NEW BIOLOGICAL BOOKS

The aim of this section is to give brief indications of the character, content, and cost of new books in the various fields of biology. More books are received by The Quarterly *than can be reviewed critically. All submitted books, however, are carefully considered for originality, timeliness, and reader interest, and we make every effort to find a competent and conscientious reviewer for each book selected for review.*

Of those books that are selected for consideration, some are merely listed, others are given brief notice, most receive critical reviews, and a few are featured in lead reviews. Listings, without comments, are mainly to inform the reader that the books have appeared; examples are books whose titles are self-explanatory, such as dictionaries and taxonomic revisions, or that are reprints of earlier publications, or are new editions of well-established works. Unsigned brief notices, written by one of the editors, may be given to such works as anthologies or symposium volumes that are organized in a fashion that makes it possible to comment meaningfully on them. Regular reviews are more extensive evaluations and are signed by the reviewers. The longer lead reviews consider books of special significance. Each volume reviewed becomes the property of the reviewer. Most books not reviewed are donated to libraries at Stony Brook University or other appropriate recipients.

The price in each case represents the publisher's suggested list price at the time the book is received for review, and is for purchase directly from the publisher.

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A. W. F. EDWARDS ON PHYLOGENETIC INFERENCE, FISHER'S THEOREM, AND RACE

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A review of
Phylogenetic Inference, Selection Theory, and History of Science: Selected Papers of A. W. F. Edwards with Commentaries.

Edited by Rasmus Grønfeldt Winther. Cambridge and New York: Cambridge University Press. $89.99. xii + 540 p.; ill.; index. ISBN: 978-1-107-11172-1. 2018.

Anthony Edwards profoundly influenced the development of mathematical evolutionary theory. In collaboration with Luigi Cavalli-Sforza, he pioneered the statistical approach to phylogenetic inference. Edwards also did important work clarifying R. A. Fisher's fundamental theorem of natural selection, and he famously took issue with Richard Lewontin's influential argument that races lack biological reality. Beyond the confines of evolutionary biology, Edwards helped de-velop the likelihood approach to statistical inference, inspired by Fisher, who was his teacher, and complementing the work of philosopher Ian Hacking (1965). Edwards also did important research on the history of statistics and evolutionary biology—for example, on Pascal's triangle, Venn's diagrams, and theorizing about the evolution of sex ratio by Darwin, Düsing, and Fisher.

The present volume, edited by philosopher of science Rasmus Grønfeldt Winther, includes 28 of Edwards's published papers, 11 new papers (by Walter Bodmer, Joseph Felsenstein, Rasmus Nielsen, Mark Pagel, Elizabeth Thompson, Ziheng Yang, Warren Ewens, Samir Okasha, Maurizio Esposito, Jean-Baptiste Grodwohl, and Noah Rosenberg) that discuss Edwards's work, the transcript of an extended interview/

conversation between Edwards and Winther, and Edwards's curriculum vitae, a list of his publications, and four appendixes.

The papers commenting on Edwards are of high quality, and the articles by Edwards collected here are still of considerable interest. Among the commentaries that I found especially illuminating are Felsenstein's discussion of phylogenetic inference, Okasha's chapter about Fisher's theorem, and Rosenberg's essay on race, which I will now briefly discuss.

Phylogenetic Inference

Felsenstein describes how Edwards and Cavalli-Sforza (1964) were led to enunciate their "principle of minimum evolution" by the conceptual difficulties they encountered in their efforts to understand phylogenetic inference in terms of likelihoods. For Edwards and Cavalli-Sforza, the principle of minimum evolution was a stopgap expedient, introduced for the nonce until a coherent likelihood approach could be developed.

Edwards (pp. 230, 431) takes pains to separate his and Cavalli-Sforza's principle from "Ockham's razor" and from the parsimony concept defended by cladists, but it is questionable whether the gap between Edwards and Cavalli-Sforza's principle and cladistic parsimony is as wide as Edwards suggests. Cladists do not insist that a lineage that evolves from state x to state y must do so via the minimum number of evolutionary changes. Their idea is that the best phylogenetic hypothesis is the one that requires the minimum number of changes; there is no commitment to the idea that the actual number of changes is identical with that minimum (Farris 1983). The vital distinction is between minimizing assumptions and assuming minimality. What distinguishes Edwards and Cavalli-Sforza from the cladists is not the meaning of parsimony, but their assessments of what it takes for the principle to be justified. For Edwards and Cavalli-Sforza, the most parsimonious tree, given the data, is the best tree only if that tree has the highest likelihood, and whether that is true will depend on the probabilistic model of the evolutionary process assumed to be at work in branches. For cladists, parsimony does not require a likelihood justification, since that would mean assuming a probabilistic model of the evolutionary process; cladists want phylogenetic inference to be prior to, and independent of, inferences about the details of the evolution processes at work in branches. In the end, likelihoodists use a plurality of methods, one for each distinct process model that applies to some phylogenetic inference problems but not to others; for cladists, parsimony applies across the board.

