BIOGRAPHICAL MEMOIRS OF FELLOWS OF THE ROYAL SOCIETY

# Theodosius Grigorievich Dobzhansky. 25 January 1900 -- 18 December 1975

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# THEODOSIUS GRIGORIEVICH DOBZHANSKY

25 January 1900 — 18 December 1975

Elected For.Mem.R.S. 1965

By E. B. Ford, F.R.S.

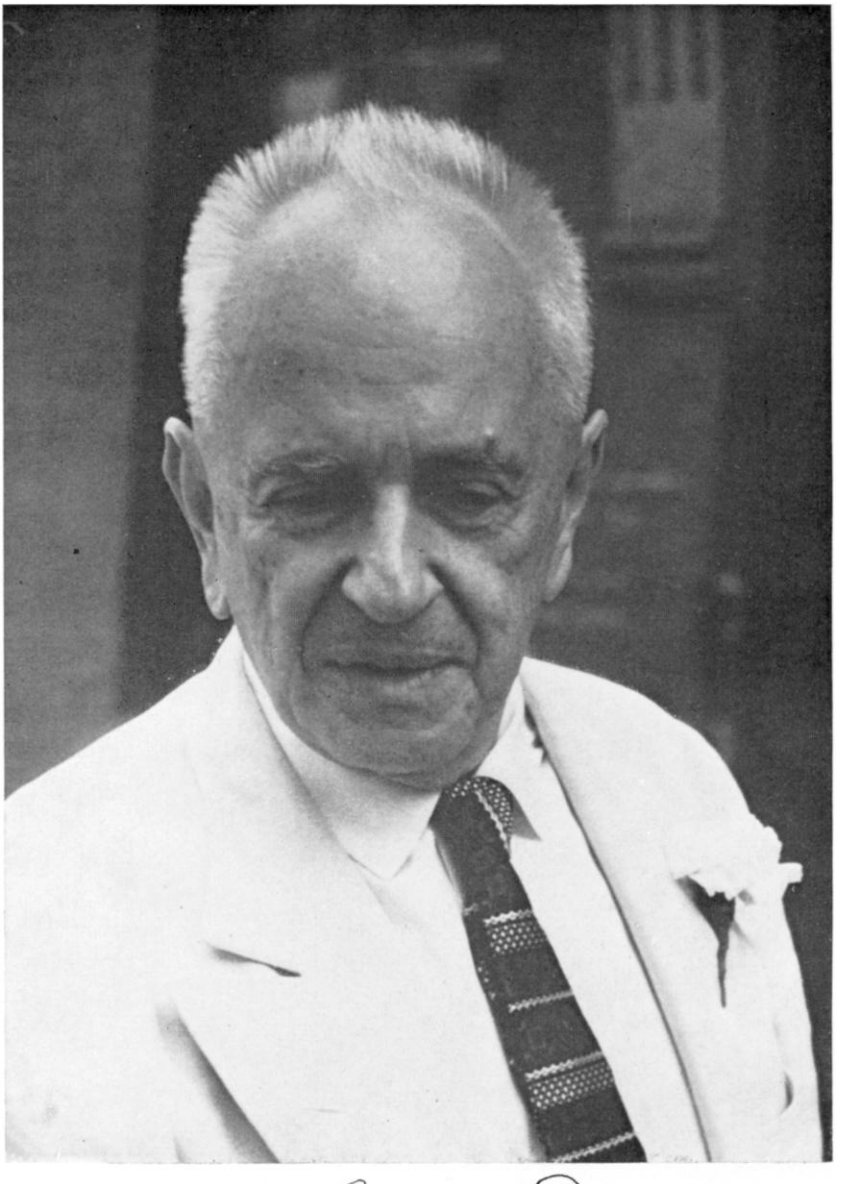
Professor Th. Dobzhansky was the most distinguished geneticist in the U.S.A. and one of the most distinguished in the world. He was well fitted to hold an outstanding position in America for, educated in Europe and being an exceptionally travelled man, he had an international outlook, while his ability to read a number of languages enabled him to keep abreast of the literature of his subject published outside North America. He had, moreover, an attribute of value in general intercourse; he was a man of wide culture and artistic perception, especially of painting and music.

