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A CHRONOLOGY OF GENETICS

ROBERT COOK

Editor, *Journal of Heredity*

THE SCIENCE OF GENETICS as of 1937 has a long and rather involved history, which has not proved easy to treat as a chronology. Made up as it has been of a fusion of diverse specialties which have developed at different rates, a simple chronological listing of discoveries and developments necessarily gives a rather fragmentary picture of the unfolding of the modern science of heredity. Various plans were considered to avoid this difficulty, but the most satisfactory treatment seemed to be to combine everything in one simple chronology, which branches out into occasional summary paragraphs to suggest, without prohibitive chronological detail, the recent developments, and to buttress this with a graphic genetic family tree to give visually the relations of the various main components that have gone to make our modern genetic organism. The difficulties that have been encountered in determining many of the "first discoveries" noted in this chronology suggest that an exhaustive history of genetics will soon be necessary. Roberts and Zirkle have recently summarized the early publications on plant hybridization, but a connected story of the development of genetics as a whole remains to be written.

The compiler takes this opportunity to acknowledge invaluable help and suggestions from a group of about 35 geneticists who generously read and commented on a mimeographed first draft of this chronology. In the time allotted it would have been impossible without this freely given aid to have done nearly so complete a job as is here presented — which remains, it is regretfully realized, even with this help, only a very rough sketch. It was the wish of the editors to present in this Yearbook a bird's-eye view of genetic progress pointing out the important highlights but not in too much detail. Without overburdening this chronology with bibliographic references, and thereby reducing its readability to a minimum, and at the same time to make available authority for the dates given, a condensed list of references is included. A more detailed bibliography giving titles of articles cited and authors in full has been deposited in manuscript form in the United States Department of Agriculture library. Copies of this bibliography may be obtained from the library through the Biblioform Film Service. It is hoped that this will make all references reasonably easily available to all who are interested.

BEGINNINGS

FIRST HYBRIDS were probably of species and varieties of cattle and dogs, by Neolithic people, possibly as much as 10,000 to 25,000 years ago.

Several varieties of dogs and of cattle and sheep are depicted on Egyptian and Babylonian monuments of 5,000 years ago. The bisexual nature of the date palm was also recognized by the early Babylonians and Assyrians 5,000 years ago. Mules are mentioned in Homer (B. C. 800) and in Herodotus (fifth century B. C.). The writings of Aristotle and other ancients abound in a wealth of observations, many of them confirmed by modern experiments. Unfortunately they also contain much very fanciful material-descriptions of astonishing and highly improbable hybrids between a great variety of animals. This very likely meant no more than that monstrosities were ascribed to hybridization, as the ancients generally looked upon the process of hybridization with abhorrence. Even angels and demons were reported on excellent authority to have produced hybrid progeny whose astonishing characteristics were limited only by the imagination of the narrator. Theories of heredity were not lacking, but facts that might verify these purely speculative fabrications were held in small esteem. Vergil tells us that the chosen seed, improved through years and labor, was seen to run back, unless man selected by hand the largest and fullest ears (Georgics I: 197). Columella and Varro also affirm the need for selection of cereal varieties. Theophrastus and Pliny discussed sex in plants but reported no experiments.

Allusions to the tendency of "like to beget like" are not hard to find in ancient literature. The Middle Ages enthusiastically added much to the fables but nothing to the factual background of the ancients. In spite of the lack of theoretical background, animal breeding, based on traditional methods ("like begets like" and various approximations to the progeny test) excellently exemplified in the New Testament aphorism “by their fruits ye shall know them”, (Matthew 7: 20) made very considerable progress.

That primitive men have been not only persistent plant breeders but fairly successful ones is evidenced by the remarkable progress made in plant breeding in many parts of the world. The ancient Chinese are credited with breeding superior varieties of rice and hybrid flowers. Russian workers have recently published most interesting accounts of the wheat breeding on the southern slopes of the Caucasus Mountains. We have only to consider Indian corn, and the remarkable varieties produced by the American Indians, to realize the fact that man has been breeding plants from very early times.

The records left by the Babylonians and Egyptians leave no doubt that at least 5,000 years ago distinct breeds of domesticated animals were recognized. Certain of the types depicted on those ancient monuments bear a remarkable resemblance to modern breeds. Excellent types of beef cattle and of merinolike sheep are to be seen in some of these ancient relics, which mark the beginnings of recorded history. Jacob’s famous agreement with Laban regarding “goats that were ringstraked and spotted” (Genesis 30: 35) has often been cited as evidence of an early belief in maternal impressions. But we read in the next verse that Jacob relied on “three days’ journey” between Laban’s solid-colored “cattle” and his own spotted flocks, and when it is explicitly stated that the rams used were spotted, it is clear that this ancient Hebrew herdsman did not depend entirely on magic to produce results in animal breeding. Early Hindu writers also discussed these matters at length.

While the philosophers and scholars of the Middle Ages were piling one improbability on another, at least two great modern breeds were being formed — the Arab horse and the merino sheep. The desert horse had very remote beginnings, and it had reached or maintained such a state of excellence by the Middle Ages that it contributed greatly to the development of the horse of today. The English Thoroughbred breed traces to two Arab horses and a Barb imported into England about the time of Charles II. From very remote beginnings the Spanish merino had reached a perfection that gave Spain virtually a monopoly of the fine wool weaving industry by the fifteenth century. This monopoly was maintained by a strict embargo. Through royal courtesy the ban was lifted in 1765 to permit the export of merinos into Saxony. Within a few years merinos were exported from Spain to several other countries. In 1786 the famous merino herd at Rambouillet, France, was established. Maintained continuously since that time with only one importation of outside blood, this herd has formed the basis for the modern Rambouillet breed, which today is spread over all the world and is raised in greater numbers than any other type of sheep.

One other "root" of modern genetics also had a very early beginning. Mathematics was a subject intensively studied in Babylon, Egypt, and Greece. Some branches of the science of numbers were highly developed among the ancients, although algebra, so essential in modern genetic experiments, was not well developed until after the Crusades. This early science of numbers formed the groundwork for the later development of statistics, probability, and correlation, all necessary tools of modern genetics.

BACKGROUND

BY THE BEGINNING of the seventeenth century a new spirit of scientific skepticism had begun to be manifest. The reaction of common sense against the cumulative absurdities of centuries of uncontrolled verbalism was reflected in the first stirrings of an age of scientific experiment. Nehemiah Grew in 1676 suggested the nature of ovules and pollen. A growing interest in biology culminated in the publication in 1694 of Camerarius' (Germany) famous 50-page letter on the sex of plants (De Sexu Plantarum Epistola), which put on record convincing evidence that plants are sexual organisms. This was followed early in the eighteenth century by the production of the first artificial plant hybrid by Thomas Fairchild (in England a short time before 1717). The practical implication of these discoveries is reflected in the founding in 1727 of the seed-breeding establishment today world-famous as Vilmorin-Andrieux et Cie. (One of the early great successes of the Vilmorins was the development of the sugar beet during the Napoleonic era.) In the next 50 years there was a veritable wave of hybridizing. Crosses between more than a dozen different plant genera were made by several investigators and reported with varying degrees of accuracy. This period culminated in the publication of J. G. Koelreuter's work (Germany, 1761-66), reporting the results of 136 experiments in artificial hybridization. This mass of evidence definitely established plant hybridization as a scientific. pursuit.

