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EDMUND BEECHER WILSON

1856–1939

BY

T. H. MORGAN

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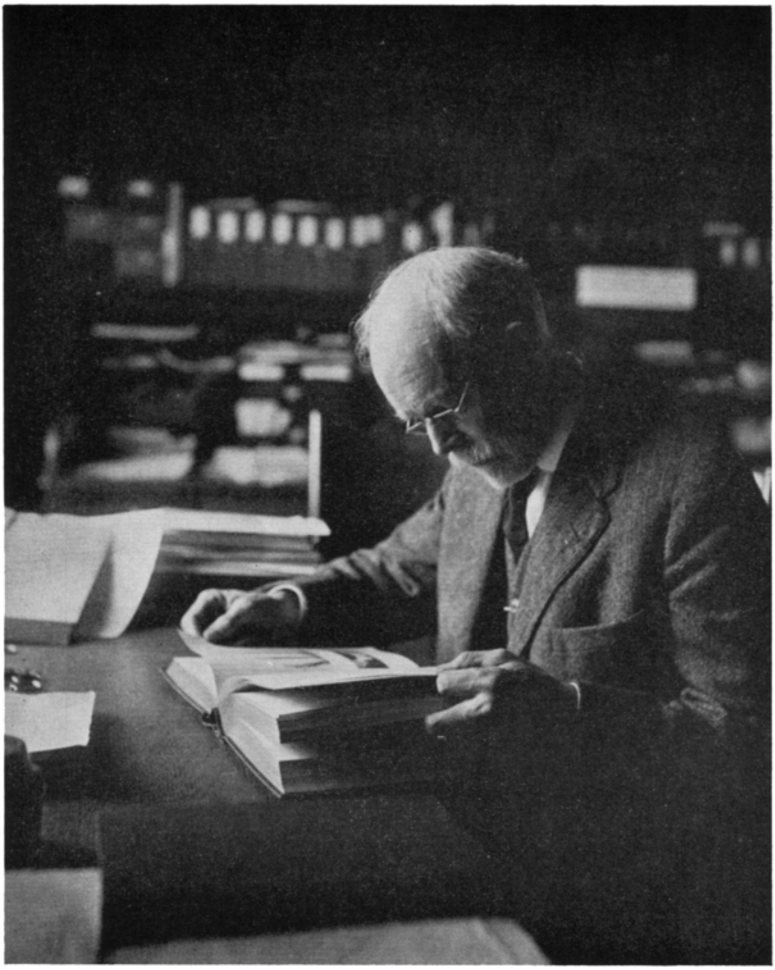

Edmund B. Wilson.

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Wilson has written in regard to his ancestry, "I will frankly confess that I am proud of certain things in my ancestry; first, because it is purely American back to 1620; second, because it is purely New England and especially Cape Cod; and third, because so many of my forefathers were seafaring men".

"I have always loved the sea and all its ways—the ships—the men who sailed them—the strange beasts that make their home in it. I am descended from Thomas Clarke, reputed mate of the *Mayflower*—who settled in Plymouth in 1623". His eldest son, Andrew Clarke, removed to Boston, later to Harwich. Wilson's maternal grandfather, Scotto Clarke, born at Harwich in 1782, married in 1809 and later moved to Boston. After the financial crash of 1837 he, with his four children, Harriet, Charles, Caroline, (Wilson's future mother) and Ellen, migrated to Geneva, Illinois. Wilson's father's ancestors came originally from Wrentham, Massachusetts. His father, Isaac G. Wilson, went through Brown University, graduating in 1838, then attended the Harvard Law School and was admitted to the Massachusetts Bar in 1841. In the following year he began the practice of law at Elgin, Illinois, ten miles up the valley of the Fox River and ten miles from Geneva. Afterwards he moved to Geneva where in 1843 he married Caroline Clarke, the second daughter of Scotto Clarke. Later Wilson's father became county judge, circuit judge and chief justice.

Edmund Beecher Wilson was born October 19, 1856, at Geneva, Illinois. The first sixteen years of his life were passed there. He has written "it would not be easy to imagine a happier environment for a boy who somehow managed to combine an early passion for natural history with an almost equal love for music; who grew up in an atmosphere of warm affection and sympathetic understanding at home, and was surrounded by a circle of intelligent and cultivated people".

When only two and a half years of age, "Eddy," as he was called, was adopted by his mother's sister, Mrs. Charles Patten, who also lived in Geneva; "with the result that henceforward I had in effect two homes and four parents between whom I hardly distinguished in point of love and loyalty". His foster parents encouraged his interest in birds, snakes, insects, toads, and all living creatures even to the extent of setting aside a room for his treasures.

The Chicago fire occurred on October 7, 8, 9, 1871. His father had taken up residence there at the time, practicing law. A schoolmate had been engaged to drive the carriage to Chicago and he took young Wilson along. The fire was at its full height, but they had not heard of it at the time. Halted at the Chicago River they could see great clouds of black smoke. They spent the night on the floor of a house and in the morning took a roundabout course to the north side of "Phil's house". They found the place but Phil's father's house was gone. Still they identified it by a pile of Laraby furniture on the opposite side of the street, including a piano on which one of Phil's brothers was playing a lively waltz, while two others were dancing on the pavement. Later in the day they found Wilson's father's house on the South Side. The fire had not quite reached it.

