

INHERITANCE STUDIES

with

Lupinus Hirsutus

Lupinus Hartwegii

Antirrhinum Majus

Phlox Drummondii.

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to

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## Inheritance Studies.

It seems to us rather strange that such a great subject as plant-breeding should have been neglected and been in the dark until comparatively recent times, the more so on account of its relation to human and animal development. Very few of the primitive people seem to have made an attempt to investigate the part either parent plays in the production of offspring. There does not seem to be the vaguest idea about the powers of transmission peculiar to each one of them. For ages and ages the domesticated races of animals and plants have been improved by man more or less consciously, but not until the time of Aristotle do we find a clear evidence of any hypothesis to explain the phenomena of inheritance. The ideas about reproduction were very crude indeed. The production of offspring was supposed to be similar to the growing of the crop from seed. The male furnished the seed and the female provided the soil, and for many centuries this theory remained unchanged. The physical basis of heredity did not become established until female was recognized to be more than simply a passive agent. This slow progress in the science of biology lasted until the advent of the microscope which furnished a way for studying more successfully the processes of life. Only with the help of the microscope the minute sexual cells could be observed and studied, and at the end of the 18th Century most scientific men settled down to the view that each of the sexes contribute a definite amount to the offspring produced by their union. Among the animals the female furnishes the ovum, and the male the spermatozoon; among plants the male furnishes the pollen, the female



the ovule.

Like in other sciences related to agriculture, also in plant breeding, isolated practical applications of breeding methods preceded the scientific investigation and explanation of them. Unconscious selection was practiced at a very early date. Among the Romans we find a type of selection which approaches very closely the scientific selection as it is practiced today, by our practical plant-breeders. Large ears and heavy seeds were picked out as Columella, Virgil, and Varro report, and with these an attempt was made to improve the strains of agricultural plants. Rice, which is now a plant of world-wide economic importance, is claimed to owe its existence to the fact that a spontaneous variation was found and preserved by the Emperor Khang-hi in China centuries ago. Even hybridization was practiced in every remote times, though evidently not so much with agricultural plants. Thus the Chinese crossed various flowers at an early date, Under the reign of the Roman emperor roses were crossed in Italy and much later in the 17th Century in Holland tulips and auriculas were crossed extensively Theophrast mentions artificial pollination of the female date-palm, but the phenomena involved were evidently not yet understood.

The scientific foundations of the carrying on of breeding experiments were created much later and progressive breeding based upon a knowledge of the fundamental natural processes involved, was therefore, made possible only at a much later period. A very important factor for the development of the science of heredity was the invention of the compound microscope by Antonius van Leenwenhoek. While there were microscopes before, he built a microscope of higher magnifying power than any other microscope built

before. Nehemias Grew and Millington first expressed the opinion that the anthers produce the male organisms in "Grew Anatomy of Plants", 1682, but Camerarius has to be considered as the founder of the theory of the sexuality of plants and his book "De sexu plantarum epistola", 1694 reports about a series of original experiments, such as have been carried on much later in America by Logan at about 1740 with corn. Camerarius also pointed out the possibility of hybridization. Miller at 1751 observed the part insects play in pollination.

Between 1760 and 1766 Joseph Gottlieb Koelreuter carried out the first series of systematic experiments in plant hybridization which had ever been undertaken. These experiments not only established for the first time the fact that the seeds of plants are a product of a sexual process similar to that known to occur in animals, but it also led to a knowledge of the general behavior of hybrids which was not much changed until Mendel made his discovery. Koelreuter originated the first agricultural hybrid produced with a knowledge of the sexual relation of plants in 1760 by applying the pollen of *Nicotina paniculata* to the stigma of *Nicotiana rustica*. The character of the hybrid offspring was of a character intermediate between those of the parents. He found also that the hybrid offspring of two different plants as a rule took about as closely after the plant that furnished the pollen as after the one upon which the hybrid seed was borne. He even found that it made no difference which of the parents furnished the pollen and which bore the ovule. Thereby he showed for the first time that the pollen was just as important as the ovule which was quite a new idea at Koelreuter's time. As early as 1681 Malpighi discovered the ovule and embryo-sac. He also examined pollen,

but regarded it as a useless secretion. Koelreuter did not know that the content of a single pollen grain unite with the contents of a single ovule during fertilization. He believed that fertilization took place by the intimate mingling together of two fluids, one present in the pollen grain, the other secreted by the stigma. These fluids were supposed to pass down the style into the ovary and arriving at the ovule to start the maturation processes of the seed. Here-in he followed simply the belief of the animal physiologists who believed that the process of fertilization in animals took place by a similar mingling of two fluids. Koelreuter also was the first to observe the different ways by which pollen is distributed from plant to plant. This may happen by the pollen grains falling directly upon the stigma or by the wind blowing the pollen to the stigma, or also, insects visiting the flowers, may act as pollen carriers. He also recognized the part the nectar of many flowers plays, namely, to attract the insects, as for instance the bees, which help to distribute the pollen. Koelreuter found that hybrids between different varieties of the same species are as a rule more fertile than those between distinct species.

As first garden-hybrid is mentioned a cross between two varieties of Dianthus produced in London by a gardener, Thos. Fairchild before 1719, though undoubtedly other crosses between flowers had been produced previously. The difference, however, consists in the fact that this cross was obtained with a knowledge of the investigations of fertilization. In spite of the work of these investigators the sexuality of plants was still considered as doubtful by some investigators, and further experiments and

investigations were carried on along this line. Sprengel reported about further observations by insect activity in cross-fertilization and expressed some ideas regarding the superiority of cross-pollination to self-pollination in 1793. The botanist, Thomas Andrew Knight, also published observations along the same line in 1799. He occupied himself to a considerable extent with the improvement of useful races of plants by cross-breeding. He experimented with peas and these experiments are of particular interest because by experiments with the same plants Mendel later on made his great discovery. Knight's experiments were carried on with a different object in view, namely, to find out whether a cross with a distinct race would stimulate a debilitated plant to restoration of new vigor. The fact was established without a doubt, that the hybrid offspring of two different strains shows a more vigorous growth than either one of the parents. Knight concluded, therefore, that "Nature intended that a sexual inter-course should take place between neighboring plants of the same species". And Darwin still more forcibly expressed this idea: "Nature abhors perpetual self-fertilization." But while this seems to hold good in many cases there seems to be some plants that apparently continue to self-fertilize indefinitely. John Goss also experimented with peas in 1822. He crossed a blue and a white pea and he found that the blue seeds all bred true, while the white ones yielded a mixture of blue and white seeds. But he, like Knight, did not observe the proportion of the different types of seed and thus missed the chance to make the discovery Mendel made. Rev. W. Herbert also conducted hybridization experiments towards the beginning of the 19th Century. He came to the conclusion that Knight

and Koelreuter were wrong in their claim that hybrids between different species were always sterile. Carl Friedrich Gaertner, 1772-1850, made a very great number of crosses between species of all branches of the natural system. In 1849 he published the result of more than 9000 crosses and shed much light upon the question of hybridization. This theoretical conclusion, however, only confirms those of Koelreuter and he made only little advance in this direction.

Amici, in 1823, saw the pollen-tubes and observed their entering into the ovary about 1830, and after Schleiden had followed up the development of the seed-buds before fertilization, the most important facts for an understanding of the fertilization processes were given, C. Naudin in 1862 published an essay, "New Researches on Hybridity in Plants", in which he pointed out the fact that the return of hybrids to the forms of their parents is due to a disjunction of the two specific essences in the pollen-grains, and in the ovules of the hybrid. This hypothesis came remarkably near to that of Mendel. Naudin considered the adult hybrid to consist of an aggregate of particles which are homogenous and characteristic of a single species when pure, but mixed in various proportions in a hybrid, which represents thus a kind of mosaic structure.

Millardet in 1894 published the results of experiments conducted with strawberries. He crossed a number of different species and varieties and found in contradiction to the general observation of such crosses, in which the offspring as a rule was intermediate between the two parents, that the hybrid resembled only one parent, from which it was indistinguishable, while it showed no likeness to the other parent. And sometimes it resem-

bled the pollen-parent, sometimes the seed-parent. Sometimes the hybrid thus produced bred true to type with complete apparent exclusion of the other parent. There is some doubt whether these experiments were sufficient to establish the result as a scientific fact, particularly as his experiments never have been confirmed by later investigators, though they never have been contradicted.

A large number of experiments have been conducted with hybridization of plants and many observations been made upon the characteristics and behavior of hybrids, but until comparatively recent times the underlying laws of transmission were still completely hidden until Gregor Mendel made his startling discoveries.

Gregor Johann Mendel was born on July 22, 1822 at Heinzendorf, near Odrau, in Austrian Silesia. His father was a small peasant proprietor. Heinzendorf was a German colony surrounded by a Slavonic population. His father took special interest in fruit culture and taught his son at an early age the methods of grafting. Mendel attended school at Heinzendorf and distinguished himself there to such a degree, that his parents consented to send him to Leipzig at the age of eleven, though they had to deny themselves in order to do so. Here again he distinguished himself so much that he was sent to the gymnasium at Troppan. One of the teachers at Troppan was an Augustinian and he probably influenced Mendel to enter the Augustinian convent at Brunn, called the Konigskloster, in 1843. In 1847 he was ordained a priest. The cloister sent him at its expense to the University of Vienna in 1851 where he studied mathematics, physics, and natural sciences until 1853. He then taught in the Realschule at Brunn until 1868 when he was elected Abbot of the Konigskloster.

He carried on his famous experiments in the large garden of the cloister. He began to experiment with plants very early. Here he conducted his crossing experiments with peas, which lasted eight years. The results he read before the Brunn Natural History Society in 1865, and published them in 1866, but no attention was paid to them. He also worked on Hieracium and published the results 1869, but with no better success. He also conducted an investigation upon a large scale on the heredity of bees. Unfortunately the notes which he made on these experiments cannot be found, and it is supposed that he destroyed them before his death. His appointment as Abbot practically ended his researches. His later years were taken up by a controversy with the government about special taxes imposed upon property of religious houses and the last ten years were passed in disappointment and bitterness. From being a cheerful, friendly man, he became suspicious and misanthropic. He died January 6, 1884 of chronic nephritis. The 2nd of October 1911 a monument of Mendel was unveiled at Brunn, in the presence of many biologists of different countries.

Mendel was very deeply disappointed by the total neglect of his work, but he had confidence that sooner or later it would be recognized. There does not seem to be any reference to Mendel's observations except that of Focke, "Pflanzenmischlinge" 1881. It was due to these references that Mendel's papers were rediscovered. Bailey found the name of Mendel's paper in Focke's bibliography and De Vries learned from Bailey's publication of the existence of Mendel's papers, which he rediscovered simultaneously with Correns and Tschermak in 1900. All three of these investigators were also able to verify Mendel's experiments in their own



work. In May, 1900, Bateson gave an abstract of Mendel's work before the Royal Horticultural Society of London(?) , England, and later a translation of Mendel's original paper was published by this society. In 1902 the knowledge of Mendel's work became widespread in the United States, mostly due to the instruction of Webber and others at the Graduate School of Agriculture at Columbus and to the discussion before the International Conference on Plant Breeding in New York, fall of 1902. Before going into details of Mendel's discovery, let us review the theories of heredity and evolution as they developed up to Mendel's time.

#### Theories of Heredity and Evolution.

Ever since the enunciation of the cell-theory by Schleiden and Schwann in 1838-39, it has become more and more evident that the cell forms the key to all biological problems. The cell-theory first brought the structure of animals and plants under a common point of view, and through the cell-theory Kolliker, Remak, Naegeli, and Hofmeister opened the way for an understanding of the nature of embryological development, and the law of genetic continuity lying at the basis of inheritance. Later on Hertwig, Van Beneden, and Strasburger solved the riddle of the fertilization of the egg, and the mechanism of hereditary transmission. The cell-theory and the theory of organic evolution have done more than any other theory to bring apparently different phenomena under one point of view, and for consolidation of knowledge. The cell-theory and the evolution-theory form the foundation of modern biology, and while they are nearly related, they have developed along very different lines of research and in recent



times they have met on common ground. The cell theory states that in all higher forms of life, whether plants or animals, the body may be considered as a host of numerous, minute, structural units, the cells, which directly or indirectly constitute each part.

It is based upon the study of microscopical anatomy and was carried on with no thought of its relation to the origin of living forms.

The theory of evolution grew out of the study of natural history, and was established long before the minute structure of living bodies was known. Lamarck and his followers paid little attention to minute details of internal structure. They were more concerned with the more obvious character of organisms, such as color, form, etc. Only in recent years a close alliance between students of organic evolution and students of the cell has become possible.

The first scientific explanation of the process of evolutions was that made in 1809 by Lamarck. He considered the habitat and the habit as the two factors which were concerned in the transformation of species. The habitat is the environment, supplying the conditions under which the organism lives. The environment calls for new habits for every change to adapt the organism to the new needs, thereby, inducing greater exercise of some organs and less exercise of others. Thus certain organs gradually become enfeebled or strengthened and the modifications thus acquired are transmitted through heredity to the new individuals that are produced by them, provided the changes are common to the two sexes, or to those that have produced these new individuals. Three factors are involved in this hypothesis: (1) Environment reacts upon organisms according to their needs or func-

tions. (2) As a result the organs are modified to adapt them to the new needs; (3) These modifications are transmitted to the offspring. This theory is known as the Lamarckian theory and emphasizes the inheritance of acquired characters.

About 50 years later Darwin proposed a hypothesis which had a greater influence upon scientific thought than any other theory. He also saw that all forms of life vary. There are no two individuals alike. He accepted Lamarckism as a whole. He saw that there must be a fierce struggle for existence among the varying individuals, and that the gardener by selecting the best individuals improved the breed. "Can it, then, be thought improbable," said Darwin, "seeing that variations useful to man have undoubtedly occurred, that other variations useful in some way to each being in the great and complex battle of life, should occur in the course of many successive generation? If such do occur, can we doubt (remembering that many more individuals are born than can possibly survive) that individuals having any advantage, however slight, over others, would have the best chance of surviving and procreating their kind? This preservation of favorable individual differences and variations, and the destruction of those which are injurious, I have called Natural Selection, or the Survival of the Fittest." Darwin recognized discontinuous variation, but he did not realize its importance. He saw the cause for variation in external influences and believed in inheritance of acquired characters, though not to such a degree as Lamarck. He formulated the theory of pangenesis. He supposed that besides the ordinary multiplication of the cell, each cell may "throw off minute granules which are disposed throughout the whole system; that these, when

supplied with proper nutriment, multiply by self-division, and are ultimately developed into units like those from which they were originally derived." These granules or "gemmules" collect by a natural affinity for each other from all the different parts of the body and from the sexual element.

Neo-Lamarckism is an attempt to revive Lamarckism and its followers claim inheritance of acquired characters caused by Kinogenesis or movement, stress, and similar agents, or by Physiogenesis or influence of environment. They also elevate the notion of inheritance of acquired character to the rank of a scientific dogma.

Another theory advanced by Wilhelm<sup>His</sup>/in 1874 is the theory of Germinal localization. It is a kind of revival of the naive early theory of preformation. It maintains that, while the embryo is not preformed in the germ, it must be predetermined in such a way that the egg contains localized areas predestined for the corresponding parts of the embryonic body. The visible process of segregation was supposed to be only the sequel of a differentiation already present, but not visible. Flemming supposed that it would be possible to search for this structure with a microscope and called the aim of this research the "Morphology of Inheritance." Other writers seek the seat of germinal localization in the nucleus as for instance, De Vries, Hertwig and Weismann.

Nägeli is the author of another hypothesis called the Idioplasm Theory. He assumes that inheritance is not effected by the transmission of a cell as a whole, but by a special substance, the "idioplasm", which is contained within the cell and forms the physical basis of heredity. The idioplasm differs sharply from

the other cell-constituents, which form a nutritive plasma or trophoplasm and has nothing to do with inheritance. The idioplasm is the determining factor in inheritance, and was supposed to be of a very complex nature, consisting of different units. Very soon after the publication of Naegeli's theory some of the foremost investigators located the seat of the idioplasm in the nucleus and concluded that it was identical with the chromatin. It was shown that the two germ nuclei which give rise to the germ were of the same morphological nature, since both produce the same number of chromosomes of the same size and form. Kolliker, Strasburger, Hertwig and Weismann came independently and almost simultaneously to the conclusion that the nucleus was the physical basis of inheritance and that the chromatin corresponded to Naegeli's idioplasm.

Mr. Galton formulated the law of ancestral inheritance.

In all ordinary cases of reproduction the offspring inherits from both parents. The contribution of each parent is made up again of contributions of the grand-parent and so on backwards. Galton's law is as follows: "The two parents between them contribute on the average one-half of each inherited faculty, each of them contributing one-quarter of it. The four grand-parents contribute between them one-quarter, or each of them one-sixteenth; and so on, the sum of the series  $\frac{1}{2} + \frac{1}{4} + \frac{1}{8} + \frac{1}{16} + \dots$ , being equal to 1, as it should be. It is a property of this infinite series that each term is equal to the sum of all those that follow: Thus,  $\frac{1}{2} = \frac{1}{4} + \frac{1}{8} + \frac{1}{16} + \dots$ ,  $\frac{1}{4} = \frac{1}{8} + \frac{1}{16} + \dots$ , and so on. Galton's law has not been disproven, but it is not yet in harmony with Mendel's discovery.

