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Erwin Schrödinger and the Origins of Molecular Biology

Krishna R. Dronamraju

Foundation for Genetic Research, Houston, Texas 77227

ERWIN Schrödinger (1887–1961) was a distinguished physicist who won the Nobel prize in 1933 for his pioneering work on wave mechanics. Yet, to biologists his name is permanently connected with a little book, entitled *What Is Life?*, that was greatly influential in inspiring a number of pioneers of molecular biology (Schrodinger 1944). Among those who acknowledged their debt to Schrödinger's book are M. Delbruck, G. Stent, J. D. Watson, F. Crick, M. F. Wilkins, and S. Benzer. Baldwin (1994) discussed the deep impact of Schrödinger's book on young Watson (also see Watson 1968).

On the other hand, a few eminent scientists, such as Linus Pauling and Max Perutz, were critical of the contribution of *What Is Life?* Pauling (1987) wrote, "When I first read this book, over 40 years ago, I was disappointed. It was, and still is, my opinion that Schrödinger made no contribution to our understanding of life." Perutz (1987) wrote, "Sadly, however, a close study of his book and of the related literature has shown me that what was true in his book was not original, and most of what was original was known not to be true even when the book was written . . . the apparent contradictions between life and the statistical laws of physics can be resolved by invoking a science largely ignored by Schrödinger. That science is chemistry."

Schrödinger was the subject of an earlier *Perspectives* (Crow 1992). In addition to noting the remarkable span of Schrödinger's intellect, it discussed Schrödinger's solution to a tricky genetic problem posed by Haldane (1945a), with reference to the breeding of hornless cattle.

There is general agreement among most biologists today that Schrödinger, like O. T. Avery, belonged to that small circle of scientists whose primary research was not in genetics, but who nevertheless had a decided impact in initiating the development of molecular genetics. There are, however, profound differences between Avery and Schrödinger. Avery conducted biochemical experiments, showing that DNA is the genetic material. Schrödinger was a theoretical physicist who happened to write an influential book on biology.

Early life and education: Erwin Schrödinger was born on August 12, 1887 in Vienna. His close relationship with his father, Rudolf, played a most important role in his childhood and teenage years. Rudolf was in the oilcloth business, but his major hobby was botany, especially plant breeding and evolution. There were frequent scientific discussions between father and son. One book of great interest was Darwin's *The Origin of Species*, which remained Schrödinger's favorite book all of his life. His mother, who came from England, and her sister taught him the English language at an early age. This may have influenced his decision in later years to go to Oxford and Dublin. It was while in Dublin that Schrödinger wrote *What Is Life?*, which profoundly influenced so many biologists. As the only child of a well-to-do family, Schrödinger received the best education available. His scholastic performance at the Wiener Akademisches Gymnasium and the University of Vienna was above average in all subjects, but he showed a special aptitude for mathematics. His mathematics professors, Wirtinger and Kohn, the experimental physicist Franz Exner, and especially the theoretical physicist Fritz Hasenohrl all deeply influenced young Schrödinger's intellectual development. Hasenohrl, who succeeded Ludwig Boltzmann, had such an impact that Schrödinger regarded him as having had as great an influence on his intellect as his own father. Throughout his life, Schrödinger maintained an intense interest in the interrelationship between physics and philosophy. While Schrödinger was serving in the First World War in Italy, he learned of the theory of relativity that was being developed by Einstein. The post-war years brought hard times for the Schrödinger family. However, a subsequent offer of an assistant professorship at Jena (under Max Wien) in 1920 and his marriage to Annemarie Bertel turned life around for Erwin Schrödinger,

Address for correspondence: Foundation for Genetic Research, P.O. Box 27701-0, Houston, TX 77227. E-mail: kdronamraj@aol.com

Erwin Schrödinger in Dublin in 1952. Courtesy of Ann Goldsmith, Librarian, School of Theoretical Physics, Dublin Institute for Advanced Studies.

launching his life and career on a long, distinguished path (Moore 1989).

In the following years, Schrödinger held brief teaching posts at Stuttgart and Breslau, but he found his niche at Zurich when he was offered the chair held by Einstein during the years 1909–1911. His inaugural lecture was titled "What Is a Law of Nature?". However, his most important work, the theory of wave mechanics, was formulated later in 1925 and was at once acclaimed by the scientific community. He was offered the chair at Berlin as a successor to Max Planck and was invited on a lecture tour of the United States during the winter of 1926–1927. In Berlin, he found several distinguished colleagues to his liking, including Einstein, Planck, Hertz, and Otto Hahn. In 1933, Schrödinger was granted leave to go to Oxford University as a guest professor and he resigned his position at Berlin while at Oxford.

