GENESIS OF GENETICS

THE GROWING KNOWLEDGE OF HEREDITY BEFORE AND AFTER MENDEL

A brief historical synopsis written in honor of the Institutum Gregorio Mendel and the International Symposium on Medical Genetics held in Rome, 6-7 september 1953

by

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Prologue

"Nonum prematur in annum" . . . is the Horatian rule for newborn manuscripts.

The rule could not be followed, however, in writing this outline of the development of genetics. Time was very short to include in the synopsis everything that was prepared for it in my preliminary work. Several appendices of the outline had to be omitted, such as *a*) National and international organizations for genetic research, *b*) Journals of genetics, *c*) Five-foot bookshelf of genetic classics, and *d*) Time-applied dictionary of human genetics.

For the same reason, the outline had to be released before the usual rhetorical follow-up could secure elegance of expressions and smoothness of language. Nevertheless, every effort was made to present an objective synthesis of the scattered data. The facts of the outline are accurate, and they are presented without prejudice, and with sincerity to the Benevolent Reader.

30 June 1953, Washington, D. C. CLAUDIUS F. MAYER

GENERAL INTRODUCTION

It is the intention of this paper to draw an outline of the changing views of the centuries concerning the problems of heredity and to show how the slowly acquired knowledge on the phenomena of life and its reproduction prepared the development of a modern science which since 1906 has been called *genetics*. The birth of this new science happened at the change of the century, in 1900 when the importance of Gregor Mendel's experiments with hybridization of plants was first recognized by the leading biologists of the world, and his conclusions from crossing peas in a monastic garden in the eighteensixties became the fundamental laws of inheritance.

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More than half a century passed by, and genetics is now a major independent branch of biology. Its growth by experimentation and observation is very rapid, and its theoretical and practical field is steadily widening. This makes it difficult to reduce the history of the last fifty years into a brief outline. As any growing science, genetics also has its prenatal period of existence which from 1900 reaches back into ancient history. A full evaluation of this ancient knowledge, though desirable, is impossible at present, and I have to restrict myself to sampling the old ideas and to providing basis for comparison with the modern thoughts on heredity.

Heredity is the conservation and transmission of the qualities or characters from parents to offspring, regardless whether it happens in the kingdom of plants, or of animals, or in human society. Thoughts on heredity are therefore inevitably connected with ideas on generation, sexual reproduction, sex, species, conservation and perpetuation of the pattern of plant species or of animal species, maintenance of the parental type, individual differences and variations, the basic relation of all life on the globe, the creation and origin of the first life, and the evolution and interrelation of all forms of life since its beginning.

The laws of heredity could hardly be accurately and properly recognized without the accurate knowledge of the basic facts of generation. But these basic facts were only very gradually discovered, by means of the microscope in the course of the last two centuries. Before the recognition of the essential elements of reproduction of life, all knowledge about inheritance served as a ground of more or less vague speculation only. *Longet* (1811-1871), French physiologist, estimated that there are about threehundred different theories which had been suggested for the explanation of the problems of generation and heredity in the course of history.

Since the time of the Greek philosophers of Antiquity the historical aspect of life had been a subject of intensive speculation. The main points of interest of most theories were the material carrier or carriers of inheritance, the mechanism of transference of characters, the characters which are heritable (especially the inheritance of sex), the distribution of characters in the offspring, and the influence of the external environment, and of the universe, upon the various phases of generation. Throughout the centuries, up to our own times, the two leading problems remained the same: 1) do the paternal and maternal elements of generation contain an already organized pattern of the offspring (theory of *preformation*) or only the potencies for its individual evolution (theory of *postformation* or *epigenesis*), and 2) are defects and acquired other characters transmitted, or not, from parents to descendants? The entire history of genetics is characterized by a continuous wave-like movement of the alternately negative and affirmative answers to these questions.

A particular difficulty in writing an outline of the history of genetics arises from the circumstance that the language of modern genetics is constantly creating many new words, for the use of geneticists, which are hardly to be avoided in a historical outline of the subject, except with some degree of troublesome circumlocution.

Another difficulty has its origin in the wide range of life which includes plants, animals, and man. Genetics is the science of the origin of *any* living form on the basis

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of inherited reaction standards, the science of the development of all new forms of life and of the nature and effects of hereditary factors (1943 Gottschewski). Even in an outline of its history one has to consider therefore the different manifestations of life. Propagation and heredity are universal functions of living beings, and knowledge acquired by breeding of plants will also benefit our scrutiny of human inheritance. Our own line of ancestry must include at least 300,000 generations according to an estimate of Hirschfeld, yet it was a plant breeder, Gregor Mendel, the Augustinian monk, who, with the aid of a much shorter line of plant generations, made himself the founder of modern genetic science.

Nevertheless, it is impossible for me to divest myself of my medical background and to make the following retrospect evenly divided for the interests of the botanist, zoologist and anthropologist. In the collection of my data I inclined toward records on human heredity, and reported on plant and animal inheritance where such knowledge was in the foreground of interest of a particular period.

HISTORIANS AND SOURCES OF HISTORY OF GENETICS

Being a considerably new science, genetics proper did not attract the attention of many historians. Moreover, modern genetics is so thoroughly different from the older doctrines on heredity that practically everything before 1900, with the exception of Mendel's laws and some basic facts of reproduction, is now deadwood. As far as present day genetic research and its success is concerned, very little of the historical material before 1900 has any importance. Hence, there are only few who took time and made some effort to revaluate the tremendous heap of single observations and loose records which throughout the several thousand years of human history had accumulated in reference to heredity.

The *original sources* for a history of heredity are manyfold, and of the same kinds as for any history of science. Among the written records this study is restricted to the sampling of a few outstanding representatives of the natural sciences in Antiquity and in the Middle Ages. It is true that reading a great number of inferior or average writers would be the surest way to learn the mind of these ages. There are very few historical analysts, however, on the field of sciences, and, notably, these few had no time yet to run through the history of all ages in search for the contemporary opinions of the people, or of the better educated scholars, concerning the ways of heredity. In a synthetical history of genetics it suffices to show the leading ideas of the most outstanding or representative naturalists, in order to compare them with modern advancements. The works of the older authors are quoted from newer editions of their books. Modern authors after 1500 are quoted from their original publications, including the contemporary geneticists. Much of this material is listed in the various sets of the Index-Catalogue of the Surgeon-General's Library (Armed Forces Medical Library, Washington, D. C.) under appropriate genetic terms, and it is available at the same place. A substantial portion of older and newer printed sources was obtained from the Library of Congress.

No doubt that many religious works of the ecclesiastical fathers, also the publications

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of general writers, geographers, jurists, even poets, and fiction writers of all ages and all countries could be searched with profit on scattered data concerning generation, sexual beliefs and parental inheritance.

In 1939 Beck stated that there was yet no comprehensive history of human genetics. The historiography of genetics is of comparatively small volume. It includes biographies and obituaries, general summaries, studies of individual achievements, general studies on reproduction, description of single or several theories, of special discoveries, etc. Many older histories were written by the investigators themselves whose publications often begin with a short résumé of previous work on the field.

Other sources of secondary information on the history of genetics are the general histories of science (e. g., Sarton's Introduction), histories of botany, of zoology, of biology, of medicine. Each textbook on genetics also contains a few chapters which refer to historical material.

Articles or books on history of genetics were written by Roth,[1] Thompson,[2] East,[3] Roberts,[4] Johannsen,[5] Punnett,[6] Sirks,[7] Du Bois,[8] Wilson,[9] Krumbiegel,[10] Lehmann,[11] May,[12] Weismann,[13] Keudel,[14] Stiles,[15] Muller,[16] Rostand,[17] Focke,[18] Pimentel,[19] Vasco,[20] and Uda in Japan.[21]

[1] ROTH E., Die Tatsachen der Vererbung in geschichtlich-kritischer Darstellung. 2. Aufl., Berl., 1885.

[2] THOMPSON J. A., The history and theory of heredity. *Proc. R. Soc. Edinburgh* (1888-89) 1890, 16: 91-116.

[3] EAST E. M., Two decades of genetic progress. *Rep. Smithson. Inst.* (1922) 1924, 285-95.

[4] ROBERTS H. F., The founders of the art of breeding. *J. Hered.*, 1919, 10: 99-106.

[5] JOHANNSEN W., Hundert Jahre Vererbungsforschung. *Verh. Ges. Deut. Naturforsch.* (1922) 1923, 87: 70-104.

[6] PUNNETT R. C., An early discussion of heredity. *Science*, 1911, 34: 800.

[7] SIRKS M. J., Praemendelistische erfelijkheidstheorieen. *Genetica*, 1920, 2: 323-46.

[8] DU BOIS A. M., Die Entwicklung der Genetik. *Ciba Zschr.*, 1937 (Mai No. 45).

[9] WILSON E. B., The cell. 3. ed. N. Y., 1925. – has a historical introduction.

[10] KRUMBIEGEL I., Die praemendelistische Vererbungsforschung und ihre Grundlagen. *Bibliogr. genet.*, 1933, 10: 250-97.

[11] LEHMANN E., Aus der Frühzeit der pflanzlichen Bastardierungskunde. *Arch. Gesch. Naturwiss.*, 1916, p. 78.

[12] MAY W., Antike Vererbungstheorien. *Naturwiss. Wschr.*, 1917, 16: 9.

[13] WEISMANN A., Zur Geschichte der Vererbungstheorien. *Zool. Anz.*, 1886, 345-6.

[14] KEUDEL K., Zur Geschichte und Kritik der Grundbegriffe der Vererbungslehre. *Arch. Gesch. Med.*, 1936, 28: 381-416. – Based chiefly on Johannsen's results; also with reference to some philosophy of genetics.

[15] STILES K. A., Recent advances in human genetics. *Proc. Iowa Acad. Sc.*, 1941, 48: 73-81.

[16] MULLER H. J., Progress and prospects in human genetics. *Am. J. Human Genet.*, 1949, 1: 1-18.

[17] ROSTAND J., Esquisse d'une histoire de l'atomisme en biologie. *Rev. hist. sc.*, Par., 1948-49, 2: 241-65.

[18] FOCKE W. O., Pflanzenmischlinge. Berl., 1881. – Its second part, 429-445, is: Geschichte der Bastardkunde.

[19] PIMENTEL W., Genetica; sintese da sua evoluçâo. *Rev. milit. med. vet.*, Rio, 1939, 2: No. 21, 1531-48.

[20] VASCO, Apuntes históricos y médicos sobre la herencia. *Pabellón méd.*, Madr., 1875, 15: 183; 195.

[21] UDA, HAJIME, Mendel iden-gaku. Tokyo, Seikatu-sya, 1948. 227 p. – includes also data on Japanese geneticists.

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The following publications treat theories of heredity or generation in Antiquity: Ballantyne [22] on heredity in Hippokratic writings, Johannsen [23] on Hippokrates and Aristoteles, Balss, [24] Hommel, [25] Montalenti [26] on Aristoteles, Stiebitz [27] on Aristoteles, Barthélemy-St. Hilaire [28] on the generation in Aristoteles, MacCartney [29] on Greek lore, Hervé [30] on Aristoteles and Réaumur, Balss on Galenos [31] and on preformation in Greek philosophy. [32]

Other publications discuss special historical problems: the parthenogenesis by Taschenberg, [33] the movement of human ovum by Kehr, [34] Virchow's attitude to heredity by Posner, [35] the chromosome theory by Franz, [36] the evolutionary ideas of Antiquity by Heinze, [37] Zeller [38] and Schwertschlager. [39]

Among the contemporary historians of genetics the most active and the most comprehensive is Conway *Zirkle*, professor of botany at the University of Pennsylvania. His various publications include journal articles and books related to plant hybridiz-

[22] BALLANTYNE J. W., Antenatal pathology and heredity in the Hippocratic writings. *Tr. Edinburgh Obst. Soc.*, 1894-95, 20: 51-66.

[23] JOHANNSEN W., Die Vererbungslehre bei Aristoteles und Hippokrates im Lichte heutiger Forschung. *Naturwissenschaften*, 1917, 5: 389-97.

[24] BALSS H., Die Zeugungslehre und Embryologie in der Antike. *Quellen und Stud. Gesch. Naturwiss. Med.*, 1936, 5: 1-82. – includes also heredity, and hybrids.

[25] HOMMEL H., Moderne und hippokratische Vererbungstheorien. *Arch. Gesch. Med.*, 1927, 19: 105 etc.

[26] MONTALENTI G., Il sistema Aristotelico della generazione degli animali. *Rass. stud. sess.*, 1926, 6: 113-39.

[27] STIEBITZ F., Ueber die Vererbung bei Aristoteles. *Arch. Gesch. Med.*, 1930, 23: 332 etc.

[28] BARTHÉLEMY-ST. HILAIRE J., Traité de la génération des animaux d'Aristote. Paris, 1887, 1: 1-124. – This is the preface; it gives a good outline of the history of comparative embryology.

[29] MCCARTNEY E. S., Acquired and transmitted characters in Greek lore of heredity. *Papers Michigan Acad. Sc.*, 1927, 7: 21-40.

[30] HERVÉ G., La génétique prémendélienne: Aristote et Réaumur. *Rev. antrop., Par.*, 1922, 32: 285-97.

[31] BALSS H., Ueber die Vererbungstheorie des Galenos. *Sudhofs Arch.*, 1934, 27: 229-34.

[32] — Präformation und Epigenese in der griechischen Philosophie. *Arch. stor. sc.*, 1923, 4: 319-25.

[33] TASCHENBERG O., Historische Entwickelung der Lehre von der Parthenogenesis. *Abh. Naturforsch. Ges. Halle*, 1892, 17: 365-453.

[34] KEHR J., Die Aufnahme des menschlichen Eies in die Tuba und seine Fortleitung bis in den Uterus; eine historisch-kritische Studie. Jena, 1885.

[35] POSNER C., Rudolf Virchow und das Vererbungsproblem. *Arch. Frauenh.*, 1922, 8: 14-23.

[36] FRANZ B., Altes und Neues über die Chromosomentheorie der Vererbung. *Natur*, Lpz., 1921, 12: 239-43.

[37] HEINZE, M., Antiker Darwinismus. *Neues Reich*, 1877, 1:

[38] ZELLER E., Ueber die griechischen Vorgänger Darwins. *Abh. Berl. Akad. Wiss.*, Vortr., No. 2, 1884, 37-51.

[39] SCHWERTSCHLAGER J., Die erste Entstehung der Organismen nach den Philosophen des Altertums und des Mittelalters. Eichstädt, 1885.

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ation,[40] inheritance of acquired characters,[41] the discovery of sex linkage,[42] history of sex in plants,[43] predarwinian ideas on natural selection.[44]

Other historical essays on genetic topics include the valuable publication of Roberts[45] on plant hybridization before Mendel which covers the years between 1761 and 1864 also. Gillespie's recent work on Genesis and Geology (Cambridge, 1951) is limited to the 1780-1850 period and the scientific thought in Great Britain. Vavilov's work[46] is valuable for its bibliographies and for its references to plant genetics. Lippmann[47] published a comprehensive work on spontaneous generation and its historical development.

In 1950 the Ohio State University organized a Golden Jubilee to celebrate the 50th anniversary of the rediscovery of Mendel's work. The various essays which were written for and presented at this occasion were collected in a volume and published in 1951 under the title Genetics in the Twentieth Century (N. Y., 1951). Among the contributors are historians as Zirkle, Iltis, etc., and pioneer geneticists as Castle, Penrose, etc. As an interesting general description of the collected essays indicates, the volume is a successful combination of the historical and the subject aspect of genetics. (The work could not be located in the Armed Forces Medical Library when I requested it for consultation and reference).

A number of biographies of geneticists have been published. Göbel[48] analyzed the life of Hofmeister. Many are the biographers of Mendel, including Boeke,[49] Correns,[50-51] Iltis,[52] and Thomsen.[53-54] Moewes wrote on the precursors of Mendel,[55] and Buddenbrock[56] published the lives of a selected group of geneticists. Karl Baer,[57] the discoverer of the ovum, wrote his autobiography.

[40] ZIRKLE C., The beginnings of plant hybridization. Phila., 1935. – includes all plant hybridizers before Kölreuter, 1761.

[41] — The early history of the idea of the inheritance of acquired characters and of pangenesis. *Tr. Am. Philos. Soc.*, Phila., 1946. – In a shorter form also in *Am. Naturalist*, 1935, 69: 417-45.

[42] — The discovery of sex-influenced, sex-limited, and sex-linked heredity. *Stud. and Essays Hist. Sc.*, N. Y., 1946, 167-94.

[43] — Some forgotten records of hybridization and sex in plants. *J. Hered.*, 1932, 23: 433.

[44] — Natural selection before the Origin of Species. *Proc. Am. Philos. Soc.*, 1941, 84: 71-123.

[45] ROBERTS H. F., Plant hybridization before Mendel. Princeton, 1929.

[46] VAVILOV N. I., The origin, variation, immunity and breeding of cultivated plants. Waltham, *Chronica Botanica*, vol. 13, 1949-50.

[47] LIPPMANN E. O., Urzeugung und Lebenskraft; zur Geschichte dieser Probleme von den ältesten Zeiten an bis zu den Anfängen des 20. Jahrhunderts. Berl., 1933.

[48] GOEBEL K., Wilhelm Hofmeister. Lpz., 1924.

[49] BOEKE J., Leeuwenhoek en Mendel. Haarlem, 1920.

[50] CORRENS C., Gregor Mendel's Briefe an Carl Nägeli. *Abh. math. phys. Kl. Sächs. Akad. Wiss.*, 1905, 29: No. 3.

[51] — Etwas über Gregor Mendels Leben und Wirken. *Naturwissenschaften*, 1922, 10: 623 etc.

[52] ILTIS H., Gregor Johann Mendel. Berl., 1924.

[53] THOMSEN O., Gregor Mendel's vaerk. *Hospitalstidende*, 1922, 65: 461-80.

[54] THOMSEN O., Fra Mendel til Morgan. *Hospitalstidende*, 1922, 65: 831-96.

[55] MOEWES, Vorläufer Mendels. *Naturwissenschaften* 1913, 12: 541.

[56] BUDDENBROCK W., Bilder aus der Geschichte der biologischen Grundprobleme. Berl., 1930.

[57] BAER K., Nachrichten über Leben und Schriften. St. Peterburg, 1865.

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Gedda,[58] in his "Studio dei gemelli", describes the history of genetics as it especially concerns the theories of twinning. Stur,[59] Brock,[60] Lorda Audera,[61] and others wrote on various aspects of the history of generation and heredity. Labus[62] discusses the history of heredopathology, while Beck[63] analyzes Morgagni's *De sedibus et causis morborum* for its genetic references.

Darwin's own work on "Variation of Animals and Plants under Domestication (2 v. Lond., 1868)" contains also the previous history of this subject, though it does not mention Mendel's experiments of 1865. Timoféeff-Ressovsky wrote a very useful work on experimental research into the problem of mutation,[64] with a chapter on the history of lamarckism. The work of Lamy[65] discusses the application of genetics to medicine, and devotes several chapters to the history of genetics. Ernst[66] contributes to the local history of genetic research in Switzerland. Useful historical data are contained in Bloch's work on the development of embryology[67] and in the essay of His[68] on the theories of sexual reproduction.

Oscar Hertwig published a study in 1918 in which he described in detail the cytological studies after 1870 which are in relation to oogenesis, fertilization, division of cell nucleus, and some adjunct theories such as the idioplasma theory, the persistence of chromosomes, etc.[69] He also wrote a series of historical essays which discussed various fields of this biological area of research.[70]

Several publications contain the historical development of the Russian doctrine of

[58] Gedda L., Studio dei gemelli. Roma, 1951. – See chapter 6, 231-263.

[59] Stur J., Zur Geschichte der Zeugungsprobleme. *Arch. Gesch. Med.*, 1931, 24: 318.

[60] Brock, Einige ältere Autoren über die Vererbung erworbener Eigenschaften. *Biol. Zbl.*, 1888, 8: 491.

[61] Lorda Audera V., Evolución de la teoria celular. *Tr. Cátedra hist. crit. méd.*, Madr., 1934, 2: 367-81.

[62] Labus J., Geschichtlicher Beitrag zu dem Problem der Vererbung von Krankheiten. *Freib. i. B.*, 1929.

[63] Beck W., Erbpathologische Hinweise in Morgagni's Hauptwerk De sedibus et causis morborum. *Virchows Arch.*, 1939-40, 305: 521-30.

[64] Timoféeff-Ressovsky N. V., Experimentelle Mutationsforschung in der Vererbungslehre. Dresd., 1937. – See Cap. 2, 8-12: Historisches und Kritik der lamarckistischen Versuche.

[65] Lamy M., Les applications de la génétique à la médecine. Par., 1944.

[66] Ernst A., Von den Anfängen der Vererbungs- und Mutationsforschung in der Schweiz. *Arch. Julius Klaus Stift.*, 1941, 16: 208-20.

[67] Bloch B., Die geschichtlichen Grundlagen der Embryologie bis auf Harvey. *Abh. Leopold. Carolin. deut. Akad. Naturforsch.*, 1904, 82.

[68] His W., Die Theorien der geschlechtlichen Zeugung. *Arch. Anthrop.*, 1870, 4.

[69] Hertwig O., Dokumente zur Geschichte der Zeugungslehre. 1918.

[70] — Allgemeine Biologie. (Various editions in 1906, 1909, 1912). See also his Der Kampf um Kernfragen der Entwicklungs - und Vererbungslehre (1909); also Zeit - und Streitfragen der Biologie (1894, Heft 1); also his Das Werden der Organismen, eine Widerlegung von Darwins Zufallstheorie (1916).

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Michurinism, [71-73] while the 2-volume work of Raikov [74] describes Russian evolutionism before Darwin's time. As mentioned before, the general textbooks on genetics and those on the history of biology also contain ready references on the development of genetics. I have used a number of them, and found them of some value on the field of the history of genetics, such as the compendium of Mainx, [75] the five-volume work of Hirschfeld, [76] the works of Rostand, [77-78] and the histories of biology by Nordenskiöld [79] and by Singer. [80]

I have also consulted Baitsell's Human biology (2. ed. N. Y., 1950) which contains a clear description of the current views in genetics and human heredity. The publications of Janicki, [81] Gottschewski, [82] Brix, [83] Beirne, [84] and especially the work of Wardlaw on Phylogeny and Morphogenesis, [85] helped in the understanding of the latest phases of genetic research work. Praechter's book on the history of ancient philosophy, [86] Brim's work on the Bible, [87] Müller's studies on eugenics among ancient Indians, [88] as well as two recent essays of Dobzhinsky [89] and Zirkle [90] on Russian genetics were also consulted. My previous study of Albertus Magnus [91] was also of help to me in preparing this outline of the history of genetics.

Further references to original literature are listed at appropriate places in the outline.

[71] Lenin Agricultural Academy, The situation in biological science; proceedings, July 31-Aug. 7, 1948; complete stenographic report. N. Y., 1949. See also Huxley J. Heredity East and West; Lysenko and world science N. Y., Schuman, 1949.

[72] U. S. S. R. Akademia. Institut Genetiki, Protiv reakcionnogo Mendelizma-Morganizma; sbornik statei. Moskva, 1950.

[73] Haldane J. B. S., New paths in genetics. Lond., 1941.

[74] Raikov B. E., Russkie biologi-evoljucionisty do Darvina. 2v. Moskva, 1951.

[75] Mainx E. F., Einführung in die Vererbungslehre. Wien, 1948.

[76] Hirschfeld M., Geschlechtskunde. 5v. Stuttg., 1928. – This was one of my valuable sources for portraits and illustrations.

[77] Rostand J., Les idées nouvelles. Par., 1941.

[78] — Esquisse d'une histoire de la biologie. 3. éd. Par., 1945.

[79] Nordenskiöld E., Die Geschichte der Biologie. Jena, 1926. (Also in English, N. Y., 1946).

[80] Singer C., A short history of biology. Oxford, 1931.

[81] Janicki D. J., Evidence of cytoplasmic inheritance. *Bios*, 1953, 89-97.

[82] Gottschewski G., Der heutige Stand der Vererbungswissenschaft. *Der Biologe*, 1943, 12: 53-64. – Also source of illustrations.

[83] Brix K., Chromosomen oder plastische Stoffe. *Umschau*, 1953, 53:234-5.

[84] Beirne C. G., Summary of important names and dates in the history of genetics. *Bull. Creighton Univ. Sch. Med.*, 1948, 5: No. 1, 12-15.

[85] Wardlaw C. W., Phylogeny and morphogenesis. Lond., 1952.

[86] Praechter K., Ueberwegs Grundriss der Geschichte der Philosophie des Altertums. Berl., 1909.

[87] Brim C. J., Medicine in the Bible. N. Y., 1936.

[88] Müller R. F., Zum Rassengedanken bei der altindischen Ehe. *Sudhofs Arch.*, 1935, 25: 382, etc.

[89] Dobzhinsky T., Lysenko progresses backwards. *J. Hered.*, 1953, 20-22.

[90] Zirkle C., The involuntary destruction of science in the USSR. *Sc. Month.*, 1953, 76: 277-83.

[91] Mayer C. F., Die Personallehre in der Naturphilosophie von Albertus Magnus. *Kyklos*, Lpz., 1929, 2: 191-257.

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As the literature of modern genetics is very large, many authors are quoted only by name (and an added number of the year when their publication appeared) since it is not my intention to prepare a bibliography of genetics. For the description of genetic trends the shorter method of " *dated pointers* " is adequate. [92]

I. PRE - MENDELIAN ERA

The history of genetics can be conveniently subdivided into three uneven parts for the sake of easy discussion: 1) the times before Mendel's experiments, or the pre-Mendelian era which ends with 1865, 2) Gregor Mendel's experiments and his laws, and 3) the period after Mendel's publication, which again has a transitional segment between 1865 and 1900 when the rediscovery of the Mendelian rules of heredity stamps this period as the era of Mendelism.

The outstanding events of the pre-Mendelian era, which extends over more than 3000 years of human history, are concentrated in its last twohundred years. The basic facts of sexual reproduction as well as the germ cells, male and female, were discovered between 1677 and 1865, only. The following table of these basic discoveries will contribute much for the understanding of the general character and the level of genetic knowledge of the pre-Mendelian era:

1672 description of the ovarian follicle
1677 description of the male germ cell (human)
1777-80 first artificial impregnation (of a bitch)
1827 description of the ovum
1839 establishment of the cell theory.

The discovery of the basic facts of sexual reproduction is a rather late achievement of mankind. This is however not surprising since there are still world-wide persistent beliefs according to the anthropologists [93] that children come by other means but natural generation. Yet, inspite of the inaccurate sexual knowledge, the concept of heredity must have developed very early in the history of mankind. But is there any evidence for such statement?

Zirkle, in his historical work on plant hybridization, states that the first species or variety crosses were made by man in the *Neolithic Age.* Domestication of cats and dogs also meant hybridization. It is also probable that cattle were graded up from wild stock through breading in this prehistoric age. [94] Similarly, the first plant hybrids were purposely made by the neolithic man for crop betterment. [95]

It can be supposed that prehistoric man recognized similarities and differences bet-

[92] The bibliography of genetics is well covered by the *Index-Catalogue* up to March 31, 1950. Thereafter, the special bibliographical lists of the genetic journals, especially that of the *American Journal of Human Genetics*, provide the most complete survey of the subject literature. The Index-Catalogue is available in all countries, in the large medical and university libraries.

[93] HARTLAND, Primitive paternity. 1909.

[94] ZIRKLE, o. c., Phila., 1935, 2.

[95] IBID., 3.

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ween father and son, and between wild and domestic animals and their offspring. It must have occurred to the most primitive people that cows have calves rather than puppies or colts. [96] These observations must have influenced, without scientific background and perhaps unintentionally, the practices of the nomad people in breeding cattle or domestic animals, and their methods of plant breeding after they had settled down.

Certain conclusions can be drawn from the beliefs of present day common people in primitive or *semicivilized countries*, since, with certain restrictions, it can be assumed that the biogenetic rule of recapitulation is also applicable beyond the sphere of physical morphogenesis. Thus, the common beliefs of the general laity concerning heredity and generation may still have certain rudiments of the opinions of the neolithic man.

One of the most frequent questions of common people is whether the child will be a boy or a girl. The various customs of ancient and contemporary folks in regard to sex determination are described by Hovorka and Kronfeld. [97] It was a general rule that a strong male animal would generate a female offspring, while a strong female would produce a male. It had been also an old belief that the sex of the embryo could be voluntarily influenced by means of various tricks.

It is not necessary to enumerate all the remedies, drugs, diets, and other means which had been employed throughout the ages for influencing the sex of the growing foetus. Since it was also an old tradition that the right side of the body produced the males, and the left side the females, various advantageous positions and other rituals were in common use during mating in order to obtain the desired effect. The belief in the right side and its maleness is basically the adherence to a genetic theory which assumes that external influences are effective in changing the character of sex during conception and prenatal life. In Steyr, Austria, people believe in a correlation between the year's crop of certain fruits and the sex of children born in the same year. If there is abundance in apples and nuts, the yearly quota of boys will be higher among the newborn; if the pears abound, the higher sex ratio shifts to the girls. [98]

Here should be also mentioned the universal belief among the women of the world of all ages that the imaginary power of a mother is sufficient during pregnancy or at the time of conception to produce similarities in her child, similarities to both ugly and beautiful things she happens to look at. This belief is still there in the modern woman's wedding chest.

Antiquity

In ancient times many observations were made about the transmission of good or bad, nice or ugly characters from generation to generation of animals as well as of man, and many phantastic theories were left over in the historical remains. The concept of heredity was tied together with the knowledge of sexual reproduction. Since the latter was based upon much ignorance, not much worthy can be found in the other.

For the speculators there were the two basic observations of life: 1) the *continuity*

[96] Cf. Beirne, footnote 84.

[97] Hovorka-Kronfeld. Vergleichende Volksmedizin. Stuttg., 1909, 2: 527-34.

[98] —

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of species in plants, animals and human beings, and 2) the *similarity and dissimilarity* of individuals according to their relationship. In these speculations, however, superiority was ascribed to the male principle of generation... a sort of Priapus cult in the minds of the ancient philosophers in Babylon, Egypt, Greece, and Rome.

ASSYRIA. There is an interesting fragment of an Assyrian inscription which Dennefeld found among the birth signs and omina: "If a sow delivers three, 2 white and 1 black pig, then among the sons of the owner... (Also) if a sow throws four, among them a white, a black, a yellow and a spotted, then... ".[99]

On some Assyrian bas-reliefs, dating back to the 9th century B. C., one may see a cherub, fertilizing with his hand the date palms. Zirkle states that the knowledge of pollination goes back among the Assyrs as far as 2,400 B. C., to the reign of Gimil-Sin, while the actual cultivation of date palm (and thus the knowledge of bisexuality among plants) dates back to 3,500 B. C.[100]

INDIA. In the Manava-Dharma-Sastra which was composed between the 14th and the 13th century B. C. there are theories for the explanation of reproduction, and others for the understanding of conception, but they are in many contradictions. One of these theories ascribes equal role to the father and the mother in the production of the child. Another theory states that the father has the overwhelming effect, and the mother only supplies the embryo with food and lodging. Hence, the heredity is considered paternal.[101]

Müller analyses the marriage rules of the *Manu-saṃhita* which was written 2-3 thousand years ago. The manuscript contains rules prohibiting marriage with a woman whose tribe *a*) does not have male children, *b*) who has much hair on the body (perhaps a desire to select young brides), *c*) who suffers from digestive diseases, loss of consciousness, and from white and black exanthemata (leprosy? and smallpox?). A 9th century commentator considered these ailments hereditary.[102]

The manuscript considers that the seed of the father and the blood of the mother are the transferers of these diseases. Another mechanism for the development of hereditary diseases is given in *reincarnation* after which a man, who had committed specific sins in his former life, would have to wear a bodily mark, a physical sign of his "*peccatum hereditarium*": — the gold thief would have sick nails; the food thief, digestive troubles; the adulterer,skin diseases; the drunkard, black teeth; the grain thief, defects of limbs; the forgerer, superficial limbs; the thief of clothes, leprosy. It is also recommended that a man should not marry a girl who has 6 fingers or 6 toes.[103]

FAR EAST. There is not much known about the ancient genetic knowledge in China and Japan. It is commonly told, however, that in both countries hybridization and selection in breeding of domestic animals and plants had been practiced for economical as well as ornamental purposes.

[99] KRUMBIEGEL, cf. footnote 10, l. c., 255.
[100] See footnote 40.
[101] Cf. MÜLLER in footnote 88.
[102] —
[103] —

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BIBLE and TALMUD. The genetic references in the Bible and the Talmud are characteristic for the ancient Hebrews. Much of their beliefs came from Greece, and, in chronological order, this paragraph should follow the notes on classical Antiquity.

The ancient Hebrews were breeders of animals. In *Genesis* (30: 32-42) there is the story in which Jacob outwitted Laban by having maneuvered his sheep to conceive while they were looking at mottled reeds. " ...And he set the rods which he had pilled before the flocks in the gutters in the watering troughs when the flocks came to drink, that they should conceive when they came to drink. And the flocks conceived before the rods, and brought forth cattle ringstreaked, speckled and spotted ". The practice to control the offspring of animals at the moment of conception was known also to Greek antiquity.

It is stated that Balaam, the son of Beor, had his magic power by heredity (Numb., 22 : 5). It is also in Genesis (2 : 24) that husband and wife are one life. This is interpreted by Brim [104] that paternal and maternal characteristics have to fuse to shape the new being, which is apparently a too liberal explanation of a simple biblical text. The belief that the sins of the fathers will be " visited upon the children and the children's children, even unto the third and fourth generation " (Ex., 34 : 7) had been further maintained by the later talmudists.

Other references in the Bible show the knowledge of natural selection (Gen., 6 : 1-2), a primitive form of race betterment (Gen., 6 : 6), and the assumption that each living being can propagate its own species for its perpetuation (Gen., 8 : 19). The sons of God selected from the daughters of men, and they took only the fittest for their wives, and their offspring was stronger and superior.