Weismann's Theory of the Germ-plasm.

No other investigator did more to advance the scientific study of heredity than did Professor August Weismann, of Freiburg, though his work has been done along different lines from that of Galton and his school and also from that of the experimental school of Mendel, Bateson and others. Weismann constructed a theory of heredity in connection with a theory of development and a theory of evolution which has inspired much research, and won the admiration even of his opponents. Weismann concluded in 1885 that "the heredity<sup>y</sup> substance is in the chromosomes of the nucleus of the germ-cell". The chromatin of the nucleus of the germ-cell forms the physical basis of inheritance. It is composed of a definite number of chromosomes or "idants". The chromosomes in turn consist of ids, which are identified with the visible chromatin-granules, and each of which contains a full inheritance. Each id again, consists of a number of primary constituents or determinants which are still beyond the limit of microscopic vision. A determinant is composed of a group of biophors, the minutest vital units. The chromatin has thus a highly complex fixed structure, which is transmitted from generation to generation and determines the development of the embryo in a definite and specific manner.

Weismann inaugurated a new period of discussion when he put forth a bold challenge to the entire Lamarckian principle. He showed the absurdity and impossibility of the inheritance of acquired characters as put forth by Lamarck, and also by Darwin. Transmission of acquired characters are impossible, for it was inconceivable that a change of the body should influence the germ-plasm to cause corresponding changes in the offspring. The offspring does

not inherit from the parent-body, but from the parent germ-cell. The germ-cell in its turn owes its characteristics not to <sup>the</sup> body which encloses it, but to a pre-existing germ-cell of the same kind. The germ-plasm continues without intermission and is handed down from generation to generation. The body is only an off-shoot of the germ-cell and also the carrier of the germ-cells for future generations. This theory is known as the theory of the continuity of the germ-plasm.

Weismann divided, for the matter of practical convenience, the cells of the body into two groups, the somatic, or body cells, and the germ-cells, which differ greatly from each other. Thus he linked the work of the evolutionists and of the cytologists together and brought the cell theory and the evolution theory into close connection. The question was how do the characteristics of the body get into the germ-cells, which <sup>it</sup> carries, while as a matter of fact, the characters of the parent do not get into the germ-cell, but the germ-cell makes the body as the germ-cell was there first. The germ-cells form the links of the chain of germ-plasm and produce the bodies of the next generation after uniting with another germ-cell of the opposite sex. The body is mortal, while the germ-cell is immortal, and only ends when the body carrying it dies without producing any offspring. The germ-cells, after fertilization, in dividing, throw off the body-cells which continue to divide and to differentiate until the whole body is formed, the germ-plasm in the meantime, produces other germ-cells to continue the line.

Hageli claimed that neither environments nor natural selection are responsible for evolution, but that evolution is due to "internal perfecting principle" and is predetermined. Environment may produce ontogenetic variation, but does not affect phylogeny

This theory stands by itself and is in some way related to the kinetic view of evolution.

Professor De.vries from Amsterdam denied that natural selection was competent to produce new species, or that progressive variation could take place by the accumulative effect of small differences or fluctuations. He advanced the Mutation theory. He divided variations in two general groups: (1) Variation proper, or fluctuation, consisting of small, fluctuating, unstable differences, peculiar to the individual, and (2) mutations or differences of a marked character, which appear suddenly without intermediate forms, and start entirely new races or species. Fluctuations are large<sup>y</sup> due to environment, unstable and only temporary. They fluctuate between two extremes and do not progress any further. Mutants are stable from the start and breed true. The causes of mutation are not yet known, but are probably physiological. He based his views that species have originated by mutations upon his observations on the Evening Primrose, *Oenothera lamarckiana*. Working with this plant he was able to witness, for the first time, the actual process of the origin of new species. There are two kinds of mutations, the one characterized by the addition of something new is called progressive elementary species; the other lacking something present in the parental type is called regressive mutation. The same mutation can arise simultaneously in several individuals. The parent form may repeatedly give rise to similar mutants, while it itself remains unchanged. Mutations are apt to appear periodically and may occur in all directions.



### Reproduction.

Reproduction can take place in several ways.

Bacteria, amoeba, and other one-celled organisms usually divide by simple division or fission, while yeast and certain lower animals reproduce by budding. In some plants we find spore formation, sometimes alternating with sexual reproduction. In higher animals and plants the reproduction is entirely sexual and takes place by the union of two germ-cells. The cell then is the basis of reproduction and of heredity.

### The Cell.

The cell is a mass of protoplasm of varying shape according to its surroundings. Isolated cells tend to be rounded. The protoplasm which forms its active basis is a viscid, translucent substance, which may be apparently homogenous or finely granular, forming a kind of network, the reticulum. There are pretty nearly always passive bodies present also. The protoplasm consists of the cytoplasm which forms the cell-body and of the karyoplasm, which represents the nucleus of the cell. Neither one of these substances, however, represents a single homogeneous mass, but they consist of several distinct elements. The terms nucleus and cytoplasm are really only topographical expressions, denoting differentiated areas of the same structural basis. The nucleus is to be found floating in the cytoplasm in all living cells. It is the controlling factor, and the basis of cell activity, and thus of prime importance in growth, development, and reproduction of cells. Without the nucleus the cell must die sooner or later. The nucleus passes through two very distinct phases, one of which is characteristic of the cell in its ordinary or "resting" stage, while the



other one occurs only during the complicated process of cell-division or mitosis. The most important structures in the nucleus are the chromosomes, little rod-shaped bodies. They represent the "ids" of Weismann. These split lengthwise when the cell divides. The chromatin is arranged in a thread or spirem, which breaks up into the chromosomes. Each species has a definite number of chromosomes in each cell. The somatic cells have twice the number of that of the <sup>germ</sup> cells. They all arise by continued division from the original germ-cell and the germ-cell again arises by division of a cell pre-existing in the parent body. By cell-division the hereditary substance is handed on from the egg-cell to every part of the body produced by it. Cell-division is one of the main factors in inheritance. There are four stages in the mitosis of the cell: (1) the prophase or preparatory changes. The chromatin losing its net like arrangement forms a spireme, which breaks up into a number of chromosomes. The nucleus disappears. (2) The Metaphase. The chromosomes split into equal halves and arrange themselves in the equatorial plane of the spindle, the two poles of which are formed by the centrosomes. (3) The anaphase. After the chromosomes have split they diverge to the opposite poles of the spindle and form daughter-nuclei. In the 4th or Telophase, the entire cell divides in two, each of the daughter-cells receiving half of the chromosomes and half of the mitotic figure. The daughter-nuclei have formed in the meantime and are in the "resting" stage. The equal division of the chromatic substance is of great significance, as it is supposed to be the basis of cell-activity. Especially in the division of germ-cells the transmission of the chromatin is of particular importance. The germ-cells arise from the primordial germ cell.

which has its origin in the hypodermal layer of the parent plant and becomes differentiated at a very early period of development. From the outset it differs from the somatic cells, not only in greater size, but also in its mode of mitosis. In all blastomeres that are to produce somatic cells, a portion of the chromatin is thrown out into the cytoplasm, but in the germ-cell the whole amount is saved. Recent research has shown that maturation of the germ-cells is of the same type in both sexes. During the last two divisions reduction of the chromosomes to half the number is effected, so that the mature germ-cells contain only half the number of chromosomes as the somatic cells. In the female only one cell forms the "ovum" proper, while the other three remain rudimentary and are incapable of development. In the male, however, all four cells become functional germ-cells. The process of reduction is evidently a provision to keep the number of chromosomes constant at the number characteristic of the species. If the number of chromosomes was doubled by the union of two germ-nuclei, an infinite complexity of the chromatin would soon arise. In the female gametophyte or embryo-sac the nucleus divides into eight nuclei, which form the four microphylar bodies, grouped near the micropyle or opening of the embryo-sac; and the four antipodal bodies arranged at the base of the embryo-sac. One of each group move to the center and fuse, forming the endosperm nucleus, (primary polar nucleus). One of the microphylar nuclei forms the egg-nucleus, the other forming the synergids.

Fertilization takes place by the pollen being carried by the wind, insects, or other agents upon the stigma of the female flower. The stigma is either rough or secretes a fluid to

hold the pollen in place. The secretion of the stigma causes the pollen to germinate which sends a tube down through the connective tissue of the style into the ovary, where it enters the embryo-sac through micropyle and the generative nucleus of the pollen passes down and fuses with the egg-nucleus forming the oospore, which develops the embryo. The other male nucleus passes to the endosperm nucleus and fuses with it, the resulting cell developing the endosperm. The embryo then develops into the seed which can be considered as a metamorphosed sporangium. From the seed again is produced a new individual with the characters of both parent- individuals which have been transmitted through the chromosomes of both germ-cells.

#### Kinds of Inheritance.

We distinguish between three different kinds of inheritance as follows: (1) Particulate inheritance, or inheritance "bit by bit", part from one parent, part from the other parent. A characteristic example of this type is the Andalusian fowl, which upon crossing of a white and a black individual with each other produces a blue colored type. This, however, is nothing but a very minute mosaic of black and white. This character is very unstable, and breaks up into blacks and whites in the offspring. The fixing of the mosaic type is a great problem for future breeders. In some cases where the mosaic color is the original one of the type it is constant, as for instance in the Barred Plymouth Rock.

The second type of inheritance is called Blended Inheritance, where two characters blend. It may be only a very fine mosaic type not distinguishable with the naked eye. Continuous or fluctuating characters are generally supposed to follow

this type of blended inheritance, also De Vries "unisexual" characters where one character unit has no antagonist in the other cell, and in such cases we have an unbalanced cross, which results in averaging the conditions in the progeny, and this type shows no tendency to segregate in the following generation. Galton's law of inheritance has been given above.

The last type of inheritance is the "Alternative Inheritance", which produces types that split up in the second and following generations. Gregor Mendel was the first one to recognize this type of inheritance, and it is therefore, also called Mendelian inheritance, and after him is named the law which governs this type of inheritance.

#### Mendel's Work.

Mendel's work is important because it upsets many of the current notions about hybridization. As De Vries' discussion did away with the current belief that evolution was gradual and slow, thus Mendel showed that the general opinion that the results of hybridization are mostly chance was false. He found uniformity and constancy of action in hybridization. About the most important point in Mendel's work is the great pains he took in selecting his plants for the crosses. He considered hybridism as a complex and intricate subject. He realized that some of the diversity experienced in crossing was due rather to instability of the parents than to the results of the crossing itself. He also took precautions to exclude all intercrossing in the offspring. The offspring itself must be numerous to be able to study the average of large numbers.

The garden pea appeared to him to possess the desired

qualities and he selected well-marked horticultural varieties. He grew these for two years previous to his experiment in order to ascertain their stability and trueness to type. Only normal plants were chosen for parents and all weak plants were thrown out. He picked out seven prominent characters for the study of the hybrids. These characters were paired as follows:

Long stem vs. short stem.

Round seed vs. wrinkled seed.

Inflated pod vs. constricted pod.

Green cotyledons vs. yellow cotyledons.

Purple flower ) vs. ( White flower.

Brown seed coat ) vs. ( White seed coat.

Green pods vs. yellow pods

Axial flowers vs. terminal flowers.

Every parent plant possessed one or the other of every pair of characters, but in order to facilitate the work, Mendel selected a special set of parents for each character, studying flower color in one set of hybrids, seed color in another set and seed shape in another, and so on. Thus he avoided complications in the results.

In planning his crossing experiments Mendel took an attitude different from all his predecessors. The seed was very carefully harvested from each individual plant separately and sown separately the following year. By this method Mendel found the clue that had escaped all the efforts of his predecessors.

In the cross between tall and dwarf individuals the offspring in the next generation ( $F_1$ ) showed only tall types, while the following generation ( $F_2$ ) produced both tall and dwarf

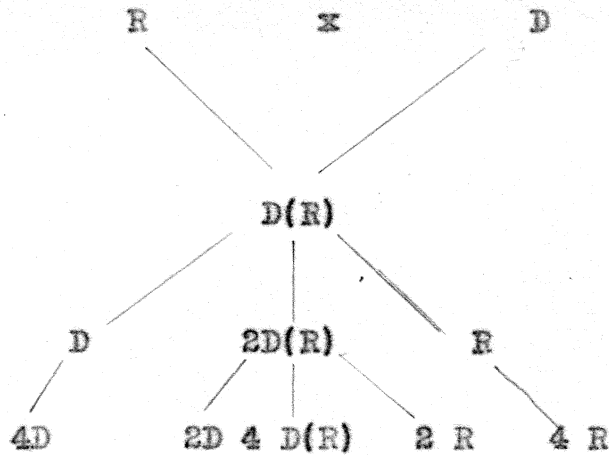


types, and these in a proportion of 3:1.

He found that the seeds from the dwarfs bred true, producing only dwarfs. But the tall plants behaved differently. Some of them bred true, while others behaved like their hybrid-parent, and broke up into tall and dwarf plants in the proportion of 3 tall ones to one dwarf. Counting showed that the number of the tall plants producing dwarfs was twice that of those tall ones that bred true. From the fact that the factor of tallness appeared exclusively in the  $F_1$  generation Mendel called it dominant. Dwarfness which disappears in  $F_1$  he called a recessive character. Further investigation showed that the tall types breeding true were pure dominants, while the other types were impure and hybrids, and thus the progeny consists of three different types:

25%	50%	25%
Pure dominants.	Impure dominants.	Pure recessives.
3 Dominants	;	1 Recessive.

In this way Mendel found tallness to be dominant over dwarfness, and in the same manner he determined the dominance or recessiveness of the other character-pairs. The dominant type always appeared in the  $F_1$  generation to the complete exclusion of the recessive type. No intermediate forms were noticed. For the dominant factor he introduced the letter D, for the recessive factor the letter R. Thus  $R \times D$  apparently give D, but the breaking up or degregation in the next generation shows that  $F_1$  is not pure D, but also has R hidden in it. Correspondingly we express the  $F_1$  generation by the symbol D (R).



In its simplest form Mendel's law would be:

Two units following the Mendelian inheritance produce, when crossed, uniform offspring in the first generation of a hybrid character. In the second generation, when self-fertilized, they break up according to a definite numerical proportion. One-fourth shows the pure type of the dominant parent character, one-fourth the pure recessive parent character, and one-half a hybrid of the dominant and recessive character, showing externally the dominant form. This hybrid form again splits up in the next generation like in the second and so on, while the pure dominant and pure recessive type breed true to type.

This type of hybrid is called a mono-hybrid and the results are quite simple, but where more than one single pair of factors are present they become quite complex.

In order to explain these uniform results Mendel formulated the law of gametic purity. According to this theory the gametes in a ripe germ-cell are divided in such a way that the germ-cell is pure to its parent type. Before maturation the cell is impure, but the other units are thrown off during the maturation process in the polar bodies and thus the cell finally is pure to type. A slight contamination may remain and cause some variation.

According to this theory the pollen-grains of mono-hybrids are not crosses, but belong exclusively to one or the other parental type. In the hybrid individual the different unit characters exist side by side, one obscuring the other, but in the formation of the germ-cells, the pairs of unit characters are segregated as mentioned above and the resulting reproductive cells contain either one or the other character, that means they are pure to type. The chromosomes are supposed to be the carriers of the unit characters, and in the reducing division previous to maturation of the germ-cells the segregation is supposed to take place. Thus hereditary characters are usually independent units which segregate out upon crossing, regardless of temporary dominance. Bateson calls this segregating character allelomorphic, that is alternating. Mendel's unit characters respond to Weismann's primary constituents or determinants, the germinal representatives of the characters of the organism.

The result of Mendel's experiment is what would be expected if both male and female germ-cells of the hybrid  $F_1$  were bearers of either the dominant D or recessive R character in equal number, but not of both. If the union of the male and female germ-cells occurs at random results would be:

$$\begin{array}{ccc}
 D & D & ) \\
 R & R & ) \\
 & & ) \quad DD: 2 DR : RR
 \end{array}$$

The appearance, however, would be 3D : 1R. The visible type is called the "phenotype," while the "genotype" refers to the internal gametic structure of the phenotype. The individual formed by the union of two gametes is called a zygote. A homozygote is an individual composed of two gametes, bearing one given character, while a heterozygote is formed by two gametes, one of which



carries the given character, while the other one does not. A homozygote is a pure type with regard to the given character, while a heterozygote is impure or a hybrid. An individual may be homozygous for one or more characters, and at the same time be heterozygous for other characters.

The problem of dihybrids was solved by Mendel by crossing green wrinkled pea with yellow smooth peas. Smoothness is dominant to wrinkledness, and also the yellow color to green color. The result in  $F_1$  was, therefore, a smooth, yellow pea. In the next generation he obtained four different types, smooth yellow, smooth green, wrinkled yellow, and wrinkled green types in the proportion of 9 smooth yellow, 3 smooth green, 3 wrinkled yellow, and 1 wrinkled green type. To illustrate the matter, let us designate smoothness with S, wrinkledness with s, denoting absence of S, the same way, yellow color with Y, green with y. A good method to show the different possibilities of combination of the gametes is the chessboard method.

