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Cytology in 1924: Expansion and Collaboration

Cytology had a bumper year in 1924, with two major books published and a third well on its way into print. Together they represented the current state of the science. But they also reveal something more. A close comparison of the second and third of these volumes shows how cytology was changing, expanding into new areas, and becoming more diverse in a way that made it difficult for any one person to handle the entire subject. This expansion of the subject and of its diverse methods of attack reflects the general expansion of knowledge, methods, and enthusiasm within biology. But it also reflects the fact that cytology in particular had reached a stage where what had been a coherent and vital field of study for more than a half century had grown so large and so diverse that it had begun to experience fragmentation and specialization. The three important textbooks that appeared in 1924 and 1925 reflect the status of the field of cell studies as well as the state of biology as a whole.

The first volume was Leonard Doncaster's second edition of *An Introduction to the Study of Cytology*. This leading British cytologist had actually died shortly after the first edition in 1920, but the work had nonetheless undergone revision and updating by assistants. As Doncaster explained in his introduction, he had not intended to provide a textbook in the usual sense. His volume was not designed to summarize known facts and offer a few inferences from them while avoiding any sustained theoretical discussions. That was the purpose of textbooks, he believed, but cytologists were not yet sufficiently unified in their interpretations to warrant such a standard text. Instead, he sought with his volume to "interest the student in the subject by pointing out some of the ways in which cytological investigation is related to the great fundamental problems that lie at the root of all biological research."[1] The organization of Doncaster's book followed his lecture series presented at Cambridge University over the course of six years, to students not previously familiar with cytology. Its chapters considered the basic biological subjects: cell definition, cell organs, cell division, the centrosome, germ cells, fertilization, parthenogenesis, sex determination, chromosomes, and heredity.

At the end of his volume, in a concluding section on the state of the field, Doncaster noted that cytology found itself in a tenuous state just as zoology had after the publication of Darwin's *Origin*. At that time, as he saw it, zoology and physiology had diverged, each pursuing separate questions. He thought that this had been to the detriment of both. Cytology now stood in a similarly precarious position, so that "if cytology is to avoid a similar misfortune, its students must keep in view the need for both the descriptive and comparative and the experimental methods, and remember that the biochemist and physicist are studying with flask and test-tube the same problems that they themselves are attacking with microscope and microtome."[2] Otherwise cytology might also fragment into diverse directions.

The second volume, Edmund V. Cowdry's *General Cytology*, agreed. By bringing together a collection of contributions by American researchers in various aspects of cytology, the edited volume sought to discuss work using both descriptive and experimental methods and work from biochemistry and physics and microscopic study, as well as examinations of both cellular structure and cellular function. The volume thereby attempted to do precisely what Doncaster urged, to keep in view the way that cytology joined different approaches and different perspectives.

Whereas Doncaster believed that a proper textbook in cytology remained premature because of the existence of so many interpretations, Cowdry's group proposed to turn the lack of a single unified view to advantage. By presenting a diversity of facts, interpretations, and methods, the volume could provide a working textbook for general cytology. Its intended audience included students of both biology and medicine, anyone concerned with the nature of the cell.

As Cowdry explained, several individuals had met at the Marine Biological Laboratory (MBL) in the summer of 1922 to begin their collective project. They had wanted to address what was known of cellular structure and function and to consider whether to attempt a cooperative study of the subjects. In particular, given the increase in information and ideas available, they debated whether they should try "to present briefly for the first time within the scope of a single volume data concerning the cell." These data and their discussions would be "fundamental, alike, to the sciences of botany, zoology, physiology, and pathology," so they decided to pursue the project and to coordinate a volume.[3] With such different approaches, and with the different background traditions from which they came, it seemed difficult to bring all the work together in one coherent volume. Some researchers emphasized cell structure using traditional morphological methods of description and comparison. Others pursued the physicochemical makeup and actions of the cells. Some stressed colloids, others chromosomes. Yet the various studies all concerned the same cells, the same fundamental units of life, and as a result a coordinated study seemed well worthwhile. Since no one person was able to cover the full range of ideas and results, the group decided to work together.

They found, Cowdry explained, that the subject "naturally fell into subdivisions." He did not also claim that these represented natural subdivision, or, in other words, that this was in any sense *the* proper way to divide up the subject of cytology. Perhaps there could have been alternative divisions instead, but this set made sense and had the advantage that an investigator at the MBL could handle each part. Each contributor could discuss his or her own line of research and offer his or her own views. This meant that different sorts of data and methods as well as varied interpretations could be included even while preserving the integrity of the whole volume. "In this way the labor involved was shared and did not fall heavily on the shoulders of any single individual. The unique opportunity thus afforded for friendly and informal consultation between the different contributors greatly facilitated the enterprise."

The fact that everyone was together at the MBL and could consult freely and easily made the project possible. And because of that advantage and "in consideration of the fact that several of the contributors had developed their lines of study by availing themselves year after year of the facilities for investigation offered at Woods Hole," the resulting book represented a major MBL effort. The volume was designed to focus on research results rather than on details of methods or historical discussion. It also provided extensive lists of references to direct readers to appropriate further study instead of attempting a comprehensive review of existing literature.

Appropriately enough, Edmund Beecher Wilson provided the introduction. Also appropriately, he devoted the first part of his contribution to some historical considerations, including a review of signal advances up to his own early years of research. Wilson was the grandest figure in cell studies by 1922. Slowed down by severe arthritis, he moved around Woods Hole on crutches, but he persisted with his research and continued to work on the third of the cytology books in 1924, the revision of his own great book, *The Cell*.[4] In his introduction to Cowdry's volume, Wilson noted several factors about the recent past: the growing cooperation between cytology and genetics in studying heredity, the increasing interest in the system of cell components and their action during histogenesis, advances in techniques to study living cells, and—most important—studies of the ways in which altered external conditions affect living cells (including artificial parthenogenesis). Over time, Wilson noted, the result had changed what had been morphological cytology into a new field of cellular biology. This had produced

> a new cytology, a new cell physiology, a new cellular embryology, and a new genetics; and these various lines of inquiry have now become so closely interwoven that they can hardly be disentangled. This much-to-be-desired result has been made possible by an always growing cooperation between lines of attack widely different in method and seemingly in point of view. Such concerted effort in cell research long seemed an almost unattainable ideal; but its realization now seems close at hand. The present book has been undertaken in hope of furthering this cooperation. In the nature of the case it is hardly possible to arrive at complete unity in a work produced by several collaborators representing widely diverse fields of research. Such a group, however, can at least bring to their task a broader and more critical knowledge of the subject than any single writer can at this day hope to command.[5]

In particular, the group as a whole could embrace both physicochemical and morphological perspectives on the cell as no one individual could hope to do. This wide scope is reflected in the selection of chapter subjects and in the overall organization of the volume. Three chapters focus on the physicochemical nature and action of the cell, two on the structure of cells, and five on cellular changes and the role that cells play in various fundamental life processes.

Cowdry's volume provides a marked contrast to the third cytological text. Wilson's own book was undergoing final revision and typesetting at the time that Doncaster's and Cowdry's volumes appeared, and was published the next year.[6] This third edition of *The Cell* followed the same basic organization as the earlier editions but also represented a much revised and extensively updated contribution. Whereas the second edition had had 483 pages, for example, the third offered 1,232 pages. And the general literature list had expanded from twenty pages to fifty-eight pages, though even then Wilson apologized that his list represented only those selected works actually cited in the text and not a comprehensive bibliography.