Brim states that in the 1st and 2nd centuries A. D. the Talmud considered epilepsy a hereditary disease. There was also the supposition that anything that affects a mother will also leave its impression upon her offspring. In the *Midrash* (Numb. R. 9-1) the example of an ass is quoted; the ass had a mole on its side, at a spot corresponding to the point where the side of its mother had been cauterized. [105]

A human example of the general belief in " *maternal impression* " is also cited from the Talmud by Hovorka. [106] Rabbi Johanan, about 200 A. D., made the following arrangement for the benefit of his synagogue. Since the Jewish women were obliged to bathe after their menstrual period and before resuming normal sexual relations with their husbands, Johanan, a man of noble stature and of fine features, placed himself at the threshold of the bathing place so that all women could look at him and could depart to their marital beds with his image in mind.

CLASSICAL ANTIQUITY. As transmitted to us by the Protagoras of Plato, and in one of the odes of Horatius, the myth of Prometheus has it that when all creatures were molted from clay at the beginning of the world, Prometheus tried to distribute the characters which the creatures were supposed to have. But his supply was exhausted at

[104] BRIM cf. footnote 87.
[105] —
[106] HOVORKA, cf. footnote 97 (l. c., v. 2: 547).

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the time when he reached man. Therefore, he was obliged to recover a small portion of their qualities from other animals in order to invest them into man. By such extraordinary way, man acquired his composite character. [107]

The early Greek philosophers spent much of their time on speculation about Nature. *Anaximander*, of Miletos, (610-546 B. C), was the first who wrote a philosophical work on Nature (*Περὶ φύσεως*). [108] In his views on the origin of animals he occasionally reminds one of the 19th century ideas of evolutionists, though he cannot be declared a precursor of Darwin. He stated that the first animal organism had developed in the water; then the aquatic animals cast off their fish-skin and went up on dry land to live. Thereafter, man developed from animals of different species. [109] This order of appearance was necessary since, without a previously developed animal life, man could hardly maintain its existence. [110]

Another early philosopher, *Empedokles*, of Agrigent, (ca 450 B. C.), who is also known as a physician, wrote a poem on Nature (*Περὶ φύσεως*) which is of more interest to us. [111] It received much attention by Albertus Magnus in the period of medieval scholasticism. [112] In his theory of the origin of life the two main principles are Love (*φιλότης*) and Hatred (*νεῖκος*). The plants were generated first, and the animals afterwards. Their parts were separate, and Love united them into complex beings. Eyes, heads, and arms first lived separately. Their union was entirely by chance, and without any ultimate leading idea in Nature. Hence many abnormities developed which later were destroyed; but there remained a sufficient number which could maintain life and propagate their species.

This idea was later objected to by Aristoteles (Physica, Lib. 2, 3) because it could not be supposed that so many formations of life had developed by chance alone. The doctrine of Empedokles is often compared with the lamarckian and darwinistic pangenesis. There is a great difference, however, between this doctrine and the later views of evolutionists. Darwinism attempted to give reason and basis of the successive differentiation into simple forms, while in the theory of Empedokles there is talk of the union of heterogenous parts only. [113]

In relation to man, Empedokles stated that the sperma of the male and the female is derived from the whole body, from each organ, whether simple or complex. Hence, it is a non-organized mixture of disconnected miniature limbs and members. The sperma which generates twins, e. g., has two heads in it, but the heads are not connected to their respective neck. The development of the individual is thus a sort of assembly of pre-

[107] Cf. McCartney, see footnote 29.

[108] It was republished by Diels: Vorsokratiker, Berl., 1912, v. 1, 11 etc.

[109] *ἐξ ἀλλοειδῶν ζῴων ὁ ἄνθρωπος ἐγεννήθη.*

[110] Cf. Praechter; footnote 86, l. c., 33. – The same idea was later repeated by Plutarchos (Quaest. symp., lib. 1, 8, 8, 4).

[111] Cf. Footnote 108.

[112] In his De animalibus, lib. 15, tract. 2, cap. 2, and elsewhere.

[113] Cf. Heinze, in Footnote 37; also Zeller in footnote 38.

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formed parts of the body. These early ideas of *preformation* were very much ridiculed by Albertus Magnus in the 13th century.

Another of the Greek philosopher preformists was *Anaxagoras*, of Klazomenai (499-428 B. C.) in Asia Minor, who also wrote on Nature (*Περὶ φύσεως*).[114] In his theory it is the *Nous*, the Intellect which put the primordial Chaos into order. This chaos was composed of unlimited number of qualitatively definite, different archaic matter which he called the seed of things, *spermata* or *chremata*. These sperms were in the air, and they fertilized the wet soil; thus, the plants developed. Animals developed in the same way, from germs which fell upon the moist earth where they were hatched under the influence of heat. In the human sperm, which is supposed to come from all members, there are the invisible patterns of the members, including patterns for hair, nail, veins, arteries, and bones; there is however only one pattern for all bones, one for all flesh, and so on.

Similar views on preformation were also held by *Demokritos*, of Abdera, (floruit ca 420 B. C.), who also taught that the seminal fluid would be a derivative of all organs, especially of the so-called " *membra similia* ", an early designation to our modern idea of " tissue ". It is the tissue which was supposed by the previously mentioned Anaxagoras, too, that is patterned in the sperm.

Among the *Hippokratic works* there are two especially which are of some historical value to genetics. One is about the seminal fluid, and is now ascribed to the Cnidian Hippokrates, while the other is the famous geomedical work on the Air, Waters, and Places, ascribed to *Hippokrates*, of Cos (460-377 B. C.). The work of the Cnidian physician considers the seminal fluid of the parents a secretion of all organs and body fluids. At this time of history, the mother's vulval secretion was considered the " *sperma muliebre* ", and this view and misconception did not change until the latter part of the seventeenth century. This view of generation also assumed that all organs are represented in both the male and the female seminal fluid. Similarity of the offspring to the parents depends upon the quantity and the heat of the seminal fluids. If the seminal fluid is sufficiently hot, or if the male semen came in overwhelming quantity so that it overpowers the female portion of the mixture then the descendant will be similar to the father. The sperma was supposed to be both cause and material in generation.

In the geomedical work of Hippokrates as well as in other places of the Corpus Hippocraticum (notably in the Aphorisms, and the Predictions) several sentences can be found which mention various aspects of human inheritance. Thus, we read that the tribe of the Longheaded (*Macrocephali*), which considered that the longer is the head the nobler is the person, attempted to mold the heads of infants by means of massage and bandages in the hope that this feature will be transmitted to future generations by heredity. It was also thought that children with blue eyes are born from blue-eyed parents, bald heads from bald-headed parents, and squint eyes from cockeyed parents. At other places, among the hereditary diseases are mentioned dropsy, consumption, gout, epilepsy, also biliousness and phlegma. There is an allusion to determination and

[114] Cf. Footnote 108.

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heredity of sex in the *Aphorisms* which supposes that boys are generated when the father's seed comes mainly from the right testicle. The character of maleness would also depend whether the embryo would lodge in the right half of the uterus.[115]

As a curiosity it should be recorded that *Herodotos* (flor. ca 446-430 B. C.), in his History, made the statement that the dark-skinned people of India and Ethiopia produce a seminal fluid of black color, which statement was later questioned by Aristoteles, " aren't the teeth of the Negro white "?[116]

Among the Greek philosophers, *Plato*, the disciple of Sokrates, is looked upon by modern biologists as the founder of biological systematization.[117] His theory of the origin of the universe and the relation of man to Nature is nevertheless a mystical cosmogony, and not entirely original. It is contained in his dialogue Timaeus, and it seems to be a repetition of the doctrines of the previous believers in preformation, and pangenesis. In his belief, the semen comes from all parts of the body, and each complex organ is represented in it in miniature; thus, the father's semen contains a part derived from his head, and this part is a miniature head, and so on. Individual development, hence, is only an assembly and growth of fragments of the body. He also assumed that there are many " souls " in a body, as many as there are principal divisions of the body.[118]

In his work on *Laws* Plato mentions the belief that pregnants are peculiarly sensitive to physical and mental impressions, especially at the moment of conception. As stated before, this belief is universal among women of all ages. The theory of maternal impression resulted in the practice of keeping nice pictures of handsome men in front of the mating woman.[119] The belief and this practice was also used as a convenient explanation for some embarrassing dissemblances between mother and child. Thus, Chariclea, the daughter of the queen of the Ethiopians, was of white color and her mother, Persina, blamed the difference upon her contemplation of a Greek statue.[120]

The most significant contribution to genetics can be found in Plato's *Republic*,[121] in which the idea is expressed that the breeding of human beings, as of animals, should be made with the selection of the best and at a ripe age. If care would not be taken, then the animals and the domestic birds would greatly deteriorate. His words are as follow: " The best of either sex should be united with the best as often, and the inferior with the inferior, as seldom as possible; they should rear the offspring of the one sort of union, but not of the other, if the flock is to be maintained in first-rate condition ". The offspring of the inferior — continues Plato — should be put away in some

[115] Cf. Footnotes 23, 24, 25, 29.

[116] COONEN L. P., Herodotos on biology. *Scient. Month.*, Wash., 1953, 76: 63-70.

[117] NORDENSKIÖLD; see footnote 79.

[118] Albertus Magnus writes of Plato's theory: " ...quod partes spermatis determinatae habeant virtutes membrorum a quibus deciduntur, et per speciales et partiales virtutes partium spermatis, quaelibet operetur membrum unum ex parte spermatis in qua est ". (*De animalibus*, lib. 15, tr. 2, cap. 1).

[119] MCCARTNEY, l. c., quotes Oppian who had recorded similar practice among the Spartans.

[120] This story was originally reported by Heliodorus (Aethiopica, 4), and thereafter repeated by many writers of Antiquity.

[121] PLATO. Republic. (Jowett translation. Ed. by J. D. Kaplan., N. Y., 1950).

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mysterious, unknown place. This has to be done if the breed of the guardians (i. e., state officials in charge of breeding) is to be kept *pure*.

Further very radical measures are recommended by Plato in relation to human breeding. Though he does not exclude from mating the people who are beyond the prescribed age of breeding under the surveillance of the state officials, he states that in an ideal state " man may not marry his daughter ", or his daughter's daughter or his mother or his mother's mother, neither can a woman marry such close relatives. Yet, if there would be conception, the offspring should be destroyed. [122]

One of the best known students and opponents of Plato was *Aristoteles*, of Stagira, (384-322 B. C.). His importance and his influence is unequalled among the philosophers. His sphere of activity was very wide, and his interest in biological phenomena was unsurpassed in Antiquity. Many of his works are on topics of medical interest, perhaps because his father was physician to Amyntas II, king of Macedon. It can be expected therefore that his knowledge on human heredity is actually at the highest level of the 4th century science before Christ.

His chief works related to genetics are the *History of Animals*, and the *Generation of Animals*. In these works his advanced ideas show him as a true precursor of the theoretical geneticists of our modern times. His teachings on the asexual and sexual reproduction of animals make him the father of modern embryology. He is also known as the first who proclaimed the perpetuity of species. In his explanations of generation he appears to be an opponent of the theories of Empedokles and of the later philosophers who had taught seminal preformation. Many of his doctrines persisted till the 19th century, almost unchanged. Inspite of his truly scientific spirit, many observations and conclusions in his works on natural history are incorrect.

The 3rd chapter of the 4th book of his work on the *Generation of Animals* is devoted almost entirely to discussion of heredity. [123] This chapter tells that dissimilarity, or the difference between a child and its parents, is a kind of monstrosity because in this case Nature deviates from the type in some measure. Even the female offspring is to be considered such a deviation; but some descendants will be female because either the father is outside the proper range of reproductive age, or for some other reasons. Another deviation from parental resemblance is found in monsters.

Sometimes there is no resemblance to the parents, except that the offspring is a human being. But this is the main point; anything else is only accidental. When it comes to generation, it is always the specific that counts. Coriscus (the favorite name of the Aristotelian " anybody ") is wholly a man and an animal But the quality that makes him a man is more specific than the quality that makes him an animal Hence, it happens that his child will be of the most specific quality, i. e., a human being.

In the same book Aristoteles states that mental characters, such as being well instructed in grammar and the like, are not heritable. There are also other qualities which cause differences in the organs, e. g., the color of eyes, of hairs, etc. The causes of such diver-

[122] See footnote 121.
[123] For the French translation of this Aristotelian work see Footnote 28.

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sities are partly specific, partly fortuitous. If specific, the differences belong to the entity of the being, to his essence. Development is part of the essence of a being, yet his essence is not the result of such development (Lib. 5, Cap. 1). The color of the eyes is normally black, while blue eyes represent a kind of deficiency in the shade (This would be perhaps restated by a Mendelian geneticist so that blueness of the eye is a " recessive " character).

In his *History of Animals* Aristoteles collected all contemporary knowledge of the life of animals, chiefly for the purpose of using this biological information as a part of his cosmogonical theory. He gave remarkably true accounts of the habits of many animals during their breeding seasons. [124] His general views on reproduction and heredity are summarized from this source as follow. The male and the female elements of reproduction are of different significance. The male semen, though it does not contribute to the material of generation, brings the fundamental elements of life, and it is the starter and the continuous mover and former during the developmental process. The female semen (i. e., the mistaken secretion of the labial glands) is the material from which the mass of the embryo takes its first building stones. The child may resemble the parents not only in shape but also in gait, in voice and external characters for which there is no substance in the semen. The similarity to anyone of the parents is determined by the dominance of one parent's semen over the other. In lack of such dominance, the daughter may resemble her father, and the son his mother (We would perhaps say that the absence of a dominant element will determine crossed heredity).

In view of such hybrid animals as the mule, Aristoteles remarked that after many generations they always regress to the original type of the ancestral mother animal. He also recorded the story of the girl in Sicily who had a white daughter from a Negro husband, but the daughter's child reverted to the black color (Generation, 1 : 18). Such natural variations as albinism among bears, leopards, and ravens, Aristoteles explained by a possible disorder occurring during the reproductive formation of the animal. For human genetics it is significant that he distinguished acquired characters which are heritable, and such which are non-heritable. Blindness, lameness, or even the scars are transmitted by the parent to the descendants, while accidentally acquired defects and the results of mutilations are not hereditary. Though this statement is of no significance today, in the times of Aristoteles it represented the essence of heredopathology. He was keen to note, however, that such defects might skip the immediate descendants, and might appear in the second generation. In his nomenclature, this phenomenon was called *regeneration*. (Now we call it reversion or atavism).

The influence of the authority of Aristoteles was a very lasting one. The next fifteenhundred years did not change it substantially, neither did they add much to it. His good friend and pupil, *Theophrastos* of Eresos (372-288 B. C.) [125] supplied and recorded the botanical knowledge of the Peripathetic scholars. By his two botanical works, the *History of Plants* and the *Causes of Plants* he became the father of botany. There is not

[124] See some descriptions in SINGER; cf. Footnote 80, l. c., 14 etc.
[125] Others state that he was born ca 380 B. C. and died 287 B. C.

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much on heredity in these works. He recognized the bisexual nature of date palms, and the role of the male pollen dust in the development of fruit; but this had been known to the Assyr-Babylonians for many centuries.

In the *Causes of Plants* (Bk 2, Cap. 13) he describes some changes which cultivation may cause in plants. It seems that he believed a successive modification of the plant under the influence of soil and climate; such changes come gradually, and they are more manifest in the third generation. This belief was in accordance with the wide-spread opinion that a plant species could degenerate or spontaneously change into another. The same idea returns in the works of all subsequent writers on plants and on agriculture.

Among the early writers of the Roman Empire there is none whose work is of any importance in the history of genetics, Plinius not excepted. It is also questionable whether the practice of occasional or regular exposure of deformed infants had any eugenic reason or it was done for economic purpose. [126] The books on *Natural History* of *Plinius* (23-79 A. D.) record many scattered curiosities which have something to do with heredity.

In the 10th chapter of Book Seven he records the family of Lepidi in which an eye abnormity was noticeable in several generations, but with some interruption in heredity. [127] Here again is the story of the nobleman who was a bastard, born from the adultery of his white mother and a Negro; he himself had white skin, but his child " regenerated " the black grandfather. [128] The mind itself is able to produce such similarity, too. [129] Nevertheless, there is constancy in the reproduction of the various forms of animal life, especially since the animals themselves have no imagination that could alter their species. [130] (Plinius apparently did not read Jacob's story in the Bible).

In the same book he describes different types of human beings who, being inhabitant of remote countries, are provided with various unusual characteristics. Most of these incredible races had been described by others, and only quoted by Plinius. Needless to say that much of this primitive classification of human races is based upon inaccurate observation and tradition (e. g., the race of the one-eyed (*monoculi*) who are also referred to as *sciapodes*). He also recognizes the environment as a factor in the formation of unusual types and species. Modern biology talks of phenotype, i. e., the form of appearance of an individual or species under the given environmental conditions. Plinius has reference to the same when he states that the animals are largest in India, and the trees grow the tallest in the same country because of the soil, the climate, and the

[126] McCartney; see Footnote 29 (l. c., 31).

[127] Liber 7, Cap. 10, Historia naturalis: " ...In Lepidorum gente tres, intermisso ordine, obducto membram oculo, genitos accepimus. Similes quidem alios avo: et ex geminis quoque alterum patri, alterum matri: annoque post genitum, maiori similem fuisse ut geminum ".

[128] — " Indubitatum exemplum est Nicaei nobilis pyctae Byzantii geniti, qui adulterio Aethiopis nata matre, nil a ceteris colore differente, ipso avum regeneravit Aethiopem ".

[129] — " Cogitatio etiam, utriuslibet animum subito transvolans, effingere similitudinem aut miscere existimatur ".

[130] — " Ideoque plures in homine, quam in ceteris omnibus animalibus differentiae: quoniam velocitas cogitationum, animique celeritas, et ingenii varietas multiformes notas imprimat: cum ceteris animantibus immobiles sint animae, et similes omnibus, singulisque in suo cuique genere ".

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abundance of water. Under the foliage of a single figtree an entire column of horsemen could hide.[131]

He repeats the belief that several acquired characteristics can be inherited, even the marks of tribal origin, crippling conditions of the body, etc. Drugs, or other things taken, could also influence the shape of the future child, or the color of his eyes. He recommends therefore a certain mixture which he calls " Hermesias "; this mixture the mother should swallow if she wants handsome and good children.[132] Plinius continues the tradition about the sex and the artificial fertilization of palm trees.[133]

A contemporary of Plinius was Dioscorides, military surgeon in the army of Nero, who wrote on plants and their medicinal virtues, but did not report on their generation. *Lucretius Carus*, who lived in the First Century B. C., left a poem on the *Nature of Things*, which was easy to memorize and quote. His reference to generation is a short line which asserts that the birth results always from mixed seeds of the male and the female.[134] This was then accepted and frequently quoted throughout the Middle Ages.

References to heredity can be also found in various writings of *Plutarchos*, of Chaironeia (50-125 A. D.), an eclectic Platonist. In his *Morals* he described discontinuous inheritance, as Plinius also did, and cited a number of characters which are transmitted in an alternating manner (e. g., warts, moles, freckles). McCartney believes[135] that the only example of homochronous heredity of blindness in Antiquity is described in *Timoleon* of Plutarchos. This Timoleon was a citizen of Corinth; he lost his sight at old age, and other descendants of his family became blind at the same year of their lives.

Some additional knowledge on heredity is indicated in the writings of *Galenos*, of Pergamon (130-210 A. D.), the best interpreter of the medical writings of Hippokrates which he, with his own practical knowledge of medicine and physiology, wished to bring into harmony with the knowledge of the Aristotelian school of philosophy. But he misunderstood Aristoteles. In the matters of generation he studied the observations of women, watched the coupling of animals, and even dissected the body of women who died soon after sexual intercourse in order to see the immediate changes that might be caused by the seminal fluid in its receptacle. His chief knowledge on generation and heredity is contained in his works on the seminal fluid (*De semine*, libr. 2) and on the formation of the foetus (*De foetus formatione*).

Against Aristoteles, he believed that both the male and the female semen take part in the animation, formation, and building of the embryo. According to his works, the two semina mix in the " horn " of the uterus, and he agrees with Aristoteles that the preformation theory of Empedokles is untainable. He believes that the form of the embryo is gradually developing and the first organ to be formed is the brain. His ideas

[131] — " ...Haec facit ubertas soli, temperies caeli, aquarum abundantia, (si libeat credere) ita sub una ficu turmae condantur equitum ".

[132] Lib. 24, cap. 102.

[133] Lib. 13, cap. 7: " Adeoque est Veneris intellectus, ut cultus etiam excogitatus sit ab homine, ex maribus flore ac lanugine, interim vero tantum pulvere insperso in feminis ".

[134] LUCRETIUS: " Semper enim partus duplici de semine constat ".

[135] See Footnote 29; loco citato.

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on heredity are mostly those of Aristoteles. As this Greek philosopher, Galenos also recognized the rigidity of the species, the resemblance to the parents, and the transfer of sex characters as the three basic problems of heredity. He confessed, however, that he did not know a satisfactory answer.

The cause of similarity is not entirely in the semen, he states, because then the child would resemble to whichever parent would contribute the larger portion of the seminal mixture.[136] At another place he repeats the old story about the ugly man who placed the picture of a beautiful boy in front of his wife so that she could look at it during intercourse in order to conceive a handsome child.[137]

Galenos comes perhaps the closest to the truth when he writes about the soul as the vital force in the formation of the foetus and in heredity of parental characters: " I confess that I do not know anything certain about the formative cause of the foetus... while on one hand I cannot accept the opinion that there is a soul in the foetus and that this soul forms it, on the other hand I cannot completely give up this idea, especially when I look upon the similarity of the foetus to the parents ".[138]

After Galenos, the Antiquity *tacet*!

MIDDLE AGES. The medieval period in the history of genetics was greatly dominated by the ideas of Aristoteles, Hippokrates, Lucretius, and Galenos. Though there was a fundamental difference in the views of Aristoteles and Lucretius as to the role of the male and female seeds in generation, they both were maintained, and served as topics of heated argumentation until the discovery of the Graafian follicles and of the spermatozoa in the 17th century. The Middle Ages widened also the interest in the discussion of environmental factors of heredity. The environment of life was now extended into the most remote boundaries of the visible Universe, and it was assumed that conception, prenatal growth, and birth of any life was modified, altered, and influenced in various ways by the radiation of the stars. As times progressed, such astrological believes became stronger and helped only to veil the facts of heredity and life in mystery. Neither were the methodology of science sufficiently advanced and the instruments of study sufficiently sharp to penetrate into Nature, beyond its gross anatomy and visible life.

I do not want to make a deep excursion into *Arab science*. The Arabs were masters of animal breeding, especially of horse breeding, but their knowledge was that of a practical stall-master. They did not know much of heredity though in their practical breeding work they recognized the importance of selection of the parent animals. That they were in the possession of a way of artificial impregnation of mares since the year of 1322 is nothing but a phantastic invention and misunderstanding which started in

[136] De semine, lib. 2, cap. 3. in KÜHN'S Med. graecorum opera, 20v. Lpz., 1822-33.

[137] De theriaca, cap. 11 (vol. 14 in the KÜHN edition of Galenos).

[138] De foetum formatione libellus: " Nam summam in horum conformatione et sapientiam et potentiam video, neque possum existimare, eam quae in foetu est animam... foetum ipsum formare, ...neque rursus ab hac opinione in totum possim recedere, quum similitudinem, quam filii habent cum parentibus, specto... " (Vol. 4 of the KÜHN edition).

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the 19th century only.[139] The Arab literature of the Middle Ages grew rapidly after the 8th century, and many of the details are still not available. Works of early travelers, of philosophers, and of physicians contain scattered remarks which are characteristic of the credulity of the era. When *Ibn Shahriyar* (912-1009 A. D.) writes in his *Marvels of India* the story that on certain lonely islands fishermen and fish enter into sexual intercourse and produce fish descendants in human shape[140] one wonders whether this early Arab traveler wanted to write a tale, later to be included in the Arabian Nights, or he wished to extol the marvels of an exotic part of the world.

As their various books on agriculture prove, the Arabs were also in the possession of the art of plant hybridization. *Ibn al'Awwam* (1150-1200 A. D.), of Sevilla, the famous naturalist of the medieval Arab world and the contemporary of Maimonides (1135-1204) refers in his agricultural work (*Kitab al-filaha*) to the cultivation of about 584 plants and of over 50 fruit trees. There he also stated that he fertilized a wild palm in el-Alxarafe at the time its blossoms were unfolding. This makes him perhaps the first conscious plant hybridizer in the world.[141]

Ibn Sina (980-1637) wrote a work on the *Deluge* in which he remarked that after the great flood there was much putrefaction; but under astral influences, the rotting cadavers gave life to new beings of all species, including man. This happened without any semen; hence, Ibn Sina, as anyone else in his era, was a believer in spontaneous generation. In one of the various " fens " of his *Qanun* he also mentions a fantastic theory that black color of the skin may be inherited by mere imagination of the parent exercised at the moment of ejaculation or orgasm (Lib. 1, Fen. 1, doctr. 2, cap. 14). Much of this speculation has the hallmark of ancient Greek philosophy which was quite familiar to the Arabs.

WESTERN EUROPE. In the Anatomy of Melancholy of Burton there is a passage from H. *Boetius*[142] where it is indicated that the ancient Scots practised castration for the suppression of heritable diseases. " If any were visited with the falling sickness, madness, gout, leprosy, or any such dangerous disease, which was likely to be propagated from the father to the son, he was instantly gelded; a woman kept from all company of men; and if by chance having some such disease, she was found to be with child she with her brood were buried alive; and this was done for the common good, lest the whole nation should be injured or corrupted ".[143]

In a work of *Alexander de Insulis* (ca. 1188 A. D.) the belief is expressed that the image of externally worn articles of dressing, e. g., a crucifix worn over the breasts, may be transmitted by the imagination of the devoted mother and impressed upon the body

[139] The Arab knowledge on generation will be included in one of my early future publications. I have historical evidence contrary to the opinion which is generally held at present by animal breeders as to the origin of artificial insemination.

[140] Cf. ZIRKLE; see Footnote 40 (l. c., 52-3).

[141] IBID., 80.

[142] BOETIUS H., De veterum Scotorum moribus; in Lib. 1.

[143] Cf. MCCARTNEY; see Footnote 40.

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of the embryo. The same author related that in 1183 he saw the white son of a Negro man and of a white girl in Erfurt. The child showed various marks on his body: 1) a bluish nose, 2) the figure of moon on his chest, 3) some white hair on the head, and 4) a black-skinned penis. *William of Aubergne* (Alvernus) (1180-1249), who was bishop of Paris from 1248 to 1249, mentioned in his work on Laws (*De legibus*) that man has tried to produce, and believed to have produced, human life in other ways than by means of regular generation.[144]

Albertus Magnus, the great Dominican interpreter and historian of the Universe, (1193-1280) is the most typical representative of medieval science. He was a true follower of the philosophy of Aristoteles, but he also relied upon his own observations. The most significant for the genetician is his *History of Animals* (De animalibus) which was republished in a very handy 2-volume edition (Münster, 1920).[145] This work contains a great deal of criticism of all previous data on generation, breeding habits of animals, seminal fluid, heredity, etc. In the following I will restrict myself to his views on heredity, since his views on generation are almost identical with those of Aristoteles.

Albertus Magnus distinguishes in the human constitution a part which is hereditary (i. e., our genotype) and one which is under the influence of various external factors (i. e., our phenotype). The basis of the hereditary part is formed by the two seeds of the parents. This secures the similarity to the species, the heredity of humaneness (" *ad naturam* "). But there is also a heredity " *ad personam* " by which Albertus means the similarity to the race and to the parents.

The hereditary characters come first of all from the bodies of the father and mother, and then from the ancestors. The ancestral characters are latent in the parents but they can be awakened by accidental developmental stimuli. Hence, the constitution of the genotype is composed of very different, heritable, dynamic elements: 1) individual characters from the parents, 2) genealogical elements up to the fourth degree of ascendancy, 3) elements of the "species" Homo, and 4) elements of the "genus" Animal. In the course of heredity these characters act in a decreasing order of force. The formation of embryo is first under the action of the individual factors. Should this formation be disturbed accidentally, then the genealogical elements will get the upper hand. The accidental disturbance can be any factor that is able to modify heredity, e. g., the wrong composition and putrefaction of semen, or the change in the complexion of the paternal and maternal sperm by a disease.

In the theory of Albertus, heredity is therefore governed by some very potent factors which the modern science would call perhaps idiotypic. Among these, the most effective is the formative power which is in the semen itself, as an expression of the so-called " *virtus generativa* " which again is the special ability of the vegetative soul. This formative power results from two other powers which Albertus names *a*) the power

[144] Cf. his Opera omnia. Venez., 1591 (De legibus).

[145] For the full description of the theories of Albertus Magnus on constitution, complexion, genotype, phenotype, etc. see my study: Die Personallehre in der Naturphilosophie von Albertus Magnus. *Kyklos*, Lpz., 1929, 2: 191-257.

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to induce species, and *b*) the power resulting from the qualities of matter. This latter, which is conditioned by the constitution of the parents, forms the true basis for all heredity.

The "*virtus formativa*" plays in Albert's theory of heredity the same role as the *id* in modern genetics. The essential difference between Albertus and modern genetics is that the theory of chromosomes and genes works with material, particulate units and assumes that small material complexes are the carriers of heredity while Albertus, whose mentality is Aristotelian and vitalistic, believes in specific *hereditary energies*.

In his further thoughts Albertus remains entirely vitalistic. The energies manifest themselves as effects of the matter. These effects are analyzed by him in an effort to come nearer to the understanding of heredity. The chief function of the formative power is digestion. After conception, this power may result in complete, undisturbed elaboration of the semen, in which case the offspring will resemble the father. If the semen is not properly elaborated, then the maternal seed will take over the chief regulation of the formation of the genotype; hence, according to its degree of success, the maternal seed will determine the later phenotype of the child, sometimes only for one or several organs, sometimes for the entire body constitution. (Today, we talk of *cytoplasmic* inheritance).

He also teaches the heredity of certain acquired characters. Thus, the children of the smiths have large arms and strong brachial musculature.[146] Sometimes even the scars of the parents are transmitted to the descendants.[147] There are dogs whose tails were cut so often that the puppies are born tailless.[148] Diseases also are heritable. The heritable acquired characters and diseases are called "*occasiones*" in the terminology of scholastic natural philosophy. They appear more intensive in the successive generations.[149] If a limb is defective in a parent it will be only partially useful in the child, too.[150].

The variations of the color of the body, of the size and of other constitutional characters are well known to Albertus. He also knows all the related parts of his Aristoteles, including the crossing of white females and Negro males. Yet, he does not tell us the cause of these variations. For the bountiful coloration of the bird feathers, his only explanation is the complexity of the semen of the birds and the variety of influence of the semina derived from different intercourses.[151] From other places of his *De Animalibus* it is evident that the variation of body color and size is ascribed to the diversity of sperms and to the volume of the uterus.[152] He confesses, however, that it is impossible to give a satisfactory solution for these problems.[153]

[146] Lib. 4, De meteor., tr. 1, c. 25.
[147] Lib. 15, De animal. tr. 2, c. 1.
[148] — tr. 2, c. 1, 60.
[149] Lib. 9, De animal. tr. 1, 6, 62; also lib. 10, tr. 2, c. 1, 39.
[150] Lib. 3, De animal., tr. 2, c. 8, 162.
[151] De Animal., Lib. 15, tr. 2, c. 8, 125.
[152] — lib. 9, 1, 6. 63.
[153] — lib. 9, tr. 1, c. 6: "In talibus enim similitudinibus et dissimilitudinibus nihil manifestum sensui aut certum secundum rationem tradi potest".

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He also discusses the heredity of abnormalities. In this development only the formative energies of the *genus* are at work, with the result that there will be either a plus or a minus, a dystopy or a monstrous form. He knows of brothers having six fingers, of hermaphrodites, animals with one kidney or without spleen(?), with situs inversus of the viscera. As an explanation he also refers to deficiency or surplus in the quantity of the sperm. The genotype is not a rigid, unchangeable concept in Albert's writings, but it possesses a certain degree of lability, and variability. He enumerates a number of factors which may bring about a change in hereditary treasures. It is especially the phenotype of the mother which is of the most effective influence, together with the mother's diet. He briefly mentions the effect of cosmic forces though he himself does not accept the sideric powers. On the other hand, he thinks much of the effect of seasons and of the weather. Thunder can, for instance, disturb the fine structure of a hen's egg and result in the destruction of the embryo.[154]

He is one of the first scholars who clearly states that women do not have sperm, and that the white fluid which had been called so for centuries has no formative function. In criticizing the theories of Empedokles and Anaxagoras he rejects the idea that the human form is present in the sperma either in a rudimentary way or in toto. As he states, such arrangement would make the sperm an organic living being, i. e., a small animal, which is an absurdity. He also recognized that the heredity of the sex cannot depend upon the position of the woman during coitus, or upon the condition whether the sperm comes from the right or the left testis. He has seen a man whose remaining left testis always produced sons. It is also the result of his observation that he separates the heredity of sex from the rest of the hereditary characters and states that the general resemblance and the sex resemblance are the work of two different powers.

The knowledge of Albertus Magnus represents the best in the scholastic Middle Ages, and none of the later medieval authors could match his science either in quality, or in amount, or in acuteness of reasoning. The later authors, such as Michael *Scot* (died before 1235), *Cecco d'Ascoli* (died 1327), and others are very strongly under the influence of superstitions and of the fashionable *judicial astrology*. Since such works were very popular they also represent the belief of the medieval majority opinion. They were sold in the form of " *Secrets of Secrets* ".

A fourteenth century rationalist stands out almost alone. He is *Heinrich*, of Hassia (*1325-1397*), a German mathematician, philosopher and astronomer. He wrote against the belief that the stars could affect human life. It is a surprise when we find in his works that new combinations may always arise in Nature; that, as in the past, also in the future there will be created new species of plants and animals. Similarly, the appearance of new diseases can also be expected. He suggested that the men of the future might be of a different kind.[155]

What about the *Regimen Salernitanum*? Therein is nothing useful for the historian

[154] De animal., lib. 5, 2, 1, 57.
[155] His chief works are 1) *De habitudine causarum*, and 2) *De reductione effectuum*. – Cf. SARTON. Introduction, 1947, 4: 1504.

