A BRIEF CHRONOLOGICAL TABLE

of

DISTINCTIVE EVENTS and the MEN CONTRIBUTING

to our

KNOWLEDGE OF CYTOLOGY

IN RELATION to GENETICS.

Rudolph

CONTENTS.

700 B. C. Babylonians

Sexuality in animals was recognised from the beginning but not in plants until in 700 B. C. when the Babylonians observed but did not prove the existence of fertile and sterile date trees.

200 B. C. Aristotle.

Gave to the world a treatise on animal reproduction particularly on the development of the chick.

1651 William Harvey.

Gave the world a theory of reproduction that constituted a step in our present knowledge. Held the view that conception in the uterus is identical with; or at least analagous to, conception in the brain; and that the ovum is the product of such unconscious uterine desire or conception and receives no material substratum from the male.

1680 Antony von Leeuwenhoek.

Perfected the simple microscope, making it superior to the compound microscopes then in use.

1665 Robert Hooke.

Made some marked improvements on the microscope and described the vesicular nature of vegetative substances. Applied the term "cell" to the apparent cavities.

1673 J. Swammerdam.

Discovered hermaphroditism in snails.

1674 Malpighi.

Gave an advanced detailed description of plant tissue and was the first to apply the microscope to both plant and animal tissues.

1676 Rudolph Jacob Camerius.

The true discoverer of sex in plants, since he was the first to base his evidence on experiments.

1677 Antony von Leeuwenhoek.

Discoverer of spermatozoa and furnished the first fundamental advance in the theory of reproduction.

1681 Sir Thomas Millington.

Was the first to claim for the stamens the character of male organs of generation in plants.

1694 R. J. Camerius.

Discovered the existence of monoecious as well as dioecious plants, and the need of pollination in corn.

1745 (Ovists).

Parthenogenesis discovered in plant lice.

1761 Joseph Gottlieb Koelreuter.

Produced hybrids artificially, and observed that the characters of both parents are found in the offspring.

1781 Fontana.

Discovered the nucleus as a definite body in the protoplasm.

1780 Spallanzani.

Was a praeformist, and at the suggestion of Bonnett was the first to practice artificial parthenogenesis.

1821 Goss.

Segregation observed in crossed peas.

1823 Amici.

Saw the pollen tube on the stigma and emerge from the pollen grain.

1824 Prevost et Dumas.

Advanced a new theory of fertilization, and was the first real advance since Spallanzi.

1826 Brongniart.

Worked out the formation of the pollen tubes, thus confirming Amici's work.

1830 Amici

Worked out the course of the pollen tubes all the way to the ovules.

1831 Robert Brown.

Showed that the nucleus to be generally present in the tissue cells of Phanerogams.

1835 Du Jardin.

Gave the name "sarcode" to the protoplasm of the unicellular animals studied by him.

1838 Matthias Jacob Schleiden.

Gave us the first comprehensive treatment of the cell, and the formation of a definite cell theory in plants.

1838 Theodor Schwann.

Established the fact that the ovum is a cell, having the same essential structures as the other cells of the body.

1840 J. Purkinje.

Applied the term "protoplasm" to the formative substance of the young animal embryo.

1841 Kolliker.

Demonstrated that the spermatozoa arise directly from cells in the testes.

1842 Bischoff.

Advanced the "contact theory" of fertilization, viz; that the spermatozoa lie close to the ovum to effect fertilization.

1844 De Bary

Established the fact that the spermatozoa do penetrate the ovum in fertilization.

1845 Steenstrup.

Introduced the term "alternation of generations", but it only carried the idea of a succession of vegetative shoots in the production of the flower.

1846 Hugo von Mohl.

Applied the name protoplasm to the living substance within the cell walls.

Recognized that cells arise by the divisionof a pre-existing cell.

1846 Amici.

Embryo sac shown to exist before the pollen tube.

1846 Naglei.

Was the first to preceive that protoplasm was a nitrogenous substance.

1849 Leuckart.

Saw the spermatozoa enter the frog's egg in the process of fertilization.

1849 Gartner.

Sexuality confirmed in a large number of plants.

1851 Bischoff.

Together with Allen Thompson proved that fertilization is accomplished by the actual entrance of the spermatozoa into the egg.

1851 Hofmeister.

Replaced the old distinction of alternation of generation based upon the methods of reproduction. Showed the existence of two life cycles. Distinguished between a spore bearing generation and another which exhibits sexual reproduction.

1853 Dzieron.

Demonstrated that in the honey bee the males always come from the unimpregnated eggs, while the females, queens and workers come from the impregnated eggs.

1854 Thuret.

Described the sexual act in Fucus. Was a step in the knowledge of fertilization.

1855 Prigsheim.

Confirmed the work of Thuret when he saw the male organ of fresh water algae penetrate into the substance of the egg and be dissolved in it.

1855 Virchow.

Maintained the universality of cell division.

1858

Supported by the work of others maintained the law of genetic continuity of cells in the since famous aphorism "omnis cellula e cellula".

1858 De Bary.

Described the sexual act in the Conjugatae.

1861 Gegenbaur.

Vertebrate egg proved to be a single cell.

1861 Kolreuter.

Found the characters of both parents in the offspring.

1863 Kolliker.

Gave the name "cytoplasm" to the protoplasmic ground substance as opposed to the granules.

1863 Max Schulze.

Established the fact that protoplasm is the

vital principle of animal and vegetable life. That the protoplasm of the botanists and the sarcode of the animal phsiologists is the same thing.

1865 Gregory Mendel.

Established the two so-called laws of Mendel, viz;

The law of dominance, and
The splitting of the hybrid race.

1865 Kolliker.

Applied the name "cell sap" to the more liquid ground substance of the nucleus.

1865 Schweigger-Seidel
La Valette St. George.

Proved simultaneously that the spermatozoa is a complete cell, consisting of a nucleus and cytoplasm, and hence of the same morphological nature as the ovum.

1866 Hackel.

Expressed the view that "The internal nucleus provides for the transmission of hereditary characters".

1867 Hildebrandt.

Observed that in crossing maize that the embryo was hybrid, and the the endosperm showed characters proper to each of the parents.

1868 Celakowsky.

Distinguished two different kinds of life cycle and applied the names "protophyt" and "antiphyt" to the two phases names replaced later by Gametophyte and Sporophyte.

1873 Butschli.

Observed in the egg of a nematode the approach and contact of two structures, which we now know to be the germ nuclei.

1873 Anton Schneider.

Published works that gave us a better insight into the process of cell division. Explained the difference in consistency in the reticular hypothesis of cell protoplasm, and suggested a binding agency for the different kinds of protoplasm recognized.

1873 Warming.

Gave the first account of the anatomical development of the stamen.

1874 Auerbach.

Described the appearance of two nuclei at the opposite ends of the elongated egg of Rhabdites.

1875 Strasburger.

Called the thickening of the spidle of fibres from which the partition wall arises during the

division of plant cells, the "cell plate".

1875 Flemming.

The minute body detected at the spindle poles, and found to be an inseparable companion of the animal cells he called the "centrosome".

1875 Oskar Hertwig.

Observed and described correctly for the first time the process of fertilization.

Later. Reached the conclusion that fertilization consists in the union of the male and female pronuclei.

1875 Eduoard van Beneden.

Observed in the rabbits egg the fusion of two nuclei before cleavage.

1875 Sir Francis Galton.

Published his law of Ancestral Heredity.

1876 Fol.

Observed the details of penetration of the spermatozoa with a clearness that has never been surpassed for these forms.

Gave the first correct account of the maturation divisions, and origin of the egg nucleus.

Gave special attention to the fertilization membrane and founded the classic theory that it was

an adaptation to prevent polyspermy.

Was the first one to adequately present the harmful effects of polyspermy.

1877 Flemming.

Discovered and named the chromatin bodies in the nucleus now known as "chromosomes".

1877 Fol.

Observed and described the occurence of the amphiaster.

1878 O. Hertwig.

First observed the approach and union of the egg and sperm nuclei.

1878 Flemming.

Showed the existence of a centrosome in animals, and in addition outlined the whole scheme of mitosis as we now know it.

1878 Klein.

Discovered the presence of a nuclear membrane separating it from the rest of the cell.

1879 Flemming.

Gave the name "chromatin" to the deeply staining substance of the nuclear net work, and of the chromosomes consisting of nuclein.

1879 Schmitz.

Observed in the Spirogyra the fusion of the egg and sperm nuclei.

1879 Flemming.

Discovered that the chromosomes arrange themselves in the equatorial plate of the spindle, and each plits longitudinally in two. This was confirmed by Retzius in 1881.

1880

Observed that "The chromatin net work is converted into a thread which whether continuous or discontinuous splits throughout its entire length into two exactly equivalent halves.

1881 Focke.

Gave the name "xenia" to the phenomenon discovered by Hildebrandt in 1867.

1882 Strasburger.

Gave the name "cytoplasm" to the substance of the cell as opposed to that of the nucleus.

1882 Flemming.

Applied the name "dispirmem" to that stage of mitosis in which each daughter nucleus has given rise to a spireme.

was also able to extend Virchow's aphorism to the nucleus also, "omnis nucleus e nucleo".

Made observations on species whose chromosomes show specific and constant differences in size and shape. Furnished much evidence for the independent existence of these bodies.

1882 Pfitzner.

Showed that the splitting of the chromosomes in the equatorial plate was only the reappearance of a split in the spireme thread, and was due to a corresponding division of each of the two chromatin granules.

1883 Roux.

Pointed out that the daughter nuclei receive precisely equivalent portions of chromatin from the mother nucleus.

1883 E. van Beneden.

First described a process of mitosis and applied the term "reduction - divisions" to it.

1884 Strasburger.

Named the four periods in mitosis, viz;

1. Prophase; 2. Metaphase; 3. Anaphase; 4. Telophase.

1885 Rabl.

Concluded that the chromosomes do not lose their identity at the time of their division, but persist in the chromatic reticulum of the nucleus.

1887 Flemming.

Was the first to name and describe the first stage of maturation divisions, and called it the "heterotypic division" because of the reduction in the number of the chromosomes.

1887 Schwartz.

Showed the existence of linin threads in the resting nucleus.

1887 Hugo De Vries.

Discovered mutations in the Evening Primrose.

1887 E. van Beneden.

Found in the fertilized ovum and blastomeres of Ascaris Megalocephala, at the poles of the nuclear spindle, definite spheres each with a dense center, which he considered as permanent cell organs in connection with the nucleus, and called these spheres "attraction spheres".

1887 Theodor Boveri.

Observed that the attraction sphere was occupied by a minute body. He called this dark central

body the "centrosome". Boveri and van Beneden regarded the centrosome as not only initiating the division of the cell body, but that of the chromatin also.

The "Individualitats Hypothese" was put forth by Boveri in '87 as a result of C. Rabl's observation on the epithelial cell of the salamander in '85. Was later supported by several prominent investigators.

1887 Oskar Hertwig.

Initiated the modern period in the physiology of fertilization, involving two considerations, viz;

The direct experimental analysis of the fertilization process itself, and

The attempt to initiate the action of the spermatozoa by chemical and physical agencies, or, in brief, the studies on artificial parthenogenesis.