In his first edition of 1896 and revised second version in 1900, Wilson had sought to survey the new field of cell biology. Thirty years later, following the rediscovery of Mendel and the resulting explosion in the study of heredity, the task of providing a full survey seemed much less reasonable. In addition, the relations of cytology to the other fields of anatomy, histology, embryology, physiology and genetics, which had been recognized in 1896, had expanded to include close relations with cell physiology, biochemistry, and biophysics. This wide range of relations made cell study "so diversified that no single work could possibly cover more than a small portion of it." As a result, "extended general treatises on cellular biology have largely gone out of fashion in favor of more circumscribed works dealing with particular aspects of the subject, and thus making possible a more intensive treatment." Yet despite the difficulties, Wilson still "ventured to think that the need of a work of somewhat more synthetic type has not disappeared."[7]

Wilson's own emphasis remained concentrated on the structure of cells and their roles especially in development and heredity. Zoological cytology and embryology predominated, while physiological or biochemical concerns and botanical study of cells remained less central. Chapters in the second edition on cell division, germ cells, fertilization, chromosome reduction, cell organization, cell chemistry and physiology, cell division and development, and inheritance and development largely remained in the third. Each chapter expanded, most about doubling by adding new information and consideration of new interpretations. In addition, new chapters appeared on reproduction and sexuality and others on chromosomes. These Wilson saw as the major areas of advance calling for inclusion.

Many of the subjects in Cowdry's volume received little attention in Wilson's. Even those included in both books, such as heredity, fertilization, and differentiation, were approached very differently. Where Wilson's book offered a meticulously detailed consideration of as wide a range of existing literature on his subjects as possible, Cowdry's included deeper exploration of several selected sets of facts, methods, and ideas. Where Wilson sought to remain judicious in his consideration of alternative theories, contributors to Cowdry's volume willingly advocated their various theoretical interpretations. While Wilson necessarily provided one particular judgment and one set of biases, the cooperative project brought together a mixture of alternative views. In the face of expanded knowledge, the two works offered interestingly different sorts of synthetic treatments of cell biology.

A Comparison of *General Cytology* and *The Cell*

In order to demonstrate the way in which Cowdry's volume differs from Wilson's, it is useful to adopt a closely descriptive and comparative approach. This will allow a careful look at each subject addressed and an examination of the data discussed, the approach, and conclusions. Since the authors in Cowdry's volume wrote their contributions expressly for this special volume, many of the papers have a somewhat different flavor than the usual professional publications by the same scientists. Here they consciously seek to reach a wider audience in both biology and medicine. Some provide relatively straightforward surveys. Others also bring more general themes and theoretical considerations into the discussion than they typically would have.

The list of contributors to Cowdry's volume includes the MBL leaders, who were also national leaders in these areas of cytology and physicochemical studies of cell processes. All members of the group had their Ph.D. degrees, except for the Lewises. Warren Lewis had received an M.D. from Johns Hopkins, and Margaret Lewis (formerly Margaret Reed) had received her B.A. from Goucher College and had then continued at Bryn Mawr for a year. Only Robert Chambers had gone abroad for his degree, the rest studying at Columbia (Albert Prescott Mathews), Pennsylvania (Merkel H. Jacobs), Chicago (both Frank Rattray and Ralph Lillie, Edmund V. Cowdry, Ernest Everett Just), Johns Hopkins (Edwin Grant Conklin, Thomas Hunt Morgan), and Kansas (Clarence E. McClung). Many had published or were soon to produce major texts in one or another cytological field, and all published extensively.

Aside from Wilson, the oldest of the group were Conklin (at fifty-nine) and Morgan (fifty-six), whereas the youngest was the editor (Cowdry at thirty-four). The others ranged from nearly forty to their early fifties. Most worked at leading research centers around the country, though not all in traditional university settings. For example, Ralph Lillie had moved to the Nela Research Laboratory in Cleveland after having taught at several schools including Pennsylvania and Clark University. Cowdry had taught at the Peking Union Medical College before he returned to the United States and moved to the Rockefeller Institute for Medical Research in 1921; Margaret Lewis worked in her husband's laboratory at Johns Hopkins Medical School. And Ernest Everett Just taught at Howard University rather than at the sort of major research institution he would have preferred.[8]

All were regulars at the MBL. Conklin and Morgan had spent most of their summers there since their graduate school days. Indeed, both had served in nearly all capacities there: teaching courses, giving public lectures, serving as trustees, actively working with fund raising, and introducing new generations of graduate students to the community by taking them along for summers of research activity. Frank Lillie had served as right-hand man to the first director, Charles Otis Whitman, since the 1890s and had become assistant director and then director of the laboratory. As his student, Just had also become part of the MBL group each summer by the 1920s, as had Ralph Lillie. McClung had probably joined the group during the time he visited Columbia to work with Wilson, as had Mathews during his studies at Columbia. Warren and Margaret Lewis were friends of Ross Harrison, another active MBL member and trustee from Johns Hopkins, and they had participated in earlier special programs related to their work on tissue culture and neurobiology. Jacobs became a trustee and then the third MBL director when Lillie retired, serving in that role from 1926 to 1937. Clearly, this group represented something like a "ruling class" at the MBL, and its interest in cytology reflected one of the central interests of the institution.

Cell Chemistry

The first chapter of Cowdry's volume following Wilson's introduction was Albert Prescott Mathews's on cell chemistry. The general chemistry and physiology of the cell was a subject that Wilson felt incompetent to discuss in full and which, as a result, he felt remained to be explored. Yet in his 1925 edition, Wilson looked briefly at colloidal theories of the cell and followed Jacques Loeb's suggestion that the cell operates essentially as a chemical machine that transforms food materials into living and functioning form. In a short half chapter, Wilson considered the available evidence about the chemical nature of the various cell parts, including the nuclear and chromosomal elements. There he offered his only brief direct references to Mathews's work, that on the nature of nucleic acids. Wilson also said little in his book about physics or about the special chemical nature of living cells, though he did insist that *organization* rather than some vital substance distinguishes life from nonlife. In effect, form characterizes living matter, but Wilson did not attempt further to define life.[9]

In marked contrast, Mathews directly tackled questions about the nature of life. He moved beyond solid reporting of data and research methods to enter the exploratory spirit of the volume by giving vent to some interpretive speculations. Mathews had taught a course on cell chemistry at the University of Chicago and presumably had developed his broader picture of the cell in that context. His essay begins by pointing out that physics and chemistry had only recently begun to provide much help for study of the cell. Recent advances had made such an enormous difference that the biochemist could, in fact, begin to make sense of the cell as a machine. Specifically, and here he disagreed with Loeb's chemical emphasis, Mathews believed that it is an electrical machine. This knowledge transformed the biochemist into an engineer, Mathews believed, though an engineer in the process of becoming rather than an accomplished expert since he could take the electrical and mechanical system apart but could not yet put it together again. Making repairs and creating similar living machines must wait.[10]

According to Mathews, to reach these constructive goals requires understanding that "most characteristic" element of living things, namely the "psychic element." Psychism must be part of the biochemistry of the cell, Mathews insisted, for without it the cell would be like *Hamlet* without Hamlet. The psychic component is just as much a part of nature as gravity or inertia, so that the biochemist must be part poet and part psychologist as well as an electrical engineer. This psychic element might well be particulate, he suggested, like matter, light, and energy. Or it might not. Yet he did not intend to suggest any sort of metaphysical dualism, for at its root life, like the physical world, is made up of material substances.

Beyond the psychic, Mathews provided a list of facts that any theory about the chemistry of cells must also explain. For example, the fact that life ceases without oxygen, or, in other words, that living protoplasm must be in a state of partial oxygenation—this is fundamental to understanding life. The ability of cells to grow by synthesizing proteins and other substances is likewise vital. So is the capacity of living things to generate electrical currents. These, then, are the "fundamental phenomena to be explained."[11] And they should be attacked through a coherent look at all the phenomena together within the context of one theory. It was particularly important for Mathews that any theory must correlate all the facts together in order to be considered successful.

Turning to physics in his lengthy essay, Mathews explained that electrons make up life. They are then organized into atoms and, further, into molecules. These bundles of moving electrons make up tiny "universes" which move through space. Yet Mathews argued that this space is not empty, as contemporary physics suggested, but is instead filled by an ether. In describing the ether and its importance, Mathews appealed to Sir Oliver Lodge's popular 1902 volume, *The Ether of Space*.[12] Living things are little universes, Mathews agreed with Lodge, with space filled with the luminferous ether. Science must study the interaction of ether and matter, he insisted, not only to understand life but also to understand physics and chemistry. "For life illumines physics and chemistry just as truly as physics and chemistry have illumined physiology and psychology. There is more in matter than meets the eye." Further, ether is space multiplied by time; ether is infinity and eternity; ether consists of particles called etherions; and ether is not a mere metaphysical construct but is a "real physical, as well as perhaps a psychic entity." Within ether, energy is an "etherial flux or motion" and is somehow "the same as mass," both being a rotation in the ether. And molecules exist within the ether, as systems of atoms.[13] Lodge's eloquence, itself inspired by Ernst Haeckel's earlier versions of materialistic monism, clearly moved Mathews to speculative enthusiasm.