At the same time independent progress was being made in fields that after 1900 were to have a profound influence on genetics. M. Malphigi (Italy) was laying the groundwork for descriptive embryology (1650-70). A. von Leeuwenhoek (Holland) was discovering the tiny world of the microscope, and with his pupil, Johan Ham (Holland), in 1677, was the first to see mammalian germ cells (spermatozoa). In 1780 L. Spallanzani (Italy) attempted to demonstrate by artificial insemination in dogs the essential part played by the male in fertilization.* The modern science of statistics had its beginnings at about the same time, in a treatise published in 1761 by a Prussian divine, J. P. Süssmilch, who undertook by appeal to vital statistics to prove the glory of God. The leisurely progress of scientific thought is suggested by the award to Linnaeus (Sweden) in 1760 of a prize for an essay on sex in plants — nearly a century after Camerarius had rather conclusively laid the groundwork of this subject. Linnaeus' publication of Species Plantarum in 1753, which attempted to classify plants according to their assumed relationships, marks an important step in the development of evolution theory. In 1760 Robert Bakewell (England) took over the management of the Dishley Estate, where for 35 years he proved to his own satisfaction that inbreeding is not necessarily injurious and that it is the quickest way to fix type. His experiments laid the groundwork for the development of many of the modern breeds of livestock. In 1793 C. K. Sprengel (Prussia) observed the cross-pollination of plants by insects.

In the matter of human heredity some knowledge had also been accumulating. From the earliest times resemblance in relatives had been noted. The inheritance of such definite anatomical peculiarities as the "Hapsburg jaw" had frequently been recognized. Man has never been well adapted for laboratory study, and little exact progress was made. A notable exception has to do with sex-linked inheritance. The peculiar inheritance of color-blindness was reported to the Royal Society as long ago as 1779 by a British divine, Michael Lort. Forty years later C. T. Nasse (Germany) formulated a law of sex-linked inheritance based on hemophilia, a disease of unusual interest because of its occurrence in the royal families of Europe.

By 1760 the stage was set for a century of biological progress that culminated in 1859 with the publication of Darwin's Origin of Species.

GENETICS IS BORN, 1760-1900

1760-1830 — Foundation of important livestock breeds through inbreeding and selection practiced by English breeders — Bakewell, Bates, the Collings, and others.

1809 — Publication of J. B. P. de Lamarck's Philosophie Zoologique (France) represented the first attempt to produce a comprehensive theory of evolution. Erasmus Darwin (England), G. L. L. de Buffon (France), and W. von Goethe (the German poet whose Metamorphosis of Plants, 1790, is a notable

* His "proof" that the fluid and not the spermatozoa was the fertilizing agent was unfortunately wrong. Not until 1824 did Prevost and Dumas correct this mistake.

milestone in biological thinking) had dealt with various phases of the problem of organic development of individuals, species, and genera. Lamarck attempted to weld these observations and speculations into a coherent theory of evolution, an important step in biological progress.

1812 — (1) Karl Friedrich Gauss (Germany), Theoria combinationis observationum erroribus minimis obnoxia (theory of least squares — basic in the statistical evaluation of data).

(2) Pierre Simon Laplace (France), Theorie analytiques des probabilités. Beginning of "the law of error concept."

1820 — (1) Gauss, evolution of the probable error — for a century the almost universally used test of the significance of experimental data.

(2) C. F. Nasse (Germany), Nasse's law of male sex-linked inheritance, based on study of hemophilia.

1822 — John Goss (England) reports but does not interpret dominance and recessiveness, and segregation in pea hybrids.

1823 — Thomas Andrew Knight (England), Knight-Darwin law of cross-breeding (value of crossing to produce better plants). Dominance, recessiveness, and segregation observed in peas without mathematical relationships.

1826 — A. Sageret (France) classifies contrasting characters in the parents of a cross in pairs, using muskmelons and cantaloupes, cites unit characters in human eye color, and uses the term "dominant."

1835 — (1) Division of cells described by H. von Mohl (Germany).

(2) Publication of K. F. von Gaertner's Memoir (Germany) reporting 25 years of hybridization experiments dealing with 107 species of plants; noted distinction between the uniformity of first hybrid generation and the diversity of later generations, and reported hybrid vigor.

1838-39 — Cell theory, M. J. Schleiden and T. Schwann (Germany). First generalized statement of the theory that all organisms are made up of cells — one of the great generalizations of experimental biology.

1840 — Word "protoplasm" coined by J. E. Purkinje (Bohemia), though used in a slightly different sense from that of today. A. Payen (France) and F. Cohn (Germany) suggested the essential similarity of protoplasm as the physical basis of all life (1846-50).

1841 — R. A. von Kölliker (Switzerland) proves that spermatozoa arise from parent body and are not parasites as was previously believed.

1840-50 — Louis de Vilmorin (France) develops the progeny test ("genealogical selection") in wheat, oat, and sugar-beet breeding.

1843 — John Le Couteur (island of Jersey) publishes a summary of his work on wheat breeding. "This summary has been the basis and origin of variety testing" (De Vries). The same methods were independently developed somewhat earlier by Patrick Sheriff (Scotland), who produced many outstanding varieties.

1846 — (1) A. Quetelet (Belgium), Lettres . . . sur la Theorie des Probabilités. Described biological phenomena in quantitative terms.

(2) Von Mohl recognizes nature and importance of protoplasm in its present sense.

1848 — W. Hofmeister (Germany) figures the chromosomes as unstained bodies, but without appreciating their significance.

1849 — (1) Sir Richard Owen (England) enunciates principle of the continuity of the germ plasm. This idea was developed by Virchow, Weismann, and others, and culminated in the modern gene theory.

(2) Union of sperm cell and egg cell (fertilization) first seen in seaweed (*Fucus*) by G. Thuret (France). A year later he showed that the egg would not develop without fertilization.

1858 — R. Virchow (Germany) enunciates the principle: Omnis cellula e cellula (every cell from a cell), finally disposing of the theory of spontaneous generation — a basic biological generalization which completed the cell theory, establishing the continuity of all life from remote beginnings.

1859 — Publication of Charles Darwin's Origin of Species (England). This contains extensive discussions of hybrids, but its contribution to genetics was mostly indirect. It marks a turning point in scientific thought and dates the beginning of the modern experimental approach to biological problems.

1861-62 — M. J. S. Schultze (Germany) and H. A. de Bary (Germany) establish the essential unity of protoplasm in all living cells.

1863 — D. A. Godron and C. V. Naudin (France) independently report experiments in plant hybridization. Naudin confirmed Sageret's work, in general discussed work of the early hybridizers, and reported dominance and segregation in *Datura* (jimsonweed) hybrids. He did not deal with single characters and reported no statistical observations on the second generation. His theoretical explanation of his facts was a forerunner of Mendel's ideas, but inferred rather than deduced.

