From Presentation to Representation in E. B. Wilson's *The Cell*

JANE MAIENSCHEIN

Department of Philosophy Arizona State University Tempe, AZ 85287 U.S.A.

ABSTRACT: Diagrams make it possible to present scientific facts in more abstract and generalized form. While some detail is lost, simplified and accessible knowledge is gained. E. B. Wilson's work in cytology provides a case study of changing uses of diagrams and accompanying abstraction. In his early work, Wilson presented his data in photographs, which he saw as coming closest to "fact." As he gained confidence in his interpretations, and as he sought to provide a generalized textbook account of cell development, he relied on increasingly abstract diagrams. In addition, he came to see that highly abstract and even schematic drawings could provide more than pictures directly from life.

KEY WORDS: Abstract(ion), cell, cytology, diagram, drawing, fact, knowledge, photograph, Wilson.

Rather than considering more familiar questions about the way that theories get represented or illustrated, this paper turns the emphasis around and asks first about the nature of illustrations or diagrams as a guide to what they are intended to illustrate. The focus, then, is on the illustrations themselves and the way that they are used within a text. Whether they are taken to be representing anything – either nature directly, knowledge generally, or theories more specifically – is a question to be addressed later. The particular example selected for discussion is the classic work of cytologist Edmund Beecher Wilson in cellular development.

Wilson began to study the details of cell development at a time when few others did, especially in the United States. By 1895, he had decided to portray the early developmental stages visually in one volume and to compile the wider range of known facts about the cell into a second volume. His path to these two books is instructive since it undoubtedly influenced his determination to present his information in what he saw as the most compelling way. Photographs and diagrams played respectively central roles in depicting what he accepted as established knowledge in each work.

E. B. WILSON

As a midwestern American who taught in a one room schoolhouse for a year, Wilson decided that he had better pursue an education. Acting on the advice of his cousin Samuel Clarke, Wilson followed Clarke to Antioch College for a year

and then on to Yale's Sheffield Scientific School. There he received a B.S. degree after completing a thesis on the sea spiders. The next year he remained at Yale as an assistant and became familiar with the work of Harvard Professor Edward Laurens Mark. As his major professor Sidney I. Smith pointed out to him when he gave Wilson one of Mark's papers, Mark had produced a very lengthy study of snail development and had "only got as far as the two-cell stage." Wilson then "wondered what the author could find to fill two hundred pages on the subject." He explained that "I looked over the paper and saw my first picture of karyokinesis. Then and there was born my determination to find out something about cells, protoplasm, cell division, fertilization, and development." He later added that "from that determination I have never swerved, although it often seems to me that cell structure and cell life seem in their essentials as mysterious today as they did fifty years ago" (Morgan 1941, p. 318). Soon Wilson followed cousin Clarke once more, this time to graduate school with the help of a fellowship in biology at Johns Hopkins University.

At Hopkins, Wilson came most directly under the influence of William Keith Brooks, who pushed him in the direction of studying later stages of development than fertilization and the first cell divisions. Brooks held the conventional view at the time that only at the germ layer stage do developmental stages begin to have significance for later differentiation; before that the cytoplasm remains largely undifferentiated and plastic. (Benson 1987; Maienschein 1987) During his Hopkins years, Wilson examined the patterns of cell cleavage in various species, and he explored the evolutionary significance of such patterns. (Maienschein 1978).

Shortly after graduating, however, he went to Europe for a year and began to look at the earliest developmental stages. There he studied with cytologist Theodor Boveri and then went on to the Naples Zoological Station. The research at both places reinforced his interest in these early stages and his conviction that exciting work was being done on that subject. In addition, he came into contact there with the very best techniques and equipment for doing cytological work (Baxter 1978; Benson 1988). After returning to the United States, he teamed up with his friend and fellow Hopkins graduate William Sedgwick to write a new textbook in *General Biology* (Sedgwick and Wilson 1886). In that work, Wilson offered his first preliminary explorations of the earliest stages of cell development.

By 1895, Wilson was established at Columbia University and heavily involved with producing his major work, *The Cell in Development and Inheritance*, which provided a textbook account of cell structure and function from the germ stage onward (Wilson 1896). By that time he had become aware of the need to present his ideas clearly and convincingly, and he carefully selected a mix of drawings, diagrams, drawings from photographs, and graphs as part of his presentation. It is the way that this major work on *The Cell* changed from the first (1896) to the third and final edition (1925) that forms the central example for this study. Yet in the process of constructing this classic volume, Wilson also produced another which tells us much about his use of different forms of presenting information.

AN ATLAS

In An Atlas of Fertilization and Karyokinesis of the Ovum, Wilson joined efforts with Columbia photographer Edward Learning to produce a series of photographs depicting the various key stages of fertilization and early cell division. The result was, as Wilson put it, "the only successful attempt hitherto made to show the early history of the ovum by means of photography" (Wilson 1895, p. vi). He then laid out what he saw as the crucial importance of photographs for conveying information in biology.

Wilson explained that "no drawing, however excellent, can convey an accurate mental picture of the real object," especially in the case of such rapidly advancing and important work as fertilization and early development studies. Necessarily, any drawing must remain schematic and includes "a considerable subjective element of interpretation." Although a photograph cannot provide a perfect likeness either, it "at least gives an absolutely unbiased representation of what appears under the microscope; it contains no subjective element save that involved in focussing the instrument, and hence conveys a true mental picture" (Wilson 1895, p. v). Though he did include a few supplementary drawings of some stages and though he provided some textual discussion of the observations, it is clear that the series of ten photographic plates was the central focus on the *Atlas* (Figure 1).

For Wilson's goal of presenting data at the highest level of accuracy, meaning in the way that was truest to life, photography could do the best job. Though he recognized that some interpretation was involved in making and selecting the preparations to be photographed, he clearly felt that the resulting photographs provided an essentially "true" picture. He felt confident in the "fidelity to nature and that the results may be trusted even for the finest details." The photographs provided what Steven Shapin and Simon Schaffer have called "virtual witnessing" (Shapin and Schaffer 1985, pp. 60–65). The observer of the photographs, which could be carefully produced and then reproduced in widely distributed book form, could "see" or witness the object under consideration almost as if he or she were actually there taking a turn at the microscope. Unfortunately, the process of photographing and then publishing the results with sufficient quality was very expensive, which restricted the audience which could share the information. In addition, different goals dictated different approaches.

