

in populations that is, according to Mayr, the source of almost every insight that has led to progress in the biology of ultimate causation. No theme is more insistently sounded than the crucial role of "populational thinking," the recognition of individual differences. No obstacle to progress in biology has been as great as essentialism, "the most insidious of all philosophies." Platonic idealism may serve for physics, but Plato was a disaster for biology, and "the rise of modern biological thought is, in part, the emancipation from Platonic thinking." Mayr's development of this theme alone, even if overstated in places, is a major contribution.

It is, of course, easy to find debatable points in any work of this magnitude, especially when it is penned by so forceful a personality. But it would take a far longer review than this to describe the book's virtues. It is a work of immense scholarship; it treats virtually every historical figure and idea that has had an impact, for good or ill, on the subjects discussed; it is above all a work of interpretation, of reflection on the larger significance of every substantial ripple in the current of biological history. Interesting facts and interpretations abound: how natural theology benefited evolutionary theory by asking questions about adaptations; how Lyell's uniformitarianism prevented him from recognizing evolution; how *Naturphilosophie* developed in reaction to reductionism; how Franz Unger's concern with the nature of species may have led his student Mendel to his work; how Darwin could find inspiration by applying Malthusianism to individuals rather than to species; how Lyell's and Weissmann's views influenced the development of evolutionary theory by their sheer forcefulness; how induction failed, and deduction succeeded, in developing a theory of genetics; how Galton arrived at a particulate theory of inheritance but failed to promulgate it in the right journals. Mayr has provided far more than a compilation of historical events; he treats history in the best tradition of evolutionary biology, offering on almost every page new interpretations and reasoned speculations to account for the origin, diversification, and extinction of ideas.

To wish for greater coverage of some topics would be ungracious, but some few questions are not developed to the fullest. How, for example, did the theory of polygenic inheritance develop and find acceptance? Why were Lamarck's ideas not accepted? What role did geology and anthropology play in the origin of evolutionary thinking? In other instances

Mayr carefully identifies questions that he leaves for future historians. For example, he discusses at some length the contributions of evolutionary natural history and systematics to evolutionary thought and notes that a detailed history of this topic is yet to be written. But it is hard to think of anything that has escaped Mayr's notice. The number of questions raised and provisionally answered is breathtaking, the amount of historical detail is overwhelming, and the challenges to future historians are innumerable.

The publisher has performed an extraordinary service by making the book available at such a reasonable price. It can, and should, find a place in the personal library of every student and professional worker in biology or the history of science. This is an extraordinary, epic, work in which Mayr once again shows himself a master of detail, interpretation, and synthesis.

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The Work of Dobzhansky

Dobzhansky's Genetics of Natural Populations, I-XLIII. R. C. LEWONTIN, JOHN A. MOORE, WILLIAM B. PROVINE, and BRUCE WALLACE, Eds. Columbia University Press, New York, 1981. xiv, 942 pp., illus., + plates. \$42.50.

The Roving Naturalist. Travel Letters of Theodosius Dobzhansky. BENTLEY GLASS, Ed. American Philosophical Society, Philadelphia, 1980. x, 328 pp. Paper, \$8. *Memoirs of the American Philosophical Society*, vol. 139.

Theodosius Dobzhansky is regarded by many as the most influential figure participating in the "neo-Darwinian synthesis" that occurred during the late 1930's. Dobzhansky's book *Genetics and the Origin of Species*, published in 1937, was his main contribution to the synthesis. In it he brought together the then recent theoretical results of Sewall Wright, J. B. S. Haldane, and R. A. Fisher with his own observations on the genetic structure of natural populations and the speciation process. The book must be ranked as one of the great contributions to 20th-century science.

In 1938 Dobzhansky published the first paper in his *Genetics of Natural Populations* (GNP) series. He continued to contribute to this series until his death in 1975. Since the granting of membership of a particular paper to the series appears to be more or less random, the series may be viewed as a representative cross-section of his work and a natural target for inclusion in a book of the "collected works" genre. This particular collection, however, is considerably more than the juxtaposing of a number of influential papers. It includes a discussion of the origins of the GNP series by William Provine, an essay by R. C. Lewontin that evaluates the scien-

tific contribution of the series, a prelude to each of the papers that places the paper in its historical context and comments on problems that have been identified since the paper's publication, and a series of photographs of the collecting localities that Dobzhansky frequented and of his numerous students and co-workers.

Provine's essay on the origins of the GNP series examines the early work of Dobzhansky, particularly his collaborations with Sturtevant and Wright. It is clear that both of these men had an enormous influence on the direction of Dobzhansky's research and, in Sturtevant's case, on his education as well. In fact, Dobzhansky viewed himself as Sturtevant's student even though he had completed his degree-gathering while still in Russia. Sturtevant's influence can be measured in the draft of a grant proposal "Status and Prospects of the *Drosophila pseudoobscura* Analysis" that Sturtevant wrote and sent to Wright in 1936. In it can be found the outline of much of the GNP series. The planned collaboration of Dobzhansky and Sturtevant on this proposal broke down because of the much-discussed falling out between them. Provine suggests several reasons for the squabble. The one I find most consistent with the personalities involved stems from Sturtevant's disenchantment with the quality of Dobzhansky's cytological work. Sturtevant was a meticulous scientist who one imagines would be very intolerant of the errors that repeatedly crept into Dobzhansky's often hastily done cytology.