In the following year when Wilson was not quite sixteen his uncle Davis suggested that he take over the "little country district school" that his brother Charles had taught the year before. The offer was thirty dollars a month and board (with his aunt and uncle). "At the end of the winter a farmer, the father of three of my pupils, said to my aunt, 'He's young but his age don't hurt him none'." "Few words of praise in my life have pleased me as much". "It was a grand experience that I would not have missed, as the saying is, for a farm. I lived at the manor house with my uncle and aunt, sleeping with one of the higher class men, during a very cold winter in the coldest room I ever entered, with no fire and often breaking the ice in the pitcher for the morning wash. The little one-room schoolhouse lay a mile away on the rolling prairie near the road leading to the village of Oswego. It was a pleasant but lonely country with the nearest house half a mile away. Every morning even in the dead of winter I walked to school carrying my luncheon in a tin pail, often with an icy wind blowing across the prairie, and had to build a fire in the schoolhouse and sweep the floor before school opened at nine o'clock. When the thermometer stood at thirty degrees below zero, as it did at times, this was, I assure you, no joking matter. I wonder how the modern city-bred youth would like such an experience. I had only twenty-five pupils or so, of all ages from six to eighteen, and I had to teach all grades, from the three R's up to history and algebra."

His father urged him to take a competitive examination for West Point which he did and found extremely easy. He came out first on the list; "for it covered only ordinary grammar and school subjects", but since it was found that he was below the legal age, he was ruled out.

In the following summer he was in Geneva where his cousin, Sam Clarke, had just returned from Antioch College. "As the summer passed I had gradually made up my mind to try for a college education and a life devoted to biology or at least to science." "I had nothing but my two hundred dollars but with this in hand I packed up my meager outfit in September and started for Antioch College in southern Ohio." He rented a room for a dollar a week, joined an eating club which cost two and a half dollars a week, and earned a dollar a week by "manufacturing" the gas by which the college was lighted. The college was a very simple one but with sound ideals. "We had good teachers. Here, for the first time I received regular instruction in zoology and botany, in Latin, in geometry and trigonometry and especially in chemistry with regular laboratory work and I reveled in it all."

In June (1873) he went back to Geneva where with a tutor he began to study Greek. Instead of returning to Antioch in the fall a new prospect opened. Sam Clarke wrote enthusiastic letters from the Sheffield Scientific School at Yale. "In turning towards Yale I was influenced not merely by Clarke's example but in part by the reputation of the professors of zoology, botany, comparative anatomy, and geology, and in part by the almost equally compelling consideration to poor students that Yale offered many advantages in the way of self-support. I felt, however, not yet fully prepared—." Wilson spent the winter with his family in Chicago in attendance at the University there, preparatory to Yale. Hearing of an opening as recorder in the Lake Survey he easily passed the examination, and was accepted at a salary of a hundred dollars a month. He took part in the primary triangulation of Lakes Ontario and Erie which lasted until September; then he started east to enter Yale.

He entered the Scientific School at Yale in 1875 and graduated three years later with the degree of Ph. B. He remained there one year more doing graduate work and acting as assistant. During the first year at Yale he took courses in zoology with Verrill, in botany with Eaton, and embryology with S. I. Smith. He then decided to regularize his work so that it would lead to the bachelor's degree. His three undergraduate years were, he writes, very busy and very happy years. It was during this year that he attended "Brewer's famous lectures, nominally on stock breeding but mainly on heredity and evolution. This was my first real approach to this subject. Brewer made an indelible impression on all who knew him, and especially on the youngsters who were fortunate enough to hear him. He lectured with the utmost fire and vehemence". At the end of the last year at Yale, Wilson was offered a position for the following year but both Sedgwick, with whom he was on intimate terms, and Wilson himself were getting roseate reports from Sam Clarke who was then at Johns Hopkins University. Both applied for fellowships there and were duly appointed. It was during the last year at Yale that Professor S. I. Smith showed Wilson a paper by Professor Mark of Harvard, saying "Here's a man who has written two hundred pages about the development of the snail and has only got as far as the 2-cell stage". "I wondered what the author could find to fill two hundred pages on that subject. I looked over the paper and saw my first picture of karyokinesis. Then and there was born my first determination to find out something about cells, protoplasm, cell division, fertilization, and development. And 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".

Before leaving Yale, Wilson had been appointed a member of the U. S. Fish Commission (summer of 1877). The party under the leadership of Baird gathered at Gloucester, Massachusetts. Several trips were made on the naval steamer *Speed-*

well, where for the first time Wilson saw dredging for marine animals.

At the end of his first year at Johns Hopkins both he and Sedgwick were reappointed to fellowships and in the third year to assistantships. His three years there opened a new world of ideals; he became aware, he says, of new horizons of research, and wider outlooks in biology. His teachers were H. Newell Martin and W. K. Brooks. It was with the latter that he carried out most of his own work. "It was through informal talks and discussions in the laboratory, at his house, and later at the summer laboratories by the sea that I absorbed new ideas, new problems, points of view, etc." "Through him I first discovered what I really wanted to do." "From him I learned how closely biological problems are bound up with philosophical considerations. He taught me to read Aristotle, Bacon, Hume, Berkeley, Huxley; to think about the phenomena of life instead of merely trying to record and classify them."