Theodosius Grigorievich Dobzhansky, originally Dobrzhansky but 'Doby' to many of his friends, was born in the little town of Nemirov in the Ukraine. He was an only child and his father, Grigory Dobrzhansky, who taught mathematics, was of Polish ancestry. His mother is generally said to have been Russian; but her name, Sophia Voinarsky, suggests that her family also had a Polish origin, no doubt more remotely than that of her husband's.

Their son, the subject of this memoir, attended a secondary school at Kiev, 130 miles from his birthplace, and passed on to the University there, reading biology and graduating in 1921. He spent the next three years at the Institute of Agriculture in Kiev, moving thence to the University of Leningrad, where he was lecturer in genetics until 1927. In 1926 he had become a Fellow of the U.S.S.R. Academy of Sciences and that same year included for him an important scientific event, for he led an expedition into Central Asia, which he had visited in 1925 and 1926, to study domestic animals.

In 1924 he married Natalia Petrovna Sivertzev, herself a geneticist whose last publication appeared in 1964. She died in 1969. This was a deep distress to her husband, for their marriage brought them both much happiness. They had a single child, a daughter, Sophia, who is married to Professor M. D. Coe of Yale University. Both are anthropologists and they have five children.

While at Leningrad, as a young Russian able to speak German, though at that time no English, he was picked upon to show William Bateson over the Hermitage Galleries. He told me that Bateson gave him his first cigar and that they conversed together in German. This is slightly curious, since we know that



Theodosius Dobzhansky

during the period 1886–87 Bateson learnt to speak Russian, and indeed Kirghiz, easily.* I regret that I never asked Dobzhansky to explain the matter or if he attempted to speak Russian with Bateson who, perhaps, had largely forgotten it.

In appearance, Dobzhansky was of middle height, thick-set with, towards the end of his life, stiff white hair kept very short and standing starkly on end on the top of his head. He retained an extraordinary accent, never to be forgotten by those who heard him, high and staccato. It was an odd vehicle for his almost perfect English. He spoke German fluently, but his spoken French was very imperfect though he read the language easily. How good were his Spanish and Portuguese I do not know, but he had sufficient command of them to converse without difficulty during his many travels in South America. He had another linguistic ability to which special attention must be drawn; the extraordinary polish and excellence of his English writing. It was plain, straightforward and free from all pedantry or any suggestion of foreign grammar. This is the more surprising because he learnt no English until after he had graduated. As Professor C. D. Darlington remarked to me, Dobzhansky had, perhaps, an inherited aptitude for writing, being some relation of Dostoevsky. Though admitting the connection, he never, to my knowledge, specified it in precise terms, calling it 'rather remote'. Yet it could hardly have been very distant or, in a family which did not possess detailed genealogical records, he would not have known about it. There seems evidence that he was, in fact, a maternal cousin.

Dobzhansky was extremely hospitable. He entertained frequently and often had colleagues to stay with him. On one occasion he lent his fine New York apartment to me for several weeks when he had to leave for some other country. His lifelong pleasures were riding—he was an accomplished horseman—and travel. He and I kept a list of the countries in which we had dined together and it was quite a long one. On one occasion while going round the world in opposite directions we parted in Australia (Brisbane). He went West and I East and we joined up again near Mather in the Sierra Nevada of California, camping in the forest at a place where his ashes, and those of his wife, now rest.

In 1927 he accepted a Fellowship from the International Board of the Rockefeller Foundation to go to the United States for two years, taking his wife with him, to work at Columbia University, New York, with Professor T. H. Morgan. It was evidently expected by the Russian authorities that he would return when this Fellowship expired. In fact, he never entered Russia again though he longed to so do as a visitor, but not to live in a Communist country.