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of genetics. It contains a few verses on the similarity of the offspring to the parents but the didactic value of these verses is not above the platitude that " as the tree is recognized by its fruits so the son used to resemble his father ".[156] And this is less than what the divine Alighieri sings in his Paradiso:

" Natura generata il suo cammino
simil farebbe sempre a' generanti,
Se non vincesse il provveder divino ".
(*Paradiso*, Canto 8).

In the Seventh Part of the Salernitan Regimen, the fourth chapter is on hereditary diseases. The two lines of hereditary diseases include morphaea, leprosy, tinea, phthisis, podagra, and lithiasis.[157] In other sections the Salernitan Rules reflect the current beliefs in the astral origin of diseases, according to the effect of the houses and the zodiacal signs.

RENAISSANCE. The knowledge of heredity did not improve in the sixteenth century. Though the renaissance created a liberal spirit of criticism, and even those who did not freely follow the revolutionary doctrines had looked with askance at the biological doctrines of previous centuries, something else was still lacking to open up new channels and new vistas to the searchers of truth.

There were still such fantastic books produced as the History of Monsters by Licetus, which described a number of unnatural crossings between man and animals, food only for the credulous. Among the botanists, Charles de *L'Ecluse* (Clusius) (1526-1609) is outstanding who is the first describer of the segregation of genetic factors in hybrid tulips and peonies.[158]

The best physicians of the renaissance believed in the force of maternal impressions and the heredity of acquired characters. Thomas More (1480-1535) wrote an epigram about it.[159] Levinus Lemnius (1505-1568) advises with all seriousness that the pregnant

[156] Cf. Regimen sanitatis. Ed. A. Sinno. Salerno, 1941. Pt. 4: Physiologica: Cap. 10: Generatio hominis (p. 303), art. 3: " De similitudine natorum cum parentibus. Fructibus ipsa suis quae sit dignoscitur arbor. Saepe solet filius similis esse patri " (p. 304).

[157] — part 7, cap. 4 (p. 396): Morphaea cum lepra, tinea, phthisis, atque podagra. Haec in senibus ut calculus haereditantur ".

[158] In his Rariorum aliquot stirpium per Hispaniae observatarum libri (Antw., 1576); cf. ZIRKLE, Footnote 40 (p. 69).

[159] Reprinted in SCHURIG, Syllepsologia. Cap. 9, Sect. 5: De gravidarum imaginatione, p. 651 (Dresd., 1731):

" Atqui graves tradunt sophi,
quodcumque matres interim
imaginantur fortiter,
dum liberis dature opera
eius latenter, et notas
certas et indelibiles
modoque inexplicabili
in semen ipsum congeri.
Quibus receptis intime
simulque concrescentibus
a mente matris insitam
natus refert imaginem ".

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woman should not look at monkeys, she should not carry lap-dogs as pets because her fetus might develop features of the monkey or the dog. [160] Girolamo Fracastoro (1484-1553), the epidemiologist and the poet of syphilis, held the opinion that the pregnant woman's desire and imagination is carried through the blood to the fetus in which it remains in form of a permanent mark such as a particular color, or sometimes a strange figurated pattern. [161] These marks were called *stigmata*.

Ambroise Paré (1510-90), Marcello Donato (ca. 1588), Bruno Seidel, Martinus Del Rio, and others had a general belief in the heredity of acquired characters. So did Girolamo Cardano (1501-76) [162] who had the misfortune to have two unworthy sons, the living examples that their father's mental abilities were not transmissible by heredity. One son was beheaded for uxoricide by poisoning while the other was disinherited for hidden reasons. In one of his works Cardano distinguishes acute and chronic contagious diseases; the first group is not transmitted by heredity but the chronic disease injures the semen and is transferred to the child. Its effect may be just a general weakening of the health of descendants, lest the effect was stronger and the exact copy of the father's disease is reproduced in the child. [163]

None of the 16th century anatomists contributed to a change of opinion as to the physiological role of semen in generation and heredity. The Aristotelian ideas prevailed, even in the books of Vesalius and the works of botanists and zoologists. As a typical example we may introduce the *History of Monsters* by Ulisse Aldrovandi (1522-1605). [164] He assumed that the origin of man was from one ancestor. Beside the normal sexual reproduction he did not accept any other mythical origin by strange crossings. In his embryological views he is an epigeneticist: the development of the embryo is a gradual differentiation and growth of the semen or seminal mixture until final consolidation. The question of heredity is not discussed, though there is a chapter on the nomenclature of consanguinity and affinity according to the *Institutions* of Justinian. [165]

On the side of much sound detailed work we find also such questions as " why are fewer giants nowadays? ". And the answer: " Because the world is getting older and people have less and less semen ". Also, his work includes the figures of monsters whose shapes are the most fantastic. It can be justly questioned whether they had ever existed in the animal world or among us.

Seventeenth century

It was in the early years of the seventeenth century when the use of the first models of the microscope began to spread. This simple instrument enabled the naturalist to penetrate into secret depths hitherto unsuspected in Nature. It helped him to discover

[160] LEMNIUS L., De occultis naturae miraculis. Antw., 1559. lib. 1, cap. 4.
[161] FRACASTORO G., De sympathia et antipathia. Op. omn. Lyon, 1554,
[162] CARDANO, De rerum varietate. Lib. 8, 40. Basel, 1557.
[163] — De venenorum differentiis. Basel, 1564.
[164] ALDROVANDI U., Monstrorum historia. Bologna, 1642.
[165] The series of male ancestors, e. g. are: pater-avus-proavus-abavus-atavus-tritavus.

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the red blood-cell, the male cell of generation, and other microcosmic structures. It also prepared the way for the recognition of the finer elements of life, the tissues of the plant and animal body, and their component units, though it took more than two-hundred years until the cell and protoplasma as life's basic units were finally recognized. With the gradual shift of the naturalist's point of view from the macroscopic to the microscopic, the opinions on generation and heredity also moved and the search for the site of hereditary characters was continued into the realm of micrography.

It was Robert Hooke (1635-1703) who saw the first cell in plants, and he used plant cells as objects to show the wonderful magnifying power of his microscope. Since then, the so-called cellular theory has been steadily growing under the influence of Malpighi, Grew, Wolff, Oken, Trevisanus, and Brown, though it was not called a cellular theory until the middle of the 19th century.

Studies of 17th century botanists and their hybridization experiments revealed several useful data on heredity, even without the use of a microscope. Giambattista Ferrario [166] described that he produced many varieties from the seed of a white carnation. He called these varieties degenerate descendants, yet he recommended their cultivation because of their beautiful, mottled flowers. These experiments of Ferrario were carried out to prove the " spontaneous degeneration " of cultivated plants. Nevertheless, they show that this planter had a practical knowledge of the phenomenon which is called now the Mendelian segregation. The same " degeneration " is best described in the work of an English planter, Robert Sharrock [167] who also observed Mendelian segregation in a number of commonly cultivated flowers. He also saw that from the seed of a single plant a number of variants could be produced, which for him was a prove that plant degeneration is a natural and real phenomenon. This " degeneration " was considered at that time an actual change of the species. As such it looked a very serious blow to any hereditary character that was supposed to conserve the species. (Later on, it was recognized that there was no degeneration or aberration from the species pattern, because all progeny belonged to the same plant species).

It had been known for some time that certain plants are bisexual. Cultivation of the date palm goes back to several thousand years. That other plants and trees might have similar bisexual character was also suspected and known to Nehemiah Grew (1641-1712), physician in London and secretary of the Royal Society in 1677. Sturm (1684), and Ray (1693), the English naturalist (1627-1705), also had knowledge of the sex of plants. But it was the merit of Rudolf Jacob Camerer (Camerarius), physician and professor of natural philosophy at Tübingen (1665-1721), to prove the existence of sex in the plant kingdom (1694). He discovered that pollen was necessary for the reproduction of viable seed, and that the plants reproduced sexually. [168]

Another physician, Marcello Malpighi (1628-1694), professor at various Italian

[166] Ferrario G., Florum cultura. Roma, 1633. – Cf. Zirkle, in Footnote 40 (l. c., 73).

[167] Sharrock R., The History of the Propagation and Improvement of Vegetables by the Con currence of Art and Nature. Oxford, 1660. – Again cf. Zirkle.

[168] Camerarius R. J., The sexu plantarum; this is a letter dated 25 Aug. 1694 and addressed to Michael Bernard Valentin, professor at Giessen University.

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universities, is also recognized as the discoverer of the sex in plants. He was interested in all forms of life, however, and studied the evolution of the chicken from the egg under the control of the microscope, making many important discoveries.[169] In fact, his wide interest in the morphology of life originated from his main hobby: —microsscopy. As a pioneer in the exploration of Microcosmos, he made a long series of important discoveries, thereby preparing the way to a better understanding of the phenomena of generation and heredity. Francesco Redi (1626-1697), Florentine physician, contributed with an experiment to the destruction of the old belief in spontaneous generation, though he could not convince even himself entirely. A hermetically closed vessel, in which he placed some putrefying material, did not show any living worm or other being; and this was declared a proof against the existence of spontaneous generation or abiogenesis. (Yet, Redi continued to teach that intestinal worms originate in the intestines).

Fig. 1. Rudolf Jacob Camerarius, 1665-1721

This is the period when the first medical publications were printed on the hereditary diseases. Luis Mercado (ca 1525-30-1611), professor of medicine since 1560 at the Valladolid University, wrote his work *De morbis hereditariis* (Madr., 1594; 2. ed. Valladolid, 1605). He was a very learned Jewish physician, later protomedicus of Spain.[170] In a popular midwifery of this era which was published in 1618 in Milano and written by Mercurio *Scipione*, physician and Roman citizen, all the previous theories of heredity and filial similarity are collected and fairly accurately described in a single chapter from the times of Empedocles to Geronimo Cardano and Scaliger. The book still supports the wide belief that it is the thought, the imagination of the lady which creates the similarity in the offspring.[171]

[169] Malpighi M., Dissertationes de ovo incubato et de formatione pulli in ovo. (1666 and 1672).

[170] Several of his sons and daughters entered various Catholic religious orders.

[171] Scipione M., La commare oriccoglitrice. Milano, 1618, Lib. 1, Cap. 11, p. 76 etc. – Prof. Luigi Gedda was kind to send me a copy of the titlepage and of a few additional pages, of the 11th chapter of this rare Italian work.

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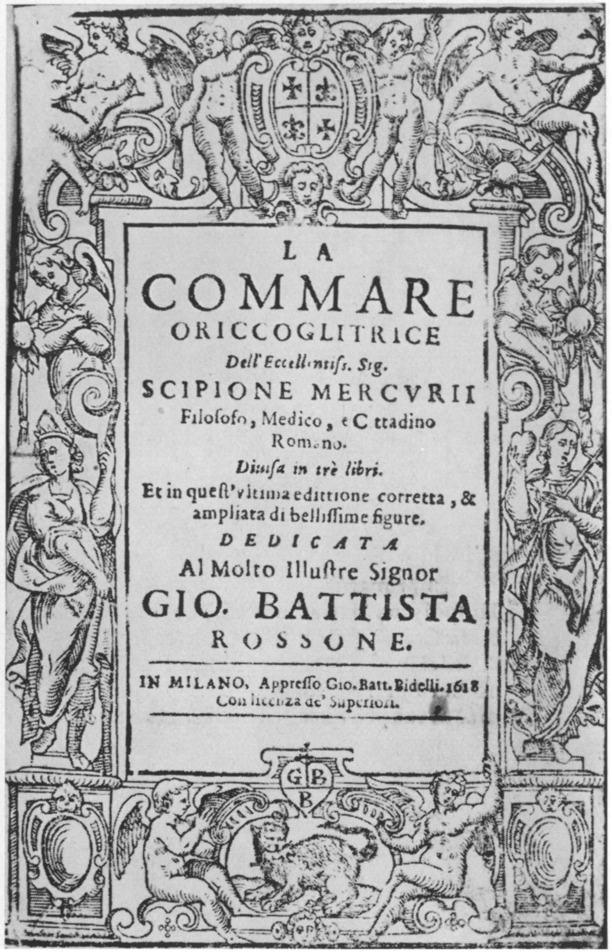
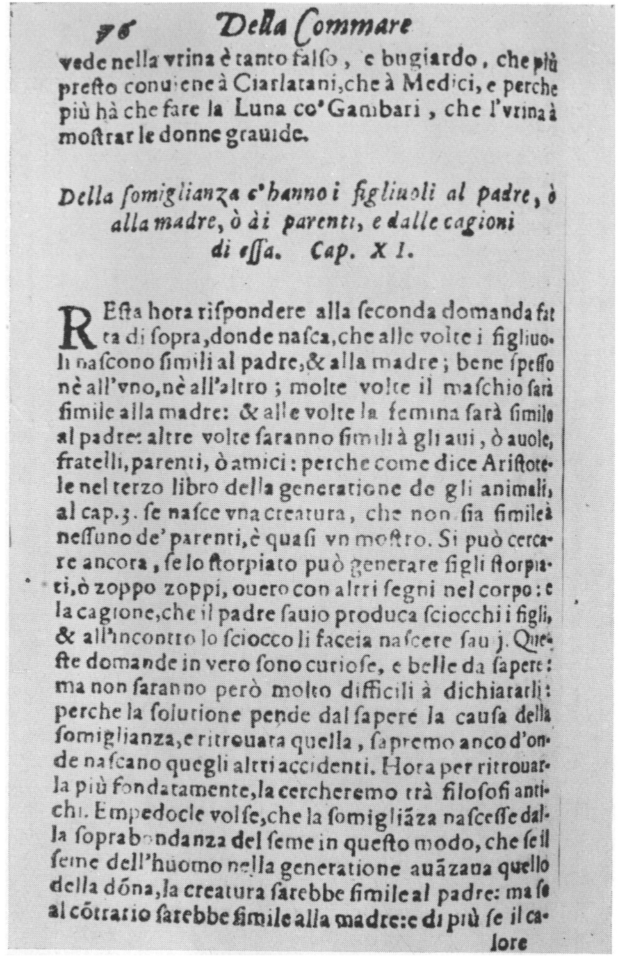


LA
COMMARE
ORICCOGLITRICE
Dell'Eccellentiſs. Sig.
SCIPIONE MERCVRII
Filoſofo, Medico, e Cittadino
Romano.
Diuiſa in trè libri.
Et in queſt'vltima edittione corretta, & ampliata di belliſſime figure.
DEDICATA
Al Molto Illuſtre Signor
GIO. BATTISTA
ROSSONE.
IN MILANO, Appreſſo Gio. Batt. Bidelli. 1618
Con licenza de' Superiori.

Fig. 2. Titlepage of " La commare " (Milano, 1618)



76 Della Commare

vede nella vrina è tanto falſo, e bugiardo, che più preſto conuiene à Ciarlatani, che à Medici, e perche più hà che fare la Luna co' Gambari, che l'vrina à moſtrar le donne grauide.

Della ſomiglianza c'hanno i figliuoli al padre, ò alla madre, ò à i parenti, e dalle cagioni di eſſa. Cap. XI.

Reſta hora riſpondere alla ſeconda domanda fatta di ſopra, donde naſca, che alle volte i figliuoli naſcono ſimili al padre, & alla madre; bene ſpeſſo nè all'vno, nè all'altro; molte volte il maſchio ſarà ſimile alla madre: & alle volte la femina ſarà ſimile al padre: altre volte ſaranno ſimili à gli aui, ò auole, fratelli, parenti, ò amici: perche come dice Ariſtotele nel terzo libro della generatione de gli animali, al cap. 3. ſe naſce vna creatura, che non ſia ſimile à neſſuno de' parenti, è quaſi vn moſtro. Si può cercare ancora, ſe lo ſtorpiato può generare figli ſtorpiati, ò zoppo zoppi, ouero con altri ſegni nel corpo: e la cagione, che il padre ſauio produca ſciocchi i figli, & all'incontro lo ſciocco li faccia naſcere ſauij. Queſte domande in vero ſono curioſe, e belle da ſapere: ma non ſaranno però molto difficili à dichiararli: perche la ſolutione pende dal ſapere la cauſa della ſomiglianza, e ritrouata quella, ſapremo anco d'onde naſcano quegli altri accidenti. Hora per ritrouarla più fondatamente, la cercheremo trà filoſofi antichi. Empedocle volſe, che la ſomigliãza naſceſſe dalla ſoprabondanza del ſeme in queſto modo, che ſe il ſeme dell'huomo nella generatione auãzaua quello della dõna, la creatura ſarebbe ſimile al padre: ma ſe al cõtrario ſarebbe ſimile alla madre: e di più ſe il calore

Fig. 3. La commare, Cap. 11: On similarity of children to parents. Text

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René Descartes (Cartesius) (1596-1650), mathematician, also composed a treatise on the *Formation of the Foetus,* in which his approach to life was entirely mechanistic. He also expressed the idea that the seeds of the male and female act upon each other as ferments; this was, however, so much speculation. Yet, he also made a very strange statement. He believed that, with the knowledge of all specific components of a particular animal's semen, e. g., of man's semen, one could deduce, by entirely mathematical and accurate reasoning, the entire design of the animal and the conformation of all its members; viceversa, the accurate recognition of the particles of the animal's body would enable one to describe the components of its semen. This statement is striking, especially when we look at the modern maps of Drosophila chromosomes which show the exact relationship of the gene particles to heritable characters.

The first who attacked the influence of maternal imagination in heredity was Daniel Sennert, physician, who in 1655 doubted that such imagination can cause any specific mutation such as change in shape or similarity to something. If the mere phantasy would have such power, — says he — then there would be many more mutations seen in embryos. He conceded, however, that, by its influence upon the emotions and the movement of body fluids, such imagination could produce abortion or death of the developing foetus. [172]

Despite of such efforts, the concensus of opinion among the scholars as well as among the common people remained unchanged as to the power of maternal imagination. It was considered a power which can produce all types of metamorphosis: it can " add, subtract, increase or decrease the shape, the color, and it can change, mutilate, construct, or destruct, not to say annihilate, anything that had been already formed and perfected in the foetus ". [173] At this time two other important discoveries began to attract general attention: the discovery of some vesicles in the " female testis ", and the successful demonstration of moving " animalcules " in the seminal fluid of man and animals. There followed a period of transition during which the modern analyst of the 17th and 18th century literature (of science and medicine) will find various contradictions in the works of the writers; there was still the old, ready to discard, yet being kept because the significance of the new knowledge was not fully perceived.

Ovarian follicles

The ovaries of women have been called " female testis " since about 280 B. C., when Herophilos had observed them at dissection. How many more saw them, and the small vesicles on their surface is hard to tell. But in the 16th century Gabriele Fallopio (1523-62) observed these vesicles, and described their watery, yellowish or clear

[172] Sennert D., De chymicorum cum Aristotelicis consensu et dissensu. Frankf., 1655. " Et si species phantastica eam vim haberet, multo plures mutationes in foetibus acciderent ". – Also: " ...contingere possunt a phantasia, mediantibus animi pathematis et motu humorum ac spirituum ".

[173] Gahrliep G. C., Misc. Naturae Curios., Decas 3, an. 7 and 8, Observ. 59, 57.

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contents.[174] He did not attribute much importance to the vesicles. Others saw them after him, and left descriptions and drawings of them. Yet, none guessed their function. Not even William Harvey (1578-1657), physician, who had a vague idea that every living being has a beginning, and this beginning might be some kind of egg. Harvey had an opportunity to dissect a doe of the Windsor Castle of Charles I and he found a small vesicle in the uterus of the doe which was filled with some sticky, white substance and a developing foetus. From his finding he concluded that the development of this animal is the same as of the chicken; that the deer also must develop from an " egg ". He never saw a mammalian egg, however, though he thought that an embryo is made by successive formation of its parts. He shows a strange mixture of old Aristotelian ideas and new knowledge on the field of embryology.[175]

Fig. 4. Regnier de Graaf, 1641-1673

Caspar Bartholinus (1655-1738), Danish physician, helped to clarify the concept of "female semen". He discovered that this so-called semen is nothing but the secretion of two glands at the side of the vulvar entrance (1673). It has no relation to the " female testis ". By this time, the knowledge of " female testis " also became more accurate owing to the efforts of several Leiden anatomists who since 1668 have repeatedly called attention to the little vesicles in this part of the internal female genitals. Jan van Horne (d. 1670), the Leiden professor of anatomy, called these vesicles " ovulum " or " ovum muliebre " but it was his pupil, Regnier de Graaf (1641-1673) who in 1672 described them in detail[176] and announced that the animals and man do not develop from a kind of egg which is formed from the union of male and female seminal fluids in the uterus but the egg exists in the woman's testis before any sexual intercourse. He thought that the male seed arrives through the

[174] FALLOPIO G., Observ. anat., v. 1, 421 (In: Op. omn., Frankf., 1660).

[175] In his *Exercitationes de generatione animalium* (Lond., 1651) the introduction contains these words: " ...omnia... ex ovo progigni... primosque conceptus... ova esse ". But at another place his definition of ovum is 1) any beginning that is capable of living, and 2) anything that has the nature of an egg though it does not look such. Cf. LIPPMANN, Footnote 47, (*l. c.*, p. 58).

[176] De mulierum organis generationi inservientibus. Delft, 1672. Also in his Op. omn., Leiden, 1677.

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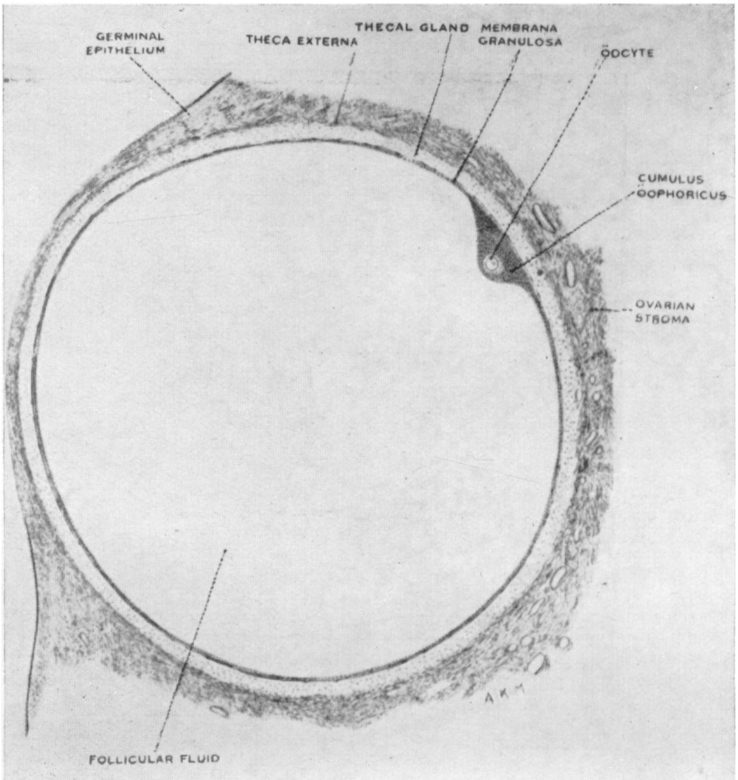

Fig. 5. A Grafian follicle (modern drawing)

tubes to the eggs, and fertilizes them by irrigation. Thereafter the eggs descend to the uterus where they develop into embryo. Others started to call the female testis an " ovary "[177] and Regnier de Graaf accepted the new term. He also observed that the excision of the ovaries is followed by sterility.[178]

It was immediately believed that the newly described vesicles, which were mistaken for the true mammalian ovum,[179] contain all parts of the future offspring and that they need nourishment only for their full growth in the way as a plant seed does. Such an

[177] It was Nicolas STENO who saw the female gonads in viviparous fish, and first called them ovaries. His work: Musculorum descriptio (1667).

[178] R. de GRAAF: Op. omn., p. 302: " communis femellarum testiculorum usus est, ova generare, fovere, et ad maturitatem promovere... potius mulierum *ovaria*, quam testes appellanda veniunt... illi ad generationem summopere necessarii existant; quod... confirmat ipsa femellarum castratio, quam sterilitas infallibiliter concomitatur ".

[179] The true mammalian ovum was discovered by Karl Baer in 1827.

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erroneous idea was further supported by occasional descriptions of cases in which well-developed parts of the foetus could be seen in the ovary.[180] Jan Swammerdam (1637-1680), another pupil of van Horne in Leiden and the rival of Regnier de Graaf, became the chief promoter of such preformation theory and was the leader of the " ovists ".

The description of the Graafian follicles and ovaries was followed by the repentant statement of anatomists and physicians that it was a pity that for so many centuries the true nature of these parts had been unrecognized. Further observations soon showed that there is a special portion, a *cicatricula*, within the follicles and it is the true " female semen ". Thus, John Ray (1627-1705), English naturalist, talks of this cicatricula or gemma which has to be animated by the " effluvium " of the male sperma. The follicles in the ovary gave opportunity for wild speculations, some of which could be now designated as early theories of pangenesis. Rosinus Lentilius published in 1698 one of the most fantastic of such theories.[181] He assumed that the seeds of all animals were put into the air at the time of Creation. These seeds are then inhaled by female animals, and enter the ovaries where they root and vegetate.

But coming back to the ovists, they did not stop at the assumption that the parts of a new descendant are ready-made in the female ovum. They wondered whether the ovaries of the first mother of mankind contained also all the ova for the entire human species so that, when the supply of these primordial ova will ever become exhausted by the successive generations, the human race will stop propagating. Swammerdam suggested this first, and many were his followers, including Johann Conrad Brunner,[182] Malebranche, Berger, Herfeld, and others. There were also skeptics who could not believe that the tiny ovary of Eve could have contained the million times million eggs which the pregnants of all ages needed for reproductive function.[183]

Spermatozoa

Soon after the discovery of the female ovarian follicles or " ova ", a chance observation of the male seminal fluid under the microscope showed that the male semen is full with small, rapidly moving worms, vermicles, or animalcules. The discovery of these formations was contested by several persons.[184] It may be true that Louis Gardin, physician at Douai had already seen them in 1623 but it was the merit of Antony van Leeuwenhoek (1632-1723) to bring the chance observation of Ludwig Hamm, a medical student, to the knowledge of the Royal Society of London in a letter dated November 1677. With the discovery of the male germ cell a new line of speculation

[180] See e. g. Theodor KERCKRING'S *Anthropogeniae iconographia* (1671), in which cases of ovarian pregnancy are reported.

[181] See his Miscellanea medico-practica. Ulm, 1698.

[182] In his treatise on the Pancreas, Brunner doubted the ovist theory.

[183] Among the skeptics were Peyer (1685), Harder (1687) and all the socalled animalculists.

[184] It was Pouchet in the 19th century who claimed the glory of discovery for Louis Gardin. I could not check the right of this claim. Others who were mentioned as discoverers of the spermatozoon are Nicolaas Hartsoeker (1656-1725), and Stenon (1638-1687).

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started. Leeuwenhoek had correctly guessed that the animalcules are essential for fertilization; that only one or two enter the cicatricula or *punctulus* in the ovarian follicle. But he made the mistake to reduce the woman's role in generation to a mere receptacle in which the " animalcule " is reared to full maturity. [185]

Leeuwenhoek's animalcules were also supposed to have the exact pattern of a future being, and some microscopists imagined that they saw a small *homunculus* hidden in the spermatozoon. Hence, a scientific discussion began between the " animalculists " and the " ovists ", both group claiming the truth for his own misconception. Both group believed in preformation, and advocated that heredity is chiefly unilateral. The scientific fight lasted more than a century. In its course, many new and useful ideas developed and our knowledge of heredity progressed.

Fig. 6. Leeuwenhoek discovers the spermatozoon

Johann Baptist Lamzweerde attempted to reconcile the differences between ovists and animalculists by saying that both the ovum and the male semen contain the parts of the body, with the only difference that in the ovum the rudiments of female genitals and secondary sex characters (such as breasts) are in a more perfect form. [186] One is very much tempted to read into this statement something from our modern gene theory of sex determination, and of the behavior of X and Y chromosomes. Herfeld, writing of the heredity and origin of diseases, calls the animalcules of the male so many " ideas ", and believes that each has the " signatures " for the production of the whole body of the offspring. [187] Schurig remarks that they make us immortal in a

[185] Leeuwenhoek was also practical breeder of Dutch rabbits and Belgian pigeons. For this reason J. Boeke considers him a precursor of Mendel. But Leeuwenhoek only mentions how rabbits are bred by crossing wild gray males with domestic females of any color, and the paternal gray will dominate in the offspring. cf. his Epistola de generatione ranarum, 26 July, 1683 (In his Op. omn., v. 1, 49).

[186] Lamzweerde J. B., Historia molarum uteri. Leiden, 1868: " ...attamen aeque ac semen masculinum omnium partium corporis feminini rudimenta et virtutem seminalem complectitur " (p. 72).

[187] Herfeld. De origine morborum. Amst., 1706: " hoc semen, sive sit animalculum, sive idea, signaturas totius creaturae producendae in sese comprehendens... " (p. 36).

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way because we are reborn in the descendants.[188] He seems to be the first who ever announced so clearly the continuity of life, and its transmission along the line of generation.

Heredopathology

The knowledge of hereditary diseases in man also received stimulus from the discoveries of the Graafian follicles and the spermatozoa, though this knowledge did not advance as far as to clearly explain the causes of hereditary disease. Many medical works contain casual references to single observations of some heritable sickness or defect (V. Coiter 1573; C. Bauhin 1614). Among the hereditary diseases the 17th century writers mentioned hernia, malignant " erysipelas " (Bierling 1679), headache (Muralti 1687), pulmonary lithiasis (Huldenreich), food idiosyncrasy to veal chops inherited by the daughter from her mother (Albrecht), melancholia and mania (Timaeus 1677), epilepsy (Zacutus Lusitanus), a form of dysuria with infrequent urination (Paullin), cataract homochronous in father and daughter, blindness and deafness, sweating inherited from mother by daughter (Tulpius 1652), and so on.

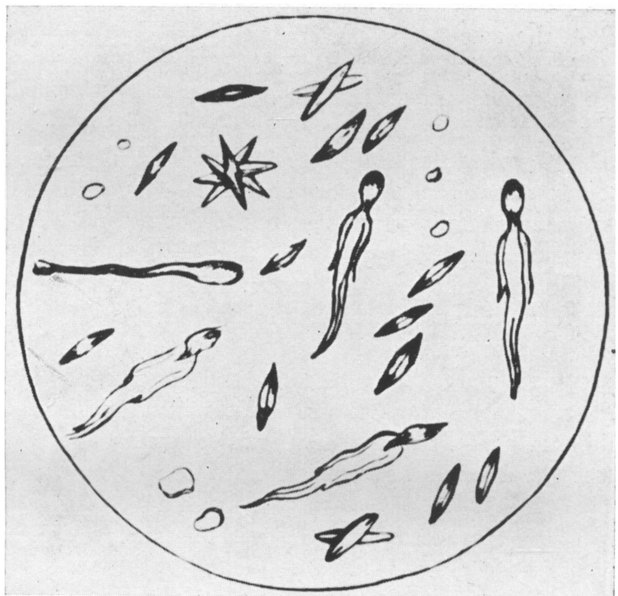

Fig. 7. What Leeuwenhoek saw under the microscope

A kind of textbook on heredopathology is Edmund de Meara's De morbis haereditariis (Lond., 1665)[189] in which he mentions certain hereditary diseases that became almost tribal marks for a family so that absence of the disease in an offspring made people speculate whether the child came from the legitimate line of ancestors. Ettmüller clearly distinguished hereditary diseases and tried to separate them from the merely congenital or connatal affections.[190] There was sometimes confusion in the meaning of " hereditary ", and some contagious diseases were also called such if they were com-

[188] SCHURIG M. Spermatologia. Frankf. a. M., 1720: " indeque nos immortales quasi reddere, dum redivivos in aliis entibus, nobis similibus... " (p. 152).

[189] This treatise was published in his Examen diatribae Willisii de febribus (Lond., 1665), 241-315. The treatise was written by Dermutius de Meara, the father of Edmund, and first published in Dublin about 1621.

[190] ETTMÜLLER M., Op. med., v. 2, Frankf., 1697. See v. 1, 202.

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municated to the child by the parents. Schurig[191] thought that for the propagation of hereditary diseases it was not necessary that the parents were actually suffering from the disease at the moment of mating. It was sometimes only the cause of the disease transmitted to the descendants. Ettmüller also stated that there was nothing material such as a ferment or a morbid seed transplanted into the embryo because the heredity of diseases was rather the implantation of a *disposition* into the fetal parts.[192]

In the medical works of this period the causes of hereditary diseases were also sought 1) in the semen alone, 2) in the semen and the blood, 3) in the mixture of the paternal and maternal seeds (the old view), 4) in the " archaeus seminalis " (Helmont), 5) in the semen and the maternal blood (Fernel), 6) in the female semen alone (Laurentius), 7) in deficiency of salts (Quercetanus). Some of the early pathologists denied the existence of heredity for disease, and they believed that the depravity of the semen of one parent can be corrected by the better quality of the other, which seems to be a primitive idea of dominance in pathological heredity. It was also pointed out as a consolation that the eruption of a hereditary sickness might be hindered by the constitution of the body, and that the observation of general hygienic rules might suppress any morbid hereditary disposition.[193]

Though there was more and more evidence which indicated that in reproduction the form of the species is rigidly maintained, I have seen first in a work of Lamzweerde (1686) that from human male semen and female semen nothing else will be born but a human child. Nevertheless, the old legend of interspecies reproduction of animals, either from normal human intercourse or by means of crossing between man and animals, was kept alive and ultimately ended, towards the end of the eighteenth century, in a general theory of evolution.

Eighteenth century

In the history of modern genetics the eighteenth century is of great interest for several reasons. It witnessed the efforts of the plant hybridizers to settle, on the field of botany, the old quarrel about the concept of *species*. It also cut short further speculation of the ovists and animalculists, and prepared an open way for the clear understanding of individual evolution from the seed.

The outstanding events of this century can be summarized as follow:

1759 Wolff's theory of epigenesis published
1760-66 Kölreuter's work on plant hybrids
1777-80 Spallanzani's experiments with animal fertilization.