The likelihood approach to phylogenetic inference requires that a single process model be assumed in a given phylogenetic inference problem, and it is understandable that cladists and others might balk at using unsubstantiated assumptions about the evolutionary process. However, this problem can be mitigated by using a model selection criterion such as the Akaike Information Criterion (AIC) to evaluate competing hypotheses; see Burnham and Anderson (2002) for a general discussion of AIC. In the context of phylogenetic inference, AIC can be used to evaluate a set of competing hypotheses in which each phylogenetic tree is paired with each of several process models. In this way, multiple process models can be considered with no prior commitment concerning which of them is true. What is more, AIC controls for overfitting. Depending on the data, a given phylogenetic tree may be best across a broad range of process assumptions (Sober 2015).

Fisher's Fundamental Theorem of Natural Selection

Okasha describes how Edwards helped clarify Fisher's (1930) fundamental theorem of natural selection. The "old" interpretation of the theorem was (roughly) this:

(Old) The rate of increase in the average fitness of the organisms in a population at a given time is equal to the additive genetic variance in fitness at that time.

This statement is false for lots of reasons. For example, average fitness can decline when there is frequency-dependent selection, but variances are never negative. The new interpretation of Fisher's theorem, championed by Price, Ewens, Okasha, and Edwards is (roughly) this:

(New) The rate of increase in the average fitness of the organisms in a population at a given time *that is due to natural selection* equals the additive genetic variance in fitness at that time.

Here the "change due to natural selection" is computed by holding fixed the average effects of the alleles, but letting their frequencies change, where the "average effect" (of an allele on fitness) is itself defined by a least squares procedure; it is a partial regression coefficient.

Okasha asks whether we should accept the claim that any change over and above this "partial change due to natural selection" can validly be attributed to

environmental change. If genotypic fitnesses change because the physical environment changes, he agrees that this counts as a genuine environmental change, but he is less persuaded that dominance and epistasis should be regarded in this way. I concur with this hesitation; it seems arbitrary to place dominance and epistasis in the bin of nonselective processes, a bin that is the proper home of mutation and migration (for example). These latter are nonselective processes because they do not require variation in fitness. In contrast, "dominance" means dominance *in fitness*, and "epistasis" means epistatic *fitness* interactions, and both require fitness variation.

If New uses an overly restrictive conception of selection, how can it deserve to be called "fundamental"? One answer is that the theorem is fundamental in the sense that it is a basis on which to build. The theorem describes the simplest kind of situation in which natural selection, narrowly defined, impinges on a Mendelian population. More complex and realistic models can be built by starting with New and developing representations of component causes other than the narrow notion of natural selection deployed in New, showing how they induce change in gene frequency, both singly and in combination.

Although Fisher's theorem is fundamental (in the sense just described) within population genetics, it does not have that status in evolutionary theory more generally. This is because the Mendelian genetic system is a product of evolution, so evolutionary theory needs to be able to explain its evolution. Darwin (1859) was able to explain a lot without knowing about Mendelian genetics. Contemporary biologists, of course, are not in the same position of ignorance, but when they endeavor to explain the evolution of the genetic system, they need to start by considering a population in which the genetic system we see around us is absent. Instead of starting with the idea that parents transmit genes to their offspring, these biologists may begin with an idea akin to Darwin's "strong principle of inheritance" (Darwin 1859:5, 127, 438), which says that offspring tend to resemble their parents.

Edwards (pp. 4, 297) sees an affinity between Fisher's theorem and the "gene's-eye point of view" popularized by Dawkins (1976). So does Okasha (2008). There is a connection here, but it should not be overstated. Dawkins, inspired in part by Williams (1966), presented the idea of "the selfish gene" as an antedote to the idea of group selection, which he viewed as poisonous and conceptually confused, an idea that should be dismissed out of hand rather than empirically tested on a case-by-case basis. However, there is nothing in the fundamental theorem that has this implication. New defines natural selection so that it excludes dominance and epistasis, but that does not mean that dominance and epistasis are conceptually confused, or that they never occur in nature. The same point applies to

New's defining "selection" as a strictly within-population process. Selection among groups is left out in the cold, by definition, but that says nothing about whether groups of organisms vary in their ability to send out migrants and avoid extinction, with the result that altruism and other group-advantageous characteristics evolve. The unwillingness to call this "selection" is not an argument. For that reason the fundamental theorem is perfectly compatible with multilevel selection theory, which encompasses selection among the genes in the same organism (intragenomic conflict), selection among organisms in the same group, and selection among groups in the same metapopulation, where in each case selection just means variation in fitness (Sober and Wilson 1998).

