TEXTBOOKS: Expectations vs. Reality

THE DNA STORY

WILLIAM D. STANSFIELD

What do teachers want or expect in the textbooks used by their students? A partial list of expectations would likely include at least the following items:

- Accuracy
- Current Knowledge
- Historical Perspectives
- Breadth
- Depth
- Scientific Methodology
- Critical Thinking
- Readability
- Illustrations

In reality, what we unavoidably often get from our textbooks is less than complete satisfaction. Whatever is in our textbooks should at least be correct and free from errors in the content provided; errors of omission (failure to mention specific topics) are often merely subjective opinions of the individual reviewer. We also want texts that are easy to read and understand, but some teachers might object that this goal has been achieved through oversimplifications and/or the misuse of metaphors. Our textbooks should be well illustrated by pictures or diagrams whenever they would aid in comprehension and retention of complex subjects. We want to challenge our students to think critically, evaluate data, and reach unbiased, well-reasoned conclusions. Our textbooks can help here by providing multiple examples of how the methods of science, logic, and reason have been applied to solving specific biological problems. Both authors and publishers of scientific textbooks are aware of the breadth vs. depth problem. Textbooks cannot be encyclopedias. Largely because of curriculum demands, most textbooks tend to superficially cover more topics rather than select fewer topics and explore each of them in greater detail. It thus often becomes the teacher's responsibility to provide important details that students need to really understand complex biological topics such as ecology and evolution.

Another dilemma facing textbook authors is the amount of attention that should be given to subjects of historical interest versus the space allotted to the latest research. New discoveries in biology can stimulate interest and excitement in both student and teacher, and sometimes may even force us to reconsider well-established beliefs. Overthrowing paradigms is one way that science progresses. However, without historical perspectives, students will be deprived of a well-rounded education and cannot be expected to develop a better understanding of, and appreciation for, how we have attained our present level of scientific knowledge (Stansfield, 2000).

There is often a lag of a year or more from the time a textbook manuscript is accepted for publication until the book becomes available. A lot can happen in fast moving biological frontiers (such as genomics, proteomics, and developmental biology) within a year, so textbooks may be out of date in some respects even before we start using them. Teachers at colleges and universities are usually free to adopt more current textbooks whenever desired. Unfortunately, most school districts are not allowed to adopt new textbooks more often than every five to seven years. Teachers in secondary public schools thus find that, as each year passes after adopting a new textbook, they must cover increasing amounts of more recent vital information missing from their textbooks.

Defining Research Goals & Test Case

I became interested in learning about this "knowledge gap" as textbooks age. How long does it take for the results of important research to get into textbooks? How accurately can the advance of knowledge in a given discipline be traced by a study of textbook evolution? As a test case, I chose to study what is commonly cited as the most important biological discovery of the twentieth century—an understanding of the structure of deoxyribonucleic acid (DNA). We all know (or should know) about the double helical structure of DNA proposed by James Watson and Frances Crick in 1953. But what was known about nucleic acids when they began working on the problem? When and by whom was this information obtained? How long did it take for their discoveries to get into textbooks?

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Defining the Primary Research Period

The most popular idea about the chemical nature of genes prior to 1944 was the "protein theory." In that year, Avery, MacLeod, and McCarty reported the results of their transformation experiments in bacteria, providing the first evidence that DNA, rather than protein, carried genetic information. There was no reason to believe that, prior to 1944, genetics textbooks would be particularly interested in reporting on progress in understanding the structure of nucleic acids (although this should have been of interest to biochemists). Thus, in selecting data for my research purposes, I chose to concentrate on sampling genetics and chemistry/biochemistry textbooks bearing publication dates during a 10-year period before and after 1953. Occasionally I was obliged to follow leads in textbook and journal sources outside this range. The results of my research constitute the bulk of this report.

