DOBZHANSKY ON EVOLUTIONARY DYNAMICS:
Some Questions about Dobzhansky's Russian Background

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The present paper poses some questions regarding the influence of Dobzhansky's Russian background on his later views regarding evolutionary dynamics. Since I know Russian materials only at second hand, I cannot seriously answer the questions raised here; my main hope is to provoke a response from those who are familiar with, or who are able to investigate, the Russian roots of Dobzhansky's work. This said, I shall focus mainly on Dobzhansky's response to the views of Iurii Filipchenko,[1] Dobzhansky's close friend and mentor[2] and the person who coined the term 'macro-evolution' (Filipchenko, 1929)[3].

I suspect that Dobzhansky's arguments for the continuity of evolutionary mechanisms at all levels of the systematic hierarchy were shaped in part by his concern to overcome Filipchenko's objections to the (neo-)Darwinian extrapolation from micro- to macroevolution. Furthermore, and this cannot have come easily, in taking this position Dobzhansky sided with Chetverikov and the Moscow school (and various Russian entomologists) against Filipchenko. Thus, the investigations that I wish to stimulate concern the role that Dobzhansky's Russian background played in the development of his views on evolutionary dynamics during the period from about 1925 to about 1950.

I shall take for granted that Dobzhansky participated in what Gould (1983) has called "the hardening of the evolutionary synthesis." This point is hardly original (see, e.g., Provine 1986,

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[1] Cf. N. Krementsov, this volume, for a discussion of another component of the Russian background of great importance in shaping Dobzhansky's views on species and speciation – to wit, his involvement with the debates on these topics among various Russian entomologists during his formative years. Cf. also Adams (1990c and in preparation) and D. Alexandrov, this volume, for further background on Filipchenko, his views on macro-evolution, and his relations with Dobzhansky.

[2] A major stimulus for the meeting leading to the present volume was the examination of the rich correspondence between Dobzhansky and Filipchenko, the bulk of which occupies the period after the former's departure for the U.S. in 1927 until the latter's death of meningitis in 1930. That correspondence, which will be available in the American Philosophical Society as well as in the Academy of Sciences of the USSR, Leningrad branch, will be published by Mark Adams in due course. It should go a long way toward clarifying the issues raised here.

[3] Cf. Adams, in preparation, to which I owe the citation, and Alexandrov, this volume. Many of the issues I raise regarding the relations of Dobzhansky and Filipchenko have been raised by Adams's work in its numerous variants, reinforced by Alexandrov's recent work.

chaps. 10-12) and is probably no longer controversial. What is partly new, in English at least, are the suggestions, pursued here, that Dobzhansky's increasing adaptationism in micro-evolutionary theory needs to be interpreted against the background of earlier disputes in Russia as well as the more familiar ones in the United States and England, and that it marks a major departure from the Russian biological traditions within which Dobzhansky was raised.

Those traditions, although partly Darwinian, are well represented by Leo Berg, Filipchenko, various orthogenetic theories, and, above all, the belief that evolution at or above the species level cannot be fully accounted for by intra-specific competition and its consequences.[4] Particularly relevant to the issues at hand are Dobzhansky's increasing conviction, from about 1940 on, that intra-specific differences among organisms and populations, although perhaps brought forth by historical accident or genetic drift, are typically maintained by selection and by intra-specific competition, and his ever-stronger insistence that no macro-evolutionary mechanisms other than the ones described in micro-evolutionary theory are required (or play an important role) in nature. Now if selection maintains the differences among organisms that cause populations to differentiate, and the differences among populations are converted to differences between species by a continuation of the very same selective processes, distinctions between micro- and macroevolution become distinctions only of scale; no distinct macro-evolutionary processes need be invoked. This extrapolationist view, parallel to Darwin's, is characteristic of the so-called synthetic theory of evolution, which Dobzhansky helped create. I take it to run against the grain of much of the Russian evolutionary biology with which he was familiar – including evolutionary theory as it was taught and practiced in St. Petersburg (later Petrograd, then Leningrad). It is Dobzhansky's growing confidence in this selectionist and extrapolationist position during the 1940s and 1950s at which my questions are directed.