1888 Theodor Boveri.

The formation of the reticulum in the telophases and its behavior in the prophases lead to the identification of the so-called "unit reticula" derived from the single chromosomes.

1888 Waldeyer.

Gave the name "chromosomes" to the deeply staining bodies of the contracted spireme.

1889 Hugo De Vries.

Published his theory of Intercellular Pangenesis.

1891 H. Henking.

Discovered a deeply staining body in the growth period of the primary spermatocyte of Pyrrocoris, and its unequal distribution in the second division, where by one spermatozoa receive one more chromatin element than the other, and were therefore dimorphic in respect to the number of chromosomes.

1891 Flemming.

First found attraction spheres and centrosomes in the resting stages of leucocytes, and in the epithelial cells of the lungs of the salamander.

1891 Guignard.

Found attraction spheres and centrosomes in the resting stage and mitosis, in reproductive vegetative cells.

1892 Hacker.

Applied the term "bivalent" to the chromatin rods representing two chromosomes joined end to end.

1892 Butschli.

Was the first to emphasize the fact that protoplasm is a complex structure. At this time Butschli advanced his "Foam Theory".

1892 O. Hertwig.

Considered that the nucleus is the bearer of (heredity) inheritence material.

The equivalence of the inheritance material in male and female.

The equal distribution of the inheritance material to all the cells of the organism.

The prevention of the summation of the inheritance material, by its reduction before fertilization.

The isotrophy of the protoplasm.

1892 Sargent.

Showed that mitosis after reduction is equal to ordinary mitosis.

1892 F. Hermann.

The discovery of the central spindle first clearly showed that two kinds of fibres must be recognized in the mitotic figure.

1893 A. Weismann.

Published his "Germplasm Theory".

1893 J. B. Overton.

Announced the discovery of reduction-divisions in plants.

1893 Strasburger.

Proved that the centrosome may at time and in some species be surrounded by a spherical mass known as the centrosphere.

1894

Placed the alternation of generations on a chromosome basis, by announcing the generalization that the reduced cell contains half the normal number of chromosomes, i. e. the gametophytic generation.

1895 Moore.

That phase of the nucleus just preceeding the heterotype mitosis was given the name "synapsis".

1897 Huie.

The direct growth of the chromatin knots which are present in the resting nuclei into the chromosomes was first observed by Huie in '97.

1898 Montgomery.

Was the first to detect that the accessory chromosome is bivalent.

1898 Nawaschin.

Discovered the phenomenon of double fertili-

zation in Lillium.

1898 Jesel.

Discovered parthenogenesis in plants.

1899 Paulmier.

Confirmed the dimorphism in spermatozoa discovered by Henking in '91.

1899 Guignard.

Presented evidence for the continuity of chromosomes in their presence through interkinesis.

1900 Juel.

Proved conclusively the generation of the microspore nuclei.

1900 Guyer.

The pairing of chromosomes discovered.

1901. Guignard.

Double fertilization in corn observed.

1902 Cannon.

Relation of pairing of chromosomes to Mendelism explained.

1902 McClung.

Suggested a theory for the function of the accessory chromosome.

1903 W. S. Sutton.

Advanced a theory on the relation between chromosomes and allelemorphs.

1904 Rosenberg.

Gave a theory on the existence of prochromosomes.

1904 C. E. Allen.

Discovered the pairing of the chromosomes and of the chromomeres in the Lillium.

1905 N. M. Stevens.

Described another type of dimorphism both classes of which have the same number of chromosomes but differ in that one class contains a large idiochromosome and the other a small one.

1905 E. B. Wilson.

Described the "m" chromosomes which are two spermatogonial chromosomes which do not unite at the general synaptic period and which may or may not condense in the early growth period to form two small chromosome nucleoli. They undergo a late synapsis in the prophase of the first division to form a bivalent which divides in both divisions.

1908 Ferdinand Payne.

Described a type of dimorphism in which there are five chromosomes, which divide as univalents in

the first maturation division. In the second divi- they do not divide but four of the five pass to one pole and the other to the opposite pole.

1909 Guyer.

The x chromosome in relation to sex extended to man.

1909 Wilson.

Presented evidence for the sexual predetermination and predestination in the germ cells.

1910 W. E. Castle.

Advanced the Presence and Absence theory.

1911 T. H. Morgan.

Sex-limited in heritance.
Sex-linked inheritance.

Chapter II.

PHILOSOPHICAL DISCUSSIONS AND THEORIES BEFORE EXACT KNOWLEDGE IS OBTAINED.

At no time has the great problem of heredity, which involves such far reaching results, received such universal attention among biologists; been more widely discussed or more diligently studied than at the present day. It is now realized that the possibility of an ultimate solution must entail the study of genetics combined with that of microscopical investigation, for it is within the cells that the factors reside which determine the morphological and physical character of the individual. But the arrival at our present day fund of knowledge of heredity has been after the elapse of several centuries of mystery, filled with divers theories, many of which to us now appear absurd, but in their period were considered as distinct advances.

By virtue of the nature of our problem we must necessarily deal with the sexuality of plants and animals, and therefore with the process of fertilization.

From the beginning of the history of man the primary fact of the necessary concurrence of two individuals to produce offspring has been recognized. Little more was known of the essential features of the sexual process in animals than had been familiar to the Assyrians, Egyptians and Greeks at least twenty centuries previous to 1850. While sexuality in plants had been suspected as early as in 700 B. C., yet it remained for Camerius 1694 to prove by his experiments on the mulberry the existence of sex in plants.

"The first discoveries pointing to the existence of sex in plants were evidently made very early in human history by peoples cultivating unisexual plants for food. The existence of fertile and sterile trees of the date palm was known to the peoples of Egypt and Mesopotamia from the earliest times, but even the keen Greeks failed to offer any interpretation for this well known fact. Aristotle and Theophrastus report the fact that some of the trees of the date, fig and terebinth bear no fruit themselves but in some way aid the fertile tree in perfecting its fruit. In this uncertain state the knowledge of sexuality in plants was destined to rest for twenty centuries, waiting for the experimental genuis of Camerius to give a conclusive answer to the question." Johnson (1915)

During the period in which the question of sexuality in plants lay dormant; and the sexuality in animals being recognized it was but natural that the investigators of natural phenomena turn their attention to the problems of heredity, and therefore necessarily fertilization in animals.

It must be remembered that the problem of fertilization was not clearly separated from the general problem of reproduction until well into the nineteenth century. In early human culture reproduction received its only interpretation at the hands of priests and mystery men; its first philosophical and scientific treatment was one of the great distinctions of the Greeks, especially of that great philosopher and father of science, Aristotle (350 B. C.) who combined observation and reflection in the interpretation of nature. Aristotle devoted a separate treatise (which has come down to us) to animal reproduction. Among other things he studied the development of the chick day by day with so much detail that William Harvey felt compelled to say 1900 years later; "Aristotle among the ancients and Hieronymous Fabrisius of Aquapendente among the moderns, have written with so much accuracy on the generation and formation of the chick from the egg that little seems left for us to do".

Aristotle says; "The male is the efficient agent, and by the motion of his generative virtue (genitures) creates what is intended from the matter contained in the female; for the female always supplies the matter, the male the power of creation, and this it is which constitutes the male, another female. The body and the bulk, therefore, are nec-

essarily supplied by the female; nothing of the kind is required from the male; for it is not ever requisite that the instrument, nor the efficient agent itself, be present in the thing that is produced. The body then proceeds from the female, the vital principle (anima) from the male; for the essence of every body is its vital principle (anima)".

Harvey 1651

"From the time of the Greeks to that of Harvey there was but little progress in the knowledge of reproduction, and none in theory. With more common sense, if with less metaphysical sublety the physicians held, according to Harvey, that conception is due to a mingling of the male and female fluids. The mixture having from both equally the facutlty of action and the force of matter; and according to the predominance of this or that geniture does the progeny turn out male or female". (Harvey Ib.L)

Harvey's observations contained much that was new and significant, but the facts that he knew were inconsistent both with Aristotle's ideas and those of the physicians. They were, however, inadequate for sound generalization. He descended deeper into the slough of metaphysics than Aristotle, and commited himself to the fantastic idea that conception in the uterus is identical with, or at least, analogous to conception in the brain, and that the ovum is the product of such unconscious uterine or desire

of conception, and receives no material substratum from the male." Lillie (1919)

The next notable theory of fertilization was that of Spallanzani (1780) He "held the view that the seminal fluid accelerated vital processes and stimulated the action of the heart. He believed that an organism was performed in the ovum, since the beating of the heart was the first observable movement of the embryo. Bonnett suggested that if the spermic fluid might stimulate the action of the heart of the embryo in the process of fertilization, why might not other fluids produce the same effect. This suggestion was taken seriously by Spallanzani, and the direct result was that he was the first to practice practical artificial parthenogenesis."

Lillie (1919)

The first real advance in the theory and knowledge of fertilization since Spallanzani in 1780 was made by Prevost et Dumas (1824). They concluded that a spermatozoon penetrates each egg, and becomes "the rudiments of the nervous system, and that the membrane (germ disk of the egg) in which it is implanted, furnishes, by the diverse modifications which it undergoes all the organs of the embryo."

We must now turn to the botanists for the foundation of our cell theory. M. J. Schleiden in "Beitrage zur Phytogenesis", 1838, gave us the first comprehensive treatment of the cell, and the formation of a definite cell theory in plants. He maintained that cells are the individuals in the vegetable kingdom, and supposed that new cells arose from very minute granules and that the new cells arose from the parent cell by the crystalization, or a crystilizing process from the cell fluid. Up until now the cell nucleus had lain undisturbed, until Schleiden suddenly made it the soul of his theory and the starting point of all cell formation, the nucleolus appearing first, then the nucleus, and finally the cell body.

"Theodor Schwann in 1839 extended Schleiden's theory to animal tissues, this being the first real step to a comprehensive cell theory including animal tissues. However with this great error, that new cells arise, not only within the mother cell as Schleiden had supposed, but also in the intercellular substances so common in animal tissues. The fact was established that the egg is a single cell, having the same essential structures as the other cells of the body." Lillie (1916)

"Bischoff in 1842 advanced the theory that only the dissolved part of the semen penetrates into the egg and thus completes fertilization." He later came to the belief that the spermatozoa were themselves the essential agents, and gave his contact theory, viz; that the spermatozoa lie close to the ovum to to effect fertilization. Lillie (1919)

Dzierzon demonstrated in 1853 that in the honey bee, from the impregnated eggs came the females, queens or workers as circumstances dictate, while from the unimpregnated eggs always came males. The absence of spermatozoa from the eggs which develop into drones has been proven in the laboratory of Weismann, by the use of modern cytological methods.

In the next year, 1854, Thuret showed how the large egg cells in species of Fucus are surrounded by spermatozoids, and he even succeeded in producing hybrids by fertilizing the egg cells of one species with the spermatozoids of another; but it was still uncertain whether simple contact of the male and female organs was sufficient, or whether fertilization is due to the mingling of the substance of the spermatozoid and the germ cell. Though a simple process the sexual act was so clear that it threw light at once on other cases more difficult to observe.