The conception of sex in plants was clearly developed by Camerer, the Tübingen physician, in the previous century. After the recognition of the sexual character of flowers, many industrious gardeners, and amateur botanists took up plant hybridization

[191] Schurig, Spermatologia historico-medica. Frankf., 1720, 204.
[192] Ettmüller, cf. Footnote 190 (ibid.).
[193] Bohne J., Circulus anatomico-physiologicus. Lpz., 1686.

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as a hobby. Zirkle[194] and Roberts[195] collected them in their books, and described their merits, comparing their achievements with those of Mendel. They leave no doubt that all these early amateurs and professional gardeners or botanists must have seen the same phenomena as Mendel did in the mid-ninteenth century but all of them lacked either the intellectual make-up, or the simple curiosity of the investigator of Nature for making a methodical research and for drawing general conclusions of value to interpret the innate rules of Nature.

In a sense any plant hybridizer before Mendel can be considered a precursor. Scientific ideas never are born without their germ's having been present in the air for many decades, if we are permitted to express ourselves in the idiom of the pangeneticians. Yet, in a narrower sense, no discovery has precursors, and an original idea has a unique character of originality. This does not subtract, however, from the importance of the findings of the earlier investigators who contributed to a field of knowledge.

Among these 18th century plant breeders we find Cotton Mather (1663-1728), the New England clergyman; Thomas Fairchild (1667-1729), English professional florist; Jean Marchant (d. 1738) in France; Thomas Knowlton (1692-1782) in England; Philip Miller (1691?-1771), gardener of the Chelsea Physics Garden; Paul Dudley (1673-1751), naturalist and New England judge; Giuseppe Monti in Italy who studied maize hybrids in 1719; Benjamin Cooke who also crossed various agricultural plants; Henri Louis Du Hamel du Monceau (1700-1782), who is also thought of as a precursor of Darwin; the Reverend Thomas Henchman (d. 1746) who was surprised what he found after the crossing of two varieties of peas, but beyond his surprise he was not further interested.

Other botanists and hybridizers before Kölreuter were Jacob Andrew Trembley (in 1734); John Mitchell (d. 1768), physician in Virginia; John Bartram (1699-1777), collector of American plants in Philadelphia; Daniel Rudberg, a student of Linnaeus, who described Linaria hybrids in 1744; Johann Georg Gmelin (1709-55) in 1745; Johann Gustav Wahlbom (1724-1808) who published a work on hybridization of tulips in 1746 in Stockholm; Per Kalm (1715-79), Swedish naturalist in 1750; William Douglass (1691-1752), physician in Boston, who described varieties of corn in 1751; John Haartman who in 1751 felt the need that studies should be carried out with fertile hybrid plants; Christlob Mylius (1722-54) in Germany in 1751; Edmé Gilles Guyot (1707-86), James Parsons (1707-70), Johann Gessner (1709-1790), N. E. Dahlberg (1755), C. L. Ramstrom (1759) who also stated that the use of hybrids is the best method for the study of heredity.

Linnaeus himself (1707-78), as several of his pupils was one of the hybridizers, and won a contest of the Academy of Sciences of St Peterburg with an essay which he wrote in 1759 to prove that plants reproduce sexually; his reference to hybrids was illustrative only. The most outstanding among the plant hybridizers of the 18th cen-

[194] For details on plant hybridizers before Kölreuter see his work; cf. Footnote 40.
[195] For plant hybridizers after Kölreuter see his work; cf. Footnote 45.

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tury was a German botanist, Joseph Gottlieb Kölreuter (1733-1806).[196] He performed his first hybridization in 1760. The merit of Kölreuter is that he introduced hybridization as an experimental method in the study of the sexual behavior of plants, but, in contrast with Mendel, he lacked mathematical exactness, and was not keen on the use

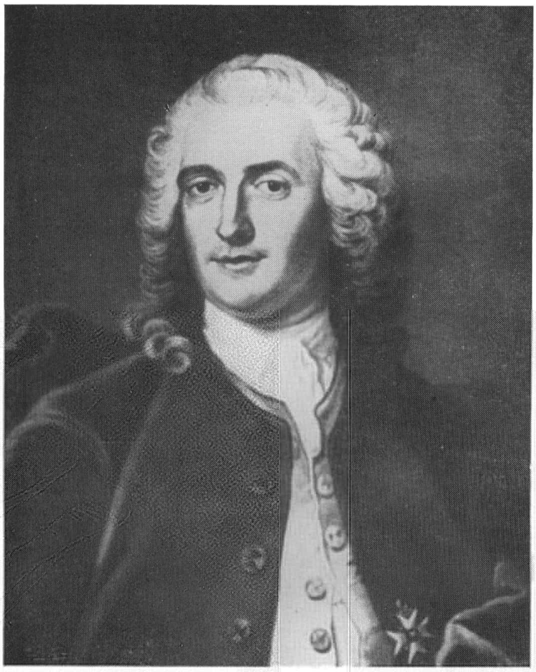

Fig. 8. Karl Linnaeus, 1707-1778

Fig. 9. Joseph Gottlieb Koelreuter, 1733-1806

of the statistical method. His experiments were carried out in his native village, in Sulz, where he made his Nicotiana hybrid. Later, he moved to Calw where the garden of Dr Achatius Gärtner, physician, served as his experimental laboratory. He also worked in St Peterburg, Berlin and Leipzig. He showed that fertile hybrids can be produced between plants of different kinds. He also saw the relation of insects to plant pollenization. It is also his statement that crossing is an ordinary and common phenomenon between plants in Nature. His fate was that of other true scholars: it took one hundred years until his merits were recognized.

Contemporary with the botanist Kölreuter was the physician Caspar Friedrich Wolff (Berl. 1733-St. Peterburg 1794) who in 1759 wrote his thesis *Theoria generatio-*

[196] Kölreuter J. G., Vorläufige Nachricht von einigen das Geschlecht der Pflanze betreffenden Versuchen und Beobachtungen. Lpz., 1761; with 3 supplements (1763, 1764, 1766); republished in Ostwald's Klassiker der exakten Wissenschaften. No. 41. Lpz., 1893. English resumé in Roberts, l. c.

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nis (Halle, 1759) in which he set forth his theory of emergence, gradual appearance of parts from the seed of the parent animal. This gradual emergence, in opposition to the preformation, is called *epigenesis*. It was essentially not a new thought, since the same idea had also occurred to naturalists in Antiquity and the Middle Ages. This theory accepts the existence of a fundamental substance, an amorph matter (which we now call protoplasma) which gives rise to the development of primordial embryonic vesicles (and the cell formation) which finally enters into the formation of the body and its organs. This emergence is moved by a " vis essentialis ", which had also produced the first life. As for the animals, he also found for the plants, from his studies of floral development, that the evolution of a plant from its seed is not a process of unfolding of pre-existing rudiments, but must be considered as new accretions, a true epigenesis.[197]

Among the 18th century naturalists there were also a few who experimented with crossing of lower and higher animals. One of the earliest was René Antoine Ferchault de Réaumur (1683-1757) who, beside his chief interest in the life of insects, also tried the crossing of domestic fowl, and reported his experiences in 1749 in a lengthy memoir. French historians of science (e. g. Hervé) are inclined to claim the fathership of genetics for this noteworthy Frenchman.[198]

A rival French naturalist, George Louis Le Clerc *Comte de Buffon* (1707-1789), just about this time, startled his countrymen and the world of science with his doctrine that all animals descended from a single primitive animal which, through the many thousands of centuries, transformed many times. Two volumes of his *Histoire naturelle* (v. 10 & 11 of the 1830 ed.) are full with details of this theory. He assumed that plants and animals are of the same order, and their chief resemblance is in the fact that they reproduce themselves. He believed in the existence of organic living molecules which are independent of each other and which may form groups according to the species of animals; they shape themselves according to an internal mold or matrix (" moule intérieur "), there being a matrix for the entire animal and separate matrices for each single member. The theory of internal matrices was sufficient to explain to Buffon the similarity of an individual to his parent, but for the explanation of dissimilarities and divergences it was not sufficient. Buffon also believed that the variations among individuals of the same species are under the effect of environment, and in the origin of a species various factors might be at work such as struggle for existence, artificial and natural selection, geographical isolation, etc. He also held the view that acquired characters are hereditary.

Another scholar of this era, Charles Bonnet (1720-1793), who is, occasionally, incorrectly taken as the first describer of parthenogenesis in insects,[199] held similar

[197] Cf. WARDLAW, p. 4. See Footnote 85.

[198] His breeding experiments are in the memoir " Esquisse des amusements philosophiques que les oiseaux d'une basse-cour ont à offrir " which appeared in: Art de faire éclore et d'élever en toute saison des oiseaux domestiques de toutes espèces, etc. Par., 1749.

[199] Parthenogenesis had been observed in 1667 by Goedart in the female of *Orgyia gonostigma* (cf. Metamorphosis et historia naturalis insectorum, pars 2, p. 106, 1667; 2. ed. Lond., 1685). – Thereafter it was noted by Leeuwenhoek (1695), Blancard (1696), Albrecht (1706), Réaumur (1741).

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ideas on transformism, and further encouraged the ovists and preformists by suggesting a remodelled version of Swammerdam's theory of encasement (*emboîtement*). Buffon's idea of transformation was further propagated by Erasmus Darwin (1731-1802), grandfather of Charles Darwin, who in 1794 published his *Zoonomia or The Laws of Organic Life* (Lond., 1794) in which he also accepted the view that the changes, caused by the environment in the parent organism, are transmitted to the descendant by heredity. Another Englishman, James Hutton (d. 1797), an atheist, published a synthesis of the contemporary knowledge about the origin of the Earth,[200] and he is considered by some the true intellectual ancestor of Charles Darwin.

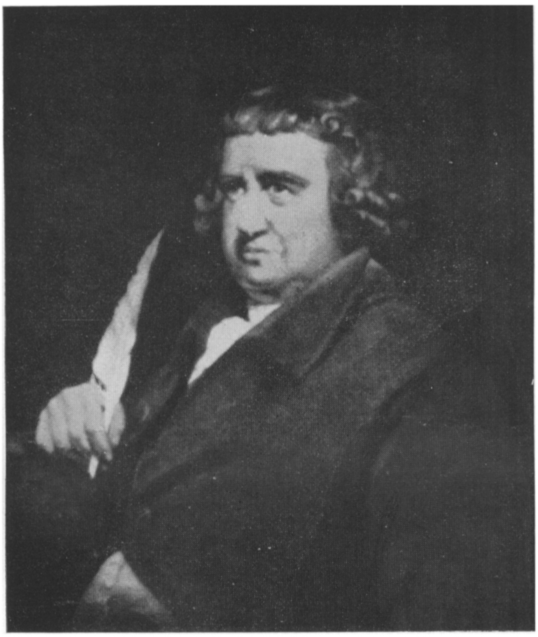

Fig. 10. Erasmus Darwin, 1731-1802

Lazzaro Spallanzani (1729-99), a very skillful experimentator, was very much interested in regeneration and fertilization. His attempts at artificial insemination started in 1777, and in 1780 he succeeded in impregnating a bitch by transfer of the sperm of a male dog, and its injection through a syringe. In 1786 he also proved by filtration of the sperm that it looses its fertilizing power after such procedure, which was an indirect evidence that the fertilizing capacity is in the spermatozoa, and not in the seminal fluid itself. The role of the " spermatic worm " in the fecundation of ova had been already proven by Antonio Vallisnieri (1661-1730), Professor at Padua and pupil of Malpighi.[201]

Further progress can be seen in the 18th century on the field of *heredopathology*. The literature on the subject of hereditary diseases was considerably increased,[202] and to say that 30 or 40 such works had been published between 1700 and 1800 is but a very conservative estimate. Inspite of the lack of knowledge of the anatomical basis of heredity, much of the material that was collected by the 18th century clinicians on hereditary disease has good standing. Indeed, a full and modern knowledge of genetics

[200] Theory of the Earth (1785).
[201] VALLISNIERI A., Historia generationis. Venez., 1721-23.
[202] For this literature see the *Index-Catalogue* of the Surgeon-Generals Library. See also LABU- Footnote 62.

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is not necessary for having good eyes for observation, and for having sound mind to make conclusions from healthy reasoning.

The finding of the previous century that " not the disease but only its predisposition is inherited " was further confirmed. The predisposition was thought of as a certain " anlage ". The central problem of 18th century heredopathology was how does the " anlage " get into the seed. It was remarked that the male seed is a sort of abstract of the entire body. If any part of the body is at fault, or at disease, such fault or disease will also appear in the seminal fluid. Various mechanical and chemical explanations were given how a small, dynamic, faulty part of the semen can produce such havoc.

The problem of hereditary disease was so acutely felt that in 1748 the Academy of Dijon had a prize set for the best essay written on the topic: " Comment se fait la transmission des maladies héréditaires "? [203] It was felt as before that, beside the hereditary " anlage " there is also another accidental factor at work which awakens the hereditary disposition, and produces the manifest disease. Perhaps, it was in the spirit of the period that the pathologists assumed a " rigidity of species " among the hereditary diseases, too. Thus, a disease of the nerves in the parents would cause a tendency to neural affections in the child. Nevertheless, it was also according to the spirit of the 18th century rising transformationism that some hereditary diseases were considered capable to mutation of their pathological species.

Among the heredopathologists of the 18th century we should especially mention Giambattista Morgagni (1682-1771), the father of pathological anatomy, who, in several letters of his great work (*De sedibus*, etc. Venez., 1761) mentions a number of diseases with the remark that the patient's brother or father, or his other relative, also had the illness. Among such diseases we read of gout, phthisis, hemoptysis, gastrointestinal ailments, cholelithiasis, manic depressive disease, epilepsy, severe headache, meningocele, cataract, strabismus, deafness, heart ailments, and apoplexy. He also noted that there is a possible aggravation of a disease in the successive generations. There is, however, no indication that in collecting these family data on sickness he was anywhere near to discovering a biological rule for heredopathology.

Several theses which were published from Halle and Göttingen about the middle of the 18th century suggested that for the control of hereditary diseases the descendants of certain sick parents should be excluded from propagation, by legal ban upon their matrimonial union. [204] The French 18th century literature also produced works on betterment of the human race. [205]

[203] Prize essay of CHAMBON. Discours de la transmission des maladies héréditaires. Par., 1749. Other essay writers: Gravier, Rey, and Louis.

[204] Such theses from Halle are by Hilbrand (1749), Oppermann (1753); and from Göttingen by Vogel (1767).

[205] VANDERMONDE, Essai sur la manière de perfectionner l'espèce humaine. Par., 1766.

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Nineteenth Century before Mendel

The first half of the 19th century struggled with the new problems which the discoveries and theories of the two previous centuries created in natural philosophy. This is the period in which general biology became a firmly established experimental science and the knowledge about generation also divested itself, almost completely, of the superstitions and speculations. The outstanding events of these revolutionary years are as follow:

1802-09 Lamarck sets forth his theory of evolution.
1812 Cuvier establishes paleontology of vertebrates.
1827 Baer sees a dog's ovum.
1839 Schleiden (in plants) and Schwann (in animals) establish the cell theory
1859 Darwin demonstrates transformism
1859 Pasteur stops speculation on spontaneous generation.

Fig. 11. Jean-Baptiste Antoine de Monet Chevalier de Lamarck, 1744-1829

Fig. 12. George Cuvier, 1769-1832

The idea of transformation and descendence from a single animal, which Buffon had promulgated in France, was further developed by Jean-Baptiste Pierre-Antoine de Monet Chevallier de Lamarck (*1744-1829*) who in his various publications, especially in his *Philosophie zoologique* (Par., 1809), declared the variability of all organisms, the effect of environment on plants and animals, and the heredity of acquired characters. He saw that the essential mechanism of species transformation is the heredity of acquired characters. His theory accepts two laws. One is that in a developing animal the

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non-usage of an organ causes weakness, deterioration, progressive diminution and final disappearance. According to the other, only those acquired characters are heritable which are common to both sexes, and which represent an active, essential adaptation to the environment.

Lamarck was essentially a botanist, and his theory was ridiculed by another Frenchman, a zoologist, George Cuvier (1769-1832), who adhered to the opinion that there is no variation possible which could make it possible to have a single common ancestor for all animal life. His views on the constancy of the types of species were followed by many zoologists though it became for him increasingly difficult to uphold his belief in straight Creation, in view of the increasing number of fossils which were uncovered. He himself did not care much about the problems of generation, and did not conduct experiments on crossing of animals. This attitude of the truly scientific Cuvier influenced other zoologists to devote their energies to the description of the anatomy of various animals, of new forms of life, and to voyages at various parts of the world. This may be perhaps one of the reasons that the laws of heredity were developed by botanists and plant breeders rather than by students of animal life.

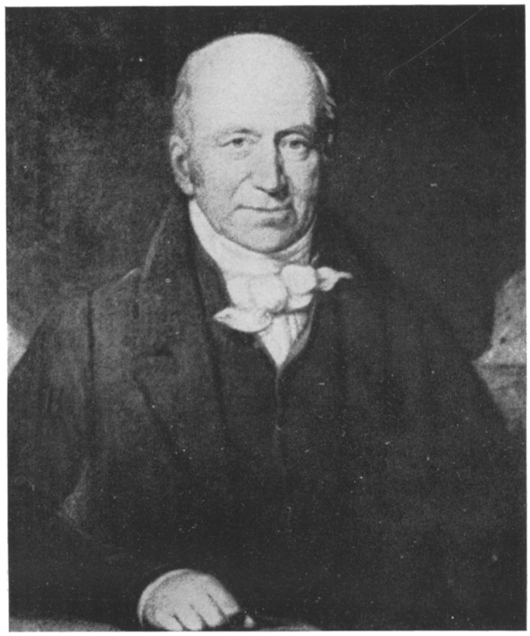

Fig. 13. Thomas Andrew Knight, 1759-1833

Toward the end of the 18th century, — owing to the advancement of capitalism as the Russian Vavilov believes [206] — there was in Western Europe and especially in England a tendency to pedigree livestock and seed production, thus affording profitable outlets for its development. Among the seed producers and plant hybridizers who followed the steps of Kölreuter, Thomas Andrew Knight (1759-1833) is of special importance, an English country gentleman, who in 1799 undertook experiments on superfetation (2 males for 1 female) of peas, the same plant on which Mendel discovered his laws of heredity. His crossing experiments with peas started already in 1787 and he was the first to record color dominance in peas. [207] In crossing several varieties of red upon white currant, he found that by far the greater number of hybrids produced red

[206] Vavilov, See Footnote 46. (l. c., p. 3).
[207] Knight T. A., in *Tr. Horticult. Soc. London*, 1823, 5: 377-80.

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fruit (later confirmed by Darwin). This hybridization rule is occasionally referred to as the Knight-Darwin Law. He also wrote on human heredity, and on the comparative influence of male and female parents on their offspring (Philos. Tr., Lond., 1809, 392-9).

William Herbert (1778-1847), a contemporary of Knight, also experimented with production of hybrid vegetables for the improvement of agricultural plants.[208] He found that the fertility of hybrids depends greatly on the constitution of the parents. Other plant breeders of this period are John Goss (1820), Alexander Seton (1824), and Augustin Sageret (1826) in France who also anticipated the knowledge of segregation.[209]

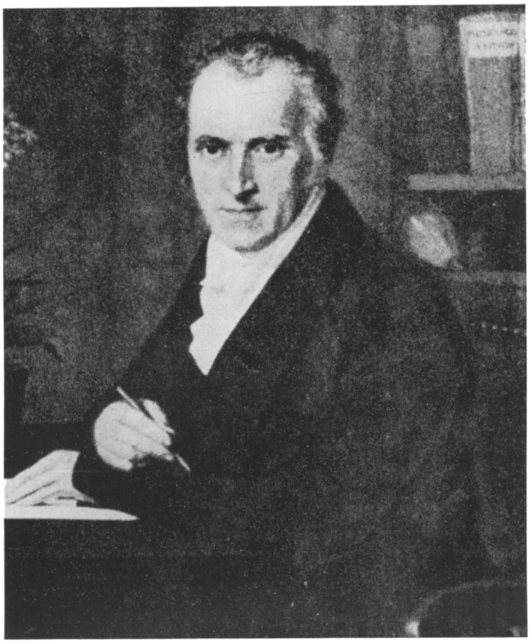

Fig. 14. Friedrich Gärtner, 1772-1850

Carl Friedrich Gärtner (1772-1850), a physician and son of a botanist, wrote an essay for a contest which was announced by the Holland Academy of Sciences at Haarlem, on artificial fertilization as a means for production of new species.[210] He also wrote on his various experiments which showed that there is a difference between first and second generation of hybrids; that there is some regularity in the segregation of hybrid characters; that hybrids have a special vigor which makes them excellent for agricultural purposes. He also had an idea of the relative dominance of one or more parental factors which he called " Wahlverwandschaft " or sexual affinity. He also experimented wiht peas, the heredity of their color and of the form of seeds, but did not make any statistical records; nor did he follow out the distribution of hereditary characters in the seeds of the second generation. Indeed, Focke[211] says that the work of Gärtner is characterized by extraordinary clumsiness.

The family of Vilmorins, including André (1840), Louis (1859) and Henry (1880), was of great importance in the history of French agriculture in the 18th and 19th centuries. Theirs was a seed-firm near Paris, since 1727. They published many articles in journals and books. As plant hybridizers they are usually mentioned among Mendel's

[208] Herbert W., *Tr. Horticult. Soc. London*, 1819, 4: 15-50.
[209] Sageret A. (1763-1851) *Ann. sc. natur.*, 1826, 8: 294-314. – Experimented on Cucurbitaceae.
[210] Gaertner C. F., Over de voorteling van bastaard-planten. Haarlem, 1838.
[211] Focke, Pflanzenmischlinge. Berl., 1881.

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precursors. It was Louis (1816-1890) who in 1859 became interested in the numerical ratio of transmission of characters from crosses of Lupinus hirsutus. His findings were published only in 1879 by his son, Henry (1843-1899),[212] (i. e., after the publication of Mendel's findings in 1865). He reports that in 40 cases during 5 years, the rose-

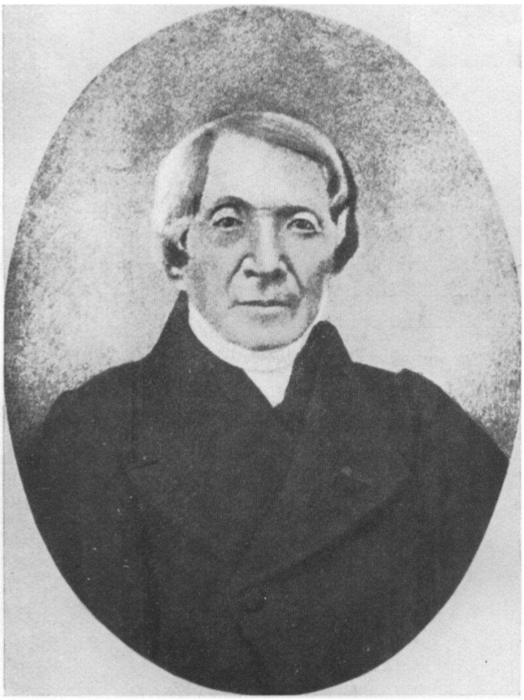

Fig. 15. Andrée de Vilmorin, ca. 1840

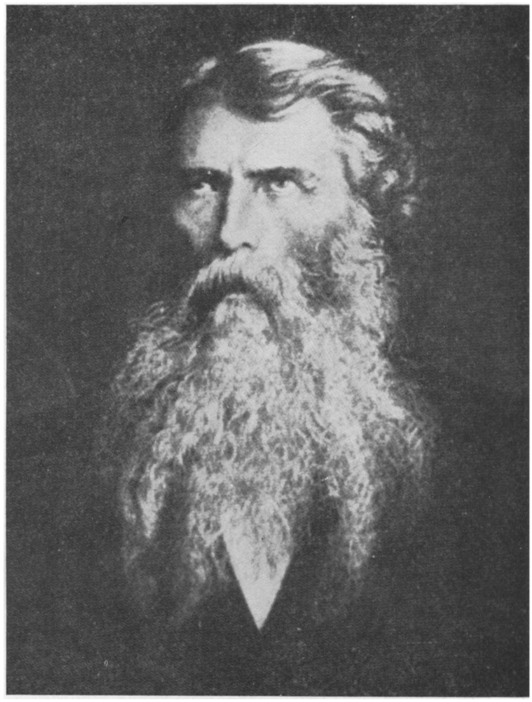

Fig. 16. Charles Naudin, 1815-1899

flowered plants broke up into blue and rose in a 3 to 1 ratio (which is exactly the Mendelian law).

Three other plant breeders in France are to be mentioned in search for precursors for Mendelism. D. A. Godron, of the University of Nancy, wrote on hybrids in 1844, and competed in 1861 with Naudin to win the prize which the Academy of Sciences in Paris put upon an essay on fecundity and perpetuity of hybrid plants. Henri Lecoq (1845) also worked on problems of hybrids. Charles Naudin (1815-1899), of the Museum of Natural History in Paris, was an ardent student of hybridization, and, in

[212] Note sur une expérience relative à l'étude de l'hérédité dans les végétaux. *Mém. Soc. nat. agr. France* (1879).

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various articles,[213] published his findings which are generally considered to be remarkably close to the results of Mendel, of whom Naudin was a contemporary. He recognized the independent behavior of characters in a cross; he emphasized the general uniformity of the first hybrid generation, and the diversity of the second generation; he noticed that the first generation is generally intermediate; and he saw the segregation in the third hybrid generation, calling this phenomenon a " disorderly variation ", and explaining it with the *disjunction* of the two specific essences in the pollen and the ovules of the hybrid. This law of disjunction is essentially the same principle that operates the Mendelian laws; yet, Naudin makes his statement more or less as a scientific *hypothesis*, and not as a conclusion which is derived from specific experiments (Roberts). He never made a numerical classification of the hybrids, and the very fact that he calls the results of hybridization by the term " disorderly variation " proves that he completely missed the regularity of the basic phenomenon in hybrid reproduction.

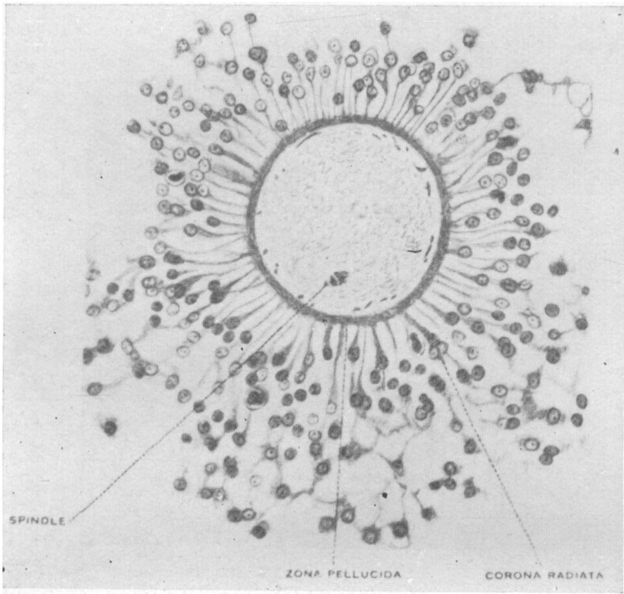

Fig. 17. An oocyte or ovum (modern drawing)

A group of interested naturalists further advanced the knowledge about generation. J. B. Dumas (1800-85), a chemist of Genève, in collaboration with J. L. Prévost, physician, published a paper on generation (1824) in which they proved that the spermatozoa are secreted in the testis of the adult, and they have spontaneous movement. They also saw " a small spherical body, of one millimeter in diameter, less transparent ", but they did not know that this body was the female ovum. It was the good fortune of Karl Baer (1792-1876), a Russian of Estonia, and professor at the Königsberg University after 1819, to discover the true mammalian ovum in 1827! Indeed, the female ovum was very elusive, and even the great Haller, the physiologist, tried to discover it already in 1752 when he was in Göttingen. The Englishman Cruikshank stated that he saw the rabbit's egg three days after mating of

[213] Nouvelles recherches sur l'hybridité dans les végétaux. *Ann. sc. natur., Bot.*, 4 ser., 1863, 19: 180-203. – Also his: De l'hybridité comme cause de variabilité dans les végétaux. *C. rend. Acad. sc.*, 1864, 59: 837-45.

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the animals. Baer found the ovum at the dissection of a bitch in Burdach's house, when he opened the dog's ovary and removed its yellow spot for closer examination under the microscope.[214]

Baer then made the following conclusions: 1) every animal which develops from sexual reproduction develops from an ovum, and not simply from a plastic fluid; 2) the

Fig. 18. Karl Baer, 1792-1876

Fig. 19. Matthias Schleiden, 1804-1881

ovum has a cuticle without pore, and the male fluid acts upon it through the cuticle; 3) first the central parts of the embryo are formed; 4) first the spine is formed, and this mode of evolution is common to all vertebrates. By his very meticulous observations of facts, reflection and explanation (i. e., the Aristotelian method) F. A. Pouchet (1800-1872), professor of the Museum of Natural History at Rouen, demonstrated in 1835 that the ovules of mammals and man are constantly growing, and are expelled spontaneously and independently from sexual intercourse; that the spontaneous ovulation comes at regular intervals; and that fecundation takes place in the presence of seminal fluid only. He also added that the fecundation takes place somewhere in the

[214] BAER K., De ovi mammalium et hominis genesi. Lpz., 1827. – A very vivid description of his discovery is contained in his autobiography (*Nachrichten*).

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uterus, or in the region of the tubes. As to the spermatozoa, he considered them real animals which are provided with will-power.[215]

Meanwhile the studies of M. J. Schleiden (1804-81), and Theodor Schwann (1810-82), helped the final emergence of the cell doctrine in general biology. The cell was recognized as a peculiar little organism in plant and animal life (1839) which is able to

Fig. 20. Theodor Schwann, 1810-1882

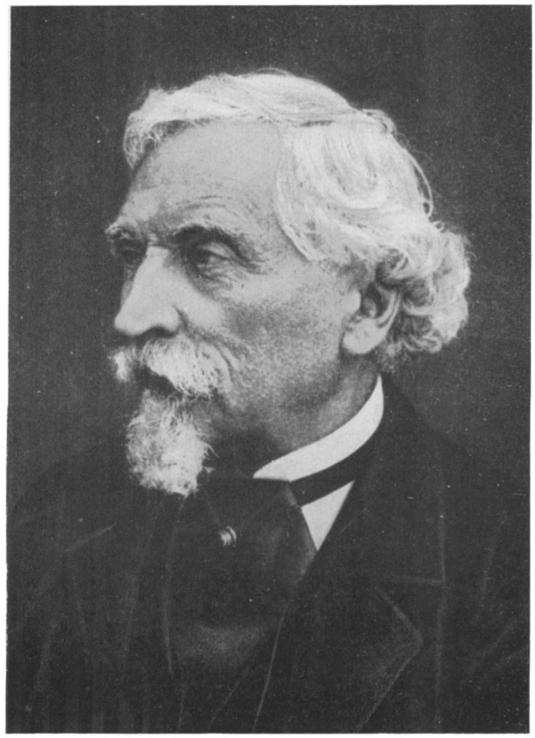

Fig. 21. Edouard Gérard Balbiani, 1823-1899

carry-on its own life to some extent, though subject to the general control withtin the organism as a whole. They thought that the cells are formed either by free primary origin, or by separation of nucleoli of the maternal substance. It was Hugo Mohl (1805-72) who described the division of plant cells. Soon after Schwann's work, Rudolf Albert Kölliker (1817-1905) showed that the spermatocytes arise in the testis by transformation of cells (1841).[216] Later (1885) he stated that the hereditary character

[215] Pouchet F. A., Théorie positive de l'ovulation spontanée et de la fécondation des mammifères et de l'espèce humaine (1847).

[216] Koelliker R. A., Beiträge zur Kenntnis für Geschlechtsverhältnisse und Samenflüssigkeit wirbelloser Tiere. Berl., 1841.

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is transmitted by the cell nucleus. Balbiani (1823-1899) first observed the sexual intercourse of unicellular beings under the microscope, and found out that conjugation of the infusoria is a real mating. He made some wrong conclusions which had to be corrected by Bütschli in 1875,[217] in his study on karyokinesis.

II. GREGOR MENDEL

On the previous pages we read a general outline of the activities of naturalists, plant breeders, zoologists, botanists, physicians, microscopists who all contributed to the development of biology. We have seen a long series of experimenters, and keen observers, professors of universities, and directors of various biological stations who devoted their time and energy to the solution of the innumerable mysteries of Nature. We have read about practical men whose methods intended the improvement of agriculture and animal husbandry; we also read about the greater and smaller thinkers eagerly concentrating on various problems of generation and heredity. We also witnessed the use of the microscope for the study of the invisible, in search for the mere satisfaction of man's curiosity, and we saw the penetration of human eyes into the depth of life, down to its smallest atoms. Yet, nowhere could we find a clearcut answer to the most simple questions concerning the heredity in plants, animals, and man.

The privilege of forging the key to the closed door of knowledge and of providing the basic rules of inheritance after correct reading the Book of Life has been reserved by Destiny to a simple high-school teacher of physics and natural history, a Catholic priest whose spare time was divided between daily readings of his Breviary and watching his plant hybrids to grow in the small spot that was designated the garden of his monastery. Our modern knowledge of heredity rests entirely upon the disclosure of his findings in 1865. He told us that many characters of an organism are inherited independently of each other rather than as a composite group. From this knowledge our modern theory of genes developed.

The essential biographical data of Gregor Mendel are commonly known. He was born at 22 July 1822 at Heinzdorf in the Austrian Silesia. His father was a peasant farmer who called his son Johann. He learned the elements of his knowledge in a village school, and continued his education at the gymnasiums of Troppau, and Olmütz. In the Troppau school one of his teachers was an Augustinian priest, a canon. Perhaps it was under his influence that Johann Mendel decided to become a priestly high-school teacher. The Augustinian order possessed several schools, and supplied various gymnasiums with professors, in Austria.

Mendel, after graduation from the Olmütz school, entered the Augustinian order in 1843, and as a novice and candidate for the priesthood he spent the next four years in the seminary of the Abbey of St. Thomas, the so-called " Königskloster ", at Brünn (or Brno). After four years study of Catholic theology he was ordained priest in 1847. This year and the next ones were very turbulent in the political history of Austria.