		Gametes			
		S Y	Sy	sY	sy
SY	SY	SY	Sy	sY	sy
	SY	SY	SY	SY	SY
Sy	Sy	Sy	Sy	sY	sy
	SY	Sy	Sy	Sy	Sy
sY	sY	sY	sY	sY	sy
	Sy	Sy	Sy	sY	sY
sy	Sy	sy	sy	sY	Sy
	SY	Sy	Sy	sy	sy

Each character pair represents a gamete, the horizontal lines one parent, the vertical line the other parent.

All squares containing a capital S. represents a smooth individual, a small s a wrinkled one, a capital Y a yellow individual, a small y. a green one. Thus we can easily see how the factors unite and form the 9:3:3:1 proportion as follows:

9 SY + 3 sY + 3 Sy + 1 Sy. In the case of a tri-hybrid we get a 27: 9:9:9 : 3:3:3 : 1 proportion, as can be illustrated by the same method. A simple way to find out the proportion of a multiple hybrid is by a plain algebraic series. 3 - 1 represents the monohybrid proportion, (3-1) (3-1) or 9 : 3:3: : 1 the dihybrid, (3-1)<sup>3</sup> the trihybrid and so on. These proportions cover all simple Mendelian cases of inheritance. Besides we have a number of other proportions which are caused by special conditions, as for instance the modified 9 : 3:3: 1 proportions 9:3:4, 9:7, 13:3, in cases where interaction of characters take place. Mendel's scheme of inheritance has been found to hold good for many diverse things, such as height, hairiness, flower color, and shape of flower and leaves, of pollen grains, coat color of animals, comb of poultry, eye color in man. The more work is done along this line the more cases are found that follow the same law of transmission, though at first they seemed to follow a different law of inheritance.

#### Presence and Absence Theory.

Accordance to the presence and absence theory the dominant character of an alternative pair owes its dominance to the presence of a factor which is absent from the recessive character. The yellow pea is yellow on account of the presence of a factor for yellow color, while the green pea is green owing to the absence of this factor. The yellow pea is a green pea + the yellow color factor. Still clearer this conception shows in the case of the fowl's comb, where R is the factor for rose-comb, P the factor for pea-comb. The presence of each is alternative to its absence. When both factors are present in the bird a walnut comb is produced. In the formation of the gametes a separation

takes place between the part of the zygotic cell containing R or P and the one which does not contain it, or r or p. Thus the chances are equal that R meets P or not. Therefore, we have two kinds of gametes containing R, RP and Rp, and the same kinds containing P, RP, rP. The same way it is with r and p. And from the chess-board method we shall see that we will get the 9:3:3:1 proportion.

Spurious Allelismorphism and Gametic Coupling.

A few instances have turned up where the distribution of the different factors to the gametes is influenced by their simultaneous presence in the zygote. This influence which they exert upon each other is of two kinds. They may repel each other and refuse, as it were, to enter into the same zygote, or they may attract each other and become coupled together and pass into the same gamete. Repulsion of factors occurs in the sweet pea, where the hooded factor refuses to combine with the red factor. If an erect red type is crossed with a hooded purple type we should expect four types: Erect purple, hooded purple, erect red, and hooded red, in the proportion 9 : 3: 3: 1, but instead we get only three types: Erect red, erect purple and hooded purple, in the proportion 1 : 2: 1. While the other forms breed true the erect purples always break up again in the same proportion. Hooded red sweet peas occur in other strains. The experimental facts are readily explained on the assumption of repulsion between the two factors for red color and hoodedness during the formation of the gametes, which are heterozygous for both. The original cross introduced one of the repelling factors with each of the two parents. When both of the factors are brought into the cross by the same parent we get coupling between them instead of repulsion.

The association is, however, not quite complete. Now this peculiar result could be brought about if the gametic series produced by the  $F_1$  plant consisted of gametes that are produced in unequal numbers. If A and B are the two factors contained in the hybrid-zygote we would expect the gametes

$$AB : A b : aB; ab,$$

in equal proportions, and we would have a dihybrid proportion 9 : 3: 3: 1 in  $F_2$ . This is not the case, however, in the case of gametic coupling, but the gametes are produced in unequal proportion according to the strength of the coupling. In one instance we have the gametes produced as follows:

Male	Female
7 AB	7 AB
1 Ab	1 Ab
1 aB	1aB
7 ab	7 ab

Such a series of ovules and of pollen grains fertilizing each other would give a generation of the following composition:

$$\begin{aligned}
 &49 AABB + 7 AABb + 7 AaBB + 49 AaBb \\
 &\quad + 7 AABb + 7AaBB + \quad AaBb \\
 &\quad\quad\quad + \quad AaBb \\
 &\quad\quad\quad + 49 AaBb
 \end{aligned}$$

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$$\begin{aligned}
 &+ AAbb + 7 Aabb + aaBB + 7 aaBb + 49 aabb \\
 &\quad 7 Aabb \quad\quad + 7 aaBb
 \end{aligned}$$

15

15

49



Male	Female						
63 AB	63 AB)	}	16384	12161	127	127	3969
1 Ab	1 Ab)						
1 aB	1 aB)						
63 ab	63 ab)						
(n-1)	)	}	$4n^2$	$3n^2 - (2n-1)$	$(2n-1)$	$(2n-1)$	$n^2 - (2n-1)$
1	)						
1	)						
(n-1)	)						

Some of these series have already been worked out experimentally.

Albinos, that are devoid of pigment, may yet bear factors which are capable of producing color when they meet with another factor in the zygote, which is called the complementary factor. Some colors may thus be due to the co-existence of several distinct determining factors, which may be distributed independently in the germ-cells. In the rabbit for instance, grey is produced by the presence of a color-element and of a factor which determines the grey color. In certain plants color depends entirely upon the co-existence of two complementary factors in the individual. This was found out by crossing two albinos breeding true to type, which produced colored offspring in  $F_1$ . Each factor by itself cannot produce color, but combined they act upon each other, giving rise to color. These factors are transmitted independently in gametogenesis and in  $F_2$  we have the ratio, 9 colored : 7 white individuals. In cases like this, where several factors are involved, we call these factors epistatic that modify factors already present. Thus grey is epistatic to black in rabbits. The opposite is called

a hypostatic character. Thus we see that a black mosaic is due to the lack of a determiner for grey. Sometimes we also find a prohibitive factor present which prevents another factor present to show itself.

There are three fundamental principles underlying Mendel's law; segregation, independence of unit characters, and dominance. While segregation and independence of unit characters have been found to hold true with exception of the cases of spurious allelismorphism and gametic coupling, dominance, though it holds good in very many cases, shows some exceptions. In the regular Mendelian inheritance we have perfect dominance, but in cases of blending inheritance we notice instances of imperfect dominance. A classical illustration for this is the Andalusian fowl, which does not show any dominance, but both parent types contribute to the hybrid-phenotype. In some cases where there is apparent dominance we can notice a difference between the homozygous dominant and the heterozygous dominant. Another instance is delayed inheritance where the dominant character manifests itself very late. Davenport reports that when a white and a black Leghorn are crossed, the chicks have white plumage with black areas on it. But at the first molt these black spots disappear and white is dominant. There are certain cases where the hybrid does not show a factor, which as a rule, is dominant, but where this factor is, nevertheless, transmitted to the next generation. Further breeding will show that this case of failure to potency is not identical with the absence of the determiner.

Mendel's Results Summarized.

1. The first result of Mendel's discovery was the demonstration of the law of dominance  $D \times R = D (R)$ .

2. The second result was the demonstration of the law of segregation of the offspring of inbred hybrids into forms showing the dominant character and forms showing the recessive character, with on the average definite proportion (3:1) between the two sets:

$$D (R) \times D (R) = 1 DD + 2 D (R) + 1 RR.$$

3. The third result was the conception of alternative pairs of "unit characters" or "allelomorphs" which behave in inheritance as if they were discrete unities.

4. The fourth result was the theoretical interpretation of the second result, as due to the segregation of the gametes into two equal groups, one bearing the dominant character and the other bearing the recessive character.

Cross Breeding Experiments with Lupines.

Lupinus Hirsutus.

From 1909-1911 Mr. F. S. Holmes conducted some crossing experiments with different varieties of *Lupinus Hirsutus*. He crossed a blue, a red and a white variety with each other and obtained a number of crosses. He carried the crosses on until the  $F_1$  generation and made several interesting observations. He was, however, prevented from growing the  $F_2$  generation and making the final observations regarding their mode of inheritance. Therefore, Professor Price asked me to finish up the work and grow the  $F_2$  generation from seeds that Mr. Holmes had saved from his  $F_1$  generation.



The Genus Lupinus.

The lupines belong to the Leguminosae or pulse family. Its name is derived from the Latin word lupus, wolf. People in early times had the notion that this plant impoverished the land and gave it this name on account of that. It is strange that a nitrogen gatherer should acquired such a bad reputation. There are over 80 species mostly confined to western North America, a few growing in eastern North America, and in the Mediterranean region. They are mostly annuals or herbaceous perennials. All of them have showy flowers in terminal racemes. The color of the flowers are blue, white, yellow, or pink, and like most legumes, papilionaceous. They grow easily in gardens except in limy soils. In green-houses they suffer from fusarium wilt which destroys them in short time. They are propagated by seed and do not stand transplanting when once established. Therefore, it is best to sow them right in the beds. Some varieties are used for soiling and as green manure. In some countries they are used on a large scale for improving sandy soils, also seed beds for forest nurseries. They make good hay, but have to be used carefully as the seed contains an alkaloid and may be harmful to stock. It makes a very beautiful ornamental plant for borders and for bedding.

*Lupinus hirsutus* or blue lupine is an annual plant. It grows two to three feet tall and its stem, leaves and branches are covered with soft silvery hair. It branches extensively towards the top. The leaves are digitately compound, having seven to nine leaflets which are oblong and have long petioles four to six inches long. The stipules are linear-lanceolate and deciduous. the inflorescence is terminal and the flowers of the raceme are somewhat verticillate or scattered. The flowers are dark blue with

a white area in the centre of the standard, which with aging turns red. The standard is reflexed, about an inch long and broad. The wings are slightly smaller and about half an inch wide, cohering below. The keel is white with a dark tip and scythe-shaped. Only the lowest whorl as a rule sets seed. The pods are broad, hairy and slightly constricted between the seeds. The seeds are about one-fourth of an inch broad and flat with a rough seed-coat of reddish brown color. The variety ruber is like the blue variety except that it has pink color instead of the blue, while the variety albus is also like the previous varieties, but with pure white flowers. Like most legumes they have ten stamens and one pistil.

Mr. Holmes made the following crosses:

(1) *Lupinus hirsutus albus* ♀ x *Lupinus hirsutus* (blue) ♂

Three F<sub>1</sub> plants were grown and these were light blue of the pattern of the blue parent.

(2) *Lupinus hirsutus albus* ♀ x *Lupinus hirsutus ruber* ♂

Six plants of the F<sub>1</sub> generation were grown which were almost identical in every way and were like those of the first cross.

(3) *Lupinus hirsutus* (b) ♀ x *Lupinus hirsutus*<sup>a</sup> ♂

This is the reciprocal cross of cross No. 1 and two plants of F<sub>1</sub> were grown. The result was the same as in No. 1.

(4) *Lupinus hirsutus* (b) ♀ x *Lupinus hirsutus r* ♂

Five plants were raised from this cross and they were all identical and like those of cross No. 1 and 3, only a shade darker.

(5) *Lupinus hirsutus ruber* ♀ x *Lupinus hirsutus*<sup>a</sup> ♂

This cross is a reciprocal of No. 2 and the four plants raised were like those of No. 2.

(6) *Lupinus hirsutus ruber* x *Lupinus hirsutus* (b)

The flowers of the four plants raised from this cross were alike and similar to those of No. 4.

Mr. Holmes forms from these results the following hypothesis: "The predominant flower color of the different varieties of *Lupinus hirsutus* L. may be represented by two Mendelian factors which are allelomorphs to their absence in each case."

Y, a factor representing a red chromogen.

X, a factor representing an oxidizing agent which acts upon Y to form blue. According to this assumption the constitution of the flowers may be regarded as follows:

- YYxx = Red
- YYXX = Blue
- yyXX = White

The presence of X, the ferment or oxidizing agent, is not sufficient to produce color and thus, the individual having only X produces only white flowers.

90 plants were raised in the F<sub>2</sub> generation of the crosses 2 and 5, and the result was as follows:

Blue	Red	White
52	13	25

This proportion would correspond about <sup>t</sup>o the proportion 9:3:4, and indicate that we have to do

Female gametes	Male gametes			
	XY	Xy	xY	xy
XY	XY	Xy	xY	xy
Xy	XY	XY	XY	XY
xY	XY	Xy	xY	xY
xy	XY	Xy	xY	xy

with a dihybrid and the proportion really is a 9:3:3:1 proportion. But by using the chess-board method we see clearly that three of the sixteen zygotes have only X, the ferment, present, which without Y cannot produce color, while one zygote is without X and Y, therefore, we have the 9:3:4 proportions.

	Blue		Red		White
Practical results:	52	:	13	:	25
Computed:	50.625	:	16.875	:	22.5.

This result confirms Mr. Holmes' hypothesis that the blue color is due to the action of two Mendelian factors upon each other.

The composition of the parents would then have been:

Albus  $XXyy$  and Red  $xxYY$

and the  $F_1$  hybrid  $XxYy$ .

The  $F_2$  hybrids are of varying composition, but all containing X + Y are blue while those having only Y are red, and the rest are white.

Fourteen plants of the cross *Lupinus hirsutus* b. x *Lupinus hirsutus* r. were grown in the  $F_2$  generation, and they broke up in the proportion of 13 blue : 1 red. In this case the composition of the parents was:

$XXYY$  blue x  $xxYY$  red

the hybrid =  $XxYY$  or blue.

Only two kinds of gametes are formed, XY and xY both of the same quantity. By independent union of these gametes we obtain according to the law of chance, a 3 : 1 proportion. Three of the zygotes have X and Y present for every one that has only Y present. Thus we should expect to get in  $F_2$  generation 10.5 blues

and 3.5 reds. The actual result was 13 blues and 1 red. The difference between theoretical and actual numbers can well be ascribed to the very small number of plants raised. This would further confirm the Holmes hypothesis.

Cross-breeding work with *Lupinus Hartwegii*.

*Lupinus Hartwegii* is another member of the Genus *Lupinus* used in this work. It has an erect stem two to three feet high and is somewhat branching. It has digitately compound alternate leaves, consisting of seven to nine oblong, obtuse, very hairy leaflets about two to three inches long on a long petiole. The whole plant is more or less hairy. The showy flowers are arranged in whorls in many-flowered elongated racemes and of a blue color similar in structure and pattern to *Lupinus hirsutus*, but of a smaller size. The stamens are monadelphous of two sets of five of different length, the sheath not cleft, ovary sessile and the style incurved. The pods are flattened and hairy about an inch and one-half long and one fourth of an inch wide and contain up to eight or ten seeds. The seeds are flattened and smooth, of a mottled brownish appearance, between one-eighth to one-fourth inch in diameter. This species differs from *Lupinus Hirsutus* in that all blossoms may set seed. The stem and the branches of the plant show more or less purple color in them, especially near the joints.

There is also a white variety, *Lupinus Hartwegii albus*. It differs from the blue variety by having pure white flowers, ivory colored seed and perfectly green stems without purple in them. The species originates from Mexico and is used as <sup>an</sup> ornamental plant and shows off effectively with its dense spikes which

attain a length of ten inches. A number of crosses were carried out between the white and the blue type, both varieties being used as pollen-parent and also as seed-parent.

#### Technique of Crossing.

The tools used in crossing were a pair of light forceps with a fine curved point, a needle, a pair of small fine scissors, a magnifying glass and paraffin paper bags. The flowers are ready for emasculation after the corolla has emerged from the calyx lobes and has reached almost its full size, sometime before the wings unfurl. At this time the keel was carefully ripped open with the point of the needle or of the forceps, to expose the stamens and the pistil, care being taken not to rupture the pollen sacs. Then the stamens were separated from the style and nipped off with the point of the forceps and thus the anthers completely removed. In case the anthers were ~~broken~~ the flower was discarded. From 6 to 8 flowers were emasculated this way sometimes on one raceme. It did not make much difference whether the flowers were selected at the base or at the top of the raceme. In most cases the flowers were pollinated immediately, only in cases where the blossoms were still very young a day or two were allowed for the stigma to ripen. The pollen was applied in two ways. If many flowers were available the point of the keel, with the anthers contained in it, was cut off with the scissors and stuck on the top of the style and slightly pressed down to bring the stigma in close contact with the pollen, and left on the style for protection. If not enough flowers of the pollen plant could be had, the point of the keel was removed again, and put on several other styles in succession, after some of the pollen had adhered to the stigmas and left on the last one to pollinate. Thus one flower served to pollinate a whole series. With the magnifying glass the stigmas were examined to see whether all of them had retained some



pollen-grains. The majority of the flowers thus treated produced seed. After pollination the remaining unmaturing blossoms were cut off and the whole spike enclosed in a paraffin paper bag, securely tied to prevent any insects from getting to the stigma, and a tag attached indicating the kind of cross made and the date of pollination. A flower that has its wings unfolded is about ready to be used for furnishing the pollen; older flowers are not quite as desirable, because the pollen becomes rather dry and does not adhere as well and a good deal of it will not stay in the tip of the keel.