Only halfway through the article did Mathews deal with more familiar biological phenomena such as respiration or growth of cells. Only two-thirds of the way through did he attempt to develop the idea of the cell as an electrical machine, or a battery, in a more concrete way.

Chromatin provided the last major subject that Mathews addressed, though it was here that he had done the most significant original research. Although nucleic acid was hard to obtain and thus to study, Mathews outlined in some detail what was known of the chemistry of chromatin. He then considered the chromosomal theory of inheritance, according to which chromosomes are the carriers of all inherited material. Echoing a view he had put forth in his *Physiological Chemistry* of 1915, Mathews rejected the chromosome theory as very improbable, partly because he felt that chromosomes are just too simple in their composition to carry out such a complicated hereditary task as was assigned them. Far from their having proved the theory, Mathews thought that the

> onus of proof is on those who assert that the chromosomes are such museums containing samples of all the chromatin of all the cells of the body, not only all the chromatins which develop during life, but all that infinite collection of old masters inherited from the past, and all the infinite number of descendants yet to appear in the eons before us, and presenting qualities usually said to be dormant. They are concealed no doubt in the chromosomal attic, ready to be produced when the occasion arises.[14]

Such an idea struck Mathews as unsupported and as probably unsupportable.

Obviously, Mathews's views were not universally held. Wilson, who accepted and had helped to develop the chromosome theory, believed that Mathews had overlooked some basic facts. Another critic found Mathews's speculative ideas rather odd, complaining that they "may mean something to the metaphysician, but one cannot help feeling that Prof. Mathews's view on the relationship between cell lipins [sic] and cell proteins, or on the biochemistry of development, would have been more useful."[15] Yet Mathews was not simply spinning out the sort of crackpot ideas that ended up in Frank Lillie's file cabinet at the University of Chicago under "C.R.A.N.K.S." Although rather temperamental and although involved in various clashes with colleagues both at Chicago and elsewhere, Mathews generally commanded high respect from other biochemical physiologists. His ideas and his approach were unorthodox but always provocative and exciting. He taught physiology at the MBL for seventeen years and remained a major figure, first as a department leader at Chicago and then at Cincinnati after he moved there to head a new physiological chemistry department in 1918.

Mathews belonged to a group of biologists in the early decades of this century who saw the organism as a unit rather than as a straightforwardly reducible set of physical parts and actions. His insistence on psychism as part of cellular phenomena did not obviously conflict with other ideas about design-in-nature by Ralph Lillie and others, or the insistence on the organism-as-a-whole by Charles Manning Child or even Thomas Hunt Morgan in his early career. Some physicists also tended to have similar views, including a few of the physicists who were invited to lecture at the MBL to encourage cross-fertilization of ideas from different disciplines. Although Lodge's popular books of the late 1800s and early 1900s and their particular details of physical theory had become rather outdated by 1924, many would have agreed with the impulse there. Somehow nature *must* be more than a bundle of separate physical pieces, such thinkers suggested. Coordination of parts might take different forms, but whatever the form, science must seek to understand the nature of the unities and the coordination. Such coordination of parts, or "organization" as Wilson called it, is what makes life work, after all.[16]

Epistemically, many scientists sought general theories such as Mathews's that could explain the whole range of facts at hand. A unified theory, even if dependent on rather questionable suggestions, might succeed better according to this view than a more careful but limited and less provocative theory. Thus, stimulating ideas that might prove horrendously wrong in the long run might very well represent first-rate science at the moment, if they provided a sufficiently suggestive framework within which to work. Mathews did provide such suggestions, though, as Robert Kohler puts it, "Not unlike the molecular biologists of a later time, Mathews was regarded by the more sober citizens with a mixture of awe and alarm."[17]

Cell Permeability and Reactions

For Wilson, cells remain individual units even while they interact with other cells to make up a whole organism. As a result, the cell membrane for Wilson serves primarily to define the cell and to separate it from its environment.[18] The cell exists, for Wilson, as a starting point; every individual organism begins as a cell. Thus he did not devote much attention to the way a cell arises or to the special role of the cell membrane in regulating the substances that are allowed to enter or those excluded. Questions about permeability of the cell membrane did not seem as central a question to Wilson as it did to others.

Merkel H. Jacobs, for example, saw the differential permeability of the cell to different substances as basic to cytology, making cells what they are. Life is dependent on the ability of cells to regulate which substances reside inside the cell and which are kept outside. This often complex regulation produces the internal heterogeneity of material necessary for life.[19] Many of the most central questions about the nature of body functions depend on the results of differential cell permeabilities.

To study permeability, Jacobs believed, the researcher had best adopt the widest range of diverse methods available. With each method, it is difficult to know whether experimental conditions remain close enough to normal conditions to provide useful information. In addition, slight differences in conditions in each case might produce slightly different and confusing results. Therefore he warned that the researcher must remain particularly careful not to generalize from single cases.

After reviewing the various alternative theories about what causes differential permeability, Jacobs insisted that no one theory had gained significant credibility as yet. It remained to generate more facts, in particular by covering a wide range of materials and by using as many different methods as possible. Convergence and agreement would strengthen the results of each separate study. Finally, examining what sorts of factors can bring changes in cell permeability under experimental conditions would also provide information about what directs normal permeability. Then, according to Jacobs, "a satisfactory theory will follow as a matter of course. Until that time, speculations should be reduced to a minimum."[20] Wilson would have agreed with such an epistemological preference even while he focused on different questions, though Mathews would not have.

In looking at cell reactions, Ralph Lillie, like Jacobs, took on a more defined topic than Mathews had. Yet, like Mathews, Lillie (who was also at the University of Chicago) was interested in what makes the whole cell and the whole organism of coordinated cells work. Like Jacobs, Lillie saw the cell as essentially interconnected with its chemical environment and with other cells. All concentrated on chemistry and physiology much more than did Wilson, who maintained his morphological focus even when he acknowledged the interrelations of cells.[21]

For Lillie, the cell is not an enclosed, isolated thing, but it lives in equilibrium with a changing environment. Lillie asked how the cells react, or adjust their functions, in response to the varying conditions in that environment. In other words: "What are these special features in the composition or constitution of living matter which render its chemical processes so susceptible to influence by changes in the surroundings?"[22]

Basically, Lillie held, the cell undergoes changes in metabolism when a stimulus acts on the protoplasm and modifies the chemical reactions, in part by affecting the reaction rate which depends ultimately on the particular structure of the protoplasm. Therefore Lillie proposed to begin by looking at studies of experimentally altered structures and the effects of changed external conditions, though he thought that studies with nonliving material could have only limited value for illuminating ordinary living processes.

Another line of research suggested to Lillie that protoplasm is like an emulsion of oil drops in water: it consists of material in two different fluid states. Stability between the two depends on the presence of thin films which act as surface layers. And research on emulsions showed that these layers can be broken down or established quite easily, with only a small change in ion concentration or the presence or absence of a tiny amount of a particular substance making all the difference between an emulsion and a layering of two different materials. For Lillie, the living cell seemed to be a proper emulsion, with a thin film in the form of the outer cell membrane keeping the cell intact and separate from its surroundings. Evidence had also accumulated that the material inside the cell is also divided by thin film partitions between chemically different parts. The semipermeable nature of the partitions accounts for the sophisticated regulations within the cell.

