Boris Balinsky: transition from embryology to developmental biology

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Summary

This is the story of a textbook that students of developmental biology have used for 45 years. ''An Introduction to Embryology'' was released soon after a role for genes in the control of development became finally recognized but not yet well documented. Thus this book manifested the transition from embryology to developmental biology. The story of its author, Boris Balinsky, who against all odds survived to write this book, is remarkable on its own. He started his scientific career in the USSR, but due to 20th century social and political upheavals, ended it in South Africa. This article will shed light on the life of Boris Balinsky, a scientist and writer and will explore the origins of his book. ***BioEssays*** **27:970–977, 2005.**

Introduction

In September 1941, Boris Balinsky faced the most momentous decision of his life. He was about to choose whether to remain a loyal citizen of Soviet Russia and evacuate to the East or to remain in territory that would be occupied by Germans. He chose the second option, which resulted in an outcome that he could not foresee. After the long ordeal of several evacuations to the West, Balinsky found himself in 1949 in C.H. Waddington's laboratory in Edinburgh. Here he wrote a plan for a textbook that would make his name famous worldwide with the notable exception of Russia. The book, "An Introduction to Embryology",[1] was published in seven English, two Japanese, two Italian and one Spanish edition.

In 2005 two anniversaries coincide, the 45th anniversary of the book and the 100th birthday of Boris Balinsky. As a professional scientist he was successful in the fields of experimental embryology and entomology. He also treated music, painting and writing very professionally. The story of Boris Balinsky and his textbook is likely to be of interest to those who grew up on modern developmental biology handbooks, which were, to a large extent, written under the influence of Balinsky. The story of his book is quite remarkable since it is a story about war and peace, human rights and scientific freedom of one scientist who tried to stick to his profession even though he was caught in the midst of social unrest at its worst.

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Stormy life

Boris Ivanovich Balinsky was born during the first Russian revolution of 1905 (19.9.1905) in Kiev. He became a student of Ivan Schmalhausen (1894–1963), one of the leading Russian zoologists and embryologists, and one of the founding fathers of the integration of embryology with evolution and genetics.[2]

The beginning of Balinsky's scientific career was exceptional. In 1924, Schmalhausen suggested that he follow up experiments initiated by one of the pioneers of experimental embryology in Russia, Dmitry Filatov (1876–1943),[3] who transplanted an ear vesicle onto the head of a frog embryo. Balinsky modified this approach. First, under the influence of Spemann and Mangold,[4] he used newts. Second, Balinsky transplanted the ear vesicle onto the flank of the embryo. This resulted in the induction of an ectopic limb, demonstrating 'competence' of the lateral mesoderm and the requirements of inductive interactions during limb formation. These experiments opened up a new avenue of studies in limb development, which had been pioneered a few years earlier by Ross Harrison and laid the foundation for Balinsky's first paper.[5] The five-legged newt became his mascot.

His scientific career developed rapidly. During 1931–1936, he rose from an assistant to full professor and deputy director of the Institute of Zoology and Biology. By that time Schmalhausen had become more focused on a theory of evolution, while Balinsky continued to work in experimental embryology (Fig. 1). In 1937, during a campaign of mass arrests and deportations instigated by Stalin, Balinsky's wife was arrested and Balinsky lost his positions. Given the circumstances, it was very fortunate that he maintained his research group. Later on, Balinsky submitted an appeal and his wife was released. Nevertheless, this episode cast a long shadow over Balinsky and, to a large extent, precipitated all the following events. In the mid-1930s, Balinsky switched to studies of endoderm development[6,7] for which he was later awarded the Kowalevsky Prize by the USSR Academy of Sciences (see Box 1).

However, the inner opposition of Boris Balinsky to the regime grew steadily. Several factors influenced this trend,