1865 — F. Schweigger-Seidel and A. von la Valette St. George (Germany) independently prove that a spermatozoon is a single cell and contains nucleus and cytoplasm.

It is impossible to tell how much of this earlier work was known to Gregor Mendel. Very likely most of it was. The work of Godron and Naudin was jointly awarded a prize by the French Academy of Sciences, so that it must have been fairly well known in scientific circles. Mendel had access to a rather extensive library, which included all of Darwin's works, and many other books on plant hybridization, etc. He was in contact with such eminent biologists as Nägeli, so that there is an excellent possibility that he had the benefit of this earlier work. But be that as it may:

1866 — (1) Gregor Mendel (Austria) publishes in the Proceedings of the Brünn Natural History Society (Verhandlungen der Natur Forschenden Verein in Brünn) his investigations concerning plant hybrids, Versuche über Pflanzen-Hybriden, one of the outstandingly lucid and detailed expositions of a fundamental discovery. For 34 years Mendel's papers lay forgotten.

(2) E. Haeckel (Germany) predicts that the cell nucleus will play a star role in heredity.

1867 — (1) Vilmorin tests immediate effect of pollen.

(2) H. S. Bidwell (United States) reports controlled pollination in maize.

1868 — Darwin's pangen hypothesis — gemmules (hypothetical particles that float in the blood stream) are given off by cells and held to modify germ cells.

1873-4 — L. Auerbach (Germany) begins experimental study of cell mechanics (fertilization).

1875 — (1) E. Strasburger (Germany) describes the chromosomes.

(2) Oscar Hertwig (Germany) proves that fertilization consists of union of two parental nuclei contained in the sperm and ovum. This demonstration that sexual reproduction is a process contributed to essentially equally by the two sexes marked an important advance. It disposed of speculation regarding the role of the two sexes in inheritance, and it showed that genetics is basically a problem of cell physiology.

1878-81 — W. J. Beal (United States) determines increased yields of corn hybrids between varieties and suggests their use in corn production.

1879-82 — W. Flemming (Germany) describes the longitudinal splitting of the chromosomes.

1881 — W. O. Focke (Germany) coins the term "xenia" to denote immediate effect of pollen on the endosperm in the maize seed.

1883 — (1) P. J. van Beneden (Belgium) begins study of early history of animal egg. Reports reduction of the chromosome number in the egg cells to half that in body cells and holds that chromosomes have a genetic continuity throughout the life cycle — basically important concepts in genetic theory.

(2) E. L. Sturtevant (United States) observes without interpreting first linkage of genes now known as tunicate and sugary (*TuSu*) in maize.

1884 — K. W. von Nägeli (Switzerland), ideoplasm concept — control of heredity seen as due to "ids", which were conceived to be solid particles. Nägeli's book was important as a precursor of Weismann's The Germ Plasm.

1884-5 — (1) Identification of the cell nucleus as the basis of inheritance "made independently and almost simultaneously by Hertwig, Strasburger, Kölliker, and A. Weismann" (Germany).

(2) Halves of split chromosomes shown going to opposite poles by Flemming and others.

1885 — C. Rabl (Austria) announces the individuality of the chromosomes.

1886 — (1) Francis Galton (England) devises the correlation table — a most useful tool in applying statistical methods to many biological problems.

(2) Hugo de Vries (Holland) discovers aberrant evening primrose plants at Hilversum, Holland. Experiments with these extending over 15 years formed the basis for his mutation theory of evolution.

1885-87 — Weismann publishes a theory of chromosome behavior during cell division and fertilization which explains earlier observations of Van Beneden, Strasburger, etc., and predicts that two kinds of cell division will be discovered — mitosis (already known) and reduction, in which the chromosome number will be reduced to half by an orderly separation of paternal and maternal chromosomes.

1887 — W. Roux (Germany) suggests that the longitudinal splitting of the chromosomes when dividing means that many different qualities are arranged single file in the chromosome, and that these are all contributed by this method of division to each daughter cell.

1887-88 — Th. Boveri (Germany) verifies Weismann's prediction of the reduction of the chromosomes by observing the phenomenon in *Ascaris*.

1888 — Chromosomes named by W. Waldeyer (Germany).

1889 — (1) De Vries revises the “pangen” theory of determiners floating in the blood stream, and denies any transfer of gemmules (determiners) from body cells to gametes.

(2) Francis Galton (England) publishes Natural Inheritance, which formulates his law of ancestral inheritance — a statistical statement of the relative influence of parents, grandparents, etc., in determining characteristics in offspring.

1890 — (1) Law of numerical equality of paternal and maternal chromosomes at fertilization in animals and plants (Boveri, Germany; L. Guignard, France).

(2) Babcock test for butterfat percentages (United States). Beginnings of dairy-cattle selection for butterfat production on scientific basis.

1891 — (1) Willett M. Hays (United States) develops the centgener progeny test, thereby recognizing that the test of the genetic quality of an individual can be adequately evaluated only by a study of its progeny. At about the same time the New York (Cornell) Agricultural Experiment Station develops rod-row method of small grain testing.

(2) W. A. Kellerman and W. T. Swingle (United States) make first count on a segregating ear of maize.

1892 — With publication of Das Keimplasma (The Germ Plasm) Weismann enunciates the then very radical principle of noninheritance of acquired characters, and expands Nägeli’s idioplasm theory to bring cell theory and “genetic theory” into organic relationship. Basing his theory on Van Beneden’s observations, Weismann explains the reduction division as a method of exactly distributing the chromosome material.

1894 — (1) W. Bateson (England) emphasizes the importance of the study of “discontinuous variation” (an approach toward the idea of Mendelian units) in solving the problem of heredity.

(2) Karl Pearson (England) publishes first of Contributions to the Mathematical Theory of Evolution, developing methods of dealing statistically with skew frequency curves.

(3) A. Millardet (France) notes “false hybrids” entirely resembling pollen parent (patrogenesis).

1897 — (1) G. Udny Yule (England), publications On the Theory of Correlation.

(2) First egg-laying contests (England).

1898 — (1) Pearson develops Galton’s Law of Ancestral Heredity and also introduces the standard deviation, an improved method of determining the significance of deviations of observed data from theoretical perfection.

(2) S. G. Navashin (Russia) discovers double fertilization in higher plants.

(3) W. J. Spillman (United States) notes segregation in wheat, which he reported in 1901 in an independent statement of Mendelian principles.

(4) G. M. Gowell (United States) installs 52 trap nests and initiates scientific breeding for egg production.

(5) Flemming counts human chromosomes, finding 24 in corneal (eye) tissue. (Later work with improved technique shows 24 pairs.)

1899 — (1) L. Cuénot (France) working with animals, and Strasburger (Germany) working with plants, advance theory that sex is controlled within the germ cell, not by environment.

(2) De Vries and C. F. J. E. Correns (Germany) publish almost simultaneously an explanation of xenia in corn as due to double fertilization.

(3) First International Conference of Hybridization (the later conferences in this series were called Congresses of Genetics) held in London.