#### The Crosses.

1. *Lupinus Hartwegii* albus ♂ x blue ♀

The F<sub>1</sub> generation produced plants that resembled in every respect the blue parent. The flowers were blue and the stem and petioles showed purplish coloring in the same degree as the blue parent.

In the second generation 34 plants were raised to maturity. Of these 25 were blue like the F<sub>1</sub> generation and showed the same characteristics in other respects, while 9 plants were pure white with pure green stems and petioles. There seems to be an association of the blue color factor in the flowers with the color factor in the stem. The same factor producing blue color in the flower seems to cause the coloring of the stem. Thus we have here presence and absence of a single factor and as a result we have a simple Mendelian proportion 3 : 1 as follows:

Observed 25 blue, colored stems. 9 white green stems.

Calculated 25.5 " " " 8.5 " " "



2. *Lupinus Hartwegii* albus ♂ x blue ♀

In this case the result is practically the same as in the first cross.  $F_1$  is like the dominant blue parent and the  $F_2$  generation again breaks up into blues and white. 144  $F_2$  plants were raised to maturity and of these 111 were blue and 33 white, with the following results:

Observed : 111 Blue flower, colored stem. 33 White flower, green stem.

Calculated. 108 Blue flower, colored stem. 36 White flower, green stem.

This gives a fairly good 3 : 1 proportion.

3. *Lupinus Hartwegii* albus ♂ x blue ♀

This cross gave a rather surprising result. Instead of the expected two blue and white type, a third type was obtained of a light pink coloring of the flower, in its pattern like the blue flower. The stem in this case showed also the coloring of the blue individual. The  $F_1$  generation appeared like the dominant parent, but in the  $F_2$  generation the result was 9 blues, like the dominant parent, 8 whites like the recessive parent and 8 pinks. The question is now, where does the pink color come from and how is it explained?

The number of  $F_1$  individuals is really too small to draw any conclusion from. I am inclined to believe that the blue color of this lupine is really made up of three complementary factors, a factor C for color, which has to be present to get any color at all, a factor P producing pink when associated with C., and a factor B producing pale blue in presence of C, light purplish blue when present with P and deep purplish blue with CP both present. Thus we would have the following types.

	27	CPB	-	Deep purplish blue	
	9	CPb	-	Pink	
	9	CpB	-	Pale blue	
	9	cPB	-	Light purplish blue	
10	(	3	cpB	)	White
		3	cPb	)	
		3	Cpb	)	
		1	cpb	)	

The colors we obtained were blue, pink and white. In a larger number the other combinations might have turned up. The expected result would have been:

	Deep purplish blue,	pink	pale blue,	light purplish blue,	white
	10.53	3.51	3.51	3.51	3.9
Observed	9	8	-	-	8

As is seen this result does not check very closely. In the next cross the result is a little different.

4. *Lupinus Hartwegii* albus ♂ x blue ♀

The F<sub>1</sub> generation was again the same as in previous crosses. Of the F<sub>2</sub> generation 45 plants were raised which showed the following colors:

Deep purplish blue	Pale blue	Light purplish blue.
25	14	6

Unexpected is the absence of white and of pink. In this case the white parent probably carried a hidden blue factor and the composition of the parents would have been:

$$\begin{array}{ccc}
 ccppBB & \times & CCPPBB \\
 F_1 & & CcPpBB
 \end{array}$$

Thus B would be present in all gametes formed by the hybrid and pink could not show at all, while only a few whites could be expected which, owing to the small number involved might not have shown up. The result expected would have been:

	Deep purplish blue.	L. purplish blue.	Pale blue.	White.
	25.2	8.4	8.4	2.8
Observed	13	18	14	-

This result does not check up very well.

5. *Lupinus Hartwegii* albus ♂ x blue ♀

The F<sub>1</sub> generation was again like that in the preceding crosses. In the F<sub>2</sub> generation 72 plants were obtained of the following colors:

D. purplish blue.	L. purpl. blue.	Pale blue.	Pink.	White.
24	8	11	16	13

Here we have all the types that we would expect according to the above theory. According to the trihybrid proportion we would expect:

	D. purplish blue.	L. purpl. blue.	Pale blue	Pink.	White
Calculated:	30.375	10.125	10.125	10.125	11.250
Observed:	24	8	11	16	13

Here the observed results do not differ very far from the calculated results, though there are some discrepancies which may be due to the small number of individuals. The pale blue type differs from the other blue types in these crosses by having no color in the stems. They resemble in this respect the white strain. In addition to these crosses a few reciprocal crosses were made with differing results.

6. *Lupinus Hartwegii* blue ♂ x albus ♀

The F<sub>1</sub> generation did not differ any from the F<sub>1</sub> generation of the reciprocal crosses. The F<sub>2</sub> generation consisted of 72 individuals which showed the following color:

D. Purplish blue.	L. Purpl. blue.	Pale blue.	White.
34	12	9	17

The pink type is absent entirely, possibly owing to the small number involved, or to some linking with other factors. The expected result would have been:

	D. Purplish blue.	L. Purpl. blue.	Pale blue.	Pink.	White.
Calculated:	30.375	10.125	10.125	10.125	11.25
Observed:	34	12	9	-	17

Whether the hypothesis regarding the three factors influencing the colors holds true is still a matter of doubt. The number worked with is too small to give any definite explanation without further investigation. A number of seeds have been saved from the F<sub>2</sub> plants to investigate the matter further, but so far it has been impossible to do so, owing to lack of space for planting the seeds. Another difficulty is to reconcile the results of the first two crosses with this theory, unless there should happen to exist a case of complete coupling of all three factors in that instance in which case we would have a simple Mendelian ratio 3 : 1 as a result.

7. *Lupinus Hartwegii* blue ♂ x albus ♀

The F<sub>1</sub> generation is again like the dominant parent, while the F<sub>2</sub> generation breaks up into two types representing a simple Mendelian ratio, namely,

	Blue	24.	White	7
Calculated:	"	23.25	"	7.75.

According to the above theory of trihybrid inheritance this case might be explained by the fact that the hybrid zygote produces two kinds of gametes, CPB and cpb, which in this case behave as unit characters. Thus  $F_2$  would be the combination:

$$(CPB)_2, 2 (CPB\ cpb), (cpb)_2$$

The homozygous dominant and heterozygous dominant both would be blue, while the homozygous recessive would be white.

7. *Lupinus Hartwegii* blue  $\sigma^7$  x albus  $\varphi$

The first generation is identical with the dominant blue parent. In the  $F_2$  generation there are 14 blues and 2 whites. This result evidently indicates a 3 : 1 proportion of inheritance, and corresponds with crosses No. 1, 2 and 7. The number of white is rather small, but sufficient to indicate the proportion. We would have expected 12 blues and 4 whites, and we might have gotten better results with larger numbers of individuals.

#### Description of Flower Colors.

1. Pink Flower: The center of the standard is white with both ends of it of a pale purplish pink color. The wings are of the same color near the outer margin, with pink veins running back to the calyx. The tip of the keel is blue with the outermost tip white. The other way the blue goes over into pink, and this into white. The upper lip of the calyx is purplish pink with green margin, the lower lip is green. The petioles are purplish above and green below. The stem is green with slight purplish flush in upper end. The stipules at the base of the petioles are also purplish in color. The rest of the plant is pure green.

2. White flower: The corolla is pure white, only the center of the standard is slightly ivory colored, and the tip of the keel is of greenish color. The upper lip of calyx is of whitish



green color, the lower lip green. The petioles and the upper part of the stem are yellowish green, and the rest of the plant is pure green. This type formed the white parent.

3. Pale blue flower: The standard is white in center, with ivory tinge towards base. The sides are a very pale blue. The outer margin of the wings is pale blue with blue veins running to the base. The blue color fades towards the base. The keel is white with the tip of bluish green color. The upper lip of the calyx is pale blue with green margin, the lower lip green, also the petioles, stem and rest of the plant. Just when the flowers open the center tip of the standard is purplish pink which soon fades away.

4. Dark blue flower: The center of the standard is white with purplish pink tip at time of opening of the flower. The sides of the standard are almost solid blue. The wings are blue with dark blue veins and darker shade near border. The keel is white with blue tip and the veins penetrating from the tip. The outermost tip is white. The upper lip of the calyx is purple at its base, changing into bluish purple, and to green at the apex of the sepals. The lower lip is green. Stipules are purplish and the flower stem and peduncles dark purple, which fades into green at the base. The lower parts of the petioles are purplish, the leaves green. The flower color fades somewhat with age. This type corresponds to the blue parent. The light bluish purple type is like this type, but not so dark in color.

While the work with lupines is more or less preliminary it seems to be certain that Mendel's law of inheritance will apply. Some modification will probably have to be made when the subject is investigated more thoroughly, and the trihybrid hypothesis may not

stand a rigid test, but for the present it seems to explain to some extent the phenomena observed.

Crosses with Antirrhinum majus.

The genus Antirrhinum of Snapdragon belongs to the family Scrophulariaceae or Figwort Family. The name is derived from the Greek and means snout-flower. This name is due to its peculiar formed corolla, resembling a mouth, which opens and closes again when pressed together from the side below the throat. Therefore, it is also called Lion's-mouth, rabbit's mouth, calf-snout and similar names.

Bailey, in the Cyclopedia of Horticulture, stated that there are about 60 species, all herbs, natives of Europe, Asia, and Western North America, in warm temperature regions. They are grown for the flowers in the open and under glass. The common varieties are perennial and most of them are hardy in the North if well covered during the winter. Snapdragons are very satisfactory for forcing in the greenhouse.

Antirrhinum majus.

Antirrhinum majus or great snapdragon is a perennial herb with alternate, lanceolate, linear or oblong lanceolate, entire leaves on short petioles, one to three inches long and about one-half inch wide. The plant grows one to three feet high and is glabrous except in the flower clusters which are downy. The flowers are large, one to two inches long, with long tubes saccate at the bottom. The calyx is five-parted, the corolla irregular, two-lipped, the upper lip erect two lobed, the lower spreading three lobed, its base produced into a palate nearly or quite closing the throat.



Stamens are four, didynamous included, the filaments and the style filiform. The flowers in cultivation are of many different colors and color-combinations; they are arranged in a long terminal raceme. See colored plate on page ( ).

For this experiment flowers were taken that had been growing for several years in Dr. Smythe's greenhouse without special attention and which, therefore, no doubt had intercrossed freely. Unfortunately there was no time to isolate pure strains from these plants and, therefore, it was not known whether the parent plants were homozygous or heterozygous. This probably accounts for the fact that no better results were obtained.

#### The Nature of Flower-Color.

Plant colors are due to two classes of constituents; those which are colored themselves, and those that act upon other substances to produce color in them. Practically all cells of plants contain these substances. Plant pigments are usually divided into two classes according to their location in the cell, namely, chromoplast colors and cell-sap colors. Chromoplast colors include green, and as a rule yellow and orange, sometimes also red. Cell-sap colors include red, blue and violet.

Buscationsi and Traverso distinguish the following classes:

1. Green (chloroplasts)
2. Yellow - orange (chromoplasts).
3. White (colorless, made white by air in inter-cellular spaces).
4. Red.
5. Violet and Lilac
6. Blue ( 4 - 6 anthocyan pigments in solution)
7. Brown (tannin probably concerned)

### Plastid Color Substances.

In most plant cells there are present in the cytoplasm outside of the nucleus small bodies called chromatophores. At growing points and in the embryonic tissue these chromatophores are colorless and refractive. As a rule colorless chromatophores develop into chloroplasts, leucoplasts, or chromoplasts. In the parts of the plant exposed to light they develop into chlorophyll bodies and are scattered in the parietal cytoplasm of the cells. The chlorophyll bodies contain a green and a yellow pigment, the green pigment often excluding the yellow pigment. The yellow pigments of the chloroplasts are termed "xanthophyll". The two pigments can be separated by treating them with benzol and alcohol. The chromoplasts arise mostly from colorless chromatophores or from chloroplasts. The color of them varies from yellow to red, according to the predominance of the yellow xanthophyll or orange-red carotin. Carotin is particularly abundant in the roots of carrots. There is a close relationship between chloroplasts and chromoplasts, and the green and yellow pigments in them. In general the yellow color in flowers and fruit is due to the yellow pigments of the chromatophores.

### Cell-Sap Color Substances.

Other color-substances are produced in the plant cell during the process of metabolism, which are in solution in the cell-sap. They are insoluble in klyol, ether, and similar solvents, but in water and alcohol and thus, they may be separated from the plastid colors. Cell-sap colors may occur with plastids or without them, but as an organized part of the plastid. They and the chlorophyll substance assume a shade of green when treated with alkalis,

potassium cyanide or sodium phosphate. They differ by the fact that the colors are strongly affected by acids, alkalies and iron salts. Their sensitiveness accounts probably for their various shades and tints.

#### The Yellow Pigments of Antirrhinum.

Miss Wheldale examined the yellow pigments of Antirrhinum and found them to be members of a group of natural yellow coloring matter, the "flavones". It is pretty certain that the flavones are universally distributed among plants and form a class comparable to sugars, proteins, tannins, etc. They occur as a rule in plants in the form of glucosides, with one or more hydroxyl groups being replaced by sugar in which condition they are almost colorless and easily soluble and in this condition they occur in the cell-sap. They react in a characteristic way with alkalies, producing an intense yellow color, which can be shown by placing white flowers in ammoniac vapors when they turn canary yellow. That the ivory pigment of Antirrhinum might be a flavone was suggested by the fact that the flowers of the ivory variety turn yellow in ammonia vapor. It contains a pale yellow flavone, epigenin. The yellow pigment was identified as the flavone, luteolin, and it owes its intense color to the ortho-position of two hydroxyl groups. Therefore, the dominant ivory factor of Antirrhinum may be considered as the inhibiting factor for the formation of luteolin. From the pure white variety, the albino form, no flavone could be extracted and ammonia vapors do not turn them yellow.

#### The Anthocyanin Pigments of Antirrhinum.

In crossing yellow or ivory with a suitable white in F<sub>1</sub> anthocyanin is produced. This suggests that some factor in the white acted on the flavone, forming anthocyanin. This process

may involve both oxidation and condensation of a flavone. There are two anthocyanins in *Antirrhinum*, a red one and a magenta one. The latter contains a factor B which is absent in red. Analyses revealed that red contains more oxygen than the flavone, and magenta more than red. The molecular weight of the red and magenta pigments also indicate that condensation has taken place.

The pigments in solution in the cell-sap are of two kinds. The first class consists of the red, purple, and blue pigments, the anthocyanin and the second class of soluble yellow pigments or xanthins. The pigments associated with specialized protoplasmic bodies or chromoplastids are characterized by a constant insolubility in water. They are usually yellow, orange-yellow, orange or orange red. The first one of this group is carotin, a hydrocarbon of definite characteristic properties. It is insoluble in water, nearly so in alcohol, slightly soluble in ether, more readily in benzine and most soluble in chloroform and carbon bisulphide. It occurs naturally and can be obtained in crystalline form. With concentrated sulphuric acid it gives an indigo blue color, at first violet; with iodine a green or greenish-blue color. The second pigment of this group is Xanthin, a plastid, and amorphous in form. It is insoluble in water, somewhat soluble in ether, chloroform, and benzine, but more so in alcohol. With concentrated sulphuric acid it gives a blue color, first green; with iodine a green color.

Anthocyanin is supposed to be a compound of a glucoside-like body with a reddening substance. The loss of the reddening substance (R) gives an ivory variety with no pigment, except in the palate, but carrying a glucoside-like body. There are two kinds

of anthocyanin. In one case decomposition possibly of the glucoside body gives a yellow xantheic form, in the other case no such decomposition occurs and no yellow form exists. Colors of varieties arising from anthocyanic types may be regarded as components of the original anthocyanin. It might be supposed to lose its components (Mendelian factors) in succession and give rise to a series of color variations. There exist two series of color variations, one containing xanthein derivatives, while the other one does not. In the first series albinism would be due to lack of both anthocyanin and xanthein, while in the second series only anthocyanin has to be absent. Xanthein includes a number of different pigments. It is not quite certain whether it is a deviate of anthocyanin. There is evidence of a correlation between the behavior of pigments in genetics and their reaction towards chemicals. In case plastid pigments are present the type may contain carotin and xanthin or both. If the power to produce carotin or some constituent of xanthin is lost variation may take place. If anthocyanin and plastid pigments exist side by side products of both forms of pigmentation are found among the varieties.

