

“Nothing in Biology Makes Sense Except in the Light of Evolution”
(Theodosius Dobzhansky)¹

Theodosius Dobzhansky (1900-1975) was one of the principal architects of the so-called synthetic theory of evolution.² Born and initially trained in Russia, where he became an entomologist and zoologist with wide-ranging interests, he brought a rich background in systematics and study of natural populations with him when he came to the United States to learn genetics in the laboratory of T. H. Morgan in 1927 (Adams 1994). In the end, he remained in the US, in part because of political developments in Russia, where he was ultimately declared a non-person. Dobzhansky utilized his double background of work with natural populations and in Mendelian genetics in writing what came to be the single most influential book in the formative period of the synthetic theory of evolution (Dobzhansky 1937). Dobzhansky is a particularly interesting figure to study because of the cultural dualities (or, rather, multiplicities) which he embodies, because his work forcibly reconciled biological disciplines (systematics and natural history on the one hand, genetics on the other) that had not only drifted apart, but had built strong evidentiary bases for conflicting claims, and because, like many of the founders of the evolutionary synthesis, he sought to relate biological findings to issues in the wider culture.

This chapter takes its title from a talk that Dobzhansky delivered to the American Association of Biology Teachers (Dobzhansky 1973a). The title of that talk, “nothing in biology makes sense except in the light of evolution,” is often cited both in controversies over the status of evolutionary studies within biology and in various cultural debates over the (supposed) conflict between evolution and religion. In this chapter I examine Dobzhansky’s claim and some of his arguments in its favor with an eye to both of these contexts. I focus first on the setting, both within biology and within American culture, of Dobzhansky’s arguments for the importance of evolutionary biology. Second, I turn to the relations among biological disciplines or fields, especially between evolutionary biology and molecular genetics, a field that “took off” after the formation of the evolutionary synthesis. Finally, I deal with some complications arising from the difference between the intellectual and the institutional positions of the field of evolutionary

¹ First published as Chap. 6 of *The Epistemology of Development, Evolution, and Genetics*. The original version of this chapter was presented in 1995 at a colloquium in honor of Marjorie Grene, “Conceptions de la science: hier, aujourd’hui et demain,” at the University of Burgundy; the French version is published in *Conceptions de la Science – hier, aujourd’hui et demain : homage à Marjorie Grene*, ed. J. Gayon and R. Burian (Brussels: Ousia, 2007). The present version has been greatly improved by discussion at the colloquium and the criticisms and suggestions of Jean Gayon and Marjorie Grene.

² About the synthetic theory and some of the current debates about its status see, e.g., Burian (1988), Gayon (1990), Grene (1983), Grene (1990), and Mayr and Provine (1980). For further biographical details about Dobzhansky, see Adams (1994), Ayala (1990), Gould (1982), and Provine (1981).

biology. I can, of course, do only partial justice to Dobzhansky's advocacy of the centrality of evolutionary studies within the biological sciences.

EVOLUTIONARY THEORY IN BIOLOGY AND EVOLUTIONARY BIOLOGY IN THE UNITED STATES

A remarkable fact about evolutionary biology, given its importance in 20th century biology, is that there have been virtually no departments of evolutionary biology for most of this century (as there have been of genetics, for example).³ It is important to start from the fact that Mendelian genetics and Darwinian evolutionary biology were in serious conflict with each other in the first third or so of this century. There are many aspects to this conflict, both intellectual and institutional.⁴ I offer here a first approximation account of some of the differences involved. Some of them follow from the practical necessity for early Mendelians to work with mutations with large effects. Indeed, since at first all known mutations were large in effect, the Mendelians held that such mutations were the norm and provided the basis on which new species were formed. In contrast, most natural historians and Darwinians insisted on the absence of large mutations in the

³ Interestingly, the major exception is Russia where, early in the century, there were intense and productive scientific debates over various Darwinian and non-Darwinian theories of evolution. At the end of the 1930s most major Soviet universities had departments of Darwinism. But in consequence of Russia's intellectual isolation in the 1930s, the controversies over Lysenkoism, and Lysenko's ascent to power, they deployed a distinctive Soviet version of Darwinism that did not match orthodox evolutionary theories and practices in the West at that time. On this topic, see Adams (1991). See also Provine (1980) for some useful material on the institutional bases for genetics. Provine does not explicitly take up the formation of departments of genetics within colleges and universities.