For the textbook purposes of compiling and presenting to a wide general audience the latest information and interpretations about fertilization and development, Wilson suggested that alternative approaches were not appropriate. When he produced *The Cell*, therefore, he did not rely on photographs. Instead, diagrams and drawings played the central role. It is precisely the interpretive character of these diagrams and drawings which made them preferable for conveying a certain type of information. No longer was it crucial for the reader actually to share the observation of the original material. Rather, providing generalized and generally accepted information within a textual context was the goal.

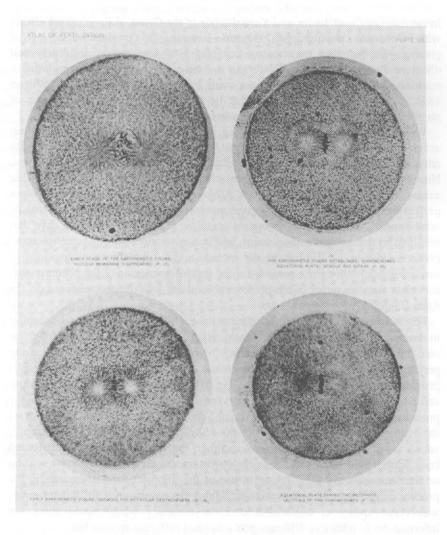


Fig. 1. Plate VII from An Atlas.

THE CELL

It is instructive to look at some examples of Wilson's use of illustrations, and especially to examine ways in which they changed from the first to the third and final edition of *The Cell*. The first edition in 1896 had 331 pages and 142 figures, which yields a ratio of not quite 43 illustrations per 100 pages. By 1925

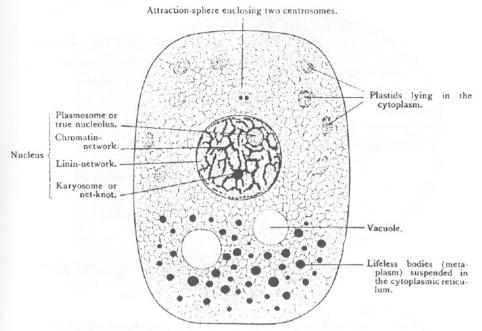


Fig. 5. — Diagram of a cell. Its basis consists of a thread-work (*mitome*, or *reticulum*) composed of minute granules (*microsomes*) and traversing a transparent ground-substance.

Fig. 2a.

the number of pages had increased to 1118, the number of figures to 529, and the approximate number of illustrations to 100 pages had risen to around 47. In addition, the illustrations in the last edition were on average more abstract, with tables, schematic diagrams, and graphic presentations of data relatively more common than in the first edition. The question is, then: what significance do these changes suggest for the role of illustration in Wilson's work and more generally? I will work through examples from each edition, taking a few samples from a sequence of developmental stages in each case. Then I shall step back to discuss just what more generally these are examples of. Yet this study remains quite preliminary and serves as a promissory note that there is more to come and as a provocation to others to enter the discussion about the use of diagrams in scientific work.²

Dedicating his book to his friend and inspiration Theodor Boveri, Wilson began with a short introduction. The first major chapter, "The General Sketch of the Cell," begins with a picture of typical cell structure. This information Wilson presented in a diagram which shows the parts of the cell and its general appearance. The third edition opens with a similar diagram, also the first in the body of the main text, but with significant revision in the light of new knowledge about the cell (Figure 2). Both show that the cell is not, as many textbooks had suggested, analogous to a monastic cell in consisting of just a

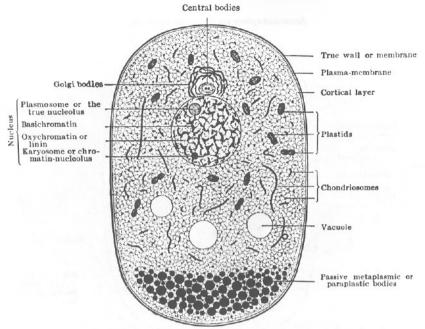


Fig. 6.—General diagram of a cell. Its cytoplasmic basis is shown as a granular meshwork or framework in which are suspended various differentiatied granules, fibrillæ and other formed components.

Fig. 2b.

Fig. 2a-b. The cell in 1896 (p. 231) and 1925 (above).

hollow or undifferentiated chamber surrounded by solid walls. Rather, each cell is a complex of distinguishable parts. By 1925, so many more parts had been identified that the text describing the basic structure of the cell as well as the number of illustrations had expanded quite considerably.

The diagram is not significantly more complex even though by 1925 Wilson had added Golgi bodies, membrane, and chromosomes. The basic parts remained nearly the same, yet the pictures nonetheless looked rather different. Both are abstract and sketch in much of the background detail. But by 1925, the picture looks less schematic and a bit more specific, more like a real individual cell might look. Simple changes such as making the plastids different sizes and shapes, or in other words making them more specific, create this effect. It seems that as Wilson became more certain about the morphology of the cell, he represented it more abstractly but also with greater detail and specificity. Wilson's next step was to look inside the cell.

Most fundamentally, each cell is filled with protoplasm, and so Wilson turned to the nature of this material. The not quite four pages of text in 1896 had expanded to twenty-two in 1925 to deal with the wealth of new information and detail, and the illustrations had changed accordingly. In particular, in 1896 Otto Bütschli's theory that protoplasm has an essentially alveolar structure, like an

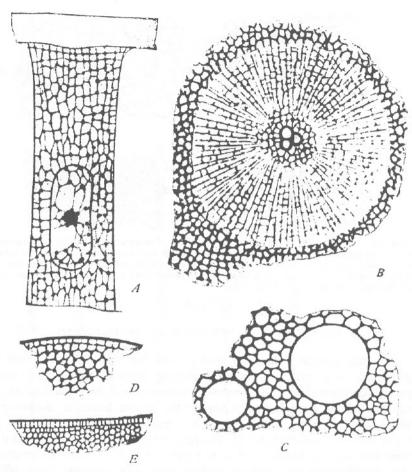


Fig. 8.—Alveolar or foam-structure of protoplasm, according to Bütschli. [BÜTSCHLI.]