Yet the films do not provide a permanent or irreversible partitioning of the cell. Their semipermeability allows diffusion of substances across the films and makes regulation possible. And even a small stimulus can have a far greater effect than might seem possible. Thus a tiny pinprick in one spot may affect the entire cell in a radical way. It seems, Lillie concluded, that the cell has some sort of transmission process to carry effects throughout the whole. The propagated effect apparently travels along defined paths, in a manner similar to that of a neuromuscular response: a stimulus in one place on the nerve can travel rapidly along the nerve and can then stimulate the reaction of muscle fibers or other reflex actions. The whole cell must regulate its response to remain in proper equilibrium with its surroundings and within itself.

All the facts seemed to favor one theory over others, namely that electrical stimuli control all the stimulation and transmission of cell reactions. Presumably the current causes polarization along the boundary of the films, with resulting chemical changes along the film. These are transmitted beyond to the rest of the protoplasmic material. A survey of various cell and organismal functions suggested that all fit within the electrical transmission theory, which therefore provided a unified way of looking at the organism as a whole as well as at the individual parts.

Wilson referred in a very positive way to Lillie's earlier study of permeability, even acknowledging that the changes in permeability of the entire cell that occur at fertilization had been well documented. Furthermore, he agreed that the process might involve a changing electrical equilibrium, as Lillie suggested. But he devoted no further attention to that subject since, as he put it, "we are here concerned more particularly with the cytological changes."[23] By this, Wilson meant morphological changes, though Lillie, Jacobs, and Mathews would clearly not have agreed that these were more truly "cytological" than the sorts of actions affecting the whole cell that they studied.

Cell Structure

Cell structure was something Wilson did regard as basic. He was centrally interested in the different special parts of the cell as well as in structure and organization within the familiar general protoplasm. Chapters on the "General Morphology of the Cell" and on "Some Problems of Cell-Organization" most directly consider the subject. Wilson traced a collection of alternative theories about the nature of protoplasm, with some theories stressing the fibrillar or reticular structure, others the gelatinous viscous nature, for example. He concluded that no one theory had yet gained general acceptance. Perhaps there is a basic invisible structure, which admittedly may force "us back upon the assumption of a 'metastructure' in protoplasm that lies beyond the present limits of microscopical vision; but in that respect the biologist is perhaps in no worse case than the chemist or the physicist."[24]

In his essay, Robert Chambers agreed with Wilson. Both maintained that the protoplasm must have a defined structure. Furthermore, it must be more than a liquid since the protoplasm serves as the center of all life and appears to be highly organized. And it must be more than a mere random collection of protoplasmic material. The cellular unit must have its protoplasm, its nucleus, its cortex, and other parts, and some organization. Therefore it "must be regarded not as a 'stuff' but as a mechanism consisting of visibly differentiated and essentially interrelated parts."[25]

The problem was to devise a way to see the structure, much of which may remain invisible even with advanced microscopy, since the protoplasm normally resides inside the cell and hence remains unobservable under normal conditions. People had tried crushing the cell to determine its viscosity. Or centrifuging it to assess the effects of displacement under a change in gravitational force, or electromagnetic experiments for parallel reasons. Or microdissection with tiny needles, using tissue suspended in hanging drops. Or even microinjection of substances to determine the effects on internal structure. None of these methods had proved perfect. None gave a definitive answer, for example, to the question whether the different areas of the cell remain structurally or functionally independent or whether they are connected through a larger reticulum.

As Chambers pointed out, the evidence had accumulated to suggest that the cell has defined and stable different parts. The nucleus maintains its integrity because of its membrane, which if disrupted releases the nuclear substance throughout the cell. Furthermore, the destruction of the nucleus leads to a disruption of cell function as it becomes unable to divide. Chambers spent considerable time discussing the nucleus and the structural changes of all its parts, including the chromosomes, during cell division. Much of this work Wilson also referred to and accepted in *The Cell*. But in his essay Chambers offered a very different emphasis, namely on the methodology of microdissection and injection more than on the results. Like Wilson and unlike Mathews, Jacobs, and Lillie, Chambers also retained a largely morphological approach to cellular protoplasm.

Like Chambers, Edmund Cowdry pursued a largely morphological topic in his essay. Yet he also sought to show the connections of structure to function of cellular parts, especially the mitochondria and Golgi-apparatus. In particular, he wanted to show how the chemical nature of cellular parts dictated their functions. Unfortunately, "our functional interpretations must necessarily lag far behind on account of the great difficulty of projecting accurate methods of chemical analysis into such very small units as cells."[26]

Cowdry lamented that researchers had tended to generate more and more data using the same observational methods. Instead, they needed new alternative experimental approaches to gather different sorts of data as well. For Cowdry held that looking at the broader picture and gathering a variety of evidence would make a stronger case:

> It is possible that we, as students of mitochondria, have allowed ourselves to become rather narrow, and have approached too closely to the problem to see it in its proper proportions, whereas our task is really a synthetic one: we must piece together information from many quarters, and build up in our mind's eye a dynamic picture of mitochondria in relation to innumerable other cellular constituents. To take a familiar example, the close study of the mainspring of a watch would not tell us much unless its behavior was carefully considered in connection with all the other parts of the mechanism.[27]

Mitochondria clearly are present in almost all the major vital phenomena, Cowdry saw, which implies that they play a central role, perhaps in respiration. But too little was known to draw any safe conclusions about mitochondrial function as yet.

In this, Cowdry and Wilson largely agreed. Wilson pointed out that a likely role offered for mitochrondria in fertilization remained completely speculative. One full-scale theory suggested that mitochondria enter the egg from the sperm at fertilization, are passed on to other cells after division, that they then give rise to more specialized protoplasmic structures, and that throughout this cycle they retain their integrity and also play vital roles in heredity and development. Wilson joined Chambers in acknowledging that parts of the theory had "far outrun the facts" or even faced contradictions with observation, but that nonetheless the emphasis on mitochrondria "has too many facts in its favor to be lightly dismissed."[28]

Likewise, Wilson felt that "too little is known of the Golgi-apparatus, morphologically and physiologically, to warrant extended discussion at this time." It was not even clear whether they retain identity for long, though some evidence suggested that they did. Nor was their function at all clear. In fact, Wilson believed that the basic studies of Golgi-bodies were, like those of mitochrondria, "still in a somewhat unformed state."[29]

Cowdry agreed. First, the Golgi-apparatus did not really appear to him to be a distinct organized "body" but rather a collection of chemical substances. Neither microscopic work with vital stains and living cells nor study of prepared materials showed the actions or exact structure of the Golgi apparatus. This left the suggestion that here was another functioning part of the cell, but the cytologist had little to work with to date.

The so-called "chromidial substances" posed similar problems for both Cowdry and Wilson. There seemed to be defined, observable (since they stained regularly) substances in the nucleus. These apparently interacted with materials in the remaining cytoplasm. Yet the exact structures of the materials and the precise nature of the interactions remained unknown even though more was known of structure than of function. Wilson and Cowdry shared the view that here was a potentially important subject warranting careful attention with both traditional morphological and newer experimental methods. And they agreed that little was yet certain. Cowdry's attempt to look at cell parts beyond the long-recognized chromosomes and other nuclear parts remained more suggestive than final. Yet it received special attention when one reviewer of the volume applauded the fact that "the much-abused Golgi apparatus has at last received official recognition."[30]

Cell Behavior

Most of Wilson's book is dedicated to the structure and activity of cells under normal conditions. Experimental manipulations provide additional useful information toward understanding the normal cases, certainly, but Wilson focused on descriptions of the normal rather than on discussions of experimental conditions or results. The Lewises' paper in Cowdry's volume followed much of the rest of their work in exploring what happens in experimental cases.[31] Specifically, what do various types of cells do and what structures do they have in various sorts of tissue cultures? Tissue cultures allow the researcher to study individual functioning cells or cell clusters, which normally would be hidden away well inside the living whole organism.