Figure 1. Boris Balinsky. Kiev, 1939. © Helen David

Box 1

The Alexander Kowalewsky (Kowalevsky) Award and Medal (for details, see http://spns.narod.ru/Eng/kov_med. htm) were established by the Imperial St. Petersburg Society of Naturalists initially in 1910 to honor the well-known Russian embryologist and early Darwinian (1840–1901), who demonstrated the close evolutionary relationship between vertebrates and tunicates. Initially the award equaled 250 gold rubles (app. 3000 US$ in 2004), which in 1910 corresponded to a professor's yearly salary and was meant to be given for studies in comparative anatomy and embryology of invertebrates. Due to delayed implementation, no awards were given before 1914. The Award (without a medal) was restored by the USSR Academy of Sciences in 1940 only to be abandoned again due to the war. Obviously, in times of war, biology is one of the first casualties. Thus Boris Balinsky happen to be one of only two scientists, who received this Award (5000 Roubles) without a medal before German invasion of 1941. Both the Award and Medal were restored again in 2001 by the St. Petersburg Society of Naturalists. Coincidently, Scott Gilbert, the author of a modern popular textbook "Developmental Biology" that continues the tradition of "An Introduction in Embryology" got this prize (with a medal) in 2004; interestingly, he also had a five-legged amphibian as a totem—a five legged frog. Since the initial capital of the Imperial St. Petersburg Society of Naturalists has been nationalized during the third Russian revolution of 1917, the modern award corresponds to a modest sum of current 250 rubles (app. $8.75).

including the murder of his grandfather during the civil war, the lowering of the quality of life of his family, the grave pictures of famine in Southern Russia and Ukraine in the early 1930s induced to force peasants to join collective farms, the oppression imposed by the Stalinist regime upon all people and, in particular, his friends and relatives, and his the first-hand experience as a visitor of the Archipelago Gulag. All these elements combined to lead him to decide to seek a better life outside of the Soviet Union, using the opportunity brought about by the German invasion in 1941.

This was not an easy decision. Being trapped in the Crimea, where he went with his family just before the war, Balinsky initially wanted to join the army to defend his country. But having witnessed mass arrests and extermination of political prisoners, he realized that, if not for their absence in Kiev, he and his wife could have been rounded up too. Possibly, his memories of the German invasion of 1918, which brought a brief period of independence for Ukraine influenced his decision. After German troops captured Kharkov, Balinsky and family returned to Kiev. To earn a living, he started to work at one of the few research institutions established by the German administration, the Fisherei Institute. Very soon his idealistic expectations of the Germans as liberators of an independent Ukraine evaporated. When German troops started retreating westwards, he realized that he was caught between a hammer and anvil. In 1943 his wife suddenly died. When the Germans evacuated Kiev, he took his mother and son into exile in Posen (Posnan).

Once in Germany Balinsky was able to visit several laboratories, including the laboratory of Otto Mangold in Freiburg. This was a rather sentimental journey since, in 1928, Schmalhausen had arranged for Balinsky to visit Mangold in Berlin-Dahlem, but such plans were not realized.

For several years before and during the war, Balinsky worked on the development of several teleost species,

including the goldfish, roach, pike and bream. He generated a complete series of illustrations covering all the developmental stages of these species. All these were lost during the evacuation from Posen. The only result of his desperate efforts in appalling conditions was a short summary of results[8] and some drawings used for a textbook.[1] In Posen Balinsky created his own special *ex libris* sign, choosing the five-legged newt. After the war he settled in Munich, where he met his second wife, Elizabeth Stengel.

In an attempt to re-launch his scientific career, Balinsky initiated job hunting with a little help from Theodosius Dobzhansky (1900–1975), who in 1927 had left Kiev for T.H. Morgan's laboratory in Columbia. Later on Dobzhansky became known for his seminal work in population genetics. In 1947 Balinsky joined Waddington's laboratory. By the late 1940s, Conrad Hal Waddington (1905–1975) in parallel with Schmalhausen had already contributed to developing a synthesis of evolution, embryology and genetics.[2] In his laboratory, Balinsky studied development of the mammary gland in mammals.[9,10] Here he briefly acted as a tutor to Mary F. Lyon, who was later to launch an illustrious and influential career in mammalian developmental biology.[11] During this period Balinsky had been thinking about the role of the scientist in society. Later on he formulated his philosophy in his novel "Seven Men in the Barrack Room"[12]: "For a scientist as myself, creativity means scientific research. All my conscious life I have attempted to penetrate the workings of nature, devised and carried out experiments, written and published papers and a book or two. The work of a scientist does not stand out as a unique, independent thing, as a work of art does, but it contributes to the general movement of advancement, and in this way goes beyond my life, beyond my personality. That is unless a scientist makes an outstanding discovery that picks out his name and places it above the host of others."

In September 1949, Balinsky moved to South Africa. Here he returned to studies of amphibians and contributed a chapter on endodermal development into the normal table of *Xenopus* development by P.D. Nieuwkoop and J. Faber.[13] Within a few years he became a professor and the head of the Department of Zoology of the University of Witwaterstrand until retirement in 1973.