Sachs (1890)

It remained for Pringsheim in 1855 to clear up the question of fertilization as raised by Thuret in 1854 when he saw the male organ of fertilization of a freshwater algae penetrate into the substance of the egg cell and be dissolved in it.

Regarding theories of cell division Virchow as early as 1855 positively maintained the univer-

sality of cell division, concluding that every cell is the offspring of a preexisting cell. The work of Kolliker 1844-46; Karl Bogislaus Reichert 1841-47, and Remak 1852-55 enabled Virchow in 1858 to maintain the law of genetic continuity of cells in the since famous aphorism "omnis cellula e cellula".

Theological Theories:-

In olden times the idea was prevalent that the germ of a new human life was at conception possessed by a spirit, which thereafter became responsible for development. As it is not so very long ago (1750 or later) that even digestion was explained as the work of a spirit, it need not surprise us that development was relegated to a similar unverifiable efficiency. We believe in mosaic or ancestral heredity, or inheritance, and though we know that this has a definite material basis, we have no warrant for denying that this has also its metakinetic or spiritual aspect. Thompson (1908)

Metaphysical Theories.

For a time, especially in the latter half of the eighteenth century, it was the custom to appeal to the "hereditary tendencies" and "principles of heredity" by aid of which the germ was supposed to grow into the likeness of its parents.

Although William Harvey (1650) working " in the harness of Aristotle" maintained that " all animals are in some sort produced from eggs", he at the same time believed in spontaneous generation as firmly as his master did. He had to fall back on a metaphysical conception of inheritance and development. "Not only is there a soul or vital principle present in the vegetative part, but even before this there is inherent mind, foresight and understanding, which, from the very commencement to the being and perfect formation of the chick, dispose and order and take up all things requisite, moulding them in a new being, with commensurate act, into the form and likeness of its parents". Thompson (1908)

"Preformationist" Theories

During the seventeenth and eighteenth centuries and even within the limits of the nineteenth, a theory of inheritance and development prevailed, according to which the germ, (either the ovum or the sperm) contained a minature organism, preformed tho invisible, which required only to be unfolded (Evolved) in order to make the future animal. A thorough going representative of the preformationist school was Charles Bonnett (1788) who discovered parthenogenesis in green flies, and made many important observations on polyps and worms. Albrecht von Haller likewise was a preformationist of the same period, and wrote "No part of the body is made from

the other, all are created at once".

To the main conception of preformation and the unfolding of all its parts within the germ, two subsidiary hypotheses were added:-

1. That of emboitement, according to which, the germ contains the preformation not of one organism only, but of successive generations; and

2. That germs occurred scattered through out the organism capable of developing into buds, or replacing lost parts, and so forth.

The preformationists divided themselves into two minor schools, viz; the "ovists" and the animalculists". The ovists held that the ovum contained the miniature, while the animalcultists supported the claims of the sperm.

The preformation theory or "theory of evolutio" as it is sometimes called, received its death blow from the hands of Caspar Friedrich Wolff (1759), who maintained a gradual development of obvious complexity from an apparently simple rudiment. The various organs of the developing embryo make their appearance successively and gradually, and are to be seen being formed. There is no "evolutio"; there is new formation or "Epigenesis".

The preformationists and believers in epigenesis came to a deadlock, and both schools usually fell back on the assumption of hyperphysical agencies.

until the genetic of germinal continuity which links generation to generation was realised, there could be no real progress in theories of development.

Thompson (1908)

Theories of Pangenesis.

Passing from the theological, metaphysical and mystical interpretations, we come to a whole series of theories, which are in varying degrees unscientific, and may be fairly enough described by the general term "pangenetic". They all have this in common that they seek to explain the uniqueness of the germ cell by regarding it as a center of contributions from different parts of the organism. At such different epochs as are suggested by the names of Democritus and Hippocrates, Paracelsus and Maupertuis, incipient theories of pangenesis--prophesies of Darwin--were suggested. Thompson (1908)

Spencer's Theory of Physiological Units.

In 1861 Brucke emphasized the usefulness of assuming the existence of biological units ranking between the molecule and the cell. In 1863 Herbert Spencer adopted a similar hypothesis of "physiological units", lower in degree than the visible cell units, but more complex than the chemical units. Representative physiological units of the body congregate in vehicles which we call ova and spermatozoa, carrying with them, on their journey to form a new

generation more definite and representative results of the modifications acquired by the parental body.

Thompson (1908)

Darwin's Theory of Pangenesis.

The best known theory of this class is the "Provisional Hypothesis of Pangenesis" (Variation of Animals and Plants under Domestication, 1861). The chief points of this hypothesis are as follows:

1. Every cell of the body, not too highly differentiated, throws off characteristic gemmules;

2. These multiply by fission, retaining their characteristics;

3. They become specially concentrated in the reproductive elements in both sexes;

4. In development the gemmules unite with others like themselves, and grow into cells like those from which they were originally given off, or they may remain latent during development even through several generations. Thompson (1908)

Jager's Theory, (1876) a hypothesis of chemical pangenesis, hard to summarize due to its technical nature.

Brook's Theory. In 1883, in his valuable work entitled "The Law of Heredity" W. K. Brooks gives expression to a modification of Darwin's theory of pangenesis. "It is in unwonted and abnormal conditions that the cells of the body throw off gemmules.

The male elements are the special centers of their accumulation the female it is that keeps up the general resemblance between offspring and parent.

Theory of Genetic or Germinal Continuity

The earliest distinct suggestion of the modern theory of germinal continuity was made by Owen in 1849.

Haeckel, in 1866 emphasized the fundamental fact of the material continuity of the offspring and parent.

Jaeger in 1875 stated the doctrine of germinal continuity as the continuity of the germ protoplasm. "Encapsuled in the ontogenetic material, the phylogenetic protoplasm is sheltered from external influences, and retains its specific and embryonic characters".

Brooks in 1876-77 notes that he had also suggested the notion of germinal continuity.

"Galton 1875-1889, expounded a theory embracing the theory of germinal continuity. He was extremely doubtful in regard to the genuine inheritance of acquired characters, but a subsidiary hypothesis allowed a limited amount of pangenesis. It is needful at the outset to notice Galton's term "stirp", which he uses to express the sum total of the germs, gemmules, or organic units of some kind, which are to be found in the newly fertilized ovum.

1. Only some of the germs within the stirp attain development in the cells of the "body". It

is the dominant cells which develop.

2. The residual germs and their progeny form the sexual elements or buds. The part of the stirp developed into the body is almost sterile. The continuity is kept up by the undeveloped residual portion.

3. The direct descent is not between body and body but between stirp and stirp. "The stirp of the child may be considered to have descended directly from a part of the stirps of each of its parents, but then the personal structure of the child is no more than an imperfect representation of its own stirp, and the personal structure of each of its parents is no more than an imperfect representation of each of their own stirps." Thompson (1908)

Nussbaum, his theory is that of a continuity of the germinal cells.

Weismann, 1893 proposed his Germplasm Theory. It is more strictly a theory of the continuity of the germinal protoplasm.

"The physical basis of inheritance-the germ-plasm-is in the chromatin of the nucleus of the germ-cell.

The chromatin takes the form of a definite number of chromosomes (or idants).

The chromosomes consist of ids, each of which contains a complete inheritance.

Each id consists of numerous primary constituents or determinants.

A determinant is usually a group of biophors, the minutest vital units.

The biophore is an integrate of numerous chemical molecules".

"The germ-substance owes its marvellous power of development not only to its chemico-physical constitution, but to the fact that it consists of many and different kinds of primary constituents--that is, of groups of vital units equipped with the forces of life, and capable of interposing actively and in a specific manner, but also capable of remaining latent in a passive state until they are affected by a liberating stimulus, and on this account able to interpose successively in development. The germ cell cannot be merely a simple organism; it must be a fabric made up of many different organisms or units--a microcosm". Weismann (1904)

Hugo De Vries's Theory of Intercellular Pangenesis

A theory different from Darwin's and Weismann's was suggested by De Vries under the above title in 1889, the substance of which is as follows:

" 1. Organisms are built up of unit-characters, independently variable and independently heritable.

2. These unit-characters are represented "in potentia" in the hereditary substance of the nucleus

of the germ-cell by definite bodies (pangenes) far too minute to be visible, but together constituting the chromosomes of the nucleus.

3. The pangenes multiply in the idioplasm of the nucleus, and some of them migrate into the surrounding cytoplasm, where they become active, dominating it, and giving it a particular character. But a representative contingent of pangenes always remains in the nucleus and is handed on from cell to cell by nuclear division into each cell as it is formed a fresh migration of pangenes occurs."

THE DETERMINATION OF SEX.

The first basis for the cytological results were laid by Henking by his fundamental discovery of the dimorphism in the Pyrrhocoris, though he did not recognize the meaning of the phenomenon. The results of this remarkably able investigator, long neglected were first confirmed by Paulmier in Anasa, and later by many others. The fruitful suggestion that the two sexes arise upon the fertilization of the eggs by the two classes of spermatozoa is due to McClung, who ably supported his view by many arguments.

The first and direct evidence produced by Stevens and Wilson showed that the x class of spermatozoa are the female and not the male producing class.

The obvious view is that the chromosomes--specially the x chromosomes are actual sex determining fac-

tors; that the egg becomes male or female according as it is fertilized by one kind of spermatozoa or the other; and that it is purely a matter of chance which kinds enters the egg. It is probable that in the differential division, which separates the x class from the y, the two poles of the dividing cell may be already predestined as male producing and female producing irrespective of the chromosomes. There is no hint of such predestination in the ordinary form of spermatogenesis; but in the phylloxerans and aphids as Morgan and von Baehr have shown, the differential division is unequal, and the x chromosome always passes into the larger cell.

It is of course, possible to assume that the inequality is itself determined by the asymmetrical distribution of the x chromosome; but on the whole it seems more natural to conclude that the x pole is predestined before the x element passes into it.

Morgan discovered in the phylloxera, the males produced parthenogenetically, possess but one x element instead of two, one of the x elements being eliminated in the maturation of the male producing egg; but this egg is already distinguishable as male producing by its smaller size, before elimination takes place. We may take the epigenetic view that sex is really first established or determined when all the essential sex factors have been brought to-

gether in the egg. The chromosome combination may be taken as the culmination of this process.

On the assumption that the x chromosome is one of the essential factors, the first impression is that the x chromosome must be the bearer of specific and opposite factors (such as chemical substances) that are per se male-determining or female-determining. In ordinary sexual reproduction all the unfertilized should after maturation, bear the male tendency, because one x element is left in the egg after reduction. If capable of parthenogenesis with the haploid (reduced) number of chromosomes, such eggs should produce males (as appears to be the case in the bees and ants). If fertilized by a spermatozoon that lacks the x element, the egg produces a female, because of the introduction, not of the dominant "female tendency" but of a second x element.

This relation is also interpretable from the Mendelian view point, so that we may say that sex belongs in the category of Mendelian phenomena. In nearly all organisms thus far studied the female is to be regarded as homozygous and the male heterozygous for sex. When the egg is fertilized by one type of spermatozoa the zygote is a female, if fertilized by the other type of spermatozoa the zygote is a male. In general, the female diploid nuclei contain two of the sex chromosomes or two groups of them when the sex chromatin is compound. The nuclei of the male contain only one of these [illegible], either with or without a synaptic mate, different from it in character.