EARLY DAYS OF GENETICS

THE TURN OF THE CENTURY was an epochal year in the experimental study of heredity. The almost simultaneous rediscovery of Mendel's paper independently by three investigators (who had, when they read Mendel's paper, experimental material of their own to verify his conclusions), was a striking symptom of an even wider trend. Bateson had for years been attacking the problem of discontinuous variation, and Haldane says that had not Mendel's paper been discovered, Bateson would undoubtedly have been buried in Westminster Abbey as the discoverer of atomic heredity. Spillman's wheat work in the United States had reached a point where he appears to have been just on the brink of making the same illuminating generalization. Other workers also were hot on the trail of the gene, and the time was ripe for a veritable explosion of genetic progress. Within 3 years of the triple De Vries — Correns — Von Tschermak announcements, abundant verification of Mendel's work had been made by many workers, and the universality of the Mendelian principles had been demonstrated in plants, animals, and man. The fecund pomace fly, *Drosophila,* was about to enter his milk-bottle kingdom and populate acres of banana-agar nutrient medium with an ever-growing progeny of mutant forms. Into the hands of the research investigator had been given the key to unlock that perennial mystery of the ages, heredity.

1900 — Rediscovery and verification of Mendel's principles independently by De Vries (Holland), Correns (Germany), and E. von Tschermak (Austria), marking the beginning of modern genetics.

1901 — (1) H. Henking (Germany), F. C. Paulmier (United States), and others report an "accessory chromosome" in spermatozoa (later identified with sex determination), based on work begun in 1891.

(2) Bateson publishes a translation of Mendel's paper.

1902 — (1) Terms allelomorph, homozygote, heterozygote, F_1, F_2, coined by Bateson. In their report to the evolution committee, Bateson and Saunders list 26 instances of allelomorphism which had been "actually proved to exist, or may be inferred from the published record." This included cases in peas, wheat, maize, *Datura, Oenothera,* snapdragon, mouse, fowl, cattle. The Mendelian nature of polydactylism (an extra finger) in man was suggested.

(2) De Vries — The Mutation Theory of Evolution, based on studies of evening primrose.

(3) T. H. Montgomery (United States) announces the pairing of homologous maternal and paternal chromosomes during synapsis (joining and separation prior to formation of germ cells with reduced chromosome number).

(4) E. C. McClung (United States) relates an accessory chromosome found in some insects to sex determination — first attempt to connect a specific character with a particular chromosome. The concept of specific sex chromosomes, which have a major influence in determining sex, has been verified, with modifications, in a range of organisms extending from the pomace fly to man.

(5) Cuénot first demonstrates Mendelism in animals (normal and albino mice).

1902 — (6) Bateson defends Mendelism against attacks of W. F. R. Weldon and Karl Pearson (England). This heated clash regarding the utility of experimental versus statistical approaches to biological problems continued intermittently until 1904. Publication of first number of Biometrika, the leading journal dealing with the statistical aspects of genetics.

1902-3 — W. W. Sutton [*sic*, actually W. S. Sutton] (United States) shows that body chromosomes are individually recognizable and points out the mutual interrelations between cytological observations. and Mendelian phenomena, closing the gap between cytology and genetics.

1903 — (1) Pure-line concept (variations in the progeny of a single plant of a self-fertilized species are not due to inheritance) first put forward by W. L. Johannsen (Denmark). Phenotype and genotype defined. Modern concept of "selection" born.

(2) R. H. Biffen (England) reports that resistance to stripe rust of wheat is governed by a single Mendelian recessive factor.

(3) Bateson (walnut, rose, and single comb in fowl) and Cuénot (albino and pigmented mice) note interaction of nonallelomorphic factors (later called epistacy).

1904 — (1) C. B. Davenport (United States) confirms Mendelian inheritance of polydactylism in man.

(2) American. Breeders Association founded under Secretary of Agriculture James Wilson, with Willett M. Hays as secretary.

(3) Thomas Hunt Morgan becomes professor of zoology at Columbia University. This represents the beginning of the former "Columbia group" of genetic research workers, which included many of the names outstanding in genetics today. Other centers also had their origin about this time, at Harvard University, the University of Chicago, the University of Indiana, and Leland Stanford University.

(4) Station for Experimental Evolution established by the Carnegie Institution of Washington.

(5) A. F. Blakeslee (United States) reports isolation of sex-different strains of molds. First called "plus" and "minus", these were later called "male" and "female" though no morphological differences could be found between them.

1905 — (1) G. H. Shull and E. M. East (United States) begin independent experiments on inbreeding in maize that opens up a field of the utmost theoretical and practical importance.

(2) N. M. Stevens and E. B. Wilson (United States) confirm McClung's sex-determination theory.

(3) "Coupling" (linkage) in sweet pea analyzed by Bateson, E. R. Saunders, and R. C. Punnett (England). Bateson and Punnett explain the walnut comb in the fowl as being due to two dominant factors, one of which alone produces pea combs, and the other, rose combs — the double recessive being single combs. This first report of interaction of Mendelian factors marked a very important advance.

(4) O. F. Cook and W. T. Swingle (United States) publish diagram and propose names for the sexual cycle (sporophyte-gametophyte) in plants.

1906 — (1) Term "genetics" coined by Bateson.

(2) C. W. Woodworth and W. E. Castle (United States) "discover" *Drosophila.* "More has been learned concerning heredity from this one species since 1910 than had been learned from all sources before that time." It produces 25 generations a year and has but 4 pairs of chromosomes, so that it is ideally suited to make linkage studies. The modern gene theory is based largely on studies of *Drosophila.*

(3) Possible relation between linkage and the chromosomes pointed out by R. H. Lock (England).

(4) George Rommel begins U. S. Department of Agriculture inbreeding experiments with guinea pigs, which have been continued ever since.

1907 — (1) Correns advances theory of two kinds of male gametes (male-determining and female-determining).

(2) J. B. Norton (United States) publishes rod-row system of breeding, first put into general use by him in 1902.

(3) Strasburger uses terms haploid and diploid for reduced and double number of chromosomes.

1907 — (4) A. M. Lutz (United States) shows that the gigas mutation of the evening-primrose has double number of chromosomes of *Oenothera lamarckiana* Ser.

The discovery of a tetraploid in the evening-primrose opened up the subject of variation of chromosome number in general, and of polyploidy in particular. This discovery that organisms might vary in their chromosome constitution by an entire set of chromosomes has today developed a very extensive branch of cyto-genetics. Discoveries of polyploid series in wheat, the roses, the *Daturas* and *Solanums*, and elsewhere have marked a distinct advance in our understanding of the development of species. The artificial production of polyploids by heat treatment and by other means has been a more recent development of great promise. Even greater in its possibilities may be the production of generic polyploids (amphidiploids) having one or more complete chromosome complements from each parent species. These forms are generally self-fertile but are usually sterile with the parent species or genera.

(5) Bateson coins terms "epistatic" and "hypostatic" to describe interrelations of non-allelomorphic genes.

1908 — (1) Cuénot discovers that the yellow gene (Y) in mice is lethal, suggesting that it kills the embryo early in development when inherited from both parents.

(2) Zeitschrift für induktive Abstammungs-and Vererbungslehre (Journal for Inductive Descendence and Inheritance Theory) founded.