[217] Balbiani thought that the infusoria are complex organisms.

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There were revolutions after revolutions, in Wien, and in other larger cities of the Empire; moreover, the Hungarians began to fight for their freedom in 1848, which made the conditions at the universities of Austria, especially in Wien, very warlike. The career of an Augustinian teacher requires professional preparation at the philosophical faculty of a university. Mendel could not travel to Wien for a while; indeed, he waited until 1851 with the continuation of his chosen studies. During the waiting period he was most likely engaged in his priestly duties around the monastery.

Fig. 22. Gregor Mendel, 1822-1884

In 1851 he registered at the University of Wien, and took up his studies in natural history, botany, chemistry, mathematics, physics and related subjects. He had the good fortune to come under the influence of three eminent scholars who themselves were newcomers to the Wien University after the 1848-49 revolution. His professor in physics was Christian Doppler (1803-54), the great mathematician and investigator whose name became an eponym in radiology and acoustics ("Doppler effect") and whose fundamental work was later incorporated in the series of Ostwald's classics. His professor in chemistry was Joseph Redtenbacher (1810-1870) who was also an investigator in botany and who contributed many articles to the contemporary literature on both subjects. Finally, his professor in the anatomy and physiology of plants was Franz Unger (1800-1870), a very prolific writer on the fields of botany, and paleontology. Some of his views were very close to darwinism; therefore, he was occasionally criticized in the public. His botanical knowledge was tremendous, though he fought against the cell theory of Schleiden. These were the scholars who took part in the education and formation of Mendel.

Gregor Mendel (called so at his entrance into the Augustinian order of canons) finished his professional studies, and left Wien in 1853. In the same year, in September, he assumed his professorial duties in the highschool of Brünn which, in contrast to the humanistic curriculum of the gymnasiums, had most of its subjects selected from natural sciences and modern philology; for this character it was called an *Oberrealschule*. In this school, Mendel has been a teacher of physics, and natural history for the next

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fourteen years. In 1868 he was elected by his brethren the abbot of both the Brünn monastery and the entire order in Austria. In vain, he hoped that he could devote more time to his interest in natural sciences. To the many duties of an abbot, he also became involved in a hopeless and useless fight with the Imperial Government of Austria which in 1872 had imposed a heavy supertax on all religious houses of the country. In addition to this, his work was also hindered by various racial controversies between Moravians and Austrians. Moreover, the civic activities of an abbot also drew on his time: chairmanship in the town's bank, chess playing and bowling with the new novices of the order, etc. An additional cross that he had to wear was a chronic nephritis [218] of which he died on the 6th of January 1884. He used to say: " My time will surely come! " (" Meine Zeit will schon kommen "). And it came! His work was recognized in 1900, and his Brünn erected a monument for his honor on 2. Oct. 1910. He was further honored at the festivity of his centennial birthday, in 1922.

As a man who had been educated at a European university of the highest level, he was well prepared for his chosen field, and his interest included all branches of natural sciences, even the study of the weather. Monasteries had always been good locations for the establishment of meteorological stations. He reported his observations on the weather of Brünn and Moravia in several volumes of the Naturalist Society of his city, [219] and he also described a remarkable tornado (" *Windhose* ") which occurred in Moravia in 1870. [220] It is also known that he also studied the heredity in bees, and collected queen bees of all races from many lands in order to make crosses. His notes on this topic disappeared.

His chief interest was, however, the study of plant life. His experiments with plant hybridization started in 1857, and they were continued until about 1864 when he began to prepare his famous lecture on the mathematical regularity of the basic phenomena of heredity. He read his paper in two portions, at the second and the third meetings of the Society of Naturalists of Brünn, which were held on the 7th of February and the 8th of March 1865. The society had monthly meetings and an additional annual session. It was a very distinguished society, with over 200 members, including a number of physicians in Brünn and from the neighboring towns. Among the honorary members of the society we read the names of Robert Bunsen (Heidelberg), Prof. Göppert (Breslau), Joseph Hyrtl (Wien), Johann Purkyně (Praha), Carl Rokitansky (Wien), Rudolph Virchow (Berlin), and F. Wöhler, the Göttingen biochemist. None of these worthy men could recognize the significance of Mendel's paper though all of them received a copy of the " Verhandlungen des Naturforschenden Vereins in Brünn " (1865, v. 5:) in 1866 when the proceedings were published.

[218] WINDLE B. C. A., in: Catholic Encyclopedia, 1913, v. 10: 180 etc.

[219] Cf. MENDEL G., Bemerkungen zu der graphisch-tabellarischen Uebersicht der meteorologischen Verhältnisse von Brünn. *Verh. Naturforsch. Verein.*] *Brünn*, 1862, 1: – Also: Meteorologische Beobachtungen aus Mähren und Schlesien für die Jahre 1863-66. Ibid., v. 2-4, 1863-65.

[220] MENDEL G., Die Windhose am 13. Okt. 1870. Ibid., 1870, 9: – This is his last known scientific publication.

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It is an odd coincidence that on the first session of the Society, on 11 January 1865, Alexander Makowsky, a teacher at the Technical High School in Brünn and a member of the Naturalist Society, lectured on Darwin's theory of organic Creation (" Ueber Darwin's Theorie der organischen Schöpfung "), giving a very representative summary of this doctrine. He ended his paper with the prophecy that the task of future investigations of Nature will be not so much the solution of the question, why the cattle possesses horns but rather, how it got them.[221]

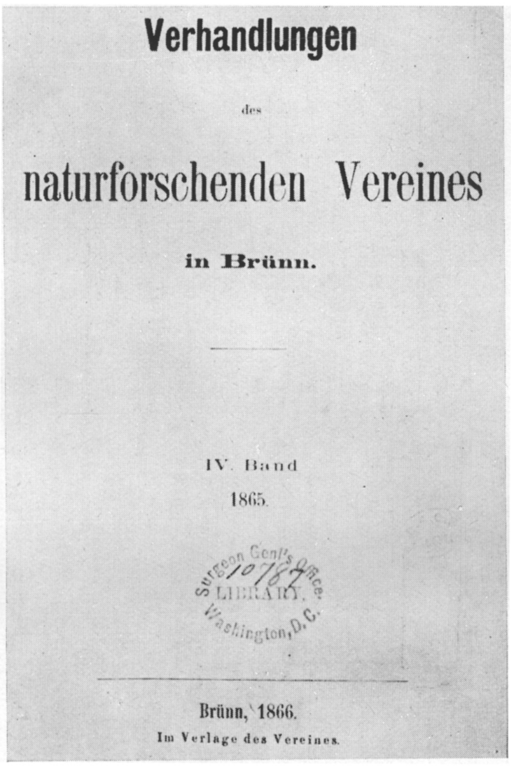

Fig. 23. Titlepage of vol. 4 of Verhandlungen des *naturforschenden Vereines in Brünn*

Pater Gregor conducted his crossings on a variety of peas which grew in a small spot, 35 meters long and 7 meters wide, called the garden. The selection of peas was a very fortunate one, because these garden peas were of seven varieties known to interbreed easily. They showed various easily recognizable structural features such as tall and dwarf, yellow or green seeds, round or wrinkled seeds, pairs of alternative characters. In his breeding experiments Mendel did not have any particular purpose. He had not to prove anything, neither the sexuality of plants, nor the fecundity of hybrids. Neither was he making his gardening for practical purposes, e. g., for improving the produce of peas for the monastic kitchen. His only guide and instigator was just plain curiosity in the ways of Nature. He was absolutely unbiased in his observations.

His method was the father of his success. It was his intention to carry out the experiments to such an extent and in such a way as to make possible the determination of the *number* of different hybrid forms which appear. He also arranged these forms with certainty according to their separate generations. Finally, he worked with correct statistical methods in order to discover the numerical relations of natural phenomena. He was not an " expert " neither a " scholar ", and his brilliancy of mind

[221] Makowsky A., " Die Aufgabe der zukünftigen Naturforschung sei beispielsweise nicht die, zu untersuchen, wozu das Rind seine Hörner habe, sondern wie es zu seinen Hörnern gekommen ". *Verh. Naturforsch. Ver. Brünn*, (1865) 1866, 5: 10-18.

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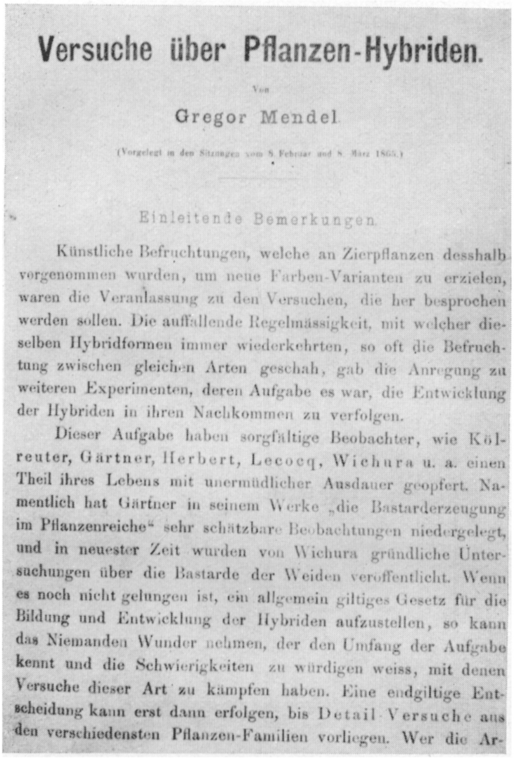
was not in his capacity of complicating things and analyzing previous results, but in his ability to simplify his experiments to a point where he had to deal with one or two variables at a time in the small garden that was his " laboratory ". Neither was it necessary for him to purchase elaborate equipments, to look into microscopes, or to have any other



Versuche über Pflanzen-Hybriden.

Von

Gregor Mendel

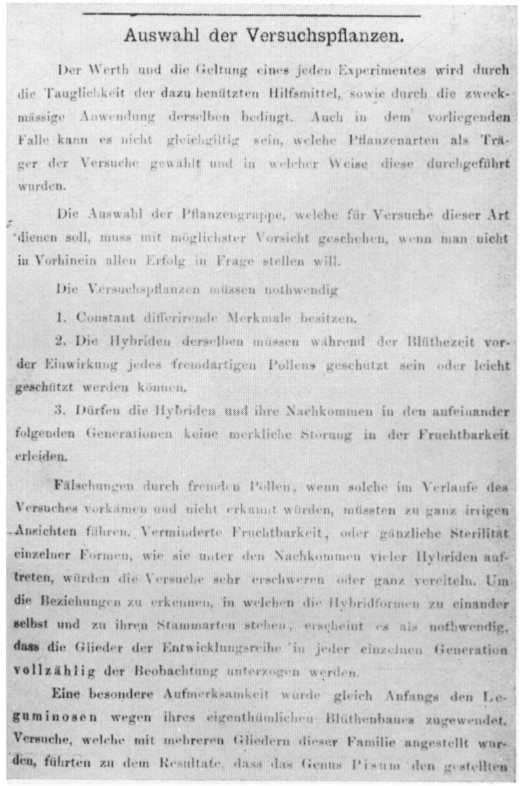
(Vorgelegt in den Sitzungen vom 8. Februar und 8. März 1865.)

Einleitende Bemerkungen.

Künstliche Befruchtungen, welche an Zierpflanzen desshalb vorgenommen wurden, um neue Farben-Varianten zu erzielen, waren die Veranlassung zu den Versuchen, die her besprochen werden sollen. Die auffallende Regelmässigkeit, mit welcher dieselben Hybridformen immer wiederkehrten, so oft die Befruchtung zwischen gleichen Arten geschah, gab die Anregung zu weiteren Experimenten, deren Aufgabe es war, die Entwicklung der Hybriden in ihren Nachkommen zu verfolgen.

Dieser Aufgabe haben sorgfältige Beobachter, wie Kölreuter, Gärtner, Herbert, Lecocq, Wichura u. a. einen Theil ihres Lebens mit unermüdlicher Ausdauer geopfert. Namentlich hat Gärtner in seinem Werke „die Bastarderzeugung im Pflanzenreiche" sehr schätzbare Beobachtungen niedergelegt, und in neuester Zeit wurden von Wichura gründliche Untersuchungen über die Bastarde der Weiden veröffentlicht. Wenn es noch nicht gelungen ist, ein allgemein giltiges Gesetz für die Bildung und Entwicklung der Hybriden aufzustellen, so kann das Niemanden Wunder nehmen, der den Umfang der Aufgabe kennt und die Schwierigkeiten zu würdigen weiss, mit denen Versuche dieser Art zu kämpfen haben. Eine endgiltige Entscheidung kann erst dann erfolgen, bis Detail-Versuche aus den verschiedensten Pflanzen-Familien vorliegen. Wer die Ar-

Fig. 24. Facsimile of Mendel's article " Versuche über Pflanzen-Hybriden " 1865-1866



Auswahl der Versuchspflanzen.

Der Werth und die Geltung eines jeden Experimentes wird durch die Tauglichkeit der dazu benützten Hilfsmittel, sowie durch die zweckmässige Anwendung derselben bedingt. Auch in dem vorliegenden Falle kann es nicht gleichgiltig sein, welche Pflanzenarten als Träger der Versuche gewählt und in welcher Weise diese durchgeführt wurden.

Die Auswahl der Pflanzengruppe, welche für Versuche dieser Art dienen soll, muss mit möglichster Vorsicht geschehen, wenn man nicht in Vorhinein allen Erfolg in Frage stellen will.

Die Versuchspflanzen müssen nothwendig

1. Constant differirende Merkmale besitzen.

2. Die Hybriden derselben müssen während der Blüthezeit vor der Einwirkung jedes fremdartigen Pollens geschützt sein oder leicht geschützt werden können.

3. Dürfen die Hybriden und ihre Nachkommen in den aufeinander folgenden Generationen keine merkliche Störung in der Fruchtbarkeit erleiden.

Fälschungen durch fremden Pollen, wenn solche im Verlaufe des Versuches vorkämen und nicht erkannt würden, müssten zu ganz irrigen Ansichten führen. Verminderte Fruchtbarkeit, oder gänzliche Sterilität einzelner Formen, wie sie unter den Nachkommen vieler Hybriden auftreten, würden die Versuche sehr erschweren oder ganz vereiteln. Um die Beziehungen zu erkennen, in welchen die Hybridformen zu einander selbst und zu ihren Stammarten stehen, erscheint es als nothwendig, dass die Glieder der Entwicklungsreihe in jeder einzelnen Generation vollzählig der Beobachtung unterzogen werden.

Eine besondere Aufmerksamkeit wurde gleich Anfangs den Leguminosen wegen ihres eigenthümlichen Blüthenbaues zugewendet. Versuche, welche mit mehreren Gliedern dieser Familie angestellt wurden, führten zu dem Resultate, dass das Genus Pisum den gestellten

Fig. 25. Text facsimile of Mendel's article (section on selection of plants)

refinement of modern research. But for correct interpretation of the laws of Nature it was important for him to have pedigreed strains of plants such as his garden peas which propagated by self-fertilization and inbreeding.

In observing the transmission of visible characters of the garden peas he did not list all characteristics of the organisms but concentrated upon the study of the sharply discernible qualities which occurred in pairs of opposites. (Such opposite pairs of hereditary characters are now called *allelomorphs* at the suggestion of Bateson in 1901). In his crossings Mendel never considered that he was crossing a whole individual against

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another whole; he was matching character against character only. Soon, he recognized that one member of the contrasting pair is usually more frequently seen in the succeeding generations than the other. One of the allelomorphs or alleles is *dominant*, while the other is a *recessive* character.

He found that 1) a character will not be blended in its transmission from generation to generation but it always returns in pure form of appearance (principle of *segregation* or *splitting*), and 2) that two or more such characters behave independently from each other so that they may reappear in independent combination in the next generation (principle of *independent assortment*). He considered the total appearance of an individual as a mosaic (*mosaicism*) of measurable elementary units; these units are constant and they are the unit *particles of heredity* (later called genes or hereditary factors). With his statistical method he formulated his law as follows:

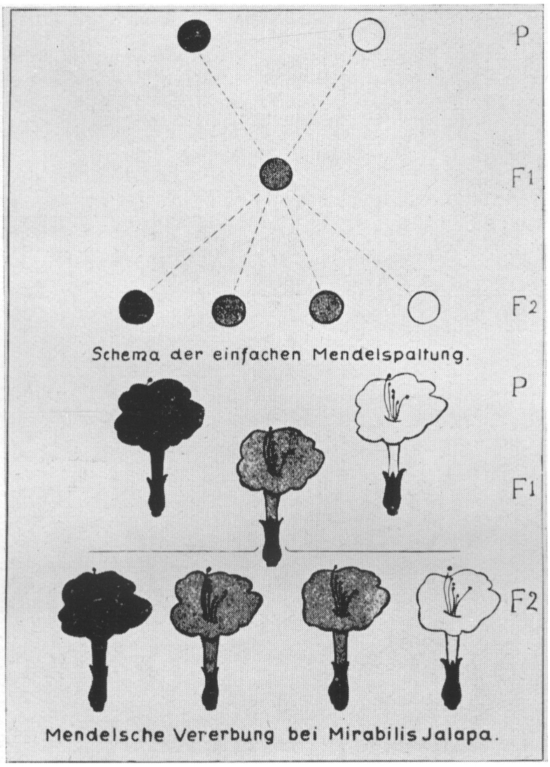

Fig. 26. Mendelism in Mirabilis jalapa

"When two varieties differing from each other in one characteristic are crossed, the hybrids preserve, for the most part, the peculiarity of one or the other parent, and do not exhibit a blend of the two. The persistent characteristic is the dominant, and the one disappearing is the recessive. When these two hybrids interbreed, the recessive appears in $^1/_4$, the dominant in $^3/_4$". It was later recognized that random of union makes this 3 : 1 *ratio* a matter of chance; the larger the number of offsprings in the second generation the closer comes the ratio of dominant: recessive to 3 : 1. Modern genetic research proved that this is the basic law of heredity. It also became manifest that many other apparent deviations from Mendel's law such as those seen in alternative and blending inheritance, or in the socalled multiple-factor inheritance and in various disturbances of the hereditary factors (e. g., crossing over) are still within the range of the Mendelian laws.

Mendel himself recognized that all fertilizations are of the same character and the phenomena (which we no call Mendelian) are really generally occurring in all union

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of sexual cells whether in plants or in animals, including man.[222] It is unfortunate that his ecclesiastical duties diverted him from the pursuit of his genetic studies. We can agree with Roberts[223] who, after a very detailed analysis of Mendel's publication, concluded with this statement: " Nothing in any wise approaching this masterpiece of investigation had ever appeared in the field of hybridization ".

III. MENDELIAN ERA

After the publication of Mendel's result with the hybridization of peas nothing happened. There were very few people who were interested in his paper even among the botanists, and those few, who saw it and read it, could not see in the paper anything of great importance. The world of biologists and physicians was kept busy with many other problems, theories and novelties. The discoveries of Pasteur, the publications of Darwin and Haeckel, the descriptions of the minute activities of the animal and plant cells, the ventures of Galton in measuring the English genius, the first steps in the advancement of microbiology, etc. – all were apt to push into the background the simple experiments of a little known monk with the simple peas in a small garden.[224]

For the easier outline of the developments on the field of heredity after 1865 we may divide the Mendelian Era into three parts: 1) the period from Mendel's publication to the rediscovery of the Mendelian laws in 1900; 2) the twentieth century which includes the birth of modern genetics and its further growth; 3) the genetic science under the political influence of totalitarianism.

Second half of the nineteenth century

The second half of the nineteenth century saw the coronation of the cellular theory, which was the insight into the cell division (mitosis; karyokinesis) and the studies of the cell nucleus. These studies revealed the existence of chromosomes and provided the investigators of heredity with a new material basis for objective research and speculation. Some of the outstanding events of this semicentury are as follow:

1858 Darwin's Origin of Species and the pangenetic theory

1874 Haeckel's perigenesis and the biogenetic law

1875 Fusion of cell nuclei in fertilization (O. Hertwig); the chromosomes (Strasburger and Fleming)

1883 constancy of chromosomes and reduction of chromosomes (Van Beneden)

1884 idioplasma (Naegeli)

[222] Another series of hybridization was carried out by Mendel on varieties of Hieracium. Cf. his Ueber einige aus künstlicher Befruchtung gewonnene Hieracium-Bastarden. *Verh. Naturforsch. Ver. Brünn*, 1869, 8.

[223] Roberts, cf. Footnote 45.

[224] As an occasional apology for the neglect of Mendel we also hear references to the lack of means of adequate promulgation of scientific thought in the 19th century. Hirschfeld believes that the advancement of Mendelism would have been different if Darwin or Haeckel had been given a reprint of Mendel's paper. Darwin never read it.

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1885 continuity of germ plasma (Weismann)
1887-88 foundation of experimental embryology (Roux)
1889 intracellular pangenesis (De Vries)
1897 law of ancestral heredity (Galton)
1899 artificial parthenogenesis (Loeb).

Fig. 27. Carl Wilhelm Naegeli, 1817-1891

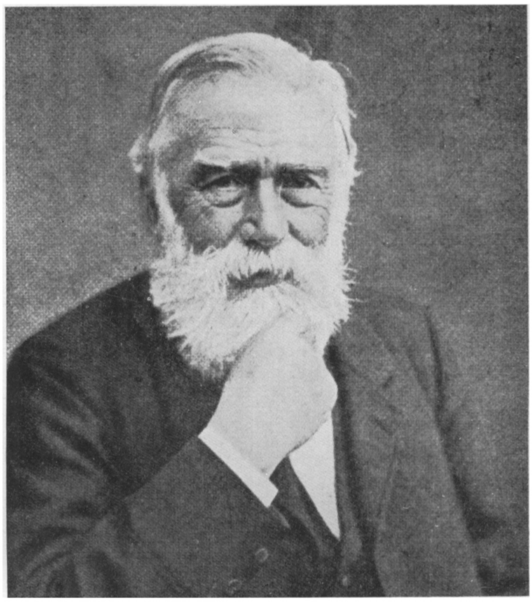

Fig. 28. Wilhelm Olbers Focke (died 1922)

There was one among the 19th century botanists with whom Mendel kept contact by means of correspondence. He was Carl Wilhelm Naegeli (1817-1891), who was the first to distinguish in the plasma of cells an *idioplasma*, composed of the finest parts, so-called micelles. He thought that the idioplasma is present in form of filaments which cross across the plasma of many cells, thereby forming an universal mesh work in the body. Nägeli published his book in 1884, the year of Mendel's death; yet, there is no place in the work where the monk's experiments on heredity are mentioned.[225]

Nägeli also studied hybridization, and with his experiments on Verbascum, Lobelia, etc., he wanted to settle the question of botany about species and variety. He read a paper about the rules of plant crossing and the general appearance of the hybrid with respect to parent. Though this paper was read at the München Academy of Sciences on 15 December 1865, i. e., 10 months after the presentation of Mendel's laws in Brünn,

[225] NAEGELI C. W., Mechanisch-physiologische Theorie der Abstammungslehre. Münch., 1884.

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it states that " facts are still lacking which are able to decide " mathematically how the descendants inherit from the parents.[226] On the field of human heredity, he speculated on the equivalence of the germ materials (1884), and stated that the characters of any parent can be transmitted by either sons or daughters to the third generation. This was

108 Leguminosae.

Ornithopus.

Lit.: P. Ascherson in Verh. Bot. Ver. Brandenb. VIII p. 118.

Zwischen cultivirtem *O. sativus Brot.* finden sich in Deutschland zuweilen einzelne Exemplare von *O. ebracteatus Brot.* und *O. compressus L.* eingemischt.

O. compressus × *sativus* ist vereinzelt zwischen *O. sativus* gefunden worden. Hülsen anscheinend unvollkommen ausgebildet.

Lathyrus.

Lit.: Darwin, Kreuz- und Selbstbefr. S. 144 ff.

Die Varietäten von *L. odoratus L.* sind in England (aber nach Delpino nicht in Italien) streng samenbeständig und kreuzen sich nicht ohne directes Zuthun des Menschen. Ch. Darwin benutzte zwei Farbenvarietäten: *purpureus* (Fahne röthlich purpurn, Flügel und Kiel violet) und *Painted Lady* (Fahne blasskirschroth, Flügel und Kiel fast weiss). Von *L. odoratus purpureus* ♀ × *Painted Lady* ♂ erhielt er aus derselben Hülse Pflanzen, die theils der einen, theils der andern Stammform sehr ähnlich waren. Die der *Painted Lady* gleichenden Blendlinge brachten indess im Spätsommer Blüthen, welche mit dunkelpurpurnen Flecken und Strichen gezeichnet waren. In späteren Generationen gingen aus diesen hybriden *Painted Lady's* verschiedene Pflanzen hervor, welche sich mehr oder minder der *var. purpureus* näherten. Die Mischlinge waren kräftiger und höher als die Stammraçen.

Pisum.

Lit.: Th. A. Knight in Philos. Trans. 1799, II p. 195; Trans. Hort. Soc. London V p. 379; Gärtner Bast. S. 316; Darwin Variiren I Cap. 9, 11; Kreuz- u. Selbstbefr. S. 151; G. Mendel in Verh. naturf. Ver. Brünn IV Abh. p. 3 ff.

Die ursprüngliche Heimath der Erbse und ihre wilde Stammform sind nicht bekannt. Man findet sie in einer grossen Zahl von Sorten oder Varietäten, von welchen indess zwei oder drei entschieden als die verbreitetsten und ausgezeichnetsten hervorgehoben werden können.

1. *P. sativum sphaerospermum* (*P. sativum L.*): Wuchs niedrig oder mittelhoch, Nebenblätter am Grunde weiss gezeichnet, Blüthen weiss, Samen kugelrund, rollend, gelblich.

2. *P. sativum arvense* (*P. arvense L.*): Wuchs hoch, Nebenblätter am Grunde roth gezeichnet; Fahne der Blüthen roth, Flügel purpurn. Samen gross, seitlich zusammengedrückt, fast von der Gestalt eines

Fig. 29. Facsimile from Focke's " Pflanzenmischlinge " with reference to Mendel

110 Leguminosae.

chen blassblau, die Flügel dunkelblau waren. Bestäubt mit Pollen von weissblühendem *sphaerospermum nanum* gab sie Mischlinge, deren Fahne und Schiffchen rosenroth, die Flügel dunkelviolet waren (Bastarderzeug., S. 316).

Knight und nach ihm viele andere Züchter haben durch Kreuzung der Erbsen zahlreiche neue streng samenbeständige Sorten erhalten. Es scheint, als ob die ältesten Sorten neuerdings nach 50 bis 60 und mehr Generationen anfangen, schwächer zu werden (Darwin a. a. O.). Mendel's zahlreiche Kreuzungen ergaben Resultate, die den Knight'schen ganz ähnlich waren, doch glaubte Mendel constante Zahlenverhältnisse zwischen den Typen der Mischlinge zu finden. Im Allgemeinen behalten die durch eine hybride Bestäubung erzeugten Samen auch bei den Erbsen genau die Gestalt und Farbe bei, welche der Mutterpflanze zukommt, auch wenn aus diesen Samen selbst Pflanzen hervorgehen, welche ganz der Vaterpflanze gleichen und welche dann auch deren Samen bringen. Es werden indess von Erbsen auch Beispiele angeführt, in denen die durch Kreuzbefruchtung erzielten Erbsen selbst eine der pollengebenden Sorte entsprechende Färbung gezeigt haben sollen. Vgl. darüber im letzten Abschnitte die Xenien.

Hardenbergia.

Ueber einen angeblichen Bastard vgl. Illustr. hort. t. 179.

Erythrina.

Lit.: W. Herbert in Journ. Hort. Soc. II, p. 102; Illustr. hortic. 291.

E. herbacea L. treibt aus der Grundachse Blüthenstände und sterile Laubtriebe, während bei *E. crista galli L.* die Blüthenstände aus Achseln der Laubblätter an kräftigen Stengeln hervorbrechen.

E. herbacea ♀ × *crista galli* ♂, von M'Leay oder von Bidwill erzogen, ist ein schöner Bastard, *E. Bidwilli* genannt, der achselständige Blüthenstände hat, wie *E. crista galli*, im Uebrigen aber zwischen den Stammarten die Mitte hält. — Später zog Bellanger in Tours eine *E. crista galli* ♀ × *herbacea* ♂, die *E. Bellangeri* genannt wurde, jedoch mit *E.* × *Bidwilli* vollkommen übereinstimmen soll. Durch Befruchtung der *E.* × *Bellangeri* mit Pollen von *E. crista galli* wurden drei Sorten erhalten: *Marie Bellanger, hybr. ruberrima, hybr. floribunda.*

Fig. 30. The same (another page)

speculation, however, and the theory needed coordination with the cytological discoveries of the period.

Several other botanists and plant hybridizers after Mendel are known who observed, on their experimental plants (willow trees, ornamental plants, peas, etc.), one or the

[226] — Ueber den Einfluss der äusseren Verhältnisse auf die Varietätenbildung im Pflanzenreich. *Bot. Mitt.*, 1865, 2: 103-58.

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other Mendelian phenomenon. They also helped in the clarification of the sexual life of plants, and of the concept of species. They are Max Ernest Wichura (1817-1866), Regierungsrat in Breslau; B. Verlot (1865); Thomas Laxton (1866); Hermann Hoffman, professor of botany at Giessen University, who is one of the few to mention Mendel in his work on species;[227] G. W. McCluer (1892); W. J. Spillman who started his wheat crosses in 1899.

Phaseolus. 111

Phaseolus.

Lit.: Ch. Fermond in Bull. soc. bot. Fr. II p. 748—752; Darwin in Garden. Chron. 1858 p. 829; Kreuz- u. Selbstbefr. S. 144; H. Hoffmann Bot. Ztg. 1874 Sp. 273 ff.; G. Mendel in Verh. naturf. Ver. Brünn IV Abh. p. 32; Fr. Körnicke in Verh. Naturh. Ver. Rheinl. 1876 Sitzgsb. 47:

Man cultivirt in Europa im Grossen zwei Arten: *Ph. multiflorus Lam.* und *Ph. vulgaris L.*, letztere in zahlreichen Varietäten. Nach der Gestalt der Samen und der Höhe des Wuchses (windend oder niedrig) werden die Hauptragen unterschieden; manche Autoren betrachten die Form *Ph. nanus L.* mit nicht windendem Stengel und wenig zusammengedrückten Samen als besondere Art.

Ph. multiflorus Lam. Nach Ch. Darwin's Versuchen wird diese Art gewöhnlich durch Insecten befruchtet; vielleicht verdanken auch die sparsam unter Bedeckung gebildeten Früchte ihre Entstehung nur den Thrips. H. Hoffmann glaubt allerdings auch bei dieser Art an Selbstbefruchtung, doch sind seine Versuche nicht ganz überzeugend.

Ph. multiflorus flor. coccineis × flor. albis. Die gewöhnliche Form von *Ph. multiflorus* hat scharlachrothe Blüthen und dunkle bunte Samen, die weissblüthige rein weisse Blüthen und Samen. Beide Sorten sind bei Isolirung samenbeständig. Ch. Fermond pflanzte die beiden Sorten neben einander; er erhielt aus einigen der geernteten bunten Samen die weisse Form, aus einigen der weissen die rothblühende, dunkelsamige. Mittelformen entstanden nicht; man cultivirt indess auch eine Sorte mit bunten (weiss und rothen) Blüthen, *var. bicolor*, die übrigens kein Gartenmischling ist, sondern aus Brasilien eingeführt sein soll.

Ph. vulgaris L. var. nanus L. ♀ × *multiflorus Lam. fl. coccin.* ♂ ist von G. Mendel künstlich erzeugt worden. *Ph. nanus* ist niedrig, hat weisse Blumen und weisse kleine Samen, *Ph. multiflorus* ist hochwüchsig, windend, hat rothe Blumen und bunte (schwarz und roth) Samen. Die Bastardpflanzen, 17 Exemplare, glichen im Allgemeinen mehr der väterlichen Stammart, dem *Ph. multiflorus*, doch waren die Blüthen blasser roth. Die Fruchtbarkeit war ziemlich gering; es wurden von den 17 Pflanzen 49 Samen erhalten, von welchen im folgenden Jahre 31 zur Blüthe gelangende Exemplare erhalten wurden. Eins derselben brachte weisse Blumen und weisse Samen, bei den andern schwankte die Blüthenfarbe zwischen roth und blassviolet; die Samenfarbe war eben so variàbel. Die Fruchtbarkeit war sehr ungleich, aber bei allen mangelhaft; die rothblühenden Exemplare waren durchschnittlich am wenigsten fruchtbar. Die Fruchtbarkeit zeigte sich

Fig. 31. The same (another reference)

Wilhelm Olbers Focke (died 1922) was also a hybridist of the old school. His work "Pflanzenmischlinge" was published in 1881 (Berl., p. 569). I mention it only because it contains 15 references to Mendel's name. He was not able to evaluate the importance of Mendel's experiments, but his references to Gregor Mendel prove that the father of genetics did not impress his contemporaries, nor were these able to comprehend the clarity of his reasoning and the accuracy of his conclusions.

The developments of the *cell theory* came chiefly after 1870. The advancements on this field can be grouped into two periods: 1) the first created our present knowledge of ripening and fecundation of the ovum and the karyokinesis on the basis of microscopic observation (Schneider 1873; Bütschli 1873-74; Auerbach 1874; Strasburger 1876; Hertwig 1875; van Beneden 1875 and Fol 1879); 2) the other is marked by the detection of suitable experimental objects (salamander larva, eggs of Ascaris megalocephala) which enabled the investigators to make a more detailed study of the finest movements of the nucleus in karyokinesis, in gametocytogenesis, and in fecundation (Flemming 1879-82; Strasburger 1883 in botany; van Beneden 1884; Nussbaum 1884). Together with the microscopical studies, there were attempts made for the utilization of the new details to the solution of the problem of heredity.

[227] Hoffman H., Untersuchungen zur Bestimmung des Wertes von Species und Varietät. Giessen, 1869. – With reference to Mendel.