A. Epidermal cell of the earthworm. B. Aster, attraction-sphere, and centrosome from seaurchin egg. C. Intra-capsular protoplasm of a radiolarian (Thalassicolla) with vacuoles. D. Peripheral cytoplasm of sea-urchin egg. E. Artificial emulsion of olive-oil, sodium chloride, and water.

Fig. 3a.

artificial emulsion, dominated. Thus in 1896, Wilson included as his primary illustration of protoplasm one of Bütschli's drawings, which represented his theory (Figure 3a). In addition, the closest generalized offering (Figure 3b) depicts a more abstract view of the regular structure of protoplasmic material. This diagram demonstrates that no one general view of protoplasm in all species had emerged. Presumably, the representation was accurate since it was Bütschli's own. Yet Wilson clearly held that this theoretical representation held a different, less secure status than his more direct depictions of the cell, for example.

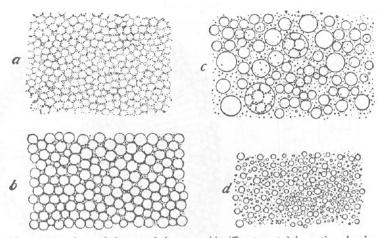


Fig. 28.—a, protoplasm of the egg of the sea-urchin (Toxopneustes) in section showing meshwork of microsomes; b, protoplasm from a living starfish egg (Asterias) showing alveolar spheres with microsomes scattered between them; c, the same in a dying condition after crushing the egg; alveolar spheres fusing to form larger spheres; d, protoplasm from a young ovarian egg of the same (all the figures magnified 1200 diameters).

Fig. 3b.

Fig. 3a-b. Protoplasm from 1896 (p. 233) and 1925 (above).

By 1925, Bütschli's dominant theory about the nature of protoplasm had given way to a variety of distinct competing theories, with no one clearly prevailing. There simply was not enough evidence available. "The fundamental structure of the protoplasm lies beyond the present limits of microscopical vision," Wilson wrote, and it "hence still remains a matter of inference and hypothesis" (Wilson 1925, p. 77). As a result of the uncertainty, he included the same drawing from Bütschli, but no new picture claiming to show *the* structure.

In the life cycle, once cells exist, they undergo reproduction. Thus, Wilson soon discussed the nature of germ cells. Here emerges a significant difference in the way he presented the information and ideas in the two editions under discussion. The first edition provides sketches, apparently made with a camera lucida, of germ cell formation. In particular with the spermatozoa, these are presented as individual cases, clearly from a number of different organisms. There is no claim that any one is typical in any way or that the information is generalizable across species. By 1925, that had changed, and Wilson had generalized to typical cases. At the same time, he also provided more specificity for each of the abstract types. This suggests that with more information and greater confidence in the interpretation, Wilson provided both a more abstract and more specifically detailed representation.

In addition to collections of illustrations of individual spermatozoa and eggs, in 1925 Wilson presented schematic diagrams of the types of sperm formation and egg formation (Figure 4). The sperm formation drawings apparently reflect

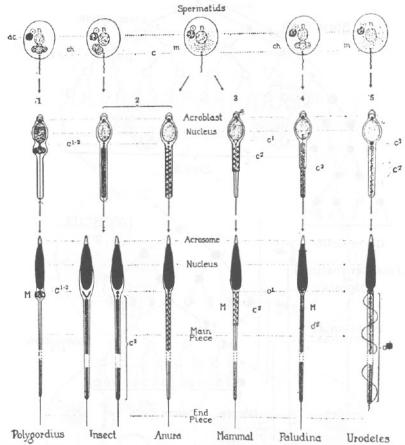


Fig. 173.—Diagram of various types of sperm-formation; c^1 , the proximal centriole or its products, c^2 , the distal.

Fig. 4a.

his increased confidence in the generality of the phenomena, and they provide a new organizational framework for such cell types. At the same time, he also included more specificity for each of the abstract types. While giving more information and a more detailed and specific picture of each type, the types are now presented as abstract and clear-cut. Perhaps surprisingly since abstraction and specificity may seem to be antithetical, abstraction away from detail of the separate individuals goes hand in hand with greater detail of the separate types. What this suggests is that Wilson had become more confident about the generalities of observable facts and also the theoretical explanation of the particular data.

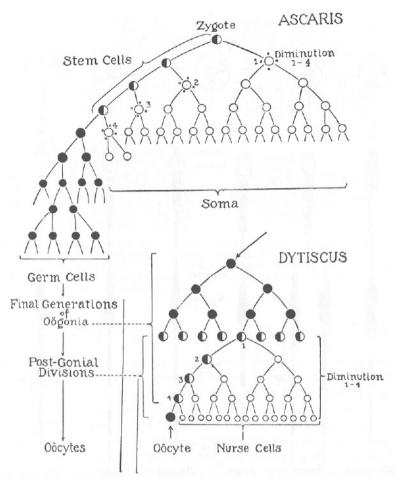


Fig. 146.—Diagram comparing the diminution-periods in Ascaris and in Dyliscus (based on the observations of BOVERI and GIARDINA).

In Ascaris it occurs during four cleavages, from the second to the fifth inclusive; in Dytiscus during the last four cleavages of the oögonia.

Fig. 4b.

Fig. 4a-b. Sperm and oocyte formation in 1925.

With egg cells, Wilson had already begun to generalize in 1896 and extended and revised his interpretation by 1925. In both cases, he was following closely the conclusions that Boveri had drawn from his work on the thread worm Ascaris. In addition, he succeeded in his larger goal of reflecting the best generally accepted views of the time. In the first edition, for example, he cautiously responded to the general uncertainty about meiosis, concluding only that "In some manner, therefore, the formation of the polar bodies is connected with the process by which reduction is effected. The precise nature of this

GENERAL SKETCH

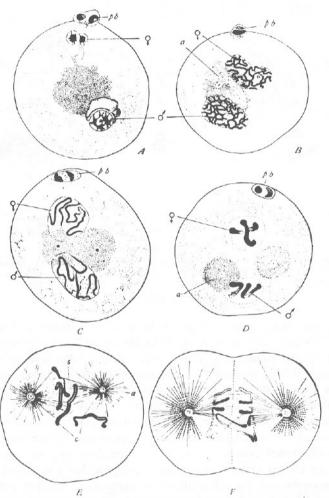


Fig. 65. — Fertilization of the egg of Ascaris megalveephala, var. bivalens. [BOVERL] (For later stages see Fig. 104.)