We have seen that flower color in *antirrhinum majus* is represented by different Mendelian factors. The pigment depends on the presence of certain organic compounds, accompanied probably by certain ferments. Magenta anthocyanin may be regarded as an oxidation product of a chromogen allied to the flavones, the oxidation being brought about by an oxydase. The loss of the power to produce oxydase by the zygote would produce ivory flowers. It is incapable of forming anthocyanin and contains pale yellow chromogen, i. e. ivory chromogen. The yellow variety in turn arises by the loss of a constituent, probably a ferment and the yellow

color is due to a xantheic pigment in the lips, of flavone nature. If modified by the ferment we have the ivory type. Yellow is the result of plants being unable to produce oxidase and the ferment. If oxydase acts upon yellow crimson, anthocyanin is the result. If all chromogens are absent we obtain an albino that is pure white, but which may carry the ferment or oxydase. Ivory is epistatic to yellow, magenta and crimson epistatic to ivory and yellow respectively. The oxidation of the chromogen by oxydase is a complex process that takes place in two stages, and is due to two factors. One factor produces tingeing of magenta, the second a concentrated factor, cannot show without the first factor. The production of the magenta color in the tube is represented by a factor which is inherited separately from the lip factor. But there is a relation between them that magenta in the tube does not show unless the color is present in the lips. Oxydase may be absent from the tube while present in the lips and thus delila types are formed with white tube and colored lips. Yellow chromogen is not found in the tube with exception of a spot at the base that is always yellow like the throat except in albinos. There are also two rows of hairs inside of the tube that are always yellow except in albinos. If the concentration factor is present only <sup>in</sup> streaks we get the striped forms. There are four shades of magenta: Tinged ivory, pale magenta, intermediate magenta, deep magenta. The corresponding shades we have of crimson.

Flower colors are represented by a number of Mendelian factors.

Y = A yellow chromogen of the nature of a flavone with the power to produce a very pale yellow (ivory) in the corolla tube, a deeper yellow in the lips and a still deeper color on the palate.



I. The power, possibly a ferment, to act on the yellow chromogen Y with formation of ivory chromogen in the lips except in the yellow palate. It has an inhibiting effect and manifests itself only in presence of Y.

R.- An oxydase producing a tingeing of red in the lips when acting upon T; when acting upon Y a tingeing of bronze results.

B.- The power to convert red anthocyanin into bluish-red or magenta anthocyanin and bronze anthocyanin into crimson anthocyanin.

T.- Presence of oxydase producing magenta in the tube. It manifests itself only with R.

D.- Probably a ferment and causes deepening of tingeing to red or magenta. It manifests itself only in presence of Y or T plus R. If Y is absent an albino is the result no matter how many of the other factors are present. Thus yyIIRRBbTTDD would only give a pure white flower:

YY(y)iiRRB(b)B(b)TT(t)DD(d)-	Yellow color.
YY(y)II(l)rrB(b)(Bb) -	Ivory "
YY(y)iiRR(r)BB(b) -	Crimson
YY(y)II(l)RR(r)BB(b) -	Magenta
YY(y)iiRR(r)bb -	Bronze.
YY(y)II(l)RR(r)bbttDD(d)-	Dep rose dori delila.

#### Technique of Crossing.

The best time for emasculation is just before the lobes of the anthers unfold. The lobes are unfolded and the throat of the corolla opened by pressing the sides gently. Thus the stamens and pistil were exposed to view. As the stamens are rather large it is



fairly easy to remove them, care being taken not to injure the style. After emasculation was accomplished a stamen of the intended pollen-parent was taken, whose anther was just breaking open ready to shed its pollen, and the pollen sac was gently rubbed against the surface of the stigma. Then the throat was released again and closed itself. A paraffin paper bag was again tied over the flower like in case of the lupine, to protect against contamination from outside and against injury. Quite a number of crosses were obtained in this way. On account of lack of space not all seed could be sown. The following crosses were grown until the  $F_2$  generation.

1. Medium Magenta ♂ x Medium Crimson delila. ♀

YyII(i)RR(r)BB(b)TtDd x YY(y)II(i)RR(r)BB(b)ttDd.

In the  $F_1$  generation three different types were obtained which seems to indicate that the parents were not homozygous:

(1) Medium crimson delila,

YY(y)iiRR(r)BB(b)ttDD(d)

(2) Medium magenta delila,

YY(y)II(i)RR(r)BB(b)ttDD(d)

(3) Medium Crimson,

YY(y)iiRR(r)BB(b)TTDD(d).

From plants No. 1 the  $F_2$  generation produced Medium crimson delila 95, yellow 1, Pale crimson delila 4, pale crimson 1, Medium magenta delila 2 individuals. This shows only two colors on ivory against 101 on yellow, and the same ratio between delila and colored tube. ~~With~~ the complex constitution of these individuals the number evidently was not sufficient to show any result.

Plant 2 gave the following  $F_2$  generation:

Medium Magenta delila 25

Pale Magenta delila 24

Medium Crimson delila	21.
Pale Crimson	3
Yellow	1
Medium Crimson	5

Here also we do not see a definite proportion of inheritance.

2. Yellow ♂ x Medium Crimson ♀

The F<sub>1</sub> generation consisted of one type only, pale crimson, with magenta tubes. The second generation had the following composition:

Pale Crimson	83
Medium Crimson	40
Yellow tinged crimson	4
Yellow striped red	3
Yellow	39

In this case we have a simple Mendelian proportion between the plants with red color and those without. There are 130 flowers with more or less red color, and 39 without a trace of color. If the yellow with red stripes is considered as yellow without color, we have the proportion 127 : 42. The expected proportion would be 126.75 : 42.25.

There appears also a dilution of color in the heterozygote and in the F<sub>2</sub> generation we have the proportion:

Yellow	Pale colored	Intense colored
42	87	39

This would indicate that yellow lacks the intensifying factor while the darker colored form is homozygous with it and the pale form heterozygous and we get a 1:2:1 proportion.

This result would indicate that red color follows Mendelian inheritance.

3. Yellow ♂ x Medium Magenta ♀

The F<sub>1</sub> generation again breaks off into pale crimson and pale Magenta delila.

In the F<sub>2</sub> generation we obtain a large number of different types from pale crimson F<sub>1</sub>.

Medium crimson	7
Medium crimson delila	3
Yellow tinged crimson	1
Yellow	7
Pink and yellow	1
D. Magenta	1

Here we have a delila factor which must have been introduced by the yellow parent, and acts as a simple recessive. We have 29 tube colored, 12 delila. The yellow type does not indicate which factor it carries. We also have a relation between color and no color: 39 red : 9 not red, which indicates a 3:1 proportion, with delila recessive. In this case also the result indicates a 1:2:1 proportion with regard to intensity of color, the heterozygote in F<sub>1</sub> and F<sub>2</sub> being pale. The calculated results would be 12:24:12; the observed result 7:30:11.

No F<sub>2</sub> generation was planted from the F<sub>1</sub> pale Magenta delila on account of lack of space.

4. Yellow ♂ x Medium Magenta delila ♀

The F<sub>1</sub> generation gives pale crimson. The color of the hybrid is diluted and the colored tube factor T, introduced by the yellow parent is dominant over the recessive delila factor.

F<sub>2</sub> generation breaks up as follows:

Medium Crimson	10
Pale Crimson	15
Med. Crimson delila	2
Pale Crimson delila	10
Deep Crimson delila	2
Yellow	16
Pale Magenta	1
Deep Magenta delila	1
Med. Magenta delila	1
Pink	1

Both red color and delila forms show a simple Mendelian proportion with their allelomorphic character. Thus we have:

Observed:	43 red color	16 yellow
Observed:	32 colored tube	16 delila
Calculated:	44.25	14.75

Yellow has been counted with the type of colored tube, as it introduced the factor, but of course the composition can not be told except by recrossing with delila forms. The intense coloring factor also follows again Mendel's law as imperfect dominant.

Observed:	16 Yellow.	27 pale color.	16 Deep color.
Calculated:	14.75 "	29.5 "	14.75 "

#### 5. Yellow x Deep Magenta delila

The  $F_1$  generation gives an intermediate type. Yellow must have introduced the factor T for colored tube and also lacks the factor D for intense color. Thus the  $F_1$  individual is medium magenta with colored tube.

F<sub>2</sub> generation breaks up as follows:

Med. Crimson	14	Med. Magenta	7
Med. Crimson del.	2	Med. Magenta del.	2
Pale Crimson	4	Pale Magenta	3
Pale Crimson del.	5	Pale Magenta del.	1
Deep Crimson	3	Deep Magenta	2
Yellow	5	Ivory	3
		Ivory striped red	2.

Delila and colored tube factors, presence and absence or red color factors, follow again the simple Mendelian proportion 3:1.

Observed:	33 colored tube	12 delila
Calculated:	33.75 "	11.25 "

Ivory striped red has to be considered as delila form, as color is absent from the tube. In the previous cross yellow has been included with the colored tubes, because yellow introduced this factor, but it was considered safest to leave out the individuals carrying no red color, as their constitution could <sup>not</sup> with certainty be determined without further crossing.

Observed:	45 red	8 no reds.
Calculated:	39.75 "	13.25 no reds.

6. Yellow ♂ x Deep Magenta delila ♀

The F<sub>1</sub> generation again indicates, as in the preceding cross, an introduction of factor T by the yellow parent and thus we have again Medium Magenta.

The  $F_2$  generation breaks up into the following colors:

Deep Crimson delila	2	Deep Magenta	2
Medium Crimson	2	Medium Magenta	5
Medium Crimson delila	2	Medium Magenta del.	4
Pale Crimson	6	Pale Magenta	4
Pale Crimson delila	5	Pale Magenta del.	4
Yellow	5	Ivory	3
Yellow striped red	3		

The factor T and that for red color are again dominant.

We have 39 red and 8 not red.

Calculated: 35.25 red and 11.75 not red.

22 colored tube 17 delila

Calculated: 29.25 " " 9.75 "

The proportion 17 deep color, 22 pale color, 8 no color, seems to indicate again a 1:2:1 proportion here.

7. Yellow ♂ x deep Crimson. ♀

The first generation gives pale crimson delila, the delila factor introduced by the yellow parent probably. The crimson parent also must have been heterozygous in this factor.

In  $F_2$  we get:

Deep Crimson delila	2	Yellow	15
Med. Crimson	7	Yellow striped red	3
Med. Crimson delila	11		
Pale Crimson	6		
Pale Crimson delila	11		

Red and no red break up in a 3:1 proportion.

Observed: 40 red 15 not red

Calculated 41.25 " 13.75 " "

8. Medium Magenta delila ♂ x Yellow ♀

The first generation gave Medium Magenta delila, which broke up in the F<sub>2</sub> generation:

Deep Crimson delila	2	Deep Magenta	1
Medium crimson	3	Deep Magenta del.2	
Medium Crimson del.	3	Medium Magenta	3
Pale Crimson	3	Med. Magenta del.5	
Pale crimson del.	1	Pale magenta	2
Yellow	3	Pale Magenta del.4	
Pink and yellow del.	1	Ivory	4
Pink del.	1	Ivory striped red l.	

We have again an indication 3 : 1 proportion in red color:

Observed:	33	red	7	not red
Calculated:	30	"	10	" "

Ivory is also dominant over yellow:

24 Ivory      16 Yellow.

9. Yellow ♂ x Medium Magenta ♀

The first generation breaks up into two forms, pale crimson delila and pale crimson. The magenta parent evidently was heterozygous in the Ivory factor, and also in the factor T, which the yellow parent was lacking.

In F<sub>2</sub> we have the following series:

F <sub>1</sub> Pale Crimson delila		Pale Crimson.	
F <sub>2</sub> Deep Crimson delila	2	Deep Crimson	3
Medium Crimson	6	Medium Crimson	6
Medium Crimdon delila	5	Pale Crimson	11
Pale Crimson	9	Pale Crimson del.	2
Pale Crimson delila	6	Yellow	10



Yellow	18	Yellow, red stripes	2
Yellow striped red	4	Ivory	2
Deep Magenta del.	1		
Med. Magenta	2		
Med. Magenta del.	1		
Pale Magenta	3		
Pale Magenta del.	3		
Ivory	6		

There are 42 reds and 24 no red in the first series, suggesting a 49:5 : 16:5 proportion, and 22 reds and 14 no reds in the second series corresponding to 27:9 proportion.

10. Medium Magenta ♂ x Yellow ♀

The first generation is of pale magenta color which breaks up in F<sub>2</sub> into:

Deep Crimson	2	Yellow	8
Med. Crimson	1	Yellow striped red	2
Pale Crimson del.	1	Pale Magenta	1

This number is too small to draw any conclusion from.

11. Medium Magenta ♂ x Yellow. ♀

The first generation gives again pale magenta and F<sub>2</sub>

Med. Crimson del.	2
Deep Crimson	1
Yellow	6

This number also is too small to indicate anything.

12. Yellow x Magenta

The first generation gave two forms: Pale Magenta delila and pale Crimson delila, showing that the magenta parent was heterozygous in the factor T and I.

F<sub>2</sub> gave the following results:

F <sub>1</sub> Pale Magenta delila.		Pale Crimson Delila.	
F <sub>2</sub> D. Crimson	1	D. Crimson	4
Med. Crimson delila	1	D. Crimson delila	6
Med. Crimson	2	Med. Crimson	8
Pale Crimson del.	5	Med. Crimson del.	13
Yellow	1	Pale Crimson	4
D. Magenta del.	1	Pale Crimson del.	19
Pale Magenta del.	2	Yellow striped red	3
Ivory	3	Yellow	9
		Pale Magenta	2
		Pale Magenta del.	1

In the first series we have a 12:4 proportion of red and no red color, in the second series the proportion is 57: 9, showing a rather wide margin.

13. Deep Magenta delila ♂ x Yellow ♀

The first generation again breaks up into two forms, Med. Crimson delila and med. Magenta delila.

F<sub>2</sub> gives the following two series:

Medium Crimson delila.		Medium Magenta delila.	
D. Crimson delila	2	Med. Crimson	2
Med. Crimson	9	Med. Crimson delila	10
Med. Crimson delila	30	Pale Crimson delila	1
Pale Crimson delila	3	Yellow	4
Yellow	21	Med. Magenta delila	31
D. Magenta delila	2	Pale Magenta	2
Med. Magenta	1	Pale Magenta delila	12
Med. Magenta delila	3	Ivory	21
Pale Magenta delila	2	Yellow striped red	1

Ivory	4
Yellow tinged pink	3
Pink and yellow (bronze)	1
Pale pink	1

In the second series we have a 3:1 proportion between presence and absence of ivory factor. Also of the red color factor:  
 Observed: 66 Ivory factors present. 18 Ivory factors absent (yellow)  
 Calculated: 63 " " " 21 " " " "  
 58 Red color. 26 No red.

In the first series we also have an indication of red color factor proportion:  
 Observed: 52 Red color. 30 No red.  
 Calculated: 61.5 " " 20.5 " "

The magenta parent is heterozygous for the ivory factor, thus giving rise to the first series where yellow color predominates.

14. Deep Magenta delila ♂ x yellow ♀

The first generation gives pale Magenta del.

In F<sub>2</sub> this breaks up into:

Medium Crimson delila, 8	Medium Magenta delila, 33
Yellow 3	Ivory 4
Pink and yellow del. 1	Pink delila 6

We have here a proportion of 3:1 in the factor for ivory, and for blueness, present in the crimson and Magenta colors.

Calculated: 41.25	1375
Observed: 43 Ivory	12 Yellow
Observed: 41 B present	7 B absent
Calculated 36	12

The yellow and ivory flowers do not show the presence of B unless R, the factor for red, is present.

15. Pink ♂ x Yellow ♀

The first generation gave Medium Crimson, due to the action of B hidden in the yellow parent on the factor R in pink. Pink was heterozygous for the ivory factor, otherwise the color would have been magenta instead of crimson. F<sub>2</sub> gave the following series:

Deep Crimson	2	Medium Magenta	5
Medium Crimson	29	Pale Magenta	1
Medium Crimson delila	14	Yellow	11
Pale Crimson	1	Ivory	1
Pale Crimson delila	4	Pink and yellow	14

There is a 3 : 1 proportion indicated in the presence or absence of the factors B, R and T.

Calculated:	61.5		20.5
Observed:	68	B present	14
		B absent	
	70	R present	12
		R absent	
	64	T present	18
		T absent	

16. Pink ♂ x Yellow. ♀

The pollen parent is the same as in the preceding cross and furnished the factor R, while yellow furnishes a hidden factor B. Pink being heterozygous for the ivory factor, we get two forms in F<sub>1</sub>.

Medium Crimson Medium Magenta

F<sub>2</sub> breaks up as follows:

Deep Crimson	2	Deep Crimson	1
Deep Crimson delila	1	Medium Crimson	21
Medium Crimson	10	Medium Crimson delila	4

Medium Crimson delila	4	Pale Crimson	5
Pale Crimson	1	Pale Crimson delila	1
Pale Crimson delila	1	Medium Magenta	9
Medium Magenta	6	Medium magenta del.	3
Medium Magenta delila	3	Pale Magenta	20
Pale Magenta	3	Pale Magenta del.	6
Pale Magenta delila	1	Yellow	10
Yellow	1	Ivory	20
Ivory	3	Pink	3
Pink and yellow	8	Ivory tinged pink	6
Pink	4	Pink and yellow	4
Pink delila	1	Yellow tinged pink	4
Pale pink	2		
Ivory tinged pink	3		
Yellow tinged pink	3		

In the first series we have an indication of 3 : 1 proportion in the factor B and T.

Calculated:	39.75		13.25
Observed:	32	B present	21
		B absent	
	42	T present	11
		T absent.	

In the second series we have 3 : 1 proportions for the factors B, R and indications for the factors T and I.