Wilson had more and more wished to study in Germany but had no means to accomplish the trip. His eldest brother offered to help him with a loan and due to this brotherly generosity he was able to carry out his longfelt desire to study abroad. At the end of the summer of 1882 he sailed to Liverpool. Newell Martin had given him a letter to Huxley who expressed much interest in the work on Renilla. Later he arranged to have the memoir on Renilla published by the Royal Society.

Wilson settled down at Cambridge. Balfour had been killed in the Alps but his assistants and students were there, and Wilson recalls meeting Adam Sedgwick, Heape, Caldwell and Bateson. He also met Michael Foster and attended his lectures. He returned to London to give his paper before the Royal Society and then left for Germany. After spending a few weeks in the small village of Thurm to familiarize himself with spoken German he went to Leipzig. Here he worked in Leuckart's laboratory and also attended a few of Ludwig's lectures on physiology. He introduced the section-cutting method that Caldwell had invented in England and it created a sensation. In Leipzig he heard a great deal of the best music.

While at Johns Hopkins, Wilson had heard about the Zoological Station at Naples. He had wanted to go there for some time but a table cost five hundred dollars and this he could not afford. At this time his cousin, Samuel Clarke, came to the rescue with the proposal that Williams College, where he was professor, would subscribe for a table and that Wilson, if he wished, might occupy it for the first year and Clarke himself the following year provided Wilson would agree to act as a substitute for him at Williams during his absence.

Naples produced a deep and lasting impression on Wilson. The Station came up fully to his expectations. There he came to know Anton Dohrn with whom he formed a sincere friendship, Hugo Eisig, Edouard Meyer, and Arnold Lang—names that are familiar to many American zoologists who have followed in Wilson's footsteps to Naples. He has written: "That first year in Naples—it was not quite a year—was the most wonderful year of my life. I despair of conveying any notion of what it meant to me, and still means, as I look back upon it through the haze of fifty years. It was a rich combination of serious effort, new friendships, incomparable beauty of scenery, a strange and piquant civilization, a new and charming language, new vistas of scientific work opening before me; in short, a realization of my wildest, most unreal, dreams."

On his return from Naples he carried out the agreement to act as a substitute for Clarke at Williams College (1883-1884). While he gained some experience in teaching and made some pleasant new associations he was not sorry when the year came to an end. Amongst other duties he was expected to give a popular evening course on modern advances in biology, which interested him, he says, more than teaching the elementary classes. Darwin's theory of evolution, while widely accepted by scientists, was by no means acceptable to the evangelical public, including the president of the college. "On the whole," Wilson writes, "the year at Williams was scientifically a dead loss; I had no time nor appliances for research, no scientific stimulus, no incentive for research."

Sedgwick and Wilson had been much interested in the course in biology at Johns Hopkins given by Newell Martin, where in the laboratory the well-known book of Huxley and Martin was used. While at Williams they began planning along somewhat different lines a textbook of general biology. In part to carry out their plan of collaboration Wilson was offered a lectureship with Sedgwick at the Massachusetts Institute of Technology. The book appeared in 1885 and was very successful.

Bryn Mawr College, a new institution for the higher education of women, was to be opened in the fall of 1885 and Wilson was invited to take charge of the department of biology. The college had been founded by Quakers and from the beginning adopted a liberal, even advanced, policy in its educational aims. This policy was largely due to Miss M. Carey Thomas who as Dean and later as President introduced the same standards as those followed by Johns Hopkins. Wilson taught at Bryn Mawr from 1885 to 1891 and had wonderful success, attracting to his classes many of the ablest students in the college.

Henry Fairfield Osborn had accepted a call from Columbia to establish a new department of zoology. He offered Wilson the position of adjunct professor to co-operate with him in organizing the new department. The offer included an arrangement by which Wilson would be given a year of foreign study before starting on his duties at Columbia. The second year in Europe was spent mainly in Munich and Naples and was even more productive and delightful than the first one, scientifically, because it settled definitely his later line of study, namely, cellular and experimental embryology. Boveri was at that time in Munich, and it was his presence there that had determined Wilson's choice of a place to work. Boveri was "far more than a brilliant scientific discoverer and teacher. He was a many-sided man, gifted in many directions, an excellent musician, a good amateur painter, and we found many points of contact far outside of the realm of science." "The best that he gave me was at the Café Heck where we used to dine together, drinking wonderful Bavarian beer, playing billiards, and talking endlessly about all manner of things."

At the end of the year he went to Naples with the Norwegian Hjort as travelling companion. At the Station he met Driesch and Herbst, both students of experimental embryology which at that time was a relatively new field and to which Wilson was soon to make valuable contributions. Driesch's work on the experimental production of twins interested Wilson intensely, because of its bearing on his own work on the development of the earthworm and Nereis, then in press. In the spring of 1892 he went to Sicily to study the embryology of Amphioxus. Returning to Naples he sailed for Genoa where he saw the famous Joseph Guarnerius violin of Paganini. "The thrill that it gave me was only equalled by my ascent of Etna."