The view that sex is determined by conditions external to the germ has in recent years given away to the belief that it is primarily established by an automatic mechanism within the germ-cells. The change of front in regard to this time honored and most interesting problem has been due to the convergence of evidence from two widely different lines of inquiry, one relating to the facts of sex heredity the other to the cytological constitution of the germ cells.

The conclusion has become in a high degree probable that sex is controlled by factors internal to the germ-cells, that the male or female condition does not arise primarily as a response of the developing germ to corresponding external conditions. Such conditions may operate to modify the action of the internal mechanism, but the process of sex production is fundamentally automatic. In so far as sex has been traced to a predestination of the fertilized egg, or to a predestination of the gametes that unite to produce it, the problem of sex production may be said to have reached a proximate solution.

Chapter III.

A BRIEF HISTORY OF THE MICROSCOPE and of MICROTECHNIQUE.

Antony von Leeuwenhoek appears to be the first to succeed in grinding and polishing lenses of such short focus and perfect figure as to render the simple microscope a better instrument for most purposes than any compound microscope then constructed. This was approximately about 1660.

Robert Hooke shaped the minutest of lenses, with which he made most of his discoveries, from small glass globules made by fusing the ends of spun gladd. Early opticians and microscopists gave their chief attention to the perfection of the simple microscope. This was due, in part, to the view held by the early opticians that a compound microscope could never produce such good images as the instrument of the simple type, but this view was later proved erroneous. The principle attention of the modern opticians has been directed to the compound instrument. Although we now know how the errors of lenses may be corrected, and how the simple microscope may be improved, this instrument remains with relatively feeble magnification, and to obtain stronger magnifications the compound form is necessary. The arrangement of two lenses so that small objects

can be seen magnified followed soon after the discovery of the telescope.

The history of the telescope is so closely linked with that of the microscope that it is necessary to say a few words about the telescope here. Though there are certain evidences of the apparent discovery of the microscope before 1600, it is quite certain that previous to that time it was unknown, except probably to individuals who failed to see its practical importance, and who confined its uses to such practices as that of "natural magic". "The practical discovery of the instrument was certainly made in Holland about 1608, but the credit of the original invention has been claimed on behalf of three individuals, Hans Lippershey and Zacharias Jansen, spectacle makers in Middleburg, and James Metius of Almaar." Ency Britt. (1911)

The first compound microscope (discovered probably by the Middleburg lens grinders, Johann and Zacharias Jansen about 1590 or a little later) was a combination of a strong biconvex with a still stronger biconcave lens: it had thus, as well as the first telescope a negative eyepiece. The development of the compound microscope depends essentially on the improvement of the objective; but no distinct improvement was made in its construction in the two centuries following its discovery. In 1668 the

Italian Divini employed several doublets, i. e, pairs of plano convex lenses, and his example was followed by Griendl von Ach. But even with such moderate magnification as these instruments permitted many faults were apparent. A microscope, using concave mirrors, was proposed in 1672 by Sir Isaac Newton; and he was succeeded by Barker, R. Smith, B. Martin, D. Brewster, and above all, Amici. More recently these catadioptic microscopes were discarded because they all yielded unfavorable results. From 1830 onwards many improvements were made in the microscope objective. Herein was the improvement that has lead to the modern compound microscope of to-day.

Amici is best known for the improvements he effected in the mirrors in reflecting microscopes and improvements in the compound microscope.

Close upon the improvement of the microscope came the improvement of the methods of technique. Methods of technique were in their infancy in 1875; their development has enabled observers to achieve the most exact study of minute anatomy, in the case of small objects, which without these methods could only be investigated by the unsatisfactory process of focusing with the microscope through the solid object.

There have been developed two methods of pre-

paring materials for examination by first sectioning the material. These two methods are: the wet method, and the dry method.

The wet method is briefly: the tissue is soaked in a solution of gum or of gum and syrup, and after being frozen by ether spray, or by a mixture of ice and salt is cut into very thin sections by a suitable section cutter. This method which today is used mainly by pathologists has two main objections; the prolonged action of the watery fluids on the tissues, and the impossibility of getting ribbons, each section having to be picked up separately.

The dry method: In the first place the tissue must be killed; in the second it must be fixed, i.e. the protoplasm must be set or coagulated as far as possible in the condition in which it appears in life; and in the third it must be hardened, i.e. in most cases dehydrated. An advanced stage in the possible perfection in the use of the fixing reagents has already been reached by the cytologists and the histologists.

"The second set of processes relates to the staining without which transparent sections are almost invisible. The stains are divisible into general stains, which dye the tissue practically uniformly and indifferently; and selective stains,

which have affinity for special tissues or cell elements. Of the latter group some fasten on nuclei, others on the chromatin of the nuclei; some on connective tissues, others on muscle fibres, and so on. It is probable that the action of all these selective stains is produced by definite chemical combinations originally in, generated in, or introduced into the tissue selected." Ency Brit. (1911)

From 1858 on there has been a very rapid progress in the matter of selective or differential stains found practical. Many highly satisfactory combinations have been worked out. The chief sources of the stains are the boxwood and the coal tar dyes.

Two methods of staining have been worked out for the use of the above mentioned stains, respectively, viz; the regressive stains, where the material is stained uniformly too deeply and the superfluous stain is washed out. The other stains are known as progressive stains, where the material is gradually brought up to a uniformly stained condition.

This advance in technique is responsible for our present intimate knowledge of the plant and animal cell, and the progress that has been made along cytological and histological research lines has been governed entirely by the rate of advancement made in microtechnique.

W. Geisbrecht was the first (1881) to fix sec-

tions on the slide, also in the same year and in the same laboratory of the Naples aquarium W. H. Caldwell first cut and fixed ribbons of sections. The first automatic microtome suitable for cutting a block of tissue into a continuous series of sections was made in 1883 in the workshops of Cambridge by W. H. Caldwell and R. Threlfall. Now there are several makes of highly efficient machines on the market.

Chapter IV

STRUCTURES

Arranged for Plants and Animals.

PLANTS

The first discovery that was a significant manner, and a direct bearing on this subject was that of Robert Hooke, who in 1665 noted and described the vesicular structure of cork and similar vegetative substances as little boxes or "cells" distinct from one another and separated by solid walls. He designated the cavities by the term "cells". He supposed them to be empty, and the whole importance was attached to the cell wall. Hooke did most of his work with a compound microscope. He was followed by Malpighi who in 1674 by working with a low power gave a more detailed description of the finer structure of plant tissue than had heretofore been known. His observations were confirmed by the works of Grew (1682) which were of a similar nature to those of Malpighi. Malpighi was the first scientist to apply the microscope alike to the study of animal and plant structures. He illustrated parts of the seed, even the history of its germination by numerous figures.

"In all accounts of the theory of sexuality in plants Sir Thomas Millington, a botanist is considered as the first person who first claimed for the stamens

the character of this organ of generation in plants."

Grew (1682)

Linnaeus (1751) was the first notable systematist, and he is responsible for the naming of the organs of fructification of plants. "He distinguishes seven parts as follows:-

1. The calyx, which represents the rind.

2. The corolla, which represents the inner rind of the plant.

3. The stamen, which produces the pollen.

4. The pistil, which is attached to the fruit and receives the pollen; here for the first time the ovary, the style and the stigma are clearly distinguished.

5. The pericarp, the ovary which contains the seed.

6. The seed, the part of the plant that falls off from it, and is the rudiment of a new plant.

7. The receptaculum, by which Linnaeus understands everything by which the parts of the fructification are connected together." Sachs (1890)

To Amici is accorded the discovery of the pollen tube. He was examining hairs on the stigma of Portulaca for another purpose and saw on that occasion (1823) the pollen tube emerge from the pollen grain on the stigma, and the granular contents of the latter, commonly known as the fovilla, execute streaming move-

plants like the [illegible] development [illegible].

"Steenstrup in 1845 introduced the term "alternation of generations", but it only carried the idea of a succession of vegetative shoots in the production of the flower." Green (1909)

The researches of Hofmeister published in 1851 placed the study of morphology on a new plane. In them for the first time a unity of plan was shown to run through all the Archegoniate plants, and all the old distinctions based on the methods of reproduction had to be abandoned. "Hofmeister showed clearly that in the Mosses, Liverworts, Vascular Cryptogams and the Gymnosperms the two forms or cycles of which their life cycle consists, and distinguished between a spore bearing generation and another which exhibits sexual reproduction.

Green (1909)

Celakovsky in 1868 gave us the following facts:- he distinguishes two different kinds of life cycle. In the Thallophytes asexual forms follow for several generations, then a sexual form occurs. In the Archegoniate plants, from the liverworts upwards, the alternation of sexual and asexual forms is constant. Celakovsky applied the terms protophyt and antiphyt to the two phases, names later replaced by gametophyte and sporophyte which are in common use today. Green (1909)

The stamen in 1850 was held to be a metamorphosed leaf, and it was not until 1873 that the first account of its anatomical development appears to have been given by Warming.

In 1863 Kolliker gave the name "cytoplasm" to the protoplasmic ground substance as opposed to the granules. Two years later he gave the name "cell sap" to the more liquid ground substance of the nucleus.

In 1875 Strasburger applied the term "cell plate" to the equatorial thickening of the spindle fibres from which the partition wall arises during the division of the plant cells.

Schwartz in 1887 showed the existence of linin threads in the resting nucleus.

In 1894 Strasburger placed the alternations of generation on a chromosome basis, and showed that not only does a reduction of the chromosomes take place which marks the passage from the Sporophyte to the Gametophyte, but that the reduced or gametophytic number is phylogenetically the primitive number, the dominance of the sporophyte with the diploid number in the life cycle having been reached chiefly in the higher phyla of plants.

STRUCTURE OF ANIMAL CELLS.

In 1781 Fontana observed the existence of a definite body in the protoplasm, and called it the

"nucleus" by which name it has since been known, but Brown failed to recognize its significance. It was not until 1840 that the term "protoplasm" came into use. At that time Purkinje applied it to the formative substance of the young animal embryo, and compared it with the granular material of the vegetable cambium.

In the following year 1841 Kolliker demonstrated that the spermatozoa arise directly from the cells in the testes, and cannot be regarded as parasites, but are the products of preexisting cells in the plant body. Kolliker did not identify them as cells, but believed them to be of purely nuclear origin.

It was not until 1865 that the spermatozoa were proven to be complete cells when Schweigger-Seidel and La Valette St. George brought forth the proof simultaneously that the spermatozoa is a complete cell, consisting of a nucleus and cytoplasm, and hence of the same morphological nature of the ovum. Wilson (1896)

In the many investigations that were being carried on regarding the phenomenon of fertilization Debary in 1844 discovered spermatozoa within the egg of the rabbit and established the fact that the spermatozoa do penetrate the egg or ova.

Hugo von Mohl in 1846 gave the name protoplasm, suggested by Purkinje, the living substance within the cell walls. It was first considered as cell sap,

...on was more carefully studied by Nageli between 1842 and 1846 and was perceived by him to be of a nitrogenous nature.

Gegenbaur in 1861 proved that the vertebrate egg was a single cell.