Tissue culture is possible because cells remain "alive" for some time even after the host organism is dead or after the cells have been removed from their initial living whole. Hanging drops of appropriate fluids provide useful culture media in many cases and offer the advantage that the researcher can easily observe the results. When successful, cells will grow and divide within the medium, then move outside as well. This makes it possible to observe changes involved in cell division, reproduction, and other crucial activities of life. As Warren and Margaret Lewis showed, some cultures can be maintained for long periods, undergoing division after division, and promising potential immortality of sorts. Some cells experience differentiation within the cultured tissue. Others undergo "dedifferentiation" as the cells begin to die when the culture medium is not renewed sufficiently or often enough; in that case renewal requires adding embryonic extracts from living materials rather than inorganic materials. As the Lewises said, such phenomena remained difficult to interpret.[32]

The major question centered on the extent to which cells in tissue cultures act normally and therefore reliably reflect normal activities. The Lewises' essay implies that the results are useful and virtually normal. Wilson agreed, despite persistent arguments to the contrary. In particular, many biologists insisted on the integrity of the organism as a whole. Indeed, Wilson acknowledged the importance of integration of the parts in a normal complex organism, in which each cell remains just a part within a whole. Yet for Wilson the composite and coordinated whole comes secondarily. Fundamentally, each cell "possesses in itself the complete apparatus of life." And "we shall therefore proceed upon the assumption, if only as a practical method, that the multicellular organism in general is comparable, to an assemblage of Protista which have undergone a high degree of integration and differentiation so as to constitute essentially a cell-state."[33]

Fertilization

The next chapter in Cowdry's volume turned to the behavior of cells in fertilization. With Frank Lillie as senior author, and with his name placed out of alphabetical order ahead of his coauthor, E. E. Just, many people naturally assumed that Lillie was the one who had written the bulk of their essay on fertilization. Yet Just's biographer, Kenneth R. Manning, suggests that in fact Just wrote at least an equal share.[34] Just had carried out his graduate work at the University of Chicago and at the MBL under Lillie from 1909 to 1916, when he finally found enough time away from his teaching position at Howard University to complete the Ph.D. During that time he had pursued the phenomenon of fertilization and was strongly influenced by Lillie's theory of the importance of a special substance which Lillie called fertilizin. After publishing several papers on various details of the fertilization process, Just turned with Lillie in this article to a defense of Lillie's point of view—with reservations. Perhaps the joint authorship allowed Just to explore some of these reservations in a friendly context.

Fertilization actually includes all stages of the union of ripe gametes and not only the stages after the union is effected, according to Lillie and Just. This phenomenon, in which two cells become fused into one, is unique and happens nowhere else in nature. The very first changes are those along the cortex, as a "fertilization membrane" forms and a "wave of negativity" (which prevents further sperm penetration of the egg) results. Both egg and sperm take active roles in the process, they said, and it is not true that the sperm simply bores into the passive egg as many had held. For example, German cytologist Theodor Boveri had suggested that the sperm carries a centrosome into the egg, which acts as the "active division center" and which then initiates all cell division. But such a theory no longer fit the facts in the 1920s, Lillie and Just maintained.

Something about the fertilization process also produces a substance that causes agglutination of the remaining sperm cells. As such, agglutination is a part of fertilization and might provide information about the normal union of one sperm with the egg. Jacques Loeb had suggested that the dissolving of the jelly coat around the egg, which occurs upon fertilization, causes agglutination. Yet Lillie's and Just's experiments suggested otherwise, though the exact nature of the chemical reaction remained unknown. Yet it was clear that Just and Lillie believed Loeb to be wrong in his views.

Historians have begun to look at the rivalry underlying this discussion of Loeb's ideas.[35] Lillie and Loeb had very different approaches to science, as to life, and perhaps were bound to clash. While both worked at the University of Chicago, Lillie remained a student and junior faculty member under Whitman whereas Loeb headed the physiology program. There Loeb developed his ideas of fertilization with relative success. At the MBL and at Chicago, Loeb discussed his work on normal fertilization and on artificial parthenogenesis. Loeb was in poor health by 1922, however, and he died in 1924, so that his side of the story is not represented in Cowdry's project.

Artificial parthenogenesis raised interesting questions since its very existence suggested that there was something nonspecific about fertilization. If altering the salt concentration in sea water could stimulate cell division, fertilization might not be such a complex or special life phenomenon as it seemed.[36] As Loeb developed the implications of his view, he objected especially to such alternative interpretations as Lillie's theory of fertilizin.

A Philip Pauly puts it, Loeb rejected Lillie's very approach, for "fertilizin was a hypothetical substance of indefinite nature whose complex structure was defined in terms of the event it was asked to explain." Further, Lillie did not appeal to knowledge of physical chemistry, as Loeb preferred, but rather he was "offering words" and "thus incorporating his theory into all descriptive discussion."[37] In putting forth his views in 1916, Loeb had directly attacked Lillie's fertilizin theory, and Just had criticized Loeb in response.[38] This essay continued the criticism, and the dispute surfaces in several places, though generally in rather restrained form. The grounds of dispute were psychological, epistemic, and methodological more than specific questions about facts.

Lillie and Just did point out some strengths of Loeb's chemical emphasis, but they then went on to criticize his cytolysis theory of parthenogenesis and fertilization, according to which fertilization allows a cytolytic agent (which Loeb had called lysin) to break down the egg cortex. For many reasons, "we cannot admit that Loeb's conception, though it was a powerful stimulus to research, contains a workable hypothesis of activities."[39] Although they suggested that "no single theory can account for all the phenomena of fertilization as we have defined it," in fact the essay serves as a defense of Lillie's theory and approach.

Wilson did not wholly adopt either Lillie's or Loeb's interpretation. Rather he accepted and rejected parts of both. Instead of developing a theory about exactly what happens in fertilization or what chemical changes occur, for example, Wilson gathered a wide range of evidence from different researchers. As he did throughout his volume, he reported the results of many experimental studies, laid out various alternative theories, discussed the theories in light of the evidence, then offered some tentative conclusions.

The fact that Wilson's chapter on fertilization also included parthenogenesis reflects the importance he assigned it. Artificial parthenogenesis could be made to initiate a sequence of events that very closely paralleled normal events in the egg. "To the cytologist," Wilson concluded, "the processes called forth by fertilization or parthenogenetic activation offer the appearance of a single train of connected events, more or less plastic in each individual case and varying materially in its details from species to species."[40] Apparently, because of heredity and organization, each egg is capable of dividing and differentiating to some extent. What was needed, Wilson saw, was further experimental study of precisely what physiological changes take place in fertilization and subsequent differentiation to determine the normal conditions.

Differentiation

Another aspect of cell behavior was differentiation of individual cells within the whole organism. In his essay in Cowdry's book, Wilson's long-time friend Edwin Grant Conklin addressed the classic question: how do individual cells undergo differentiation from a "more general and homogeneous to a more special and heterogeneous condition?"[41] Protoplasm goes through cycles of differentiation, he suggested, then cycles of dedifferentiation. Yet there is no such thing as undifferentiated protoplasm, for every cell is differentiated into parts from the beginning: nucleus, cytoplasm, centrosomes, aster, sphere, and so on. The life cycles of individual organisms exhibit development patterns of "progressive differentiation" combined with integration to effect the whole. The differentiation transforms the general material into specialized structures and functions.

Differentiation arises, Conklin explained, through epigenetic processes and certainly not through any process of qualitative division of predifferentiated parts. He directly rejected the sort of predeterminist interpretation of development and differentiation that Wilhelm Roux and August Weismann had proffered in the 1880s and 1890s. Nuclear division does not serve to separate out particulate inherited determinates into different cells, which become structurally and functionally differentiated simply in accordance with that differential inherited information.

The details of cell lineage demonstrate this fact, Conklin said. Tracing the exact fate of each cell and the pattern of each cell division through many cleavage stages shows that some cleavages are determinate and others are indeterminate, for example. This means that some organisms and some cells do not exhibit the regularities in cleavage that others do. Where regularity and determinate division occurs, there must be some underlying "structural peculiarity of the protoplasm," Conklin concluded. The divisions serve to isolate different materials into different cells.[42] In these cases, the cytoplasm thus largely directs differentiation. Yet in determinate and indeterminate cases alike, the nucleus and the interaction of cytoplasm and nucleus remain vital as well. Most of what Conklin said in this essay summarized his conclusions from his cell lineage study from 1890 to 1905. After that time, he continued to work on different organisms and on different details of each. But the principles had all been in place by the time of his major 1905 publication on ascidian development.[43]

After 1905, Conklin addressed questions of heredity more directly. Based on a careful reading of other research and on his own results, he decided that a Mendelian interpretation of heredity best fit with the facts. By the time of this essay in 1925, he had long argued for a Mendelian-chromosomal interpretation of heredity and had coordinated it with his cell lineage studies of cytoplasmic development. At the end of this essay, he asserted that there was conclusive evidence in favor of: the existence of Mendelian factors (or genes) on chromosomes, the halving of chromosomes during mitosis, and the resulting similarity of chromosomal makeup in every cell of the same body. But one major question remained for Conklin: given these facts, how can we explain how identical genes correlate with differentiated cells?