In 1904 Wilson married Anne Maynard Kidder, the daughter of Dr. Jerome Henry and Anne Maynard Kidder. Dr. Kidder was a friend of Spencer F. Baird who established the United States Fish Commission at Woods Hole. The Kidder family, who lived in Washington, D. C., built a summer cottage at Woods Hole and were on the most friendly terms with members of the Marine Biological Station. After the death of Dr. Kidder, Mrs. Kidder continued to go to Woods Hole. Many of us will remember her as charming, cultivated, witty, and hospitable and she was regarded by us as much a member of our group as though an official member of it. It was at Woods Hole that Wilson first knew Anne Kidder whose marriage to him added officially another valuable member of that family to the Woods Hole group. Their daughter, Nancy, Mrs. John Lobb, became a professional cellist of outstanding ability, and, during the latter years of Wilson's life, one of his greatest pleasures was watching her progress in her profession. This, in a sense, rounded off Wilson's passion for music.

In the summer of 1906 Wilson, accompanied by his wife, made an extensive collecting trip, first through the southeastern states, then to Knoxville, Tennessee, which was the early home of Mrs. Jerome Henry Kidder (the mother of Mrs. Wilson) and of her grandfather, Horace Maynard. From New Orleans they went to Tucson, Arizona, where they found in abundance the insects for which they were searching. The trip carried them as far as Wyoming and Southern California. This extensive journey was undertaken to collect insects in the study of whose chromosomes Wilson was then interested. He had taken part in the discovery of the role of the sex chromosomes in sex determination, and wished to extend the work over a wider field. The material collected served as a basis for some of the work carried out in following years at Columbia University.

It is difficult for one not himself a musician to describe Wilson's deep interest in music, and I shall follow his own words as far as possible. He has left a memorandum of his connection with musicians and music that shows how much music meant to him throughout his life. He writes, "I have always loved music and to it I owe some of the greatest pleasures of my life." His father played both the violin and cello, his mother played the piano and so did both of his aunts; his brother Charles was a good violinist, and his sister Ellen was an excellent pianist. There were many music lovers in Geneva and they formed, with a small group of professionals from Chicago, an orchestral organization.

His own musical experience began with singing lessons, but while he had no singing voice, as he says, he owes to these lessons "an inveterate habit of recalling all music in do-re-mi language." He learned to play the flute but later gave it up. It was in Baltimore that a new era in music opened for him when he attended the concerts of the Baltimore Conservatory of Music. He resolved never to touch the flute again and began to take lessons on the cello. He writes, "I was too old to take up so difficult an instrument with any hope of mastering it," but nevertheless he finally became an accomplished player in quartets. At Bryn Mawr he got in touch with a number of amateur musicians and had an immense amount of pleasure from these contacts. Later his first real introduction to quartet playing took place in Germantown at the house of Judge Penrose. After three or four years he became "a confirmed quartet lover of chamber music".

When he moved to New York he soon found a group of musical friends who formed a quartet that played for several years. Later when at Naples he was introduced through the invitation of Anton Dohrn, himself "music mad," to some of the best musical society of Berlin. Here he came to know Joachim and the brothers Robert and Franz Mendelssohn who "between them owned a whole quartet of fine Stradivari fiddles". Needless to say Wilson had a wonderful time which he characterizes as a "musical debauch". "Music," Wilson writes, "has always seemed to me the most mysterious of the fine arts," "a language *sui generis* and one that often cannot really be translated into words."

Wilson's first extensive work "The Development of Renilla" was published in 1883 in the Philosophical Transactions of the Royal Society, London.* It was a splendid piece of descriptive work, admirably presented. The sixteen plates that illustrate the text are an example of his skill and taste in drawing. It is worthy of note that by the use of serial sections, a procedure that was just coming into practice at that time, he was able to show in detail the cellular changes taking place in the interior of the opaque larvae of Renilla. The drawings of the sections also illustrate the excellence of his draftsmanship. The materials for the paper were collected at Beaufort, North Carolina, during two summers, when Wilson was a member of the Chesapeake Marine Station established by Johns Hopkins University.

During the six years he taught at Bryn Mawr College (1885-1891) he published a brief account of the movements of Hydra, and an extensive paper on the embryology of the earthworm (1889). After his appointment to Columbia University (1891) his research productivity steadily increased. In 1892 he published "The Cell-Lineage of Nereis". Dr. E. A. Andrews of Johns Hopkins was the first to discover the abundance of the night swimming Nereis at Woods Hole, and called attention to the splendid material it supplies for embryological study. Ever since that time it has furnished fine material to the embryologists working at the Marine Station there. Wilson's beautiful paper on the development of Nereis may be said, in America at least, to have inaugurated a long line of research on cell lineage.