Edwards (1971) thinks that New shows why the fundamental theorem fails to undergird Sewall Wright's (1932) idea of adaptive landscapes, since Wright's conception concerns the total change in average fitness, not just the part of that total change that is attributable to natural selection. However, if Fisher's theorem describes only the change in average fitness attributable to natural selection (narrowly defined), what is wrong with interpreting Wright's landscapes in the same way?

THE BIOLOGICAL REALITY OF RACE

Lewontin (1972) argued that races are biologically unreal; Edwards (2003) replied, accusing Lewontin of committing a fallacy. Rosenberg separates the problem that Lewontin addressed (of partitioning the total variance in traits into three components—between races, between populations of the same race, and within populations of a single race) from the problem that Edwards discusses (of deciding whether an individual's traits can be used to classify that individual as belonging to this race rather than that). Edwards taxes Lewontin for committing a fallacy, but the criticism Edwards makes is not that Lewontin provided a flawed analysis of the problem that he, Lewontin, addresses; rather, Edwards's beef is that Lewontin did not address the problem that Edwards wants to consider. Edwards (pp. 418–421) discusses the history of his work on Lewontin's argument and what he takes "fallacy" to mean (see also Appendix 2).

Lewontin and Edwards both start with a set of assumed races and then pose their separate questions. As Rosenberg notes, this leaves open the question of why the races that are assumed in both analyses are the ones that ought to be considered. Perhaps the races recognized by ordinary people do not coincide with the races that ought to be considered as candidates for biological reality. This idea might be developed from a cladistic point of view, where the question is not whether people of the same race have some degree of overall similarity, but whether

there are subgroups of present-day human beings whose genealogy is a branching phylogenetic tree. This is an idea that Cavalli-Sforza (1991) explored, although he decided to talk about human "groups," not "races."

A cladist assesses the biological reality of a proposed taxonomic group by examining a phylogenetic tree to see which monophyletic groups it contains. A monophyletic group is comprised of an ancestor and all of its descendants, regardless of how different those descendants are from each other, and regardless of how different they are from their most recent common ancestor. There is a monophyletic group that includes human beings and chimpanzees but excludes gibbons, however, there is no monophyletic group that includes placental and marsupial wolves but excludes moles, nor is there a monophyletic group that includes lizards and crocodiles but excludes birds. The cladist's equation of taxonomic reality with monophyly should not be confused with the cladist's methodology of using parsimony to discover phylogenetic trees. Monophyly may be the right criterion for taxonomic reality even if there are better methods of phylogenetic inference than cladistic parsimony. The idea that identifying monophyletic groups is the proper goal of taxonomy was Hennig's (1966) fundamental and lasting contribution.

Cavalli-Sforza's phylogenetic tree of human groups entails that there is no monophyletic group that includes Asians but excludes Africans and Europeans. His data and methods of inference have subsequently been improved upon, with the result that newer trees differ somewhat from older ones, but the take-home messages remain the same: a scientific attention to the branching pattern of human evolution can show that some or all of the races recognized by "common sense" lack biological reality, and the analysis may also reveal the identity of hitherto unrecognized subspecific taxonomic groups.

When cladists attempt to discern monophyletic groups in a phylogeny, they encounter a problem if the genealogy is not tree-like. However, it is not essential that migration between branches and horizontal gene transfer are zero. A little "noise" is tolerable, as long as there is a strong tree-like phylogenetic "signal." In addition, it is compatible with the idea that races are clades that cladistic races used to exist but are now on their way out, thanks to massive and prolonged migration (Andreasen 1998). If so, it may turn out that the only present-day human groups that are related to each other by a tree-like genealogy are ones that have been isolated for a very long time.

Concluding Comment

The image of science that scientists present in their publications is often restricted to final products; for example, a finished theory is described or a well-conducted experiment is explained. These finished products are important, of course, but those interested in the scientific process want to look behind that public image. How did these theories and experiments develop? What were the false starts and confusions that were embraced initially and then overcome? In what way do ethical and political factors affect the scientific process, and ought they to do so? One of the virtues of this volume is that it does not shortchange this set of questions.

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