The apparent mysterious nature of protoplasm continued to command the attention of the zoologists especially, and between 1850-1870 Max Schulze with Brucke, Kuhne and others studied both animal and vegetable protoplasm. In 1863 Schulze and his associates established the fact that protoplasm is the vital principle of animal and vegetable life, and that the living substance is of similar nature if not identical. This discovery is one of the most important results of research in modern natural science. Schulze was the first to prove that the protoplasm of von Mohl, studied by Cohn, Unger, De Bary and others is practically the same thing as sarcode of the animal phsiologists, though Unger had suggested it in 1855.

A minute chromatic body was detected at the spindle poles in 1873 by Flemming, and was found to be an inseparable companion of the nucleus in animal cells also by Flemming and independently by van Beneden in 1875-76. Flemming named this chromatic body the "centrosome".

"Parallel with the changes in the chromatin during mitosis a complicated structure known as th

"amphiaster" (so described and named by Fol in 1877) makes its appearance in the position formerly occupied by the nucleus. The amphiaster arises under the influence of the centrosome of the resting cell which divides into two similar halves, an aster being developed around each while a spindle stretches between them. This structure consist of a fibrous spindle shaped body, the spindle, at either pole of which is a star or aster formed of rays or astral fibres, radiating into the surrounding cytoplasm. The whole strongly suggesting the arrangement of iron filings in the field of a horseshoe magnet." Wilson (1896)

The centre of each aster is occupied by a minute body known as the centrosome (Boveri in 1887 observed the sphere and its centre being occupied by a minute body. He called the dense central body the "centrosome" and regarded it as a contribution from the spermatozoan to the attraction sphere of the ovum. Boveri and van Beneden in their papers in 1887 regarded the centrosome as initiating not only the division of the cell body, but that of the chromatin also), which may be surrounded by a spherical mass known as the centrosphere. (Strasburger in 1893 announced that the centrosome may at times and in some species be surrounded by a spherical mass known as the "centrosphere"). As the amphiaster forms, the chromosomes group themselves in a plane passing through the equator of the spindle, and thus form what is known as the equatorial

plate. (Flemming in 1879 discovered that the chromosomes arrange themselves in what he called the "equatorial plate" of the spindle and each splits longitudinally in two. This was confirmed by Retzius in 1881).

In 1878 Klein discovered the existence of a nuclear membrane separating it from the rest of the cell. Flemming in 1878 showed the general existence of the centrosome in animals. In addition he outlined the whole scheme of mitosis (karyokinesis) substantially as we now understand it. In 1879 he gave the name "chromatin" to the deeply staining substance of the nuclear network, and of the chromosomes, consisting of nuclein. (Their substances form what is known as the chromatic portion of the mitotic figure.) There is in addition to the chromatic figure the achromatic figure consisting of the spindle and asters, which in general stain but slightly. The next year he discovered the splitting of the chromosomes. "The chromatic network is converted into a thread which whether continuous or discontinuous, splits throughout its entire length into two exactly equivalent halves". In 1882 he applied the term "dispireme" to that stage of mitosis in which each daughter nucleus has given rise to a spireme. In the same year he also set forth his theory on the continuity of the nucleus by extending

Virchow's aphorism to the nucleus, viz; "omnis nucleus e nucleo".

"Strasburger in 1882 applied the term "cytoplasm" to the substance of the cell body as opposed to that of the nucleus." Wilson (18[illegible])

"To van Beneden belongs the honor of having discovered the attraction sphere. In the year 1887 he found in the fertilized ova and the blastomeres of "Ascaris megalocephala" at the pole of the nuclear spindle, definite spheres each with a dense center which he considered as permanent cell organs in connection with the nucleus. Van Beneden suggested that the pull of the mantle fibres caused the division of the chromatin in the equatorial plate stage."

Schaffner

"The resting nuclei of many species of plants show a finely divided reticulated chromatin. A study of the formation of the reticulum in the telophases and its behavior in the prophases, however, has led in many cases to the identification of the so-called "unit reticula", derived from single chromosomes, and was advanced by Boveri in 1888 and also in 1904, both observations being made on Ascaris. Among those who have contributed positive evidence for the existence of the unit reticula in plants are: [illegible]ggaerts, 1904; Martins Mano, 1905; Yamanouchi, 1910; Stomps, 1911 and Overton, 1911. The evidence strongly suggests that such reticula are present in all [illegible]

whose nuclei possess a finely divided reticulated structure during the resting condition." Stout (1912)

Flemming first found attraction spheres and centrosomes in the resting stage of leucocytes, and in the epithelial cells of the lungs of the salamander. Guignard found them in the same year in the resting stage and mitosis, in the reproductive vegetative cells. Others have found them as follows:

Burger	'91	Resting cells.
van der Stricht	'92	In blastomeres of Triton and amphibia.
E. de Wildeman	'92	In Spirogyra.
Butschli	'92	In Surirella.
Schottlander	'93	In Antheridia of Gymnosperms.
	'93	In spermatozoids and ova of Chara.
Heidenhain	'94	In lymph cells and giant cells in marrow of bone of rabbit.

They remain outside the nucleus during the resting stage. They persist in cells which they have ended their growth and division. Also they seem to be the organs which institute and direct the nuclear division.

"Butschli in 1892 was the first to emphasize the fact that protoplasm has the structure of a foam or network with the interstices filled with material of a physical nature different from the network, or finally, the structure of an emulsion. His anatomical observations led him to study foams, and emulsions experimentally in the hope of being able to interpret his anatomical studies more rationally. He was the

first to point out that protoplasm is heterogeneous, consisting of at least two phases touching each other by minimal or capillary surfaces." Alsberg (1911)

The discovery of Hermann in 1892 of the central spindle first clearly showed that two kinds of fibres must be recognized in the mitotic figure. Those in the central spindle correspond to the continuous spindle fibres of Flemming 1891 and of Strasburger '84, and the mantle fibres, i.e. half spindle of Polstrahlen; of van Beneden '87; and Boveri '89.

In 1884 Strasburger announced the generalization that the reduced cell contains half the "number of chromosomes found in the somatic cells, or sporophyte generation".

Juel in 1900 proved conclusively that three of the microspore nuclei degenerate, thus confirming and extending the work of Elfving 1879; and Strasburger 1884 on Heleocharis.

Chapter V.

MENDELISM.

Joseph Gottlieb Koelreuter in 1761 made a most important contribution to science in the production of hybrids, and the observation of the characters proper to both parents found in the offspring. This artificial production of hybrids by his experiments threw light on the nature of sexuality. He was the first who carefully studied the arrangements for pollination and pointed out the remarkable relation between them and insect life.

The next important work the history of hybridization records for us is that of John Goss, who in 1821, made some crosses on the garden pea, and actually witnessed the true phenomena of dominance and segregation as well as the true breeding of recessives but failed to note the significance of his results.

It remained for Gregory Mendel in 1865 to place before science certain explanations concerning the phenomena exhibited by hybrids. The romantic story of Gregory Mendel is well known to everyone interested in heredity, and breeding work, be it with either plants or animals. He spent long years in obscurity in hybridizing garden peas, and made a great discovery, but died to see it scarcely noticed and soon forgotten. His publication was practically buried in the "Proceedings of the Natural History Society" of Brunn; [illegible]

who knew it, as Naegeli for instance did, failed to realize its importance; in fact, Mendel's remarkable work was lost sight of amid the enthusiasm and controversy which the publication of Darwinism (1858) had evoked.

Darwin's theory was an answer to the question "How do the characters of the parents get into the germ cells which it produces." Pangenesis died not because Galton's experiments designed to test it had a negative result, but because Weismann's criticisms effected a swinging around of biological opinion to a statement of the problem of heredity which was the diametric opposite to that which had prevailed before.

The real question was not "How do the characters of the organism get into the germ cells which it produces?", but "How are the characters of an organism represented in the germ cell which produces it?" he knew this fact so well that he did not know that he knew it. Others reading his paper could not conceive how the characters got into the germ-cells, and the result was that no point was seen in Mendel's theory and it quickly lapsed into oblivion. Certain facts of alternative inheritance were clearly stated and accounted for by Mendel, he thus not only formulated loaw of alternative inheritance, whose correctness has been fully confirmed by a number of inde-

pendent observers, but he thus laid the foundation for a general theory of heredity. The conclusions he drew in regard to the inbreeding of hybrids is briefly referred to as Mendel's Laws; viz,

The Law of Dominance, and

The Splitting of the Hybrid Race.

With these facts he connected the theory of genetic corruption. In the history of the study of heredity his discovery is the most fundamental and far reaching. Only under the fertilizing influence of Weismann's ideas was the rediscovery of Mendel's law accomplished independently by DeVries, Correns, and Tschermak in 1900. To its further development no one has contributed more than Bateson.

Chapter VI

The Nucleus.

Within the protoplasm of the cell lies a body, known as the nucleus, first described by Fontana in 1781, though historical views generally refer the discovery of the nucleus to Robert Brown, who in 1831 reported it as being present in the cells of the epidermis of Orchidaceous plants, and in 1833 recognized it as a normal element of the cell, and showed that it was very generally present in the tissue cells of Phanerogams, perhaps adding that before Brown's work the nucleus had occasionally been figured.

"In a paper published in Linnaea 2:428: 1827 by F. J. Meyen he gives an account of the nucleus of Spirogyra, which for accuracy of observation and clearness of detailed description leaves little to be desired." Marquette (1911)

The nucleus arises through division of a corresponding element of a preexisting cell. It is separated from the streaming protoplasm of the normal cell by a [illegible] definite membrane known as the nuclear membrane.

The next observable structure of a resting nucleus is the nuclear reticulum, which is an irregular branching network of linin, invisible until treated with suitable reagents, when it takes on a

deep stain. This [illegible] is known as chromatin and is apparently [illegible] handed [illegible] from division to division. After staining there are visible in the reticulum scattered granules and small [illegible] of chromatin of different sizes and shape and form, and of a greater number than that characteristic for the chromosomes [illegible] known as chromomeres.

There are also usually one or more larger rounded or irregular bodies staining differently from the chromatin and known as nucleoli. Of these there are recognized two kinds; plasmosomes and karyosomes.

The fourth structure of importance in the resting nucleus is the ground substance or the nuclear sap. It is a clear substance occupying the interspaces of the network and is not stained by dyes that affect the linin chromatin and plasmosomes. When the cell prepares for division the chromatic fibres of the irregular network of the reticulum shorten and thicken, until a long thread or spireme thread is formed. This forms a closely convoluted mass in the nucleus, and this is the stage that has come to be known as "synapsis". From this condition there emerges a thread that shows sooner or later evidences of its double origin (i.e. maternal and paternal). In the heterotypic division this spireme breaks up into the characteristic number of reduced chromosomes.

SYNAPSIS.