It is interesting to look back and ask what motivated these enormously laborious studies on cell lineage. They followed closely on the heels of the descriptive period of embryology whose leading idea was that the history of the race was repeated in the development of the individual. The current phrase was Ontogeny repeats Phylogeny, a speculation that had reached its climax in the exaggeration of Ernest Haeckel. As facts accumulated skepticism increased as to the validity of this postulate, especially when different observers drew different conclusions

* Wilson had earlier (1879-1881) published two systematic papers on Pycnogonida or sea spiders while at Yale. These served as his graduate thesis for the degree of Ph. B.

from the same facts, particularly when the interrelations of the larger groups were concerned. Nevertheless certain evidence could not be ignored, such, for example, as the presence of gill slits in the early stages of the bird and mammal which appeared to repeat the gill system of the adult fish. However, when attention was called to the fact that gill slits, similar to those of the bird and mammal, were present in a corresponding early stage of the fish it became evident that it was not the adult gill system of the fish that was repeated in the higher form, but rather the retention of the same stage of development as that in the embryo fish. This conclusion seemed more consistent than the older somewhat mystical idea of adult stages of the lower forms being telescoped back into the early stages of the higher forms. Furthermore, the theory of the repetition of similar embryonic structures could be used to support the evolution theory just as well as the older phylogenetic theory. It furnishes as good evidence as that from comparative anatomy, but goes even further in offering earlier clues as to relationships between the great groups of the animal kingdom.

Wilson was not much concerned with the ontogeny-phylogeny theory, although in his earlier paper on Renilla he had followed the spirit of the times in his discussion of the gastraea theory as a recapitulation of a two-layered ancestor of the higher animals. He was, however, more concerned with comparisons between the cleavage stages of annelids, molluscs, and flatworms (1895-98), and still more concerned with phenomena of cleavage in these forms as having a bearing on what was called the "organization of the egg".

The problem of the organization of the egg was an old one, but after the experimental work of Roux on frogs' eggs and that of Chabry on ascidians' eggs, and the experimental work of Driesch on sea urchins' eggs, the theoretical deductions that they drew from these experiments, which were opposed, aroused wider and wider interest. From that time onwards the older phylogenetic problems lost interest, and embryologists took up the experimental study of embryology with increasing success and enthusiasm. Much of Wilson's later work was concerned with the evidence and its discussion in this new field.

Wilson's first piece of work in experimental embryology was carried out at the Faro, Sicily, in 1892 and published in 1893. The Faro was the original hunting ground of Kowalevski and Hatchek, where they obtained their material for their splendid papers (1867 and 1881). Wilson found great variability in the early cleavage stages of Amphioxus, but it is not quite clear to what extent they are due to abnormal conditions. In the light of the later work of Conklin (1932, 1933) it appears that, in the redistribution of the protoplasm of the egg of Amphioxus preceding the early stages of cleavage, the egg follows the mosaic type about as closely as does the Ascidian egg. Wilson found that the isolated first blastomeres produce whole embryos, as do the first four blastomeres also, and even the ⅛ blastomere. More recent work (Conklin 1933) confirms Wilson's conclusion for the two-cell stage, but it seems probable that only certain isolated blastomeres of the four-cell stage are capable of giving whole embryos.

Wilson's second work in experimental embryology (1901) dealt with the effects of agents inciting artificial parthenogenesis of the eggs of the sea urchin. The cytasters that appear after treatment with various salts had already been described in some detail by me (1896, 1899, 1900), but Loeb had been more successful in rearing embryos from eggs treated with magnesium chloride, and Wilson, by use of Loeb's procedure, described in more detail the role of the artificially induced cytasters. In the same year he published results that dealt with the suppression of the incipient cleavage plane by treatment with ether. He followed especially the disappearance of the asters and their reappearance when the eggs were returned to sea water, and drew certain conclusions as to their nature. In the same year he described results that followed shaking the eggs of the sea urchin just at the beginning of the first division. "The cleavage furrow, which may have begun to cut into the egg, is thus caused to fade out more or less completely and a binucleate condition results closely similar to that seen in the etherized eggs, but in most cases differing from the latter distinctly in that the elongation is still retained and its general outline at this time is very nearly identical with that of the 2-cell stage in which the cleavage furrow is obliterated. In such eggs the second cleavage takes place as a rule in the manner described by Boveri, two parallel amphiasters being formed through the equatorial plane of which the cleavage furrow passes exactly as though the first division had been completed. Two binucleated blastomeres are thus formed, and in typical examples this process is repeated at the third cleavage to form four binucleate blastomeres". Boveri had previously studied the same problem (1897), suppressing the first cleavage by placing the egg under pressure. "My observations", Wilson writes, "differ from Boveri's, however, in showing very clearly that after this point had been reached the first cleavage is restored, at least in some of the cells, and it may be restored even earlier".

In 1902 a graduate student, W. S. Sutton, pointed out that the two maturation divisions furnish an explanation of Mendel's laws. Wilson writes, "during the past year working in my laboratory he has obtained more definite evidence in favor of this result (the separation of maternal and paternal chromosomes), suggested by Montgomery (1901), which led him to the conclusion that it probably gives the explanation of the Mendelian problem". This conclusion of Sutton's has turned out to be more than "probable", and is today the basis for the mechanism of Mendel's two laws.

At Beaufort in the summer of 1903 Wilson repeated on Alpheus the experiments that Przibram had made in 1901 on the reversal of the large and small claw of Alpheus after removal of the smaller one, and confirmed Przibram's conclusions.