Observed:	70	B present	17	B absent
	73	T present	14	T absent
Calculated:	65.25		21.75	
Observed:	87	R present	30	R absent
Calculated:	87.75		29.25	
Observed:	67	I present	50	I absent (yellow)
Calculated:	87.75		29.25	

17. Pink ♂ x Yellow ♀

The parents being of the same constitution the result is the same. Medium Magenta and Medium Crimson are produced in the F<sub>1</sub> generation, but only the seed of the Magenta hybrid was sown on account of lack of space. In F<sub>2</sub> we get:

Deep Crimson	1	Deep Magenta	3
Deep Crimson delila	2	Deep Magenta delila	2
Medium Crimson	10	Medium Magenta	19
Medium Crimson delila	1	Medium Magenta delila	6
Yellow	3	Pale Magenta delila	3
Pink and yellow	4	Ivory	15
		Ivory tinged pink	6
		Pink	6
		Pink delila	2

Here we have a 3 : 1 proportion, the factors I, B, R

and T.

Observed:	62 I present (Ivory)	21 I absent (yellow)
	65 R present	18 R absent
Calculated:	62.25	20.75
Observed:	47 B present	18 B absent
	49 T present	16 T absent
Calculated:	48.75	16.25

These results show that as far as we are able to see the color factors in *Antirrhinum* follow the law of segregation and of gametic purity. The number of individuals obtained in some of the crosses was too small to get any good proportions, and besides the fact that the parent constitution, with regard to their gametic purity was unknown, made it hard to get very good results. A number of other crosses were made besides these, but not carried beyond the first generation on account of lack of space for the F<sub>2</sub> plants. As far as results were obtained they confirmed those of

Miss Wheldale, E Baur and other workers with shapdragons.

### Crosses with Phlox Drummondii.

#### History and Description.

Phloxes are among the most satisfactory of garden plants. Their showy flowers, profuseness of bloom, and easy cultivation make them favorites every where. They are all herbs, about 30 to 40 species, most natives of North America, a few of Siberia. There are two kinds of Phlox; the annuals and the perennials. The perennials comprise many species. The annuals are all derivatives of Phlox Drummondii.

Phlox Drummondii is a native of Texas. In the spring of 1835 the seeds were received first in England from Texas, where they had been collected by Drummond. In the fall of that year it was described with illustrations in Botanical Magazines, by W. T. Hooker and named after Drummond. It was described as "pale purple, without, within or on the upper side, of a brilliant rose-red or purple, varying exceedingly in different individuals in intensity." Lindley described and figured it in Botanical Register, 1837, where he describes the flowers as "either light or deep carmine on the inner surface of their corolla, and a pale blast on the outside, which sets off wonderfully in general effect. A bed of this plant has hardly yet been seen, for it is far too precious and uncommon to be possessed by any one, except in small quantities." It has been much modified by domestication, so that there are a large number of garden varieties. These vary in stature, color, size and shape of flowers. It is an erect branching herb, six to eighteen inches tall with entire oblong or lanceolate leaves, the upper ones more or less clasping. The flowers are showy and arranged in broad, mostly flat-topped cymes. The calyx lobes are



long and narrow, and spreading in fruit, throwing out the seed from the pod. The corolla lobes are five, broad-obovate. In some varieties they are deeply cut, forming a star. The five stamens are straight and inserted on the corolla tube. The pistil has three styles with a single stigma each. At its base is the three-celled ovary with one seed in each cell. The colors vary from violet, purple and scarlet shades to pink, cream and white colors, sometimes with traces of darker color around the center. The photographs give an idea of the variety of sizes, shapes and patterns. The plants used for this experiment were grown from seed obtained from a commercial seed-house and raised in the greenhouse beds.

#### Technique of Crossing.

The flowers of Phlox, being perfect and self-pollinating, had to be emasculated before pollination took place. As the stamens are inserted on the corolla-tube, emasculation was a rather simple process. The buds are selected just before the anthers break open, that is, before the corolla is unfolded, but after it is fairly well formed. The writer found out that if the whole corolla was removed the flower was emasculated. If the corolla is caught by its tip and gently pulled, it comes off very easily and all the stamens with it, while the pistils are left on the top of the ovary. Only the emasculated flowers were left on the cyme. Then a <sup>flower</sup> of the male parent was taken, pulled off and the stricture at the bottom of the tube cut off. The tube was now put <sup>over</sup> the pistil of the emasculated flower in place of the one removed during emasculation, and slightly pressed down so that the top of the pistils reached the anthers in the corolla tube. If

you now blow from above into the corolla tube the pollen is blown in thick masses onto the stigmas. Now the flowers were bagged securely and the bags left until the seed was about ripe. The seed was harvested before it was dead ripe, as it was liable to get lost when the caspule dehisced.

#### Description of Parent Plants.

About ten different types of colors and shapes were used in the following crosses:

With regard to shape we have two large groups, those with round entire petals and those with the petals cleft, or the stars. The photograph in the appendix gives an idea of the different kinds of stars and round forms. Then we have the doubles and singles. The singles have five petals, while the double flowers have from six to ten petals. But the doubleness is not complete. There are always some single flowers on the plants with the doubling factor.

About ten different color combinations were used as parent plants.

- (1) White without any trace of color, pure white.
- (2) Cream, a plain buff color, without pattern.
- (3) Pink, of a rose pink shade with a white and purplish center.
- (4) Purple-eyed cream, like No. 2, but with a ring of purplish violet color around the throat.
- (5) Violet and white star, a star of deep rich violet color, with a white rim around it, the pattern like 4 C in the large photograph. It may be mentioned here that all stars have a more or less narrow rim of white on the outer border.
- (6) Purple, an amaranth-purple color with more intense

color in the center, which gradually turns into a violet shade.

- (7) Purple star, of the same color as the preceding and of the same pattern as the violet star.
- (8) Violet, of the solid rich violet color with center more intensely colored.
- (9) Lilac and white, a brilliant lilac color of the petals with a white circle around the center and another purplish violet ring inside of this around the throat.
- (10) Scarlet, a rich rose-red color, slightly more intense in the center.

All these colors, where red and blue pigments are involved, take on a more bluish tint with age, so that an old purple flower looks violet, and an old scarlet flower purple. On account of this change which begins soon after the flowers open, it is necessary to determine the exact flower color as soon as the flowers are open. With regard to the growth of the plants, there is no difference between the differently colored varieties. The double varieties are of the same color as the single varieties and differ only in the number of petals present. The description of the flower color in the  $F_1$  and  $F_2$  generations follows the nomenclature of Ridgeway.

The Crosses.

1. White ♂ x Cream with Purple Eye. ♀

F<sub>1</sub> gave, as expected, white with purple eye, but besides also pure white and rose pink with a center of Tyrian rose and white. The mother-parent evidently was heterozygous and contained a color factor, indicated by the purple eye, which stimulated by a factor present in the white parent produced a pink flower, while the gamete that did not contain this color factor gave pure white with the gamete of the pollen parent. In F<sub>2</sub> the pure white flower produced an offspring of 6 whites and 2 creams, a simple 3 : 1 proportion as expected. The pink hybrid gave one Rhodamine purple flowered plant. The third did not produce any seed.

2. Violet Star ♂ x Pink. ♀.

In F<sub>1</sub> we got a Rhodamine purple star with darker center of purplish violet color.

F<sub>2</sub> broke up into the following series:

- Amaranth purple star, pansy purple center 4
- Rhodamine purple star 1
- Light mallow purple star, dark in center 1
- Magenta and amaranth purple center 4
- Deep rose pink with rose center 1
- Hermose pink with eosin pink center 1
- White with violet purple center 1
- Lavender violet with manganese violet star 1

The color inheritance seems to be blended a 1:2:1 proportion, being indicated as follows:

Observed:	2 Violet	10 Purple	2 Pink
Calculated	3.7	7.6	3.7

There seems to be also Mendelian inheritance of the intensity of the color, 11 individuals having dark flower color, while 3 have light colors, 10.5 to 3.5 being the 3:1 proportion. Stars and round shape are equal in number, but if a larger number had been produced the stars probably would be dominant.

3. Pink x White c Violet Star.

F<sub>1</sub> is a amaranth purple star with pansy purple center.

In F<sub>2</sub> we have:

Lilac with solid white center	3
Lilac with solid star center	1
White star flushed pink	2
Indian Violet star	1
Rose red star	3
Purple star	6
Purple round	1
Tyrian rose and white star	1
Venetian pink star with white center	1
Violet and white star	1

Here we have dominance of the star shape:

Observed: 17 stars 4 rounds

Calculated: 15.75 5.25

There seems to be also blended color inheritance.

Observed: 7 violets 7 purples 7 reds

Calculated: 5.25 10.5 5.25

The purples would be heterozygotes, and the others the homozygotes.

4. Rose Pink ♂ x Violet Star ♀

In first generation we have again an amaranth purple star as intermediate of Pink and Violet.

In  $F_2$  we have the following:

Magenta Star	4
White Star	8
Lilac with white center	4
Lilac with white center star	2
Purple star	9
Rose pink with white center	1
Rose pink with white center star	2
Bluish violet star	4
Hortense violet and white star	5
White round	1

Stars are dominant:	34 stars	6 round
Also color to white	31 colored	9 white
Also blue factor B to absence of B	28 purple and violet	12 white
Calculated	30	10

The factor B produces purple with a red factor R and violet blue by itself, both in presence of a color factor C.

5. White  $\sigma^{\uparrow}$   $\times$  Cream with purple eye  $\varphi$ .

$F_1$  breaks up similar to cross No. 1, a pure white and a purple eyed white being produced. White is dominant to cream.

From the white flower we get in  $F_2$ :

White	16
Cream	3
Magenta and purple center	3
Deep rose pink star	1
Rose color round	1

There seems to be a hidden color factor in white which crops out in  $F_2$ . White and cream form a 3 : 1 proportion together. The star is probably a mutant, mutation being stimulated by cross-

ing. In several instances a star appeared where no star was expected. The other F<sub>1</sub> plant produced only one flower, a white purple striped star.

6. White ♂ x cream with purple eye. ♀

The first generation is like the preceding cross:

1 white, 1 white with purple eye.

F <sub>2</sub> produced:	White	41
	Cream	12
	Pink and white	3
	Pink and cream	1
	White with purple eye	3

Here we have 47 plants showing white in the flowers and 13 showing cream color, showing 3 : 1 proportion 45, and 15 being the theoretical result.

In F<sub>2</sub> of the plant with purple eyed white flowers we have:

White	17	Pink star, rose red center	1
Cream	4	Pink and white	2
Cream and pink	5	White star	1
Purple eyed cream	4	Indian lake	1
Purple	1	White with purple eye	14
		White with star	1

White and cream again break up in 3: 1 proportion.

Observed: 37 Whites 13 Creams

Calculated: 37.5 13.5

7. Lilac and white ♂ x Rose red ♀

F<sub>1</sub> gives an intermediate color, dark rhodamine purple with pome-granite center. F<sub>2</sub> produces:

Lilac with solid white center	3
Dark rhodamine purple	2
Magenta	3
Rose red	1



This would indicate a blended color inheritance.

Rose red 1, purplish colors 5, lilac 3.

Theoretical:            2.25                            4.5                            2.25

There seems to be also a dominance of intense color over light color; 6 intense colors and 3 light colors, lilac, being produced.

8. Violet ♂ x Rose red ♀

F<sub>1</sub> gives us an intermediate color, amaranth purple.

F<sub>2</sub> breaks up into:    Amaranth purple    6  
                          Pansy violet        2  
                          Rose red            1

As in the preceding cross blended inheritance seems to take place. 2 violet, 6 purple    1 rose red.

Theoretical: 2.25                            4.5                            2.25

9. Rose red ♂ x Violet Star ♀

F<sub>1</sub> gives again an intermediate type, amaranth purple star, the star being dominant to round shape. F<sub>2</sub> breaks up into:

Amaranth purple star	28
Amaranth purple round	14
Rose red star	11
Rose red round	6
Lilac and solid white center star	2
Lilac and solid white center round	2
Dull Magenta purple star	1
Dull Magenta purple round	1
Indian lake star	8
Indian lake round	4
Purplish violet star	3
Purplish violet round	3

Magenta purple star, solid white center	1
White star with Amaranth purple rays	11
White star with Tyrian red rays	4
White star with lavender rays	3
White star	1

Stars are dominant: 73 stars 20 round

Calculated: 77.25 25.75

Color inheritance is blended: 25 violet shades, 56 intermediate purplish shades, 21 rose color shades, 25.75: 51.5: 25.75:, being the expected numbers.

10. Rose red ♂ x Violet ♀

F<sub>1</sub> is intermediate, amaranth purple and in F<sub>2</sub> breaks

up into:

Amaranth purple	45
Rose red	5
Pansy violet	8
Indian lake	1
Rhodamine purple	6

The result seems to indicate blended inheritance, though the intermediate type, purple, seems to be unexpectedly numerous.

Red 5 Purple 51 Violet 9

Expected: 16.25 32.5 16.25

11. Rose color ♂ x Violet ♀

F<sub>1</sub> generation is again amaranth purple. F<sub>2</sub> gives:

Purple star	3
Purple round	4
Violet	5
Cameo pink star	1

The proportion, 5 violet, 7 purple, 1 pink indicates

a blended color inheritance, though the number is rather too small for definite results. The appearance of the stars is unexpected and may possibly be explained by mutation.

12. Rose Red ♂ x Violet ♀

The first generation is intermediate again, dark rhodamine purple. In F<sub>2</sub> we get the following colors:

Purple	60
Violet	20
Tyrian Rose	20
Indian Lake	2
Rose Red	6

Another instance of blended inheritance:

Observed:	21 violet	59 purple	26 red
Expected:	26.5	53	26.5

13. Violet ♂ x Purple ♀

F<sub>1</sub> generation breaks up into three colors; Fluorite violet, dull blueish violet, and Pansy Purple. The purple may have been self-fertilized or the Violet parent must have been heterozygous for the factor red. The fluorite violet hybrid gave in F<sub>2</sub>:

Fluorite violet	13
Dull bluish and Nigrosin violet	2
White with purple eye	3
Purple	2

The violet color seems to be dominant over purple.

15 plants containing violet and 5 purple color.

Purple produced:	Fluorite violet	1
	Raisin purple	1
	Amaranth purple	1
	Magenta	1

This number is too small for results.

14. Purple x Violet Star

F<sub>1</sub> gave three colors.

(1) Rose Red Star

(2) Light violet and white star with pansy violet center

(3) Magenta star with pomegranite center.

In F<sub>2</sub> number 1 gave:

Rose Red star	26	Indian lake and white star	13
Rose Red round	3	Indian lake and white round	7
Tyrian Rose star	17	lavender star	1
Tyrian Rose round	9	White star with purple rim	1
Amaranth purple star	16		

Star shows dominance over round shape again.

Observed: 74 Star 19 round

Calculated: 69.75 22.25

Number 2 game in F<sub>2</sub>:

Magenta Star	1	Violet	1
Purple Star	1	Violet star	1
White star with violet center			1

Proportion of stars to round form, 4:1.

Number 3 gave:

Tyrian rose star with Amaranth purple center	17
Tyrian rose round with Amaranth purple center	6
White star with flush of Indian lake	5
White round with flush of Indian lake	1

Star Dominates: 22 star 7 round

Expected: 21.75 7.25

The color inheritance is not clear. Evidently the parents werannot heterozygous.

15. Purple ♂ x Violet Star.♀

The first generation gave a rose red star and a light violet and white star, with dark violet center.  $F_2$  of the rose red star broke up as follows:

Rose red star	17
Rose red round	2
Tyrian rose star	10
Tyrian rose round	5
Venetian pink star	13
Venetian pink round	4
White and Venetian pink star	1
Pomegranate and Amaranth purple star	3
Indian lake star	11
Indian lake round	1
Purple eyed white	2

Star againis dominant. 55 star. 14 round

Expected: 51.75 17.25

The  $F_1$  violet star produced only one plant like itself.

16. Violet star  $\sigma$  x Purple  $\varphi$ .

In  $F_1$  we have again three colors:

- (1) Hyacinth and Amethyst violet star.
- (2) Dark rhodamine purple star, pansy purple center.
- (3) Indian lake star, with amaranth purple center.

No. 1 game in  $F_2$ :

White/star with some bluish violet markings	5
Dauphin's violet with dark center	1
Hyacinth violet star	8
Lavender violet, manganese violet center	2
Lavender violet, star violet center	2
Indian lake on white ground	1

Indian lake on cream ground 1

Star dominates. 15 stars 5 round.

The other F<sub>1</sub> hybrid did not produce sufficient plants to discuss them.

17. Violet x Purple Star.

F<sub>1</sub> broke up again into two colors, amaranth purple star and pansy and hortense violet star.

The purple star gave in F<sub>2</sub>:

Pansy purple star 3

Hortense and Amethyst violet 1

Magenta and amaranth purple 2

The violet star produced in F<sub>2</sub>:

Pansy violet star 10 Violet striped white star 3

Amethyst violet star 3 Violet round striped white 2

Amethyst violet round 5 Rhod. purple star 5

White with violet eye 1

Star is dominant: 21 star 13 round

Also violet to purple: 24 violet 10 purple

Calculated: 25.5 8.5

The number of F<sub>2</sub> is rather small for good results, particularly in the first case.

18. Violet ♂ x Purple ♀

F<sub>1</sub> gave manganese violet with pansy violet center.