That phase of the nucleus just preceding the heterotypic mitosis in which the fusion of the simple chromosomes into multiple ones, usually of a bivalent nature takes place, was named synapsis by Moore in 1895, and has come to be regarded as an important and critical period in the life cycle. It was called synapsis because of the apparent concentration and contraction of the chromatin at one side of the nuclear cavity. The peculiar appearance of the nuclear thread at this period seems to have been first observed by Schlevianoff in 1875. He gives a very good representation of a synaptic nucleus in the pollen grain of Cupressus. The figure is plainly that of a pollen mother cell. Synaptic figures were observed in various pollen mother cells by Tangl, 82; Strasburger, 82; Lenoir, 84; Guignard, 84; van Beneden and Julin, 84; Moltschilsky, 88; O. Hertwig, 90; Overton, 91; and Brauer, 93, all of whom, however, considered the peculiar appearance to be an artificial condition caused by imperfect fixation. It was however confirmed in 1897 by Miss Sargant, who found this condition in the fresh material of the Lilium. It is now considered an end result of fertilization.

Allen, Farmer, Gates, Mottier, Overton, Yamanouchi, Davis, Miss Fraser and Cardiff are a few of the present

many cytologists supporting the (view) synaptic phase.

It is interesting to note that Weismann insisted on the theoretical necessity for reduction division in connection with his views as to the relation of ancestral characters with material principles. The term synapsis, has in the last few years received wide currency among cytologists as a designation for real and hypothetical processes supposed to take place in the early stages of reduction divisions. At the present time cytological literature abounds with contradictory accounts of various cell activities supposed to be normal, until the reader is certainly confused.

The remarkably constant and characteristic phenomenon associated with the reduction division in plants and animals, have long attracted attention, but the interpretations which have been suggested have been many and various, until today there are but two important interpretations held at the present.

There are some points in common and they are to the effect that it is generally admitted that a qualitative separation does take place in the heterotypic, but there is no such harmony as to the manner in which it is supposed that this end is attained. Early attention was directed on the changes involved in the actual heterotypic division, i.e. on the late prophase and metaphase of this division; it is now recognized that the true interpretation must rest on accurate knowledge of the nuclear changes which take place at an earlier stage--the earliest stages of prophase.

The two interpretations held today are; Parasynaptic, and Telosynaptic, by the parasynaptists and telosynaptists respectively.

Parasynapsis.

"The parasynaptists or the greater number of supporters parasynapsis involve the idea of a lateral pairing of the chromosomes, brought about by the the approximation towards one another of two previously independent spireme threads, which are generally assumed to be derived respectively from the male and female germ nuclei which united in fertilization. During the early prophase, or earlier, these two threads arrange themselves in parallel, becoming closely approximated until at the time of synapsis a more or less complete, though temporary fusion takes place. From the contracted condition of the spireme, characteristic of synapsis, the spireme emerges a thread which shows sooner or later distinct traces of its double origin. This double thread gives rise to the "bivalent" chromosomes of the heterotypic division. That is to say, two pairs of somatic chromosomes which lie side by side having been brought into this position by the approximation of the threads towards one another, which took place in the prophase.

The heterotypic division consists in the separation from one another of the two members of each pair of chromosomes, one member passing to the one daughter nucleus, its mate to the other. This process of separation takes place throughout the whole series of pairs of chromosomes, and thus a quantitative reduction is brought about, each of the daughter nuclei containing a single series of chromosomes, as compared with the paired or double series which is found in the somatic cells." Gregory (1909)

The most widely known investigators supporting the pairing of homologous maternal and paternal elements in the form of parallel threads are: Allen, 05; Berghs, 04; Carduff, 06; Gregorie 04-07; Miyake, 08; Overton, 09; Rosenberg, 05-09; Yamanouchi, 08. Overton brings forward evidence supporting views put forward by him in connection with Strasburger, Allen and Miyake when the occurrence of a lateral pairing in the prophase of the heterotypic division was advocated.

Telosynapsis.

"The alternative interpretation provides the same final result, but involves a different method of pairing. It is a characteristic feature of the heterotype division, that the spireme, as it emerges from the contracted condition known as synapsis is thrown into a series of loops. According to the interpretation we are now considering, the pairing of the chromosomes is brought about by the approximation towards one another of the limbs of these loops. Thus each pair of chromosomes is at first a "U" shaped structure, the two chromosomes being joined end to end, the point of junction forming the bent portion of the U.

The parallel limbs of the U come closer and closer together, and sooner or later a transverse fission takes place at the angle, the paired chromosomes now lying side by side for the separation which takes place in the metaphase of the heterotypic division. This method of attaining the paired arrangement,-by the looping of the thread and the subsequent approximation of the loops towards one another-involves an "end to end pairing" of the chromosomes. Since the loops are generally continuous with one another at their inner ends it follows that the chromosomes are arranged in a single linear series.

Although direct proof is necessarily lacking, the evidence is very strong in favor of the correctness of the hypothesis that the two chromosomes which are united in each pair are respectively of maternal and paternal origin. It, therefore, follows that the looped thread, as it emerges from the contracted state, chromosomes of maternal and paternal origin must be arranged alternately in a single linear series."

Gregory (1909)

These supporting the view that the split which occurs at the time of synapsis is a true split, and is not preceeded by a pairing of parallel threads, but the thread is single from the beginning. Farmer & Moore 03-05, in Lillium, Osmunda and Psilotum; Farmer & Shove, 05, Tradescantia; Schaffner, 06; Mottier, 05-07, Lillium, Podophyllu, & Tradescantis.

These studies of chromosome reduction in different plants indicate that there are two general methods of reduction in organisms, viz; parasynapsis and telosynapsis. "The difference, however, is not of phylogenetic significance, because the whole chromosome must be regarded as the unit of nuclear morphological structure. In general, genera having shor chromosomes will show telosynaptic pairing, while in forms with long thread like chromosomes, the chromosomes are likely to pair parasynaptically.

In organisms having heteromorphic chromosomes, both methods may occur in the same nucleus, whether the pairing shall be side by side or end to end is, therefore, not of phylogenetic or of hereditary importance, but is merely a matter of cell mechanics; and the two methods of chromosme reduction are therefore essentially one." Gates (1911)

Those supporting the synaptic conditions are:

Cardiff	Botrychium obliquum.
Farmer & Moore	Osmunda regalis.

Gregoire	Osmunda regalis.
Yamanouchi	Nephrodium molle.
"	Polysiphonia violacea.
Burlingame	Ophioglassiales.
Marquette	Isoetes Lacustris.
"	Marsilia quadrifolia.
"	Equisetum hyemale.
Strasburger	Many species of Marsilia.
Cardiff	Ginko Biloba.
Noren	Juniperus communis
Allen	Coleochaete.
Blackman	In the rusts.
Harper	In Mildews.
Miss Sands	In Mildews.
Olive	In Myxomycetes.

Overton (1909)

FERTILIZATION

From the beginning of the history of man the primary fact of the necessary concurrence of two individuals in the production of offspring has been recognized. Little more was known of the essential features of the sexual process in animal than had been familiar to the Assyrians, Egyptians and Greeks at least twenty centuries previous to 1850. While sexuality in plants had been suspected as early as in 700 B. C., yet it remained for Camerius (1694) to prove experimentally the existence of sex in plants.

From the time of Aristotle onwards many theories regarding fertilization were held by as many authors. True, some of the more notable theories constituted distinct steps of advancement towards our present day knowledge of sex. Notable were those of Harvey, Spallanzani and of Prevost et Dumas.

Among the botanists Schmeidel 1747, Esenbeck 1822, Bischoff 1828, Unger 1834-37, Nageli 1844, observed motile spiral filaments, animalculae, as they thought to be in several of the lower plants, viz; liverworts and ferns. Unger (1837) in his studies on the Mosses declared that they were male fertilizing cells.

At about this time the zoologists were making some interesting observations on the spermatozoa of animals. Barry (1844) had seen a spermatozoa within the egg of a rabbit. Leuckart (1849) saw them enter the frog's egg; and Bischoff together with Allen Thompson proved that fertilization is accomplished by the actual entrance of the spermatozoa into the egg.

De Bary for the botanist in 1858 described at length the simplest form in the sexual act of the Conjugatae, and regarded it as a sexual process.

Butschli in 1873 published his discoveries on the nematode in which he observed in the egg of a nematode the approach and contact of two structures, which we now know to be germ nuclei, immediately preceeding the first cleavage of the ovum. Butschli did not assign an interpretation to this phenomena at the time.

Auerbach in 1874 described the appearance of two nuclei at the opposite ends of the elongated egg of Rhabdites, these increase in size, migrate towards the centre of the egg, meet, rotate through 90^{o} and fuse together. A dicentric figure appears and cleavage follows. It was supposed that the nuclei at the ends of the elongated egg arose freely.

Oskar Hertwig in 1875 observed and described correctly the principle phenomenon of fertilization in the sea urchin egg. He did not actually see the

spermatozoa penetrate the egg but observed the sperm nucleus and its aster soon after, and interpreted therefrom correctly the process of fertilization. (The egg nucleus was regarded as being the persistent nucleus of the germinal vesicle). He reached the definite conclusion that fertilization consists in the union of the male and female pronuclei.

Edward van Beneden (1875) observed in the rabbit's egg the fusion of two nuclei before cleavage. He did not see the spermatozoa enter the egg, but found them with their heads closely applied to the surface in every unsegmented egg. He concluded that fertilization consisted essentially in the fusion of thespermic substances with the superficial layer of the vitellus. At a little later stage he found a small nucleus in the cortical layer of the egg; this he called the peripheral pronucleus, a central pronucleus appeared simultaneously. They grow, approach one another and meet in the centre, later there is only one nucleus, probably formed by the union of the two.

Fol made some observations in 1875-6, partly in dependent and partly after the publication of Hertwig's first paper.

1. He observed the details of penetration of the spermatozoa with a clearness that has never been surpassed for these forms.

2. He gave the first correct account of the

maturation divisions and origin of the egg nucleus.

3. He paid special attention to the origin of the fertilization membrane, and founded the classic theory that it was an adaptation of prevent polyspermy.

4. He was the first to adequately present the harmful effects of polyspermy.

Hertwig first observed in 1876 the approach and union of egg and sperm nuclei. Schmitz one year later observe in Spirogyra the fusion of the egg and the sperm nuclei.

Hertwig in 1887 initiated the modern period in the physiology of fertilization. The one is the direct experimental analysis of the fertilization process itself. The other is the attempt to initiate the action of the spermatozoa by chemical and physical agencies, in short, the studies on artificial parthenogenesis.

"Our insight into the nature of the process of fertilization was very materially promoted by the discovery, made by van Beneden (1883) that the number of chromosomes is the same in both the conjugating nuclei. Further investigations established the fact, for both plants and animals, that a reduction to one half the number of the chromosomes in the generative nuclei preceeds the sexual act, and that in consequence of the coalescence of the male and female nuclei, the nucleus of the fertilized ovum possesses the number of chromosomes characteristic of a vegetative cell."

Strasburger (1894)

Chapter VII

XENIA.

In 1867 Hildebrandt noticed a peculiar phenomenon resulting from crossing a dark brown and a yellow race of maize. The embryo was hybrid and the endosperm showed characters proper to each of the two parents. This same phenomenon was observed again in 1872 by Kornecke. Again in 1881 by Focke who gave the name "xenia" to it. Xenia may be defined as the effect of pollen of another race upon the tissue of a seed plant apart from that initiating the formation of the embryo. The term originally meant the effect of pollination upon mother tissue, but has come to be applied to the appearance of the F_1 hybrid endosperm produced by the fusion of the second male nucleus with the so-called endosperm (fusion) nucleus of the embryo-sac, when its characters are different from those exhibited by the mother plant after self fertilization. The endosperm shows the characteristic features of the plant from which it is formed and also of that from which was derived the pollen the pistil received.