A. The spermatozoon has entered the egg, its nucleus is shown at β ; beside it lies the gramular mass of "archoplasm" (attraction-sphere); above are the closing phases in the formation of the second polar body (two chromosomes in each nucleus). B. Germ-nuclei $(\hat{\mathbf{Y}},\hat{\mathbf{Z}})$ in the reticular stage; the attraction-sphere (a) contains the dividing centrosome. C. Chromosomes forming in the germ-nuclei; the centrosome divided. D. Each germ-nucleus resolved into two chromosomes; attraction-sphere (a) double. E. Mitotic figure forming for the first cleavage; the chromosomes (c) already split. E. First cleavage in progress, showing divergence of the daughter-chromosomes towards the spindle-poles (only three chromosomes shown).

Fig. 5. Fertilization in 1896.

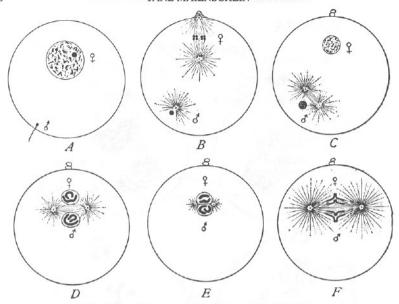


Fig. 187.—Diagram of Ascaris type of fertilization.

A, unmatured egg, entrance of sperm; B, sperm-aster and first polar spindle; C, sperm-amphiaster, polar divisions completed; D, union of the pronuclei; E, ensuing "pause," reduction of asters; F, first cleavage-figure.

Fig. 6. Fertilization in 1925.

process is, however, a matter which has been certainly determined for only a few cases." (Wilson 1896, p. 176) By 1925, Boveri had generated significantly more detailed understanding of which stages involve what sorts of divisions. And although Wilson presented the information for two different species, the text makes it clear that he believed that this mode of cell division, with only a few typical modifications, held quite generally.

The next stage of development, fertilization, brought the reader to the subject matter of *An Atlas*, which had just recently appeared in print. What Wilson offered as his central example in the first edition, however, was not from his own work on the sea urchin *Toxopneustes variegatus* but a sketch of Boveri's conclusions on *Ascaris*. The information was presumably, as he put it elsewhere, "drawn from life," through the microscope and perhaps with a camera obscura (Figure 5). In 1925, he provided instead simplified diagrams of the types of fertilization (Figure 6).

What had happened in the thirty intervening years was the progressive refinement of knowledge that allowed Wilson to gain certainty in his interpretations and representations. The higher level of abstraction and schematic simplifications in his last edition reflects that greater reliability of interpretation. Yet once again, the more confident, more abstract diagram also provides more specificity of detail. We see precisely what the spindle fibers, for example, are doing.

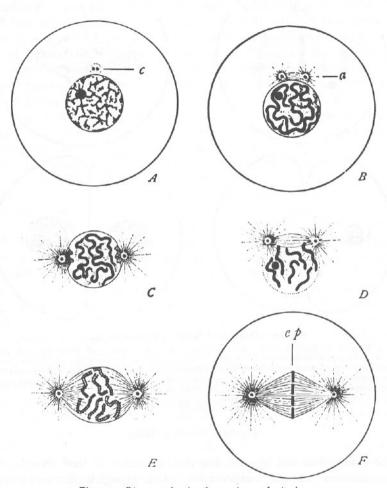


Fig. 19. - Diagrams showing the prophases of mitosis.

A. Resting-cell with reticular nucleus and true nucleolus; at ε the attraction-sphere containing two centrosomes. B. Early prophase; the chromatin forming a continuous spireme, nucleolus still present; above, the amphiaster (a). C.D. Two different types of later prophases; C. Disappearance of the primary spindle, divergence of the centrosomes to opposite poles of the nucleus (examples, many plant-cells, cleavage-stages of many eggs). D. Persistence of the primary spindle (to form in some cases the "central spindle"), fading of the nuclear membrane, ingrowth of the astral rays, segmentation of the spireme-thread to form the chromosomes (examples, epidernal cells of salamander, formation of the polar bodies). E. Later prophase of type C; fading of the nuclear membrane at the poles, formation of a new spindle inside the nucleus; precocious splitting of the chromosomes (the latter not characteristic of this type alone). E. The mitotic figure established; e.p. The equatorial plate of chromosomes. (Cf. Figs. 16, 21, 24.)

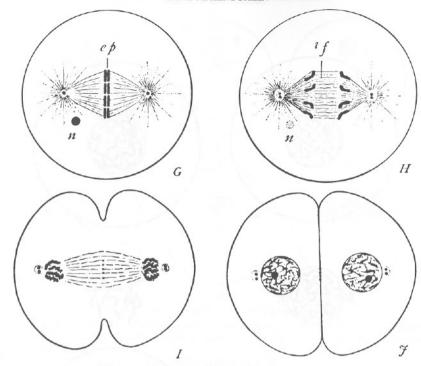


Fig. 20. — Diagrams of the later phases of mitosis.

G. Metaphase; splitting of the chromosomes (e, p,); n. The cast-off nucleolus. H. Anaphase; the daughter-chromosomes diverging, between them the interzonal fibres (i, f), or central spindle; centrosomes already doubled in anticipation of the ensuing division. I. Late anaphase or telophase, showing division of the cell-body, mid-body at the equator of the spindle and beginning reconstruction of the daughter-nuclei. \mathcal{T} . Division completed.

Fig. 7b.

Fig. 7a-b. Mitosis in 1896.

These simplified and abstract diagrams, he seems to have thought, were appropriate now that he felt confident that he knew enough to offer his interpretations as general knowledge worthy of reliable textbook presentation. Since we know that he regarded diagrams as interpretive and since he had made clear that he wanted this text to offer the best possible compendium of fact and alternative interpretations without prejudging any questions, certainly he intended the interpretation to present established fact, that is the best and most reliable knowledge available. Beyond such direct depictions, he also began to realize that diagrams serve to represent theory. Yet for Wilson, a good theory still had to be closely grounded in significant empirical data, should not go far beyond that data, and must remain tentative and always subject to revision in the face of new data. By 1925, fertilization theory (about the morphological changes in fertilization) had achieved such a status.

