Wilson's earlier work [22]. R. C. Lewontin declared this effort fruitless because it rested on a reductionist approach that produced nontestable hypotheses and assertions. In his review, Lewontin [23] stated:

> The argument is now complete. A small difference in natural selection will cause a small change in gene frequencies, the small change in gene frequencies will cause a small change in "epigenetic rules," and a small change in epigenetic rules will lead to a huge change in the culturgen frequency in different populations. So, the multiplier effect works after all, and sociobiology is saved. The only trouble is that each step of the model-building process is carefully designed to achieve that end. The authors have tried to cover their tracks by dusting their path with epsilons and deltas, but the plan is clear.

Segerstrale, reviewing the conflict between Wilson and Lewontin, concluded:

> One could describe the situation between these two opponents in the sociobiology controversy as really one of symbiosis. It is in both parties' interest to keep the controversy going, not to clear up misunderstandings, and not to introspect too much about where the real differences lie. This shows that the terms of a scientific debate, while set by the protagonists, may not be a true representation of what the conflict is, in fact, about. [22, p. 79]

Wilson responded to the arguments by stating that Lewontin did not criticize the substance of *Genes, Mind, and Culture* [22]. Such an analysis was provided later by another review [24], which appeared in *Evolution:*

> Our conclusion is that little that is not self-evident emerges from the models, and that the results which LW [Lumsden and Wilson] regard as important, like the

"thousand year rule," do not depend on the cultural components of the model, but follow directly from the assumption of high heritability and strong selection. [24, p. 624]

Criticism and countercriticism surrounding sociobiology continue to be heated, perhaps in part because of the political and social implications of these studies. An example is the recent publication of a book on aggression that is critical of sociobiology [25] and a review of this book in *Nature:*

With apparent ease the complex observations of Charles Darwin, Sigmund Freud, Konrad Lorenz, Paul MacLean, E. O. Wilson, Richard Dawkins, Jose Delgado, Robert Axelrod and other contributors to this debate (including, alas, myself) are disposed of. The treatments have a depth of insight and freshness worthy of examination essays. . . . There is not a single new fact, idea, analysis or synthesis that might move forward, even a bit, the frontiers of knowledge about this grave human and scientific problem on which the world's future may hinge; only breezy criticisms of the best efforts of others. . . . Respected opponents of sociobiology! Surely you can do better than that! [26]

Is There a Trend in Evolutionary Controversies?

The three examples described here lead to the conclusion that evolutionary controversies tend to be heated exchanges that rarely end in victory for one of the opponents or for a reasoned compromise. Once ideas are presented, the controversy builds up steam and reaches a peak at some point, then slowly recedes. This somewhat undramatic conclusion to most controversies can be due to the absence of further counterarguments or lack of interest in the scientific community. Frequently, this results from a lack of data to falsify one of the competing views. When such data become available after the debate subsides, readers who have lived through the "war" can reflect on who was right or wrong. However, by that time the original contestants have moved on to different areas—often new controversies.

When, through logic, a scientist demonstrates that his or her particular conclusions follow from accepted premises, we acknowledge that he or she has produced a proof [27]. Although we must hope that "proof" represents an approximation of empirical truth, they may not always correspond. It is the core of the scientific method that this approach does indeed bring us closer to the empirical truth. Why is it, then, that most controversies involving the evolutionary process do not seem to follow a resolvable pattern involving proof? Conflicts involving the subspecies concept in the 1950s, cladistics and phenetics in the late 1960s and in the 1970s, and sociobiology in the 1980s are but three examples among many. Other examples of controversies in evolutionary and systematic biology abound. Mayr [28] enumerates a great many unresolved

issues in natural selection including the level of genetic variability in natural populations, variability due to chance, Haldane's genetic-load controversy, group selection, and punctuated equilibrium. Why is it that after thousands of pages of journal articles and seemingly endless books on the subject, scientists still disagree about whether natural selection operates on levels above and below the individual organism (species and higher taxa sensu Eldredge and colleagues and genes sensu Dawkins) [29]?

The answers to these questions lie in the nature of the field or subject matter and of the people involved. Evolutionary change occurring over geologic times cannot be examined directly, and scientists must use such clues as the variation observed between living organisms and fossils. Limitations on experimentation in this science are perhaps only paralleled by similar limitations on some aspects of physics (e.g., hypotheses on the origin of the universe). In addition, characterization of evolution involves a study of complex interactions of living things with their environment, an extremely complicated endeavor. It is therefore not surprising that most evolutionary biologists are so involved in their highly focused research that they are not concerned with the holistic or reductionist approach of the theoreticians. For example, while the cladistic/phenetic controversy was raging, most practicing systematic mammalogists blithely continued their work and refused to take sides. To the potential dismay of both sides, mammalogists began using techniques from both phenetics and cladistics in their research. Similarly, many other biologists used the most practical methods or totally avoided the issues described here.