⁴ There is a huge literature on the debates involved. Important references include Bowler 1983, 1988, 1989; Depew and Weber 1995, Part II; Gayon 1992, 1998; Provine 1971. On this last topic, for a contrasting point of view see Nordmann (1994). In a recent paper, Scott Gilbert ("Back to the Future: Resynthesizing evolutionary and developmental biology," presented at the Fifth Mellon Workshop on History and Social Sciences of Contemporary Life Sciences, MIT, 1995) points out an important institutional aspect: during the fifties, population genetics received considerable funding from the U.S. Atomic Energy Commission in connection with concerns about the effect of radiation on populations. As he puts it: "Whereas most evolutionary studies have difficulty getting funds and students, concerns about the genetic effects of radiation enabled Dobzhansky and others a constant supply of money and graduate students" (MS p. 5). On this topic, see also Beatty (1991) and his "Opportunities for genetics in the atomic age," presented at the Fourth Mellon Workshop on History and Social Studies of Contemporary Life Sciences, MIT, May, 1994. The lines of work thus funded thrived, but they did not have significant impact on the organization of academic departments or on the larger theoretical issues in evolutionary biology.

field and on the gradual character of changes from one species to another. Thus, early Mendelians and turn-of-the-century Darwinians agreed that the effects of Mendelian mutations were too large to allow natural selection on Mendelian mutations to control the features of organisms with any precision, including features of organisms in a new species. Natural historians did not find significant numbers of Mendelian mutants in natural populations; accordingly, the Darwinians derided Mendelian mutations as experimental freaks that would be eliminated immediately from natural populations and as irrelevant to evolutionary history. Geneticists, in contrast, argued that Darwinians had no adequate causal basis from which to explain the changes that took place in speciation and which were marked by the striking visible differences between “good species.”

Turning to the institutionalization of biology, the term ‘biology’ came to be employed rather self-consciously in some quarters around the turn of this century for *experimental* biology. The insistence on experiment was used to help legitimize a series of new sciences, genetics among them, as distinct from natural history, botany, zoology, systematics, paleontology, and speculative Darwinian evolutionism. Part of the point of excluding these old-fashioned sciences was that they did not have adequate means of testing explanatory hypotheses or, worse yet, they did not even offer genuine explanatory hypotheses. One aspect of the movement toward experimental biology was the physics-envy of biologists and their long struggle of biology to demonstrate that their science is as legitimate as physics, a struggle in which Darwin himself had been engaged. Many participants in the experimental movement deliberately excluded Darwinian theory from (their kind of) biology precisely because it was ‘too speculative’ and had no means of adequately controlling or testing its speculations (especially after the impact of Haeckel and Weismann).⁵ The success of this ‘experimentalist’ movement is marked internationally by the dominance of the new experimental disciplines in the departments and research units begun after, say, 1910.

Although this is only an approximate account of one part of the deep background to the matters of primary concern here, it usefully marks Dobzhansky’s accomplishment. During the twenties and into the thirties, the founders of mathematical population genetics, especially Fisher, Haldane, and Wright in the Anglophone world,⁶ using models employing large numbers of mutations with small effects, provided mathematical demonstrations that Mendelism is compatible with Darwinian gradualism. Indeed, given enough mutations of small effect, large enough populations, stable enough conditions, and enough time to approach equilibrium, the mathematics demonstrated that the

⁵ Mark Adams forced me to recognize the importance of the experimentalist movement. I am very grateful to him for many helpful discussions of this topic. A major debate on this issue was triggered by Allen (1979) and a symposium on the topic edited by Jane Maienschein, Ronald Rainger, and Keith Benson, *Journal of the History of Biology* 14 (1981), pp. 83-176.

⁶ Dobzhansky of course also knew the work of Chetverikov and Timofeeff-Ressovsky.

selection would be the dominant factor in shaping the changing characteristics of organisms within a population. At the same time, laboratory work in Mendelian genetics had demonstrated that there are many more mutations with small effects than mutations of large effect and that the mutations of small effect can modify what is done by those with large effects. Thus the groundwork was laid for reconciling genetics with studies of natural populations. But the relevant communities of investigators were not sympathetic with one another and did not read each other's work. And there were certainly plenty of serious questions to be asked about whether the assumptions of the models corresponded to the biological realities to be found in natural populations and about the relevance of change within populations to speciation. It was Dobzhansky's virtue to bridge the communities of naturalists and geneticists, to find a methodology for doing experimental work with natural populations, and to write a book that so formulated the issues that, after much dispute, both communities were, by and large, persuaded.