Schrödinger was invited to Oxford by F. A. Lindemann, who, at the time, was a Fellow at Magdalen College (October 1933–September 1936). It was while at Oxford that Schrödinger was awarded the Nobel Prize, which he received on December 10, 1933. During 1934–1935, he visited Princeton and later Spain, lecturing in English and Spanish respectively. In 1936, he accepted a professorship at Graz, but in 1938 he moved once again (because of the worsening political situation in Austria), first going to Rome, and finally to Dublin to head the School of Theoretical Physics, which was part of the newly established Dublin Institute for Advanced Studies. He described the 16 years that he spent in Ireland as very good years. He enjoyed full freedom to pursue his research and teaching activities, producing a prolific output of books and papers on a number of important topics, including a unified field theory. It was also during that period that Schrödinger wrote *Statistical Thermodynamics*, *What Is Life?*, and *Nature and the Greeks*. He found time to indulge in various literary and artistic activities, for instance, poetry writing and translating Homer from ancient Greek into English and old Provençal poetry into German.

Schrödinger's final move in his long career came in 1956, when he accepted a professorship in Vienna. For his inaugural lecture he chose the topic, "The Crisis of the Nuclear Concept." He taught for two and a half years, but illness forced him to retire from his chair at the end of September 1958. During his last years, he wrote his autobiographical account, *My Life*, and *My View of the World*. He died on January 4, 1961, after a brief period of ill health.

What Is Life? The Physical Aspect of the Living Cell: The chapters of this book are listed as follows:

1. The classical physicist's approach to the subject
2. The hereditary mechanism
3. Mutations
4. The quantum-mechanical evidence
5. Delbruck's model discussed and tested
6. Order, disorder and entropy
7. Is life based on the laws of physics?

At the outset, Schrödinger posed the question: "How can the events *in space and time* which take place within the spatial boundary of a living organism be accounted for by physics and chemistry?" Schrödinger continued, "The preliminary answer which this little book will endeavor to expound and establish can be summarized as follows: The obvious inability of present-day physics and chemistry to account for such events is no reason at all for doubting that they can be accounted for by those sciences."

In *What Is Life?*, Schrödinger focused attention on two topics in biology: (a) the nature of the hereditary material and (b) the thermodynamics of living systems. In a review of the state of knowledge of genetics at that time, Schrödinger considered a number of topics related to genetic phenomena. These are briefly listed below.

The hereditary code-script (chromosomes): Schrödinger used the term "pattern" to include not only the structure and function of the organism but also its ontogenetic development from the fertilized egg to the adult. He then considered the role of the nucleus, especially the role of chromosomes in heredity. He wrote, “It is these chromosomes, or probably only an axial skeleton fibre of what we actually see under the microscope as the chromosome, that contain in some kind of code-script the entire pattern of the individual’s future development and of its functioning in the mature state. Every complete set of chromosomes contains the full code; so there are, as a rule, two copies of the latter in the fertilized egg cell, which forms the earliest stage of the future individual.” Schrödinger suggested that one can predict the precise phenotype from the code-script. But he acknowledged that the term code-script is too narrow. He described chromosome structures as “law-code and executive power” or they are “architect’s plan and builder’s craft” in one.

After considering mitosis, meiosis, and crossing over, Schrödinger dealt with the subject of the maximum size and permanence of a gene. He considered the gene to be a large protein molecule in which every atom, every radical, every heterocyclic ring plays an individual role. Schrödinger’s discussion was largely based on the work of Timofeef-Ressovsky and Delbruck, although he took into account the ideas of some eminent geneticists of that period, especially Haldane, Muller, and Darlington. As a theoretical physicist, he had to depend on the findings of others.

Delbruck’s model: Much of Schrödinger’s discussion in *What Is Life?* was based on an article by Timofeef-Ressovsky *et al.* (1935) on the mutation rate induced by X rays in *Drosophila melanogaster*. A third section of that article was by Delbruck (a model of genetic mutation based on atomic physics). Perutz (1987) summarized Delbruck’s results.