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The fecundation by the spermatozoon was evident from the experiments of Spallanzani in the 18th century. Yet, the mechanism of fecundation was not known until 1875. It was Oscar Hertwig (1849-1922) who proposed his fecundation theory in this year, and thereby put the investigations of heredity upon a new basis. In his research

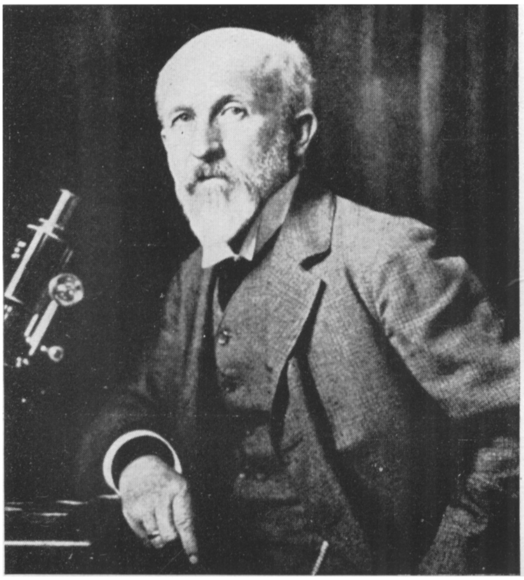

Fig. 32. Oskar Hertwig, 1849-1922

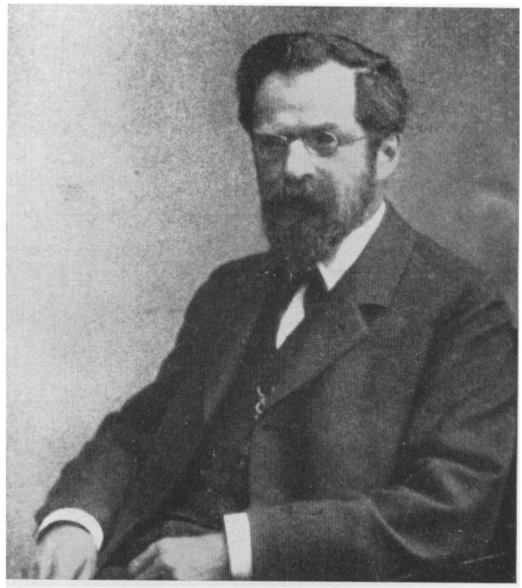

Fig. 33. Carl Rabl, 1853-1917

he proved that only one spermatozoon fecundates; that fecundation is a fusion of the nuclei of ovum and spermatocyte; that not the protoplasma but the nuclear substances are the fecundating elements; that the nuclear substance acts as a formed, organized element. Since the fecundation also transfers the paternal characters to the ovum, he concluded that the nuclear substances are also the *carriers of hereditary characters* which go from parents to the offspring. He declared also that it is very probable that the nuclein (chromatin) is both the fertilizer and the transmitter of heredity, and as such it is identical with Nägeli's idioplasma. [228]

He was in constant discussion with other cytologists and their hypotheses on morphology and physiology of the cell. By his studies on the chemical environment of the egg and artificial hybridization of the ovum, he prepared the way to Loeb's experiments on artificial fecundation and parthenogenesis (1899). In 1890 he disproved the theory of Van Beneden which this cytologist proposed for the explanation of the reduction

[228] HERTWIG O., Das Problem der Befruchtung und der Isotropie des Eies; eine Theorie der Vererbung (1884).

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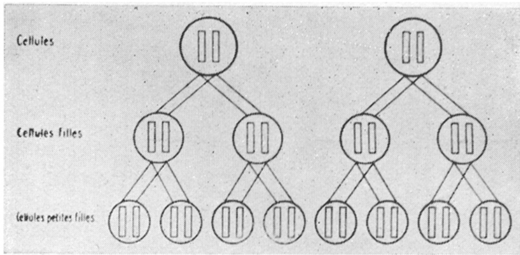
of chromosomes (during the ripening of the germ cells) which he discovered in 1883. Van Beneden believed that every cell is a hermaphrodite. Hertwig showed that there is no sex difference in the nuclei of the germ cells; the nuclei are not in a sexual contrast with each other, yet one carries the hereditary characters of the maternal, the other

Fig. 34. Theodor Boveri, 1862-1915



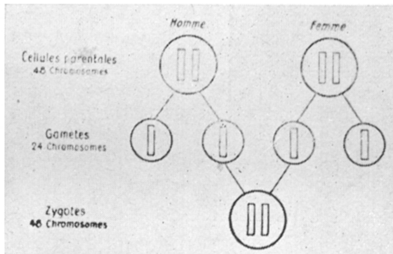


Fig. 35. Schematic illustration to show difference in mitosis and meiosis (modern)

those of the paternal organism. (It took more years to discover the true cause of sex inheritance).

Walter Flemming (1843-1915) described the splitting of the chromosomes of the cell nucleus during karyokinesis (1879) (They were named chromosomes a few years later by Waldeyer). He saw that they split lengthwise, and one set goes into each of the daughter cells. Already in 1882 he saw that there is some numerical regularity in the chromosomes. It was however Karl Rabl (1853-1917) who in 1884 discovered that the number of chromosomes, which in the same year Oscar Hertwig announced the carriers of heredity, is fixed in each species. He published this observation in 1885, and it took many years until its accuracy had been generally proven.

In the same year, Rabl also expressed the concept of the continuity or individuality of chromosomes, or persistence of chromosomes. There is a priority dispute whether

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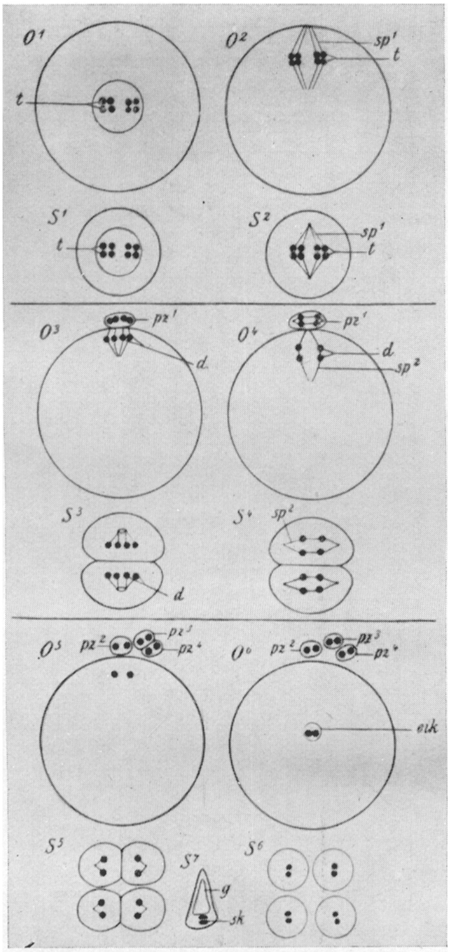

Fig. 36. Schema of O. Hertwig to show steps of oogenesis and spermatogenesis

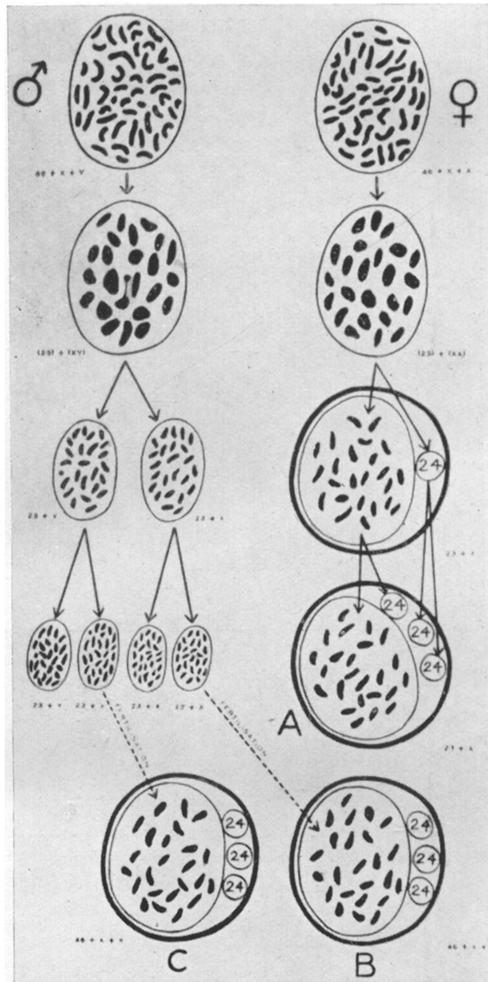

Fig. 37. Modern schema to show human oogenesis and spermatogenesis

this hypothesis originated from Rabl, or Van Beneden or Theodor Boveri (1862-1915).

There were further studies continued on the genesis of the ovum (*oogenesis*) by Schneider (1883), Nussbaum (1883)[229] and van Beneden (1884). Moritz Nussbaum (1850-1915) also emphasized the genetic continuity of the germ cells from generation to generation. He believed that the germ cells of the next generation separate themselves very early (in the course of the cell-division of the ovum) from the cell material,

[229] Nussbaum M., Ueber Befruchtung. *Sitzber. Niederrhein. Ges. Natur. Heilk.*, 1883.

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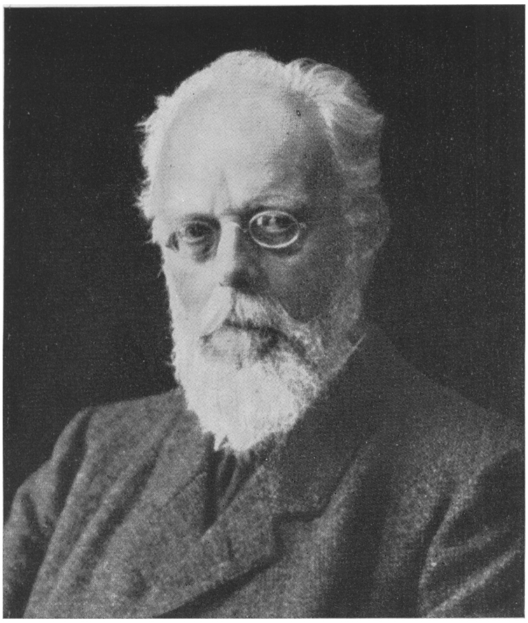

Fig. 38. August Weismann, 1834-1914

and from that point on the " accounts of the individual and of the species are completely separated ".[230] With such statements he prepared the ground for Weismann who, on cytological evidence, challenged the doctrine of lamarckism (i. e., the heredity of acquired characters).

Edouard Van Beneden (1845-1910), of Liège, made various important observations in the life of cells. He discovered the so-called *reduction process* in the course of the divisions of the ovum (1884). He showed that the nuclei of the ovum and of the spermatozoon have only one half of the chromosomes which, according to the constancy of chromosome number, could be expected. For the explanation of reduction he suggested that the cell is hermaphrodite. Weismann suggested a theory of the reduction of ancestral plasma, while the correct assumption was that the reduction of chromosome number in the germ cells is a device to prevent the accumulation of hereditary characters. In the same year (1884) Julin published his studies on spermatogenesis, the evolution of the male germ cell, in which similar reduction of chromosome numbers takes place.

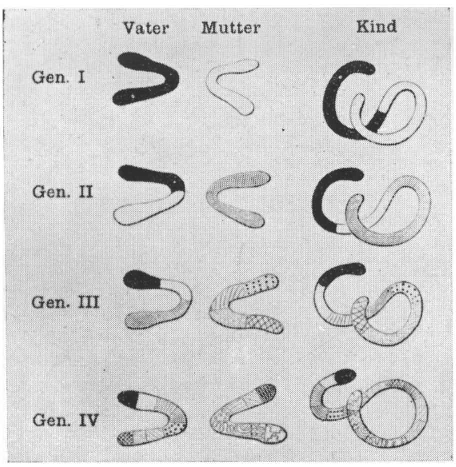

Fig. 39. Weismann's ancestral plasma and its mixture in generations

These morphological and physiological studies of the germ cells prepared the way for August Weismann (1834-1914) who took over the theory of Nägeli's idioplasma and further developed it (1885). He also accepted certain views of the botanist Eduard Strasburger (1844-1912) about ancestral generations. According to his conception, the idioplasma of the 4th generation is composed of 16 ancestral plasmas (" Ahnenplasma "); the 10th generation's idio-

[230] — Ueber die Veränderungen der Geschlechtsprodukte bis zur Eifurchung; ein Beitrag zur Lehre der Vererbung. *Arch. mikr. Anat.*, 1884, 23:

https://doi.org/10.1017/S1120962300027098 Published online by Cambridge University Press

plasma has 1024 different ancestral plasmas; the *n*-th has n^2. Finally a point is reached where further fragmentation is impossible because we reach indivisible units. The ancestral plasma (which is also called ID) was supposed to be a system of numerous subordinate hereditary atoms, the *determinants* and the *biophores*, which Weismann worked into a special " Keimplasma " architecture.[231] (The theory has very close relation with various general problems of heredity such as preformation and epigenesis, Mendelian laws, etc.). He considered that the germ plasma is only in the germ cells, while the " Kernplasma " of the rest of the body cells contains only fragments of the true idioplasma. Accordingly, he accepted two forms of cell division; 1) hereditary or integral, and 2) non-hereditary or differential. By the continuity of the germ plasm an individual becomes immortal. His theory rejected the idea that bodily characteristics are hereditary. This was a very serious attack upon the growing army of darwinists and lamarckists.

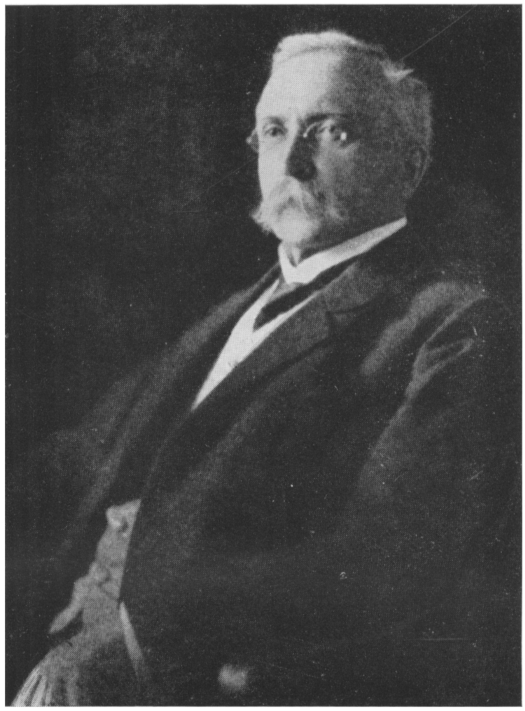

Fig. 40. Wilhelm Roux, 1850-1924

Weismann found a supporter in Wilhelm Roux (1850-1924), the founder of developmental mechanics. In his work on " *Entwicklungsmechanik* " (1885) he suggested that the two main principles of ontogenesis are 1) the true reproduction of the many parts of the body, and 2) influences of changes by evolution. His experiments with halving the egg of frog and thereby producing half an embryo convinced him that all parts of the egg are necessary for the development of a full animal. This made him to agree with Weismann's hypothesis. Others disagreed. Herbert Spencer attacked him (1893); so did Brown-Séquard who criticized the theory on the basis of heredopathological facts (1892).

The theory of *evolution* touches on the problems of genetics for two reasons: 1) because it assumes that the species is not fixed but it changes under environmental effects, 2) because it believes in the heredity of the acquired characters. The idea of evolution in its present form is the creation of the nobleman Lamarck. Charles Darwin (1809-1882), in his *Origin of Species* (1859) and in an earlier (1858) letter to the Lin-

[231] Weismann A., Das Keimplasma. 1892.

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nean Society of London, outlined his system (*Darwinism*) in which he still considered the same acquired characters and their heredity as proposed by Lamarck, but he put more stress upon the accidental variants which are in his view multiplied and fixed by *natural selection*. He erred however when he believed that such a selection by Nature

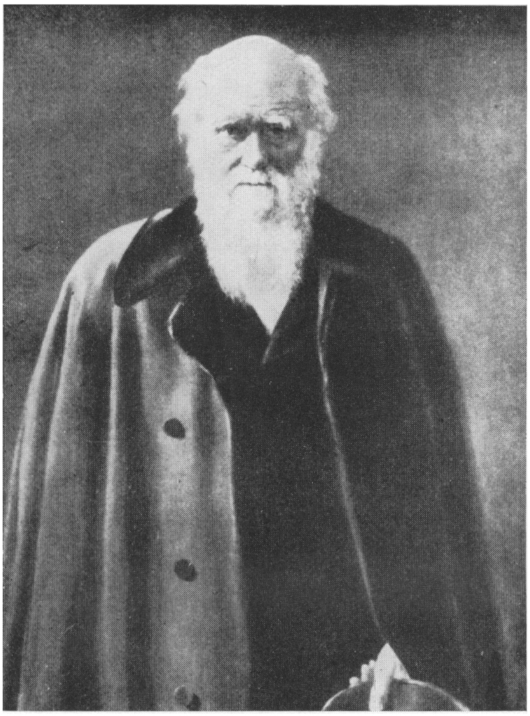

Fig. 41. Charles Darwin, 1809-1882

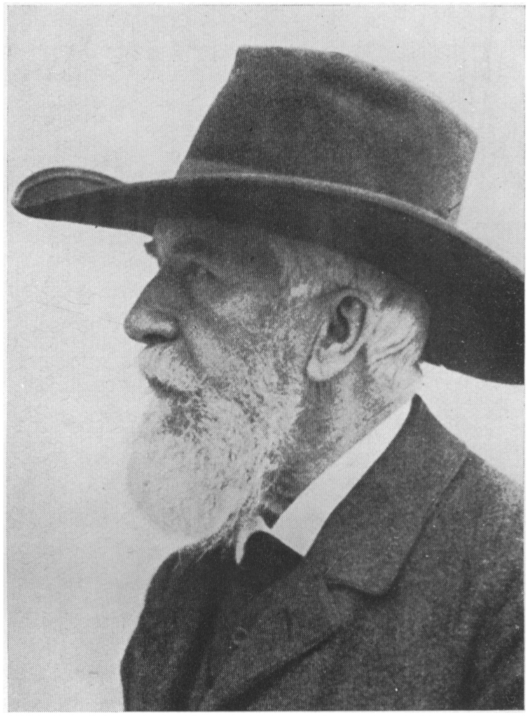

Fig. 42. Ernst Haeckel, 1834-1919

(which is guided by the *struggle for existence*) is of as much value as the skilled work of a human breeder of plants and animals. How could he accept an idea that natural selection would be able to make a *constant* species from variations when it is the experience of human breeders that, after their efforts had ceased, the variations again return to the original ancestral form?! Darwin also proposed the theory that moleculoid particles (*gemmulae*) are given off by the cells and these particles finally congregate in the germ cells which are influenced in their development so that they will reproduce the parental organism. [232]

[232] DARWIN C., The effects of cross and self fertilisation in the vegetable kingdom (N. Y. ,1892) refers to his own hybridization experiments, also to those with the common pea (Pisum sativum). In this part he remembers of Andrew Knight, and Mr Laxton too, but he does not mention Mendel.

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Ernst Haeckel (1834-1919), who in his recapitulation theory suggested that the individual's development is a short abstract of the development of Life (" biogenetic law "?) did write much about heredity though he was the founder of evolutionary embryology. What he wrote however, is in a chaos, and hard to understand. His hypothesis is that of the wave-production of the life particles, or the *perigenesis* of the plastidule (molecules). Heredity transmits not only the chemical qualities of the plasma of each cell but also the specific form of molecular motion which is active in it. He further developed Darwin's evolution or descendence theory.[233]

There was another man in the 19th century who, as Mendel, used mathematics and statistical methods in the study of heredity and variation. He was Sir Francis Galton (1822-1911) who happened to be born in the same year as Gregor Mendel. He was a cousin of Charles Darwin. He became interested in human heredity and, with mathema-

Fig. 43. Haeckel's pedigree of vertebrates and man (1866)

[233] HAECKEL E., Anthropogenie. 1874.

https://doi.org/10.1017/S1120962300027098 Published online by Cambridge University Press

tical methods for the measurement of the degree of resemblance, he tried to draw conclusions as to the share of each parent in heredity. His material of observation was, however, unfortunately selected, because the color of Basset hounds, the stature of man, and the color of *Papaver* show a complex form of inheritance. Nevertheless, between 1865 and 1900, until the rediscovery of Mendelism, his was the most accurate attempt at developing laws of heredity on a mathematical basis. He recognized particulate inheritance because he thought that eye color always comes from one single parent. He also was aware of the existence of latent characters.[234] His paper on heredity of twins (1875) is one of the earliest of modern twin research. He also suggested that heredity must be studied on huge populations, entire nations so that, on the basis of the law of probabilities, predictions could be made. His critics say that his mind was along mathematical lines, and his writings have only the shine of exactness. Yet, his results are only statistical statements and not genetic analysis. This does not detract from his value, however.

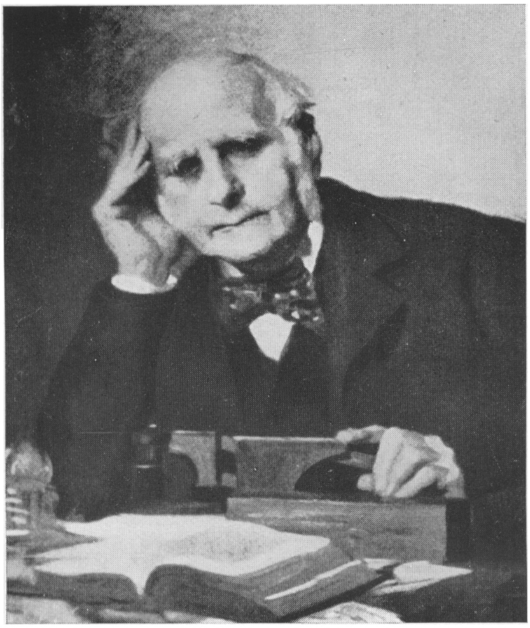

Fig. 44. Sir Francis Galton
1822-1911

In 1897 he formulated his *law of ancestral heredity:* " Two parents contribute between them an average, one half or 0.5 of the total heritage of the offspring; the four grandparents, one quarter or 0.5^2; the eight great-grand-parents one-eighth or 0.5^3, etc. which being equal to 1, accounts for the whole heritage ". He was active in organization of genetic research. In 1905 he left his wealth for an academic chair to teach eugenics at London University. In 1908 he founded the Eugenics Education Society. He was a physician, and is generally honored as the father of eugenics. His work was continued by Karl Pearson (1857-1936) whose merit is the foundation of the correlation theory in biometrics.

The progress in morphology and biology of the cell, and the increasing interest in heredity and evolution was also a great stimulus to clinical studies. The range of investigations widened and Richet, French physiologist, proposed a questionnaire for the study of " psychologic inheritance " (1884).[235] It was questioned whether virtues,

[234] Galton F., Hereditary genius, 1869. – Also: Natural inheritance, 1889.
[235] Richet C., *Bull. Soc. anthrop.*, 1884, 3. ser., 7: 734-40.

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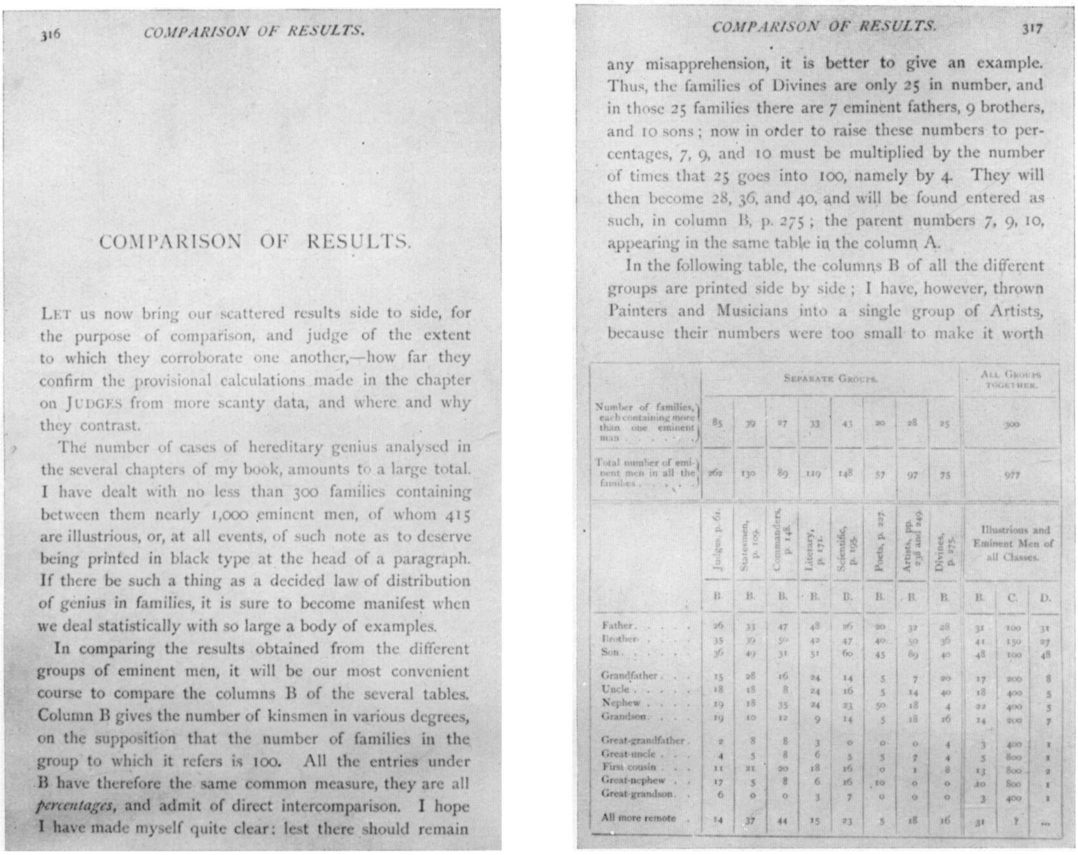

316 *COMPARISON OF RESULTS.*

COMPARISON OF RESULTS.

LET us now bring our scattered results side to side, for the purpose of comparison, and judge of the extent to which they corroborate one another,—how far they confirm the provisional calculations made in the chapter on JUDGES from more scanty data, and where and why they contrast.

The number of cases of hereditary genius analysed in the several chapters of my book, amounts to a large total. I have dealt with no less than 300 families containing between them nearly 1,000 eminent men, of whom 415 are illustrious, or, at all events, of such note as to deserve being printed in black type at the head of a paragraph. If there be such a thing as a decided law of distribution of genius in families, it is sure to become manifest when we deal statistically with so large a body of examples.

In comparing the results obtained from the different groups of eminent men, it will be our most convenient course to compare the columns B of the several tables. Column B gives the number of kinsmen in various degrees, on the supposition that the number of families in the group to which it refers is 100. All the entries under B have therefore the same common measure, they are all *percentages*, and admit of direct intercomparison. I hope I have made myself quite clear: lest there should remain

COMPARISON OF RESULTS. 317

any misapprehension, it is better to give an example. Thus, the families of Divines are only 25 in number, and in those 25 families there are 7 eminent fathers, 9 brothers, and 10 sons; now in order to raise these numbers to percentages, 7, 9, and 10 must be multiplied by the number of times that 25 goes into 100, namely by 4. They will then become 28, 36, and 40, and will be found entered as such, in column B, p. 275; the parent numbers 7, 9, 10, appearing in the same table in the column A.

In the following table, the columns B of all the different groups are printed side by side; I have, however, thrown Painters and Musicians into a single group of Artists, because their numbers were too small to make it worth

	SEPARATE GROUPS.								ALL GROUPS TOGETHER.		
Number of families, each containing more than one eminent man	85	39	27	33	43	20	28	25	300		
Total number of eminent men in all the families	262	130	89	119	148	57	97	75	977		
	Judges, p. 61.	Statesmen, p. 109.	Commanders, p. 148.	Literary, p. 171.	Scientific, p. 195.	Poets, p. 227.	Artists, pp. 238 and 249.	Divines, p. 275.	Illustrious and Eminent Men of all Classes.		
	B.	B.	B.	B.	B.	B.	B.	B.	B.	C.	D.
Father	26	33	47	48	26	20	32	28	31	100	31
Brother	35	39	50	42	47	40	50	36	41	150	27
Son	36	49	31	51	60	45	89	40	48	100	48
Grandfather	15	28	16	24	14	5	7	20	17	200	8
Uncle	18	18	8	24	16	5	14	40	18	400	5
Nephew	19	18	35	24	23	50	18	4	22	400	5
Grandson	19	10	12	9	14	5	18	16	14	200	7
Great-grandfather	2	8	8	3	0	0	0	4	3	400	1
Great-uncle	4	5	8	6	5	5	7	4	5	800	1
First cousin	11	21	20	18	16	0	1	8	13	800	2
Great-nephew	17	5	8	6	16	10	0	0	10	800	1
Great-grandson	6	0	0	3	7	0	0	0	3	400	1
All more remote	14	37	44	15	23	5	18	16	31	?	...

Fig. 45. Double page from Galton's Hereditary genius (1869)

vices, and habits are also transmitted from parents to descendants. Partly under the influence of Mantegazza, Lombroso and of the French and Italian school of criminologists, serial studies were made in mental asylums toward the end of the 19th century. Among the heritable psychopathic characters were mentioned feeblemindedness, viciousness in children (Baer 1897), alcoholism, and a number of mental diseases.

In heredopathology the topic of continued controversy remained the heredity of mutilations and other injuries. There were always a few who could detect one or another case to prove the inheritance of mutilations. Rath (1893) made critical study of such cases. Zacharias (1888) and Weismann himself (1888) [236] also contributed their

[236] WEISMANN, Ueber die Hypothese einer Vererbung von Verletzungen. *Tagebl. Versamml. deut. Naturforsch.* (1888) 1889, 61: pt. 2, 45-57.

https://doi.org/10.1017/S1120962300027098 Published online by Cambridge University Press

own theories. Orshanski wrote a series of papers to the St. Peterburg Academy of Sciences in which he revealed his findings from the study of unhealthy families (1891-99).

In my opinion the most outstanding heredopathologists of this period were C. E. Brown-Séquard and J. Hutchinson. Brown-Séquard studied the hereditary transmission of certain injuries to the nervous system (1875), also the inheritance of certain eye changes in rabbits (1880), while Hutchinson discussed the "laws" of heredity in relation to disease (1881) and described retinitis pigmentosa and allied affections to show the operation of these laws.[237]

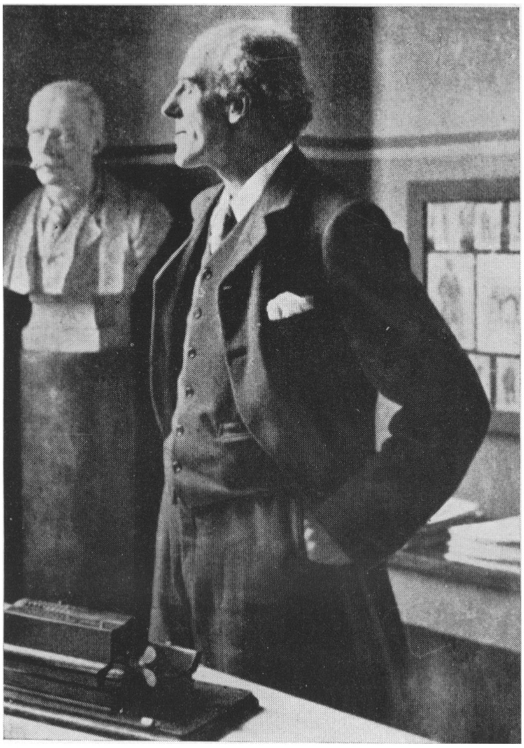

Fig. 46. Karl Pearson, 1857-1936

Paget suggested the hereditary transmission of tendencies to cancerous and other tumors (1857). Others discussed the inheritance of stiff knee-joint (Clark 1857), cleft palate (Jamieson 1880), hypospadias by indirect atavismus (Lingard 1884), disposition to liver diseases (Marmisse 1862), transmission of microphthalmus with irideremia and nystagmus (Page 1874). It was thought by Sedgwick (1861-63) that some of these diseases may be limited to, or linked with, sex.[238]

Twentieth century

The foundation of modern genetics needed many centuries to build. Its development on that foundation is entirely the merit of the twentieth century. During the fifty years which we had already passed, the science of heredity became a huge palace, with many rooms in many separate wings, in which whoever enters needs a special guide and a special language for easy orientation. A bird's eye-view of this proud palace is only of the external shape and surface, and it cannot penetrate into the depth. A short list of the outstanding events and important steps in the development of modern genetics is as follow:

[237] Cf. his article in *Arch. Surg.*, Lond., 1895, 6: 125-30. Also *Ophth. Rev.*, Lond., 1881-82, 1: p. 2; passim.

[238] Sedgwick W., On sexual limitation in hereditary system. *Brit. Med. Chir. Rev.*, 1861, 27: 477. See also Ibid., 1863, 31: 445.

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1900 rediscovery of Mendelism
1901 mutation theory (De Vries)
1902 sex chromosome (MacClung)
1903 research on pure lines, phenotype-genotype (Johannsen)
1905 immunogenetics (Biffen)
1906 crossing-over (Bateson, Punnett)
1910 Drosophila studies and chromosomic theory of heredity (Morgan)
1913 chromosome maps
1917 physiological genetics (Goldschmidt)
1925 position effect (Sturtevant)
1927 cytoplasmic genetics (Wettstein); x-ray mutations (Muller)
1932-34 giant salivary-gland chromosomes (Painter).

REDISCOVERY OF MENDELISM. It was in 1900, sixteen years after the death of Mendel, that three botanists, working independently and experimenting with plant crossings, discovered the laws of inheritance, the character-pairs and their splitting in subsequent generations. Before writing and publishing their papers, however, they came across Mendel's article of 1865, and each of them recognized that not only their findings but also their conclusions are identical with the principles of inheritance first announced by Gregor Mendel. The three botanists worked in three different countries: Hugo de Vries (1848-1935) in Belgium, Carl Correns (1864-1933) in Germany, and Erich von Tschermak-Seysseneg (1871) in Austria. Their papers were published in the course of 1900 in the same 18th volume of the reports of the German Botanical Society.[239, 240, 241]

The confirmation of Mendel's findings and the restatement of his laws opened a new era in research which was based upon the recognition that heredity is a natural phenomenon, open to examination by reliable methods of science, and it is not a mystery for speculation but a biological process that follows the simple rules of Nature.