His entomological studies occupied a large portion of his time. While in Scotland he published two entomological papers.[14] After moving to South Africa, 20 out of his 50 research articles were related to entomology. Yet the experimental manipulation of amphibian embryos by means of transplantation to induce ectopic structures and to understand the underlying developmental mechanism still remained at the forefront of Balinsky's interests. The last of these papers appeared in 1974 almost 50 years after the first one. Balinsky repeated transplantations of the first paper and using electron microscopy demonstrated that both normal and induced formation of the limb required absence of the basal lamina in regions destined to develop the limb. He hypothesized that this would provide the supply of morphogenetic factors involved in limb induction.[15] Indeed, recently it was found that the ear rudiment secretes FGF.[16]

Ironically, escape from political turbulence dominated his entire life. When leaving for South Africa, he was warned that this country was ripe for revolution. He ignored this caution and even became rather sarcastic on that matter at the time when he completed his memoirs in 1988.[17] He could not have been more mistaken on that issue. Within a couple of years South Africa experienced one of the most significant shakeups in its history, but without a bloodbath. Nevertheless, it was evidently his destiny to live a stormy life.

Writing a book

Balinsky wrote his first small book in 1927 and followed it by the publication in 1936 of a book that he produced by modifying a 1931 lecture.[18–20] It remains the most clearly written textbook on embryology in the USSR. Its author was only 31, and this was only the beginning. Before his famous embryology textbook of 1960, Balinsky published six books and monographs, several review articles and chapters. He was well prepared for the advent of a big book and yet he was not in a hurry. After all, the plan for this book was conceived in 1949.

From the very beginning, Balinsky had a very clear idea of how his book should look. It was supposed to be divided both "horizontally" and "vertically" (see Box 2)

When the book was finally written and published in 1960, its first edition strictly followed this plan. The novelty of his approach was an attempt to combine in an embryology textbook a core of descriptive embryological data with that of experimental embryology, supplemented by elements of physiology, biochemistry and, importantly, the role of genes in development, which was very controversial at the time.

Box 2
Initial idea for layout of book

The vertical subdivision followed the periods of development, such as:

- Gametogenesis
- Fertilization
- Cleavage
- Gastrulation
- Organogenesis
- Growth and Differentiation

In each of these sections, he planned four "horizontal" aspects:

Descriptive morphology; Causation (experimental); Physiology and Biochemistry; Genetic background.

Figure 2. The front page of the V edition of "An Introduction in Embryology".

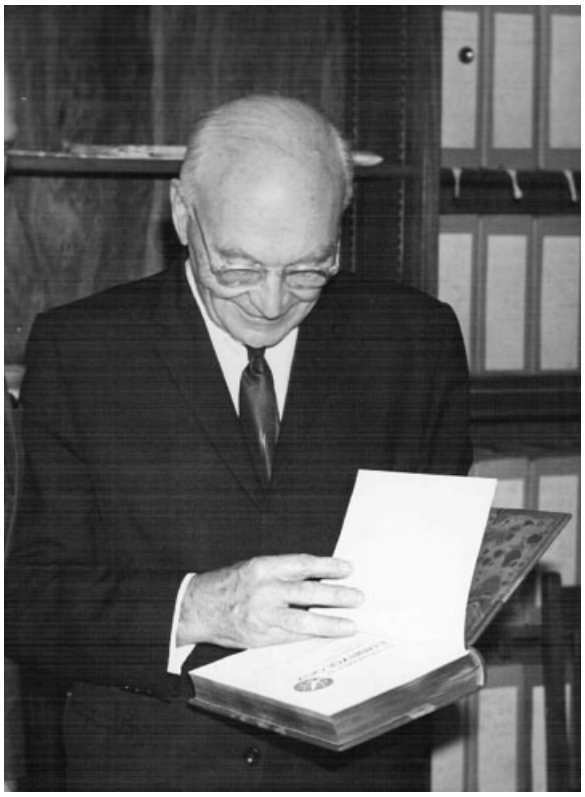

Figure 3. Boris Balinsky with a 100.000 copy of his book in 1971. © Helen David

According to this plan, Balinsky organized the lecture notes for a course in general embryology for third year students that he developed at the University of Witwatersrand in 1949. In 1952 the first draft of his notes was distributed amongst students who were asked to provide feedback. In 1953 he added a chapter on regeneration. In 1958-59 he revised the text, updated it to accommodate new developments in science and modified according to the requirements of American universities. The first edition was published in 1960.[1] For the cover Balinsky used the same five-legged newt (Fig. 2).