Stage Setting

What do I assume about Dobzhansky's Russian background? I assume that, unlike many of the American geneticists who were his contemporaries, his primary training was not as a breeder or an experimentalist, but as a natural historian, entomologist, and field biologist (Gould 1982). I assume that he acquired his deep interest in fundamental questions of evolution from his earliest days as a biologist and that he was not taught, as were his American colleagues, that evolutionary questions are hopelessly speculative. In any case, he clearly would not have been satisfied to work in genetics or any other discipline unless he could bring his work to bear on evolutionary problems – including Darwin's fundamental problem concerning the origin of species and the question, much debated in the Russian and the American settings, of the causes of variation among organisms. From this perspective, perhaps by 1927 and surely by the time that he had been in Morgan's laboratory for a few years, he had an advantage that few American geneticists of his generation enjoyed: he was in a sound position to bring both field and laboratory studies of genetic variation in natural populations to bear on evolutionary issues.

I also assume that accounts of Russian Darwinism like those offered by Adams (1968, 1979, 1980, 1990a-e, and in preparation), Dobzhansky (1980), Todes (1989), and others are generally reliable. Thus I take it that the inheritance of acquired characters remained an open question and

[4]For relevant background regarding the anti-Malthusian tendencies of Russian Darwinism and anti-Darwinism, see Todes, 1989.

that a majority of important Russian evolutionists from Beketov and Korzhinskii to Filipchenko resisted Darwin's reliance on the Malthusian mechanism of intra-specific competition. Many of those from whom Dobzhansky first learned evolutionary biology denied the importance of intra-specific competition as a major cause of evolutionary change. Not that they denied the importance of competition altogether, but that they conceived of it mainly as inter-specific competition or as "competition with the environment."

For present purposes, the views of Filipchenko and Serebrovskii appear particularly interesting, though my knowledge of their work rests mainly on secondary literature (e.g., Adams 1990c and e; Gaissinovitch 1980). To put it briefly, Filipchenko held a form of autogenesis from before his close association with Dobzhansky (which began in 1924) until his death in 1930, denying that within-group variation is comparable with, or able to explain, the differences among higher taxa. Thus he distinguished sharply, as Goldschmidt would later, between micro- and macroevolution,[5] denying that selection acting on within-group variation could explain macroevolution. Genetics could solve the problems of micro-, but not those of macroevolution. Serebrovskii, who had worked in Chetverikov's group in the Kol'tsov Institute, held, in contrast, that variation within populations, though perhaps partly random in character, provided the basis for a full theory of evolution. "All evolution is in essence ... the evolution of the gene fund" (Serebrovskii 1928, quoted in Adams 1990e).

It is worth noting that Dobzhansky's early allegiance was with Filipchenko, not with Serebrovskii.[6] Yet it was Serebrovskii who originally coined the term 'gene fund' ('genofond', Serebrovskii 1926) and Serebrovskii's use of that term that appears to have led Dobzhansky, by a long and ironic pathway, to coin the English term 'gene pool' in 1950 (Dobzhansky 1950; Adams 1979). I turn to an exploration of some aspects of that path.

Filipchenko's Variabilität und Variation

I suspect, but cannot document, that the evolutionary issues that most concerned Dobzhansky when he left Russia in 1927 were (1) the causes of variation within populations and (2) the relation between micro- and macroevolution. At the very least, he was deeply familiar with them; they were central to Russian evolutionary biology. They can be united by a bridging question, which played an important role in Dobzhansky's early work (bibliography in Lewontin et al. 1981): are the causes of variation within populations the same as the causes of variation between populations, between species, and between higher taxa? Already in Dobzhansky's early field studies, as in parallel work by Chetverikov and his school, material is gathered to address this question.

This suspicion is heightened by a reading of one of the few works of Filipchenko accessible to me, his Variabilität und Variation (Philiptschenko, 1927). In it, Filipchenko drew a number of fundamental distinctions. Three are crucial for my argument, for they help explain the structure of Dobzhansky (1937). The distinctions are: (1) variation as a condition ['Variabilität'] vs. variation as a process ['Variation'], (2) individual variation vs. group variation, and (3) statics vs. dynamics.