When Morgan moved to the California Institute of Technology in 1928, Dobzhansky accompanied him and settled there for the next twelve years, becoming Assistant Professor of Genetics in 1929 and full Professor in 1936. His subsequent appointments are listed on p. 66. It will be seen that they led him to New York. Until latterly, he was happy there, at Columbia and, especially, at the Rockefeller University with its splendid facilities. These were arranged to provide men of genius with every opportunity for research, free from the

* Bateson, W. (1928) *Letters from the Steppe*. London: Methuen.

responsibilities of formal teaching, unhampered by interference and with but a minimum of mere administration. The use he made of them was admirable, but the end of his live was saddened by trouble both private and academic.

His wife died when he was 69, the year before he was due to retire. He had expected that the laboratories he had developed with so much success would continue after he had ceased to be their nominal head, and that in them he would retain full facilities for his own work and students. It was not to be. Detlev Bronk, the wise President of Rockefeller, retired in 1968, and in time Dobzhansky learnt that as a result of subsequent arrangements his department was to be disbanded and his staff dismissed.

At this point, and with the help of Professor R. W. Allard, a position was found for him as adjunct professor (without salary) in the University of California at Davis, where he went in 1971 and where his former student F. J. Ayala had become Professor of Genetics in the same year. It was there that Dobzhansky built a house and spent the brief remainder of his life.

He had friends there: Ayala, Ledyard Stebbins and others; also Mrs Olga Pavlovsky, except latterly when she had to move back to New York. Many colleagues came to see him, especially Michael Lerner to whose visits he so much looked forward. But there is no doubt that Dobzhansky felt professionally isolated at Davis, even from the genetics department. Yet, though suffering from leukaemia, he maintained his rewarding laboratory work, for which he had good facilites, almost to the last; and he was still able to undertake his studies of *Drosophila* in the field: in South America, in Mexico and at his beloved Mather in the Sierra Nevada. In his final years it was above all the devoted friendship of a young man, his last doctoral student, who moved with him from New York, that in Dobzhansky's eyes made life worth living and encouraged him to continue his research on genetics and evolution.

## Scientific work

The tenor of Dobzhansky's work will be evident from an inspection of his vast bibliography (pp. 67–89). While still in Russia, he was mainly concerned with a study of Coccinellid beetles, *Adalia*, *Harmonia* and others. His initial approach was chiefly that of the systematist, but under the influence of Chetverikov, to whom he owed much in his earlier years, he turned his attention to their genetics and geographical variation.

As early as 1924, however, he published a paper on *Drosophila melanogaster*, and in 1927 appeared his important work, using that species also, in which he studied the multiple effects of single genes, showing that each could control characters of extreme diversity such as eye-colour, proportions of an internal organ and viability. Though he did not reach the conclusion that dominance and recessiveness can result from selection, he did make it clear that they are properties of characters not of genes. Yet one finds the expressions 'a dominant gene' or 'a recessive gene' pervading genetics long after Dobzhansky had demonstrated that one gene can have effects some of which may be recessive and

others not. Unfortunately he did not throw his weight against the habit of using the word 'mutation' in two distinct senses, to the well-deserved scorn of philosophers; an elementary confusion of thought by no means absent from genetics today.

It was natural that, on arrival at Columbia, Dobzhansky should develop his interests in *Drosophila melanogaster*. He devoted himself with enthusiasm to some of the studies already in progress there, such as the sex-determination work of Bridges, while he was able to carry further other triumphs of the Morgan school. In particular, he was attracted to the conclusions to be derived from chromosome aberrations. These he used to supply independent evidence for the order of the genes. Also he was the first to build up a chromosome map based on cytological evidence, showing the strength, and the weakness, of such maps when derived from cross-over values.

