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Original Paper

Photograph 51, Rosalind Franklin and DNA Structure

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Abstract

The Nobel Prize in Physiology/Medicine was awarded in 1962 to Watson, Crick and Wilkins, after the death of Rosalind Franklin who passed away in 1958. This mini-review focuses on Franklin's contributions to the double helix discovery. The title of this paper, Photograph 51, describes a x-ray diffraction image of DNA (B form) taken by Franklin and her graduate student Raymond Gosling (Note 1). Its importance will be described, as well as Franklin's other contributions to the double helix discovery. Of immense importance is what Crick and Watson themselves said: Without Franklin's data, "the formulation of our structure would have been most unlikely, if not impossible" (Note 2). This statement makes it clear that Franklin rightly deserves to be the 4th partner in the discovery of the structure of DNA, along with Crick, Watson and Wilkins.

1. Introduction

Matthew Cobb's and Nathaniel Comfort's 2023 Nature Commentary, What Watson and Crick Really Took from Franklin, Nature 616: April 27, 2023, pages 657-660, is a major reference for this mini-review (Note 3). It, like this paper, concludes that Franklin is rightly a 4th partner in this great discovery (Crick, Watson, Wilkins, Franklin), one of the greatest of all time. The references in this paper are twofold: One: those based on the DNA story (Notes 1-4) and Two: why am I telling this story (Notes 5-97)? These latter references show my credibility in research science, some recognition: US Presidential Award, AAAS Fellow, CSU system statewide Trustees Outstanding Professor; and my personal friendship with the late Dr. Crick, who visited here for about 10 years in the 1990s.

There are two DNA forms. The A form—is crystalline and "dry." The second is the B form, that is "wetter" and called the paracrystalline form. A form can be converted to B form by increasing humidity. B form can be converted to A by reducing humidity. Cells contain lots of water and therefore the B form of DNA is likely the biologically functional form. Maurice Wilkins who supervised Crick, Watson

and Franklin obtained some very pure A form DNA from Swiss chemist Rudolf Signer and some less pure DNA from the Austrian biochemist Erwin Chargaff (Notes 3).

Attention is often given to the purest form of a chemical, in this case the A form of DNA. Watson and Crick had many interactions with colleagues. For example, Erwin Chargaff told them that there was rough equivalences of thymine (T)/adenine (A) and guanine (G)/cytosine (C). This helped them think that A binds with T and C binds with G (Notes 4). At first Crick and Watson in building models thought the bases were in the aldose form that was wrong and their models did not work.

Watson and Crick showed their models to Jerry Donohue, an American crystallographer who shared an office with Watson.

Jerry said that the DNA bases would most likely be in the ketose form in water, not the aldose from that they had been using. An aldose contains an aldehyde group (CHO) consisting of carbon, hydrogen and oxygen while a ketose contains a ketone group (CO) consisting of carbon and oxygen.

When they switched their thinking that the bases were in the ketose form, the cardboard models "worked." A paired with T and C paired with G. Here again, interactions with colleague(s) helped Watson and Crick arrive at a correct piece of the puzzle.

From Ross Hardison, the Pennsylvania State University (denoted by " "):

2. B-form of DNA

- "B-DNA is the Watson–Crick form of the double helix that most people are familiar with.
- They proposed two strands of DNA — each in a right-hand helix — wound around the same axis. The two strands are held together by H-bonding between the bases (in anti-conformation).
- The two strands of the duplex are antiparallel and plectonemically coiled. The nucleotides arrayed in a 5′ to 3′ orientation on one strand align with complementary nucleotides in the 3′ to 5′ orientation of the opposite strand.
- Bases fit in the double helical model if pyrimidine on one strand is always paired with purine on the other. From Chargaff's rules, the two strands will pair A with T and G with C. This pairs a keto base with an amino base, a purine with a pyrimidine. Two H-bonds can form between A and T, and three can form between G and C.
- These are the complementary base pairs. The base-pairing scheme immediately suggests a way to replicate and copy the genetic information.
- 34 nm between bp, 3.4 nm per turn, about 10 bp per turn
- 9 nm (about 2.0 nm or 20 Angstroms) in diameter.
- 34^{o} helix pitch; -6^{o} base-pair tilt; 36^{o} twist angle"

3. A-form DNA

- "The major difference between A-form and B-form nucleic acid is in the confirmation of the deoxyribose sugar ring. It is in the C2′ endoconformation for B-form, whereas it is in the C3′ endoconformation in A-form.
- A second major difference between A-form and B-form nucleic acid is the placement of base-pairs within the duplex. In B-form, the base-pairs are almost centered over the helical axis but in A-form, they are displaced away from the central axis and closer to the major groove. The result is a ribbon-like helix with a more open cylindrical core in A-form.
- Right-handed helix
- 11 bp per turn; 0.26 nm axial rise; 28^{o} helix pitch; 20^{o} base-pair tilt
- 33^{o} twist angle; 2.3nm helix diameter"