Relatively little had changed with respect to his understanding of the general patterns of mitosis, except that further cytological studies had added some detail

and clarification about just what was happening in each stage. These revisions and additions appear in parallel diagrams in each edition (Figures 7 and 8). The result was actually a loss of generality so that by 1925 Wilson thought it necessary to present two sets of data for what he then saw as two distinguishable types of mitosis. This bifurcation became necessary only after new observations showed greater specificity of detail in spindle fiber and chromosome changes in different types of organisms. No substantial change in theory about mitosis had occurred during this time.

In contrast, understanding of the chromosomes and their movements and changes was certainly an area in which much had changed. Chromosomal structure and changes thus provide a striking example of the effects of accumulating knowledge and a resulting increasing abstraction and yet also specificity. In 1896, Wilson was grappling with recent new information from cytological studies about chromosomes. It appeared that these nuclear structures might have some ontological reality, that is persist throughout the various cell divisions and other changes through which the cell passes. As Wilson put it, despite skepticism and even direct opposition, "The opinion is nevertheless gaining ground that the chromatin-granules have a persistent identity and are to be regarded as morphological units of which the chromatin is built up" (Wilson 1896, p. 27). Yet that "opinion" was not at all clearly established yet. As a result, though he provided a discussion of emerging views about the chromosomal role in mitosis, in 1896 his depiction of chromosomes remained rather generic. In other words, he treated the chromosomes as all pretty much the same, with each as a separate but not necessarily differentiated unit. He was not sure about their individuality or significance and so did not represent them as having any such differentiation. This was necessary since he sought to present in his textbook only what he felt was well-established and reliable knowledge.

By 1925, of course, the situation had changed radically. The first decade of the new century had brought considerable evidence for the individuality of the chromosomes – evidence provided especially by Wilson's friend Boveri and his student Walter Sutton.³ In addition, evidence accumulated in the laboratory of Wilson's friend and colleague at Columbia Thomas Hunt Morgan. Morgan and his students reinforced the conclusion that the chromosomes are actually differentiated in important ways. It was most reasonable to conclude that each has a different makeup and holds a different significance for the development of the organism.

In addition, shortly after the publication of Wilson's first edition, Mendel's work had been rediscovered and Mendelism had emerged. Though not persuading many at first, by 1925 various versions of Mendelism had come to dominate biology. Therefore, both the chromosomal studies and the Mendelian interpretations of heredity called for substantial revision of Wilson's work. In fact, he had adopted such a careful approach from the beginning that he had to "take back" very little. Instead, what he did was largely to fill many of the numerous gaps which had required him before to conclude quite often that "we do not know as vet."

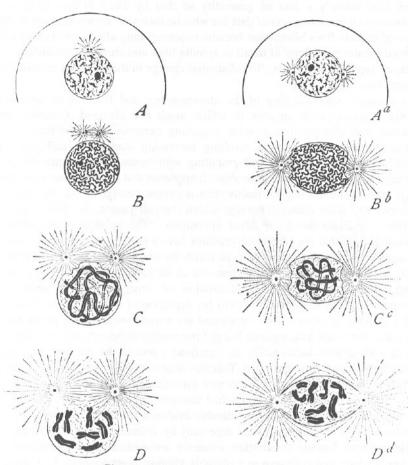


Fig. 45.—Diagram of the prophases of mitosis.

A-D, "Type A," (Ascaris); A^a-D^d, Type B (sea-urchin).
A, vegetative nucleus; B, fine spireme; C, coarse spireme; D, late prophase with chromosomes, spindles forming.

Fig. 8a.

By 1925, the Mendelian-chromosomal interpretation of heredity and development had become sufficiently well established, and Morgan and others had produced a sufficiently widely recognized way of presenting both data and theoretical interpretations of the data that Wilson adopted the same general approach. For example, he added a schematic diagram to illustrate what happens with each of the chromosomes in the course of fertilization during sexual

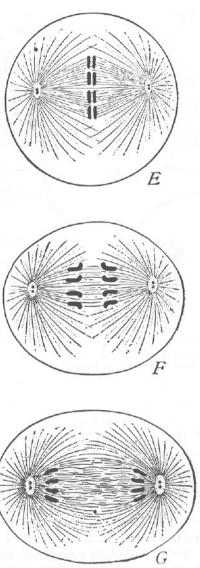


Fig. 46.—Diagram of the middle phases of mitosis.

E, metaphase; F, G, earlier and later anaphases.

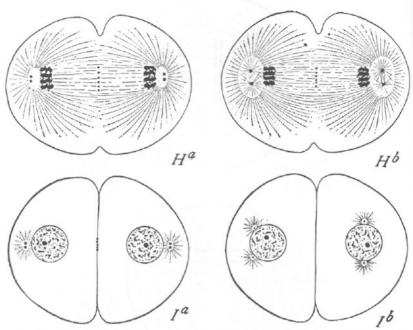


Fig. 47.—Diagram of closing phases of mitosis. II^a and I^a, "Type A"; II^b and I^b, "Type B"; I^b showing two slightly different conditions in the interphase.

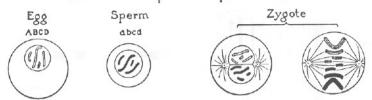
Fig. 8c.

Fig. 8a-c. Mitosis in 1925.

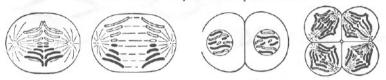
reproduction (Figure 9). Another showed the various typical ways in which chromosomes become attached during mitosis (Figure 10). Both of these are highly abstract and even stylized, yet they are also highly specific and give all the available information that is reliable and holds for all cases.

Figure 11 moves yet a step further, going beyond the observable data into the admittedly theoretical world. As Wilson pointed out, this diagram could be taken as representing either chromosomal units of heredity or theoretical hereditary factors. It shows how the individual units come together, recombine, and go on to produce variations in the next generation of gametes. If this is taken to represent diagrammatically what the chromosomes do, it still involves a good deal of interpretation since the observer certainly cannot actually see these chromosomes recombining at each of the stages. Thus the diagrams move further away from "fact" and become more recognizably representations of theory. Yet at least it was possible to gather *some* direct observational evidence, as Wilson and others recognized the existence of different individual

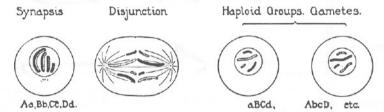
FROM PRESENTATION TO REPRESENTATION Union of the Haploid Groups. Fertilization.