With Sturtevant out of the picture Dobzhansky turned to Wright for assistance with the quantitative aspects of his

work. The Wright-Dobzhansky collaboration was one of the most successful theorist-experimentalist efforts ever in evolutionary biology. The papers that came out of this joint venture are high points in the history of population genetics. The picture of natural populations that was emerging was one in which genetic drift was the main factor causing the genetic differentiation between populations in the frequencies of inversions and lethal alleles. At this time Dobzhansky felt that inversions were neutral chromosomal rearrangements. This view changed radically when he observed temporal changes in inversion frequencies that were so large as to be incompatible with the predictions of Wright's genetic drift calculations. Natural selection seemed to be the only known force strong enough to account for these fluctuations. Thus the picture changed to one in which natural selection was the primary force molding the genetic structure of natural populations. Wright seemed to lose interest in the collaboration at this point, in part because of other pressing commitments, but perhaps also because of Dobzhansky's demotion of genetic drift to a minor role in shaping those aspects of natural populations that could be observed experimentally.

Provine's account of these early years of Dobzhansky's scientific development is convincingly done. Provine is an excellent writer and a very competent historian. Lewontin's essay on Dobzhansky's scientific accomplishments is somewhat less satisfying, although it does contain some good material. For example, there is a useful classification of the GNP papers according to their subject matter. This makes it easy to read as a unit all the papers that bear on a single question. What Lewontin attempts but fails to do is to provide a penetrating analysis of the scientific merit of the entire corpus of Dobzhansky's work.

From the beginnings of the GNP series in the late '30's until the early '50's almost every observation Dobzhansky made was a significant contribution to our knowledge of the genetic structure of natural populations. When most of us conjure up a picture of the temporal and spatial pattern of genetic variation in natural populations the chances are that the picture is very close to what Dobzhansky would have conjured up even in the late '50's (although we might see somewhat more alleles per locus). However, from the late '50's until his death Dobzhansky's view of the nature of the selective forces acting in natural populations became less and less compatible

with the experimental results coming out of other laboratories. These other results are ignored by Lewontin and in the annotations to the papers.

It could be argued that if there were one parameter that would provide the most information about the maintenance of genetic variation in natural populations that parameter would be the average heterozygous effect of alleles. In a common notation this parameter is called h . It is interesting to watch the evolution of h in the GNP series. In the early years Dobzhansky felt, along with almost everyone else, that mutant alleles affecting fitness were recessive and deleterious ($h = 0$). The experience with inversion polymorphisms, and later with interpopulational hybrids and lethal alleles, convinced Dobzhansky that most pairs of alleles exhibited overdominance ($h < 0$). This was the point of view that he was to hold until his death. (It has been a convenient interpretation for theoretical population geneticists because it

provides an easy way for their dynamics to yield stable polymorphic equilibria.)

In the early '60's James Crow and Rayla Temin began an experimental program to estimate h by a series of complementary experimental designs, some direct, some very indirect. This program was continued and refined by Terumi Mukai and later by several of Crow's students. Included in these experiments were naturally occurring alleles, spontaneous mutants, and induced mutants. Both in scope and in the care with which they were executed these experiments far exceeded most of those previously attempted. Insofar as they can tell us anything, they certainly suggest that alleles with small effects on fitness (that is, viability in most cases) are almost additive ($h \approx .5$).

Dobzhansky had attempted experiments similar in design to those of Crow's group but always failed to see the correlation of heterozygous and homozygous effects routinely observed in



"Dobzhansky's method of capturing flies. This fascinating sequence of photographs was made by Wyatt W. Anderson when he and Dobzhansky were collecting at Ferron, Utah, August 18-19, 1963. The sequence, beginning with the upper left, shows Dobzhansky approaching the bait bucket at the base of the tree, placing the net over the bucket and tapping the bucket to encourage the flies to enter the net, swirling the net to force the flies to the bottom, placing a vial in the net, tapping the flies into the vial, and etherizing the flies for examination. The flies were reported on in GNP XXXVIII." [From *Dobzhansky's Genetics of Natural Populations*, I-XLIII]

Crow's lab. Even a cursory glance at a typical Mukai paper shows that his designs were both better and larger (more chromosomes sampled and more flies counted) than Dobzhansky's. For some reason both Dobzhansky in his GNP series and Lewontin in his assessment of Dobzhansky's work have ignored this entire effort by Crow and his followers. This is not a trivial point. If the Crow-Mukai interpretation that for naturally occurring alleles h is close to .5 is correct for most loci, then Dobzhansky's theories about the maintenance of genetic variation are quite simply wrong. Moreover, since much of equilibrium population genetics theory relies on overdominance to maintain variation, a good part of it would also be a casualty. No matter how much we may wish that Crow's results were different, they will not go away, and to ignore them when trying to assess the contributions of Dobzhansky is unacceptable.