After briefly reviewing the gene concept, Delbruck dealt with the nature of mutations and the stability of the gene. Since no direct methods for studying the chemical nature of the gene were then available, the problem was attacked indirectly by studying the nature and limits of gene stability and by asking whether the known facts about genes are consistent with the known facts of the atomic theory, especially with reference to the behavior of well-defined assemblies of atoms. Delbruck considered both vibrational and electronic transitions. He derived the relationship between the rate of such transition (W) and its activation energy (U). Delbruck stated that chemical bond energies are of the order of several electron volts, but argued that the activation energies of molecules cover an even wider range than his estimates indicate, so that reaction rates of any magnitude can result from a given set of circumstances. He concluded that evolution had stabilized the molecular structure of genes to the extent that their natural frequency of rearrangement is smaller by several orders of magnitude than the frequency of their reproduction. A single ionization, because of its much greater energy, should be sufficient to produce any given mutation, regardless of its natural frequency. On the basis of Delbruck’s speculations with respect to the atomic structure of a gene, Schrödinger pointed out that “there is a fair chance of producing a mutation when an ionization occurs not more than about 10 atoms away from a particular spot on the chromosome.” However, Perutz (1987) summarized evidence indicating that Schrödinger’s estimate was incorrect. An article published while Schrödinger’s book was in press showed that the biological effects of ionizing radiation are due primarily to the generation of hydroxyl radicals and hydrogen atoms in the surrounding water (Weiss 1944). Other evidence since then has shown that the hydroxyl radicals and hydrated electrons can diffuse to their targets even if they are generated more than a thousand atomic diameters away (see Perutz 1987).

Delbruck concluded that mutations are quantum transitions resulting from either random thermal fluctuations or the absorption of radiant energy, spontaneous mutations arising predominantly from thermal fluctuations rather than from natural radiation. Schrödinger, although relying heavily on Delbruck’s work, failed to mention the discoveries of H. J. Muller on radiation-induced mutagenesis or the important role of *complementariness* in the specific attraction between molecules and their enzymatic synthesis, which was already suggested by Haldane (1937) and Pauling and Delbruck (1940).

Negative entropy: Perutz (1987) pointed out that what was true in Schrödinger’s account was already known. Indeed, he was paraphrasing the works of others, especially the article by Timofeef-Ressovsky *et al.* (1935) on the mutagenic effects of X rays and γ-rays on the fruit fly *Drosophila melanogaster*. Even Schrödinger’s most famous hypothesis, that the gene is like an aperiodic one-dimensional crystal, is a reformulation of Delbruck’s suggestion that “the gene is a polymer that arises by the repetition of identical atomic structures.” In a chapter entitled “Order, disorder and entropy,” Schrödinger stated that living organisms do not approach thermodynamic equilibrium (defined as a state of “maximum entropy”), which they achieve by feeding on negative entropy. Schrödinger wrote, “How does the living organism avoid decay? The obvious answer is: By eating, drinking, breathing and (in the case of plants) assimilating. The technical term is *metabolism* . . . a living organism continually increases its entropy—or, as you may say, produces positive entropy—and thus tends to approach the dangerous state of maximum entropy, which is death. It can only keep aloof from it, *i.e.*, alive, by continually drawing from its environment negative entropy—which is something very positive. . . . What an organism feeds upon is negative entropy. Or, to put it less paradoxically, the essential thing in metabolism is that the organism succeeds in freeing itself from all the entropy it cannot help producing while alive.” Schrödinger further stated that entropy is not a hazy concept, but a measurable physical quantity: “At the absolute zero point of temperature (roughly −273°C) the entropy of any substance is zero.”

Perutz and others have argued that we live on free energy and that there was no necessity to postulate negative entropy. Pauling (1987) commented that when Schrödinger was discussing a change in the entropy of the system, he never defined the system. Pauling wrote, “Sometimes he seems to consider that the system is a living organism with no interaction whatever with the environment; sometimes it is a living organism in thermal equilibrium with the environment; and sometimes it is the living organism plus the environment, that is, the universe as a whole.” Pauling wrote that Schrödinger failed to recognize the most important question: “How biological specificity is achieved; that is, how the amino-acid residues are ordered into the well-defined sequence characteristic of the specific organism.”

Lederberg (personal communication, 1999) suggested that Schrödinger’s intended meaning may have been “elements of crystallinity” or “near-crystal” rather than “aperiodic crystal.” With hindsight one can say: “DNA has elements of periodicity (the backbone), and of aperiodicity (the message in the base sequence).” This is Lederberg’s surmise based on what Schrödinger may have meant at that time.

