

The Ogre of the Story

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Chicago Literary Club

[April 23, 2018]

“She spoke to an audience of about fifteen in a quick, nervous style that suited the unornamented old lecture hall . . . There was not a trace of warmth or frivolity in her words. And yet I could not regard her as totally uninteresting. Momentarily I wondered how she would look if she took off her glasses and did something novel with her hair. Then, however, my main concern was her description of the crystalline X-ray diffraction pattern.”¹ This is James Watson’s description in *The Double Helix* of Rosalind Franklin at the King’s College, London, colloquium in November 1951, in which she presented her first X-ray results on the structure of the nucleic acid DNA molecule. *The Double Helix* is an idiosyncratic memoir published in 1968, fifteen years after the publication of the structure of DNA by Watson and Francis Crick in 1953. My impression on a reading when the book first came out, was that the thrill of a major scientific discovery was well portrayed. The book was on the New York Times bestseller list for

many weeks, has sold over a million copies, and has gone through subsequent critical and annotated editions.² The memoir was initially viewed by some as revelatory in revealing the inner workings of a major scientific discovery. In Watson's memoir, Rosalind Franklin is alone singled out for criticism of her scientific abilities as well as her personal behavior. Yet It was largely Franklin's experimental X-ray data, that was the key to the discovery of the molecular structure of DNA, often regarded as the most significant biological discovery of the 20th century. Nonetheless, Franklin's crucial research contributions did not prevent Watson from presenting her as the "Ogre of the Story." ³

Rosalind Franklin joined the King's College biophysics laboratory, directed by J. T. Randall, in January 1951. She had completed a Ph.D. in physical chemistry at Cambridge University in 1945, worked for several years at the British Coal Utilization Research Association, followed by three years at the Central Laboratory of Chemical Services in Paris from 1947-49. During these years she did fundamental research as a crystallographer on the X-ray diffraction analysis of carbon and coals, publishing 17 research papers, including three in the prestigious journal, *Nature*, and one in the *Proceedings of the Royal Society*. Franklin then received a three-year research fellowship at J. T. Randall's King's College lab to work on the

X-ray diffraction of proteins, but when she arrived in January 1951, Randall changed this to DNA research. He told Franklin that it would be her exclusive research topic and re-assigned Maurice Wilkins' graduate student, Ray Gosling, to work under Rosalind. Randall, however, failed to inform Wilkins of this and the change transpired while the latter was vacationing. Wilkins had been doing X-ray diffraction research on DNA for several years and he had assumed that Franklin was to work jointly with him. A problematical situation was thus created, severely heightened by the fact that Franklin and Wilkins were never to get along personally, eventually barely speaking to each other. Indeed, according to Anne Sayre, Rosalind's close friend, long-time correspondent, and first biographer, "it is very possible that the history of molecular biology might be rather different from what it is today if Rosalind and Maurice Wilkins had not hated one another at sight." ⁴ Gosling and Franklin, however, worked well together and this was her main, if not only collegial association for the three years she was at King's.

At the November 1951 King's College colloquium on nucleic acids, Rosalind Franklin presented a number of fundamental results arrived at after less than a year: DNA occurred in two different forms in terms of X-ray diffraction patterns, the "B" form is probably helical, the sugar-phosphate

backbone of the molecule must lie on the outside with the bases on the inside, and she identified the crystal class (monoclinic) of the molecule. All of these proved to be part of the final DNA molecular structure. James Watson was in the audience as noted at the outset of this essay. Watson was from the University of Chicago, graduating in 1947 at 19 as was common in the Hutchins' era, had a Ph.D. from Indiana University with a dissertation in genetics in 1950, and was now on a three-year fellowship at the Cavendish lab in Cambridge University, probably the world's leading laboratory of crystallographic research. He had decided on DNA research after hearing Maurice Wilkins' lecture at a conference in Naples earlier that year. And now Watson was involved in intensive daily discussions on molecular research with office mate, Francis Crick, a physicist now turned to biology and working on the molecular structure of the protein hemoglobin.