In part on the basis of his extensive work with natural populations, Dobzhansky had always held that there is an immense reservoir of variation within populations in nature. In *Genetics and the Origin of Species* (1937), he synthesized his findings and those of many others to provide an integrated account, consistent with genetics, of the origin of species as an extrapolation of the microevolutionary changes that the naturalists had described in detail. He also argued that these results are entirely consistent with the models of population genetics (particularly Wright's). Furthermore, his account did not employ the difficult mathematics of the population geneticists. In consequence, it made their results accessible to both the larger genetics community and the natural historians, who were largely unequipped to handle the mathematics (as was the case with Dobzhansky himself). In the early papers of a series of 43 experimental papers on the genetics of natural populations, the first 18 of which were published from 1938 to 1948 (Lewontin et al. 1981), he managed to show that natural populations have a large reservoir of (mostly recessive) Mendelian mutations, that there are significant genetic differences between local populations, and that the predictions of certain of Wright's mathematical models are compatible with the changes found in the populations of *Drosophila pseudoobscura* that he studied.

It is worth noting a controversial problem on which Dobzhansky took a strong stand. The issue stems from a paradox. The more powerful natural selection is, the more likely it is to consume the variation that it requires in order to change the characteristics of the organisms in a population. The reason is simple: where there are selective difference among conspecific organisms within a population, there is some likelihood of losing traits that are less advantageous in favor of a single optimal solution to the physiological and ecological problems faced by the members of the population (or the closest to optimal among the traits that are available). The stronger the coefficients of selection, the more rapidly alternative traits are lost. So how can there be high degrees of variation within a population if the traits of the organisms in that population are shaped by

selection? To the extent that the proponents of the synthetic theory, Dobzhansky among them, hold that the dominant factor shaping organisms in evolution is natural selection, to that extent they should expect variation to be minimized. How can Dobzhansky's insistence on the power of selection in leading to the origin of species be reconciled with the high degrees of variation he found, required, and advocated as the typical condition of natural populations?

Many geneticists, e.g., Herman Muller, who occupied the 'classical' position, applied this argument at the genetic level. They argued that selection tends to *reduce* genetic variation, and that a population near equilibrium will be largely homozygous, with only an occasional mutant allele here and there. Dobzhansky, in contrast, advocated what came to be known as the 'balance' position, to wit that at equilibrium, most loci would be heterozygous, that there were many more than two alleles available within the population at most loci, and that the action of the genes will be balanced in such a way that the external phenotype will be rather homogeneous, masking the enormous amount of genetic variation within the population.⁷ To support this view, Dobzhansky argued that the availability of different alleles enables organisms to respond successfully to the wide range of environmental conditions that they encounter in their lifetimes.⁸ Putting it crudely, selection favors phenotypes capable of responding to a wide range of humidities, temperatures, constituents in food, toxins, and so on, and to adjusting developmental schedules to meet environmental conditions. The best way to do this is to have (to use Waddington's term) a *canalized* phenotype⁹ plus high amounts of genetic variation, so that most individuals have two distinct alleles available at most loci unless there is specific harm done by one of those alleles.

⁷ There is continuing controversy about the extent of justification for, and truth in, these two polar positions. During Dobzhansky's lifetime the epistemological difficulties involved in resolving the dispute were insuperable; they remain severe even now. The *locus classicus* for setting out the biological side of the epistemological issues is Lewontin (1974). Lewontin's analysis of the subsequent ramifications of the controversy is controversial (see, e.g., Dietrich, 1994).

⁸ I have ignored some important shifts in Dobzhansky's position over time. Two issues on which his views changed concern the extent of coadaptation among the alleles represented in a given local population (see Lewontin 1993) and the importance of the effects of small population size on the variation within populations. (This factor made an essential contribution in Wright's models of evolutionary change.) As Dobzhansky became more selectionist and the synthesis 'hardened' (cf. Gould 1983a), random variation in small populations came to play less of a role in Dobzhansky's and many other synthetic theorists' accounts of evolution.