The experiments of De Vries with hybrids started in 1894. His plant was the *Oenothera lamarckiana.* He found that in 1895 the second generation of this plant showed splitting of characters, and after these experiments he found a work of Bailey on plant breeding (1895) in which Mendel's paper was also listed among the references. De Vries read Mendel's paper, then he wrote his own which appeared both in German and French.[242] Though in his own German paper De Vries referred to Mendel in a footnote only, later in the same year (21 Nov. 1900) he published another article in the organ of the German Botanical Society[243] in which he attributed the law of segregation

[239] De Vries H., Das Spaltungsgesetz der Bastarde. *Ber. Deut. bot. Ges.*, 1900, 18: 83-90 (14 March).

[240] Correns C. G., Mendel's Regel über das Verhalten der Nachkommenschaft der Rassenbastarde. *Ibid.*, 158-168 (22 Apr.).

[241] Tschermak E., Ueber künstliche Kreuzung bei Pisum sativum. *Ibid.*, 232-9 (received June 2).

[242] For the German article see Footnote 239. The French was published on 26 March in *C. rend. Acad. sc.*, Par., 1900, 130: 845-7.

[243] De Vries, Erbungleiche Kreuzungen. *Ber. Deut. bot. Ges.*, 1900, 18: 435-43.

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to Mendel, with the remark that this law has general applicability to the entire kingdom of plants.

The name of De Vries is also memorable for his theory of *intracellular pangenesis* (1899). This was a modification of the Darwinian pangenetic theory, and assumed

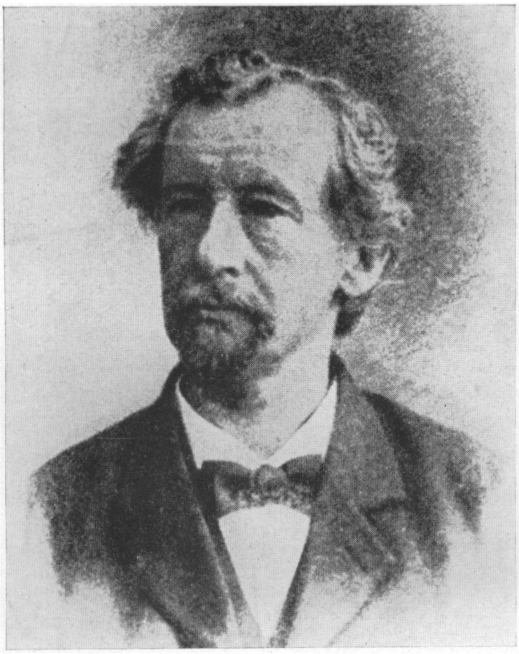

Fig. 47. Hugo de Vries, 1848-1935

Fig. 48. Carl Correns, 1864-1933

that the gemmulae or pangens, instead of wandering through the entire organism, are present in each cell, and each pangen is the material substrate of a hereditary tendency. The main principle of this assumption is that the hereditary characters are units. The pangenetic theory led De Vries 1) to the theory of the origin of species by means of *mutations* and 2) to his hybridization experiments which were able to show the recombination of hereditary units. Under mutation he understood any hereditary variation or sudden unexplained change in a filial generation. Sudden changes in type had been observed by many, not only among the plants of experimental stations but also among domestic animals. A change always seems anti-hereditary. Such changes are recognized as mere variations under the influence of environment, or as a reappearance and recombination of genetic factors. But some of the changes are inexplicable with our present knowledge; these are called *mutations*.

Carl Correns, professor of botany at Tübingen, began his genetic research in 1891.

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He experimented with hybridization of corn and pea races. He found the basic principles of heredity sometimes in October 1899, and a few weeks later he read the article of Mendel. In April, 1900, a reprint of De Vries' article reached him, which encouraged him to put his own observations into print. He did know of Mendel, however, both

Fig. 49. Erich von Tschermak-Seysseneg, 1871

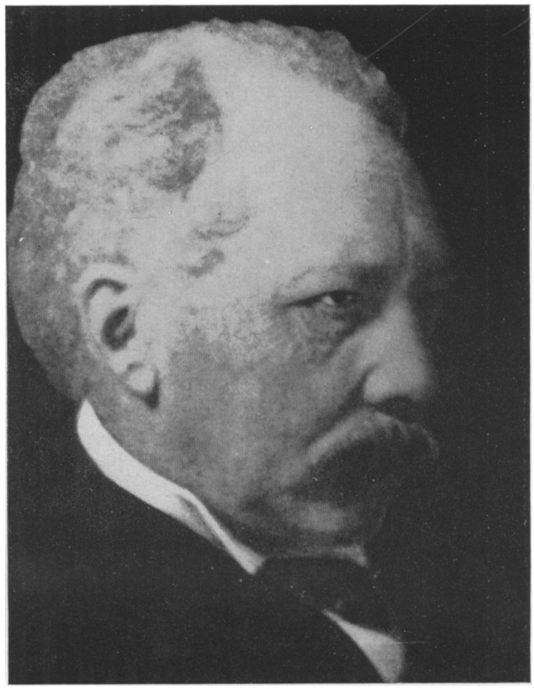

Fig. 50. William Bateson, 1861-1926

from Nägeli and from the book of Focke. Correns was the first who thoroughly understood the basic nature of Mendel's experiments and he called the principles of heredity the Law of Mendel (1900). But he was also the first who discovered that many character pairs might not follow the law of dominance, and the law of segregation might not be of universal value. Tschermak was at the beginning of his career at this time. His interest in horticulture and a lecturing tour in Germany secured him a position at the Agricultural College in Wien where he became assistant of Prof. A. Liebenberg. His experiments with peas began in Ghent, and were continued later on an experimental field of the Austrian Emperor. In 1899 he also discovered the laws of heredity. By Focke's work he was referred to Mendel whose classical significance he immediately understood so that he made provisions for the inclusion and republication of Mendel's paper in the Ostwald series of Klassiker der exakten Wissenschaften.

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Further popularization of Mendel and further spread of the Mendelian laws of heredity is the value of William Bateson (1861-1926), who, himself a plant hybridizer, became acquainted with Mendel's work through the papers of the above mentioned three in 1900. Before doing so, however, he already felt the need for a thorough statistical investigation of the hybrids (1899).[244] He is the first who introduced Mendel to English-speaking investigators in 1900[245] and translated Mendel's 1865 article into English (1901).[246] In 1906, he also discovered the role of *linkage* in heredity. This was the year when he gave the name of *Genetics* to the growing new science. Together with Lucien Cuénot, in France, he also worked on the application of Mendelism in animal breeding. It was also Bateson's task to defend Mendel against the attacks of the English school of biometrists, especially against Karl Pearson, who completely disregarded the Mendelian facts.

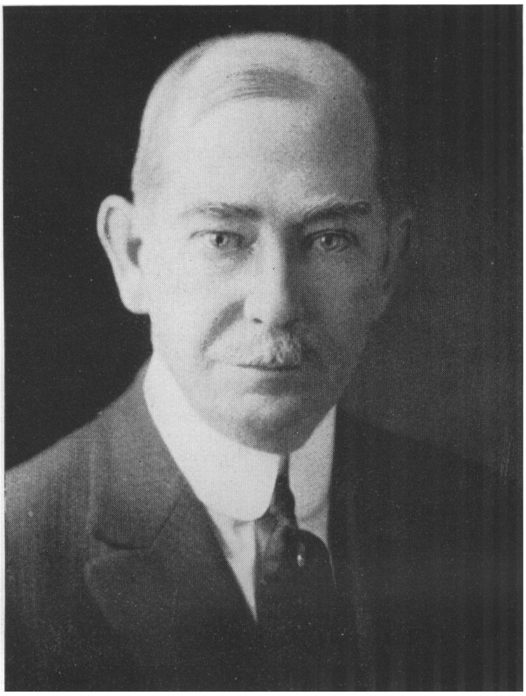

Fig. 51. C. E. McClung, 1870-1946

The best comparison of the merits of Galton's mathematical system of hereditary laws and of the Mendelian principles was given by Bateson in 1913[247] in the following way.

In Mendelian cases in which the characters behave as units, only three types of individuals are considered with respect to any pair of alleles, two being *homozygous* (pure bred, produced by unlike gametes) and one *heterozygous* (produced by unlike gametes); in a system such as Galton's the number of possible types is indefinite. The Mendelian system states that purity of type may be absolute, and that it may arise in individuals of the second filial or any later generation bred from heterozygotes. The Galton inheritance considers purity as relative which arises by continued selection of a long series of

[244] Bateson W., Hybridization and cross breeding as a method of scientific investigation. *J. R. Horticult. Soc.*, Lond., 1899, 24: 59-66.

[245] — Problems of heredity. *Ibid.*, 1900, 25: 54-61.

[246] — Mendel's principles of heredity; a defence. Cambr., 1902. – This contains a modified translation. The original translation was made by Mr C. T. Druery. Bateson later (1909) published a larger book on Mendel.

[247] Bateson W., Mendel's principles of heredity. 1913.

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generation. In any ancestral system no account is taken of dominance though this is a phenomenon which is essential part for the practical application of any worthy theory of heredity. While the Galtonian system cannot be applied universally, the Mendelian system is for universal application. So much for Mendel's defense by Bateson.

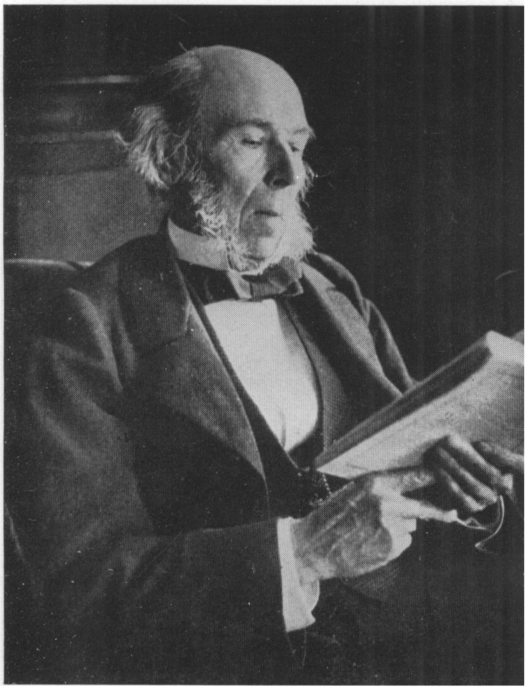

Fig. 52. Herbert Spencer, 1820-1903

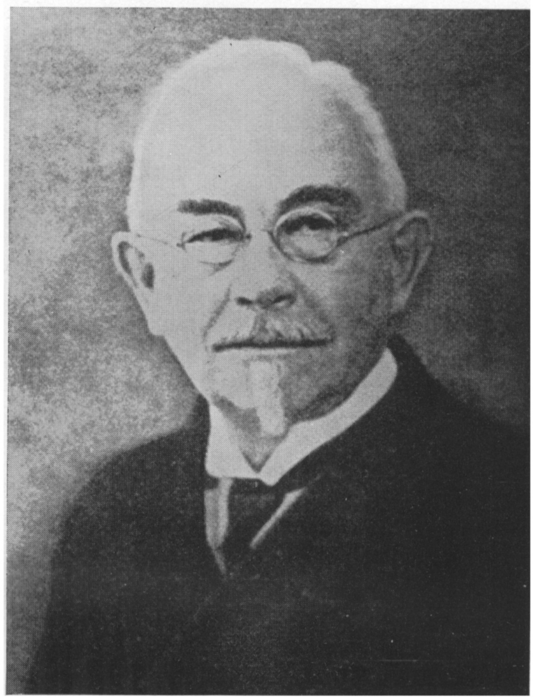

Fig. 53 Wilhelm Johannsen, 1857-1927

SEX INHERITANCE. Since Antiquity many theories had been propounded for the inheritance of sex, but the causes of maleness and femaleness could not be found until the cytomorphological research of the late 19th century. In 1891 the German H. Henking wrote an article on spermatogenesis and its relation to oogenesis in Pyrrochoris apertus.[248] He saw that in certain Hemiptera and in other insects the constitution of the nucleus of spermatozoon is of two different type, one half of the germ cells is provided with an extra chromosome (accessory, *heterotropic*, or *X chromosome*) while in other germ cells this chromosome is lacking. In 1902 Bateson suggested that sex might be a Mendelian character. In the same year McClung (1870-1946) developed a hypo-

[248] HENKING H., in *Zschr. wiss. Zool.*, 1891, 51.

https://doi.org/10.1017/S1120962300027098 Published online by Cambridge University Press

thesis of sex production, based upon the conjecture that the heterotropic chromosome is a sex determinant, and that the spermatozoa containing this chromosome will produce males. The hypothesis implied that the cells of the female must contain one chromosome less than those of the male. [249]

This hypothesis was further elaborated by Castle in 1903. Soon however, Edmund B. Wilson (1856-1939) proved that McClung's conjecture is to be reversed; for it is the female and not the male that possesses the additional chromosome. [250] We know now that the ovum has the X chromosome, while the spermatozoon is of two types: one with X and another with Y chromosomes. From the fusion of an ovum and an X type male cell, i. e., from X plus X, a female will develop. From the union of an ovum and a Y sperm, i. e., from the fusion of an X and Y cell, the male offspring will develop.

Fig. 54. Thomas Hunt Morgan, 1866-1934

GENE THEORY. The modern gene theory of heredity was gradually built up by the various theories of the 19th century, but its development was largely the result of the rediscovery of Mendelism. One of the fundamental elements of the gene theory is that the hereditary factor is particulate in nature. Such particulate theory was also the " theory of physiological units " which Herbert Spencer (1820-1903) proposed in 1863. [251] This supposed that each species of animal or plant is composed of fundamental units which are all alike for each species; the units are larger than protein molecules and more complex. Spencer speculated that, in some cases, any part of an organism can reproduce the whole again. Another particulate theory was Darwin's pangenesis which we shortly mentioned above. This gave way to Weismann's theory of the germ plasm (which he considered to be continuous). Then, the cytologists of the eighteen seventies and eighties suggested the chromosomes as the carriers of hereditary factors.

It was Walter S. Sutton (1876-1926) who in 1902 remarked that the behavior of

249 McClung, *Biol. Bull.*, 1902, 3.
250 Wilson E. B., *J. Exp. Zool.*, 1906, 3.
251 Spencer H., *The principles of biology.* Lond., 1864.

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the chromosomes in the course of the vital cycle of an individual is the same as it could be expected from a hereditary material factor according to the Mendelian way of heredity.[252] H. Friedmann also spoke of the chromosomes as carriers of the hereditary substance (1902). It was then the Danish Wilhelm Ludwig Johannsen (1857-1927), professor of the Agricultural College in København, who proposed to call

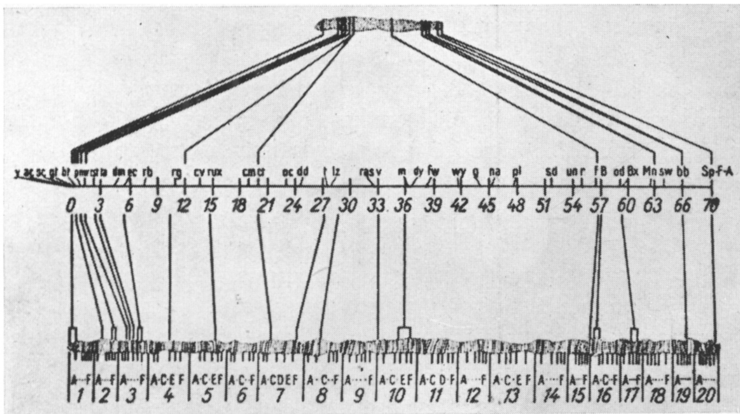

Fig. 55. A combined chromosomal (cytologic, genetic and giant-chromosomal) map.

Mendel's factors *genes* in 1909.[253] In an earlier work (1903) he published his experiments with hybridization of beans, with *pure line* breeding.[254] These experiments showed to him that any individual is composed of a part that is determined by heredity (this he called *genotype*) and another part which, together with the individual's inherited characters, makes the appearance in life (this he called *phenotype*). The genotype is the sum total of all the hereditary factors or genes in a gamete (germ cell) or a zygote (offspring of germ cells after union and cell division). Johannsen showed the occurrence of phenotypic variations under the influence of environment, and the possibility of transmission of acquired characters to the offspring. He never fully believed that the bearers of hereditary qualities are located in the chromosomes (i. e., in the nuclei) alone. His studies were also of great interest to the constitution pathology and medical research.

It is undoubtedly the merit of Thomas Hunt Morgan (1866-1945) and his school to establish, by direct experience, the localization of the Mendelian units in the chromosomes.[255] About 1910 Morgan selected, as an object of his studies of heredity, the

[252] Sutton W. S., *Biol. Bull.*, 1902, 4: 230.
[253] Johannsen W. L., Elemente der exakten Erblichkeitslehre (many eds.).
[254] Johannsen W. L., Om arvelighed i samfund of rene linier. (1903).
[255] Morgan T. H., *American Naturalist*, 1910, 44: 449-96.

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vinegar fly (*Drosophila melanogaster*) since it is easy to rear, it shows large number of races or mutations each of which behaves according to the Mendelian rules; also this insect has only four chromosomes in its germ cell. In collaboration with C. B. Bridges (1889), A. H. Sturtevant (1891), and H. J. Muller (1890) he could demonstrate that each chromosome of the insect contains a group of Mendelian units or genes. It was assumed that these are in a linear arrangement, and the Morgan school attempted to show the chromosomic position of each gene; thereby *chromosome maps* were prepared of the Drosophila. The linear map was established by Sturtevant in 1913.[256] W. E. Castle (b. 1867) has proposed a three-dimensional map to show the arrangement of linked genes.[257] The breeding experiments with Drosophila showed that there are between 2500 and 3000 genes in a single chromosome of this insect. These are as many distinct characters. It was also discovered that genes can exchange or interchange from one chromosome into another.

In 1933 Painter found that the cells of the salivary gland of the larva of Drosophila contain very large, so-called giant chromosomes on which the study of various gene locations, and the different phenomena of gene life, can be very clearly studied. This inspired further work in all countries, and on other test animals and plants. We now know, especially by the efforts of Bridges, not only the exact topography of *chromomeres* (these are groups of genes in the form of knots along the thread-like *chromonemata* which are wound together to form a chromosome) but also we are aware of deficiencies in these structures, and we know that such deficiencies cause lack of certain hereditary characters.

The experiments with Drosophila have led Morgan to two principal conclusions in 1911: 1) that sex-limited inheritance is explicable on the assumption that one of the material factors of a sex-limited character is carried by the same chromosomes that carry the material factor for maleness; 2) that the association of certain characters in inheritance is due to the proximity in the chromosomes of the chemical substances (factors) that are essential for the production of those characters. He found that even the extremely complicated results of the combination of two or more of these sex-limited characters must be explained upon the same general principle of heredity. " It is this evidence — says he — that has convinced me that segregation, the key note to all Mendelian phenomena, is to be found in the separation, during the maturation of the egg and sperm, of material bodies (chemical substances) contained in the chromosomes ".[258]

MUTATIONS. The problem of influencing heredity by external factors of the environment had been also studied in earlier centuries of the classical Antiquity and of the Middle Ages. Such studies increased at the end of the 18th century. In the 19th century the two main thoughts on the problem of heredity of acquired characters were

[256] STURTEVANT., *J. Exp. Zool.*, 1913, 14: 43-59.
[257] W. E. CASTLE, *Proc. Nat. Acad. Sc. U. S.*, 1919, 5: 25-32.
[258] MORGAN T. H., *J. Exp. Zool.*, 1911, 11: 365-414.

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embodied in the evolutionary theories of the lamarckists and darwinists. Their discussions about their differences were chiefly theoretical and Timofeef-Ressovsky (1937) thinks that this was very fortunate for the development and rediscovery of the Mendelian laws.

In the 20th century one began to test the validity of mutation theories. There were three possible approaches: 1) cultivation of different individuals under different milieu conditions to detect the possible changes; 2) experimental modification of nuclear structures that are known to be of importance for heredity; 3) study of the effect of different external factors upon the quantitatively comprehensible and measurable mutation ratio of favorable objects, under well-chosen experimental conditions. All three approaches were tried during the last fifty years, some with less success than the others.

The first method was used by a group of lamarckists at the early years of this century (e. g., Dürcken, Guyer, Przibram, Tower, etc.). Since the test objects were wrong, and the hypothesis was wrong, and the experimenters showed ignorance of the Mendelian laws, the results of this approach were doubtful.

The second approach, i. e., the modification of nuclear structures by artificial influences began with the experiments of Gerassimov (1901) in which he was able to double the chromosome number in Spirogyra by application of cold (this is now called *ploidy* e. g. di-ploidy when the chromosome number is doubled, poly-ploidy when it is increased many times of the normal). It was discovered in these experiments that the nuclear structures, including the hereditary factors (the genes) are extremely resistant to external forces.

After the discovery of radium and roentgen rays (*gamma rays*) a much more rapid progress was made in the study of mutations and genotypic environment. Already in 1907, Bardeen showed that röntgen rays damaged the spermatozoa of frogs. Similar observations were made by Regaud and Dubreuil (1908) on rabbits, Gager (1908) and Guilleminot (1908) on plants. Further advance was prompted by the work of Oscar Hertwig (1911-1913),[259] G. Hertwig (1911-1920), and P. Hertwig (1913-1927) with radium rays on eggs and sperms of fish, amphibia, etc. It was shown that the nuclear changes which developed under the effect of these factors will inhibit or change future development of the cell. No breeding experiment was connected with this research.

The third approach developed from the Mendelian ideas on genes and mutations, and was carried out with breeding experiments on plants. The idea of mutation as a sudden jumpy change in development was born before the Mendelian Era, but, thereafter it grew together with Mendelistic experiments and with modern genetics. These sudden changes in heredity were taken for the support of the evolutionary theories in the 19th century where the phenomenon was also called *heterogenesis* (Korschinsky). They were studied also by Bateson (1894), and especially by De Vries who called the sudden changes mutations, and followed up their future through successive generations by Mendelian laws.

This experimental mutation research was further developed under certain pre-

[259] HERTWIG O., *Arch. mikr. Anat.*, 1911, 77: Abt. 2, 97-164 (on the radium disease of germ cells).

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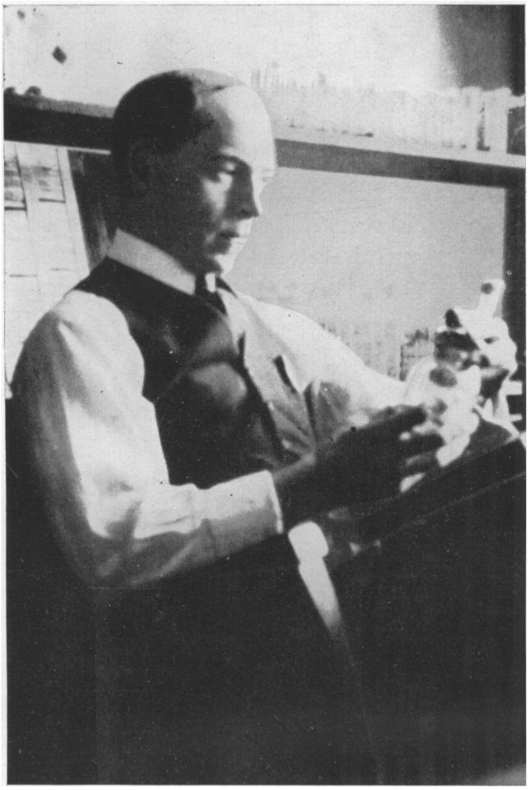

Fig. 56. Herman Joseph Muller, 1890

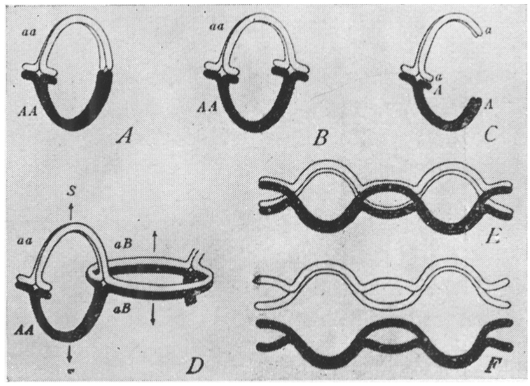

Fig. 57. Single ring, double crosses and multiple ring types of tetrads

cautions. It was found that the breeding has to be pure line (or homozygotic) which can be obtained by inbreeding only, since free population is always heterozygote and not suitable for mutation research. It was also essential that the number of crossings and generations be sufficiently large; that the breeding technic should provide a large number of first filial generation with easily recognizable hereditary changes; and that the occurring changes should be exactly analyzed. [260]

Around 1924 several investigators experimented with x-ray mutation, with more or less success. Bagg and Little (1924) produced hereditary structural defects in descendants of mice that were exposed to x-rays. In the same year (1924) Herman Joseph Muller (b. 1890) reported that he was able to produce breakage of chromosomes by roentgen irradiation. [261] His classical experiments on producing mutations by roentgen rays in Drosophila opened a new era and a new branch ("*radiation genetics*") in modern genetics. [262] He described his findings in many papers. He was able to increase the ratio of mutation by means of gamma irradiation so that mutations occurred 150 times more often than under normal conditions. He produced all types of natural

[260] For the details of this research see Timofeeff-Ressovsky, Footnote 64. I based the paragraphs on history of mutation research upon the second chapter of his work.

[261] Muller H. J., Chromosome breakage by x-rays. *Ann. Rec., Phila.*, 1924, 29: 150.

[262] — Artificial transmutation of the gene. *Science*, 1927, 66:

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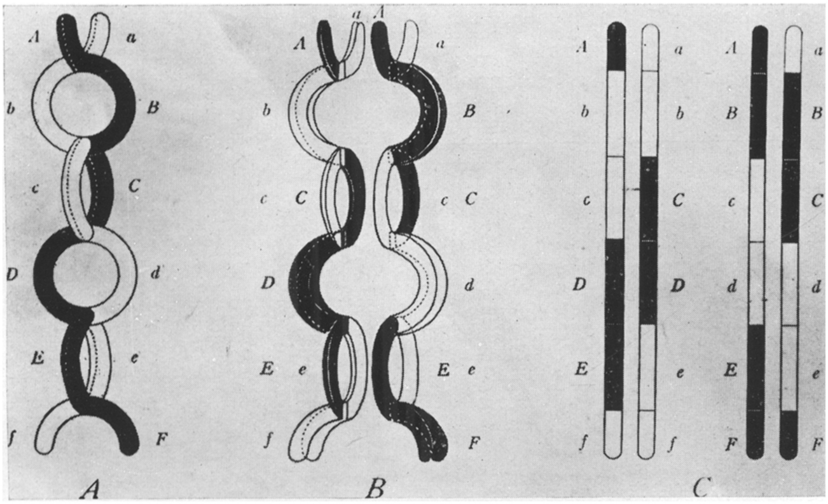

Fig. 58. Jannsen's interpretation of compound chromosomal rings

mutation such as recessive lethal factors, mutations in chromosomes and genes (deficiencies, deletions, inversions in their regular arrangement, translocations, etc.). His results were confirmed on many test objects, and for the understanding of such genovariations the work of Timofeeff-Ressovsky brought most fruitful results.

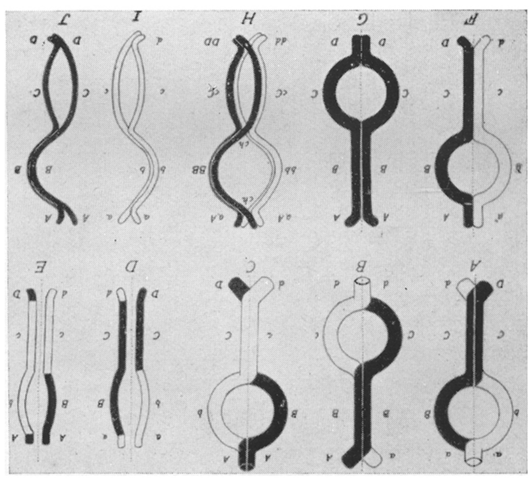

Fig. 59. Fate of double rings (Jannsen)

Inspite of this excellent research it is believed that there is a great difference in natural and artificial mutations, unless we want to consider that the mutations which had brought on the chain of evolution of all species, plants and animals, from a primordial protoplasma, had been also caused by the continued bombardment of cosmic rays and gamma rays of paleonuclear fissions. On the basis of the gene theory of heredity it is assumed that the genes are very stable chemical substances, and they pass unchanged to the descendants from the parents. Slight structural changes are held possible which might be manifested in the offspring as new characters. But, to have a new character, genes have to be either displaced from their normal *locus* on the chromosome map, or they

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must be more or less than the normal. Under such conditions, there might come a mutation in type. Such a mutant may have undesirable characters; hence, a breeder has to make *selection* for the betterment of the race. But, if a species is to develop

Fig. 60. Erwin Baur, 1875-1933

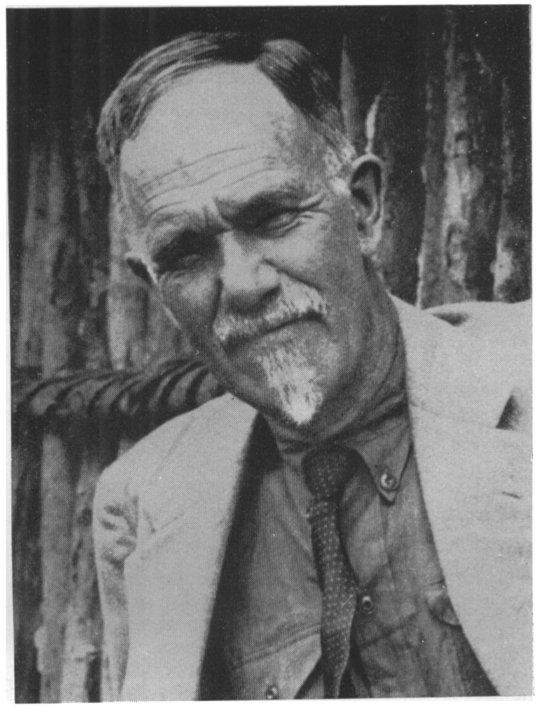

Fig. 61. Charles Benedict Davenport, 1866-1944

through mutations, as the evolutionists believed, there should be many more mutations visible in the world than they occur now.

" Phylogeny (the reconstruction of what has happened in the past) is no science — says the neodarwinist Lotsy [263] — but a product of phantastic speculations which can be held but little in check by the geological record, on account of the incompleteness of the latter ". Nevertheless, the basic fact of evolution is that there has been life on this globe long before the Cambrian epoch, and we may feel certain as Darwin said that " the ordinary succession by generation has never once been broken ". And only in this sense is phylogeny a fact. Lotsy holds that species arise by crossing, perpetuate themselves by heredity, and are gradually exterminated by the struggle for life, those

[263] Lotsy J. P., Evolution by means of hybridization's. Gravenhage, 1916.

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last exterminated obtaining the epitheton ornans: selected ones.[264] Selection is just a nice phrase for extinction. He is very skeptical about the existence of mutations and their influence on evolution.

In the development of modern genetics we should remember of the merits of Albrecht Brachet (1869-1930) who further developed the old Aristotelian idea of *general heredity* the mechanism of which is still unknown. This form of heredity provides for the rigid conservation of general bodily constitution of each species. Erwin Baur (1875-1933), the eminent German breeder and theoretical genetician, was one of the earliest scholars in Germany to study Mendel's laws (1904), using Antirrhinum majus as his main object. He was first a practicing physician before he changed over into a botanist. The first chair for genetics at the Agricultural Academy of Berlin was founded and held by him (1914). Later he became the director of the Genetic Institute in Berlin (1922-1929), and of the Institute for Research in Breeding at Müncheberg. His textbook on genetics (1911) saw many editions. He was also the founder of several German periodicals devoted to evolution, genetics, and breeding.

In the United States Charles Benedict Davenport (1866-1944) was doing the same service which Galton did in England. He was the leading geneticist in the U. S. Though zoology was his main interest, he devoted much of his time to eugenics, human heredity, and anthropology, especially the study of races. He believed in races, and that the races differ in mental capacities. Race intermingling was for him a disharmony: " Hybridized people are a badly put together people and a dissatisfied, restless, ineffective people ". With such ideas he organized (1904) the Genetics Department (first called Station for Experimental Evolution) of the Carnegie Institution, and in 1910 he established the Eugenics Record Office, and two years later the Eugenics Research Association.

Nils Herman Nilsson-Ehle (1873-1949) was professor of genetics at the University of Lund, and botanist who, in search for an explanation of some discrepancies in Mendelism, discovered the phenomenon which is known as the action of *multiple genes* (or factors); this is simply a kind of heredity where the development of a single character depends on several pairs of genes (1909). The recognition of such gene interaction strengthened, however, the validity of Mendelism, since, inspite of the multiplicity of factors, some of the character ratios in the filial generations are predictable by the Mendelian laws.

RESEARCH TOPICS. Human genetics became very soon a special branch of the newly developed science of heredity. Bateson (1914), Baur (1908), Davenport (1908), Morgan (1924), and others published valuable observations of human heredity. Boas studied the heredity of head formation (1903) while Gossage (1907-08) investigated the inheritance of abnormalities. The various laws (Buchanan 1923), Mendelism and human heredity (Fischer 1921), and the mathematics of the human germ plasm (Laughlin 1920) were described. Genealogy and family research were examined as to

[264] — 157, etc.

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their value in the methodology of human genetics.[265] Heredity and the fate of various famous and infamous families were scrutinized such as the Zero family in Germany (Jörger 1905), the Habsburgs (Strohmayer W. 1911), the inbred descendants of Charlemagne (Jordan D. S. 1921), the Dack family characterized by hereditary lack of emotional control (Finlayson A. W. 1916), or the Fick family in Germany (1921). Davenport selected a series of naval officers for objects of his genetics research (1919). In the U. S. F. A. Woods (1902 to 1919) spent many years on the genetic setup of royalty, American men of science, etc.