Crick, a colleague and friend of Wilkins in the British Admiralty during the war, was still working on his Ph.D. at 35 but nevertheless was recognized by many as a genius. For example, he was completely self-taught in crystallography but his depth of knowledge in this field rivaled that of the senior scientists at Cavendish, including the laboratory's head, Sir Lawrence Bragg, the pioneering developer of the field. It is a significant

point that Crick was not at Franklin's presentation, leaving only Watson from the Cavendish. Watson's perennial modus at all lectures he attended was not to take any notes, and because he had only started reading in crystallography recently, much of the lecture was over his head. When he accompanied Crick on a train to Oxford the following day he could not answer most of Crick's probing questions, reporting significant quantities in error by an order of magnitude (especially the amount of water in the molecule) and failing to mention Franklin's identification of the crystal class to which DNA belongs. It is possible that had this omission not occurred, the Watson-Crick model published in 1953 might have been obtained much earlier.⁵

Despite the errors and omissions Watson reported to Crick, a week later they had built a model of the DNA molecule in three chains (instead of two) with the sugar-phosphate backbone incorrectly on the inside, the bases incorrectly on the outside, and with a vastly inadequate amount of water. A group from King's including Wilkins, Franklin, Ray Gosling, and Willy Seeds were invited to view the model. After a brief talk by Crick, Franklin quickly pointed out the fundamental errors according to her experimental X-ray data and declared the model worthless.⁶ "Rosalind was polite enough as she spoke – according to Seeds (although Watson described her as

‘positively aggressive’).”⁷ Bragg, the head of the Cavendish lab, and Randall, head of the King’s lab, agreed investigating the structure of DNA would be left to King’s and Bragg further ordered Watson and Crick to stop further research on the subject.⁸

The most prominent person working on the DNA structure was Linus Pauling of Cal Tech, probably the outstanding chemist in the world at that time and the author of the most important book in the field of structural chemistry, *The Nature of the Chemical Bond*. Pauling was an expert exponent in the use of model building to unravel molecular structure. Using this method in the late 40s – early 50s he determined the structure of the alpha helix, the most important regular structure found in proteins.⁹ When Pauling turned his attention to DNA there were not good X-ray diffraction photographs at Cal Tech, and he was refused copies of Wilkins’ photographs by Randall, as Pauling was misinformed that no one at King’s was working on DNA. Furthermore, he was refused a passport by the U.S. State Department (because of his outspoken anti-nuclear pacifism) to visit a London conference at which he might have had the opportunity to see good photographs. Nonetheless, together with a colleague, Robert Corey, who had seen some of Franklin’s photographs, he proposed a three-chain model for DNA not unlike that of the Watson-Crick initial attempt with the

sugar-phosphate backbone in the wrong place. On January 28, 1953, the soon-to-be-published manuscript was shown to Watson and Crick, who though not then model building were obviously still thinking about DNA. Watson immediately spotted a fundamental blunder: the phosphates were not ionized contradictory to the fact that DNA is an acid.¹⁰

Two days later (January 30) Watson went to King's with the Pauling MS in hand to show Wilkins, who was not immediately available. What ensued was an epic confrontation between Watson and Franklin, as told in *The Double Helix*. Barging in on her lab without knocking, Watson offered to show her the Pauling MS, which she declined. After an increasingly heated argument, Watson described the following account: "I was more aware of her data than she realized. Several months earlier Maurice had told me the nature of her so-called antihelical results. Since Francis had assured me that they were a red herring, I decided to risk a full explosion. Without further hesitation, I implied that she was incompetent in interpreting X-ray pictures. If only she would learn some theory, she would understand how her supposed antihelical features arose from the minor distortions needed to pack regular helices into a crystalline lattice. Suddenly Rosy came from behind the lab bench that separated us and began moving toward me. Fearing that in her hot anger she might strike me, I grabbed the Pauling

manuscript and hastily retreated to the open door.”¹¹ [“Rosy” was a nickname used behind her back, by Willy Seeds (who had nicknames for most everyone in the lab) and by Wilkins; Watson uses it throughout *The Double Helix*, which reads as exceptionally disrespectful.]

In May of the previous year, Franklin and her Ph. D. student Ray Gosling took an outstanding and the best photograph yet of the B form of DNA, famously termed Photograph 51. [In X-ray diffraction single crystal photography, a thin fiber of DNA is mounted on a goniometer in the center of a metal cylinder and an X-ray beam is directed through the fiber. The atoms in the cell lattice diffract the X-ray beam as reflections onto the film positioned on the cylinder’s inside. The reflections identify the kind of atom and its spacing in the lattice. In the technology of that time the photographic exposure could require many hours].