Historical Background

A large, acidic, phosphorous-rich substance was isolated from the nuclei of cells by J. F. Miescher in 1871 which he called nuclein (now known to be a mixture of nucleic acids and protein, called nucleoprotein). Its function was unknown. This seems to be the first bit of information about the chemical composition of nuclear material, but it is missing from most genetics textbooks in my sample. His pupil, R. Altmann, coined the term "nucleic acid" in 1889. There are five common nitrogen-containing organic bases now known in nucleic acid polymers: guanine (G), adenine (A), thymine (T), cytosine (C), and uracil (U). Guanine was first found in bird excreta (guano) in 1844, 40 years before it was recognized as a component of nucleic acid. This was followed by adenine (1885), thymine (from the thymus gland, 1893), cytosine (1894), and uracil (1900). The pyrimidine bases (T, C, U) have single ring structures, whereas the purine bases (A, G) have double ring structures. The combination of a phosphate group, 5-carbon sugar, and nitrogenous base is referred to as a nucleotide. Individual nucleotides may become polymerized into polynucleotide chains of various lengths. By the 1920s, two kinds of nucleic acid polymers had been identified: one from yeast (ribonucleic acid [RNA] thought to represent plants) and one from thymus glands (DNA, representing animals). This notion was discredited in the early 1930s when both RNA and DNA molecules were found to be universal in all cellular life. RNA nucleotides contain bases A, G, C, U and the pentose (5-carbon sugar) ribose, whereas DNA nucleotides contain bases A, G, C, T and the pentose deoxyribose. DNA molecules were located in the chromosomes of the nucleus, whereas RNA molecules could be found in both the nucleus (where they were later found to be synthesized) and in the cytoplasm. Aside from these distinctions, "It was assumed that the main features of the structure of both nucleic acids [RNA and DNA] were the same and that the conclusions derived from experiments with RNA would be applicable to DNA and conversely" (Davidson, 1950, p. 24).

In the 1860s, G. Mendel conducted breeding experiments with peas that led him to conclude that their heredi-

tary material resided in particulate units (now called genes). His theory broke from the prevailing "fluid theory" that the hereditary material of cells resided in fluid forms such as plant sap and animal blood. Unfortunately, Mendel's work was mostly ignored for almost 30 years until it was rediscovered in 1900. As early as 1883, W. Roux suggested that the filaments within the nucleus that stain with basic dyes are the bearers of the hereditary factors. W. Waldeyer in 1888 coined the word "chromosome" for the filaments referred to by Roux. By 1909, W. Johannsen had invented the word "gene" for Mendel's hereditary/genetic units; he also coined the words "genotype" and "phenotype" for the hereditary constitution and physical appearance of an organism, respectively. The chromosomes were identified as the carriers of genes during the years 1910-1920, and were shown to be composed of nucleic acids and protein molecules. In those early days, it was hypothesized that only the protein component of chromosomes carried genetic information, whereas the nucleic acids served only as a scaffold on which blobs of genetic proteins were arrayed in linear fashion, like beads on a string, as linkage groups. The most likely rationale for this belief was the fact that nucleic acid polymers consisted of only four nucleotide monomers, whereas protein polymers could contain as many as 20 kinds of amino acid monomers. It thus appeared that the more structurally diverse proteins were able to carry much larger amounts of genetic information than nucleic acids. As stated earlier, it was not until 1944 that experimental evidence began to appear supporting the hypothesis that DNA was hereditary material. Prior to this time, biochemists worked on nucleic acid structures without a clue that any of them might be carriers of hereditary information.

Results

By 1921, a tetranucleotide theory had been proposed for the structures of plant and animal polynucleotides, in which groups containing undetermined sequences of four different RNA nucleotides in plants, or four different DNA nucleotides in animals, were linked together into polymeric chains. Davidson (1950, pp. 24-25) cites five major pieces of evidence in support of a tetranucleotide theory for the structure of nucleic acids; both linear and cyclic models of the four bases are presented.