Dobzhansky's unassailable contributions to evolutionary biology are easy to identify. One of these that was new to me was his formulation of the biological species concept. He appears to have been the first to realize that the definition of a species must involve the nature of the gene flow between populations rather than the conventional morphological criteria used by systematists. He differed sharply from Sturtevant in this point of view. Sturtevant at that time was more persuaded by the requirements of museum workers than by the biology involved.

The contributions of the first half of the GNP series are manifold and are well covered in Lewontin's essay. These early papers are the core of observations that all of us in the business rely on for our notions of the genetic structure of populations. I often find it surprising that Dobzhansky's work, particularly my favorite papers from the mid '50's, are not cited more often by theoretical types. For example, in the six 1981 issues of *Theoretical Population Biology* there were only two citations of Dobzhansky, and neither one of these was to a GNP paper. Perhaps the publication of this collection will stimulate theoreticians to begin incorporating more of Dobzhansky's (and Crow's!) results into their theories.

Another contribution of Dobzhansky's that cannot be overlooked is the enormous number of students he produced. Many of the most conspicuous contributors to both theoretical and experimental population genetics are former students of his. Among these are two of the editors of the GNP book, Lewontin and

Wallace. Most of these students harbor a great deal of affection and admiration for their mentor.

There is another side to Dobzhansky that is revealed in the collection of his "travel letters" edited by Glass. These engaging letters were written from various countries over a span of 12 years, from 1948 to 1960. They are mostly descriptions of events that occurred during collecting safaris to some often remote and primitive areas of the world. The letters are light reading. They do not indulge in profundities about the conditions in underdeveloped countries or the state of mankind, although they too often reflect some dated notions about the state of womankind. This collection would have been more interesting to the uninitiated if the cast of characters had been identified in the introduction. As it stands I had little idea who these people were that Dobzhansky was describing. Occasionally a well-known geneticist appears, but in general most readers will know nothing about most of those men-

tioned. The first letter is actually from the Columbia University Oral History Project. It describes three collecting trips to Central Asia that Dobzhansky took while in his mid-20's, before he came to this country. It is a somewhat self-conscious monologue that nonetheless gives some insight into Dobzhansky's strong roots as a natural historian.

The vastness of Dobzhansky's scientific output has probably been a deterrent to its assimilation into the thinking of younger population geneticists who were brought up outside the Columbia sphere of influence. It is to be hoped that the reprinting of these works in addition to Columbia University Press's planned reissue of the first edition of *Genetics and the Origin of Species* will focus attention back on this older experimental literature.

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Products of a Centennial

The items discussed here are celebrations of Einstein's 100th birthday that by chance and publishers' design have accumulated on the bookshelf of *Science*. They well represent the general celebratory literature; purely technical festschriften have been set aside for separate review.

The most important and substantial of the works from *Science's* shelf are the products of symposia held in Berlin (Nelkowski *et al.*), Jerusalem (Holton and Elkana), and Princeton (Woolf), which brought together scientists, historians, and philosophers. Contrary to much previous experience, it appears that the different sets of savants have something to say to one another if they study the same texts. The Jerusalem and Princeton volumes are further enriched by the craftsmanship and style of distinguished straight (not science) historians: Isaiah Berlin on "Einstein and Israel" and Fritz Stern on "Einstein's Germany" (Holton and Elkana) and Felix Gilbert on "Einstein's Europe" (Woolf).

A second genre consists of collections of mainly new material (Aichelburg and Sexl; Consejo Nacional; Kinnon *et al.*) and compendia of old and new (the fine sampler of Einstein commentary and

reminiscence edited by A. P. French). The remaining works apart from Broda are printings or reprintings of source material: Einstein's *Autobiographical Notes*, his nontechnical writings on general relativity (Tauber), a few letters (Rosenthal-Schneider), and the charming chrestomathy edited by Dukas and Hoffmann. Unfortunately, the most important new collection of source material, two volumes published by the Berlin Academy of Sciences (1), is not present. Nor is there a centennial biography, no one apparently having had the courage to try. (An account of the older biographies is given by D. Cassidy in Nelkowski *et al.*, pp. 490-510.)

Science's shelf contains no more than 20 percent of the serious centennial literature. And this literature, though large and important, does not greatly augment the volume of Einstein studies. The recently published *Literature on the History of Physics in the 20th Century* (2) lists 7000 items, of which over 10 percent directly concern Einstein. Long before his hundredth birthday he was already the most quoted physicist of modern times (3).

The attention paid Einstein derives in large part from the tendency of histori-