The fact of this fusion was proved cytologically by Guignard (1899) and by Nawaschin (1899).

In view of certain considerations East considers it possible to formulate the following law regarding

xenia. "When two races differ in a single visible endosperm character in which dominance is complete, xenia occurs only when the dominant parent is the male; when they differ in a single visible endosperm character in which the dominance is incomplete or in two characters both of which are necessary for the development of the visible difference, xenia occurs when either is male." East (1913)

Chapter VIII

CHROMOSOMES.

As the cell prepares for division the most conspicuous fact is a transformation of the nuclear substance involving both physical and chemical changes. The chromatin substance rapidly increases in staining power, loses its net like arrangement, and by resolving itself into a spireme finally gives rise to definite number of separately intensely staining bodies, usually rod shaped, curved or straight, and known as chromosomes. This phenomena was best described by Flemming in 1887 who is considered to be the discoverer of chromosomes, but were named by Waldeyer in 1888 because of the deeply staining qualities of these bodies of the spireme.

The remarkable fact has been established with high probability that "every species of plant or animal has a fixed and characteristic number of chromosomes which regularly recurs in the divisions of all its cells, and in all forms arising by sexual reproduction, the number is even."

Flemming in 1880 observed the splitting of the chromosome that is, when the chromatic net work is converted into a thread, continuous or discontinuous, splits throughout its entire length into two exactly equivalent halves. This was closely followed by the

observations of Roux who in 1883 stated that "the daughter nuclei receive precisely equivalent portions of chromatin from the mother nucleus." This was based to a certain degree on the work of W. Pfitzner who in 1882 was the first to show that the splitting of the chromosomes in the equatorial plate was only the reappearance of a split in the spireme thread and was due to a corresponding division of each of the two chromatin granules.

Eduoard van Beneden in his observations on the germ cells of Ascaris in 1883 was the first to describe this process of mitosis wherein the chromosomes were halved, and named it reduction divisions.

Strasburger, one year later, 1884, in his observations on this form of cell division recognized four rather distinct period and suggested the names or terms prophase, metaphase, anaphase and telophase respectively for them. These terms have been in use since their proposal, and each means as follows: The prophase covers all the changes of the nucleus up to the completion of the mitotic figure. The metaphase is the parting of the sister chromosomes in the equatorial plate. The anaphase is the term applied to their passage to the opposit poles of the spindle; and their reco struction to form the daughter nuclei, the telophase.

Flemming in 1887 working on the same phases of meiosis as did Strasburger described and named the first stages of maturation divisions and called it the heterotypic division because of the reduction in the number of the chromosomes.

There sprang up in 1882 at the instance of Strasburger certain theories in regard to the probable individuality and permanence of the chromosomes when Strasburger made observations on species of plants whose chromosomes showed specific and constant differences in size and shape, thereby furnishing much evidence for the independent existence of these bodies. Heteromorphism in the chromosomes in plants as observed by Strasburger have been ably supported by the work of more recent cytologists, notably Rosenberg, 04; Miyake, 05; Schaffner, 09; Clemens Muller, 09; Thara, 10; and Ishkawa, 10. There is also a vast literature regarding heteromorphism among chromosomes in animals, regarding which adequate summaries have been given by Stevens, Wilson and Montgomery, all well known present day authorities.

The hypothesis of chromosome individuality dates back to Rabl who in 1885 " concluded that the chromosomes do not lose their identity at the time of division, but persist in the chromatic reticulum of the nucleus." The organization of the nucleus as described by Rabl involves directly the permanence of the

chromosomes. A comparison of the position and form of the chromosomes during reconstruction stages in the epitherlial cells of the Salamander, with their position and form during the prophases of division, convinced Rabl that the chromosomes do not lose their individuality in the resting nucleus, and that they appear in the same relative position and forms in which they entered the reticulum. In the resting nucleus Rabl believed he could find traces of the chromosomes, and described a distinct polarity of the nucleus, in which the chromosomes converge towards a definite point. Out of the resting nucleus the chromosomes again come into view due to the chromatic substance flowing back along predetermined paths into the primary chromosome bodies.

A large number of figures of recent workers, especially among the Zoologists, which relate to the synaptic contraction, strongly support Rabl's conception of polarity and permanence of the chromosomes.

Those supporting the synaptic contraction of the nucleus

Eisen	01	Batrachoseps.
Janssens	01	Triton alpestris, T, punctatus.
Schoenfeld	01	Spermatogenesis of the bull.
Meves	02	Paludina.
Schreiner, A & K.E.	04	Myxine, and Spinax.
Farmer & Moore	05	Periplaneta.

Moore & Robinson 05 Periplaneta.

Janssens 05 Batrachoseps.

The individuality of the chromosomes.

From the standpoint of heredity the critical stages in an organism are at fertilization and reduction. That in fertilization there is an approximate doubling of the chromosomes, half of which were contributed by each gamete, there is no longer any doubt. The "Individualitats Hypothese" was originally put forth by Theodor Boveri in 1887 as a result of C. Rabl's observation in 1885 that in the epidermal cells of the Salamander larva the chromosomes reappear in the mitosis of the mother cell,--the angles of the U shaped chromosomes being directed towards one pole of the nucleus. Boveri secured positive and similar evidence by his results in 1888. His Individualitats Hypothese was ably supported by the work of Fula, 93; L. R. Moja, 95; and Ozur Strasses, 98. The evidence supporting this hypothesis is based largely on:-

1. On the uniformity in the number and character of the chromosomes appearing in successive divisions,

2. On the proof that whenever more or less than the usual number of chromosomes enter a nucleus in the egg of Ascaris the same number always appears

in the later divisions of that nucleus,

3. On the evidence that the loss of chromosome identity during the reticulate condition is only apparent,

4. On the proof that nuclear fusion doubles the number of chromosomes, while the reduction division reduces the number by half.
Boveri extended the conception of individuality to the extent of regarding the chromosomes as elementary organisms rather than merely as permanent cell organisms.

Then too, that the number of chromosomes is proportional to the number of nuclei that have fused together was shown by zur Strassen, supported by Boveri in 1893-95, and by Morgan, 95, the latter by his observations on the fertilization of enucleated sea urchin egg fragments.

In 1897-99 Miss Huie observed the direct growth of the chromatin knots which are present in the resting nuclei into chromosomes. It was not until 1909 that Huie's work was confirmed by Rosenberg.

Continuity of the chromosomes.

Evidence for the continuity of the chromosomes is found in their presence through interkinesis. It is generally conceded that in many forms the chromosomes scarcely change their form in passing from the heterotypic to the homotypic division. This fact was shown

early as 1899 by Guignard (1899). Stout (1912)

Prochromosomes.

Rosenberg in 1904 was the first to discover that in Capsella Zostera and Calendula the number of definite chromatic masses in the resting nucleus is the same as that of the long known chromosomes of the division figures; that is, the chromosomes are in reality represented in the resting nucleus by these chromatic masses. Rosenberg called these "Pseudo-nucleoles". Overton (1905) proposed the name "Pro-chromosomes". Prochromosomes or bodies corresponding thereto, in the resting nuclei which bear some relation to the chromosomes either in number, form or size have been described for a large number of plants by many investigators.

The most prominent of these investigators are:-

Rosenberg	04-07	Capsella bursa pastoris, Zostera marina, Calendula sp., and Hieracium auricula.
Overton	05	Thalictrum purpurascens, Calycanthus floridus, Helleborus foetidus, and Campanula grandis.
Miyake	05	Galtonia candicans.
Yamanouchi	06	Polysiphonia violacea.
Laibach	07	Sisymbrium strictissimum, Brassica Napus, Stenophragma Thalianum, Alyssum Wierzbikcr A. argenteum, Iberis pinnata, & Lunaria biennis.
Lundegard	09-10.	

The Chromosomes in Heredity.

"There is reason to believe that there is a definite relation between chromosomes and allelomorphs, or unit characters but we have not before inquired whether an entire chromosome or only a part of one is to be regarded as a basis of the single allelomorph. The answer must unquestionably be in favor of the latter possibility for otherwise the number of distinct characters possessed by an individual could not exceed the number of chromosomes in the germ products; which is undoubtedly contrary to fact. We must, therefore, assume that some chromosomes at least are related to a number of different allelomorphs. If then, the chromosomes permanently retain their individuality it follows that all the allelomorphs represented by any one chromosome must be inherited together. On the other hand it is not necessary to assume that all must be apparent in the organism, for here the question of dominance enters and it is not yet known that dominance is a function of an entire chromosome. We observe that there cannot be more than x (x meaning the reduced or haploid number of chromosomes) independent pairs of allelomorphs in any discussion. The remainder of the inheritance is correlated or tied together in the chromosomes in x possible independent groups.

It is conceivable that the chromosome may be divisible into smaller entities (somewhat as Weismann

assumes) which represent the allelomorphs and may be dominant or recessive independently. In this way the same chromosome might at one time represent both dominant and recessive allelomorphs." Sutton (1903)

Chapter IX

THE ACCESSORY CHROMOSOME.

H. Henking in 1891 discovered a deeply staining body in the growth period of the primary spermatocyte of Pyrrhocoris, but did not detect its origin. He did not recognize its chromatic nature and its unequal distribution in the second division whereby one spermatozoan received one more chromatin element than the other. Payne (1909)

It remained for Paulmier (99) to confirm the dimorphism in spermatozoa discovered by Henking by his studies on Anasa Tristis. He described what he called a "chromatin nucleolus", which he thought originated at the time of synapsis by the union of two small spermatogonial chromosomes, divided in the first maturation division, but passed over undivided in the second.
The work of Montgomery supporting that of Paulmier showed that Henking's observations on Pyrrhocoris were largely true of the Hemiptera in general.

The results of Montgomery agree with those of McClung who is considered to be the founder of the theory of the accessory chromosome so named by him in 1902, when he had observed the essential features characterizing the accessory chromosome, outlined its

history and suggested a theory in explanation of its function, as that of a sex determiner. McClung observed the resemblance to a nucleolus in the resting stage, and the similarity to a chromosome during the period of division. In the monaster it is destined to lie in the equator among chromosomes where it also becomes divided inthe metaphase of mitosis, (Metakinesis), and so terminates by acting like a chromosome, as at the commencement it had formed one.

"There is in the spermatocytes of all the insects so far studied an unusual nuclear element which is characterized:-

By a remarkable uniformity in staining power, similar to that exhibited by the chromosomes in the metaphase;

By a continuous peripherial position during the spirem stage;

By an isolation from the chromatin reticulum and non-participation in its changes, and

By fission during metakinesis after the manner of chromosomes." McClung (1902)

Sutton (1902) was first able to distinguish the accessory chromosome in the cysts of 8 or 16 cells. "Here as in the spermatocytes, it seems to be removed as far as possible from the influence of the ordinary chromatin. This is accomplished by an enclosure ina separate nucleus. A distinct existence is maintained

during all the stages when a possible exchange of material between the accessory chromosome and the other chromosomes might be accomplished. Only after the chromosomes are definitely established as independent bodies are the barriers removed, and then only long enough to permit the act of metakinesis to take place.