In the summer of 1902 Wilson made experiments with the nemertine egg, that Coe had previously shown to offer "an almost ideally perfect illustration of this type (mosaic) of cleavage". The material was studied at the marine laboratory of South Harpswell, Maine. Wilson studied both egg-fragments and isolated blastomeres. He concluded that localization of regions of the egg is a progressive (epigenetic) process. Before ripening the germinal regions of the egg of Nemerteans are equipotential (since fragments from such eggs may give rise to normal embryos) as regards the factors for cleavage and localization. The factors are to a certain extent localized between the beginning of ripening (the extrusion of the polar bodies) and the completion of the first cleavage; nevertheless, owing to the property of regulation a complete embryo develops out of an isolated blastomere. The localization process takes place through a new distribution of cytoplasmic materials. Cleavage is a means of localizing this material and is not the cause of differentiation. Here Wilson faced an apparent contradiction between whole and part development—a problem that is today still taxing the ingenuity of experimental embryologists. Wilson's own experiments showed that certain fragments of the Cerebratulus egg, that have reached the blastula stage, may still give rise to complete or nearly complete larvae. Also while the isolated blastomere cleaves, as though still a part only of the whole, it gives rise to a perfect embryo. Other and later experiments by Yatsu, Zeleny and Hörstadius have added further information concerning the potencies of parts of the egg and isolated blastomeres of Cerebratulus.

The most complete and outstanding papers that Wilson published in 1904 deal with "Experimental Studies on Germinal Localization". The first deals with the egg of Dentalium; the second with Patella and Dentalium. These papers were the outcome of eight months' residence at the Naples Zoological Station in 1903. The egg of the mollusc Dentalium has three distinct zones that can be traced to definite parts of the segmented egg. The first two blastomeres are unequal in size. If the smaller is isolated the embryo lacks certain organs; if the larger is isolated it gives rise more nearly to a whole embryo. A yolk lobe normally appears on one of the first two blastomeres. If removed the blastomere develops into a larva lacking certain organs present in the normal embryo. The unfertilized egg was also cut into fragments and these were fertilized. If cut in two in a horizontal plane, Wilson writes:—

"The upper fragment segments symmetrically without the formation of polar lobes and produces a larva similar to the lobeless ones. The lower one segments like a whole egg of diminished size, and may produce a normally formed dwarf trochophore. Fragments obtained by vertical section through the lower white area may segment like whole eggs and may produce nearly normally formed dwarf trochophores. Enucleated fragments, containing the lower white area of fertilized eggs, pass through alternating periods of activity and quiescence corresponding with the division-rhythm of the nucleated half, and form the polar lobes as if still forming part of a complete embryo. The same is true of the isolated polar lobe. The foregoing observations demonstrate the prelocalization of specific cytoplasmic stuffs in the unsegmented egg and their isolation in the early blastomeres. The lower white area contains such stuffs as are essential to the formation of the apical organ and the complex of structures forming the post-trochal region, including the shell-gland and shell, the foot, the mantle-folds and probably the coelomesoblast. These stuffs are contained in the first polar lobe, but the second lobe no longer contains those necessary for the basis of the apical organ. Progressive changes therefore occur in the original distribution of the specific cytoplasmic materials. Comparison indicates that the conditions observed in the molluscan egg differ only in degree from those in the nemertine or echinoderm. These differences reduce themselves to differences in the period of segregation (or differentiation) and in its pattern, and are explicable under the general theory of precocious segregation. The early development of egg-fragments indicates that the specification of the cytoplasmic regions is primarily qualitative, but not quantitative, or if quantitative is still subject to a regulative process that lies behind the original topographical grouping of the egg-materials. The development of the molluscan egg is in its essential features a mosaic-work and sustains the theory of 'Organbildende Keimberzirke' ".

The second paper deals largely with another mollusc, Patella, and describes the development of isolated blastomeres. The results are the same as those on Dentalium, but are carried further including the differentiation of later isolated blastomeres. The conclusion is reached that "the development of both Patella and Dentalium is essentially a mosaic work of self-differentiating cells".

In the same year Wilson stated his general conclusions as follows:

"I would express the opinion that, so far as the early stages of development are concerned, it is difficult to escape the hypothesis of formative stuffs or specific morphoplasmic substances, in some form. But while this hypothesis facilitates an understanding of the modus operandi or immediate causes of differentiation, it leaves us as much as ever in the dark as to the localizing or form-determining factors which are responsible for the determination of the segregation pattern. This problem, which is essentially one of correlative action, is not only unsolved, but suggests the existence of specific energies for which it is difficult at present to find an analogy outside the field of protoplasmic action".

A year later (1905) in a public address Wilson posed the two outstanding problems of development, as follows:

"I need not dwell on the absorbing, almost tantalizing, interest with which the problem of development has held the attention of naturalists from the earliest times. Twenty centuries and more have passed since Aristotle first endeavored to trace something like a rough outline of its solution. The enormous advances of our knowledge during this long period have taken away nothing of the interest or freshness of the problem; they have left it, indeed, hardly less mysterious than when the father of science wrote the first treatise on generation. I will not dwell on the epoch-making work of Harvey, Wolff and von Baer, or the curious, almost grotesque controversies of the eighteenth century, when embryology invaded the field of philosophy and even of theology. I will only point out that even at that time, when embryology was almost wholly limited to the study of the hen's egg, embryologists were already occupied with two fundamental questions, which still remain in their essence without adequate answer, and though metamorphosed by the refinements of more modern observation and experiment still stand in the foreground of scientific discussion. The first of these is the question of preformation versus epigenesis—whether the embryo exists preformed or predelineated in the egg from the beginning or whether it is formed anew, step by step in each generation. The second question is that of mechanism versus vitalism—whether development is capable of a mechanical or physico-chemical explanation, or whether it involves specific vital factors that are without analogy in the non-living world".