It took him almost ten years to prepare the first edition. He kept working on this book for more than twenty years. Between 1960 and 1981 seven English, two Japanese and one Spanish edition of "An Introduction to Embryology" were published. Given the amount of effort and time spent, this book was obviously the largest investment of his life and, probably, the biggest achievement (Fig. 3).

Unfortunately, this book was never published in Russian. Several copies of this book were given by Boris Balinsky to his Soviet colleagues during international conferences. However, overall its impact in Russia remained limited. In the absence of a comprehensive textbook on developmental biology, preparations for examinations in this subject were an uphill struggle. Sadly this situation persisted until the early 1990s.

Balinsky's book influenced all the later textbooks on developmental biology. Some illustrations in these even now contain original drawings of Balinsky or are based on their concepts. Leon Browder, an author of one such textbook said: "Like many of my contemporaries, Balinsky's textbook, *An Introduction to Embryology*, created for me the foundation that still underpins my understanding of embryonic development. In turn, I used later editions of the book as the textbook in the developmental biology course that I taught. A good textbook is a knowledge bank that provides the foundation of the discipline and creates the framework that helps scholars place new information into context. *An Introduction to Embryology* served that purpose for me as I began contemplating writing my own textbook."

Balinsky's book occupies a special place in embryological literature since it was probably the first handbook in embryology that represented a fusion of the classic 'descriptive' embryology textbook typical of courses in embryology given for medical students with the experimental embryology learned by students taking advanced courses in this specialty. This,

to a large extent, stems from the fact that its author became an experimental embryologist from the very beginning of his scientific career to remain an ardent supporter of this approach. However, he also understood the need for descriptive studies. After all one can only interpret the results of experiments knowing the manifestations of the developmental process that is being investigated. Balinsky spent long years describing developmental processes in various species of teleosts and insects and used descriptive techniques like electron microscopy to analyze the results of his experiments. Thus this book represented a novel integrative approach towards the teaching of embryology where presentation of the material gathered using both the descriptive and experimental approaches became linked together contributing to a better understanding of the ontogenetic development of organisms. It came as a continuation of a long tradition of Russian science reflected, for example, in the emergence of a Russian school of evolutionism characterized by a combination of the 'experimentalist' and the 'naturalist' tradition.[21] In fact, a detailed analysis of Balinsky's publications clearly demonstrated that a combination of descriptive and experimental approaches characterized his research both in Russia and in South Africa. In addition, his own training as amphibian experimental embryologist and entomologist provided him with a unique opportunity to generalize concepts derived from experimental embryology where, due to Spemann's influence, amphibians were for a long time the model animal of choice, and classical genetics, where due to the impact of Morgan most data came from *Drosophila* studies.

Finally, taking the point of view that processes of development are under the control of genes, Balinsky introduced the connection between inheritance and development. Thus the textbook in embryology published in 1960 recognized the role of genes in development, a concept that became firmly established only in the 1980s with the cloning of developmental genes. It is interesting to trace the formation of these ideas starting with the first sketch in his 1936 book. Here, he attempted to summarize the emergence of various types of competence in different specialized domains of germ layers, namely the neural plate, epidermis and lateral mesoderm as follows "...where do the new morphogenetic tendencies that appear during the critical phase of formation of new morphogenetic systems emerge from? Here investigation encounters the hereditary properties of every organism, or using the language of modern genetics, its genotype."[20]

Given the fact that Balinsky was closely associated with the two leaders of the unification of embryology, heredity and evolution, Schmalhausen and Waddington, it could be interesting to explore his relation to these scientists. Although, in the absence of correspondence, it is difficult to assess their direct influence on Balinsky, the syntheses of embryology, genetics and evolution put forth by Waddington and Schmalhausen[2,22] would have impacted on Balinsky.