A paper by Levene and London (1928) states that "The plant nucleic acid is regarded as a tetranucleotide, each nucleotide being composed of phosphoric acid, a sugar (ribose) and a nitrogenous component." An analogous structure for thymonucleic acid was suggested with the sugar being either an anhydro- or a desoxyhexose (*sic*). In his 1934 organic chemistry book, Conant states that nucleic acids contain a pentose, but he shows no diagrams of a nucleoside (base plus sugar), nucleotide (base plus sugar plus phosphate), nor even a two-base polynucleotide. From this, I initially inferred that sometime between 1928 and 1934 the fact that animal nucleic acids also contain a pentose (rather than a 6-carbon sugar or hexose) became established. After obtaining a copy of Davidson's 1950 book *The Biochemistry of the Nucleic Acids*, I found that the sugar in yeast RNA was

shown to be a pentose in 1909 (p. 7) and that the sugar in thymus DNA was shown to be deoxyribose as early as 1929 (p. 9). Conant identifies three pyrimidines (cytosine, uracil, thymine) and two purines (guanine, adenine), but makes no mention of DNA or RNA molecules. He states that yeast and thymus glands contain somewhat different nucleic acids, but their physiological function is not understood. Conant also points out that "The problem of the tautomerism of the pyrimidines ... is still in a somewhat uncertain state." This problem remained a stumbling block when Watson and Crick began their studies of DNA structure in the fall of 1951.

Neither DNA nor RNA are mentioned in Snyder's third edition of *Principles of Heredity* (1946). However, there is a diagram labeled "The Probable Chemical Structure of Yeast Nucleic Acid" which is based on determinations by Levene (1921). Snyder's model is a single linear chain of four different nucleotides (in a presumed arbitrary order U, A, C, G) incorrectly linked by phosphodiester bonds between carbons 4 and 5 of adjacent sugars (instead of 3 and 5). The model is unidentified as either RNA or DNA. The word "tetranucleotide" does not appear in the figure caption. The sugar contains 5 carbons (a pentose). Like RNA, the nucleic acid contains a uracil, but like DNA a hydroxyl (OH) group is missing on the number 2 carbon of the sugar. It is thus a nonexistent hybrid nucleic acid. Carbon numbers 1 and 5 in the pentose are incorrectly O-linked (instead of 1 and 4). The glycosidic bond is incorrectly shown connecting a carbon of the sugar to a carbon of the base (instead of a sugar carbon to a base nitrogen). In purine bases, Snyder's model incorrectly shows double bonds between positions 8 and 9 (instead of between 7 and 8).

The 1921 paper by P. A. Levene, cited by Snyder (1946), proposed a tetranucleotide model for thymus nucleic acid that contained thymine (like DNA), but he did not call it DNA. The four bases (in presumed arbitrary order A, T, G, C) were each coupled to a 6-carbon sugar (hexose) rather than to the pentose 2-deoxyribose that we now know to be present in DNA molecules. Carbon 2 in the hexose is bonded to an OH group as in ribose. This is another nonexistent hybrid nucleic acid. Levene's paper posed the question "Are the nucleotides united one to another in an ether linking through their carbohydrates, or in ester form, the phosphoric acid of one combining with the carbohydrates of the other?" Levene favored the latter linkage that later was confirmed to be correct. He did not show any structural details of the bases, but simply gave a molecular formula (e.g., adenine is $C_5H_4N_5$), so the way the glycosidic bond forms cannot be seen. Carbons 1 and 4 in the hexose are O-linked. The phosphate linkage between adjacent sugars involves carbons 5 and 6. Even with all of its flaws, Levene's model superficially looks very much like a DNA chain described 32 years later by Watson and Crick and did not appear in any genetics or biochemistry textbook other than Snyder's that I sampled up to 1950. Snyder cautioned, "It is not meant to be implied that this is the formula for a gene, but simply that, if genes are large organic molecules, their chemical structure would probably be at least as complicated as this."

The titration work of J. M. Gulland et al. (1947) indicated that the phosphate groups were probably on the

outside of the molecule; they also suggested that at least some of the bases formed hydrogen bonds with one another (Watson, 1980). This is the first indication I could find that DNA chains might associate with one another. By 1950, E. Chargaff and his coworkers had found that the molar ratios of A and T bases in DNA were almost equivalent regardless of species or tissue type, as were those of G and C bases. However, the ratio of (A+T)/(G+C) varied from species to species. These observations destroyed the tetranucleotide theory.