Division of the Diploid Group. Mitosis.



Reduction of the Diploid Groups to Haploid. Meiosis.



Recombinations in Fertilization.



Fig. 102.—General diagram of the chromosome-cycle in animals, the haploid groups assumed to contain four chromosomes of different sizes. Paternal and maternal chromosomes in white and black respectively. Complete gonomery of the diploid groups in the initial stages, later lost. Only two of the 16 possible chromosome-combinations in the gametes shown (cf. Fig. 105), and only seven zygote-combinations out of 256 possible ones.

Fig. 9. Chromosome cycle in 1925.

chromosomes which they then could follow – in studying killed and prepared cytological sections – through the various developmental stages. This representation then provided the best interpretation of the available data.

The claim that the diagram also could be taken as representing the mixing of hereditary Mendelian factors rested on different grounds. Here it was indirect evidence alone that supported a Mendelian interpretation. Wilson could in no way be illustrating something observed. Rather he was diagrammatically representing theoretically derived interpretations. He had avoided such inter-

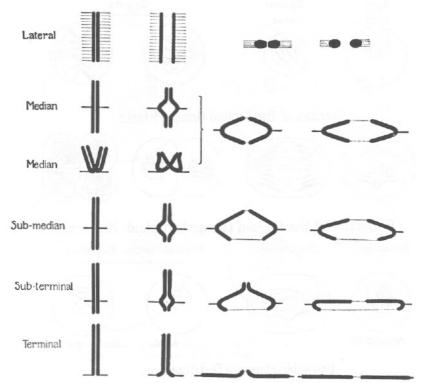
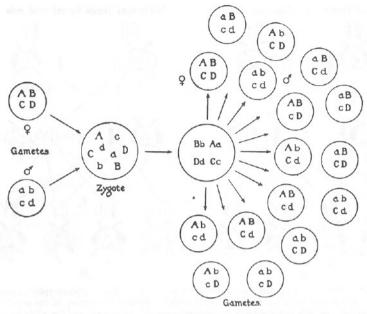


Fig. 56.—Types of chromosome-attachments and their results during the somatic mitoses. The spindle-über attachments indicated by fine lines.

Fig. 10. Types of chromosome activity in mitosis in 1925.

pretations beyond the evidence in the first edition, and it is a sign of his certainty about the strength of the evidence in favor of the chromosome-Mendelian interpretation that he presents it so confidently in the third edition. But since he was seeking to provide a compendium of the very best data and interpretations available at the time and since Mendelism had gained wide (though by no means universal) acceptance, his decision to represent theory rather than simply to present "fact" made sense.

It is worth pausing here to consider the implication of Wilson's turn to such schematic and highly theoretical diagrams. This particular example raises questions about just what role the diagram itself played in Wilson's thinking. The examples discussed so far have been relatively straightforward efforts on Wilson's part to capture the most reliable available data and to represent them consistently with the most well-established theory. His illustrations have stuck very close to what he saw as the facts. Here that changes in important ways.



Recombinations with Independent Assortment.

Fig. 105.—Diagram applicable either to chromosomes or to hereditary factors, to show Mendelian segregation and independent assortment. (Linkage phenomena are here left out of account.) Maternal components (chromosomes or factors) in capitals, paternal in small letters. The haploid number assumed to be four (cf. Fig. 102).

Fig. 11. Chromosomes or hereditary factors in 1925.

Because of the impossibility of studying movements of parts of chromosomes or their effects on inheritance of characteristics, Wilson had no reliable data of the sort that he preferred. He could not rely on direct observation and then illustrate what he saw in the most reliable way. To generate a diagram at all, he had to look past the observable to the theoretical.

The particular result is instructive. There is no A, b, c or D out there in the world, for example. Yet Wilson followed his friend Morgan's suggestion that it will fit the evidence and the theory if we represent chromosomes as if they were abstract A, b, c, D's. Capital letters represent maternal contributions, small letters the paternal. The diagram illustrates the way chromosomes recombine during fertilization and undergo division during subsequent cell divisions. We cannot see this happening, but the chromosomes theory says it does and the theory fits with the available (indirect) evidence. Therefore, the schematic representation gains the status of sufficiently reliable knowledge to fit within the textbook.

For Wilson, who had early on remained skeptical about the existence and nature of Mendelian factors, this part of the diagram may have held useful

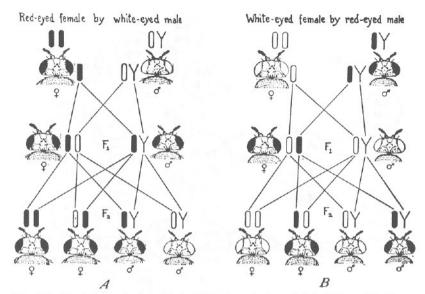


Fig. 444.—Sex-linked and criss-cross heredity of a pair of sex-linked allelomorphic characters, dominant red-eye and recessive white eye, in Drosophila, showing the history of the sex-chromosomes X and Y. In each case the black X-chromosome stands for red-eye and the white for white-eye (Morgan).

A, the result of crossing female red-eye with male white-eye. By crossing white-eyed males with heterozygous females may be obtained homozygous white-eyed females (shown in B).

B, the reverse cross, showing criss-cross heredity, the F_1 daughters like the father (red-eyed) and the sons like the mother white-eyed.

Fig. 12. Character crosses in 1925.

analogic value as well as representing what he thought he already knew. For it also makes sense of the existing Mendelian theory and also fits the available (indirect) evidence. Just substitute "factors" for "chromosomes." Since with chromosomes there is at least something to see and to build from, accepting a parallel with completely invisible factors helps to strengthen the Mendelian theory. For now the reader can visualize, by analogy, how the Mendelian factors might act in fertilization and cell division.