Such chromosome studies led, in 1933, to the use of *Drosophila pseudoobscura* as experimental material, so opening up the main work of Dobzhansky's life. Quickly he saw the advantage of that species for work on evolution and adaptation in nature, being much superior for that purpose to *Drosophila melanogaster*, which Dobzhansky came to call the 'garbage fly'. Indeed the ecology of the latter insect does not well fit it for population studies in the field.

*Drosophila pseudoobscura* inhabits the west and south of the United States, extending far into Mexico. Dobzhansky's great series of papers on its chromosome inversions was initiated by one written jointly with A. H. Sturtevant in 1936. At the outset, that work was coloured by Dobzhansky's early interest in systematics, using inversions to illustrate phylogeny. Soon, however, he began to investigate their occurrence in wild populations today.

This type of chromosome polymorphism has no visible effect on the flies. It is to be detected solely by an examination of the giant 'polytene' chromosomes found in the cells of the larval salivary glands.

At an early stage of the work we recognize the true scientist in Dobzhansky: a a man ready to adjust his views in the light of increasing knowledge and not ashamed to admit a past error, nor concerned to disguise it. In his 1936 paper with Sturtevant, he had held that these chromosome inversions are of neutral survival value, a statement picked upon by Sewall Wright (1940)* in his desire to demonstrate the occurrence of 'random genetic drift'. Yet subsequently, in 1947, Dobzhansky was himself the first to show that the apparent neutrality of the inversion polymorphism in *Drosophila* is wholly deceptive and that it is, in fact, subject to powerful selection.

This indeed is suggested by the high frequencies of the phases over vast areas, a situation which obviously could not arise as a result of random drift. However, Dobzhansky soon established their selective importance by means of observation and experiment. This he did both by analysing wild material and, experimentally, by establishing laboratory populations in *Drosophila* cages of the type invented by l'Héritier and Teissier.

* Wright, S. (1940) *The new systematics* (ed. Julian Huxley), pp. 161–183. Oxford University Press.

The inversions are labelled by a pair of upper-case letters, not in italics, so as to distinguish the terminology from that of genes. More than two dozen of them have now been identified in the third chromosome of *Drosophila pseudoobscura*.

Dobzhansky showed that the inversion-frequencies are adjusted to altitude, and also that they undergo a cycle of abundance and rarity in relation to the season. These features are to be found throughout the range of the fly. An instance of such adjustment, at first anomalous, proved explicable by means of a special technique. In a locality, Piñon Flats, Southern California, studied in much detail, it was found that the frequency of the 'Standard' inversion (ST) increases, and that of 'Chiriachua' (CH) declines during the hot summer months. The two frequencies then remain approximately unaltered during the winter but in natural conditions they are reversed in the spring: an example of *cyclic variation*. Though such environmental changes had been mimicked in the laboratory, no situation in which CH was at an advantage had ever been encountered experimentally. However, Birch (1955)*, working with Dobzhansky, realized that in the wild the spring population is a strongly expanding one. That condition is never seen in the population-cages in which the larvae always live at the numerical limit imposed by their food-supply. Birch therefore arranged a special situation in which larvae carrying both the ST and CH inversions were freed from competition. As a result, the CH/CH genotype proved of superior viability to ST/ST, and this for the first time in bred material. Here then we have an example of the fact that numerical increase favours genetic diversity because it is associated with reduced selection, while numerical decrease has the opposite effect owing to the stricter selection then operating (Ford & Ford 1930).†

The different inversions in concurrent wild populations of *Drosophila pseudoobscura*, as well as in other *Drosophila* species with which Dobzhansky worked, are examples of genetic polymorphism. That is to say, they constitute clear-cut distinctions occurring together in the same population, even the rarest of them being too common to be maintained merely by (chromosome) mutation. Such polymorphism is associated with the formation of supergenes which, of course, the inverted chromosome segments in this case constitute. They do so because they hold distinct genes together owing to the absence of crossing-over between the structurally heterozygous segments. Such polymorphism tends, in addition, to generate heterozygous advantage. The existence of such 'heterosis' and its production are matters to which Dobzhansky gave special attention.