We must look at the whole cell, he insisted, for the cytoplasm holds the answer. Recall that Conklin stressed the interaction of nucleus and cytoplasm. Yet the nucleus need not direct the cytoplasm. Indeed, the evidence lay in the other direction.

> Differential cell division is the result of definite movements of the cytoplasm, of definite orientations of spindles and cleavage planes, and ultimately of a definite polarity, symmetry, and pattern of the cytoplasm. There is good evidence that these movements, orientations, and localizations in the egg are the immediate results of cytoplasmic activity; these activities may themselves be the results of the interaction of nucleus and cytoplasm at an earlier stage, and possibly the inherited differential for all these orientations of development may be found in chromosomes or genes.

In short, "some of the differential factors of development lie outside of the nucleus, and if they are inherited, as most of these early differentiations are, they must lie in the cytoplasm."[44] Conklin was not about to become a friend of the nucleus alone—or of the cytoplasm—but remained an exponent of cytoplasmic as well as nuclear direction of development and inheritance.

Since Wilson's work had closely paralleled Conklin's, he had a great deal more to say about differentiation than about such physiological concerns as the early essays in Cowdry's volume had discussed. Differentiation appeared as a section in Wilson's lengthy chapter on "Development and Heredity," the final and conceptually central section of his book. There Wilson explained that though the egg operates as a "reaction-system" which responds to external conditions, "the specific differences of development shown by these various animals must be determined primarily by internal factors inherent in the egg-organization." Heredity, or the "innate capacity of the organism to develop ancestral traits," contributes to the particular organization of each egg. So does development, or "the sum total of the operations by which the germ gives rise to its typical product."[45] The organization remains absolutely central, yet we know little about what causes it. What is clear is that both heredity and development play vital roles in effecting and directing organization.

Differentiation within the organized egg occurs at all stages: before, during, and after each cell division. To date, the "existing knowledge of this subject is still too fragmentary and discordant to offer a sufficient basis for adequate discussion," Wilson insisted. The problem was to discover the mechanics of localization and differentiation and to determine what role heredity plays and how. Whereas Conklin had insisted on the dual importance of cytoplasm and nucleus, Wilson left open the question of exactly how the mechanisms of differentiation work. Chromosomal interpretations, and specifically Mendelian accounts, had begun to suggest answers to many questions already. Therefore Wilson reserved judgment but adopted a hopeful view that though "we are confronted still with a formidable array of problems not yet solved, we may take courage from the certainty that we shall solve a great number of them in the future, as so many have been in the past."[46]

Theories of Heredity

The last two essays of Cowdry's volume turned to those sources of Wilson's optimism, to the chromosomal and Mendelian theories of heredity. In the first, Clarence E. McClung addressed the chromosomal theory and maintained that it explained a great deal. While working as an advanced student in Wilson's laboratory at Columbia in 1902, McClung had discovered that in some insects (the Orthoptera) all and only the males have an accessory chromosome. At first he had remained cautious in his interpretations of that accessory chromosome, saying that "regarding the theory of its function advanced in this paper, I can say only that it has, if anything, been strengthened by later researches, and more nearly explains the phenomena involved than any other that has been conceived."[47] Despite his hesitations and despite some initial errors in his research, McClung quickly gained clarity of results and confidence in his interpretation. By 1925, he had become a defender of the chromosomal interpretation of heredity.

Yet like Conklin, McClung did not see the chromosomes as sharply distinct cellular bodies that sit there in a superior way giving out orders and receiving none. Instead, he believed that the chromatin is a semifluid colloidal material that acts as part of a connected system and remains continuous with the rest of the cellular material through a network of tiny fibers. The chromatin, and the chromosomes and other sets of parts into which it is organized, therefore act in an important developmental way in the individual in question. Since each individual has two sets of each chromosome, one from each parent, the individual experiences an interaction between the inherited influences of the two parents, in a way such that no two results even of the same two parents will be exactly the same. Chromosomal interactions therefore direct development, yet they also connect the existing individual with the past, through heredity. For McClung, heredity thereby brings continuity but also diversity.

McClung asked the same question that Conklin had raised: how can we explain the existence of different cells given the sameness of chromosomal material? Yet he did not conclude that the cytoplasm also exercises an effect on heredity, as Conklin had. Rather, according to McClung, the cytoplasm is controlled by the nucleus so tightly that "the character of the reaction depends upon the nuclear composition" and, further, that the "nucleus is indispensable in the functioning of the cell."[48]

"This does not at all constitute a denial of other elements of the problem, for which an open-minded attitude should always be entertained," he urged. Yet at least for the time being adopting the chromosomal theory "is a practical measure required by our own mental limitations. To deny or to minimize the value of a consistent body of evidence merely because it is not complete in all details is illogical and unfair. . . . Until some other theory is developed, more consistent with known facts and fuller in its reach, this theory will stand as our best working hypothesis in a most difficult field." For, the theory "stands as one of the highest achievements in biology and offers the most promising guide to further advances."[49] Yet for the moment, McClung offered little in the way of explanation about how chromosomes might effect their influence; he was neither chemist nor physiologist but a morphologist, primarily concerned with chromosomal structures.

In the next essay, Wilson's friend and colleague at Columbia, Thomas Hunt Morgan, took up the related subject of Mendelian heredity. By this time, Morgan had accepted the value of Mendelian genetics, theoretical as it necessarily was. In earlier decades, he had criticized Mendel and Weismann for their unscientific reliance on the existence of hypothetical inherited units, eventually called genes. In fact, Morgan had rather vehemently and insistently rejected the sort of fanciful appeal to invisible germs and to unscientific speculation that Weismann exhibited.[50] He had instead urged the study of living organisms as a whole, with a focus on developing differentiated structures and functions rather than on underlying hereditary factors.

But in the aftermath of his successes with the white-eye male *Drosophila* in 1910, he had decided that "genetics has proved a more refined instrument in analyzing the constitution of the germinal material than direct observation of the germ cells themselves, and while this advance may appear more theoretical than the conclusions based on observations of the cell, this need not mean that it is less reliable." In fact, despite the fact that he had initially been one of the major objectors, Morgan regretted that "the disrepute, into which Weismann's speculations [about quantitative nuclear division] then fell, carried over . . . for a time at least, and prejudiced needlessly the Mendelian situation."[51]

Mendelism involved the law of segregation of factors, law of independent assortment of factors for different characters, and the fact that germ material must consist of discrete units rather than inextricable wholes. Yet since many factors work together to produce a character, the coordinated interactions of parts within the whole remains fundamental. In fact, the genes are coordinated along chromosomes. They do retain some degree of individuality, Morgan believed, but they also interact in some way and to some extent. Morgan regretted that researchers did not at all agree on the way and the extent to which interchange occurs.

After reviewing the Mendelian and chromosomal theories, Morgan suggested that some of the best evidence about chromosomes comes from mapping. This mapping is very like that on a railroad where the reader of the timetable knows the times at which the train is to arrive at a sequence of different stations. By making various simplifying assumptions, the prospective rider can judge the relative distances between the stops. In addition, "Knowledge of the speed of the train and of the condition of the road-bed and of the grades would make it possible to judge more accurately the number of miles between the stations from the number of minutes between the stations."[52] Like the railway passenger, the geneticist must make assumptions but may learn a great deal from carefully considered indirect observations. It is not necessary to have actually taken the ride and directly observed the stations.