F<sub>2</sub> broke up into:

Violet 34 White and Indian lake 2

Purple 7 Lavender violet and pansy violet 5

Indian lake 8

Violet here is dominant: Violet 39 Purple 17

Expected: 42 14

One of the parents and also F<sub>1</sub> apparently was heterozygous for a factor I for intensity of color. Thus we have in F<sub>2</sub>:

41 Intense color, 15 diluted color.

Indian lake and lavender-violet are light colors.

19. Violet ♂ x Purple Star ♀

F<sub>1</sub> gave again two colors, identical with F<sub>1</sub> of cross

17. Amaranth purple star and pansy and hortense violet star. The violet star produced in F<sub>2</sub>:

Violet star	12	Violet and white star	2
Violet round	7	Violet-purple star	1
Purple round	1		

Star is dominant: 15 star 8 round

Expected: 17.25 5.75

20. Double White ♂ x Violet ♀

F<sub>1</sub> gave two types: 1 plant with double Rhodamine purple flowers, 3 plants with double light lavender violet flowers. The purple individual gave in F<sub>2</sub>:

Double rhodamine purple	5
Single rhodamine purple	1
White double	2
White single	2
Pale Indian lake double	1

Doubleness dominant to singleness:

Observed: 8 double 3 single

Expected: 8.25 2.75

Color seems to be dominant to white, 7 color types appear to 4 white.



21. Double White ♂ x Violet Star ♀.

F<sub>1</sub> broke up into three types:

- (1) Double white star with violet purple eye.
- (2) Double white star flushed violet.
- (3) Double pale mauve star, manganese violet center.

Only Number 1 produced seed and F<sub>2</sub> gave the following

forms:

Double white star	2
Single white star	2
Double white star, purple eye	5
Single white star, purple eye.	1
Double white	2
Double cream star, purple eye	1
Single cream star, purple eye	1
Single white star, pinkmays.	1
Double purple eyed white	1
Single purple eyed white	3

Doubleness is dominant to singleness, star to round shape, presence of color to absence, white color to cream. The violet parent must be heterozygous for the white factor or not have it at all.

11 double	8 single
12 star	7 round
13 color present	6 color absent
17 white present	2 white absent(cream)

Calculated: 14.25                      4.75

22. Double White ♂ x Violet Star ♀

In F<sub>1</sub> appears a double purplish-violet star. F<sub>2</sub> breaks

up into:

Deep lavender, violet purple center, single	1
Double white, violet purple eye	7
Double star, lilac and white striped	7
Single star, lilac and white striped	2
Cream star, double	6
Cream star, single	1
Cream round, double	2
Double white star	6
Indian lake on cream double	1
Indian lake on white single	1
Double Indian lake and white star	10
Single Indian lake and white star	2
Double Indian lake on cream star	4
Single Indian lake on cream star	2
Double cream purple eye star	3
Single cream purple eye star	1
Double white star, purple eye	1
Double white	2
Single white	1
Double cream, purple eye	4
Single cream, purple eye	1

In the following plants the character for doubleness and singleness was not observed:

Cream round	1	White and Indian lake star	28
Cream star	5	White and Indian lake center	10
White star	13	White and Indian lake star	6
White round	2	Cream and Indian lake center	1
		Cream and Indian lake star	1

Doubleness is dominant over singleness, the result observed is:

	53 double	12 single
Expected:	48.75	16.25

Also star is dominant to round shape, presence of color to its absence, white color to cream color.

Observed:	109 Star	23 round
	94 color	38 no color
	98 white	34 cream
Calculated:	99	33

23. Double White ♂ x Violet ♀

The F<sub>1</sub> generation breaks up into double rhodamine purple and double manganese violet. White apparently introduced a heterozygous factor, acting on violet.

Violet breaks up into the following series:

Double violet	3	Double white	1
Single violet	3	Single white	1
Double white violet eye	3	Double purple	1
Single white violet eye	1	Single purple	4
Hortense violet double	3	Double lilac violet	2
Hortense violet single	1	Double Indian lake	1
Double Magenta	1	Star Indian lake	1

Doubleness shows dominance over singleness.

Observed:	16 double	10 single
Calculated:	19.5	6.5

Purple breaks up as follows:

Double white	5	Violet double	7
Single white	2	Violet star	3
Single white star	1	Violet single	6
Purple double	5	Pink and white single	2

Purple single	5	Violet single star	1
Purple single star	5	Magenta star single	1
Magenta double	1	Lilac and white single	1
Magenta single	4		

Color appears dominant to absence of color.

Observed: 41 color present            8 color absent

Expected: 36.75                      12.25

Double and single types are about even, 21 double, and 28 single flowers being produced. The parents evidently were not homozygous in several factors.

24. Double white ♂ x Violet ♀.

The parents were the same as the preceding cross and the results are very similar.  $F_1$  is like  $F_1$  of Number 23.

Double White	6	Single violet	3
Single White	3	Double purple	3
Double purple eyed white	4	Single purple	2
Single purple eyed white	1	Light purple star	2
Single purple eyed star	1	Hortense violet double	2
Double violet	17	Hortense violet single	4

Doubleteness is dominant to singleness and presence of color to absence of color:

Observed: 32 double    16 single

39 color present    9 color absent

Calculated: 36                      12

Purple give the following  $F_2$  proportion:

Double purple	3	Double Tyrian rose and pink	3
Single purple	2	Single " " " "	1
Double white	2	Single lilac and white star	1
Single purple eyed white	1	Single Hortense violet	3
Single purple	2	Double H <sub>o</sub> rtense violet	1
Double Phlox-purple	1		

Double and single forms are here about even. Color is dominant over absence of color: 18 color present; 2 color absent.

Expected: 15 \* 5

25. Pink ♂ x Cream.♀

In F<sub>1</sub> we get Rose-pink with white and Tyrian rose center. In F<sub>2</sub> the following series appear:

White with purple eye	3	Pale pink and white center	2
Bivid pink and Venetian Pink	1	Rose pink and white	1

White color is dominant to cream.

Pink and white are dominant to pink and cream. 6 plants show white color in their flowers and only one has cream in pink, Venetian pink.

26. Rose Pink ♂ x White x Cream.♀

First generation was white and pink, color and white being dominant factors. F<sub>2</sub> broke up as follows:

Pink and white	25	White and Pink eye	9
Pink and cream	9	Cream and Pink eye	3
White	7	Cream	2

Result: 41 white 14 cream.  
 46 color present 9 no color present.  
 Expected 41.25 13.75.

27. Rose Pink and white ♂ x Cream ♀

F<sub>1</sub> was like the dominant parent pink and white. F<sub>2</sub>

broke up as follows:

Rose Pink and white	25	Rose Pink with rose center	3
Rose Pink and Cream	10	Rose color, rose center	2
White	12	Cream star	1
Cream	6		

Result: 46 White                      17 Cream  
 40 color present              19 color absent  
 Expected: 44.25                      14.75

28. Rose Pink and white x Cream.

The first generation gave Tyrian rose and white, which in F<sub>2</sub> produced:

Rose pink and white	9	Purple eyed white	4
Rose pink and cream	1	Rose color	1
White	2	Pink and white star	1
Cream	1	Amaranth purple star	1
Magenta	2	Amaranth purple round	2

Result: 16 white                      2 cream

Expected: 13.5                      4.5

A factor for intensity of color was probably introduced by the cream parent producing the darker colors.

29. Rose pink and white ♂ x cream. ♀.

The first generation was like the dominant parent, rose, pink and white. In F<sub>2</sub> segregation took place as follows:

Rose pink and white	116	White	56
Rose pink and cream	29	Cream	16
White and pink eye	30	White star, pink eye	2
Cream with pink eye	10	Rose pink star	1
Tyrian rose	1	Magenta round	1
		Magenta star	1

Results:	222 White	55 Cream
	205 color present	72 color absent
Expected:	207.75	69.25

30. Rose Pink and White ♂ x Cream ♀

First generation was like the dominant parent, Rose pink and white. F<sub>2</sub> gave the following series:

Rose pink and white	106	Pink and white star	2
Rose pink and Cream	26	Lilac and white	7
White	29	Magenta	3
Cream	11	Magenta star	1
Tyrian rose	1		

Result: 144 White 37 Cream

Expected: 135.75 45.25

146 color present 40. color absent.

Expected 139.5 46.5

31. Rose Pink ♂ x Cream ♀

F<sub>1</sub> gave Rose color with rose red center. F<sub>2</sub> gave:

Rose Pink and white	5	Purple eyed white	4
Rose pink and cream	5	Pink and white star	1
Purple	1	Indian lake	1
Purple star	1	Tyrian rose	1

Result: 12 White 6 cream

Expected: 13.5 4.5

Here again apparently an intensifying character has been introduced by one of the parents, producing the dark colors in F<sub>2</sub>.



32. White ♂ x Rose Pink and cream. ♀

In F<sub>1</sub> we find the two dominant factors, colors, and white, combining, forming rose pink and white. Besides by intersection of some hidden factors we get a white star with rhodamine purple eye. In F<sub>2</sub> the first hybrid gave:

Rose pink and white	19	Venetian pink and cream	5
Rose pink and "star	4	Venetian pink and "star	1
White			12.

Result:	29 color present	12 color absent
	35 white	6 cream
Expected:	30.75	10.25
	23 Pink and white	6 pink and cream
Expected:	21.75	7.25

33. Cream ♂ x white ♀

F<sub>1</sub> was pure white and F<sub>2</sub> gave the following colors:

White	3	Cream	1	Rose color	1
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White and cream form a 3:1 proportion, Rose color probably arose by union of some hidden factors, one possibly a ferment.

34. White ♂ x Cream ♀

F<sub>1</sub> again was pure white as in the reciprocal cross and F<sub>2</sub> gave:

White	25;	Cream	4;	Purple eyed white	1.
Results:	26 White		4 cream		
Expected:	22.5		7.5		

Here again a color factor crops out in the purple eyed white.

35. White ♂ x Cream ♀

F<sub>1</sub> is pure white and F<sub>2</sub> gives the following proportions: White 23; Cream 3; Purple eyed white 3.

Results:	White	26;	Cream	3
Expected.		21.75		7.25

This result is about the same as in cross No. 24.

36. Cream ♂ x White ♀.

F<sub>1</sub> was pure white. F<sub>2</sub> broke up into:

White 3; Cream 1; Rose color 1.

The result is exactly the same as in No. 33.

37. White ♂ x Cream ♀.

F<sub>1</sub> was pure white again. F<sub>2</sub> gave the series:

White	45	Indian lake star on cream	1
Cream	14	Magenta on white	1
Pink and white	1	Violet on white	1
Results:	48 White	15 Cream	
Expected:	47.25	15.75	

One of the parents seems to contain a hidden color factor that is brought out by the complementary factor of the other parent, as happened in every case.

38. White ♂ x Cream ♀.

F<sub>1</sub> gave pure white. F<sub>2</sub> broke up into:

White	27	Rose pink and white	3
Cream	12	Rose pink and white star	1
Result:	White 31	Cream 12	
Expected:	32.25	10.75	

39. Cream ♂ x White ♀.

The first generation was pure white and F<sub>2</sub> broke up again

into:	White	33	Magenta and rose	2
	Cream	11	Purple eyed white	2
	Pink and Cream	2	Violet eyed white	3
	Lavender violet and cream	1	Pink and white	1
	Purple eyed cream	1	Pink and white star	1
	Rose	1		

Result: 40 White 15 Cream

Expected: 41.25 13.75

In this case the number of plants exhibiting color is especially large, about one-fourth of F<sub>2</sub>. In all these cases two complementary factors, a color factor and a ferment, must have been introduced by the two parents, each of which had one of the factors and by their union they probably produced the colored specimens of F<sub>2</sub>.

40. Cream ♂ x Lilac and white. ♀

The first generation was like the dominant parent,

lilac and white. In F<sub>2</sub> appeared the series:

White 6 White with purple eye 2

Cream 3 Magenta on white 6

Lilac and solid white center 4; Lilac and cream with

lilac and white with violet ring around "14; violet ring in center 7

Result: 32 White 12 Cream

33 Color present 9 color absent

Expected: 31.5 10.5

41. Lilac and white ♂ x Cream. ♀

The first generation was again identical with the dominant parent, lilac and white. F<sub>2</sub> broke up as follows:

Lilac and white 8 White 5

Lilac and cream 2 Cream 3

Lilac with solid white center 3 White with lilac flush 1

Cream and lilac eye 1

Results: 13 Lilac 8 Color absent

15 White 6 Cream

Expected: 15.75 5.25

42. Cream ♂ x Lilac and White. ♀

F<sub>1</sub> was like in the preceding cross, lilac and white.

F<sub>2</sub> broke up into:

White	17	Lilac with solid cream center	3
Cream	13	Lilac with solid white center	7
Purple eyed white	10	Lilac and white	27
Purplish pink	2	Lilac and cream	9

Result: 63 White                      25 Cream  
           58 color present            30 color absent

Expected: 66                              22

43. Rose red ♂ x Double Cream. ♀

The first generation was double rose red. In F<sub>2</sub> the following series appeared:

Rhodamine purple	9	Cream star	2
Mallow purple	7	Indian lake on white	4
Rose red	20	Indian lake on cream	1
Tyrian rose	4	Purple eyed white	2
White	11	Purple eyed cream	1
Cream	2	Lavender violet on white	1
Lavender violet star on cream			1

Result: 34 Double                      12 Single

Expected: 34.5                            11.5

Observed: 18. White                    7 Creams

Expected: 18.75                         6.25

Observed: 50 Color present            15 Color absent

Expected: 48.75                         16.25

44. Rose Red ♂ x Cream. ♀

F<sub>1</sub> generation was rose red. F<sub>2</sub> broke up as follows:

Rose red	6	Indian lake and white	1
White	1	Indian lake and cream	1
Violet and white	1	Solid Indian lake	1

Cream and white broke up in 3:1 proportion.  
3 white; 1 cream

Colors are predominant, 10 plants having color and only one being white. Larger numbers would give better results.

45. Cream ♂ x Rose Red ♀

F<sub>1</sub> was rose red again. F<sub>2</sub> gave:

Rose red	25	Tyrian pink and white	2
Cream	6	Tyrian pink and cream	1
Rose pink with rose red center	3	Purple eyed cream	3
Rose red on cream	4	Purple	2
Indian lake	3	Rose red star	2
Pale Indian lake	1	Pink and cream star	1
White and Indian lake center	2	Tyrian red	2
White	16		

Result:	51 Color present	22 Color absent
Expected:	54.75	18.25
Observed:	29 White	15 Cream
Expected:	33	11

46. Rose Red ♂ x Double Cream ♀

The first generation was double purple. A blue factor evidently was introduced by the cream parent. F<sub>2</sub> gave the following series:

Double rose red	4	lilac and white single	1
Single rose red	1	Purple eyed cream double	1
Purple eyed white double	2	Double white	2
Purple eyed white single	1	Single white	2

Indian lake double	1	Double Magenta purple	1
Tyrian pink and white star single	1	Single Magenta purple	1
Result:	11 Double	7 Single	
	14 Color present	4 Color absent.	
Expected:	13.5	4.5	

There were also 10 white, 1 cream.

Expected: 8.25 2.75

47. Red and White Star ♂ x Cream ♀

The first generation gave lilac and white star and also a purple star, a blue factor being introduced by the cream parent.

F<sub>2</sub> gave the following series from lilac, white star:

Cream and pink star	2	White	2
Cream and pink round	1	Cream	1
Rhodamine purple star	7	Rose pink and white	6
Lilac and white star	25	Rose pink and white star	2
Lilac and white round	9	Cream star	4
Lilac and cream	3	White star with lilac flush	7
Lilac and cream star	5	White round with lilac flush	4
Magenta purple star	5	Purple eyed white	1

Result: 57 Star 27 Round

Expected: 63 21

Observed: 56 White 16 Cream

Expected: 54 18

From the purple star F<sub>2</sub> gave:

Violet and white star	1	Pink and white	2
Purple and white star	1	Lilac and white star	4
Purple eyed white star	3	Lilac and white round	2
Purple star	2	Cream and lilac star	1
Pink and white star	3	Cream and lilac round	1

Result:	15 Star	5 Round
Expected:	15	5
Observed:	16 White	2 Cream
Expected	13.5	4.5

48. Double purple ♂ x Cream. ♀

F<sub>1</sub> broke up into: (1) Double dull magenta purples with pomegranate purple center. (2) Double rose red. Purple gave in F<sub>2</sub>:

Double white	1	Double purple	1
Single cream	1	Single purple	1
Tyrian pink and rose double	1		
Tyrian pink and rose single.	1		

The doubles and singles are even, the number probably being too small to show the dominance of doubleness. In color presence there is a dominance over absence: 4 color present; 2 color absent. Expected: 4.5 1.5

Rose red gave in F<sub>2</sub>:

Double rose red	2	Double Indian lake	1
Single rose red	1		

Here is an exact 3 : 1 proportion of doubleness to singleness.

49. Cream ♂ x Red and White star. ♀

F<sub>1</sub> split up into: (1) White star with purple stripes.  
(2) Purple eyed white star.

F<sub>2</sub> of No. 1 broke up into:

White star	2	Jasper pink and cream star	1
Rhodamine purple and rose color star	1.		

Result: 3 white ; 1 cream, 3:1 proportion.

The other hybrid produced only one white plant.



50. Red and White star ♂ x Cream ♀.

The first generation split up into two types:

- (1) Purple lilac and white star
- (2) Amaranth purple star with pansy purple center.