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[5] E.g., Goldschmidt, 1940. As Adams and Alexandrov point out, Goldschmidt's use of the terms 'micro-' and 'macro-evolution' derives from Dobzhansky, who got them from Filipchenko. See n. 3 above.

[6] Additionally, there was the influence of Berg's Nomogenesis. Cf Dobzhansky (1980), p. 233.

For Filipchenko, these distinctions may be applied only at or below the level of Linnean species, i.e., to individuals, pure lines (biotypes), Jordanons (races or subspecies) or species. "In this regard we go no further, ..., that is [not] beyond the species, for we hold that one must understand by variability ['Veränderlichkeit'] the unlikeness or diversity of individuals or groups of individuals within the boundaries of a species, so that species boundaries are at the same time the natural boundaries of variation" (1927, p. 15).[7]

These distinctions divide the study of variation in relation to evolution as follows: Statics studies variation in individuals (norms of reaction, responses to environmental variation) and groups (differences among groups in the distributions of characters of all sorts, including their extremes and means), over specified ranges of environments. Since statics concerns variation as a condition, its results do not turn on the heritability of that variation, and hence do not reveal its evolutionary significance. Heritability, together with its consequences in relation to selection, population size, etc., is studied in dynamics. Study of the dynamics of variation within species requires entirely different methods than those of statics; they include the methods of what we would now label 'population genetics'. This is the proper domain of the familiar laws of Mendelian-Morganian genetics, of Vavilov's law of homologous series, and of their elaborations for the dynamics of populations.

Near the end of the book, Filipchenko returns to the relation between his account of variation and the problem of macroevolution. He affirms that small "stepwise" mutations can accumulate to transform Jordanons and that the Jordanons that form a Linnean species, geographically separated, can be transformed to yield distinct species. Nonetheless, he goes on to reinforce some arguments against Darwin's principle of divergence of characters, stating his own position as follows: "It seems to us highly likely that the origin of the characters [that differentiate the] higher systematic categories [requires] some other factors than does the origin of the lower taxonomic units" (p. 91). Two pages later, he speculates, with Boveri, Conklin, and Loeb, and against Morgan, that "generic characters, like those of the first developmental stages of the egg, and also those of the higher systematic categories, are determined, not by the nucleus, but by the cytoplasm" (p. 93). Repeating the distinction between micro- and macroevolution he insists that "contemporary genetics removes the veil from the evolution of biotypes, Jordanons, and Linneons," but not from the evolution of higher systematic categories (p. 93).

The "Physiology of Populations"

In order to keep the present analysis within bounds, I shall concentrate on certain features of the first and third editions of Genetics and the Origin of Species, drawing also on the series of papers on "Genetics of Natural Populations" (GNP). The analysis has two purposes: to show that the structure of the first edition of his magisterial book (Dobzhansky 1937) is helpfully understood as a direct response to Filipchenko and to illustrate some of the ways in which Dobzhansky's vision of the dynamics of evolutionary processes changed as this focus disappeared – as it had by the third edition (Dobzhansky 1951).

To appreciate these points, start with the organization of chapters in the first edition, lost in the third. In the first edition (p. 14), but not the third, Dobzhansky says he will treat evolutionary statics in Chaps. 2-4 and dynamics in Chaps. 5-10. Statics examines "whether the differences

[7] Free translations from this source by RMB.

between forms encountered in nature can be resolved into the elements whose origin is known in experiments" (p. 14). Dynamics, in contrast, deals with "the evolutionary process in the strict sense" (p. 14) – the 'physiology of populations' and the fixation of differences among populations.