As to that recurring question about the relative importance of nuclear and cytoplasmic contributions to development, Morgan answered that it really did not matter and that we do not know enough to give a final answer. Claiming that the cytoplasm is really more important than the nucleus is "an example of obscurantism rather than of profundity." For, in fact, "all the examples of heredity that have been sufficiently worked out show that all adult characters and most embryonic ones . . . are accounted for by the known behavior of the chromosome." In other words, the chromosomes direct whatever happens during development, no matter what the character of the cytoplasm. As a result, "it is clear that whatever the cytoplasm contributes to development is almost entirely under the influence of the genes carried by the chromosomes, and therefore may in a sense be said to be indifferent."[53]

Nevertheless, the chromosomes could not direct if there were nothing to direct. So the cytoplasm is absolutely vital to the actual carrying out of the developmental processes. It might very well be that the cytoplasm is inherited in its own right and divides and differentiates following its own internal inheritance. But for Morgan that remained an open question, since at the moment he knew only that

> the cytoplasm of the eggs of two mutants *may* be as different as are the genes that constitute the chromosome complex of the two mutants; but the cytoplasm in the two mutants *may,* so far as we know, be identical in so far as it changes in reference to whatever kind of genes are present when it develops. On the other hand, the cytoplasms of two types may be different in the sense that in some respects they are affected differently—if affected at all—by the genetic chromosome groups. These questions must be kept entirely free from predilections until we have found out more about the physiological processes that take place in the chromosomes and in the cytoplasm. Whatever the future has in store for us in these respects, the answer does not prejudice the present situation so far as the observed effects of the genes in heredity are concerned.[54]

Although Morgan remained agnostic on the role of the cytoplasm in heredity and development, he did stress the value of pursuing a productive research program in a Mendelian-chromosomal interpretation of heredity.

That Wilson had high respect for Morgan and for the research by his group at Columbia is evident in the contents of Wilson's book. The bulk of new material in Wilson's third edition centered on heredity: on the discovery of accessory sex chromosomes, on which Wilson had worked directly, but also on the role of chromosomes in Morgan's favorite subject, *Drosophila.* Evidence of mutations, of crossing-over, and of alterations in the hereditary chromosomal material held promise for future discoveries of how heredity works, Wilson maintained. Mendelian heredity had begun to seem simple and regular and had brought many divergent facts into a coherent explanation. So Wilson concluded his massive volume with a last sentence sounding a note of hope for unraveling that critical problem of explaining organization. After all, "if Mendelian heredity, at first sight so inscrutable, is effected by so simple a mechanism, we may hope to find equally simple explanations for many other puzzles of the cell that lie beyond our present ken."[55]

Conclusion

Cowdry's volume, wrote one reviewer, is "the largest and most comprehensive ever published on the subject of cytology." It would "stand for many years to come as the most authoritative exposition of a branch of zoology which has grown considerably in recent years."[56] The reviewer noted that the work obviously represented more than the work of any single individual, and indeed that no one person could have covered the breadth of subject matter that the study encompassed. The reviews of *General Cytology* nearly all mention the "exhaustiveness," "extensiveness," and "comprehensiveness" of the work and include other such adjectives stressing scope.

When Wilson's third edition appeared the next year, it also generated rave reviews. Yet, as Conklin admitted in reviewing Wilson's opus,

> probably no single book can ever again deal so comprehensively and judicially with the whole field of cytology. Few other workers are left who were in at the birth of this science and who can speak of its development with the knowledge which comes from intimate contact with persons and problems. It is a monumental work, one of the most complete and perfect that American science has produced in any field, and biologists throughout the world will unite in extending thanks and congratulations to its author on the successful completion of a great work which will always stand as a golden milestone on the highway of biological progress.[57]

Only the unique and aging Wilson could have succeeded, and only then in revising a book rather than in starting from "scratch." No longer could anyone even hope to discuss all of cytology in one book. Cytology—along with biology more generally—had undergone expansion that had carried it beyond the reach of any one scientist or any one approach. Even the leading textbooks reflected widely different methods, interpretations, and emphases.

Wilson's volume offers a compendium of facts, theories, bibliography, and references to an almost incredible range of works by numerous Americans and Europeans concerned with questions about the cell. Yet the focus remains on cell morphology and the central theme is organization: organization of individual cells, of all parts, and of whole multicellular organisms. The volume provided a sustained interpretation of what the cell is, how it arises, and how it works.

Cowdry's volume is much different. It begins with chapters on the chemistry, permeability, reactivity, and therefore general physiological activity of cells; then moves on to questions of structure of protoplasm and cell parts; on to behavior of cells in tissue culture, fertilization, and differentiation; and concludes with chapters on chromosomal and Mendelian heredity. The ordering presents an organized approach to cytological questions. But the volume does not provide the sort of coherent work that Wilson's does. No one praised Cowdry's volume as "monumental." It was, instead, "comprehensive."

The collaborative approach allowed each contributor to focus on his or her strengths and to specialize, while also providing a wide range of subjects covered. The multiple authorship also provided a ground for disagreements or variations of opinion. Rather than presenting a perfectly united front, as if everyone agreed on all points, the collection of essays showed that numerous questions, approaches, methods, theories, and data were acceptable. This was a textbook that showed the interactions and the exchanges within science rather than just a standardized, static result. It left considerable room for suggestions, and for revisions in accepted work.

The collaboration showed that cells could be thought of as little electrical machines, or perhaps as colloidal substances, as sophisticated self-regulating individuals, or possibly as inherited units. Depending on which view one adopted, different things would count as evidence for what was thought to be interesting about cellular structure and function. Different sorts of results would count as knowledge and therefore as legitimate scientific products.

Cowdry's book represented a cooperative effort by researchers who believed that expansion of cytology called for a group of experts to study the whole field. This was, more generally, a time when scientists had begun to move on occasion to the edited volume as a way of presenting a fuller consideration of a number of biological topics. The single-authored textbook remained, of course, but such a text drew heavily on the work of a wide range of other researchers and served largely to systematize the bulk of available information. Such a textbook sought to provide an overview, presenting a package as if to say this-is-what-is-known. The group-generated textbook coverage of a field could provide more depth and more consideration of work in progress and of the best available (but admittedly working) hypotheses; it could also advocate several lines of research from different perspectives rather than being constrained to provide a balanced overview of several alternative viewpoints or an argument for only one. The coordinated conference, the collaborative symposium, and the edited volume increasingly began to come into their own as the century progressed.

Increasing expansion of research into new specialty areas was occurring at the same time and also demanded changes. As more people entered scientific research, and as techniques and problems became more specialized, there were fewer "grand old men" who knew it all. There was simply too much to know, and too many different ways to know it. Groups of biologists had much less in common than they had around 1900, when they would have read a set of the same books and kept up with articles in the same journals. What had briefly come together as "biology" had begun to expand again in new directions.[58] Different problems, different methods, different types of research settings and approaches, and different ways of presenting one's ideas and results further separated biologists into myriad different research directions, as did different audiences and different sources of funding.

As the research enterprise became increasingly specialized and compartmentalized, with people talking less and less to those outside their own special domains, and with fewer people capable of dealing with an entire subject area individually, the collective approach offered a corrective. Properly conceived and executed, collaboration among individual researchers with their different problems, approaches, methods, and presentations could yield products greater than, or at least different from, the sum of the individual parts. Fortunately, to this end, a growing number of research centers also existed which could support such cooperative cross-disciplinary and cross-institutional work. The MBL was one such institution, among many.

These institutions provided a place for scientists to talk to a variety of other specialists with whom they might normally never have discussed their work "back home." Whether summer havens, special research laboratories, or centers where visitors could work temporarily for various periods, places that allowed discussion across the increasingly hardening disciplinary boundaries played important roles in encouraging coordinated and cooperative work. The products reflect the special institutional setting out of which they grew as much as the individuals who contributed. The individuals alone could not have produced the same results, since no one scientist could possibly have been fully familiar with all the varied research represented or have held such a wide diversity of sometimes contradictory views.

General Cytology falls into this category. It could not have been written by one author. Indeed, no one person would have agreed with all of it. Nor would any one person have thought of using all those different approaches or those widely different ways of presenting the ideas. The ways in which Cowdry's book differs from Wilson's illuminates more general changes in biology by the 1920s.

