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A Hypothesis on the Secondary Structure of DNA

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Abstract: **The Watson-Crick double helix is unable to explain the topological difficulties in DNA replication satisfactorily. Disproved by several experiments, the classical double helix model needs an amendment from plectonemically to ambidextrously. The present hypothesis not only can remove the topological troubles in DNA replication, but also can explain some extraordinary phenomena that are normally beyond comprehension. Several predictions were proposed for testing the validity of this amendment.**

Keywords: **Left-handed DNA, Ambidextrous double helix, Linking number, Positive supercoiling, Pea vine.**

1. INTRODUCTION

On the foundation set up by many previous scientists, a reasonable DNA structural model was proposed by Watson and Crick at the right time and the right place.[1] at the beginning, the DNA double helix is a theoretical hypothesis without sufficient experimental demonstrations. Afterwards, many evidences confirmed that the two complementary strands are coiled around each other in opposite directions with 10 base pairs per turn and they are held by hydrogen bonds between paired bases. Except the model building, the evidence supporting the winding direction of the two strands in DNA is very scarce. It is the only weak point in the classical double helix model.

2. SIDE EFFECT OF THE DOUBLE HELIX

No doubt, the discovery of the double helix is one of the greatest achievements in the science of 20th century, which stimulated many important ideas and findings, leading to the recognition of the central dogma of molecular biology. And so, the double helix becomes an icon of the molecular biology today. Disagree with the validity of the double helix may be deemed as a blasphemy against modern science.

It is likely that the glory of Watson-Crick Model is so bright and dazzling that made many people believe there is no problem in DNA structure. The fast advancement of molecular biology concealed the topological problems involved in the double helix. Surely, most people don't have enough knowledge or ability to question the classical double helix model written in almost every textbook of biochemistry or molecular biology which has an effect of brain wash for generations of molecular biologists. Repeatedly reading or hearing the same story from various books or seminars would make most people to have the impression that the DNA is really a right-handed double helix. Many students and experts were unintentionally or imperceptibly misled by the double helix. Hence, the side effect of the double helix on the scientists' psychology is probably indescribable and impalpable.

In the mid-1970s, Robert W. Chambers, chairman of the biochemistry department at the New York University School of Medicine, had successfully made a plasmid by annealing a pair of single stranded circular (SSC) DNA. That result strongly repudiates the assertion of the right-handed double helix. Normally, a scientist with such a surprising finding would continue his investigate carefully and desperately until it is perfect and then to declare his finding. The strange fact is that professor Chambers kept silence [2]. One of the understandable reasons is that the famous double helix and its prestigious Nobel Prize laureates may deter a scientist who has not psychologically prepared to get ready for further investigation.

Likewise, Tai Te Wu, a tenured professor of Cornell Medical College was compelled to switch his study from DNA to immunology simply because his research questioning the validity of the double helix and subsequently lost his grant. Evidently, anyone trying to question the legitimacy of the double helix needs not only enough courage and knowledge but also needs an open-minded society allowing the performance of independent experimentation and expression of heretical opinions.

3. THE ACHILLES HEEL OF THE DOUBLE HELIX

It is interesting that the spatial problems involved in the DNA structure was noticed by Watson and Crick themselves shortly after the publication of the double helix[3]. They were quite optimistic that that spatial objection is not insuperable.

Since the discovery of the double helix, a lot of scientists plunged into the investigation of DNA, consequently many important findings emerged. Some of them cast shadow on the acceptability of the double helix.

1) Genetics and autoradiography revealed that the chromosome of *E.coli* is a very long circular DNA containing 4×10^6 base pairs [4, 5, 6]. If the DNA is really a right-handed double helix, the two strands of *E.coli* DNA would inter-wind 4×10^5 times. In other words, the linking number of circular *E.coli* DNA is 4×10^5.

2) The replication mechanism in the *E.coli* is semiconservative and bi-directional[7]. Hence after each round of replication, the two parental strands have to unwind 4×10^5 times, i.e. reducing the linking number from 4×10^5 to exactly 0.

3) The DNA replication is a very fast biochemical process. At each replication fork, new DNA replicates at the rate of 1kb per second[8]. That needs the right-handed double helix to unwind at the rate of 100 rounds per second, i.e. 100 rps or 6,000 rpm.