On the preformation view:

"Development was conceived to be only the unfolding and transformation of a pre-existing structure, not the successive formation of new parts—a process of 'evolution', not of epigenesis. In this particular form the doctrine of preformation was conclusively overthrown by Wolff; but the principle underlying it has repeatedly and persistently reappeared in later speculations on development, and still contests the field of discussion with its early antagonist".

With respect to the second question Wilson wrote:

"Hand in hand with this controversy has gone one of still more general scope between the two opposing conceptions that

I have referred to as mechanism and vitalism. Is development at bottom a mechanical process? Is the egg a kind of complex machine, wound up like a piece of clockwork, and does development go forward like the action of an automaton, an inevitable consequence of its mode of construction? Or, on the other hand, does development involve the operation of specific vital entelechies or powers that are without analogue in the automaton and are not inherent in any primary material configuration of the egg? This question, I hardly need say, is included in the larger one, whether the vital processes as a whole are or are not capable of mechanical explanation. As a problem of embryology it is very closely connected with that of preformation or epigenesis, and in point of fact the two have always been closely associated. Evidently, by its very form of statement, any theory of preformation or prelocalization in the germ assumes at least a mechanical basis for development, i.e., a primary material configuration upon which the form of development in some measure depends. With theories of epigenesis the case is not so clear; for such theories may or may not be mechanical. Without further preamble I now ask your attention to certain facts which will place clearly before us the form in which these time-honored problems appear to us today".

These quotations serve to show the philosophical morass in which the embryologists were floundering at that time. The older dispute between preformation and epigenesis has been largely laid aside in its original meaning, but to some extent has been brought forward under the evasive term of "organization of the egg". Today vitalism, as propounded by Driesch, has almost been forgotten, as embryological research has advanced, but in another form called the "Organism as a Whole" or the organismal theory it still has advocates and serves to keep the philosophical ball rolling—but to what goal is as unclear as it was forty years ago.

Wilson's most outstanding contributions are his eight studies on chromosomes published from 1905 to 1912. These deal almost exclusively with the reduction divisions during spermatogenesis. Here accuracy of observation and care in interpretation of the behavior of the chromosomes are shown in a high degree. The actual counts of the number of chromosomes is in itself not difficult, at least in those forms that have a small number, and Wilson chose mainly such forms, but the changes that take place during the ripening of the sperm cells call not only for extraordinarily careful observations but also for skill in interpretation. In both respects Wilson was unusually gifted. None of his results has been rejected by later workers while some of the erroneous chromosome counts of other contemporary cytologists held back for several years the solution of the role of the sex chromosomes in the determination of male and female.

In 1891 Henking described in the sperm cells of an insect Pyrrochoris a body that he called a chromosome nucleolus that finally went to half the sperm cells. But he did not even suggest that it had anything to do with sex determination. In 1902 McClung described a similar body in grasshoppers and called it the accessory; later it was called the X-chromosome. He suggested further that since half the sperm came to contain it and half lacked it, it had to do with sex, the male having one more chromosome than the female. Unfortunately the reverse turned out to be true in the insects under consideration. It is surprising that between 1902, when McClung published his hypothesis, and 1905, no one tested this view by an examination of the chromosomes of females. The reason is that it is difficult to procure good material of the maturation stage in the female while the corresponding stages in the male are readily procurable and give beautifully clear preparations. It is true there were a few records of oögonial chromosomes in females, but it turned out that the counts were wrong or else the male count was wrong, which stood in the way of acceptance or rejection of McClung's hypothesis. Then in 1905 Miss Nettie Stevens at Bryn Mawr College published in the Publications of the Carnegie Institution of Washington an account of the role of the sex chromosomes in the beetle Tenebrio. She showed that the male had 19 large and 1 small chromosome (the Y), the latter going to half the spermatozoa. She also showed that at the reduction division it (the smaller one) was the mate of one of the large chromosomes. Consequently half the ripe sperm had 10 large chromosomes and half had 9 large and 1 small chromosome. In the oögonial cells there were 20 large chromosomes which would reduce to 10 in the egg after maturation. She pointed out that an egg fertilized by a sperm with 10 large chromosomes would give a female with 20 such chromosomes, and that an egg with 10 large chromosomes fertilized by a sperm with 9 large and 1 small chromosome would restore the number characteristic of the male.

In the same year (1905)[1] Wilson published a similar conclusion in regard to the role of the sex chromosomes in two other insects in which the female has one more chromosome than the male; thus Anasa tristis ♀ has 22, and the male 21; and Protenor ♀ has 14, and the ♂ 13. The Stevens type XX-XY and the Wilson type XX-XO are the same in principle. It has turned out that the former is much commoner than the latter as a sex determining mechanism occurring widely in groups other than insects.