In the first place, he found that the heterozygous inversions generally exceed their calculated value in wild populations. Thus the relative viabilities, not gene-frequencies, of AR/AR, AR/CH and CH/CH (AR = 'Arrowhead') in a stock from Piñon Flats proved to be 0.71 : 1 : 0.43. Indeed there have been numerous instances in which more than 50% of the individuals in a wild population are heterozygotes, of course an impossible situation unless that type

* Birch, L. C. (1955) *Evolution*, **9**, 389–399.

† Ford, H. D. & Ford, E. B. (1930) *Trans. R. ent. Soc. Lond.* **78**, 345–351.

were favoured by selection. Dobzhansky then proceeded to examine the evolutionary aspect of the matter by, as it were, taking it to pieces. He had shown that the heterozygotes have a significant advantage over both homozygotes in comparisons involving CH, ST and AR at Piñon Flats as well as Mather. Though both in California, these two localities are 300 miles apart, and in crosses between flies taken respectively at them, the heterozygotes were no longer superior but of intermediate viability between the two homozygotes. Carrying the matter a stage further, when strains from Chihuahua and Piñon Flats, 700 miles apart, were crossed, the heterozygotes between CH and AR were actually the least viable of the three genotypes. It is clear therefore that such heterozygosity is not in itself beneficial but that its advantage has *evolved*.

Dobzhansky was naturally fascinated to observe an evolutionary change taking place in the wild population of *Drosophila pseudoobscura* at the present time. The Pike's Peak (PP) inversion was already common in Texas when his work began. It was then a great rarity in California; up to 1946 only four instances of it had been encountered among 20 000 chromosomes studied. During the next twelve years it increased throughout the vast area represented by the greater part of that State, to the extent that about 8% of all third chromosomes came to carry it while there was a corresponding decrease in one of the other inversion-types (CH).

Evidence obtained by Dobzhansky seemed to exclude migration of the flies from Texas, which would mean traversing Arizona. He was therefore driven to consider alternative explanations for these changes. On the other hand, the Californian climate may have altered, either naturally or as a result of human interference, in a way favourable to the PP inversion but to the detriment of CH. It is difficult to prove a negative, but at any rate no widespread climatic change has been detected there. Moreover, the State is immensely diverse in its ecology and climate, while it includes large urban districts, extensive agricultural regions and huge areas of unaltered countryside; yet the spread of PP seems quite unrelated to such distinctions. Dobzhansky seems correct, therefore, in attributing the phenomenon to a genetic readjustment: a gene mutation or a cross-over in the right place might well give advantage to an inversion not previously favoured. It must, however, be remarked that one difficulty faces this and every other explanation of the recent increase of the PP type; that is to say, the immense area over which it has occurred. This is wholly unrelated to the rate at which the fly can normally spread, about 1.76 km in ten months. Whatever combination of circumstances may be involved, it is clear that Dobzhansky has here detected a striking instance of contemporary evolution.

In his later years, he found valuable material for research in *Drosophila paulistorum*. Working with Olga Pavlovsky, he reported (1966) an important occurrence in a stock of this fly, the 'New Llanos' strain, which had been maintained in the laboratory. They found that this had become so adjusted as to produce sterile males, though fertile females, in crosses with an Orinocan race with which the F1 had previously been fertile in both sexes, a change that had taken place between 1958 and 1963. This fascinated Dobzhansky as it evidently

threw light upon the early stages of speciation, a matter of critical importance in evolution. It requires much further study today. As he realized, we need far more information on the genetic adjustments that can build up in isolation He had indeed been greatly interested by some early work of H. B. D. Kettlewell on the moth *Lasiocampa trifolii*. This is a large species, powerful on the wing, subdivided into isolated coastal populations in southern England. Kettlewell studied two of these 300 miles apart; a reddish brown form from Cornwall and a pale one from Dungeness, Kent. The colour distinction is unifactorial (brown being dominant) but they have already taken the first step towards speciation for on crossing them Kettlewell found that the female progeny are intersexual, though the males, being homogametic in the Lepidoptera (the reverse situation to that in the Diptera), are sexually normal.