Each of these results was supported by solid evidence. Their combination causes some doubt which is difficult to be explained by the traditional double helix model. For example: it is unlikely that the delicate thin DNA strand can unwind at the rate of 6,000 rpm in the viscous cytosol where the friction and hindrance is supposed to be very high. Additionally, separating two tightly interwound parental strands will encounter with awful topological difficulties since the complicated replication processes are confined within a very limited space.

Trying to avoid the topological problems involved in DNA replication, Rodley et al. proposed that the two strands do not coil round each another but laid side-by-side [9]. Refuted by Crick et al.[10], the side-by-side DNA was no more considered as a reliable DNA model by most scientists.

The finding of many topoisomerases greatly alleviated the topological difficulties. It is hoped that the magic power of enzymes can remove the topological difficulties in DNA replication. Up to now, many scientists still believe the discovery of topoisomerases has taken "the sting" out of the topological objection to the plectonemically double helix.

During the last four decades, numerous new findings occurred, which made the old double helix model more vulnerable to the new facts. Here are some of those evidences:

1) It is getting clear that under physiological conditions, DNA molecule is dynamic and polymorphous. DNA can exist in many different forms, including A, B, C ….Z[11]. The winding of the two strands in the DNA duplex can be affected by many factors, such as monovalent or divalent cation ions, various solvents, temperature, intercalating agents etc. An interesting fact is that a left-handed Z-DNA is determined by X-ray crystallography prior to the confirmation of the right-handed B-DNA[12].

2) Replication is a very complicated process. Various enzymes and factors combined to form a replication factory, namely replisome. At each replication fork sits a replisome in which one gyrase and one helicase are acting as a pair of cooperating pioneers leading the quick separation of the two inter-winded parental strands[13].

3) As a major player in reducing the linking number of *E. coli* chromosomal DNA, the reaction rate of gyrase is very slow, only 6 times / minute / molecule [14]. It is questionable how can the gyrase perform the job of quick unwinding of 6,000 rpm during DNA replication.

4) Although helicase can quickly open the hydrogen bonds between the double helix, it cannot change the linking number of DNA [15]. If the double helix is really right-handed, it will push the two parental strands twist more tightly in front of the replication fork that would cause serious problems.

All these facts put the most vulnerable part of the double helix model on fire. The quick unwinding of the DNA duplex, i.e. 6,000 rpm calculated from double helix model, becomes the focal point. No indisputable evidence has verified that the quick DNA unwinding is actually happened in *E.coli* that is acting as a typical model microorganism in biochemical and molecular biological studies.

4. AN AMENDMENT OF THE DOUBLE HELIX

All these troubles indicated that the old structural model of the double helix needs an amendment. It naturally and logically leads to the proposal of a hypothesis that in a native DNA molecule, a relatively high percentage of left-handed DNA co-existents with the right-handed DNA. Hence, during replication, the quick DNA unwinding is no more necessary. Consequently, the estimated linking number of a plasmid in ambidextrous model should be much less than that of the same plasmid in classical double helix model. However, these doubts are not sufficient to change the paradigm of right-handed double helix. Science needs solid evidence and reasonable logic, rather than eloquent remarks or theoretical speculations. So we started our experimental investigation almost 40 years ago.

Serendipitously, the linking number of supercoiled and relaxed pBR322 DNA was found to be very low[16, 17]. pBR322 DNA is a circular DNA with 4361 base pairs. According to the classical double helix model, the linking number of a relaxed pBR322 molecule should be around 436, which is greatly different from what we have seen under the electron microscope (EM). One presentation of it is shown in figure 1.

A zero linking number topoisomer of relaxed head-to-tail dimer pBR322DNA was finally found which cannot be explained by the old DNA model [18]. This set of experiments provides a disproof to the claim that most native DNA is a right-handed double helix.

The merit of disproof is well expressed by psychologist Mihaly Csikszentmihalyi: *"The advantage of disproof over proof in science is that whereas a single case can disprove a generalization, even all the cases in the world are not enough for a conclusive positive proof. If I could find just one white raven that would be enough to disprove the statement: 'All ravens are black.' But I can point at millions of black ravens without confirming the statement that all ravens are black"* [19].

Since the EM results are not always trusted or accepted by many scientists, additional evidence of falsification is needed. The annealing product of two complementary single stranded circular DNA was found to be similar to a relaxed plasmid as shown in figure 2 [18]. The formation of such a circular DNA duplex is not aided by enzyme; its linking number has to be zero. It can be taken as second disproof of the classical double helix.