(3) Delaware Agricultural Experiment Station begins inbreeding experiments with swine.

Many practical breeders before this time had used intensive inbreeding in their operations, but the degree of inbreeding actually practiced is very hard to determine. Several instances are on record of herds being maintained for a number of generations without the introduction of new blood. N. H. Gentry's work with Berkshire swine in Missouri was a notably successful example of the use of inbreeding in breed improvement. The Delaware experiment represents the first attempt to attack this problem in a scientific manner with farm animals. All of the swine inbreeding experiments (and they are practically the only experiments in the intense inbreeding of livestock, by brother X sister matings, that have been undertaken, though considerably more has been done with poultry) have been only partially successful from a practical standpoint. The hoped-for production of highly inbred lines of swine that could be crossed to utilize to the full the principle of hybrid vigor in the first generation has failed to materialize because of the practical difficulties encountered in maintaining the inbred lines. Theoretically there appears to be no reason why robust inbred lines cannot be produced as has been done with rats and guinea pigs. Among the outstanding later experiments are those at the University of California, the Oklahoma Agricultural Experiment Station, Iowa State College (poultry), the Minnesota Agricultural Experiment Station, and the United States Department of Agriculture.

Many less direct attempts to produce highly inbred herds of livestock have been started and are continuing. Notable among these is the United States Department of Agriculture's development in dairy-cattle breeding, which has continued since 1912. The intention is to produce dairy sires pure or homozygous for high production by line breeding as intense as possible to the foundation sire of the herd. While many practical breeders have used this method with livestock for short periods, this continuing project, with accurate records for many generations, is unique.

(4) H. Nilsson-Ehle (Sweden) explains that inheritance of color of seed in wheat is largely due to three Mendelian factors — multiple factors and blending inheritance begin to be added to Mendelian concepts. This principle was confirmed a year later by East in corn.

1909 — (1) Crossing-over hypothesis (exchange of segments in paired chromosomes) advanced by F. A. Janssens (Belgium).

(2) R. A. Emerson (United States) reports multiple allelomorphs (more than one alternative factor) in beans and maize.

(3) Sir Francis Galton's bequest to found the Galton Laboratory at the University of London establishes the first laboratory devoted to the study of human heredity.

(4) Shull suggests use of first-generation hybrids between inbred lines as a basis of practical corn breeding.

1910 — (1) L. Epstein and R. Ottenberg (United States) point out that human blood groups (discovered by K. Landsteiner, Austria, in 1900 and classified by Jansky, Germany, in 1907) follow Mendelian principles in inheritance.

(2) Morgan proposes explanation of sex-linked inheritance; publishes first gene mutation in *Drosophila* (white eye).

(3) Announcement of the gene theory by Morgan, which includes the principle of linkage of genes resident on the same chromosome. This brilliant hypothesis has been upheld in a multitude of experiments. Beginning of chromosome maps compiled by linkage and cross-over data.

(4) A. B. Bruce, and F. W. Keeble, and C. Pellew (England) suggest that hybrid vigor is due to dominant favorable growth factors.

(5) A. Lang (Switzerland) suggests multiple factor hypothesis to account for size differences in rabbits.

(6) H. Winkler (Germany) publishes method of producing *Solanum* chimaeras artificially. The explanation of these chimaeras as layers (periclinal) and sectors (sectorial) of cells from stock and cion was furnished by Erwin Baur (Germany) 1914.

1911 — (1) Journal of Genetics (England) established.

(2) Raymond Pearl (United States) publishes the first of his studies of egg production in the fowl.

(3) G. N. Collins and J. H. Kempton (United States) report first linkage in maize.

(4) Baur publishes the first edition of his Introduction to the Experimental Study of Heredity, Einführung in die experimentelle Vererbungslehre.

(5) Richard Goldschmidt (Germany) publishes the first edition of his Einführung in die Vererbungswissenschaft (Introduction to the Science of Heredity), which summarizes his theory of sex determination as a matter of rate of developmental expression of sex-determining genes — demonstrated by the production of intersexual forms in hybrids of the gypsy moth.

(6) W. E. Castle and J. C. Philips (United States), ovary transplantation experiment in the guinea pig, showing nonmodification of genetic characters through change in embryo environment.

(7) Cuénot, explanation of multiple allelomorphism in mice.

1912 — (1) R. R. Gates (England) identifies *Oenothera semi-gigas* Vries as a triploid — the first to be recognized (triploids have three sets of chromosomes).

(2) H. S. Jennings (United States) shows that with self-fertilization the percentage of heterozygosis is halved in each successive generation.

This principle was elaborated by H. D. Fish (United States 1914) and Pearl 1913-17, and expanded by Jennings in 1917. In 1923 Sewell Wright (United States) published a general inbreeding coefficient applicable to irregular systems of mating. Since that time the evolutionary implications of Mendelian heredity have been developed by Wright, R. A. Fisher, J. B. S. Haldane, and others.

1913 — (1) C. B. Bridges (United States) reports nondisjunction of sex chromosomes (both sex chromosomes going to one gamete and none to the other). Important confirmation of chromosome theory.

(2) Nils Hansson (Sweden) publishes first formula for a sire index, an improvement in the progeny test for characters not expressed by the sire.

More recently the sire-index idea has been elaborated by a number of suggested modifications of Hansson's original idea. All of these are based on the concept that the sire's transmitting ability for a character he does not himself show (such as milk or egg production) can be measured by comparing the production of his daughters with that of their dams. This concept is one of the bases of the "proved, sire movement" started in 1918 by the United States Department of Agriculture, which attempts to discover and to utilize to the maximum the sires that transmit desirable qualities to the greatest degree.

1915 — Morgan, A. H. Sturtevant, Bridges, and H. J. Muller (United States) publish The Mechanism of Mendelian Heredity — an epoch-making book.

1916 — (1) Castle confirms Lang's multiple-factor hypothesis of blending inheritance in rabbits.

(2) Winkler produces polyploid forms from the callus tissue of decapitated grafts.

This method of doubling, tripling, and quadrupling the chromosome number has been rather widely used in experimental procedures by other workers. By applying it to haploid tomatoes, E. W. Lindstrom (United States, 1927) was able to obtain a pure line by doubling of identical chromosome complements — a procedure of considerable value in genetics and plant breeding.

(3) Castle and Wright discover first linkage in a mammal (rat).

(4) Pearl demonstrates effectiveness of pedigree selection contrasted with mass selection in the fowl.

(5) Shull suggests the word "heterosis" to designate the vigor of first-generation hybrids.

1917 — (1) O. Winge (Denmark) elaborates theory of polyploid origin of new species by multiplication of a basic chromosome complex.

(2) Emerson finds variegated pericarp in maize due to an unstable gene.

(3) The Connecticut Agricultural Experiment Station produces the first commercial "crossed corn."