Dobzhansky gave much attention to the genetics of behaviour. His work on phototaxis, closely paralleled by that on geotaxis, opens up exciting possibilities for the future which he would certainly have pursued had he lived. Using *Drosophila pseudoobscura*, he had shown that though the heritability of both these traits is quite low, about 9%, it was possible to build up positive and negative phototactic and geotactic populations; such that after twenty generations of selection very few of the flies made a wrong choice when offered a series of alternatives in a maze. It is of much interest that when the selection was relaxed the positive or negative phototaxis achieved by the previous treatment was almost obliterated in forty generations. Dobzhansky was also carrying out studies of much potential interest on phototaxis in response to different wavelengths of light.

Developing further the question of dispersal, of obvious significance in some of Dobzhansky's work already mentioned, he turned again to this subject when it became possible to mark *Drosophila pseudoobscura* in the wild. It may be questioned whether attracting the flies to bait gave an unbiased picture of what was occurring in nature, but the method could have been refined in the future and is of potential importance.

Finally, one further and particular aspect of Dobzhansky's contribution to science must be mentioned. In 1973, he had been approached by authorities in Mexico to ask if he would take steps to start the study of ecological genetics in that country. This he did with enthusiasm; it was characteristic of him. He would always give up his time to encourage research and especially young research workers. The stimulus he provided can never be assessed, but it was great. There must be many within his field of science who owe to him far more than they can specifically record, more indeed than they realize.

While recognizing the importance and the outstanding achievements of molecular genetics, Dobzhansky was of opinion that too much research is directed to that aspect of the subject and that evolution, the fundamental concept of biology, needs to be studied intensively upon the whole organism. The molecular approach is indeed the conventional one in science, that of analysis. Dobzhansky turned his eyes in the other direction, towards synthesis, integrating the organism into the environment of which it is itself a part. In this

he had much success in the field which he valued most: that of interpreting Darwinism in terms of modern biology.

I should like to express my sincere gratitude to Dr J. R. Powell, now of Yale University, for the care and trouble he has taken to give me a detailed account of Professor Dobzhansky's last years. No one is so well qualified to do so as he. Moreover, he has with great labour provided a bibliography of Professor Dobzhansky's writings from 1970 onwards. Before that, I checked my own lists of his works, with which he supplied me at intervals, against that published in the special volume in honour of Professor Dobzhansky which appeared as a Supplement to *Evolutionary biology* (ed. M. K. Hecht & W. C. Steere), 1970, New York: The Meredith Corporation.

I am most grateful to Dr V. Pavlovsky for his photograph of Professor Dobzhansky which illustrates this memoir and for his permission to use it for that purpose.

## Appointments in the U.S.A.

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|---|---|
| 1927–28 | Fellow, International Education Board, Columbia University, New York |
| 1928–29 | Fellow, International Education Board, California Institute of Technology |
| 1929–36 | Assistant Professor of Genetics, California Institute of Technology |
| 1936–40 | Professor of Genetics, California Institute of Technology |
| 1940–58 | Professor of Zoology, Columbia University, New York |
| 1958–62 | da Costa Professor of Zoology, Columbia University, New York |
| 1962–70 | Professor, Rockefeller Institute and Rockefeller University, New York |
| 1970–75 | Professor Emeritus, Rockefeller University |
| 1971–75 | Adjunct Professor of Genetics, University of California, Davis |

## Awards

National Academy of Sciences, U.S.A., Daniel Giraud Elliot Medal, 1946
National Academy of Sciences, U.S.A., Kimber Award and Medal, 1958
Academia Leopoldina, Darwin Medal, 1959
Anisfield–Wolf Book Award, 1963
Pierre Lecomte du Nouy Award, 1963
The President of the United States, National Medal of Science, 1964
Yale University, Addison Emery Verrill Medal, 1966
American Museum of Natural History, Gold Medal for Distinguished Achievement in Science, 1969
Franklin Institute, Philadelphia, Benjamin Franklin Medal, 1973