⁹ This means, roughly, that the development of the organism is so programmed that it lands in more or less the same adult (and intermediate) external phenotypes in spite of wide variation in environmental conditions. For an early text setting forth this important concept, see Waddington (1942).

This argument depends crucially on denial of the assumption that genes are ‘the target of selection’ (a term due to Ernst Mayr).¹⁰ This strategy is natural for those who study natural populations, for they understand selection in terms of the differential consequences of possessing different *phenotypes*, but it is less natural for geneticists, who calculate selection coefficients wholly in terms of *changes of gene frequencies*.¹¹ Curiously, Dobzhansky himself adopted the formula that evolution equals change of gene frequency, a position for which Mayr criticized him severely.

Turning briefly to larger contexts, two topics serve as emblems of the larger situation in the US – the institutionalization of research support within biology and the tendency in American society to see evolutionary biology as standing in conflict with organized religion and with creationist doctrines. These two issues are intertwined to a surprising degree. One way of showing the connection is to reflect on the teaching of biology in US high schools. Stephen Jay Gould did so in an essay written in December 1981, while attending a trial in which a law from the state of Arkansas was being challenged. The law, ultimately declared unconstitutional, required equal treatment in schools of ‘Creation Science’ and ‘the Evolution Theory’ (supposedly equally justified and scientific). Gould’s essay (Gould 1983b, chap. 21) describes the lack of evolutionary content in the dominant high school biology textbook, from which both he and I were taught in the 1950s. The book, *Modern Biology* by Moon, Mann, and Otto, was the lineal descendant of *Biology for Beginners* by Truman J. Moon, first published in 1921. Gould points out that the frontispiece of the original text was an image of Charles Darwin and that the book was organized around the idea of evolution. He shows that after 1925, the date of the infamous Scopes trial, the evolutionary content was removed from the text. Not only is Darwin’s image gone, the very term *evolution* is replaced by the cowardly paraphrase, ‘the hypothesis of racial development’! The 1956 edition, for example, contains a brief chapter (the 58th of 60) touching on evolution. The chapter evades the issue of creation vs. evolution by such circumlocutions as these:

¹⁰ See, e.g., Mayr 1959, 1962, and 1963. It should be noted that the argument also depends on assumptions about mechanisms of gene expression.

¹¹ Mayr has repeatedly criticized Dobzhansky and others for *defining* evolution in terms of change of gene frequencies. There are many additional reasons for resisting such a definition, e.g., the way in which it underemphasizes the centrality of speciation (which cannot be defined in terms of gene frequencies) in evolutionary change. The issue of the extent to which *natural selection* can be understood primarily by means of calculations at the genic level continues to be actively debated, e.g., in controversies over the *genic selectionism* of R. Dawkins, G. C. Williams and others. See, e.g., Dawkins (1976, 1982; Williams (1966). There are a number of important connections to some issues about biological hierarchies – see, for example, Grene 1987, especially the relations of ecological and genealogical hierarchies and various debates over the level(s) of selection.

During these ages [of geological change], species of plants and animals have appeared, have flourished for a time, and then have perished as new species took their places.... When one race lost in the struggle for survival, another race appeared to take its place.

This is how high school biology was taught to my generation. This sad fact reflects the political power of biblical fundamentalism in the US and the country's genius for intellectually unsatisfactory compromise. Against this background, is it any wonder that there was no impetus, even among professional biologists, to place evolution at the center of biology curricula or to organize biological disciplines so as to ensure that evolutionary studies played a key role in the organization of biological work in general? Dobzhansky was keenly aware of this situation and faced it head-on in the address whose title stands at the head of this chapter.

Although it is not simple to demonstrate, it is extremely plausible that this cultural background had an important influence on the structure of professional biology. Scott Gilbert, for one, connects the strength of creationism to the structure of the NSF: "In the United States, evolution is still so suspect that no National Science Foundation study section is designated evolutionary biology." Difficult as it is to make a direct connection to the cultural milieu in such a matter, I believe that there is widespread consensus among evolutionary biologists that this has been a central problem in the institutionalization of their (would-be?) discipline. The contrast with genetics, which receive major public and private funding in virtue of its economic importance, is striking.