Following the early experiments of Beal, and the inbreeding experiments of Shull and East, inbreeding experiments with maize enjoyed a considerable vogue. It was found that where some of these uniform but usually rather unpromising inbred lines were crossed, an extremely vigorous and uniform first-generation hybrid was produced, which exceeded the yields of commercial varieties by 30 percent or even more. The production of this crossed corn seed on a commercial basis was first attempted at the Connecticut Station. Unfortunately the lack of vigor and the small quantities of seed produced by the inbred strains made seed production difficult and expensive. To obviate this difficulty the system of "double-crossed corn" (suggested by D. F. Jones in 1919, first commercial production attempted in 1921 by George S. Carter, Clinton, Conn.) was perfected, whereby four inbred lines were used. These lines (designated A, B, C, D) are crossed in pairs (A × B and C × D), and the resulting two extremely vigorous hybrids are crossed to produce the commercial seed. These varieties have great vigor and uniformity, and production of seed in commercial quantities is entirely feasible. Many workers have contributed notably to this development, among them D. F. Jones, H. A. Wallace, F. D. Richey, and M. T. Jenkins, and many others in the United States Department of Agriculture and in the Corn Belt experiment stations.

The concepts developed by inbreeding have been applied in other ways, such as that of shifting a single desirable character from one variety to another by crossing and then by repeatedly back-crossing, to the other parental variety with the majority, of desirable characteristics, those segregates that have the one desired character. H. V. Harlan and M. L. Martini (United States) first used this technique in barley in 1922, and it has been applied with equal success by several other workers.

(4) W. B. Kirkham, H. L. Ibsen, and E. Steigleder (United States) prove the lethal action of the yellow gene in the mouse by embryological studies.

The attempt to trace the beginnings of gene effects in the earliest possible stages of development (and to follow through to maturity the developmental history of a gene) has grown into a new and promising but often very difficult branch of genetic research — the "genetics and development" studies. The problem has also been approached by experiments in the transplantation of tissues and organs, by hormone injections, and by studies of the gene chemistry involved in color development of hair, etc. The field is just beginning to be explored.

(5) J. Jeswiet (Netherlands) working in Java proves that the Kassoer sugarcane (used in breeding mosaic-resistant P. O. J. hybrid sugarcane) is a second-generation hybrid of true sugarcane with a wild grass, *Saccharum spontaneum* L., that contains little or no sugar. This initiated large-scale sugarcane breeding in many countries, with wild relatives used to secure disease resistance. Later researches showed that the vigorous, disease-resistant, high-yielding sugarcane hybrids all showed a much higher chromosome count than true sugarcane (polyploidy).

1918 — H. D. King (United States) reports results of inbreeding rats for 25 consecutive generations, showing that close inbreeding is not necessarily deleterious, and that fertility and vigor can be maintained in some lines.

1919 — Morgan and others publish The Physical Basis of Heredity, setting forth in detail the gene theory, and summarizing *Drosophila* genetics.

RECENT DEVELOPMENTS

EVEN FROM THE SAFE VANTAGE of a third of a century it is not easy to evaluate the developments that followed the rediscovery of Mendel's work. As we advance nearer to the present our task becomes more difficult, for discoveries that now seem not especially revolutionary may, in the light of later work, be as epochal as Mendel's pioneer contribution. The time is too short to place a final value on many advances, and progress is being made on too many fronts to attempt to cover adequately the multitudinous work in genetics and related sciences. Some recent developments that may have been overlooked may be much more important 20 years hence than they seem today. Thus the compiler is sure only that in this most hazardous part of his journey he is treading on very dangerous ground indeed.

It was planned in compiling this chronology to avoid mention of any names in this final part, simply citing significant developments and trends, letting the perspective of the years determine more fairly those who have made fundamental contributions to genetic progress. In practice this has proved difficult, because some names are so closely linked to certain discoveries that anonymity seems unfair. Thus radiation genetics and salivary-gland chromosomes immediately bring to mind the names of the pioneers whose work has very recently led the way to new bonanzas of genetic facts. Certain developments have been so interesting and significant that to stop the chronology 10 or 15 years ago purely through the promptings of the instinct of self-preservation would destroy much of its interest and value. The following compromise, which attempts to maintain perspective at very short range, is put forth with many misgivings and with a painful realization of the hazards involved. In the short summary paragraphs frequently interspersed with names and dates, an attempt has been made to suggest the extent and significance of some of the important developments.

1920 — (1) Tobacco variety "made to order" by genetic methods (East and Jones in the United States).

(2) H. D. Goodale's (United States) studies of effects of selection on egg production.

(3) E. B. Babcock (United States) begins *Crepis* investigations, which are adding much to our knowledge of chromosome evolution within a genus.

(4) G. Tackholm (Sweden), monograph on polyploid series in *Rosa*, suggesting how a genus may have evolved through changes in chromosome number.

1921 — (1) Triploid discovered in *Drosophila* by Bridges.

(2) Morgan estimates that the gene has a diameter between 20 and 70 microns.

Since Morgan first attempted to estimate the size of the gene several other approximations have been attempted. These have been based on the volume of the chromosomes, the number of genes known to reside in the chromosomes, and the number of mutations that have been known to occur in a given chromosome; or on the number of mutations alone. As our knowledge of the number of genes increases, the maximum estimated size of the individual gene is necessarily reduced. Very recently the problem of gene action has begun to be attacked from the angle of the physical chemist by D. Wrinch (England) and other biochemists. It is thus shown that the giant protein molecules of which the chemists have built mental pictures through X-ray analysis and by other means come within the range of size postulated for the individual gene. At the present time no experimental evidence exists to prove the speculations that the gene in fact consists of a single molecule.

(3) East makes genetic analysis of partial sterility in tobacco hybrids.

1922 — (1) Haploid *Datura* discovered by A. F. Blakeslee, J. Belling, M. E. Farnham, and A. D. Bergner (United States). This is the first discovery of a flowering plant developing with single instead of paired chromosomes.

(2) R. E. Cleland (United States) shows that characteristic arrangement of chromosome chains (rings) in *Oenothera* are typical of different species.

1923 — (1) K. Sax (United States) demonstrates linkage between quantitative and qualitative characters in the garden bean.

(2) F. A. E. Crew (Great Britain) presents evidence to show that the "bulldog" calf, a nonliving monster frequently appearing in crosses of Dexter and Kerry cattle, is due to a lethal factor.

While other workers had suggested the inheritable nature of this defect, Crew was the first worker to suggest the possibility of its being a lethal Mendelian character, the first lethal character identified as such in the livestock breeds. Since that time many other lethals have been recorded. C. Wriedt (Norway) has noted a tendency for outstanding dairy sires to transmit lethal factors, suggesting a linkage between such lethals and factors of economic value. They are thus a matter of some importance to the practical breeder. Their genetic interest is considerable because of the studies they have made possible in the developmental history of genes, from fertilization to adult organisms — the first of these being the study of L. C. Dann and W. Landauer (United States) on the "creeper" fowl.

1924 — (1) Blakeslee and Bolling produce pure-line *Datura* by self-fertilization of a haploid.

(2) W. R. Taylor adapts smear technique to plant cytology, simplifying previous cumbersome methods and making possible the study of a much larger amount of material.

(3) Blakeslee, Bolling, and Farnham explain certain *Datura* mutants as being plants with an extra chromosome. Blakeslee suggests the term "simple trisomic" for such forms in a classification of chromosomal types.