The chief characters which were selected for genetic observation by the investigators were color, size, and certain extreme degrees of qualities. A special group of so-called *genetic psychologists* investigated the inheritance of various mental faculties such as memory (Meyer S. 1906; Darwin F. 1908), emotional traits (Davenport 1914), etc. Some of the studies of the biometric school of Karl Pearson were especially fruitful (1901).

Heredopathology also made its progress in the early decades of the 20th century. W. C. Krauss published valuable statistics of hereditary diseases which were collected in the New York State insane asylums (1901-02). Wagner-Jauregg in Austria (1902), Jendrassik and Kollarits in Hungary (1902-07) studied the heredodegenerative diseases of the nervous system. In Germany the researches of F. Martius (in 1901-14), the founder of the pathology of constitution, were of outstanding value.[266] Weeks investigated the influence of heredity in eye diseases (1903), and F. A. R. Jung observed the frequency of inheritance in gastrointestinal diseases (1902).[267] Punnett (1907-08), K. Dresel (1917) and R. Bénard (1924) investigated the Mendelian ratio in relation to disease. The Swiss Adolf Steiger (1913) showed the influence of heredity in myopia. F. Lenz (1912) investigated the transmission of hemophilia. The Italian Gradenigo (1924) wrote on hereditary deafness which was also investigated by the Swiss E. Hanhart (1924) at various regions of human inbreeding where people in their isolation often manifest various pathological characters that are transmitted by heredity (e. g., heredoataxia, dwarfism, etc.) . The American C. C. Little and M. Gibbons described evidences of the existence of a self-linked lethal factor in man (1920),[268] while the German H. W. Siemens (1925) called attention to the dominance of sex-linked character as an unusual mode of spread of a heredopathosis.[269]

By the efforts and clinical observations of the group of human geneticists we are now able to follow up the normal and morbid characters which are transmitted according to the laws of Mendel from parents to children. A fairly long list of such inherited

[265] See especially J. Groeber (*Arch. Rassenb.*, 1904, 1: 664-81). – Also K. R. Sommer: Familienforschung und Vererbungslehre. Lpz., 1907. – Also A. Crzellitzer (*Sex Probleme*, 1912, 8: 221-43).

[266] Martius F., Krankheitsanlage und Vererbung. Lpz., 1905. Also his: Konstitution und Vererbung in ihren Beziehungen zur Pathologie. Berl., 1914.

[267] Cf. *Am. J. M. Sc.*, 1902, 123: 996-1008.

[268] Cf. *Proc. Soc. Exp. Biol.*, 1920, 18: 111-5.

[269] Cf. *Arch. Rassenb.*, 1925, 17: 47-61.

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human characters was prepared by Baitsel.[270] According to this list the hereditary characters which had been observed in man are classified into the following groups:

1. Mendelian alternative characters: (normal allele not mentioned)

a) Skin:

Dominant characters: dark pigmentation, tylosis and ichthyosis, epidermolysis, beaded hair.

Recessive characters: blondness, albinism.

b) Eyes:

Dominant characters: black or brown color, hereditary cataract, night blindness.

Recessive: blue iris.

c) Skeleton:

Dominant characters: various abnormities of finger, exostosis, fragilitas ossium.

d) Metabolism:

Dominant: diabetes insipidus.

Recessive: alkaptonuria.

e) Nervous system:

Dominance in heredity of Huntington chorea.

Recessive: hereditary feeblemindedness.

2. Mendelian blending:

In heredity of size, stature, weight, skin color, hair form, head shape, features.

3. Mendelian and sex-linked:

Recessive: Gower's muscular atrophy, hemophilia, color blindness, night blindness.

4. Probably Mendelian, with uncertain dominance:

Defective hair and teeth, extra teeth, double set of teeth, harelip, cryptorchism, hypospadias, *twinning*, lefthandedness, otosclerosis.

5. Hereditary, but mechanism unknown as yet:

Mental ability, memory, temperament, musical ability, literary ability, artistic ability, mathematical and mechanical inclinations and abilities, congenital deafness, liability to abdominal hernia, cretinism, heart defect, certain forms of epilepsy, insanity, longevity.

Totalitarian Biologies

The science of genetics is dangerously close to certain fields of human activities where the application of knowledge of human heredity may bring one in conflict with national politics, national economics, and current ideologies of the planners of states, as Muller pointed out (1949). The totalitarian states of Hitler and Stalin developed their own theories on human biology, and influences of the political ideas might be discovered in the development of genetics in these countries.

[270] Baitsel, *Human biology* (1950) 444-445.

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HITLERISM. The national politics of Germany under Hitler were in very close coordination with genetic doctrines. In Darlington's opinion however (1947) these doctrines were distortions of the truth. Hitler assumed the permanent, unconditional, and homogeneous genetic superiority of his people. On the basis of this assumption he applied genetics to national politics. The prevalent views of Hitler's regime on racial superiority and on the undesirable effects of inter-racial crossings were, however, partly supported by the past experiences of breeders of plants and animals.

It is also a matter of record that the idea of a super-race was originally propagated by various people of Antiquity, including the Jews of biblical times. [271] It is always bad when a theory which happens to be prevalent under a particular political regime has so much power that it becomes the central, leading idea not only in society but also in science. Extreme statements of the theory of racial superiority are positively without ground. [272]

MICHURINISM. As Hitler created a genetics of his own, the communist Russians also attempted to produce a theory of genetics on the basis of Marxian philosophy, mixed with a good deal of discarded darwinism and lamarckism. For the adornation of this Marxist genetics or Soviet Darwinism (Darlington, 1947) the Russian government dragged out from the past the names of two Russian naturalists: Klimenty A. Timirjazev (1843-1920) and Ivan Vladimirovich Michurin (1855-1935). Timirjavez was professor of botany at the St Peterburg Agricultural Academy and at the Moskva University. He studied photosynthesis and its relation to the wave-length of light. Above all he was a practical botanist who wanted to improve the fate of the Russian farmer. Among his many publications there is one about the teachings of Darwin; it was very popular in 19th century Russia. [273]

Michurin came from a family of horticulturists. As a child he began to experiment with hybridization, and after his graduation from highschool (gymnasium) he rented a garden for the continuation of the experiments. In 1888 he founded his own agricultural nursery which in 1919 was taken away by the Communist Government though he was permitted to continue his agricultural experiments. (This nursery is now called the Michurin Research Institute). He was especially successful in producing many varieties of fruits of unusual size and quality. In this theoretical views he was a lamarckian, and therefore an opponent of Mendelism. But above all he was an agrobiologist, and a friend of Lenin, which made his doctrines acceptable to the Communist Party.

The teachings of these early Russian botanists and agrobiologists were made into a doctrine entirely by Trofim Dennissovich Lysenko (b. 1898), who mixed genetics with a good deal of communistic doctrines approved by the Central Committee of the Communist Party in Russia. He himself is an agrobiologist [274] and, since 1938, the

[271] Cf. HALDANE J. B. S. Heredity and politics. Lond., 1938.

[272] On Galtonism and Gobineauism see also HIRSCHFELD, l. c., v. 2, 647-9.

[273] TIMIRJAZEV K. A., Ch. Darwin i ego uchenie (1. ed., 1882; 8. ed., 1924). He also wrote three articles on Darwin (1864).

[274] LYSENKO T. D., Agrobiologia. 1948.

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president of the Russian Academy of Agriculture. He called the new doctrine Michurinism and, on various meetings of the breeders and geneticists of Russia, he opposed this doctrine very sharply against the modern genetics of the western world, calling the western science of heredity " Mendelism-Morganism " which in his view is reactionary and is serving the interests of capitalistic nations only.

The deterioration of genetic sciences in Russia and the causes of transformation from Mendelism to Michurinism are analyzed in a recent article of Zirkle (1953).[275] He states that this transformation really started with Marx and Engels, who, inspite of their apparent praise of Darwin's doctrine on evolution, were in fact very hostile to the evolutionary concept. Though this is true, the real trouble began about 1936, and the controversies between Mendelism and the communist ideology became so numerous that, at the 1948 Fall meeting of the Agricultural Academy, genetics was outlawed and denounced in the Soviet Republic. It was replaced by the doctrines, some of them Michurin's but most of them the beliefs of previous centuries, which might be called really a twisted form of the old lamarckism.[276]

Fig. 62. Trofim Dennissovich Lysenko, 1898

The new Russian version of lamarckism differs, however, from the old doctrine by the following features: 1) it assumes that heredity (i. e., the genotype) can be " shattered " by various treatments which render the heredity more labile and *plastic*; the changes become hereditary (environmental change or vegetative hybridization, or crossing of very distant varieties will do such shattering); 2) it assumes that heredity (i. e., hereditary constitution) is inherent in every particle of the living body, and is determined by the type of metabolism; hence, change in metabolism would result in change in heredity; 3) it assumes that heredity is able to assimilate external conditions; indeed, heredity is nothing but " the concentration of the action of external conditions assimilated by the organism in a series of preceding generations " (Huxley).[277]

Of the shattering methods, only the environmental changes could be considered to

[275] Zirkle, *Scient. Month.*, 1953, June.
[276] Cf. Huxley. See Footnote 71.
[277] — p. 18.

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play any role in evolution. Hence, Michurinism depends chiefly upon the effect of such environmental conditions upon heredity when the hereditary constitution is brought into a " plastic state ". Though the Michurinists claim success with the application of their doctrines in agriculture, none of the claims could be verified outside of Russia. There was, e. g., the claim of Mme Olga Borisovna Lepeshinskaja that she had produced nuclear substance from nonnuclear living forms of matter. [278]

Huxley sums up the differences between Mendelism and Michurinism in a simple statement. Mendelism represents a coherent development of a central scientific concept which was formed in order to explain certain observed facts. The development was partly generalization, partly refinement. On the other side of the fence, Michurinism represents the spread of a central idea which is not the only way to explain certain facts. It is a preconceived idea, imposed upon facts, instead of arising from them. When the facts do not fit the idea they are denied. Michurinism is not quantitative; hence, it lacks precision. It is just a doctrine, essentially non-scientific.

One basic doctrine of this new brand of " science " is that there are no inborn class and race differences in man. Genetics, of course, relies upon the presence of class and race differences in plants and animals. The acceptance of such differences is, however, politically inconvenient to the communist governments which are forced to deny the existence of genes, and must believe only in the effect of environment, political or other, which they can manipulate. It never occurs to the Michurinists that neither the racial mark of Abraham nor the foot-mutilation of Chinese women have become heritable characters inspite of their continued use from generation to generation through thousands of years. [279]

To what extreme the Michurinist agrobiologists may go is shown by a book review of Dobzhansky (1953) who gives a few samples from Lysenko's recent pamphlet. [280] In this pamphlet Lysenko announces that a large body of facts has been accumulated showing that rye may arise from wheat, and wheat can generate barley and so on, depending entirely upon the environment in which these plants develop. Indeed, it is now completely demonstrated — according to Lysenko — that in the bodies of plant organisms of various species there are also formed and generated the rudiments of bodies of individuals of *other* species. Life does not need cells for its development; it may come from granules of the body which lack any cellular structure. In other words, the Michurinist biology rejects the cellular theory and puts us back into the 17th century.

[278] Cf. Gruber G. B., Einführung in Geschichte und Geist der Medizin. 4. *Aufl.*, *Stuttg.*, 1952, 87.

[279] On the other hand, McCartney (cf. Footnote 29) mentions that an anonymous magazin article referred to the elongation of the earlobes of Masailand women and of the neck of a certain tribe's women in Africa where the large ear lobes and the brass neckrings produced an artificial elongation that has become hereditary since a " good purpose " is served by these acquired characters.

[280] Dobzhansky T., Lysenko progresses backwards. *J. Hered.*, 1953, 20-22. – The work of Lysenko is entitled: New in the science of biological species (Novoe v nauke o biologicheskom vide), Moskva, 1952.

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PRESENT STATUS AND PROBLEMS OF GENETIC RESEARCH

Let us now consider briefly the most recent tendencies and views of genetic research. The gene theory of heredity and the knowledge of the Mendelian laws helped the rapid development of genetics. But more and more new problems came to light as research progressed from the larger to the smaller units. It was desirable to subdivide the field of genetics further, according to the new problems. Thus, now we have a number of *specialties* which investigate the inheritance of various characters of the organism (physiological function, mental qualities, chemical and metabolic functions of the body, immunological properties, including the heredity of blood groups, inheritance of twinning, cytogenetics, radiation genetics, mutation genetics, human or medical genetics, etc.).

NATURE OF GENES. It is now assumed that the gene is more than a hypothetical unit. It has real existence. In the view of Wright, [281] it is an organic particle of specific constitution, a block of self-duplicating chromosome material that is not divided during the process of crossing-over, or by chromosome breakage and rearrangement. On the other hand, Sansome and Philp (1939) say that there is no definite view as to the material cause and its functional effect in gene-transmitted heredity. It is believed that the gene is a very large nucleoprotein molecule (Schrodinger, 1944), [282] and genic mutation would mean a change in the constitution of this molecule.

It is easier to describe a gene in its biochemical effects. Already Hagedorn (1911) stated that genes possess the qualities of catalysts. It remains the question: what makes each gene to act in a specific manner? Since 1925, from the studies of Sturtevant, we also know that the position within the linear arrangement in the chromosome also influences the particular effect of a gene's action. This would permit the assumption that phenotypical changes might result from a great number of causes and from slight alterations in the gene.

Genic action is a contemporary problem of genetics, and chiefly biochemical in nature. *Biochemical genetics* as a subdivision of modern genetic sciences is based upon the protein nature of the gene. It is an attempt to coordinate the facilities and methods of two different disciplines, for the understanding of the relation between genes and chemical reactions. This branch of genetics started very early in the 20th century, perhaps with the hormone theory of the heredity of somatic characters proposed by Cunningham (1908). [283] In 1909, the biochemist Onslow mentioned the possibility of a close relationship between single gene and simple biochemical differences in flower colors. [284] She recognized that chemical differences in flower colors are good material for the study of Mendelian heredity. Later, the fact was established that many simple biochemical effects follow the Mendelian rules. Then, Garrod (1923) wrote on inborn

[281] Cf. *Amer. Naturalist*, 1945, 79: (289 etc.).
[282] SCHRODINGER. What is life. Cambr., 1944.
[283] CUNNINGHAM J., *Arch. Entw. mech.*, 1908, 26: 372-428.
[284] Cf. *Proc. Cambridge Philos. Soc.*, 1909, 15: 137 etc.

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errors in metabolism, and provided human genetics with valuable principles for future work on this field. He suggested to measure genetical differences by means of chemical tests whenever possible, and to assume that every gene has a specific chemical effect in the body.[285]

These studies revealed that *the cytoplasm* is the substratum on which the genes work, though, once started, the action is further a chain reaction. This is a highly speculative topic, however, since the cause of the initial activation of the gene is very little known. The metabolic aspect of genes was studied on microorganisms as test objects, such as the fungus Neurospora tetrasperma. The observations of Beadle and Tatum (1941), and of Horowitz (1945) showed that single genes may produce single steps in the chain of metabolism. A certain *polyurgic* effect was attributed to the gene by Wright (1945) who assumed that each hereditary character is affected by many genes as well as by environmental factors, and each gene in general has multiple effects so that gene and environment together are modifiers of a pattern residing in the whole organism.[286]

The genic system as seen today is very complex. Geneticists suggested *plastogenes* (plastids), and *plasmagenes* in the cytoplasm, and genes, major genes, supergenes, and polygenes in the chromosomes. More and more facts come to light which show that heredity is not only nuclear but also *cytoplasmic*. This is also called extranuclear heredity. This hypothesis supposes that there is a wholly or partially autonomous character in the cytoplasm which can be transmitted to successive generations, independently of the genotype. While the nuclear part of heredity was called *genome*, the extranuclear part was named *plasmon* by F. V. Wettstein (1926; 1928; 1930).[287]

Morgan originally considered that the cytoplasm of the germ cell can be ignored genetically. Some modern geneticists hold, however, that cytoplasmic inheritance is a reality, and it also follows the Mendelian rules. The *plasmon* of Wettstein includes the plastids, too, and any other particulate component of the cytoplasm. Of course, during the fusion of male and female elements it is the female ovum which contributes the largest amount of cytoplasm to the zygote (as the ancient Greeks had supposed it with Aristoteles). True cytoplasmic inheritance is tied to the plastids which are supposed to be never formed anew and to be propagated through division of preexisting plastids. Guilliermond (1941) suggested that the plastids are made out of mitochrondria. Cytoplasmic inheritance is also accepted by Muller (1951) who speaks of cytoplasmatically located genes and mitochondrioids that have retained the power of self-reproduction and biochemical functions. The plastids are partners of the genes in the interpretation of Sonneborn (1950). They are made responsible for inheritance of male sterility, of resistance to infection, of variation in germinating power, etc.

There is another form of apparent cytoplasmic inheritance, called *maternal predetermination*, which simply means that certain characters of an organism are already

[285] Cf. Biochemical aspects of genetics, a symposium (1949) Cambridge, 1950.

[286] WRIGHT. *Amer. Naturalist*, 1945, 79: 289, etc. – See also WARDLAW in Footnote 85.

[287] WETTSTEIN F. V., Ueber plasmatische Vererbung. *Nachr. Ges. Wiss. Göttingen*, 68: 276.

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decided before fertilization of the ovum. The effect of such predetermination is supposed to be only temporary, during the early developmental period of the phenotype.

In all these discussions one may hear the ring of the older speculations about preformation and epigenesis of the individual life. Each of the genes or hereditary units is within groups, and disposed according to a specific plan, a fixed order. Each particle has its own function, yet genes are not organs, nor the rudiments of organs. They are not units in the sense of Empedokles, nor representatives in the sense of Weismann. Though there is no preformation, there exists an organization of extraordinary nature. Hence, neither the preformists nor the epigeneticists are right. Wilson (1925) expressed the modern idea by saying that heredity is the result of the transmission of a *nuclear preformation* which, in the course of development, shows itself by a process of *cytoplasmic epigenesis.*[288] The same idea was expressed by Zimmermann (1942) in a somewhat different form that the nucleus determines what kind of developmental pattern will be followed, the cytoplasm being the agent which brings the construction into being.[289]

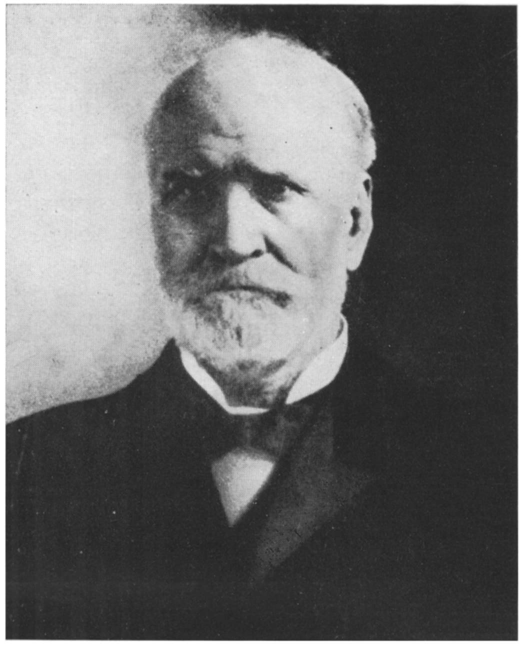

Fig. 63. James Wilson, 1835-1920
first president of American Genetic Association

A relatively new branch of genetic studies was introduced by those investigators who use physiological and morphological methods for the study of materials of known genetic constitution during the development of the new individual. The chief representative of this branch of research is R. Goldschmidt who published many papers on the topic (1927-1938).[290] *Physiological genetics* has the task to establish relationship between the presence of particular genes in the nucleus and the eventual appearance of characters in the adult organism.[291] The present view is that the genetic control of morphogenesis is exercised by means of chemical substances such as auxins, hormones, enzymes, etc.; perhaps, that the genes regulate the life of these substances (Goldschmidt 1938; Avery 1942). The literature on this topic is increasing daily.

[288] Wilson, Cell. N. Y., 1925.
[289] Zimmermann, *Cold Spring Harbor Sympos.*, 1942, 10: 152 etc.
[290] Goldschmidt R., Physiological genetics. N. Y., 1938.
[291] Cf. Wardlaw, l. c., 139. See Footnote 85.

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Biometrical genetics, or mathematical genetics as a study of continuous variation, did not lose any from the number of its followers. Contributions on this field were made by Wright (1939), R. A. Fisher (1941), L. F. Hogben (1946), and others. Dahlberg, in Uppsala, wrote a monograph from his results of the mathematical analysis of heredity in the Swedish population. Recently (1949), K. Mather published his textbook on mathematical genetics.

Cytogenetics is not a new branch, but its study received added impetus after the rediscovery of Mendelism. Its current representatives spend their time on investigation of the nuclear and extranuclear basis of heredity in various uni- and multicellular organisms, including the Paramecium (Preer 1946), the common fly (Perje 1948), and the various bacteria. Guides and textbooks were published by Demerec & Kaufmann (2. ed. Wash., 1941) for the cytogenetics of Drosophila, while H. F. Riley wrote an Introduction to general and cytogenetics (1948).

Evolutionary genetics as a branch science was outlined by Huxley at the Seventh International Congress of Genetics in 1939. One of the latest steps on this field is a synthesis of the common ideas of genetics, paleontology, and evolution under the general tutelage of Princeton University in the United States (1949).

It was R. H. Biffen in 1905 [292] who first showed that immunity of wheat from rust infection follows Mendel's laws. Nilsson-Ehle's studies in 1911 [293] are the classics of *immunogenetics*. The genetics of immunity to disease is however very complex, and its study is further complicated by the numerous races of parasites. Environmental conditions and their effect upon both host and parasite has also to be considered. One of the latest representatives of this branch of genetics is Irwin (1947).

Radiation genetics for the study of mutations and of the heredity of acquired characters was developed by Timoféef-Ressovsky (1940-42), Delbrück (1940), and the many others who followed J. H. Muller's (1924-27) method of genetic research. It was found that the changing hereditary factor is a homogeneous atom bond. Change of a single atom or electron is sufficient to provoke mutation. The experiments with gamma ray irradiation showed that the relation between ionizing dose and the rate of mutation is constant.

Great advances were made in *human* and *medical genetics*. This was made possible especially by organization of teaching, establishment of research institutes at universities, of departments in larger institutions of learning, etc. L. H. Snyder (1941), C. E. Keeler, J. A. F. Roberts (1940), M. D. Schwitzer, and many others are working on the field of medical genetics. A very detailed study of inherited biochemical deficiencies was found associated with mental defect. Jervis (1937) described among these deficiencies the so-called phenylpyruvic oligophrenia which has an autosomal recessive gene. Others who contributed to the studies of genetic deficiencies in man are Myersons (1936), Sachs (1936), Tredgold (1937), Murphy (1940), Davidenkov (1940) etc.

[292] BIFFEN, *J. Agric. Sc.*, 1907, 2: 109-128.
[293] NILSSON-EHLE, *Lundss Univ. arssk.*, n. f., afd. 2, 7, No. 6: 57-82.

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Kramp (1939) and a special group of investigators devoted their time to the scrutiny of the hereditary transmission of blood groups.

The gene exchange and chromosome aberrations in men were also studied by G. Just (1934) who also discussed the higher problems of Mendelism in human genetics. H. F. Falls and C. W. Cotterman tried to detect the relations of ageing and human heredity (1945-46). There were many useful guides and textbooks prepared on the advancements of human genetics, and there is probably no country now without a practical or theoretical manual on human heredity. Some of them were reprinted in several editions. Such manuals are by Baur-Fischer-Lenz (5. ed., 1940), Just (1939), M. J. Sirks (1941), Gianferrari (1942), Ford (Lond., 1942), Kemp (Kbh., 1943), C. Jucci (Milano, 1944), Rousseau (Montréal, 1945), Gates (N. Y., 1946), Dahlberg (Stockh., 1946), Muller (Ithaca, 1947), and by many others.

A special field of human genetics is *twin genetics* which is now practiced both as a separate field of knowledge (*gemellology*) and as a research method. Twins are especially suitable, under given conditions, for the decision whether environmental influences can impress and modify the genotype. The method was preconceived by Francis Galton (1876). Thereafter it was forgotten, with the exception of a few examples, until H. W. Siemens raised it again to the level of a scientific method. The study was put upon a Mendelian basis about 1908 when Weinberg maintained that Mendel's laws are also applicable to twinning. [294]

Further studies on twins were made by Oliver (1912), Friedenthal (1914), Meyer (1917), Bonnevie (1919), Davenport (1920), Wehefritz (1925), Luxenburger (1939), Verschuer, and Gedda. Gedda's monumental *Studio dei gemelli* (Roma, 1951) is a treasure house of the development and modern status of our knowledge on twinning.

Among the modern heredopathologists Otmar Freiherr von Verschuer (b. 1896) is outstanding. His Erbpathologie (3. Aufl. Dresd., 1945) and his Leitfaden der Rassenhygiene (2. Aufl., Lpz., 1944) are the basic guides in Germany on heredopathology and eugenics. During the Second World War, Germany developed a special branch of heredopathology which we may call comparative or experimental. This branch, under the influence of the misleading concepts of politics, did not find it ethically objectionable to use human test objects for genetic experiments, without the free will of the victims.

Heredopathologists studied many problems such as the relation of chromosome mutations to hereditary disease (Besell G. 1939), the role of recessivity in heredopathosis (Touraine 1942), crossing-over and hemophilia (Riddell 1946), etc. As examples of polyphenic gene action the dysostosis multiplex, and the Bonnevie-Ullrich status (first described in 1930) were cited (Ullrich 1943). The heredity of mental diseases was investigated by F. J. Kallman (1943-46), Myerson (1942), Ross (1942) and others. The geography of hereditary diseases was first discussed by Verschuer (1943). Problems of heredodiagnostics also received full attention of the geneticists. Neel (1947) suggested methods for the detection of the genetic carrier of inherited diseases, while

[294] See GEDDA L., *Studio dei gemelli*. Roma, 1951, Cap. 6, 231-63.

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Cotterman (1948) described the subclinical manifestations of some hereditary affections.

The rapid advances of modern genetics were made possible by the successful development of accurate and adequate *methods of research*. The spirit of experimentation is innate in any breeder; it needs only a little prompting to bring accuracy and exactness into the research method. The success also depends upon the proper selection of the experimental objects. Since the beginning of modern genetics various new forms of approach were elaborated for the solution of the main genetic problems. Many of them, or at least the most effective ones, are described on the preceding pages. It was Raymond Pearl (1879-1940) especially who, in several of his articles and in a book, contributed to the perfection of research methods in genetics.[295] The idea of a biological farm for experimental investigation of heredity, variations, evolution, and similar problems was suggested by C. O. Whitman (1902). In the near past (Phillips 1948) it was also proposed that an international cooperation be obtained for cataloguing and perpetuating genetic stocks and for promoting the exchange of such stocks for breeding purposes.

Fig. 64. Raymond Pearl, 1879-1940

Various other facilities were suggested for genetic studies. Jollos (1921) introduced the infusoria as experimental objects for heredity studies.[296] Penrose (1946) and Schelling (1941) suggested the sib-pair linkage method of study. Russell (1946) proposed ovarian transplantation as a tool in genetics. One of the most important methods is, of course, the technic of irradiation of the giant chromosomes of the Drosophila, which is the most convenient approach to determine altered gene complex in the synaptic mates. The chromosomes are also approachable through direct microchemical examination (Casperson 1940).

The *methodology of human genetics* is well described by Lenz.[297] There are many

[295] PEARL R., Modes of research in genetics. N. Y., 1915.
[296] JOLLOS V., *Zschr. indukt. Abstamm.*, 1921, 24: 77-97.
[297] LENZ, In: *Baur's Grundriss*, etc. 2. Aufl., 1923, 1: 327-69.

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difficulties in securing accurate knowledge in human genetics. There can be no control over human matings, and the observations of a single investigator can cover a few generations only. We have no written records of human breedings (except when they are abnormal), and the family album gives only a very inadequate record which can be hardly completed by hearsay and other legends.

Further difficulties arise from the nature of hereditary diseases.[298] These are well understood by Lamy (1944) who enumerates the various sources of error in heredopathological investigation. A disease, even if it is hereditary, is not necessarily the result of the same gene's action. Once it may appear as a dominant character; again, it may come as a recessive character; sometimes, it may be sexlinked. This possibility occurs in such diseases as hemeralopia, deaf-mutism, and other eye or nerve diseases. Again, the same gene of pathological inheritance may manifest itself in the form of different clinical diseases. It just shows that while experimental genetics made great progress with such excellent test objects as the vinegar fly (Drosophila), human genetics lacks the same simplicity.

MENDELISM TODAY

The principle of segregation, which seemed to be of rather limited applicability at first, is now extended so that it seems to be the key to all possible inheritance among plants, animals, and human beings. The cytological studies of the 20th century provided a physical basis of the Mendelian formula (Woodruff). The application of Mendelian principles to animals was first made by Bateson (1902) and Cuénot (1903). Since then, many characters have been studied, and there is no question of the wide application of Mendel's discovery (Morgan 1919).

The bitter fights of the early years in this century are now forgotten, and there is nobody who would doubt the priority of Mendel's research and who would ascribe a major share in his discovery to the precursors and his contemporaries than what they deserved.

Some investigators, such as R. A. Fisher[299] talk of *Neomendelism* as a generalized extension of Mendel's discovery. This is genetics in a restricted sense, a science of variation and a science of transmission of characters. It is a science of particulate heredity by means of a special *organ of heredity* which is composed of the genes (and perhaps the plasmatic components). Neomendelism recognizes modifications or variations as well as mutations. In the latter changes there may be qualitative and quantitative differences produced in the organ of heredity. Thus, Neomendelism accepts the possibility of reaction between genotype and environment. Should we attach to Neomendelism the added burden of natural selection the result will be evolutionary genetics or Neodarwinism (Fisher).

[298] Cf. Lamy, in Footnote 65 (l. c., 141 etc.).
[299] Fisher R. A., The genetical basis of natural selection. 1930.

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Future

The future of genetics is easy to guess. The many fields which are benefitting from the application of the data of genetic research include the whole life, especially practical horticulture, agriculture, agrobiology, animal husbandry, and human affairs. A recent publication by F. B. Hutt and R. K. Cole of the Department of Poultry Husbandry (Cornell University, N. Y.) indicates the great economic value of applied genetics, e. g., on the field of animal pathology. Leukosis among the fowl is one of the most serious problems in many countries. In the U. S. it may cause loss as much as 65 million dollars annually. These investigators show that it is possible to develop a stock of poultry by proper breeding which will be very markedly resistant against infection with the virus of leukosis.[300]

Such studies have been carried out for the last 18 or 20 years in zootechnics. But the example also shows that the problems of applied genetics are much wider than the tasks of genetics as a pure science. Practical breeding is the " study of producing varieties for human needs " (Vavilov). As a practical discipline it sits now on the same wide basis as genetics. The theory of hybridization brings breeding the nearest to genetics since this theory is entirely on the basis of Mendel's laws and Morgan's gene theory of heredity. The chief aims of breeding include the development of changes which increase the resistance against disease. This again brings breeding near to the special branches of modern genetics, such as immunogenetics, heredopathology, biochemical genetics, etc.

Genetics itself will become a general research method for the solution of the many obscure problems in physiology and pathology. It is not a study of gene and chromosome alone. Among its future problems there are two major fields of operation: 1) genetic physiology, and 2) genetic pathology. Among its many unsolved problems we may list the origin and reproduction of genes, the dynamics of hereditary factors, the origin of pattern in the phenotype, and the exact relation of phenotype to the heritage (genotype) of the individual.

The genes represent a future *nuclear energy*, which can be turned into destructive force as well as into a force which, in a truly humanistic sense and by ethical methods, could be used in the service and for the betterment of mankind.

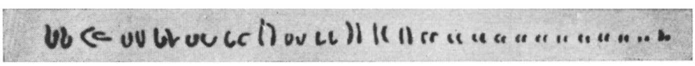

Fig. 65. Human chromosomes pairs

[300] Hutt F. B., etc. *Science*, 1953, 117: 695-7, June 19.

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Summary

The historiography of genetics is not very extensive. As a tribute to Gregor Mendel the Genesis of modern Genetics is briefly described in its full range, from the Paleolithic Age to Lysenko. Since the earliest times, the knowledge of heredity had been growing in proportion with the development of ideas on reproduction and continuity of the species. For various forms of life, the basic problems of interest remained essentially the same during all historical periods; only the emphasis shifted from the gross to the more detailed, and the answers oscillated between the theories of preformation and epigenesis. Against this historical background, Mendel and the Mendelian laws stand out as the basic foundation of genetics.

The vital growing ideas on generation and evolution of plants, animals, and man are briefly reviewed and exposed as they had occurred before and after Mendel. The historical sketch leads us to ancient Assyria, India, the biblical times, and the classical Antiquity, to the early Greek philosophers and physicians whose works are sampled to illustrate the ancient beliefs concerning the role of male and female semen in generation, and concerning the proportional share of parents in the formation of body and mind of the offspring. The medieval knowledge on heredity is at its highest in the writings of Albertus Magnus whose work represents the refinement of scholastic science.

In these earlier times people did not know the exact functions of the organs of generation, or the true nature of sex. After the invention of the microscope in the 16th, and with a more liberal spirit of research in the 17th centuries, the sexual life and the male and female germ cells of many bisexual beings, including man, were gradually discovered during the 200-year period from 1677 to 1877. This happened with all sorts of speculation about heredity and about the origin and evolution of life. Meanwhile, many practical and theoretical hybridizers saw the various peculiarities in the filial generations, and many observed normal and abnormal characters transmitted from parents to offspring. Yet, none could formulate these observations into a mathematical regularity of inheritance until the reports of Gregor Mendel in 1865 on the result of his plant-crossings.

His discovery was buried, however, until 1900 when other biologists came to the same results, and revived and accepted his rules as the laws of heredity. From then on, modern genetics advanced rapidly and branched into many activities, everywhere fully supporting the views of Mendel. Thus, Mendel is truly the father of genetics, except for communist Russians whose political theories demand the denial of Mendelian heredity and the adherence to older discarded theories.

Genetics has the destiny to solve many practical problems in the life of nations, and to investigate a number of important yet unknown factors, in order to utilize the gene theory of heredity, and the " nuclear energy ", for a wider and brighter service of humanity.

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