## Honorary degrees

| | |
|---|---|
| University of São Paulo | 1943 |
| Wooster College, Ohio | 1945 |
| University of Münster | 1958 |
| University of Montreal | 1958 |
| University of Chicago | 1959 |
| University of Sydney | 1960 |
| Columbia University, New York | 1964 |
| University of Oxford | 1964 |
| University of Louvain | 1965 |

| | |
|---|---|
| Clarkson College of Technology, New York | 1965 |
| Kalamazoo College, Michigan | 1966 |
| University of Michigan | 1966 |
| Syracuse University, New York State | 1967 |
| University of Padua | 1968 |
| University of California, Berkeley | 1968 |
| Northwestern University, Illinois | 1968 |
| Wittenberg University, Ohio | 1970 |
| St Mary's College, California | 1970 |
| St Vladimir Theological Academy, New York | 1970 |
| Mazatlan University, Mexico | 1974 |
| Sorbonne, Paris | 1975 |

## Society membership

*President*

| | |
|---|---|
| Genetics Society of America | 1941 |
| American Society of Naturalists | 1950 |
| Society for the Study of Evolution | 1951 |
| American Society of Zoologists | 1963 |
| American Teilhard de Chardin Association | 1969 |
| Behaviour Genetics Association | 1973 |

*Membership*

National Academy of Sciences
American Philosophical Association
American Academy of Arts and Sciences

*Honorary Member*

Genetics Society of Japan

*Foreign Member*

Royal Swedish Academy of Sciences
Royal Danish Academy of Sciences
Brazilian Academy of Sciences
Academia Leopoldina
Accademia Nazionale dei Lincei
Royal Society of London

A special volume in honour of Professor Dobzhansky was published as a Supplement to *Evolutionary biology* (ed. M. K. Hecht & W. C. Steere), 1970. New York: The Meredith Corporation.

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1922 Über Massenauftreten und Wanderungen der *Coccinellidae*. *Report of Bureau of Applied Entomology* **2**, 103–124. (In Russian, with German title.)

Über die imaginale Diapause bei den *Coccinellidae*. *Report of Bureau of Applied Entomology* **2**, 103–124.

1923 (With A. Semenov-Tian-Shanskij) Tres novae *Coccinellidarum* species e fauna Rossiae Asiaticae. *Revue Russe d'Entomologie* **18**, 99–102. (In Latin and Russian.)

1924 Die geographische und individuelle Variabilität von *Harmonia axyridis*. *Biol. Zbl.* **44**, 401–421.

Die weiblichen Generationsorgane der Coccinelliden. *Ent. Mitt.* **13**, 18–27.

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Die geographische und individuelle Variabilität von *Adalia bipunctata* und *A. decempunctata*. *Revue Russe d'Entomologie* **18**, 201–212. (In Russian with German synopsis.)

Zur Erforschung der Anschwemmungsfauna des Dnjeprs bei Kiev. *Russian Hydrobiological J.* **3**, 221–223. (In Russian with German synopsis.)

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1925 Zur Kenntnis der Gattung *Coccinella*. *Zool. Anz.* **62**, 241–249.

Die palaarktischen Arten der Gattung *Coccinula Dobzhansky*. *Zool. Anz.* **64**, 277–284.

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1926 Die palaarktischen Arten der Gattung *Coccinella*. *Revue Russe d'Entomologie* **20**, 16–32.

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1927 Die Coccinelliden Heptapotamiens. *Revue Russe d'Entomologie* **21**, 43–52. (In Russian.)

Neue und wenig bekannte Coccinelliden. *Revue Russe d'Entomologie* **21**, 212–217. (In German.)

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