This structure connects intimately to the position Dobzhansky takes on the extrapolation of micro-evolutionary processes to handle macro-evolutionary problems. Near the beginning of the first edition (1937), he laments our inability to understand "the mechanisms of macro-evolutionary changes, which require time on a geological scale," adding, notoriously, that "we are compelled at the present level of knowledge reluctantly to put a sign of equality between the mechanisms of macro- and micro-evolution" (1937, p. 12). This reluctance, I believe, is not feigned or coy; among other things, Dobzhansky took Berg's, Filipchenko's and others' reservations about Darwinian extrapolation seriously. Thus, although the equality of mechanisms is maintained consistently throughout the first edition of the book it remains, in an interesting way, problematic. By the third edition, (1951), this problematic character has disappeared.[8]

What are the mechanisms of microevolution? In both editions, he lists three: (1) "mutations and chromosomal changes[9]; (2) "the dynamic regularities of the physiology of populations," including "selection, migration, and geographical isolation"; and (3) "the fixation of the diversity already attained on the preceding two levels" (1937, p. 13; 1951, p. 18).[10] Strikingly, these mechanisms are used to set aside the sorts of problems regarding macroevolution that preoccupied Filipchenko. Here are the fundamental conclusions that Dobzhansky expressed on this topic in the final chapter of the first edition (Dobzhansky, 1937): species are the only (and thus the highest) systematic category to have withstood critical analysis (p. 306); thanks to physiological isolating mechanisms such as the chromosomal ones revealed by his own empirical studies,

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[8] The sentence about the equality of mechanisms is replaced with the following paragraph in the third edition: "Many authors believe that microevolutionary changes are different in principle from macroevolutionary ones, and that while the former can be understood in terms of the known genetic agents (mutation, selection, genetic drift), the latter involve forces that are experimentally unknown or only dimly discerned. Views of this kind have been entertained by few geneticists (among whom there is, however, so eminent a man as Goldschmidt, 1940), but they have been popular among those who approach evolutionary problems on the basis of data of paleontology and comparative anatomy. Well-known writers have supposed macroevolutionary changes to be engendered by some directing forces either inherent in the organism itself or acting on it by some inscrutable means from outside. These guiding forces received a variety of names, including orthogenesis, nomogenesis, aristogenesis, hologenesis, and finalism, but they escaped precise definition which would make them subject to experimental test or to any kind of rigorous proof or disproof (see Simpson 1949)" (1951, pp. 16-17).

[9] Both explicitly included in Filipchenko (1927). One of the most important differences between Dobzhansky's and Filipchenko's treatments of micro-evolution is the former's emphasis on chromosomal changes. The increased appreciation of chromosomal phenomena and their potential evolutionary significance is largely a consequence of the decade of empirical work that Dobzhansky had performed with various colleagues, especially Sturtevant, in Morgan's laboratory. An examination of the technical papers of that decade or of the early papers in the GNP series is quickly convincing on this point. It should also be noted that the only sorts of variation that Dobzhansky investigates in his treatment of evolutionary statics in the first edition are genic and chromosomal variation.

[10] The word "already" is omitted from the last quotation in the third edition.

"discrete groups of organisms frequently coexist in the same territory without losing their discreteness, ... [thus causing] a more or less permanent fixation of organic discontinuity" (p. 312); and "the conclusion that is inexorably forced on us is that the discontinuous variation encountered in nature, except that based on single gene differences, is maintained by means of preventing the random interbreeding of the representatives of now discrete groups" (p. 308). With these claims, apparently, the problems of macroevolution have been set aside.

From the First to the Third Edition

The above account sheds light on both the structure of Dobzhansky (1937) and its claims regarding macroevolution. But those claims were, in many respects, less controversial in the American context in the 1940s than others that played a central role in Dobzhansky's book. The shift in Dobzhansky's views is subtle, requiring careful examination of the details of his increasing selectionism and adaptationism. Let us examine some of the changes that occurred all too briefly, especially those bearing on the importance, and precise role, of natural selection.

Of particular interest is the changing interplay between selection and "the scattering of variability," Dobzhansky's (1937) term for the effect of drift in small populations. In chapter five of the first edition, which contains the transition from evolutionary statics to evolutionary dynamics (and which was broken up and redistributed in the third edition), this topic is developed at length. There, the scattering of variability is crucial; it ensures that differences between natural populations arise and are maintained in such a way as to allow selection to operate on those differences. Thus, in context, a claim made near the end of the chapter is quite important: "the available data, meager as they are, tend to show that the effective population sizes may prove to be small, at least in some species" (1937, p. 145).