Rosalind Franklin, a jewish woman scientist, was not allowed in the scientist lounge, as anti-female and anti-semitic culture prevailed at that time. So while Crick and Watson had the "luxury" of interacting with many other scientists, Rosalind Franklin did not. And it is often said that Franklin's science suffered for it (Note 3). It is not likely that Crick and Watson would have achieved the correct model before others such as Linus Pauling, who was close on their tracks and had won two Nobel Prizes, had they not had extensive interaction with others.

Rosalind Franklin should have shared in the glory of the discovery. She likely would have shared in the Nobel prize had she not past away before it was awarded. Her input included photograph 51. When Wilkins showed this photo to Watson, he quickly thought that it was probably a helix. Franklin left for a position elsewhere and was instructed to leave her DNA work with Wilkins. Franklin's student Ryan Gosling, who together with Franklin produced photo 51, gave it to Wilkins when Franklin left. Wilkins showed it to Watson, who after conversations with Crick, thought it was a likely helix. The models built by Crick and Watson, by themselves, were not experimental evidence for a helix. But photo 51 was experimental evidence, helping to confirm the helix structure. One photo, photo 51, is just one piece of experimental evidence. But together with the modeling, a strong case was made for the helix structure of DNA. It made sense.

For photo 51 the B form of DNA was exposed to x-rays for 62 hours to produce one of the finest and clearest x-ray photos ever taken. It was the 51st photo taken. The cartoon by Emily Willoughby shows some of the features of photo 51. Franklin said that photo 51 suggests a helical structure, most likely a double helix with ten bases per turn with the bases on the inside and the phosphate groups on the outside. She suggested that the DNA double helix had a diameter of 20 Angstroms with 3.4 Angstroms between base pairs and 10 base pairs per turn with 34 Angstroms between repeated units. A missing layer line suggested a double helix not a single helix. This all is shown in the cartoon that helps in the understanding of what Photo 51 shows. There is some controversy about what came first, Crick and Watson's models or Franklin and Gosling's experimental evidence, photo 51. The statement made by Crick and Watson regarding Franklin's data, "the formulation of our structure would have been most

unlikely, if not impossible," (Note 2) without Franklin's data, This statement suggests that Crick and Watson knew about Franklin's work before they completed their correct model of the structure of DNA. They suggest that Franklin's work was instrumental in the development of the correct DNA model (Note 2)

This conclusion was stated in Cobb and Comfort's 2023 Nature Commentary (Note 3) and represents a new twist to the DNA story. Also noted was a Medical Research Council report in which Franklin and Wilkins independently suggest that the B form of DNA is helical with two intertwined chains with a sugar-phosphate backbone on the outside of the helix and a 34 Angstrom repeat (Note 1). The correct model of the DNA double helix was displayed at the Royal Society Conversazione in June 1953 and signed by Crick, Watson, Wilkins and Franklin (Note 3).

4. Conclusions

While the exact timeline of who did what first may be controversial, there is no doubt that Rosalind Franklin deserves to be a 4th partner in the DNA structure discovery along with Crick, Watson and Wilkins. This discovery is one of the most important of all time. Franklin's experimental evidence as well at Watson and Crick's modeling were both essential in the DNA structure discovery as stated by Crick and Watson. Franklin's contributions were instrumental. Without them… "the formulation of our structure would have been most unlikely, if not impossible." While the 2023 Nature Commentary is read by practicing scientists, this mini-review is primarily for educators and everyone, bringing a new understanding of one of the greatest discoveries of all time. While it is generally known that Rosalind Franklin had something to do with the discovery, what is presented here is not widely known. The discussion on Photograph 51 is an especially relevant addition to frontiers in education technology. As a US Presidential Awardee, Fellow AAAS, CSU system Trustees Outstanding Professor, friend of Dr. Crick, and author with my students of many peer reviewed publications (Notes 5-97), I am happy to present this paper to the public.

