Mendel's Principles of Heredity and the Maturation of the Germ Cells

Edmund B. Wilson

Zoological Laboratory of Columbia University

December 11, 1902.

Wilson, E. B. 1902. Mendel's principles of heredity and the maturation of the germ cells. *Science,* N. S. vol. 16: 991–993.

ESP

Electronic Scholarly Publishing

http://www.esp.org

Electronic Scholarly Publishing Project

ESP Foundations Reprint Series: Classical Genetics

Series Editor: Robert J. Robbins

The ESP Foundations of Classical Genetics project has received support from the ELSI component of the United States Department of Energy Human Genome Project. ESP also welcomes help from volunteers and collaborators, who recommend works for publication, provide access to original materials, and assist with technical and production work. If you are interested in volunteering, or are otherwise interested in the project, contact the series editor via email: *rrobbins@fhcrc.org*.

Bibliographical Note

This ESP edition, first electronically published in 2000, is a newly typeset, unabridged version, based on a reprint of the original paper as it appeared in Křiženecký, J. 1965. *Fundamenta Genetica, The Revised Edition of Mendel's Classic Paper with a Collection of 27 Original Papers Published during the Rediscovery Period*. Prague: Publishing House of the Czechoslovak Academy of Sciences.

Production Credits

Scanning of originals:	ESP staff
OCRing of originals:	ESP staff
Typesetting:	ESP staff
Proofreading/Copyediting:	ESP staff
Graphics work:	ESP staff
Copyfitting/Final production:	ESP staff

Wilson, E. B. 1902. Mendel's principles of heredity and the maturation of the germ cells. *Science*, N.S. vol. 16: 991–993.

MENDEL'S PRINCIPLES OF HEREDITY AND THE MATURATION OF THE GERM CELLS

EDMUND B. WILSON

Zoological Laboratory of Columbia University

December 11, 1902.

IN VIEW OF THE GREAT INTEREST that has been aroused of late by the revival and extension of Mendel's principles of inheritance it is remarkable that, as far as I am aware, no one has yet pointed out the clue to these principles, if it be not an explanation of them, that is given by the normal cytological phenomena of maturation; though Guyer and Juel have suggested a possible correlation between the variability or sterility of hybrids and abnormalities in the maturation-divisions, while Montgomery has recognized the essential fact in the normal cytological phenomena, though without bringing it into relation with the phenomena of heredity. Since two investigators, both students in this University, have been led in different ways to recognize this clue or explanation, I have, at their suggestion and with their approval, prepared this brief note in order to place their independent conclusions in proper relation to each other and call attention to the general interest of the subject.

Bateson, in his recent admirable little book on Mendel's principles, is led to express the surmise that the symmetrical result in the offspring of cross-bred forms 'must correspond with some symmetrical figure of distribution of gametes in the cell-divisions by which they are produced' (p. 30). It is needless to remind cytologists that the study of the maturation-mitoses, especially in the case of arthropods, has revealed a mechanism by which such a symmetrical distribution may be effected; for the germ-cells in the great majority of cases arise in groups of fours, formed by two divisions, of which one is in many cases described as differing in character from the ordinary somatic mitoses in that it separates whole chromosomes by a transverse division ('reducing division' of Weismann). Wholly independently of Mendel's conclusions a considerable number of cytologists (von Rath, Rückert, Häcker) early reached the conclusion that the chromatin-masses from which arise the 'Vierergruppen' (tetrad-chromosomes, or their equivalents) represent double or 'bivalent' chromosomes, each of which was conceived to arise by the union (synapsis), end to end, of two single chromosomes. An actual conjugation of chromosomes in synapsis was inferred by Rückert in some cases (*e. g.*, in *Pristiurus*), and more recently described in a far more detailed way in *Peripatus* and certain insects by Montgomery (1901), who reached the remarkable conclusion that 'in the synapsis stage is effected a union of paternal with maternal chromosomes, so that each bivalent chromosome would consist of one univalent paternal chromosome and one univalent maternal chromosome.' The ensuing transverse or reducing division, therefore, leads to *the separation of paternal and maternal elements and their ultimate isolation in separate germ-cells.* This conclusion rested upon evidence too incomplete to warrant its acceptance without much more extended investigation it was, indeed, more in the nature of a surmise than a well-grounded conclusion. During the past year Mr. W. S. Sutton, working in my laboratory, has obtained more definite evidence in favor of this result, which led him several months ago to the conclusion that it probably gives the explanation of the Mendelian principle. In the great 'lubber grasshopper' *Brachystola* the chromosomes of the spermatogonia were found to be grouped in eleven pairs of different sizes, which reappeared in essentially the same relation through at least eight successive generations of these cells. In synapsis the graded pairs are converted into similarly graded bivalent chromosomes that appear to arise by a conjugation, or union at one end, of the two members of each of the earlier pairs. Cogent reason is given by Sutton for the conclusion that the chromosome-pairs consist each of a paternal and maternal member. It is known that in fertilization chromosomes are contributed in equal numbers by the two gametes ('Van Beneden's Law'). Boveri's recent remarkable experiments on sea-urchins have proved that a definite combination of chromosomes is necessary to complete development, and strongly suggests, if they do not prove, that the individual chromosomes stand in definite relation to transmissible characters taken singly or in groups. Every nucleus, however, contains two such combinations; for the facts of parthenogenesis and merogony prove that either the paternal or the maternal group alone may suffice for complete development. It is a natural conclusion from these facts that the constant morphological differences of the chromosomes observed in the grasshopper are correlated with constant physiological differences. If such be the case it appears highly probable, though the argument can not here be presented in all its weight, that those of corresponding size, associated in pairs, are the paternal and maternal homologues (*sit venia verbo*)! Sutton has pointed out that if this be indeed the case, the union of these homologues in synapsis, and their subsequent separation, which this preliminary union involves, in the reducing (second maturation) division, leads to the members of each pair being isolated in separate germ-cells; and this gives a physical basis for the association of dominant and recessive characters in the cross-bred, and their subsequent isolation in separate germ-cells, exactly such as the Mendelian principle requires.

A similar conclusion was subsequently, but independently, reached by Mr. W. A. Cannon, of the Department of Botany, though by a different and less direct path of approach. A study of hybrid cotton-plants, which are fertile, showed the maturation-divisions to be entirely normal, in contradistinction to the sterile hybrids of *Syringa*, where Juel has shown that the maturation-divisions are abnormal in character. It thus appeared that a sifting apart of paternal and maternal elements, such as Mendel's law demonstrates to occur, cannot be explained on the hypothesis of irregularities in the maturation-divisions (as had been suggested by Guyer's earlier work on pigeon-hybrids). Cannon therefore concluded, on this *a priori* ground, that such a separation of paternal and maternal elements must occur in the normal maturation-divisions, not only in the cross-bred, but also in the normal forms, and that in the character of these divisions must be sought the basis of the law. It is interesting that such a conclusion should have been reached by a botanist, on account of the fact that most recent botanical workers in this field have reached the result that transverse or reducing divisions do not occur in the maturation of the germ-cells in higher plants. It has, however, become clear that only the most exhaustive study of the most favorable material, particularly in the earliest stages of the maturation-divisions, can positively decide this question, and the importance of the most accurate and detailed further study of the phenomena is now manifest. The results I have indicated are already in part in press and will in due time be fully discussed by their authors. Should the study of the maturation-divisions indeed reveal the basis of the Mendelian principle we shall have another and most striking example of the intimate connection between the study of cytology and the experimental study of evolution.