F<sub>2</sub> of No. 1 gave:

Tyrian pink and white star	1	Magenta star white center	1
Lilac and white star	1	Magenta round white center	1

Result: 3 Star 1 Round

3 B factors for blue present; 1 B absent.

Lilac and Magenta contain a blue factor in their make-up, white pink is pure red.

F of No. 2 gave:

Purple star	8	Venetian pink and cream	1
Purple round	1	Cream and purple star	1
Rose color star	3	Cream and lilac	2
Rose color round	1	Purple eyed cream star	1
White star with hortense violet marks	1		

White round with hortense violet marks, 1.

Result: 15 White 5 Cream

14 Star 6 round

Expected: 15 5

51. Double purple ♂ x Cream ♀.

F<sub>1</sub> gave double dark rhodamine purple. F<sub>2</sub> split up

into:

Double amaranth purple	62	Double Magenta white center	
Single amaranth purple	19	Single Magenta white center	23
Double white	38	Double cream	6
Single white	10	Single cream	13
		Double magenta and cream	6
Double violet	11		2

Double white and violet	5	Single magenta and cream	1
Single white and violet	2	Double rhodamine purple and white	11
Double lavender-violet on cream	5	Single rhodamine purple and white	3
Round " " " "	2		
Double lavender-violet on white	2		
Single lavender violet on white	15		

Result: 185 Double	52 Single
170 color present	67 color absent
Expected: 177.75	59.25
Observed: 116 white	29 cream
Expected: 108.75	36.25

52. Cream ♂ x Red and white star. ♀

F<sub>1</sub> gave a white star with rhodamine purple center and purple stripes. F<sub>2</sub> split up into:

Rose pink and white 1 ; Indian lake star 1;

White star pink center 1.

Result: 2 star	1 round
Expected: 2.25	.75

53. Cream ♂ x Purple ♀

First generation was dark rhodamine purple which split up in F<sub>2</sub> as follows:

White 3	Rose on cream 1
Violet 1	Purple 1

Results: White 3 Cream 1

Observed: Color present 4; color absent 3.

Expected	5.25	1.75
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54. Purple ♂ x Cream. ♀

The first generation was rosalane purple. F<sub>2</sub> gave the following series:

Rhodamine purple			36
Dark Magenta purple with amaranth purple center			31
White	15	Red Rose	4
White star	1	Violet on white	12
Purple eyed white	11	Violet on cream	2
Purple eyed cream	6	Dark Magenta purple and white	1
Cream	5	Violet	5
Purple eyed cream star	1		
Rose pink with rose red and white center	8		
Rose pink with rose red and cream center	1		

Result: 114 Color present 21 color absent  
 Expected: 101.25 33.75  
 Observed: 48 White 15 Cream  
 Expected: 47.25 15.75

55. Cream ♂ x Purple ♀

F<sub>1</sub> was rhodamine purple and F<sub>2</sub> split up into:

White	14	Indian lake and white	1
Cream	3	Purple eyed white	2
Purple	12	Rose and Cream	1
Purplish violet	1	Rose red	2
Magenta	3		

Result: 22 color present 17 color absent.  
 Expected: 29.25 9.75  
 Observed: 17 White 4 Cream  
 Expected: 16.75 4.25

56. Violet star ♂ x double cream ♀

The first generation split up into three types:

- (1) Lavender-violet double star
- (2) Double large white star with violet stripes.
- (3) Double white with lavender-violet center.

In F<sub>2</sub> No. 1 split up as follows:

Double violet star	4	Double white	1
Double violet single	3	Double star	4
Double purple eyed cream	4	Indian lake X Cream star	2
Double purple eyed star	5	Double violet star	5
Double purple eyed white	8	Double white X violet "	1
Pansy purple star	1	Single white X Indian Lake	1

Result:	Star	25	Round	14
	Color present	34	Color absent	5
	Double	30	Single	9
	White	28	Cream	11
Expected:		26		13

No. 2 gave in F<sub>2</sub>:

Double purple eyed cream star	3	Double violet X white star	10
Double purple eyed white star	3	Double violet X white single	2
Double purple eyed cream	2	Double white	2
Double purple eyed white	1	Double white Indian lake centre	2
Double cream X violet star	1		
Double cream X violet round	1	Double cream Star	1

Result:	White	20	Cream	8
	Double	26	Single	2
	Star	20	Round	8
	Color present	25	Color absent,	3

Expected:		21		7
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No. 3 gave in  $F_2$ :

Double violet star	2	Double cream star	2
Single violet star	2	Double white	2
Double violet	1	Double white star	1
Double white star with rose purple	2	White single	1
Double white, purple eye	3	Double pansy purple star	1
Double cream, violet eye	2	Single cream and pink	1
		Single lavender-violet and cream star,	1.

Result:	Star	11	Round	10
	Double	16	Single	5
	Color present	15	Color absent	6
Expected:		15.75		5.25

57. Violet star ♂ X Double Cream ♀ .

The first generation showed two types:

1. Double light lavender star.
2. The same color round shape.

No. 1 gave rise in  $F_2$  to the following series:

Single cream, violet centre	3	Single purple star	1
Single lavender violet star	3	Double purple star	2
Single purple eye white	2	Single white star	6
Double purple eye white	1	Double white star	5
Double cream	1	Double white	5
Double cream star	1	Single white	5
Double violet & cream star	1	Double violet star	6
Single purple eyed white star	2	Single violet star	10
Double " " " "	2	Double lavender violet *	4
Double cream & violet "eye "	2	Single " " star	7
Single " " " " "	1	Double cream star	2
" violet eyed cream star	4	Double lavender star	8
Double " " " "	2	Double lavender star	3
Single white, violet center	5	Single cream X violet "	1
Double " " " "	4	Double white star, " flush	1
Double white star, violet eye	1		

Result:	Double	51	Single	50
	Color present	76	Color absent	25
	Star	72	Round	29
Expected:		75.75		25.25
Observed:	White	64	Cream	18
Expected:		61.5		20.5

No. 2 hybrid split up as follows:

Single magenta	1	Single purple star	2
Single lavender violet	10	Double lavender star	1
Double lavender violet	10	Single lavender star	1
Single cream X lavender, violet star	1	Double white	4
Single white & violet eye	4	Single white	1
Double " " " "	5	Single cream	1
Single purple eyed cream	1		

Result:	Color present,	36.	Color absent,	6
	Double,	20	Single,	22
Expected:	31.5		10.5	
Observed:	14 White		3 Cream	
Expected:	12.75		4.25	

58. Violet Star ♂ X Double Cream. ♀

F<sub>1</sub> gave violet purple, double and round.

F<sub>2</sub> gave:

Double Tyrian red	1	Single violet	4
White, violet eye double,	1	Double violet	1
" " " single	2	Double violet star	1
Single white star,	1	Single violet star	1
Double white	1	Single cream	1
Double purple star	1	Single Indian lake & white	1

Result :

	Color present,	13.	Color absent,	3
Expected:		12		4
Observed:	Double	6	Single	10

59. Red White Star ♂ X Cream ♀ .

F<sub>1</sub> split up into two types:

1. Amaranth purple star.
2. White star with purple ring around throat.

F<sub>2</sub> of No. 2 gave the series:

Cream	1	White star	1
Cream with purple ring,	1	Purple eyed white star	4
White with purple ring	3	Purple eyed white round	1
Result:	White 9	Cream	2
	Stars 5	Round	6
Expected:	8.25		2.75

60. Purple Star ♂ X Cream ♀ .

F<sub>1</sub> split up again into a violet and a purple star.

The violet star gave in F<sub>2</sub>:

White and purple eye	5	Violet	1
White and purple star	3	Violet star	1
White star	1	Cream star	1
Tyrian pink star	1	Purple star	1
Result:	Star 8	Round	6
	Color present 12	Color absent	2
Expected:	10.5		3.5
Observed:	white 9	cream	1
Expected:	7.5		2.5

From the purple star only 8 plants bloomed in F<sub>2</sub>:

Purple star	5	Purple round	3
Expected:	6		2



61. Double Purple ♂ X Cream ♀ .

F<sub>1</sub> gave double purple. F<sub>2</sub> split up as follows:

Double purple	37	Double Cream	2
Single "	10	Single "	2
Double cream and lilac	2	Double white	17
Double lilac and dark	3	Single white	12
Magenta & white double	7	Double magenta	4
" " " single	8	Double purple eyed cream	1
Magenta & cream double	2	Double lavender violet & cream,	4
" " " single	2	Single lavender violet & cream	1
Double lavender violet & cream,	4		
Single lavender violet & cream,	1		
Double lavender violet & white	11		
Single lavender violet & white	5		

Result: Double 89 Single 40

Color present 96 Color absent 33

Expected: 96.75 32.25

Observed: White 63 Cream 15

Expected: 58.5 19.5

62. Purple star ♂ X Cream. ♀

A purple star and a magenta star appeared in  $F_1$ .

The purple star gave in  $F_2$ :

Indian lake	1	Magenta	5
Purple star	11	White star	4
Round purple	3	Round white	3
Cream star	1	Cream & pink star	2
Cream round	1	White & pink star	1
White with violet eye	1	Hortense, violet,	1
" " " "star	1		

Result: Star 20 Round 15

White 11 Cream 4

Color present 26 Color absent 9

Expected: 26.25 8.75

The magenta star gave in  $F_2$  the following colors:

White	2	Indian lake on cream	1
Purple eyed white star	1	Cream and lavender star	1
Purple eyed white round	1		

Result: Color present 5. Color absent 2.

Star 3 Round 4

Expected: 5.25 1.75

Observed: White 4 Cream 2

Expected: 4.5 1.5

63. Purple ♂ X Cream ♀ .

F<sub>1</sub> is of a purple color. F<sub>2</sub> gives the following series:

Purple	25	Cream and purple	2
White	13	Red rose star	2
Violet	1	Cream star	1
Violet on cream	1	Rose red round	2
Purple star	1		
Result:	Color present, 34	Color absent,	14
Expected:	36		12
Observed:	White 13	Cream	4
Expected:	12.75		4.25

64. Purple Star ♂ X White ♀ .

The F<sub>1</sub> generation splits up into three types:

1. Violet purple star.
2. White and purplish violet star.
3. Purple star.

In F<sub>2</sub> the first hybrid brings the following series:

White star with purple eye	4
White round with purple eye	1
White with violet centre	1
Hortense violet	1
Result:	Star 5      Round 2
Expected:	5.25      1.75

The second F<sub>1</sub> hybrid split up as follows:

Pale violet star,	115	Violet star	1
Purple eyed white star	5	White star	3
" " " round	7	White & purple violet star,	5
		" " " " round	1
Result:	Star 28	Round 8	
Expected:	27	9	

No results were obtained from the <sup>third</sup> hybrid.

While the color inheritance is in general still of an uncertain nature, there are certain factors that undoubtedly follow the Mendelian law of inheritance.

A number of unit characters might be suggested as taking part in the heredity and make-up of the flower colors of phlox as follows:

C = a color factor, probably a ferment. It acts upon the chromatophores and produces color. Without it a flower is either a cream or white. All other colors are epistatic upon this factor.

B = a factor for bluish violet.

R = a factor for red, forms pink or rose colors. With B it produces purple shades of colors.

I = a factor for intensity of color. It produces the dark colors. Without it the flower colors are pale.

S = a factor producing the star shape.

D = a factor for doubleness. Absence of this character produces singleness.

W = a factor for white, dominant over cream. If it is absent, cream color appears.

E = a factor forming a dark eye in the centre of the corolla.

According to this preliminary hypothesis the different combinations would produce about the following effects:

b r w c =	cream
b r W c =	white
b R w C =	pale red color on cream (pink).
b R W C =	pale red color on white
B R W C =	light purple on white
B r W C =	pale violet on white
B <sub>2</sub> RrW C =	lilac
D <sup>2</sup> B R W C =	pale double purple on white
S d B R W C =	pale single purple star on white
S D B R w C =	pale double purple star on cream
S D B R Wc =	white

I S D B R W C = dark purple double star on white  
E I S D B R W C̄ = dark purple double star with a darker  
area around the centre.

Of these, W, S, D, and C, show good evidence that they follow Mendelian inheritance as dominants over their absence. A large number of plants died during the early parts of experiment, due to some kind of fungous disease in the soil. Therefore the results are not as good as they might have been. A few more crosses were made, but they were not carried beyond the F<sub>1</sub> generation. Seed was also saved from a number of individuals, in order to find a clue, if possible, in the third generation, but owing to lack of space they could not be planted thus far.

#### SUMMARY

1. In Lupinus hirsutus color is composed of two complementary factors, one producing red, the other one oxidizing the red to blue. Absence of both or of the oxidizer gives a white color. In F appears therefore the modified dihybrid proportion 9:3:4.

2. Lupinus Hartwegii follows partly simple Mendelian inheritance, formula 3:1. In some crosses, however, it splits up and the blue seems to consist of a number of unit characters, which in some cases couple and act as one unit. There are 3 factors, C color factor, P factor for pink color, B. factor for blue color. None of them produces color in the flower by itself.

3. In Antirrhinum there exists a complex series of unit characters that determine the color of a flower. There are two series, one based on a yellow underlying color, the other on a white or ivory color. The members of the white series are epistatic on and dominant over the yellow series. In each series the darker color factors are dominant over the lighter colored forms. Ivory is dom-

inant to yellow, pink dominant to ivory, magenta dominant to pink, intense color to light color, and light colored tube to delila. These unit characters all seem to follow Mendelian inheritance.

4. In phlox we have apparently a similar series of colors. The number of color combinations is very large. Corresponding to the yellow and ivory series in *Antirrhinum* we have in phlox two series, one on a cream colored background, the other one on a white background. The white is epistatic and dominant to cream color. Red and violet are dominant to white, purple to red. There is a color factor, probably a ferment, without which colors cannot appear. The star shape is dominant to round shape, and doubleness dominant to singleness.

These results are intended merely as suggestions for further investigation, not as definite conclusions. The number of plants in the different crosses was too small to get any definite results. Some of the facts correspond with those of former workers on the same subjects, and there is every indication that they hold good. Particularly the flower patterns of phlox require a great deal of investigation to learn their relation to each other and their behavior in inheritance. A thorough knowledge of the behavior of the unit characters in the offspring of hybrids is of great importance and is destined to play a great part in the development of new forms of plants. Not only new varieties of flowers can be produced but the agricultural crops can often be improved by judicious crossing with regard to higher yield and increased resistance to diseases.

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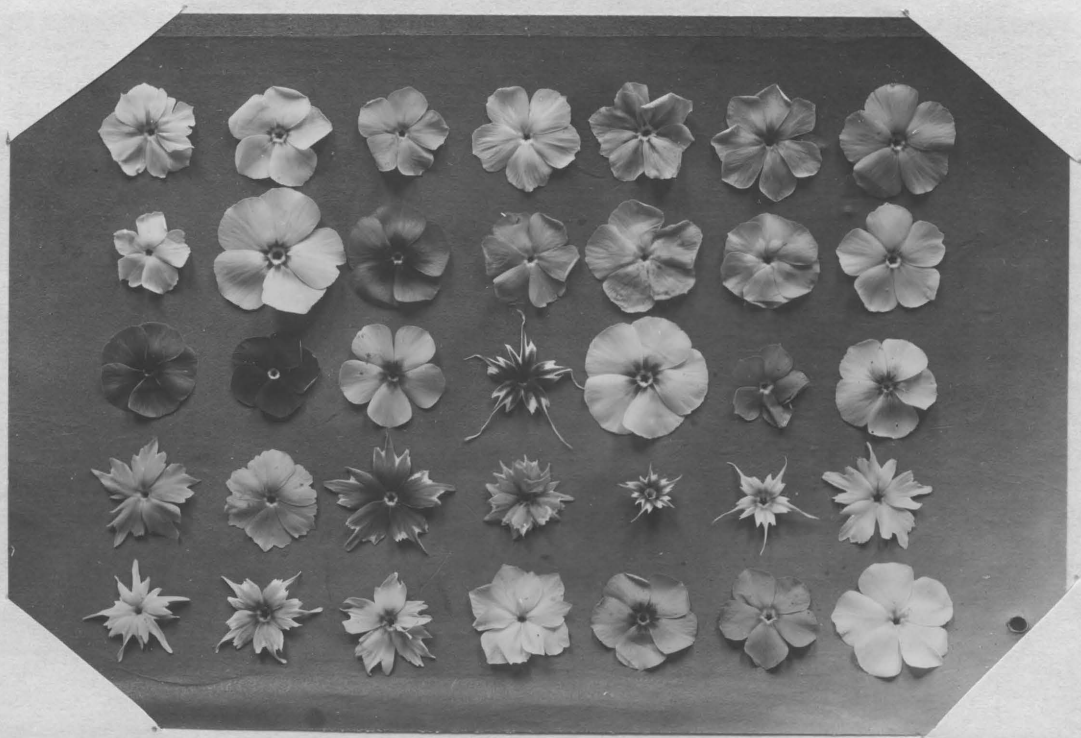
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*Fig. 1. Lupine.*



*Fig. 2. Types of Phlox.*



*Fig 3. Types of Snapdragon.*



*Fig. 4. Types of Phlox.*



*Phlox in Greenhouse. Lupine to the right.*