The third disproof is the formation of figure 8 structure which is the annealing product of two SSC DNAs each inserted with one of the 2 kb complementary λ Hind III fragment. The annealing product appears as figure 8 or θ [18]. The two single stranded loops share with a common border which is the 2kb double stranded DNA. If this 2 kb DNA is a right-handed double helix with 10 bases per turn, than the rest of the SSC DNA would wind 200 times left-handedly, which is never found under the EM. This experimental result is inconsistent with the claim of classical double helix.

The fourth disproof is the dynamics of denaturing singly nicked plasmid. It was found that the two strands of the singly nicked DNA can be separated very quickly which is almost unbelievable. If the two strands of that nicked DNA were tightly interwound, their separation would be very hard due to spatial difficulties. Because the two broken ends of the single stranded linear (SSL) DNA have to quickly wind in opposite directions that would inevitably causing them tangled and preventing the SSL DNA separate from its complementary SSC DNA[18].

All these 4 experiments were specially designed to test the winding directions inside the native DNA duplex to see if the two complementary strands are winding plectonemically or ambidextrously. It is interesting that all the observed facts are consistent with each other and cannot be explained by the right-handed double helix. Each of these experimental results independently supports the hypothesis that in native DNA, the two strands are winding ambidextrously rather than plectonemically. Naturally, the left-handed DNA is no more a rare DNA and Z-DNA is probably a special member with alternative purine and pyrimidine sequences.

In 1996, an experimental investigation of the secondary structure of the double helix was conducted by Wu & Wu[20]. Their result also challenges the traditional double helix.

Actually, there are many interesting results that were unable to be explained by the classical double helix model. It is not appropriate to list all of them here; some of them were mentioned in our published papers [18, 21]. Careful readers may find more clues from literature.

Crick et al.[10] once stated: *"In science ten weak arguments do not add up to one strong one."* The finding of a zero linking number topoisomer remarkably contradicts the traditional double helix model. Additional evidence of the figure 8 test and dynamics of denaturing singly nicked plasmid strongly suggest that the two strands of the double helix are not always winding unanimously in one direction. These results constructed a chain of evidence, indicating that they are not randomly occurred or coincidently happened. It is sufficient and strong enough to disprove the model of plectonemically double helix.

Albite we don't know if our experimental results have been reproduced by other scientists or other labs, we are confident that they can be repeated in the hands of careful scientists.

The problem is that to find out the winding direction in a native DNA duplex is rather difficult. Up to now no protocol or single instrument can clearly and definitely demonstrate it. The combination of topology and biophysical, biochemical methods makes it possible to let us have a relatively clear glimpse to the winding directions in a long native plasmid DNA.

5. THE CONSEQUENCE OF THE AMENDMENT

Although the ambidextrous double helix is a slight amendment of the classical double helix model from plectonemically to ambidextrously; this modification may have great consequences. Our experiments indicated that the absolute linking number of positively supercoiled DNA or negatively supercoiled DNA is higher than that of their relaxed counterparts. This understanding differs greatly from the conventional knowledge of the present day's DNA topology.

It is reported that doubling time of a hyperthermophilic strains is 7 hr. or 24 hr. at 115ºC or 121ºC[22]. It is difficult to know why the hydrogen bonds between the double helix are still able to hold the two strands at high temperatures. Probably the protection is due to positive supercoiling which comes from excess amount of left-handed DNA. And the excess left-handed DNA can be deduced from ambidextrous double helix[23]. Thus, the stability of the DNA in hyperthermophilic strain at high temperatures is no more implausible.

Perhaps many readers are familiar with the famous EM picture of chicken ovalbumin gene DNA hybridized with its mRNA, the 8 exons of the gene pair with the mRNA[24]. It is interesting to note that these regions appeared as parallel double stranded hybrids of DNA and RNA. It is comprehensible that the stereo structure of these regions has to have equal amount of right-handed and left-handed turns, though naked eyes cannot see these turns exactly from the picture of EM.

An unexpected phenomenon triggers the connection between the exon hybrids and self-adjusted winding of sweet pea vine.