In 1952, a year prior to announcement of the Watson-Crick model, Srb and Owen published *General Genetics*. Essentially all of the major facts about the chemistry of nucleic acids that Watson and Crick needed were already available. "Each nucleotide seems to be like a plate, composed of a *nitrogenous base*, a *sugar*, and *phosphate* (sic). The phosphate binds adjacent nucleotides together, and the plates appear to be piled in tall stacks." The authors note that deoxyribose is found in DNA whereas ribose is in RNA. "There are other chemical differences as well, in the bases they contain [true] and in the way in which the phosphate binds the nucleotides together [false]." Where they obtained this last bit of misinformation is anyone's guess. Mistakes in textbooks may often be traced to the sources used by authors rather than to the authors themselves. Many textbooks do not adequately cite the source of their information, making it impossible to trace the origin of misconceptions or disinformation.

Watson and Crick toyed with two-chain and three-chain models, but finally settled on the former. During the years 1952 and 1953, M. H. F. Wilkins and R. Franklin provided x-ray diffraction data of DNA (in crystalline and wet forms, respectively). These data suggested that the molecule was a right-handed double helix, the sugar-phosphate backbone of each chain was on the outside of the molecule, and the bases were stacked on the inside. Crick noted from Franklin's own notes that the two chains should run in opposite directions. Watson discovered how specific pairs of bases (A with T, and G with C) could form interchain hydrogen bonds, thus accounting for Chargaff's rules. The following characteristics of the DNA double helix were calculated from the x-ray data: The diameter of the molecule is 20 Å, each nucleotide pair is rotated 36° from the pair below it, the distance between base pairs in rungs of the resulting spiral ladder is 3.4 Å, and the distance of one complete turn of the double helix is 34 Å.

The Essentials of Organic Chemistry (Porter & Stewart) was published in 1953, the same year Watson and Crick published their model of DNA structure. This textbook devoted an entire chapter to proteins and amino acids, but only acknowledged the existence of nucleoprotein. It gave a formula for the sugar ribose, but did not cite any functions for ribose or nucleoproteins, nor did it even mention DNA or RNA. Apparently, these authors were not aware of the evidence that had been mounting during the preceding decade that implicated nucleic acids (especially DNA) as the bearer of genetic instructions.

A segment of double-stranded DNA containing four base pairs and showing the structural formulas of all its

components was published in the fifth edition of *The Principles of Heredity* by Snyder and David (1957). If we assume that the authors were aware of the latest research, one might infer that, as late as 1956, it was still not known that three hydrogen bonds normally form between the G and C bases. This bit of information was missing from the two 1953 papers in *Nature* by Watson and Crick. However, in the *Proceedings of the Royal Society* (1954), Crick and Watson explain that it might be possible for a third hydrogen bond to occur between guanine and cytosine bases in DNA. Snyder and David (1957) state that, "Running through the center of the spiral (or more properly, *helix*) is a protein core." This is not exactly true, but it foreshadowed the later discovery that histone proteins associate with DNA to form nucleosomes that aid in the condensation of chromosomes during nuclear divisions and tend to silence genes (prevent transcription of RNA molecules) in such regions.