Code and entropy: In Schrödinger’s time, the genetic material was generally considered to be a protein, rather than a nucleic acid. It was already known that a protein, especially a particular protein, human hemoglobin, has a well-defined sequence of amino-acid residues in its polypeptide chains. Pauling (1987) traced Schrödinger’s argument as follows: “Schrödinger seems to have asked himself the question: ‘what is the process that leads to the production of these well-defined polypeptide chains, with their low entropy?’ He seems to have answered the question, in a rather vague way, by saying that the organism ‘feeds upon negative entropy’, attracting, as it were, a stream of negative entropy upon itself. The real question about the nature of life, which Schrödinger failed to recognize, is the question as to how biological specificity is achieved; that is, how the amino-acid residues are ordered into the well-defined sequence characteristic of the specific organism.”

However, Pauling concluded that the development of molecular biology has resulted almost entirely from the introduction of the new ideas into chemistry that were stimulated by quantum mechanics. He wrote, “It is accordingly justified . . . to say that Schrödinger, by formulating his wave equation, is basically responsible for modern biology.”

Is life based on the laws of physics? The final chapter in *What Is Life?* is entitled “Is life based on the laws of physics?”. It is assumed that the gene is a molecule, but the bond energies in molecules are of the same order as the energy between atoms in solids, for example, in crystals, where the same pattern is repeated periodically in three dimensions, and a continuity of chemical bonds extending over large distances exists. Following this argument, Schrödinger suggested that the gene is a linear one-dimensional crystal, which lacks the periodic repeat, *i.e.*, an aperiodic crystal. Under the influence of the theoretical physicist Ludwig Boltzmann (1886), Schrödinger concluded, “We are faced with a mechanism entirely different from the probabilistic one of physics, one that cannot be reduced to the ordinary laws of physics. . . . Living matter, while not eluding the laws of physics . . . is likely to involve other laws of physics hitherto unknown. . . .” Unfortunately, Schrödinger was advised by the cytogeneticist C. D. Darlington of Oxford that genes are likely to be proteins, a belief that was prevalent among biologists at that time. However, Schrödinger stopped short of mentioning that proteins are long-chain polymers (with 20 different links with aperiodic patterns). Quite understandably, Schrödinger was not aware of the important discovery of Avery *et al.* (1944) that genes are made of DNA, a finding that had just been published while his book was in press. The lectures were delivered in February 1943, and the book was published in 1944. It was successful beyond the author’s expectations. It was translated into seven languages, and the total sales exceeded well over 100,000.

Epilogue: The epilogue was entitled “On determination and free will.” Schrödinger wrote, “As a reward for the serious trouble I have taken to expound the purely scientific aspects of our problem . . . , I beg leave to add my own, necessarily subjective, view of the philosophical implications.”

Schrödinger wrote that, contrary to the opinion held by some physicists, *quantum indeterminacy* plays no biologically relevant role in the space-time events in the body of a living being, except perhaps by enhancing the purely accidental nature in mutation, meiosis, and so on. The two major premises considered by Schrödinger are (a) the body functions as a pure mechanism according to the laws of nature; and (b) we also know that we are directing its motions, knowing fully the consequences of our actions and taking responsibility for them. From these premises, Schrödinger concluded that I (in the widest sense) am the person, if any, who controls the “motion of the atoms” according to the laws of nature.

It was this particular aspect of *What Is Life?* that shocked several distinguished scientists. Schrödinger goes on to say: “In Christian terminology to say: ‘Hence I am God Almighty’ sounds both blasphemous and lunatic. But please disregard these connotations for the moment and consider whether the above inference is not the closest a biologist can get to proving God and immortality at one stroke.” He stated that a similar belief was recorded more than 2500 years ago in the early great Upanishads in ancient India, where the concept that *Athman* equals *Brahman* equals omnipresent, all-comprehending eternal self was taken for granted. To the Hindus (the ancient scholars of Vedanta), it represents the quintessence of deepest insight into the happenings of the world, as Schrödinger put it. From these beginnings, Schrödinger then extrapolated the concept of "I have become God" to all saints and mystics throughout centuries.

To Schrödinger, the idea of plurality of consciousness (so clearly opposed in the Upanishads), which is widely accepted by the Western philosophers, is not meaningful. He wrote, "It leads almost immediately to the invention of souls, as many as there are bodies, and to the question whether they are mortal. . . . Much sillier questions have been asked: Do animals also have souls? It has even been questioned whether women, or only men, have souls." He preferred to consider the so-called plurality as being a series of different aspects of *one* consciousness. In a subsequent note to the epilogue, Schrödinger found some comfort in similar views expressed in a book by Aldous Huxley (1946) called *The Perennial Philosophy*, which was published shortly afterward.