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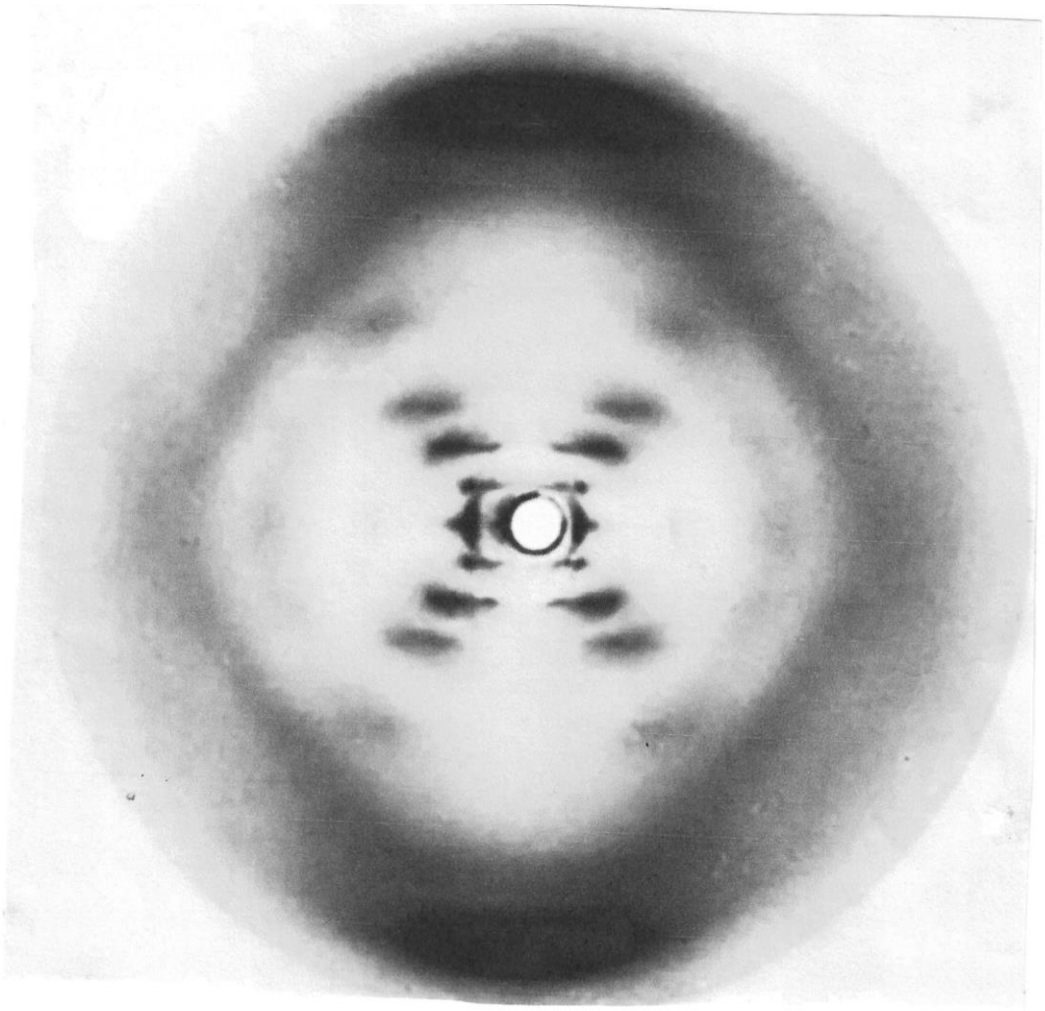
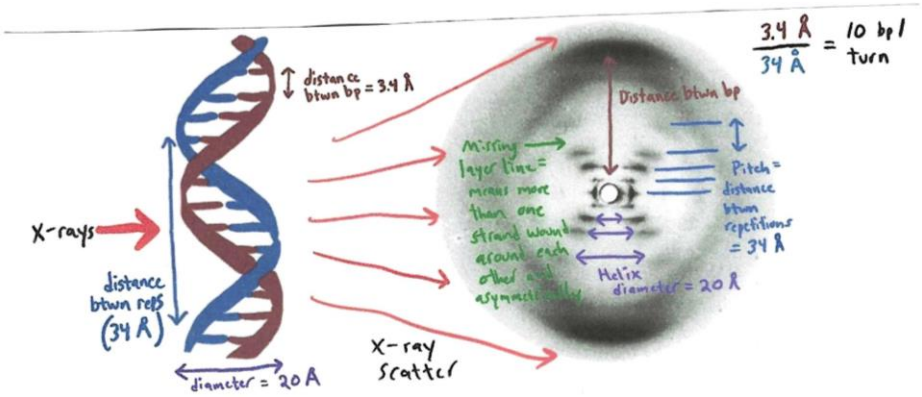


Photograph 51 from Franklin, R.E. and Gosling, R.G., Molecular Configuration of Sodium Thymonucleate, Nature 171, 740-74 (1953). This x-ray diffraction image of the B form of DNA provides evidence that DNA is a helix. Such evidence places Franklin in the group of 4 (Watson, Crick, Wilkins, Franklin) who discovered the molecular structure of DNA.



Reviewed Cartoon by Dr. Emily Willoughby of how Photograph 51 captured the helix structure of DNA

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