A *Textbook of Biochemistry* (Harrow & Mazur, 1958) discusses nucleic acids in general, noting that they "generally have a maximum ultraviolet absorption in the region of 260 m μ (which is due to the absorption by the bases). This property helps to identify nucleoproteins, nucleic acids and various individual bases" (pp. 98-99). Nothing is said about this wavelength as being the one that causes most genetic mutations. They do mention (p. 96) that the Feulgen test specifically stains DNA. However, Davidson (1950, p. 10) states that the colorimetric reactions of Feulgen and of Dische "indicate the presence of a deoxy sugar and are not specific for a deoxypentose, far less deoxyribose." Harrow and Mazur, (page 100), state in a footnote that, "The slight change in structure between the uracil on page 98 and the uracil here is explained by the shifting of an enol to a keto form." Although the source of this "change" is not given, the references at the end of the chapter list J. N. Davidson: *The Biochemistry of the Nucleic Acids*, 1950. This is the same reference initially used by Watson and Crick in an attempt to build a structural model of DNA. Watson claimed (1980, p. 110) that he had copied the molecular structures for G and T bases from Davidson's 1950 book. J. Donohue pointed out that "organic chemistry textbooks were littered with pictures of highly improbable tautomeric forms [of the bases]" and that both G and T bases were wrongly assigned rare enol configurations rather than their common keto forms. Without the knowledge of the common forms of the bases provided by Donohue, it would have been difficult for Watson and Crick to build a successful model. On page 6 of Davidson's book, guanine is indeed represented in the rare enol form, but T is in its common keto form.

The numbering of the atoms in the pyrimidine rings of T and C used by Davidson apparently was still being used by Watson et al. as late as 1987, making the glycosidic bond form between the N-3 position of the

pyrimidine ring and the C-1 position of the pentose. Other textbooks (e.g., Stryer, 1981 and Lewin, 1990) have a different numbering system in which the glycosidic bond forms between the N-1 position of the pyrimidine ring and the C-1 position of the sugar. I was unable to pinpoint when this new system of numbering positions in the pyrimidine ring began, but it was a source of confusion to me when comparing nucleoside diagrams from older textbooks.

Five years after the Watson-Crick model was published, Harrow and Mazur apparently were still not aware of the tautomeric error in Davidson's book, nor did they present even the rudimentary double helix diagram (sans diagrams of how the bases pair) that was in the earliest Watson-Crick 1953 paper. The fact that the DNA molecule is a right-handed double helix, with the sugar-phosphate chains aligned in opposite directions is not even mentioned. Harrow and Mazur present a diagram (p. 308) of the life cycle of a virulent phage and an outline of an experiment (reported in 1952 by A. D. Hershey and M. Chase) without naming either person. The results of the Hershey-Chase experiment were offered as evidence for the "role of DNA in the duplication process" of bacteriophage. "Further evidence [for the genetic function of DNA] comes from the phenomenon of bacterial transformation, but such a discussion is outside the scope of this book" (p. 308). Why was it easier to describe the 1952 Hershey-Chase experiment than that of the 1944 transformation experiments of Avery, MacLeod and McCarty which indicated that DNA carried genetic information in at least one bacterial species? In addition to these "errors of omission" there is at least one more "error of commission" in the *Textbook of Biochemistry*. "Whereas in DNA there is little evidence of branching of chains, in RNA considerable branching takes place" (p.104). Localized branching does occur momentarily during post-transcriptional processing that removes introns (non-coding regions of genes) from nascent messenger RNA molecules, but branching does not occur during the synthesis of any primary RNA transcripts. Split genes (containing introns) were not discovered until

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1977, so Harrow and Mazur could not have known this. Davidson (1950, p. 29) cited a report by Fletcher, Gulland, and Jordan (1944) that proposed three possible alternative structures for sections of a polynucleotide molecule, one of which is branched. Perhaps this is where Harrow and Mazur obtained the notion of "considerable" RNA branching.