Each kind of climbing vine can wind around a stem in one direction. The winding direction is probably determined by the gene of each plan[25]. Once the tip of a vine is holding something, the vine has to be tightening so that the plant can hold tightly with that vine. A way of doing so by sweet pea was observed on my balcony as shown in figure 3. Since the length of the vine is almost fixed, to make it tighten, the vine simply twists in both directions simultaneously until its stem is tightly holding the supporter. It is amazing that the plant with no brain can find a way to solve such a tough question. The question is: How to shortening a tube with length L to l (L>l)? Myriads different ways can be designed. However, it is likely the plant finds the best way to solve the question. Since the vine of sweet pea is usually winding left-handedly or clockwise (CW), this new way of holding a supporter was not completely determined by its gene. The vine simply twists itself in both directions, i.e., CW and CCW (counter-clockwise).

Likewise, the stereo-structure of the hybrids from exon DNA and mRNA is probably in a similar way to solve the topological problem. It is very likely that the stereo-structure of those double stranded region contains oppositely winding strands. A similar duplex from two single stranded DNA was found from figure eight structures[18] which may imply **the**

formation of left-handed DNA can be affected by topological factors, rather than determined by sequence. It may be a new type of DNA polymorphism that has not been reported yet.

The stereo structure of benzene and graphite notably differs from the tetrahedral structure of carbon in diamond or most chemicals. It indicates that topology can even affect the chemical bond and bond angle which is normally unchangeable. In the long strand of a DNA duplex, there are enough variations for the two complementary strands to adopt its most suitable tertiary structure. It is reasonable to guess that there is no chemical bond or bond angle change in the whole double helix.

The dynamic and polymorphous DNA is especially revealed by the fact that singly nicked DNA can be made from supercoiled plasmid in the presence of enough ethidium bromide (EthBr) only under strictly controlled conditions[26]. If the temperature, incubating time or the concentration of DNase 1 is over the limit, the plasmid would be degraded to small pieces. This phenomenon is difficult to be explained. Most likely, the EthBr insertion turns all the right-handed double helix into left-handed DNA which is un-cleavable by DNase 1. Whereas the short fragment cleavable by DNase I may occasionally present due to the constant movement of the double helix. As soon as the intact plasmid is nicked by DNase 1, the molecule loses its topological constrain instantly and allows more EthBr insert into the plasmid. The result is that the nicked plasmid becomes all left-handed DNA which is un-cleavable by DNase 1. The dynamic movement of DNA makes the DNA vulnerable to DNase 1 when higher temperature, longer incubation time or excess amount of enzyme is provided.

DNA is one of the most important macromolecules in biology. The fascinating self-replication property inspired great interest and curiosity in it. Starting from Friedrich Miescher's finding in 1869, the story of DNA is very long. Like reading a good detective story, guided by knowledgeable scientists, the public opinion on the structure, function and the replication mechanism of DNA had been misled several times. From time to time, new findings emerged abruptly and surprisingly which lead to new clues to follow. As an intelligent detective can always find the clue from slightest details, a research scientist should not only collecting meaningful information from all the corners all over the world, but also to do something actively, either acting as a whistle-blower by pointing out how, where, why, what the problem is, or acting as an detective to solve the puzzle. The traditional double helix model has served science community more than 60 years. However, in front of many facts and new findings, it cannot afford the commitment or obligation as a self-consistent and coherent scientific theory. Our hunch tells us that the story of DNA is not finished yet.

Epistemology teaches us that no theory is perfect. Even a theory as sound as Newtonian physics, is not assailable. K. Popper had pointed out that no matter how a theory survived in the most rigorous tests, it does not mean it can pass future test. Except in the field of mathematics, all scientific knowledge is provisional and has to be modified or improved by new findings or discoveries[27].

The finding of zero linking number topoisomer argues that the two complementary strands in the DNA cannot always wind plectonemically in right-handed direction. It is the signal from nature telling us that native DNA may have alternative structures. Our ambidextrous double helix model is probably an appropriate hypothesis that can explain almost all the known phenomena and get out of the trouble in elucidating the mechanism of DNA replication.

While dealing with scientific arguments, before making any comment or conclusion, a genuine scientist would put his/her personal cherished assumptions, bias, reputation or benefits aside, to scrutinize all the available evidence and to compare different claims or statements. It is realistic that different people carries different ideas. Truth may generate from the clash of different ideas. Disagreement is not always harmful.