Another mechanism was discovered later in birds and moths in which the male was homozygotic for the sex chromosomes,

[1] The question is sometimes asked as to the priority of Stevens' and Wilson's papers. Stevens' paper was handed in on May 15, 1905, and printed in September of that year. In Wilson's paper "Studies on Chromosomes" I (dated May 5, 1905; published August 1905) he says in a footnote: "The discovery, referred to in a preceding footnote, that the spermatogonial number of Anasa is 21 instead of 22, again goes far to set aside the difficulties here urged. Since this paper was sent to press I have also learned that Dr. N. M. Stevens (by whose kind permission I am able to refer to her results) has independently discovered in a beetle, Tenebrio, a pair of unequal chromosomes that are somewhat similar to the idiochromosomes in Hemiptera and undergo a corresponding distribution to the spermatozoa. She was able to determine, further, the significant fact that the small chromosome is present in the somatic cells of the male only, while in those of the female it is represented by a larger chromosome. These very interesting discoveries, now in course of publication, afford, I think, a strong support to the suggestion made above; and when considered in connection with the comparison I have drawn between the idiochromosomes and the accessory show that McClung's hypothesis may, in the end, prove to be well founded."

In Wilson's "Studies on Chromosomes" II (dated October 4, 1905; published November, 1905) he says, "During the summer, and since the foregoing paper was entirely completed in its present form, I have obtained new material which shows decisively that the theoretic expectation in regard to the relations of the nuclei in the two sexes, stated at p. 539, is realized in the facts. In Anasa, precisely in accordance with the expectation, the oögonial divisions show with great clearness one more chromosome than the spermatogonial, namely, twenty-two instead of twenty-one; and the same number occurs in the divisions of the ovarian follicle-cells. Again in accordance with the expectation, the oögonial groups show four large chromosomes instead of the three that are present in the spermatogonial groups. In other respects the male and female groups are closely similar. In like manner, the oögonial divisions in Alydus and Protenor show fourteen chromosomes, the spermatogonial but thirteen; and in Protenor the spermatogonial chromosome-groups have but one large chromosome (unquestionably the heterotropic) while the oögonial groups have two such chromosomes of equal size."

here called ZZ, and the female heterozygotic, or WZ. The mechanism is the same in principle here as in the other cases.

In 1929 and 1930 Wilson returned to the problems of experimental embryology. Centrifuging the unfertilized eggs of Chaetopterus breaks them up into fragments. These fragments may contain any part of the materials stratified by the centrifuge, nevertheless if fertilized many of them with different inclusions may develop into larvae "closely similar to the normal whole trochophores." The cleavage of the normal egg is typically determinate, and many of the fragments, even very small ones, may show the same type of cleavage as the whole egg. Of course, only relatively few of the fragments cleave or develop normally. Whether the eggs orient on the machine was at the time undecided, but in his second paper Wilson considered the question and concluded that the eggs orient themselves on the centrifuge to a large extent.

In 1916 and again in 1925 Wilson described the remarkable changes that take place during spermatogenesis in the chondriosomes of the scorpion, and in 1937 in collaboration with Pollister a more detailed study, including the Golgi bodies.

Five years after his appointment at Columbia University he published his book on "The Cell" (1896) which was at once recognized as the outstanding summary of the work in this field. Wilson drew upon his wide experience covering, as it did, the role of the cell in fertilization and development, in experimental embryology, in spermatogensis as well as a thorough familiarity of the work of his contemporaries dealing with the cell. A third and greatly extended edition appeared in 1925. During the interval between the first and third editions, work in cytology had advanced in many directions and a voluminous literature had grown up. In a masterly way Wilson summarized this literature, separating the wheat from the chaff. I can not do better than quote here the words of Professor E. G. Conklin spoken at the time of the award to Wilson of the Daniel Giraud Elliot medal (for 1925) by the National Academy,

"The third edition of 'The Cell in Development and Heredity' has been written out of this unique experience; it represents not only the mature point of view of the world's leading student and teacher of cytology, but it is to a large extent the work of its leading investigator in this field. Few other workers are left who were in at the birth of this science and who can speak of its development with the knowledge that comes from intimate contact with persons and problems, and no one could deal with this subject in a more comprehensive and judicial manner. Though called a third edition of the earlier work, this is in reality an entirely new book, rewritten from cover to cover and almost three times as large as the previous edition. It is in every respect a monumental work, one of the most complete and perfect that American science has produced in any field, and while we congratulate Professor Wilson upon this consummation of the work of a lifetime, we are proud of the fact that the National Academy of Sciences can bestow the Elliot Medal on a fellow member for a book of such outstanding worth as 'The Cell in Development and Heredity.' "

Wilson was a member of all the leading learned societies of Europe and America. He was a recipient of honorary degrees from the universities of Columbia, Harvard, Yale, Johns Hopkins, Chicago, Louvain, Cambridge (England), Lwow, and Leipzig. He was awarded the gold medal of the Linnean Society, London; the Elliot Medal of the National Academy of Sciences; the John J. Carty Medal and Award. He will be lovingly remembered by his many friends as a reserved, cultured gentleman whose sincerity, judgment, and breadth of knowledge were shown by the perfection of his lectures and his scientific papers.

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