Nine years after the Watson-Crick model of DNA was proposed, the popular textbook *Elementary Genetics* by W.R. Singleton (1962) was published. On page 412, only a bare-bones double helix is diagrammed. Like Snyder and David (1957), guanine and cytosine are connected by only two hydrogen bonds. In 1965, three bonds are shown between G-C bases on page 100 of *The Evolution of Genetics* by A.W. Ravin (1965). Assuming that these two textbooks (Singleton and Ravin) were equally timely in reporting the latest information about DNA structure, it might appear that the idea of three hydrogen bonds regularly forming between G and C bases in DNA molecules became established sometime between 1962 and 1965 (or perhaps a year earlier allowing for a year between acceptance of a manuscript by a publisher and its actual publication date). However, one of the most widely publicized sets of data regarding melting temperatures of artificially and biologically synthesized DNA molecules is that of Marmur and Doty (1959). They found that the dissociation (melting or denaturation) of the two chains in a DNA molecule occurs at lower temperatures for DNA molecules rich in A-T base pairs than those rich in G-C pairs. This difference was attributed to the greater number of hydrogen bonds between G-C pairs than A-T pairs. Pauling and Corey (1956) were cited by Marmur and Doty as the original source proposing that G-C pairs should have three hydrogen bonds: "Consideration of the available evidence has, however, permitted us to reach the conclusion that cytosine and guanine should form three hydrogen bonds with one another, rather than two, as suggested by Watson and Crick." Was Singleton unaware that this information had been available for five or six years or was it more detail than he felt belonged in his introductory text?

Even at the time that Watson and Crick published their model structure for DNA (April 25, 1953) they were not sure if the chromosome contained one long pair of complementary DNA chains, or if it consisted of patches of DNA molecules joined together by protein (Watson & Crick, May 30, 1953). Nine years later, Singleton (1962) states that, "It is not fully understood just what is the relationship between the strands of [a] DNA molecule and the strands of chromosomes" (p. 415). A report by D. Steffensen in 1959 is cited, from which Singleton claims that "A pair of chromosomes as originally seen under the microscope actually may contain as many as 64 strands, which could represent strands of the DNA molecule." The giant polytene chromosomes found in the salivary gland cells of fruit fly larvae do consist of many identical replicated chromatid strands bundled together like the strands of a coaxial cable. But polytene chromosomes were long known to be relatively rare exceptions to the general rule that there are only one or two chromatids in somatic cell chromosomes, depending where they are in the mitotic cycle. The book ends, unfortunately, with this bit of missing information.

Conclusion

Textbooks have their place in the educational process, collecting vast amounts of facts from a wide variety of sources. However, my research found that they often contain errors of commission and/or omission and fail to adequately relate the history of how we came to have our present level of knowledge. The history of the search for the structure of DNA, presented in this paper, is just one example of how teachers might provide in-depth instruction of an important biological problem through historical analysis, and at the same time develop understanding and appreciation of how the growth of scientific knowledge occurs (Weider, 2006). In reality, biology instructors are so pressed for time to cover the essentials in their courses that they will not be able to use all of the information in this report. But perhaps they might find time to relate to their students a greatly abbreviated DNA story, emphasizing that it contains the birth and death of at least three major scientific hypotheses:

- RNA for plants; DNA for animals
- Tetranucleotide structures
- Protein genes

Some high schools have a course, called scientific independent study, where they offer students a period in their schedule that they can use to research the history of how specific scientific discoveries were made, as exemplified in this report.

From this brief study of the DNA story, as revealed in the evolution of textbooks, it is obvious that they can be very tardy as a means of communicating new developments in genetics and biochemistry. If the textbooks sampled in this study generally failed so miserably to accurately and timely relate the story of how the structure of DNA was deciphered, what are teachers to expect about the quality and quantity of information their current textbooks give to discoveries of lesser import? Awareness of the results of this study might aid biology teachers in the selection and/or use of textbooks and encourage them in their vital function of supplying to their students supplementary information via lectures, handouts, Internet resources, and/or reading assignments in recent journals to compensate for textbook inadequacies. Textbooks can never replace teachers! Teachers know that, by attending and participating in meetings of their professional associations, and by reading their journals (such as *Bioscience*, *The American Biology Teacher*, *Journal of Biological Chemistry*, *Journal of Chemical Education*, *Journal of Heredity*, *Genetics*, *Science*, *Nature*) and science magazines (e.g., *Science News*, *New Scientist*, *Discover*, *Scientific American*), they can gain the kind of current knowledge they need to impart to their students. We simply cannot afford to turn out graduates whose scientific knowledge is three or more years out of date and expect them to compete successfully in the technological sector of today's economy.

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