I would suggest that there are three approaches to any controversy: collection of data, construction of models, and undermining of the models. These three approaches are more clearly defined in evolutionary science than in other fields, and each appears to characterize a group of evolutionists. Only a few evolutionists would claim to do all three. The model builders are generally philosophically oriented, positive thinkers who have high expectations of their hypotheses. Critics either have their own models or are synthesizers of opposing models. The practicing scientists who collect the data try to understand such data in light of practical consequences regardless of the model used. It is unfortunate that the ardent opponents in any controversy receive the most attention in discussions of issues at all levels, from specialized scientific debates or roundtable discussions in university courses and seminars, to newspaper articles written for the lay people. Practicing scientists and synthesizers of evolutionary knowledge seem to receive little attention. When the competing parties do pay attention to such moderate views, it is to attack a third and less clear view. Thus, the contestants in major evolutionary controversies paid little attention to writings of such evolutionists as

Ernst Mayr, who attempted to bring together opposing ideas and who proposed that evolutionists use their own experience and logic to make conclusions rather than follow a circumscribed set of rules [28].

Because of this emphasis on the extremes in any controversy, the literature is more biased toward the opponents' views of each other than to the practical issues and the "real data." For the new evolutionists, this bias in literature, combined with the passion of their mentors for certain ideas, can be unsettling. In my own experience as a graduate student, I moved from the extremes of phenetics to the extremes of cladistics, depending on the institution, the mentors, and the literature made available to me. After much reading, experimenting, and maturing I did come to understand something of the nature of the conflict *despite* the many publications of the opposing schools that claimed to represent "the truth."

In my view, the most unfortunate result of this obsession with theory and controversy is that some journals that have espoused theoretical frameworks reject data-gathering efforts, labeling them descriptive. I agree with Futuyama [5] that, in this age of evolutionary-hypothesis bashing, we have a much greater need for new data than for new hypotheses. Such data should come from both historical and nonhistorical evolutionary biology, and the techniques of molecular biology should be used to their fullest potential.

Some scientists who espouse and vigorously defend controversial views in evolution seem to be impatient with the progress of data acquisition and have come to rely on a combination of rhetoric and meager data to support major theoretical frameworks. A prime example is provided by the controversy surrounding the level and structure of natural selection. Despite the meager data on natural selection, there are thousands of pages about punctuated equilibrium, selection at the level of the gene, group selection, kin selection, and so forth. In the short run, this may seem to be a harmless endeavor. One might even argue that controversies are essential to stimulate the collection of data. Certainly, the publication of *Origin of Species* did just that. However, it was 20 years from the time Darwin conceptualized natural selection (in 1838) until he was forced, by the independent formulations of Wallace, to publish *Origin* in 1859 [30]. In the intervening years, Darwin patiently collected data and arguments that would support his theory and refute any potential counterarguments. Who among us, in this age of publish or perish, can afford to be so rigorous or patient? But we owe it to the next generation of scientists to present our views clearly and to accurately represent the data (or lack thereof) concordant or discordant with these views. More important, strong published convictions that lack adequate data can lead to a lack of interest in a topic that appears to have been resolved. This may backfire on the contestants by making their fields less attractive to the new generation of scientists seeking more open areas (niches) of research and who might otherwise have collected the crucial data to resolve the controversy.

Conclusion

The evolution of ideas in the field of evolutionary biology is analogous to evolution of genes and characters: both require variation and selection. Ideas in evolution are the mutations that provide the variety for natural selection (the data) to operate on. Like mutations, a load on the organism (in this case the field) is exerted because most mutations and ideas are not beneficial, aside from being the price to be paid for variation.

Controversy in science allows one to question his or her practices and rigorously examine the methods employed in evolutionary studies. However, devotion to a particular theoretical framework can significantly decrease one's ability to collect data and may even hinder prospects for additional data-gathering efforts by newer generations if these frameworks are presented with such acid conviction that readers may think all is answered. Thus, although debate and controversy are essential aspects of science, one must guard against an overzealous belief in one's position—the hazards of which are well known. Like others, I am not always able to avoid such traps and have on occasion vigorously defended one approach or another (*mea maxima culpa!*). Evolutionary biology is a dynamic and progressive field with great social and political implications. It is unfortunate that it is also a field in which the boundary between science and "faith" is most easily crossed.

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