(4) W. T. Swingle and R. W. Nixon (United States) coin the term "metaxenia" to describe the effect of the pollen on maternal tissue outside the embryo. They confirm earlier observations, hitherto generally discredited, that date pollen has a profound effect on time of ripening and some other genetic characters.

1925 — (1) T. H. Goodspeed and R. E. Clausen (United States) publish an analysis of their "artificial species", *Nicotiana digluta*, showing that this form (which arose as a fertile seedling from a normally sterile first-generation hybrid) contains a complete diploid set of chromosomes of each parent species of the original cross (*N. glutinosa* L × *N. tabacum* L.). This amphidiploid ("double diploid") is self-fertile but is sterile with the parent species. This mechanism for the production of fertile polyploids by doubling the chromosome number of sterile first-generation hybrids has been found to be of rather wide occurrence in plants.

Primula kewensis W. Wats. was the first of the amphidiploids to be noted. It arose as a fertile branch of a sterile hybrid. The phenomenon remained an enigma until Goodspeed's and Clausen's publication. *Nicotiana digluta* explained the origin of a considerable number of such "artificial new species." Among forms recognized as amphidiploids on the basis of Clausen's and Goodspeed's work are Karpetchenko's *Raphano-Brassica*, C. A. Jorgensen's *Solanum luteonigrum,* wheat-agropyron hybrids of the Russian workers, etc. Other true-breeding interfertile forms, essentially new species, have been produced by chromosomal rearrangement in *Datura.*

(2) E. S. McFadden (United States) produces the two wheats, Hope and H-44, from a cross between Marquis wheat and Yaroslav Emmer. In the mature plant stage these wheats have been found to be nearly immune from almost all the physiological races of stem rust now known.

(3) J. A. Clark and E. R. Ausemus (United States) point out that the near-immune reaction in Hope wheat is a new character in common hard red spring wheat, inherited as a dominant character. The Hope and H-44 wheats have since become successfully and extensively used in further breeding for stem-rust control.

(4) East and A. J. Mangelsdorf (United States) offer a genetic interpretation of self-sterility in *Nicotiana* as due to rate-of-growth genes affecting the pollen tubes.

1926 — (1) Bolling advances the segmental interchange theory of chromosome evolution (exchange of segments between chromosomes that are not homologous).

(2) J. Percival (England) publishes explanation of polyploid origin of 14 and 21 chromosome wheats.

1927 — (1) Artificial (X-ray) transmutation of the gene, Muller in *Drosophila* and L. J. Stadler in plants (United States).

The discovery made almost simultaneously by Muller and Stadler and Goodspeed that X-rays, and by F. B. Hanson (United States) that radium produces abundant gene mutations is one of the great bonanzas of modern genetic research. In the short time since this discovery was made it has been shown that X-rays produce a variety of effects ranging from mutations in a single gene to profound rearrangements and reassortments of entire chromosomes. Since Muller's original announcement the radiation technique has been extended to other forms of wave energy. It is impossible to give in any detail the development in this very widespread and fertile field of research.

(2) T. S. Painter (United States) finds a chromosome deficiency in mice which, with associated genetic evidence, establishes the first case in mammals of locating a definite gene on a definite chromosome.

(3) J. H. Craigie (Canada) reports hybridization of rust fungi to produce new physiological forms; reports mutation in rust fungi.

The discovery by Craigie that hybridization of rust fungi is possible has opened up a wide field of most interesting research in microgenetics. Other workers have shown that the disease-producing fungi that attack plants mutate rather frequently in respect to their ability to infect and affect a given strain. The problem of the plant breeder seeking resistance has been enormously increased in complexity by these discoveries, which necessitate methods of protection by breeding against an enemy whose physiological reactions change with no visible outward alteration.

(4) Belling, iron-aceto-carmine technique of chromosome staining, makes possible more detailed studies of chromosome structure.

(5) B. O. Dodge (United States) publishes first report on the genetics of *Ascomycetes* (fungi), which have some advantages for genetic research because their haploid nature makes direct observation of all gene effects possible. With this material C. L. Lindegren (United States) has recently produced the first chromosome map of genes in a lower plant.

1930 — (1) Stadler finds that maize genes vary widely in rate of mutation (no mutation in 1½ million waxy gametes, 492 per million in red pericarp [P] gametes).

(2) H. A. Timofeeff-Ressovsky (Union of Soviet Socialist Republics) reports induced reverse gene variations in *Drosophila,* demonstrating that X-ray effects are not purely destructive.

1930-37 — The perfecting of the gene-frequency technique for the analysis of human inheritance by F. Bernstein (Germany), L. Hogben, J. B. S. Haldane, and L. S. Penrose (England), A. S. Wiener and L. S. Snyder (United States) makes possible much greater precision in the use of pedigree data, when the samples are too small to allow statistical treatment by older methods.

1931 — (1) B. McClintock and H. Creighton (United States) in maize, and C. Stern (Germany) in *Drosophila,* prove crossing-over cytologically.

(2) McClintock and others of the Cornell group relate maize linkage groups to specific chromosomes by use of trisomics (diploid plants with one extra chromosome).

(3) Cleland and Blakeslee unify *Oenothera* and *Datura* cyto-genetic observations through segmental interchange theory.

(4) Wright gives first comprehensive picture of evolution in Mendelian terms, with stress on the balance and interplay between selection intensity, mutation rates, inbreeding, isolation, and migration.

1932 — (1) L. F. Randolph (United States) produces tetraploid maize by heat treatment.

(2) Th. Dobzhansky (United States), and Muller and Painter show that "chromosome map" distance and actual (cytological) distance do not coincide.

(3) Variegation in *Drosophila* shown to be dependent on chromatin not organized into chromosomes (heterochromatin) by J. W. Gowen and E. H. Gay (United States).