By January of 1953, Franklin was thoroughly fed up with the working conditions at the King’s College lab. She applied successfully to transfer her fellowship to J. D. Bernal’s biomolecular research lab at Birkbeck College and was scheduled to move there in March. Randall, the director at King’s, agreed Franklin should leave and that she should stop all further DNA research. Nevertheless, she and Gosling did not stop writing up their research that eventually was published in three papers that year. Since she

was leaving, Franklin had Gosling turn over Photograph 51 to Wilkins as a parting gift. Wilkins was surprised and asked for reassurance that Franklin was actually giving him permission to use the photograph in whatever way he chose.¹²

Thus, the stage was set for the key event that led to Watson and Crick's discovery of the structure of the DNA molecule. After Watson retreated from Franklin's lab, he joined Wilkins in his office, who then proceeded to show him Photograph 51 of the B form. Wilkins is on record as saying he did this naively as he assumed that Watson and Crick were no longer working on DNA. Watson wrote in *The Double Helix*: "The instant I saw the picture my mouth fell open and my pulse began to race. The pattern was unbelievably simpler than those obtained previously [of the A form].

Moreover, the black cross of reflections which dominated the picture could arise only from a helical structure." ¹³ Watson also obtained data from Wilkins on key measurements derived from the photograph. *It is important to emphasize that Rosalind Franklin was never told by either Watson or Crick in subsequent years that Watson had been shown Photograph 51, even though Crick and Franklin eventually became good friends and she thought of him as a genius.*

Watson and Crick were apparently the only ones that thought they were in a race, especially with Linus Pauling, to solve the DNA structure. And those at King's College did not know they were in a race. With Sir Lawrence Bragg's permission, Watson and Crick resumed model building with not only the insight gained from Photograph 51, but other information from Franklin's experimental research. This was contained in an unpublished report that summarized much of the information presented by Franklin at the November 1951 colloquium that Watson but not Crick had attended. Among other results this gave the identification of the crystal class to which DNA belonged, a key fact that Watson had failed to tell Crick after the colloquium. The unpublished report thus told Crick with his much deeper understanding of crystallography that the two chains of the helix had to run in opposite directions. Crick insisted that the reluctant Watson put the sugar-phosphate backbone on the outside, and the bases inside, because that had been one of Franklin's main criticisms of their first model. Furthermore, Crick had a reasonable conversation with Franklin at about this time, in which she showed him convincing evidence that the backbone must be on the outside. This left the main unresolved problem the configuration of the four bases (adenine, thymine, guanine, and cytosine, abbreviated as a, t, g and c). [Note that the precise sequence of the bases

eventually proved to be the code which carries the genetical information¹⁴].

In the early going on the new model, Watson and Crick tried to pair like-with-like (i.e., adenine with adenine, etc.). Jerry Donohue, who had done his Ph.D. under Pauling at Cal Tech was on a postdoctoral at the Cavendish lab and shared the office with Watson and Crick. When Donohue was shown the model, he told them two things: one; they should not pair like-with-like, in contrast it should be a with t, and g with c, and two; they were using incorrect chemical forms of the four bases derived from out-of-date textbook information. These were crucial insights that solved the configuration of the bases, opening the way to the final successful model, for which Donohue was inadequately acknowledged in Watson and Crick's groundbreaking paper published in Nature in April 1953. "Donohue later was one of many who felt that his part in the great discovery was underplayed. 'Let's face it,' he wrote in 1976, 'if the fates hadn't ordained that I share an office with Watson and Crick in the Cavendish in 1952-53, they'd *still* be puttering around trying to pair 'like-with-like' [chemically incorrect] forms of the bases' ". ¹⁵

The Watson-Crick model was completed on March 7, 1953,¹⁶ and Crick sent several drafts of their manuscript to Wilkins. He was offered co-authorship but declined and convinced Crick to delete an early draft

reference to the “beautiful” Photograph 51. No reference to this crucial item of data survived in the final publication by Watson and Crick on April 25 in *Nature*. Wilkins, and later Franklin and Gosling were invited to Cambridge to view the model. Rosalind offered no criticism this time, as she realized that her experimental X-ray data were not incompatible with this newer version of the model.