DOBZHANSKY'S ARTICLE¹²

Dobzhansky begins his article by discussing the rejection, on scriptural grounds, of the Copernican theory of the heavens as a 'mere theory', not a 'fact' by a Saudi fundamentalist, Sheik Abd el Aziz bin Baz. Dobzhansky lays out a very standard argument against this view in a Darwinian style, arguing that the hypothesis that the earth orbits the sun "makes sense of a multitude of facts that are otherwise meaningless or extravagant." Dobzhansky is ready to grant, for the sake of the argument, that no direct observations demonstrate the 'fact' that the earth orbits the sun, but insists that we must dismiss the geocentric alternative as making nonsense of many facts we *have* observed. Similarly, there are no direct observations of the age of the earth or of the evolution of new species, but an enormous multitude of facts show both the diversity and the unity of life that would be meaningless or extravagant except in the light of evolution.

Rhetorically, Dobzhansky makes excellent use of the parallels between the pro-Copernican and pro-Darwinian arguments and the fact that the anti-Copernican fundamentalist is a Muslim from Saudi Arabia. By adding the cultural

¹² Throughout this section, page numbers refer to Dobzhansky (1973a).

distance between a Saudi fundamentalist and mainstream Americans to the strongly held belief in a heliocentric solar system in the US, Dobzhansky makes it difficult for a biblical literalist to contest the pro-Copernican argument. Dobzhansky argues that the literalist is put in the position of blaspheming if he treats the Koran or the bible as a primer of natural science, for when scientific developments outrun the literal reading of scripture, the literalist is forced to deny well established fact or to make God into a deceiver by planting misleading evidence.¹³ Beyond that, he argues, scripture is meant to deal with far more important matters, “the meaning of man and his relation to God,” matters that require the use of poetic symbols comprehensible both to the people of a given era and to people from other times (p. 125). In the main body of the paper, Dobzhansky spells out the parallel argument illustrating at some length the multitude of facts in biology (but also geology, radiometric dating, and much more) that evolution is required to explain.

Of particular interest here is Dobzhansky’s treatment of molecular biology. The diversity of life is quickly evident from the sheer number of species and bodily diversity among plants, animals, and microorganisms, the extraordinary diversity of the ecological niches they occupy, and the narrowness of the adaptations that many organisms exhibit. It is somewhat harder to establish the unity of life. Dobzhansky treats molecular findings as the most decisive, but by no means the only, evidence for the unity of life. (He also cites, e.g., traditional evidence of homologies and of shared developmental pathways from comparative anatomy and embryology and illustrates the ways in which diversity can come from unity by the remarkable radiation of drosophilid flies on the Hawaiian Islands.¹⁴) Molecular evidence for the unity of life includes the universality of DNA and RNA as the genetic materials, the universality of the genetic code and the mechanisms by means of which the code is translated into sequences of amino acids, the high uniformity of cellular metabolism (cf. the roles played by such compounds as adenosine triphosphate, hemes, riboflavin, pyridoxin, etc. in nearly all organisms), and the consistency of the rate of substitution of amino acids into such highly conserved proteins as the cytochromes. Such

¹³ For example, in dealing with the massively coherent radiometric evidence of the age of the earth, dismissed as ‘mere theory’ by “Sheik bin Baz and his like,” one must ask “What is the alternative? One can suppose that the Creator saw fit to play deceitful tricks on geologists and biologists. He carefully arranged to have various rocks provided with isotope ratios just right to mislead us into thinking that certain rocks are 2 billion years old, others 2 million, while in fact they are only some 6,000 years old” (p. 126).

¹⁴ We now know that over 800 of the world’s more than 2000 species of drosophila, including some of the most aberrant ones, are found on a geologically isolated landmass 3% the size of France. Because of their volcanic origin, the islands have well-defined ages; the oldest is less than 6 million years old, the youngest less than 1 million years. The immense diversification and speciation of a founding stock must have taken place in that time.

biochemical or biological universals ... suggest that life arose from inanimate matter only once and that all organisms, no matter how diverse in other respects, conserve the basic features of the primordial life. (It is also possible that there were several ... origins of life; if so, the progeny of only one of them has survived and inherited the earth.) But what if there was no evolution, and every one of the millions of species was created by separate fiat? However offensive the notion may be to religious feeling and to reason, the antievolutionists must again accuse the Creator of cheating. They must insist that He deliberately arranged things exactly as if his method of creation was evolution, intentionally to mislead sincere seekers of truth (p. 127).