During the period intervening between the acts of division the conduct of the accessory chromosome parallels that of the nucleus containing the remainder of the chromatin. A vesicle is formed, the chromatin substance is deposited upon its wall in intimate relation with the cytoplasm, a concentration ensues, and a definite chromosome is produced.

Paulmier held that the accessory chromosome was degenerating and considered it in the process of disappearing from the species, and reaches this conclusion after observing that in the last spermatocyte mitosis it fails to divide and is thus unequally apportioned to the resulting spermatozoa.

From the spermatogonia, each spermatocyte received one chromosome (the accessory) which through all the subsequent stages exists as a chromosome and never suffers extensive disturbance of its chromomeres, either for the purpose of metabolic activities, or for the possible exchange for the mutual influence with the other chromosomes. Montgomery assigns the origin of the accessory chromosome to a single spermatogonial chromosome, and it must be regarded, therefore, as a single element and as the possessor of two chromatids, after its longitudinal division, and so differs from the other elements which are constituted of four chromatids. Other chromosomes of the spermatogonia are lost in the spireme, in which condition their chromomeres exist in relation far removed from those prevailing in the component individual chromosome.

The prophase occupies a relatively long time and profound changes take place in the nucleus, as a result of which the chromatin emerges in the form of chromosomes, the like of which we are unable to find in any other cells of the body. Instead of having two chromatids at the time of the metaphase each of these has four. Throughout all the time involved in the production of these fundamental differences, the accessory chromosome has existed quite apart from the field of mutual influence in which the other chromosomes operate. It is thus apparent that it has its characters fixed, not in the generation which witnesses its division, but in the previous one. In other words, it is a spermatogonial chromosome which divides in the spermatocyte mitosis." McClung (1902)

McClung's conception of the function of the "X" or accessory chromosome is that it is the bearer of

those qualities which pertain to the male organism, primary among which is the faculty of reproducing sex cells that have the form of spermatozoa.

Requirements:-

a. The element should be chromosomic in character and subject to the laws governing the action of such structures.

b. Since it is to determine the germ cells are to grow into passive yolk laden ova; or into minute motile spermatozoa, it should be present in all the forming cells until they are definitely established in the cycle of their development.

c. As the sexes exist in about equal proportions it should be present in half the mature germ cells of the sex that bears it.

d. Such disposition of the element in the two forms of germ cells, paternal and maternal, should be made to admit of the readiest response to the demands of environment regarding the proportion of sexes.

e. It should show variation in structure in accordance with the variations of sex potentiality observable in different species.

f. In parthenogenesis its function would be assumed by the elements of a certain polar body. It is conceivable in this regard, that another form of polar body might function as the non-determinant germ cell.

Finally, with respect to the evidence derived from parthenogenesis, it should be remembered that we are here dealing with a practical expression of sexuality, and it is to be expected that extensive modifications of the ordinary process will follow. If the egg takes upon itself all the functions commonly exercised by it in conjunction with the spermatozoan, it must be that the determination of sex is included."

McClung (1902)

Since McClung announced his discoveries in 1902, a few other cytologists, stimulated by McClung's results have carried out independent investigations with the net result that several additional types of dimorphism have been discovered.

One of these types was discovered simultaneously by Wilson and Stevens in 1905, confirmed by Nowlin 1906, and occuring in the insects have the same number of chromosomes in the spermatozoa but differ in that one class contains a large "idiochromosome", and the other a small one. These chromosomes may or may not unite in synapsis, depending on the order of insects to form a bivalent body.

Another type of dimorphism is that known as the "m" chromosomes as described by Wilson. They are two spermatogonial chromosomes which do not unite at the general synaptic period, and which may or may not condense in the early growth period to form two chro-

mosome nucleoli. They undergo a late synapsis in the prophase of the first division to form a bivalent, which divides in both divisions.

Ferdinand Payne (1908) describes an additional type of accessory chromosome. In this type there five chromosomes which divide as univalents in the first maturation divisions. In the second division they do not divide but four of the five pass to one pole, and the other one to the opposite pole. In this form the female has three more chromosomes than the male, and the spermatozoa which contains the three extra chromosomes must therefore be the female producing class.

The situation may be briefly summarized as follows: The view that sex is determined by conditions external to the germ cells, has in recent years slowly given way to the belief that it is primarily established by an automatic mechanism within the cell. By far the most work has been done on the insects, and with them we are now rather familiar. In many species of insects their two kinds of spermatozoa equal in number, which in the early stages of their development differ visibly in respect to nuclear constitution, while there is but one kind of egg which is in nuclear type indetical with one of the classes of spermatozoa. That is to say, if the two classes of spermatozoa be designated as the "X" class and the "Y" class, respectively, the eggs are all of the "X" class. The male may

accordingly be designated as the "heterogametic" sex, and the female as the homogametic. The evidence demonstrates that fertilization of the egg by the "X" class of sperm produces females, by the "Y" class, males. In insects and some animals, those spermatocytes, and those alone, which produce the functional spermatozoa receive the accessory chromosome. In these animals accordingly only the X class, or female producing spermatozoa come to maturity, while the Y class or male producing spermatozoa are abortive." Wilson (1910)

Hypothesis of Mendelian Heredity.
by Castle

The female is characterized by the presence of something that is absent in the male, but two general classes must be distinguished.

A. In the first case, where the male is heterogametic, the presence of two x elements in the zygote means the female conditio the absence of one of them the male.

B. In the second case, the presence of one x element means the female condition, its absence the male. This assumption may apply to cases where the female is the heterogametic sex; and it will explain such cases as the dioecious plants, where the asexual spores may produce either males or females.

From Wilson 10

Chapter L

SEX LIMITED INHERITANCE

Morgan's extensive experiments, principally on the Drosophila, have led him to draw certain conclusions, which are:-

"1st. 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 femaleness.

2nd. That the association of certain characters in inheritance is due to the proximity in the chromosomes of the chemical (factors) substances that are essential for the production of these characters."

Morgan (1911)

The evidence that Morgan has obtained has convinced him that segregation, the keynote to all Mendelian phenomena, is to be found in the separation, during maturation of the egg and sperm to material bodies (chemical substances) found in the chromosomes.

"This conclusion need not mean that the material bodies present in the chromosomes are the substances out of which the unit characters are built up. On the contrary all that this evidence goes to show is that the bodies represent some material necessity for the development of the particular in question, and it is certain that other parts of the cell also contribute

to the elaboration of the unit character. The supporting evidence is that the red color of the wild fly is due to the coloration of at least four different factors in the cell, namely a red, a pink, and an orange determiner and a color producer. The pink determiner and color producer are carried by the X chromosome, but are not otherwise related." Morgan (1911) The red factor is contained in some other chromosome; the orange factor remaining unsolved.

The numerical departure from expectation must be due to special disturbing factors. During segregation certain factors are more likely to remain together than to separate, not because of any attraction between them but because they lie near together in the chromosomes. Morgan in his investigations has tried to show the mechanism of heredity, provided we deal with particles or chemical substances in the chromosomes rather than with the chromosomes as units. A second point of significance in the results is that while in the female there may be an interchange between homologous chromosomes, no interchange takes place in the male of these factors connected with sex-limited factors.

A third point is the necessity of assuming some combination or rather localization amongst some of the substances resident in the same chromosome. Couplings and linkages have been described before to account for

observed ratios, notably by Bateson and his collaborators, but we see here for the first time that these unions are not due to inherent relations, or affinities or attractions, or correlations or repulsions but to juxtapositions of particles in the chromosomes.

It has been shown in a considerable number of cases that at one stage in the process of union of homologous chromosomes the members of each pair twist around each other like the components of a rope. Subsequently these chromosomes fuse and shorten. Later, a longitudinal split occurs or appears in the shortened double chromosome. This split now lies in one plane, i.e. does not follow the turns of the united chromosomes. In consequence of the position of the new plane of splitting or division each half, or new chromosome must be made up of parts of one and part of the other of the original chromosomes that united in pairs as Janssens has shown. As a result of the subsequent reduction division the cells that are produced will contain new combinations of the materials composing the original chromosome. If the chromosomal materials that represent the factors of heredity are placed linearly along the chromosome and in corresponding linnear series the usual Mendelian random segregation will take place in the latter case, groups of factors will tend to remain together or be associated in heredity.

What is more important is the discovery that the X chromosome contains not only one of the essential factors in sex determination, but also all other characters that are sex limited in inheritance. This leads at once to the inference that it is not the X chromosomes, as such, that is, a factor in sex determination but only a very small part of its material. If the X is the sex chromosome, then the Y is the sex limited in a double sense. Its final disappearance in certain forms represents the total loss of all characters that can become sex-limited in inheritance.

SEX LIMITED INHERITANCE.

In recent years a new fact in Mendelian inheritance has come to light, which while it obscures the Mendelian expectation based on independent segregation of the factors of inheritance, shows that the main Mendelian principles are by no means in validated; for, they too are manifest, but obscured by the linkage or coupling of certain factors.

"The parallel between the behavior of the chromosomes in reduction and that of Mendelian factors in segregation was pointed out by Sutton (02), though earlier in the same year Boveri (02) had referred to a possible connection. In this paper Boveri brought forward considerable evidence from the field of experimental embryology indicating that the chromosomes

play an important role in development and inheritance. The first attempt at connecting any given somatic character with a definite chromosome came with McClung's (02) suggestion that the x chromosome is a sex determiner. Stevens and Wilson (05) verified this by showing in a large number of cases or rather forms there is a sex chromosome present in all the eggs, and in the female producing sperm, but absent, or represented by a smaller homologue, in the male producing sperm. A further step was made when Morgan '10 showed that the factor for color in the eyes of the fly Drosophila follows the distribution of the sex chromosome already found in the same species by Stevens'08. When certain somatic characters are associated with sex, as in Drosophila, we have the best opportunity yet afforded, for studying in its simplest form this sort of "associative Inheritance" for in certain combinations the relation between linkage and breaking of linkage (crossing over) is shown at once by the male flies which indicate without complication the kind of eggs that the F_1 female produces. In certain combinations both males and females give this result. Such cases are those in which the sperm of the F_1 generation contains only sex-linked recessive characters.

Later, the appearance of a sex-linked winged mutation brought out a new point. This could happen only if "crossing over" were possible; which means,

on the assumption that both of these factors are in the sex chromosomes, that an interchange of materials between homologous chromosomes occurs (in the female only, male has only one sex chromosome).

Also it became evident that some of the sex-linked characters are "associated", i.e. crossing over does not occur freely between some factors. This means, on the chromosomal view, that the chromosomes, or at least certain segments of them are more likely to remain intact during reduction than they are to interchange materials." Sturtevant (1913)

The phenomenon of linkage was studied on a relatively large scale to reduce the occurrence of error. The results show that whatever sex-linked enter in the grandchildren. Moreover, it makes no difference from the point of view of linkage whether a "present" factor is linked with another present factor or to an "absence" or even whether two absences are linked together in one of the parents. The phenomenon is the same. Bateson and Morgan's work both support these facts.

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