It was agreed by all participants that three papers would be submitted to be published in the same issue of *Nature*: Watson and Crick’s, a paper by Wilkins and two co-authors, and a paper by Franklin and Gosling presenting the results of their X-ray research, including an illustration of Photograph 51. Franklin and Gosling had completed a draft of their MS on March 17, prior to learning that the DNA structure had been solved at Cambridge. They had only to modify their manuscript by adding one sentence: “Thus our general ideas are not inconsistent with the model proposed by Watson and Crick in the preceding communication.”¹⁷

In the *Nature* paper Watson and Crick wrote this famous sentence: “It has not escaped our notice that the specific pairing [of the bases] we have postulated immediately suggests a possible copying mechanism for the genetic material.”¹⁸ Their solution of the molecular structure of DNA is regarded as the most significant biological discovery of the 20th century, for

it created an entirely new field of science, molecular biology, with its many consequent discoveries such as the genome project.

From the perspective of the history of science, however, there is something glaringly absent from the Watson-Crick first Nature paper [and the second one as well]. Namely, adequate acknowledgment of the experimental data developed at King's College, none of which had been obtained at Cambridge. Their paragraph stating acknowledgments reads as follows: "We are much indebted to Dr. Jerry Donohue for constant advice and criticism, especially on interatomic distances. We have also been stimulated by a knowledge of the general nature of the unpublished experimental results and ideas of Dr. M. H. F. Wilkins, Dr. R. E. Franklin and their co-workers at King's College, London." ¹⁹ Leaving aside the question of the adequacy of the acknowledgment for Donohue, there is no reference to how crucially important were Rosalind Franklin's contributions to the DNA structure. In the text, Watson and Crick state: "We were not aware of the details of the results presented there [i.e., the papers by Wilkins et al. and by Franklin and Gosling in the same Nature issue] when we devised our structure . . ." ²⁰ "This sentence marks what many consider to be an inexcusable failure to give proper credit to Rosalind Franklin . . . Watson and Crick are saying here that they 'were not aware of' Franklin's unpublished data, yet Watson later admits

in his book *The Double Helix* [in 1968] that these data were critical in solving the problem.”²¹ There is no citation of the importance of Franklin and Gosling’s Photograph 51. Their second Nature paper published in 1953 also does not contain adequate acknowledgment of Franklin’s research. In contrast, however, it is true that Crick and Watson in their detailed 1954 paper in the Proceedings of the Royal Society, have the following statement in a footnote:²² “The information reported in this section was very kindly reported to us prior to its publication by Drs Wilkins and Franklin. We are most heavily indebted in this respect to the King’s College Group, and we wish to point out that without this [sic] data the formulation of our structure would have been most unlikely, if not impossible.” In the formal acknowledgments section of the 1954 paper, however, there is mention of Wilkins and Donohue, but not of Franklin or of the specific nature of her contributions used in the model. Echoing the Royal Society footnote, here is an evaluation by Jerry Donohue in 1976: “on leaving King’s College, Rosalind Franklin was forbidden to work on DNA [by Randall, the director of the King’s lab] and was even forbidden to have any contact whatever with Gosling, the graduate student with whom she had so amicably worked at King’s, the two of them having discovered how to obtain from DNA the diffraction data without which Watson and Crick would have *discovered*

nothing." ²³ [Franklin and Gosling ignored Randall's directives as they were completing three papers for publication after Rosalind left King's, and Gosling completed his thesis with Franklin continuing to advise him, although now unofficially].

According to both biographies, Anne Sayre's *Rosalind Franklin and DNA* and Brenda Maddox's *Rosalind Franklin: The Dark Lady of DNA*, ²⁴ *The Double Helix* is characterized by inaccurate statements about her research results, many of which Watson misunderstood secondhand from Wilkins, plus gratuitous sexist remarks about her appearance and behavior. Maddox suggests that making Franklin the villain of the memoir may have been a rationalization on Watson's part to cover up his guilt.²⁵ Francis Crick is quoted by Sayre as regarding *The Double Helix* as a "contemptible pack of damned nonsense" ²⁶ and both Crick and Wilkins tried to persuade Watson not to publish. In fact, a strong letter from Crick condemning the memoir reversed Harvard University Press' decision to publish, resulting in Watson going to a trade publisher, Atheneum.