The claimed centrality of evolution within biology was meant both for biologists and for a larger public. This is demonstrated by the whole tenor of Dobzhansky's career. To cite but one piece of evidence regarding the larger public, one need only look at the books he published aimed at a larger audience.¹⁵ Within biology I note his constant efforts to place all biological questions within an evolutionary framework and to ensure an institutional footing (and funding) for evolutionary studies. It is a minor, but indicative, symptom that the phrase "nothing in biology makes sense except in the light of evolution" serves as the epigraph of a co-authored textbook on evolution, published posthumously (Dobzhansky et al. 1977).

MORE ON THE RELATIONS AMONG BIOLOGICAL DISCIPLINES

I now leave Dobzhansky to examine some complexities concerning the relationship between evolutionary studies and molecular biology. There is considerable irony in the interactions between the two, especially with regard to the stance that Dobzhansky and other leading 'non-molecular' evolutionists took in favor of the centrality of evolution within biology. I will speak to the relevant developments briefly and abstractly, first in terms of the relationships among biological disciplines, institutions, and funding, then in terms of some issues about the molecularization of biology.

An interesting way of thinking about the history of biology in the twentieth century is in terms of the founding of moderately autonomous disciplines and their subsequent interactions. Thus, as indicated in the first section of this chapter, early Mendelian genetics was fairly sharply separated from (Darwinian) evolutionary biology. An enormous gulf also arose between genetics and embryology. The two disciplines employed different techniques, came to adopt conflicting experimentally grounded presuppositions (e.g., concerning the nuclear vs. cytoplasmic origin or control of key traits of multicellular organisms),

¹⁵ The list includes Dobzhansky 1956, 1963, 1964, 1967, 1972b; Dobzhansky and Dunn 1946; and Dobzhansky, Boesiger, and Wallace 1983. Dobzhansky's activity along these lines includes a considerable amount of periodical literature and editorial work as well.

and employed different organisms (with strikingly different properties) for the exemplary research on which disciplinary consensus was built.¹⁶ Specialization became ever more important in the course of the century, and it brought with it the price of significant barriers among biological disciplines, both within the experimental tradition and between experimentalists and naturalists. There were, of course, always those who sought to integrate the findings (and occasionally the techniques) of different specialties, but this was no simple matter. It is, of course, the job that Dobzhansky believed could be accomplished by evolutionary biology. But insofar as the institutionalization of biology is concerned, as already indicated, no firm institutional setting was developed to serve as a base for evolutionary biology as an integrative discipline, at least into the 1980s.

The roots of molecular biology (which are currently much disputed),¹⁷ are to be found in transmission genetics, crystallography, information theory, biochemistry, the application of physical techniques from physics, and a number of allied sources, none of which are centrally interested in evolutionary questions. I have argued in a number of articles (as have many others) that molecular biology is best understood as a loosely interrelated collection of tools, wedded to the ideal that one can elucidate and clarify biological function by analyzing molecular structures.¹⁸ To the extent that this characterization is fair, at least as a first approximation, the problems of evolution do not belong to the initial core problems of molecular biology although, of course, someone interested in evolutionary questions can apply the new molecular tools to them – something that has been done with a vengeance in recent years with the development of a major (sub?)discipline of molecular evolution and the flourishing of evolutionary studies within a number of the specialties of molecular biology. Nonetheless, as I will argue in the concluding section of this chapter, the pathway by means of which the development of studies of molecular evolution came into being was neither straightforward nor obvious.

MOLECULAR BIOLOGY AND EVOLUTION

There are two aspects to the difficult birth of molecular evolutionary studies. One is the weak institutionalization of evolutionary studies in general. The other

¹⁶ On this topic, see chap. 10 below or Sapp (1987). For one embryologist's view of the threat posed by genetics to his discipline see Harrison (1937). For my views on some more recent developments, see chaps. 11 and 12 below.

¹⁷ The broadest standard history is Judson, 1996 (1979). For an unusual position on the proper delimitation of molecular biology, see Zallen (1993). Michel Morange provides a useful synthesis of conflicting views on this topic, including a criticism of Zallen's point of view in Morange (1994, 1998).