With its variety of perspectives and its substantial guide to the literature in the form of lengthy bibliographies, the volume provided the latest word—or rather a collection of latest words—on cytology but also made it clear that these were just the latest words in a long line of continually revised words about the subject. The effect was to earn the volume considerable attention for several years. Then, new work and new interpretations replaced the old, and the contributors each went on with their own revised contributions. *General Cytology* was not continually reprinted and reissued as a classic. Unlike Wilson's volume, it did not concentrate on the presentation of a valuable array of data and thus serve as a standard reference text for decades to come. Rather, it reflected the best work and an intriguing mix of ideas, methods, and questions for a particular slice of time. It showed the exciting way that cytology had expanded and continued to expand. It illustrated the processes and suggestions rather than the apparently fixed products of science. Whereas Wilson's work was "monumental," Cowdry's was "extensive" and "suggestive." Both reflected the remarkable expansion of cytology in the United States.

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Notes

1. Leonard Doncaster, *An Introduction to the Study of Cytology,* 2nd ed. (Cambridge: Cambridge University Press, 1924; 1st ed. 1920), p. v.

2. Ibid., p. 265.

3. Edmund V. Cowdry, ed., *General Cytology. A Textbook of Cellular Structure and Function for Students of Biology and Medicine* (Chicago: University of Chicago Press, 1924), Preface, p. v. It would be interesting to know such things as whose idea the volume was, who decided what subjects and authors to include and according to what set of criteria, and other details that might illuminate the nature of and reasons for the project. Unfortunately, correspondence relating to the project at the University of Chicago Press has been placed in the Archives, where it remains closed.

4. Edmund Beecher Wilson, *The Cell in Development and Heredity* (New York: Macmillan, 1925; 1st ed. 1896 and 2nd ed. 1900 as *The Cell in Development and Inheritance*).

5. Wilson, Introduction to Cowdry, *General Cytology,* pp. 10–11.

6. Wilson, *The Cell,* p. xii, explained that he had had no time to respond to Cowdry's volume or to include many references to it since his volume was nearly complete when Cowdry's appeared.

7. Ibid., p. xi.

8. Statistics come from Cattell's *American Men of Science* (various editions) and from other standard biographical notes on each of the individuals.

9. Wilson, *The Cell,* pp. 635, 670–672, 59.

10. Albert P. Mathews, "Some General Aspects of the Chemistry of Cells," in Cowdry, *General Cytology,* pp. 13–95, on p. 15.

11. Ibid., p. 18.

12. Ibid., pp. 21, 22–23, 27, 32.

13. Sir Oliver Lodge, *The Ether of Space* (New York: Harper Brothers, 1909).

14. Mathews, "Chemistry of Cells," p. 90.

15. J. Brontë Gatenby, review in *Nature,* 1925, *115*: 185–187, on p. 186.

16. Philip Pauly discusses a similar point in "General Physiology and the Discipline of Physiology, 1890–1935," in Gerald L. Geison, ed., *Physiology in the American Context, 1850–1940* (Bethesda: American Physiological Society, 1987), pp. 195–207.

17. Robert E. Kohler, *From Medical Chemistry to Biochemistry. The Making of a Biomedical Discipline* (Cambridge: Cambridge University Press, 1982), p. 301.

18. Wilson, *The Cell,* pp. 54–57.

19. Merkel H. Jacobs, "Permeability of the Cell to Diffusing Substances," in Cowdry, *General Cytology*, pp. 97–164, on p. 99.

20. Ibid., p. 155.

21. Ralph S. Lillie, "Reactivity of the Cell," in Cowdry, *General Cytology,* pp. 165–233. Wilson on reactivity, *The Cell,* pp. 101–106.

22. R. Lillie, "Reactivity of the Cell," p. 170.

23. Wilson, *The Cell,* pp. 410–411, 475.

24. Ibid., p. 78.

25. Robert Chambers, "The Physical Structure of Protoplasm as Determined by Micro-Dissection and Injection," in Cowdry, *General Cytology*, pp. 237–309, on p. 238.

26. Edmund V. Cowdry, "Cytological Constituents—Mitochondria, Golgi Apparatus, and Chromidial Substance," in Cowdry, pp. 313–382, on p. 355.

27. Ibid., p. 332.

28. Wilson, *The Cell,* pp. 706, 707.

29. Ibid., pp. 714, 716.

30. Gatenby, review in *Nature,* p. 186.

31. Warren H. Lewis and Margaret R. Lewis, "Behavior of Cells in Tissue Cultures," in Cowdry, *General Cytology,* pp. 383–447.

32. Ibid., p. 429.

33. Wilson, *The Cell,* pp. 102–103.

34. Frank R. Lillie and E. E. Just, "Fertilization," in Cowdry, *General Cytology,* pp. 449–536. Kenneth R. Manning, *Black Apollo of Science. The Life of Ernest Everett Just* (New York: Oxford University Press, 1983), says on p. 149 that "contrary to general opinion Just had done most of the work." And on p. 310, Manning asserts that "Just wrote an equal share, if not more, of the article." Lillie evidently suggested as much in a letter to a potential supporter of Just's research, Julius Rosenwald.

35. Philip Pauly, *Controlling Life. Jacques Loeb and the Engineering Ideal in Biology* (New York: Oxford University Press, 1987), pp. 153–160. Manning, *Black Apollo of Science*, pp. 78–84.

36. Jacques Loeb, "On the Nature of the Process of Fertilization," *Marine Biological Laboratory. Biological Lectures,* 1900, *1899*: 273–282.

37. Pauly, *Controlling Life,* p. 155.

38. Jacques Loeb, *The Organism as a Whole* (New York: Putnam's, 1916), chaps. 4 and 5.

39. Lillie and Just, "Fertilization," p. 522.

40. Wilson, *The Cell,* p. 486.

41. Edwin G. Conklin, "Cellular Differentiation," in Cowdry, *General Cytology*, pp. 537–607, on p. 539.

42. Ibid., p. 599.

43. Edwin Grant Conklin, "The Organization and Cell-Lineage of the Ascidian Egg," *Journal of the Academy of Natural Sciences, Philadelphia*, 1905, *13*: 1–119. He also discussed the theoretical points in "Mosaic Development in Ascidian Eggs," *Journal of Experimental Zoology*, 1905, 2: 145–223.

44. Conklin, "Cellular Differentiation," pp. 600, 601.

45. Wilson, *The Cell*, p. 106.

46. Ibid., pp. 1085, 1118.

47. Clarence E. McClung, "The Accessory Chromosome—Sex Determinant?" *Biological Bulletin*, 1902, *3*: 43–84.

48. Clarence E. McClung, "The Chromosomal Theory of Heredity," in Cowdry, *General Cytology*, pp. 609–689, on pp. 666, 665.

49. Ibid., pp. 668–669, 682.

50. Thomas Hunt Morgan, "Regeneration: Old and New Interpretations," *Marine Biological Laboratory. Biological Lectures*, 1900, *1899*: pp. 185–208, on p. 191.

51. Thomas Hunt Morgan, "Mendelian Heredity in Relation to Cytology," in Cowdry, *General Cytology*, pp. 691–734, on pp. 693, 714. For more on Morgan and his *Drosophila* research, see Garland E. Allen, *Thomas Hunt Morgan* (Princeton: Princeton University Press, 1978), chap. 5.

52. Ibid., p. 713.

53. Ibid., pp. 727, 728.

54. Ibid., p. 728.

55. Wilson, *The Cell*, p. 1118.

56. Gatenby, review in *Nature*, p. 185.

57. E. G. Conklin, review of Wilson's *The Cell*, *Science*, 1925, *62*: 52–54.

58. Ronald Rainger, Keith R. Benson, and Jane Maienschein, eds., *The American Development of Biology* (Philadelphia: University of Pennsylvania Press, 1988) explores the establishment of a biological core. Another interpretation appears in Joseph Caron, "'Biology' in the Life Science: A Historiographical Contribution," *Hist. Sci.*, 1988, *26*: 223–268.