Balinsky analyzed the role of genes in development in several chapters (4–9,8,13,17). In particular, chapter 13 "The Genetic Control of Organogenesis" contains discussion of the results of Wright and Wagner[23] and Little and Bagg[24] on the cyclopic guinea pig and mouse, respectively. Further, he reviewed the results of Gluecksohn-Schoenheimer[25,26] on the analysis of kidney formation in the Danforth' short-tailed mice and the increase in the number of digits in the "luxate" mice[27] [due to ectopic expression of Sonic hedgehog[28]] as well as the duplication of body structures in the Danforth's and "Kinky" mice[29] [recently the Danforth's mice phenotype has been linked to gain-of-function of Etl-4[30] while Kinky phenotype to HoxB5 mutation (OMIM#142960), V. K.]. Balinsky mentioned three homeiotic mutants of *Drosophila: aristopedia*,[31] *ophtalmopedia*,[32] *podoptera*.[33] *Aristopedia/spineless* since has been linked to basic helix–loop–helix PAS transcription factor.[34] The two other mutant alleles were studied further,[35,36] but the identity of the genes affected still remains unknown.

Ivan Schmalhausen acted as a father figure and, under his guidance, Balinsky became an influential experimental embryologist. He remained forever loyal to his teacher, which is clear from his short biographical article about Schmalhausen.[37] It contains many details including nicknames of Schmalhausen given by his schoolmates that could be known only to a very close friend. Despite loss of direct contact, Balinsky followed the publications of Schmalhausen. For example, in chapter 17 (pp. 438–439), Balinsky uses a peculiar crest of feathers found on the head of the Houdan fowl as an illustration of the role of genes in the formation of an apparently new structure. This description and a corresponding illustration were adapted from Schmalhausen's "Factors of Evolution"[38] and demonstrate the impact of this book on Balinsky at the time of preparing his textbook. Thus, it is possible that the coincidence of dates of publication of Schmalhausen's book in the West (1949) and that of the development of the concept of Balinsky's textbook in 1949 is not accidental after all.

His relations with Waddington were more complex. Balinsky received a very good classical biological training, published his first paper in embryology at the age of 20 and all his life worked on closely related embryological subjects. Unfortunately, he was unable to communicate with colleagues abroad and never attended any conferences outside the USSR. On the contrary, Waddington had a quite different although rather broad education. He graduated in geology, studied paleontology and published his first paper in biology at the age of 25. Enjoying personal freedom, he attended the formal and informal scientific meetings without any restrictions and visited laboratories in Germany, Austria and USA. He met Hans Spemann, Otto Mangold, Ross Harrison, Leslie Dunn, Thomas Morgan, A. Sturtevant, and T. Dobzhansky and learned fast. Interestingly, Waddington became aware early on

of Balinsky's first paper. In 1932, Waddington explicitly refers to "...an implanted ear-vesicle for the limb-mesoderm..."[39] which is a reference to Balinsky's paper of 1925.

And yet while Balinsky received his professorship at 28 only to lose it four years later because of political persecutions, Waddington obtained his first professorship and a chair of genetics in Edinburgh at 40 in 1945. By the time that Balinsky arrived in Scotland in 1947, Waddington had become the Head of the Institute of Animal Genetics. His activity during this period has been characterized by one of his biographers, E. Yoxen as follows: "He helped to create a large research institute in Edinburgh after 1945, but he moved so rapidly from project to project that he neglected its consolidation. The legacy of his writing and research is considerable but it is very diffuse."[40] Perhaps, it was due to these factors and heavy administration duties that Waddington spent little time in discussions with his collaborators, including Balinsky. In this context, it might be of interest to bring in what Balinsky had to say about Waddington: "...As Head of the Department of Genetics, and director and scientific leader of the Institute of Animal Genetics, Waddington was conspicuously inactive. He never gave any talks in the Institute about his work, he did not conduct any seminars and during the almost two years that I was working at the Institute, there has been not a single scientific meeting or discussion in the Institute. From my stay in the Institute I learned nothing at all about Waddington's current interests, or the work he was doing at the time. From reading scientific publications, I guess that he was working, or had work done for him, on the influence of selection on the expression of mutations in the fruitfly Drosophila."[17] Thus, even if Waddington had an impact on Balinsky, it is difficult to trace. Indeed, despite the fact that several publications of Waddington were amongst the references in Balinsky's book, there is a noticeable absence of the key references mentioned by S. Gilbert in the context of Waddington's contribution to the evolutionary synthesis.[41–43] Most of publications that Balinsky referred to were experimental embryological studies, including for example fate mapping in birds,[44] measurement of pressure of migrating cells,[45] induction of a secondary chick embryo[46] or a neural plate in rabbit,[47] usage of radioactive tracers.[48] In the context of genes in development, the early Waddington's monograph[49] is mentioned along with two others.[50,51] Yet it is very clear that Balinsky felt obliged to Waddington, whose support helped him to re-launch his scientific career. Interestingly, he depicted Waddington in his novel "Seven Men in the Barrack Room"[12] under the name of a professor of genetics Alistair Edmonds, who expresses views about the role of scientists in science and society as quoted above. Both Balinsky and Waddington discussed the same *aristopedia* mutation described by Balkaschina in 1929 in Russia.[1,31,41] Even a title of Balinsky's book closely resembled that of one of the books of Waddington (An Introduction to Embryology versud An Introduction to Modern Genetics).[49]