Rosalind Franklin moved to Birkbeck College in March 1953 and began fundamental research on the molecular structure of viruses, especially the

tobacco mosaic virus although she worked on others. The tobacco mosaic virus “is the classical virus, the first to be recognized, the first to be purified, the first to be studied by x-ray diffraction.”²⁷ Between 1955 and 1958 she published 14 papers, four in the prestigious journal, *Nature*. Five were under her sole authorship and six were co-authored with her main Birkbeck collaborator, Aaron Klug.²⁸ Klug was a theoretician but “in no way saw Rosalind as a mere experimentalist, an unequal partner.” He had this to say about Franklin: “It takes imagination and intellect to know precisely what experiments to do, to design them, prepare the specimens and then to observe the results. . . She worked beautifully. Her single-mindedness made her a first-class experimentalist, with the sort of skill that blends intelligence and determination.”²⁹

Rosalind Franklin was diagnosed with ovarian cancer in the fall of 1956 but worked intermittently on her research until near the end, which occurred in April 1958 at the age of 37. Aaron Klug³⁰ was willed all her notebooks and papers, and his analysis of these showed that Franklin was extremely close to the solution of the DNA structure in early March 1953, before Watson and Crick had communicated their solution to the researchers at King’s College.

Klug noted that he and Crick agreed that Franklin would have solved the DNA structure had the Watson-Crick solution not appeared.³¹

Watson, Crick, and Wilkins were awarded the Nobel Prize in physiology or medicine in 1962. Franklin was never nominated. In their Nobel addresses neither Watson nor Crick mentioned Franklin's name or contributions. Wilkins cited her name along with another King's researcher as having "made very valuable contributions to the X-ray analysis."³² However, when Aaron Klug won the Nobel Prize for Chemistry in 1982, "he spoke movingly of his late colleague. Rosalind Franklin, he said, had introduced him to the study of viruses and set an example of tackling large and difficult problems."

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I want to repeat the acknowledgment of Franklin's research in the Nature paper of April 1953 that first presented the discovery of the correct molecular structure of DNA. "We have also been stimulated by a knowledge of the general nature of the unpublished experimental results and ideas of Dr. M. H. F. Wilkins, Dr. R. E. Franklin and their co-workers at King's College, London."³⁴ Aside from the lesser point that they, here and subsequently, always listed Wilkins ahead of Franklin, this "oblique acknowledgment

misrepresented Franklin's role and, whatever its intention, left most people with the impression that her work mainly served to confirm that of Watson and Crick. It has to be one of the greatest understatements in the history of scientific writing," according to the biologist, Lynne Osman Elkin.³⁵

In the Epilogue to *The Double Helix* (1968), Watson wrote about his later view of Rosalind Franklin, "since my initial impressions of her, both scientific and personal (as recorded in the early pages of this book), were often wrong, I want to say something here about her achievements. The X-ray work she did at King's is increasingly regarded as superb. The sorting out of the A and B forms, by itself, would have made her reputation; even better was her 1952 demonstration . . . that the phosphate groups must be on the outside of the DNA molecule." ³⁶ He also mentioned Franklin's fundamental later work at Birkbeck College on the tobacco mosaic virus. Concerning this corrective statement in the Epilogue, Anne Sayre after interviewing Watson, noted the following: "According to both Aaron Klug and Francis Crick, they each pressed upon him the necessity for adding something to rectify the picture of Rosalind as it stood in the original manuscript. It seems significant to me that

such pressure was needed, that in Watson's mind nothing more was required.”³⁷

According to Brenda Maddox, “Over the years, Watson repeatedly indulged in public admissions of unease. In 1999, in his book *A Passion for DNA*, he looked back to the publication of *The Double Helix* and joked: ‘I daydreamed that the *New Yorker* might print it under the rubric ‘Annals of Crime’ because there were those who thought Francis and I had no right to think about other people’s data and had in fact stolen the double helix from Maurice Wilkins and Rosalind Franklin.’ “³⁸ Maddox quotes other similar statements made by Watson almost 50 years after the crucial day he barged into Franklin’s lab in 1953 and then was shown Photograph 51 by Wilkins.³⁹ Maddox asked could Rosalind Franklin have dreamed that James Watson “would be declaring from public platforms half a century later that they could not have found the double helix in March 1953 without her experimental work.”⁴⁰ All Watson and Crick had to do was to acknowledge her properly in the initial 1953-1954 papers.

¹ Watson, James D., 2012, *The Annotated and Illustrated Double Helix*, edited by Alexander Gann & Jan Witkowski, p. 63-64: Simon & Schuster, New York, November 2012, 345 p. Hereafter cited as Watson-Annotated.

² The original edition is Watson, James D., 1968, *The Double Helix*: Atheneum, New York, 226 p. The Norton Critical Edition is: Watson, James D., 1980, *The Double Helix: A Personal Account of the Discovery of the Structure of DNA*, edited by Gunther S. Stent: W. W. Norton, New York and London, 298 p. The Annotated edition is cited in ¹.