¹⁸ See, for example, the symposium edited by Soraya de Chadarevian and Jean-Paul Gaudillière on "The tools of the discipline: Biochemists and molecular biologists," *Journal of the History of Biology* 29 (3) (1996): 327-462. I state some of the points at stake here more forcefully in Burian (1996).

concerns some aspects of the intellectual history of early work in molecular biology. Let me take these one at a time. Institutionally, as I have argued above, there were few natural bases for evolutionary biology, especially in connection with molecular biology, rooted as it was in the experimentalist traditions that tended to exclude evolution as a serious topic of study. As I did not argue explicitly, early molecular biology drew heavily on biochemical and molecular studies and other lines of work initiated by the ‘invasion of the physicists.’¹⁹ In spirit, it was experimental and mechanistic. It required experimental demonstration of the specific action of particular genes or physical-chemical influences, such as particular radiations, chemical mutagens, and metabolites. One characteristic of the new generation of molecular biologists was the drive toward quick and decisive experimental resolution of experimentally tractable questions. This meant that they favored the use of microorganisms in virtue of their experimental tractability and the rapidity of the experiments they permitted. Indeed, studies based on microorganisms displaced slower evolutionary projects both in funding and in the post-war institutionalization of biology. Studies of long-term evolutionary scenarios were looked on unfavorably, whereas short term mechanistic questions, for which rapid techniques were available (cf. ultracentrifugation, electrophoresis, use of radioactive tracers, plating of phages), came to dominate molecular genetics.

Work on the mechanisms of molecular action displaced work with traditional genetic and evolutionary organisms (and was favored with better funding) in part because of the obvious potential for applications to human health and improvement of agricultural production. The diversion of funding to these purposes tended to displace more general evolutionary studies. The reshaping of departments of biology in the post-war years followed the same trends. Accordingly, in many leading institutions, evolutionists felt that they were fighting rearguard actions to retain their positions and prestige in the face of the expansion of molecular biology and the indifference of most molecular biologists to evolutionary issues.

One particular consequence of the concentration on microorganisms in the early days of molecular biology is particularly ironic. Since microorganisms (especially viruses and procaryotes, organisms with no true nuclei and relatively limited amounts of DNA) experience enormous pressure for economy in the use of genetic material, they are under much greater pressure to find optimal solutions to environmental problems than are eucaryotes (nucleated organisms, mostly multicellular, with excess DNA buffered by a variety of protective devices).²⁰ Again, because of lack of buffering of the genome, there is a tendency for non-functional genetic variation in microorganisms to be more readily eliminated than

¹⁹ Two classical sources on this topic are Fleming 1968 and Judson 1996 (1979).

²⁰ Including diploidy; many of the microorganisms studied were haploid and so each and every allele was required to function properly for survival, a claim that is not true for diploid organisms.

in eucaryotes.²¹ As a result, many geneticists who worked with phage and bacteria were prepared to infer that the organisms they studied were ‘perfectly adapted’²² or very nearly so. What this means is that microorganisms were perceived as having eliminated genetic variants that interfered with optimal performance in physiological conditions. In this respect, they do not carry obvious stigmata of their history; rather, adaptation dominates over historical pathways. Thus the early findings in microbial genetics tended to find relatively less variation than Dobzhansky expected and, thus, to support the notion of ‘perfect adaptation’ at equilibrium, and with it the classical, rather than Dobzhansky’s balance theory. These conclusions were, of course, resisted by those evolutionists who worked with natural populations, especially populations of diploid eucaryotes. Such naturalists had long since developed evidence for the presence of large amounts of covert variation in populations of eucaryotic organisms.