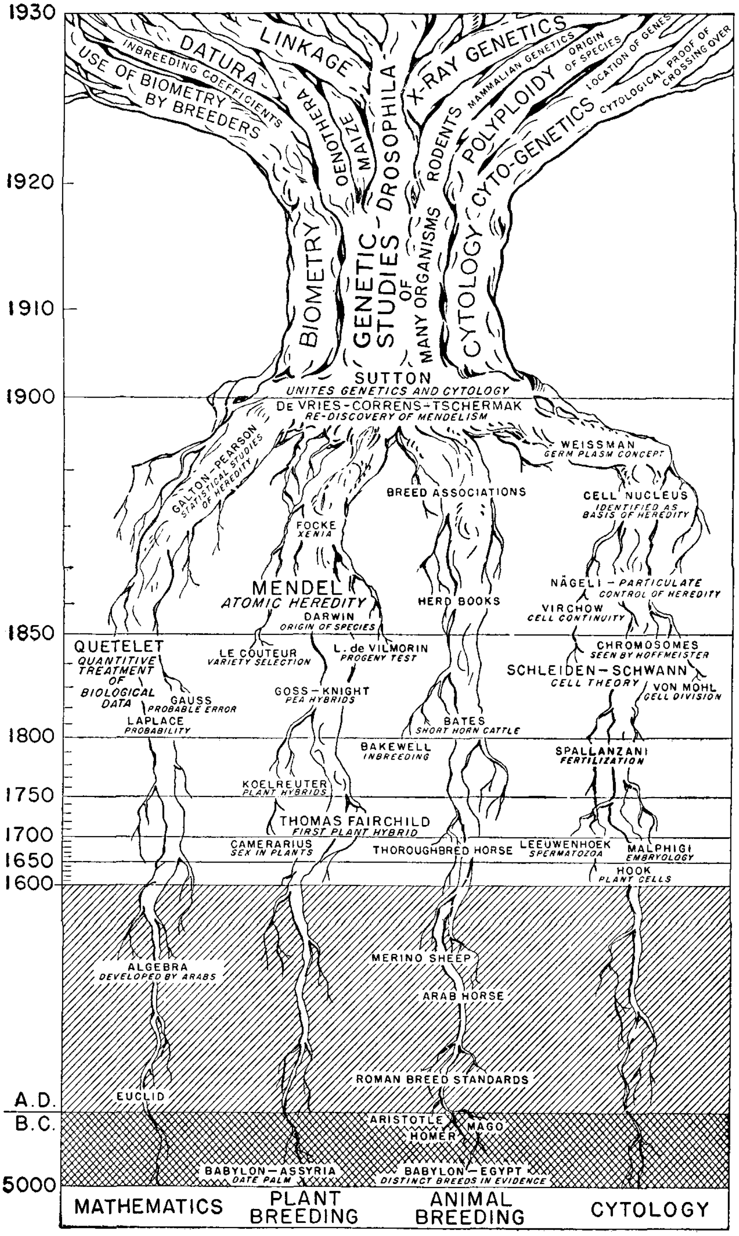
(4) J. M. Rasmusson (Norway) formulates hypothesis of interaction of genes to interpret certain observations of quantitative character inheritance.

1934 — Painter discovers genetic value of giant salivary gland chromosomes (discovered many years earlier, but considered a cytological curiosity), making possible detailed studies of chromosome structure, and leading to very exact location of genes.

THE FAMILY TREE OF GENETICS

IT IS CUSTOMARY TO VISUALIZE historical development by analogy to a tree, whose roots go back into the distant past, whose trunk symbolizes a nicely unified development, and whose spreading branches denote the wide ramifications of our pet discipline at the moment we are considering it. Under any circumstances such an analogy is probably hazardous, and with some misgivings we shall symbolize genetics as a tree which has drawn its sustenance from four main roots.

These four taproots of modern genetics are: (1) The genetics root, leading back through Morgan, Bateson, De Vries, Mendel, Koelreuter, etc.: (2) the cytological root, tracing through Belling, McClung, Wilson, Sutton, Van Beneden, Leeuwenhoek, to Hooke, who first saw and named the cell; (3) the biometrical root, tracing through Wright, Fisher, Pearson, Galton, Laplace; and (4) the animal-breeding root, tracing through the stud and herd books, through the breed founders (such as Bakewell, the Collings, and Bates of a century ago) to Mago the Carthagenian, who is to be credited with compiling the first recorded score card — which is still used, with surprisingly little modification. Other "roots" could also be thought of.



THE FAMILY TREE OF GENETICS.

It should be borne clearly in mind that these roots have generally been entirely distinct through much of their developmental history. No experimental connection existed between the observational work of the hybridizers and that of the microscopists until Sutton in 1902 confirmed Haeckel's prediction (1866) that the nucleus would prove to be the vehicle of heredity. The observed facts of Mendelian heredity fitted the cytologists' finding that meiosis and fertilization were a method for keeping the chromosome complement constant. The heretofore independent concepts were thus mutually confirmatory and together made a complete picture. Since that time it has been increasingly difficult to ignore cytology in studying strictly genetic phenomena. Without the cytologist's aid much genetic work would remain purely speculative. In the case of polyploidy, for instance, cytological counts of chromosome number and observation of chromosomal behavior at the reduction division have been of tremendous importance. Similarly the mathematical root developed entirely independently until Galton and Pearson bridged a gap that previously had been so wide that few students of the subjects involved would have admitted any close relationship.

What of future developments? The chronologer can do no better than quote one of the greatest geneticists, T. H. Morgan:

> I have been challenged recently to state on this occasion what seemed to be the most important problems for genetics in the immediate future. I have decided to try, although I realize only too well that my own selection may only serve to show to future generations how blind we are (or I have been, at least) to the significant events of our own time.
>
> First, then, the physical and physiological processes involved in the growth of genes and their duplication (or as we say their "division") are obviously phenomena on which the whole process of reproduction rests. The ability of the new genes to retain the property of duplication is the background of all genetic theory. Whether the solution will come from a frontal attack by cytologists, geneticists, and chemists, or by flank movements, is difficult to predict.
>
> Second: An interpretation in physical terms of the changes that take place during and after the conjugation of the chromosomes. This includes several separate but interdependent phenomena — the elongation of the threads, their union in pairs, crossing over, and the separation of the four strands. Here is a problem on the biological level, as we say, whose solution may be anticipated only by a combined attack of geneticists and cytologists.
>
> Third: The relation of genes to characters. This is the explicit realization of the implicit power of the genes, and includes the physiological action of the gene on the rest of the cell. This is the gap in our knowledge to which I referred already at some length.

> Fourth: The nature of the mutation process — perhaps I may say the chemico-physical changes involved when a gene changes to a new one. Emergent evolution, if you like, but as a scientific problem, not one of metaphysics.
>
> Fifth: The application of genetics to horticulture and to animal husbandry, especially in two essential respects — more intensive work on the physiological rather than the morphological aspects of inheritance; and the incorporation of genes from wild varieties into strains of domesticated types.
>
> Should you ask me how these discoveries are to be made, I should become vague and resort to generalities. I should then say: By industry, trusting to luck for new openings. By the intelligent use of working hypotheses (by this I mean a readiness to reject any such hypotheses unless critical evidence can be found for their support). By a search for favorable material, which is often more important than plodding along the well-trodden path hoping that something a little different may be found. And lastly, by not holding genetics congresses too often.

It is probable that we are even now witnessing the development of another major branch of the genetic tree — the biochemical branch. It has long been guessed that genes must be chemical in their action, and the molecular nature of the gene has more than once been suggested and speculated on. Studies of the analysis and synthesis of the sex hormones, of growth hormones and cancer-producing substances, and of the filterable viruses are bringing to light effects that closely resemble the action of genes. The next great important advance may be to link the gene with the newer biochemistry, which will make it necessary to revise our "genetic tree" and to add another important root tracing through Wilstetter, Mendeleeff, Dalton, and Lavoisier, to the alchemists of the Middle Ages!

Thus while specialization has been essential to promote the progress of science, it is distinctly a danger that too much specialization may endanger continued progress, if it prevents the formation of such fruitful graft-hybrids in ideas as those that have contributed so greatly to the progress of genetics. The geneticist and the breeder of the future must be intelligently cognizant of many fields of knowledge that are more and more impinging on their chosen specialty. Synthesis of these increasingly complicated factors seems essential if progress is to continue.

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