³ Perutz, Max, 1981, Undercurrent of Revelations (Review of *The Double Helix*, ed. G.S. Stent): *New Scientist*, 26 March, p. 827 [paraphrased from quotation in Glynn, Jenifer, 2012, *My Sister Rosalind Franklin*, p. 131-132: Oxford University Press, 172 p].

⁴ Sayre, Anne, 1975, *Rosalind Franklin and DNA*, p. 95: W. W. Norton, New York, 221 p.

⁵ Ridley, Matt, 2006, *Francis Crick: Discoverer of the Genetic Code*, p. 53: Atlas Books, HarperCollins, New York, 213 p.

⁶ Ridley, p. 55.

⁷ Maddox, Brenda, 2002, *Rosalind Franklin: The Dark Lady of DNA*, p. 165: HarperCollins, U.K.; First Perennial edition, 2003, 380 p.; *Watson-Annotated*, p. 91-92.

⁸ Maddox, p. 165; *Watson-Annotated*, p. 95, 99.

⁹ Maddox, p. 147; *Watson-Annotated*, p. 29.

¹⁰ *Watson-Annotated*, p.173; Maddox, p. 191; Ridley, p. 64-65.

¹¹ *Watson-Annotated*, p. 178; Maddox, p. 193-194.

¹² Gosling, in *Watson-Annotated*, p. 182.

¹³ *Watson-Annotated*, p. 181.

¹⁴ Klug, Aaron, 2004, *The Discovery of the DNA Double Helix*, p. 21: *Journal of Molecular Biology*, v. 335, p. 3-26.

¹⁵ Maddox, p. 204 [Donohue's emphasis].

¹⁶ Maddox, p. 205.

¹⁷ Franklin, Rosalind E. and Gosling, Ray G., 1953, *Molecular Configuration in Sodium Thymonucleate*, p. 741: *Nature*, v.171, p. 740-741.

¹⁸ Watson, J. D. and Crick, F. H. C., 1953, *A Structure for Deoxyribose Nucleic Acid*, p. 737: *Nature*, v. 171, p. 737-738.

¹⁹ Same as ¹⁸ but quote extends from p. 737-738.

²⁰ Same as ¹⁹ but p. 737.

²¹ www.exploratorium.edu/origins/coldspring/printit.html [annotation 11 in this reference, accessed in May, 2017]

²² Crick, F. H. C. and Watson, J. D., 1954, The complimentary structure of deoxyribonucleic acid, p. 82, footnote: Proceedings of the Royal Society A, v. 223, p. 80-96.

²³ Donohue, Jerry, 1976, *Honest Jim?* p. 289 [my emphasis]: The Quarterly Review of Biology, v. 51, p. 285-289.

²⁴ Sayre, Anne, 1975, Rosalind Franklin and DNA: W. W. Norton, New York, 221 p.; Maddox, Brenda, 2002, Rosalind Franklin: The Dark Lady of DNA: HarperCollins, U.K.; First Perennial edition, 2003, 380 p.

²⁵ Maddox, p. 317.

²⁶ Sayre, p. 212.

²⁷ Sayre, p. 179.

²⁸ Sayre, p. 216-217.

²⁹ Maddox, p. 254-255.

³⁰ Klug, Aaron, 1968, Rosalind Franklin and the Discovery of the structure of DNA: Nature v. 219, p. 808-810, 843-844; 1974, Rosalind Franklin and the double helix: Nature, v. 248, p. 787-788; 2004, The Discovery of the DNA Double Helix: Journal of Molecular Biology, v. 335, p. 3-26.

³¹ Klug, 2004, p. 16.

³² Maddox, p. 325.

³³ Maddox, p. 325.

³⁴ Watson, J. D. and Crick, F. H. C., 1953, A Structure for Deoxyribose Nucleic Acid, p. 737-738: Nature, v. 171, p. 737-738.

³⁵ Elkin, Lynne Osman, 2003, Rosalind Franklin and the Double Helix, p. 46: Physics Today, p. 42-48.

³⁶ Watson-Annotated, p. 239-240.

³⁷ Sayre, p. 221.

³⁸ Maddox, p. 315.

³⁹ Maddox, p. 315-316.

⁴⁰ Maddox, p. 317.