Hybrid paradigm: With the application of quantum theory to biological phenomena, Schrödinger (1944) attempted to elucidate gene structure and function in terms of a hybrid paradigm. It is often at the intersection of two or more disciplines that innovative scientific progress takes place. Heisenberg (1962), writing in *Physics and Philosophy*, had earlier stated that "in the history of human thinking the most fruitful developments frequently take place at those points where two different lines of thought meet" (p. 175). Novel branches of science arise by a synthesis of different viewpoints, concepts, and methods from several disciplines, because it leads to "hybrid vigor" on the intellectual plane. For instance, X-ray diffraction techniques have contributed to the elucidation of DNA structure (Watson and Crick 1953). However, in the present case, the physicist Schrödinger indicated a new way of looking at biology, thus invigorating and stimulating the thinking of a new generation of biologists. The rise of molecular biology, the human genome project, and various environmental health sciences are the direct result of a successful synthesis among multiple scientific disciplines. This process has been called "intellectual hybridization" (Dronamraju 1989). It was not so much a discontinuous "revolution" in the Kuhnian sense (Kuhn 1962), but a gradual synthesis (or "evolution") of ideas, concepts, and methods from several disciplines.

The place of *What Is Life?* in biology: Schrödinger's book received mixed reviews. Haldane (1945b) reviewed it favorably: "I wonder if posterity will find crossing-over as interesting as exchange energy, or mutation as atomic transition. However this may be, every geneticist will be interested in Schrödinger's approach to his or her science." Muller's (1946) review was highly critical of the epilogue. He predicted that this little volume should prove valuable in furthering the much needed liaison between the fundamentals of the physical and the biological sciences. With a great deal of foresight, Muller wrote that an elucidation of the structure and function of the gene will "entail not only physics but also a good deal of chemistry." Muller pointed out that Schrödinger's limited knowledge of genetics (evidently learned quickly from reading a few publications) led him to make certain incorrect statements, *e.g.*, in explaining why mutation occurs in only one allele at a time, and the estimation of the size and minimum number of genes and so on. However, Muller also stated that Schrödinger's book should render a valuable service in focusing attention on some important problems in biology. Muller's review was further helpful in explaining Schrödinger's terminology in terms that are more familiar to biologists. For instance, "negative entropy" is "potential energy," "aperiodicity" is "complexity," etc.

However, Muller's most critical comment was with reference to the Epilogue. Muller wrote, "It is . . . legitimate to hold the author to account very rigorously when he sails off, in his epilogue . . . to use his foregoing conceptions as the means of projecting his boat on the sea of straight old-fashioned mysticism. . . . If the collaboration of the physicist in the attack on biological questions finally leads to his concluding that 'I am God Almighty', and that the ancient Hindus were on the right track after all, his help should become suspect. It is hoped, however, that the unfortunate revelation of this physicist's inner urge will not keep the relatively sound expositions in the body of the present book from being taken seriously, and that an increasingly useful rapprochement between physics, chemistry and the genetic basis of biology is at last on the way."

In his introduction to the volume dedicated to Max Delbruck on his sixtieth birthday, Stent (1966) evaluated Schrödinger's contribution to biology. He stated that it probably had little influence on professional biologists. But it had a great impact on physical scientists, who were only too happy to focus their intellect on a new and refreshing problem in the post-war years. Stent pointed out that there were significant gaps in Schrödinger's genetic knowledge. He made no attempt to include chemistry in his discussion. Schrödinger's knowledge was derived from a few published papers and earlier conversations with Delbruck. He conducted no experiments in genetics. His grasp of genetics was outdated. In *What Is Life?,* Schrödinger made no mention of the latest advance in genetics, namely the "one gene–one enzyme" hypothesis that was supported by the discoveries of Beadle and Tatum (1941), which ultimately contributed to molecular biology. He emphasized research on Drosophila even though by the 1940s genetics was taken over by those working with microorganisms, *e.g.*, Neurospora. Even though it was Delbruck's model that inspired Schrödinger's interest in genetics, ironically Schrödinger did not seem to know that Delbruck had been working with bacterial viruses for the past five years—leading to the phage school in genetics, which later provided the answers to many of the questions that Schrödinger raised in *What Is Life?*. The significant date was 1940, when Alfred D. Hershey, Salvador E. Luria, and Max Delbruck founded the phage group at Cold Spring Harbor—long before Schrödinger was preparing his lectures in Dublin that eventually became *What Is Life?*.

Among other biologists who were influenced by *What Is Life?* were James Watson (1968) and Francis Crick (1988). Watson (1968) wrote, "This book very elegantly propounded the belief that genes were the key components of living cells and that, to understand what life is, we must know how genes act" (p. 13). Crick (1988) wrote that Schrödinger made it seem as if great things were just around the corner.

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