Chapter 13 directly addresses the genetic control of organogenesis, where Balinsky reviewed publications of other members of the Waddington's Institute of Animal Genetics, including T. C. Carter.[27] According to Balinsky he "...did some very interesting work on the embryonic development of some mutant mice",[17] and C. Gordon, the *Drosophila* geneticist.[33] Notably it was Gordon, who when acting in Waddington's absence as the Head of the Institute, involved Balinsky in student practicum at the university and supervision of Mary Lyon in a clear break with Waddington's policy.

Balinsky remained very attentive to new discoveries in the field of molecular genetics. As one of his associates at the University of Witwaterstrand and co-author Prof. Barry Fabian remembers: "Balinsky was always very aware of Schmalhausen's genetic and evolutionary interests. At staff seminars in the '50s he would initiate a discussion series on many aspects of contemporary biology, including population biology/genetics and later on the first developments in DNA. He was very sensitive to new developments in DNA biology and how it could code for proteins, and with the proviso that he could see where it could help to unravel the basic problem of how DNA coded for form. In talking to me about the last 5th edition, with which I was involved, he had a concern that insect embryology was underrepresented, an area he knew a lot about, and perhaps anticipating the genetic/developmental fruit that was to come from this area in later years. But there was a limit as to how much could be included in the book. Further, his last study on inducing mutation in butterflies and looking for the inheritance of variation was at the core of the genetic/embryology/variation/evolution quest that is mainline today. He kept abreast, as far as was possible, with the new developments in molecular biology, and was fully appreciative of and totally behind the new developments of the molecular basis of the gene, and the need to study embryology at this level, in conjunction with other levels." (Personal communication).

So, it seems that Balinsky's views on the role of genes in development were a reflection of his experience as an experimental embryologist and naturalist–entomologist developed under the influence of genetics in the Soviet Union as early as in 1930s and evolutionary theory of Schmalhausen later on. These were also influenced due to interactions in the Institute of Animal Genetics in Edinburgh and discoveries in developmental genetics of *Drosophila* and mammals in 1930–1950s.

The several editions of Balinsky's book clearly reflected the tremendous changes that happened in embryology between 1960 and 1981 resulting in its transmutation to developmental biology. Given the breadth of the approach towards the teaching of embryology taken by Balinsky, he himself humbly admitted that the first edition of his book could only be "an introduction to embryology". After its publication, his circle of correspondence increased substantially. As a result of this feedback, different chapters of the book were substantially rewritten or new chapters added. In particular, the trend of

presenting the science of embryology as a wider discipline—developmental biology, became quite obvious. In the preface to the third edition, Balinsky wrote: ". . .the general outlines of a comprehensive theory of development are gradually emerging, though as yet not clearly enough to put them down on paper; a number of links are still missing." Later on when preparing the fifth edition, Balinsky became convinced that: "Although there are still obvious gaps in our understanding of the development of the animal egg, enough progress has been made to tempt me to synthesize the guiding ideas behind the presentation of the factual material in this book, in a new addition, Part Nine: "Theory of Development—Recapitulation". So it comes as no surprise that most of the later textbooks in embryology feature "development" in their titles in one way or another."

Boris Balinsky lived long enough to see the almost simultaneous collapse of communism and apartheid in the early 1990s. After retirement he focused on entomology. According to his daughter, Mrs. Helen David, in February 1995 he sent almost 40 boxes containing his *Lepidoptera* collection to the Zoological Museum of the Ukranian Academy of Sciences at the Schmalhausen Institute of Zoology in Kiev as a last gesture of appreciation towards his distant motherland. Boris Balinsky died September 1, 1997 in South Africa just a few days before his 92nd birthday. His book can still be found in most university libraries all around the world.

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