The so called "topological problem" can be easily dissolved in the ambidextrous double helix model which also provides explanation for many acknowledged facts and some phenomena that are normally beyond comprehension. Inevitably, there are many questions arose from this amended model. At the moment, we don't know if the secondary structure of DNA duplex is completely determined by its primary structure. In what extend the secondary structure is affected by the topology of the DNA molecule? How is the junction between the oppositely winding segments? Perhaps there are more questions may be raised by our readers.

6. THREE PREDICTIONS

The way to evaluate the correctness of a theory is to test its ability in forecasting some uncertain things correctly and precisely. Based on our hypothesis of the ambidextrous double helix, several predictions can be announced:

1) There is no quick unwinding rotation of the double helix during replication in *E.coli*.

2) A zero linking number topoisomer can always be made and found in most kind of plasmids.

3) The melting temperature (Tm) of the zero linking number topoisomer is always the same as that of its nicked or linear counterparts.

It is unpredictable when these predictions can be proved or falsified by future scientists. No matter what happened, the quantitative analysis of the double helix would make biology more attractive and more accurate.

It seems likely that more investigation is needed in this repeatedly plowed field to solve the mystery in the secondary structure of the double helix.

7. EPILOGUE

Our hypothesis may arose great difficulties to be consented or accepted by many readers since it violates the concept in their minds which have been tightly set up by many years of education and training. It especially conflicts with the truthiness of those scientists who have their personal experience in dealing with the DNA manipulations, such as cloning, sequencing, hybridization, PCR, etc. Besides, the first the impression of the beautiful double helix in many readers' brain is very stable and the psychological function would automatically against our proposal.

But we are confident that our hypothesis is closer to the truth of the secondary structure of DNA, since our idea is set up on the base of several reproducible experiments. Besides, it fit to the frame of biochemistry and molecular biology.

It is expected that out publication on this journal would attract the attention of more scientists to notice the problem hidden in the double helix which was neglected by the main stream science community for so many years.

The emerging epoch of Science 2 or Open Science gives us an opportunity to let our difficultly earned experience and knowledge to be easily and quickly disseminated to every interested scientist[28]. It may greatly speed up the investigation of the secrets in the double helix, since everyone has the equal rights and convenient way to step on the scientific arena and display one's ability and wisdom, rather than waiting for someone's permission as it is necessary in the past or present times. The consequence of the emancipation of science or knowledge creation from ivory tower to the civilized public would be beyond anyone's optimistic imagination.

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APPENDIX - A

LEGEND:

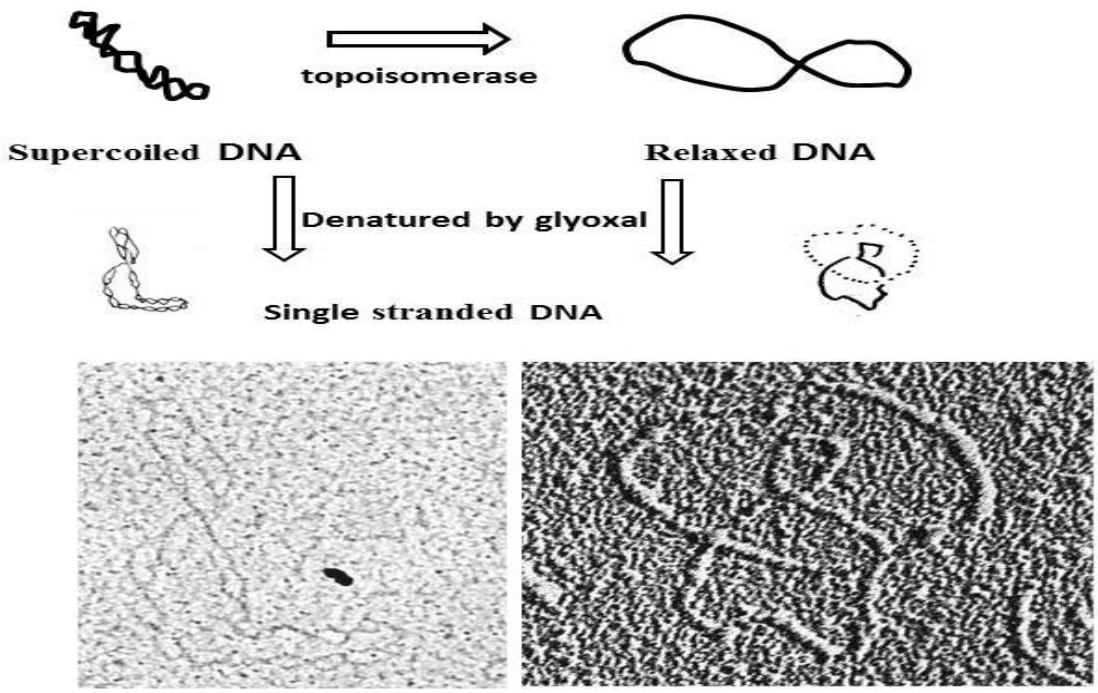

Figure 1. Supercoiled or relaxed pBR322 DNA can be denatured to single stranded DNA and examined by electron microscope.

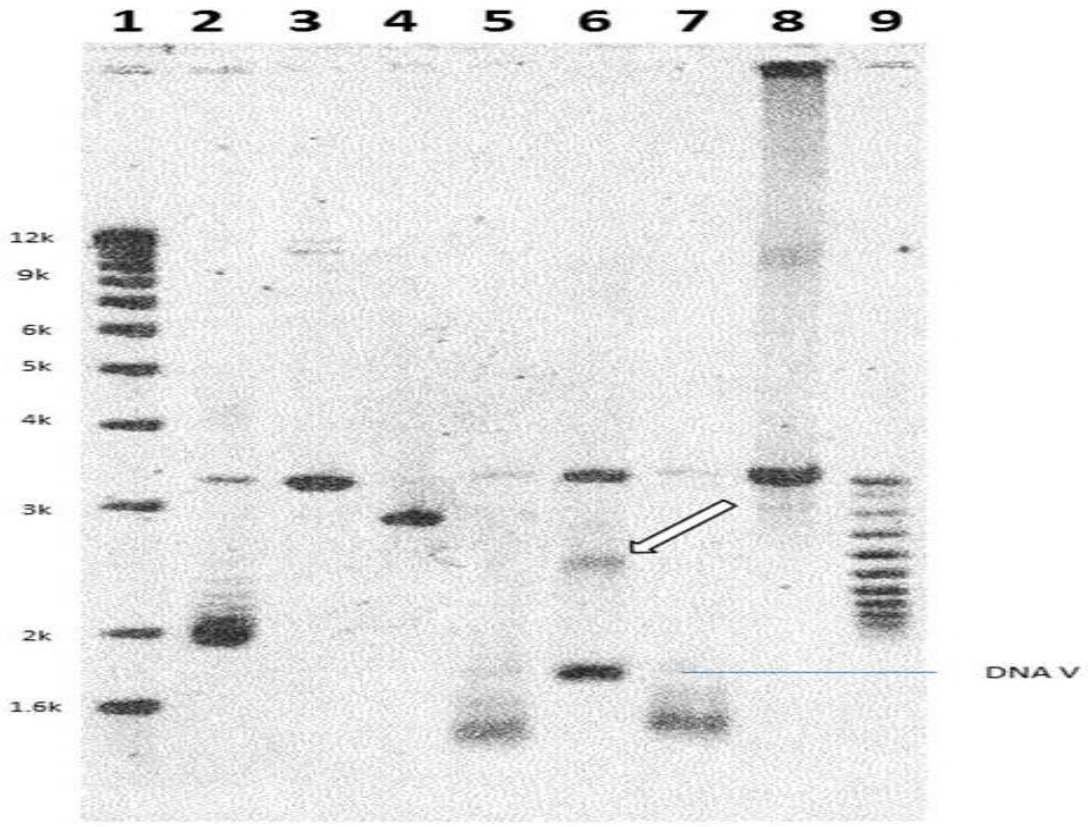

Figure 2. Figure 2 Agarose gel electrophoresis of various pBluescript DNA

Lane 1 1 kb DNA marker

Lane 2 supercoiled DNA (DNA I)

Lane 3 nicked DNA (DNA II)

Lane 4 linear DNA (DNA III)

Lane 5 Single stranded circular DNA (SSC DNA)

Lane 6 annealing product of SSC DNA

Lane 7 single stranded linear DNA (SSL DNA)

Lane 8 annealing product of SSL DNA

Lane 9 relaxed DNA (DNA I')