Small size, as Sewall Wright had shown, allowed fixation of selectively neutral variation; it thus provided for the differentiation of populations. In the last section of the chapter, this Wrightian mechanism served as the basis for the formation of microgeographic races (a term comparable to Filipchenko's 'Jordanon', coined by Dobzhansky). Dobzhansky interprets such races as exhibiting non-adaptive differences that are probably not the product of natural selection (p. 148).

The predominant view in the 1937 edition and the first eight papers of GNP is that microgeographic races are expansions of small Wrightian demes, i.e., of populations with distinctive gene frequencies and constellations of traits produced mainly by isolation and genetic drift. GNP IX (1943), however, announced the discovery that the frequency of chromosome inversions in isolated populations of Drosophila pseudoobscura vary cyclically with the season. It, together with a huge body of allied work pointing to larger population sizes and migration rates than Dobzhansky had anticipated, marks the beginning of the shift to the much more selectionist views expressed in subsequent articles in the GNP series and in the 1951 edition. This change eliminates the need to rely on the scattering of variation (drift) to maintain microgeographical races. It thus marks the abandonment of an 'internal dynamic' in the physiology of populations based on the intrinsic (if accidental) character of the populations over and above their interactions. Put hyperbolically, the "founder effect" (Mayr's term) produces variation whose fate in the hardened synthesis is solely in the hands of selection. More soberly, after the shift, the 'intrinsic character' of a population is mainly the product of selection.

This marks a major change from the problematic that Dobzhansky inherited from Filipchenko and which, as I have argued, helped structure the first edition of Genetics and the Origin of Species. Now the study of variation within and between groups is automatically a part of evolutionary dynamics, a part of the study of the changes wrought by selection and other evolutionary 'forces'. To this extent, there is no reason for a separate study of evolutionary statics. Thus, the abandonment of the large-scale chapter organization separating statics from dynamics in the third edition makes good sense: the differences among the mechanisms at the different levels are not serious enough to bear much weight. The distinction between statics and dynamics has been subtly undermined by the reduced importance assigned to drift.

Though the point cannot be developed here, I suggest that this shift (together with many other factors) helped remove Dobzhansky's remaining ambivalence regarding the relation of micro- to macroevolution. Once he supposed that selection is dominant at all levels, he no longer had any ground for supposing that the intrinsic character of organisms or populations plays a significant role in macro-evolution independent of the scrutiny of selection.

Concluding Questions

As I began, so let me end, by placing questions. Is it true, as I have suggested, that as late as 1937 Dobzhansky was still to some extent working out the consequences of abandoning views like those of Berg and Filipchenko in favor of those of Chetverikov, Serebrovskii, and Wright? Is it right that the reduced importance he came to assign to drift in maintaining differentiation of populations marks a more clear-cut allegiance to views like Serebrovskii's? Do these considerations, joined with those of Adams (1979 and in preparation), help us to understand the significance of Dobzhansky's introduction of the term 'gene pool' into the language of evolutionary biology in 1950? (Adams shows that one specific stimulus to this was Dobzhansky's reading of the 1948 Lysenkoist repudiation of Serebrovskii's concept of 'genofond'.[11]) And is the introduction of 'gene pool' itself a marker of a phase shift in Dobzhansky's career, the one that Provine describes as a shift "away from [concern with] population structure, more toward the analysis of selection in nature and in the laboratory" (Provine 1986, p. 398)?[12] While Dobzhansky himself would have resisted most of these suggestions (Dobzhansky 1980, p. 242), I think that there is enough in them to be worth further investigation.

However one answers such questions as these in the end, it is clear that we will not have a full understanding of the work of Theodosius Dobzhansky until we can integrate the Russian and the American aspects of his career and thought. It is to be hoped that this volume will mark a fruitful step in that direction.

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[11] As Adams argues, we must be careful to consider the full context for even narrowly scientific arguments: the pretension to have set aside the problems in the way of Darwinian extrapolationism clearly has an ideological component, both in the US and in the USSR. See Adams, in prep., MS pp. 35 ff.

[12] Although the third edition (1951) is far more selectionist than the first, there is still a very large difference between it and Genetics of the Evolutionary Process (Dobzhansky 1970) which is clearly a text in a new tradition, one that works within the hardened synthesis and tries to assimilate molecular data and techniques

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