There is no evidence that Wilson himself actually reasoned in this way, from chromosomes to Mendelian characters, though it seems plausible that the analogy may have helped to strengthen his willingness to accept Mendelism. It does seem clear, however, as the text shows as well, that he wanted the readers of his textbook to understand the parallel. That factors act like chromosomes would help people understand both. In addition, some philosophers of science have argued that the existence of such an analogical model can give the new theory (the Mendelian in this case) predictive power that it would not have had otherwise as one plays out the implications of the analogy.⁴ Wilson may have hoped for such an effect, to help strengthen both the chromosome and the

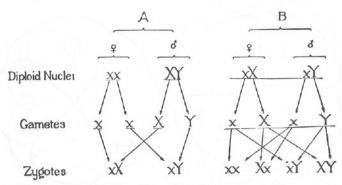


Fig. 443.—Diagrams of sex-linked heredity and the X-chromosome; X is assumed to bear the factor for a dominant and x that for its recessive allelomorph.

A, criss-cross heredity. The homozygous recessive female $xx \times t$ the dominant male XY, gives F^1 daughters xX, showing the dominant paternal character and sons xY showing the maternal recessive. B, the F^1 offspring crossed together give the grandparental and the F^1 forms in equal numbers.

Fig. 13. Abstract crosses in 1925.

Mendelian theories with his diagrammatic juxtaposition. He may well have intended both a heuristic and pedagogical effect with his diagrams in 1925, whereas those of 1896 remained primarily pedagogical. The diagram therefore suggests a different level of confidence for Wilson – not just in the observed facts but in the explanatory and predictive success of the theory.

The same sort of confidence underlies his including diagrams borrowed from Morgan to illustrate Mendelian crossing (Figure 12). Morgan's illustration of *Drosophila* eye color combined an abstract diagrammatic representation and the effort to make the schematization more "real." Thus, factors are represented as black or white colored ovals, and the crosses by lines. But sketches of fly heads also remain to show what the resulting living fly would really look like. Wilson's own abstract representation of the idea (Figure 13) does not rely on this device. In fact, much of what Wilson added to the third edition concerns positive assertions about the nature of the chromosomes, discussion of what they do in heredity, and the significance of such ideas for what Wilson saw as the vitally important chromosome-Mendelian interpretation. Without the fly eye pictures as a guide, the reader can stretch beyond the abstract lines and letters to imagine a wider range of examples and even to predict the effect for characteristics not discussed at all.

After mitosis and fertilization, cell cleavage provides the next subject of central interest. In fact, Wilson spent much of the mid 1890s examining the way that cells divide and the evolutionary significance of such divisions. He had, by 1896, developed a standard for presenting information derived from observa-

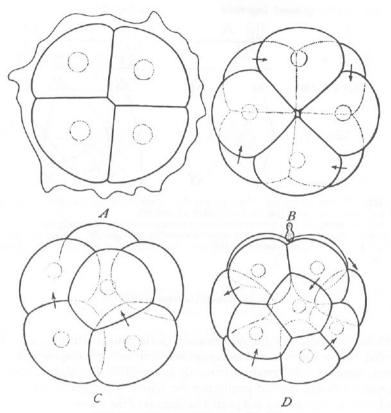


Fig. 121. — Cleavage of *Polygordius*, from life.

A. Four-cell stage, from above. B. Corresponding view of 8-cell stage. C. Side view of the same (contrast Fig. 120, C). D. Sixteen-cell stage from the side.

Fig. 14. Abstract changes in 1896.

tions of cell lineage. This was a standard adopted by others working in the line of research, which examined in excruciating detail and with meticulous care the patterns of each cell division beginning with the fertilized egg (Figure 14).

Wilson continued some of his cell lineage studies into the first decade of the new century, as did a number of other primarily American embryologists, and he provided similar, though increasingly detailed, illustrations for each. By 1925 he had also introduced something new, namely the attempt to capture diagrammatically the mechanical changes during those cell divisions. A comparison with soap bubble models, for example, shows the parallel to development in the *Trochus*, while a schematic diagram shows which parts of the egg move to produce the resulting subsequent cells, in this case as a result of spiral cleavage (Figure 15).

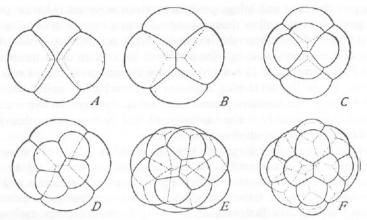


Fig. 461.—Soap-bubble models of cleavage-figures in *Trochus*. Compare Fig. 464 (ROBERT). A and B, models of 4-cell stages; C, D, 8-cell models; E, 12-cell model; F, 16-cell model.

Fig. 15a.

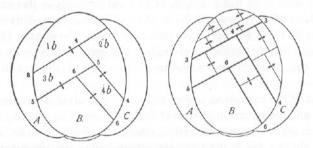


Fig. 463.—Diagram of the quartet-formation in spiral cleavage.

A, the four primary quadrants, showing the plan of formation of the first four quartets, $_1b$, $_2b$, $_3b$, $_4b$, in the B-quadrant. Successive cleavages from the third to the sixth indicated by numerals, $_B$, scheme showing the subdivisions of the quartets up to the 64-cell stage. Displacements of the cells not shown.

Fig. 15b.

Fig. 15a-b. Cleavage representations in 1925.

Once again, we see Wilson's move to increasing abstraction based on a solid base of reliable evidence. Once again also, we see him going beyond a striaghtforward presentation of his data to a representation of a more theoretical view. He can discuss parallels between cell cleavage patterns and soap bubble division in the text, but the diagrammatic representation makes the analogy strikingly clear and even allows us to suggest theoretical explanations about cells based on our knowledge of soap bubbles. Thus, we see that cleavage behaves like soap bubbles do. This carries with it broad implications about how

to interpret the facts and brings predictions about expected behavior as well. These predictions may allow the researcher to extend beyond the available data and even beyond the observable to predict what occurs deep inside the organism, of mechanical necessity. The additional illustrations of the mechanics of quartet formation (Figure 15 bottom) reinforce the interpretation and encourage the reader to see the developing organism as a mechanical object underlying physical change. The diagrams present information, represent the best interpretation, and simultaneously invite extension of that best available theory well beyond the observed or even observable data.

A wide variety of other diagrams, drawings from life, graphs of various sorts of data points, and lists of established references and conclusions fill the rest of each volume. They cover every accessible stage of cell structure and some functioning, as Wilson intentionally retained his morphological rather than physiological emphasis. Both versions of *The Cell* remain classics, each serving as the best record of ideas and evidence at its time.