The arrow indicates the new topoisomer

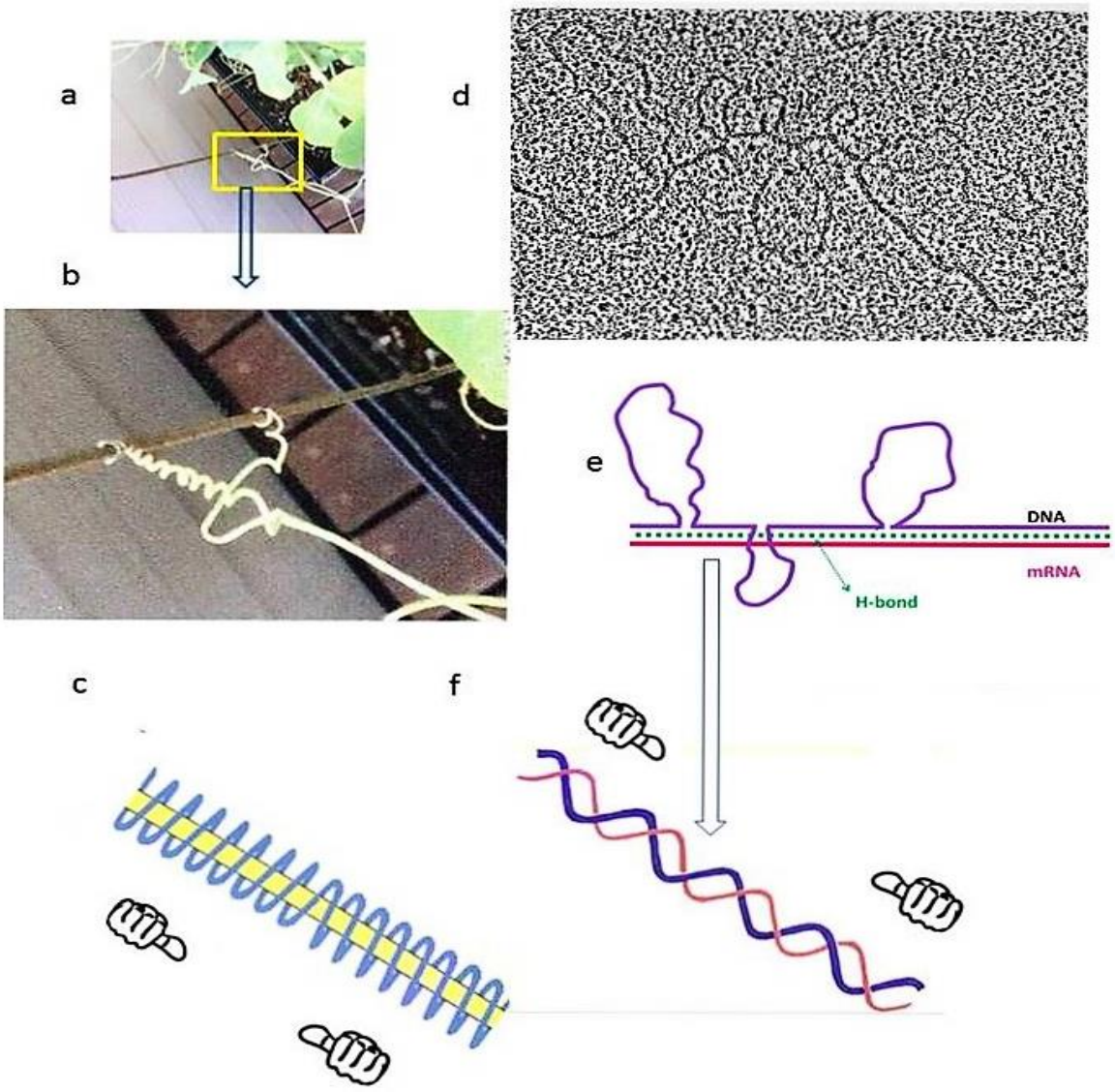

Figure 3. Sweet pea vine and EM of chicken ovalbumin gene hybridized with its mRNA

a. Sweet pea vine; b Enlarged sweet pea vine; c. oppositely twisted helix; d. EM of chicken ovalbumin gene hybridized with its mRNA; e. 8 exons; f. oppositely twisted double helix