It was only in the mid-1960s, with the adaptation of the biochemical technique of gel electrophoresis to population studies of multicellular eucaryotes,²³ that is, with the development of techniques that could, and did, detect enormous amounts of variation in the amino acid composition of particular proteins in natural populations, that the molecular techniques began to address the question of the amount of variation in diploid populations and, thereby, indirectly, the potential for evolutionary change in seemingly monomorphic populations. The

²¹ Among the many reasons for this, eucaryotes are typically diploid. Many genes that would be lethal if they were present in a single copy or when homozygous, are harmless or even beneficial, when heterozygous because they are protected by being paired with a functionally normal allele. Because of interactions among genes and gene products, the heterozygotes containing such “lethal” genes can even be beneficial, as in the example of sickle cell anemia. Again, eucaryotes often have highly evolved systems of gene families. Multiple copies of physiologically important genes allow some copies to evolve silently since other copies of the gene perform the required function. Similarly, other features of eucaryotic genomes can increase the protection of a particular gene from the immediate action of selection. For example, the separate pieces of “interrupted genes” in eucaryotes (which have separated units, often corresponding to functional parts of the corresponding protein) can be duplicated independently of one another, and combined with pieces from other genes. This allows *parts* of genes to be stabilized and recombined, and to evolve independently of one another. Yet again, eucaryotes often do a great deal of “post-transcriptional modification” of messenger RNA. That is, they have multiple means of processing genetic information after it is transcribed onto RNA and before it is “translated,” i.e., decoded to yield a protein. These devices allow evolution of the *modulation* of a genetic signal without a direct change in a particular gene. There are literally hundreds of complex phenomena that could be listed here.

²² For development of the importance of the doctrine of perfect adaptation in Darwin’s work and the struggle he had to go through to replace it with the weaker notion of relative [sufficient, but imperfect] adaptation, see Ospovat (1981). For one digest of the importance of this shift for the evolutionary synthesis, see chap. 4 above.

²³ The breakthrough papers, which set off an entire industry, were Hubby and Lewontin (1966) and Lewontin and Hubby (1966).

results led to immense and continuing controversy. However, to a first approximation it is safe to say that they supported Dobzhansky's balance against the classical position at least in this respect, that they showed there to be immensely more variation present in natural populations than could readily be accounted for on the classical hypothesis. Precisely how these findings affect the debates about the power of natural selection and what bearing they have on the paradox caused by the tendency of natural selection to consume the variation that is relevant to the formation of an optimum remains a matter of controversy to this day.²⁴ This is a story that we cannot follow here, but one that allows us to bring to closure this brief study of the status and influence of Dobzhansky's stance about the importance of evolution within biology.

CONCLUSION

During the last twenty years, molecular biology has produced a series of extremely startling findings. As was once said by astronomers of the system of the heavens, if God had consulted the biologists, they would have been able to devise for Him simpler ways of building the systems that maintain life. In particular, organisms are built of a variety of pieces and systems that were not designed to fit together. As is now well known, this is true down to the molecular scale. Genes of eucaryotes are built in pieces that have to be spliced together, the intermediate products encoded by those genes are sometimes altered as much as six or seven times at six or seven different stages of construction, both within the nucleus and after being exported into the cytoplasm.²⁵ In many organisms, mitochondria (organelles required for respiration in air) employ slightly variant genetic codes than the rest of the cell. This list could be expanded indefinitely. Suffice to say that the complications of the machinery out of which organisms are built are nothing short of incredible. And these complications bear the stigmata of a complex history. Systems of control that turn on the machinery for making eyes in mice have recently been shown to turn on the machinery for making eyes in fruit flies.²⁶ Yet the sorts of eyes that are made, and the steps by which they are made, are entirely different. The only sensible understanding of this mixture of conserved control systems and novel constructional apparatus is that the control system is a historical remnant, one that has for reasons we do not understand very well, been retained for over 500 million years. There can be no pretense of perfect adaptation here. Organisms are cobbled together. To use François Jacob's word,

²⁴ The *locus classicus* for discussion of this debate is Lewontin (1974). See also Dietrich (1994).

²⁵ For amplification on these topics see chapters 9 and 11, and for a far stronger account of the nature and impact of recent findings, see chapter 12.

²⁶ Halder, Callaerts, and Gehring 1995. Chap. 11, below, was an early reaction to the findings of the Gehring laboratory.

they are constructed by a process of *bricolage* (roughly, tinkering). This bricolage means that the different parts of organisms and even cells (cf. mitochondria) have different histories. Careful examination of the current features of organisms thus reveals a great deal about the contingent pathways by means of which they were constructed. The importance of this deep truth within biology was central to Dobzhansky's perspective. To this extent, the last two decades of work in molecular biology have helped to justify his claim: nothing in biology makes sense except in the light of evolution.

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