CONCLUSIONS

What do we learn from this example, or of what precisely is this case a case? Clearly, Wilson relied heavily on illustrations of various sorts. This was typical for textbooks by 1925, but there were relatively few similar texts in 1896. It may well have been true that Wilson's exemplary and enthusiastically reviewed first edition set the standard and influenced the style of illustration for later textbooks.

While part of the expansion in the third edition involves the addition of new information and the inclusion of a great deal more detail and more examples to illustrate each point, the most interesting changes probably lie in the addition of much more abstract but at the same time more highly specific diagrams. This apparent tension between abstraction and specificity arises because of the increasing abstraction with respect to general features and the specificity of more of the shared features. In the early stages of research, Wilson tried to identify just the fewest details that seemed important but tried to present them realistically. With increased knowledge, he provided more detail in abstract form as long as it held generally.

In addition, Wilson turned to more schematic and abstract diagrams when he felt more certain about his facts and their proper interpretations. While there are cases in the first edition in which he presented some observations "from life" and the text makes clear that he regarded their interpretation as not at all clear, by the third edition he had become much more confident about many points. The text reveals an established interpretation with which Wilson apparently felt comfortable; at the same time the diagrammatic representation becomes more abstract and schematic. They move, that is, from presenting data to representing theory.

This was especially true of his discussion of the necessarily theoretically

based ideas such as Mendelism. By 1925, the Mendelian and the chromosome theories had become sufficiently familiar and were accepted as sufficiently well established that Wilson was willing to rely on quite abstract diagrams to convey the essential points. In addition, he used a new kind of schematic presentation (such as in Figure 11) to provide new knowledge even about things that he could not see.

Apparently, Wilson did come to feel increasingly comfortable with doing the sort of interpretation which he recognized necessarily always accompanies the presentation of diagrams. Of course, he also realized that interpretation is involved in drawings as well, but presumably the use of a camera lucida and a resolute desire to "present the facts" could serve as more of a corrective if the drawing remained as close to the observed facts as possible. In abstracting part of an observation for presentation in a diagram, much more interpretation was required, with the incumbent dangers. But he saw the advantages and apparently recognized that in representing less detailed factual information, he could actually present more knowledge. Thus the changes from the first to the last editions reflect his increasing certainty about what he saw, the increase in the sheer volume of observationally-based knowledge, but also a greater sophistication on Wilson's part in recognizing the pedagogical – and perhaps also heuristic – value of less rigorously observation-based diagrams.

Wilson did not follow the line which his *Atlas* might have suggested and which many modern publications seem to have adopted, that scientific work should always offer photographs since they provide the closest possible representation of the real thing. Rather, he seems to have recognized the value of adopting a variety of modes of illustration. Indeed, he knew that there are times when a schematic and abstract diagram is preferable to the confusion which exists in a photograph. One can actually depict the essence of the idea better with a diagram in some cases. Photographs and drawings present the "facts" themselves, while diagrams present abstracted and generalized interpreted information and theoretical ideas. The diagrams also go beyond established fact to represent the central concepts of established cytology. For a textbook such as Wilson's, then, in which he wanted to present the best available data and interpretations, diagrams play an absolutely central abstracting and at the same time informative role.

ACKNOWLEDGEMENTS

Responses to an early draft of this paper at the 1989 meeting of the International Society for the History, Philosophy, and Social Studies of Biology provided new ideas to guide revision. In addition, I would like to thank Peter Taylor, Michael Ruse, Jennifer Tucker, Richard Creath, and Krister Knapp for their helpful suggestions. A grant from Arizona State University has made it possible to duplicate the photographs.

NOTES

¹ The second edition in 1900 remained substantially like the first for our purposes.

² Of course, there is a vast literature on representation generally and in science particularly, as well as on abstraction. Some of the classic studies of abstracting data out of excessive detail in the production of maps, for example, are instructive. So are classic discussions such as those by Nelson Goodman and E. H. Gombrich on representation and realism/conventionalism in art. Yet much of that literature participates in one side or another of different larger debates. I have found nothing that deals directly with the use of abstraction in the production of diagrams for scientific textbooks. This study remains preliminary, but points toward the larger goal of rigorously embedding the latter discussion within the framework of the former and ongoing debates.

³ For discussion of attribution of credit for establishing the autonomy and hereditary

significance of chromosomes, see, for example, Baltzer. (1967, pp. 98–99)

⁴ For example, see Mary Hesse's delightful dialogue between Duhem and Campbell in *Models and Analogies in Science* (Notre Dame: University of Notre Dame Press, 1977), pp. 7–56.

REFERENCES

Baltzer, F.: 1967, Theodor Boveri. Life and Work of a Great Biologist, University of California Press, Berkeley, Calif.

Baxter, A. L.: 1978, 'Edmund Beecher Wilson and the Problem of Development: From the Germ Layer Theory to the Chromosome Theory of Inheritance', Ph.D. dissertation, Yale University.

Benson, K. R.: 1987, 'H. Newell Martin, W. K. Brooks, and the Reformation of American Biology', *American Zoologist* 27, 759–771.

Benson, K. R.: 1988, 'The Naples Stazione Zoologica and Its Impact on the Emergence of American Marine Biology', *Journal of the History of Biology* 21, 331–341.

Maienschein, J.: 1978, 'Cell Lineage, Ancestral Reminiscence, and the Biogenetic Law', Journal of the History of Biology 11, 129–158.

Maienschein, J.: 1987, 'H. N. Martin and W. K. Brooks: Exemplars for American Biology?', *American Zoologist* 27, 773–783.

Morgan, T. H.: 1941, 'Edmund Beecher Wilson 1856–1939', National Academy of Sciences, Biographical Memoirs 21, 314–342.

Sedgwick, W., and E. B. Wilson: 1886, General Biology, Henry Holt, New York.

Shapin, S., and S. Schaffer: 1985, Leviathan and the Air-Pump. Hobbes, Boyle, and the Experimental Life, Princeton University Press, Princeton, New Jersey.

Wilson, E. B.: 1895, An Atlas of the Fertilization and Karyokinesis of the Ovum, Macmillan, New York.

Wilson, E. B.: 1896, *The Cell in Development and Inheritance*, Macmillan, New York. (Second edition, 1900.)

Wilson, E. B.: 1925, The Cell in Development and Heredity, Macmillan, New York.