PLANT HYBRIDIZATION BEFORE MENDEL

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H. F. ROBERTS

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PREFACE

IN the present work it is intended to present, in some fulness and detail, all the significant results obtained in the field of plant-hybridization, down to the discovery of Mendel's papers in 1900. The work of the early hybridists has never hitherto been adequately analyzed and discussed as a whole. Attention has been so concentrated upon Mendelian problems, that the contributions of the precursors of the present scientific period in genetics have been mostly overlooked, and not infrequently underestimated. To bring these contributions out of oblivion, to present them in sequence, and in their relation to one another and to our present knowledge, is the aim and purpose of the writer. In assembling this material, the work of individual breeders upon the improvement of some single species of plant, usually conducted entirely from an empirical or purely practical standpoint, has generally been omitted, those investigators only being included who have contributed in some essential manner to the theory of fertilization and hybridization in plants, and who have thereby laid a foundation for the synthetic development of genetic theory. If Mendel's papers themselves have been analyzed with unusual minuteness and detail, it is because the writer feels that such a thoroughgoing analysis is generally omitted in the current text-books on heredity, and that in a work of this sort, intended to be historical rather than genetic in character and also intended to be useful for reference purposes and to the general reader, it should be his duty to make as complete an exposition as possible of each investigator's contribution. It should be therefore stated that in the presentation of the Mendel material the details have been given with the same thoroughness and simplicity as though the paper were being reviewed for the first time. It was thought by this means to be more nearly possible to bring Mendel's actual work into its deserved relief, too often obscured by brief statement. This will also suffice to account for the simple and elementary re-statement of the dominant-recessive character relations. For a discussion of the extended development of theory and investigation based upon the Mendelian discovery, reference must naturally be made to the various general text-books and handbooks in genetics, and to the multitude of papers in the journals of biological science.

It has been necessary to make frequent use of the resources of various libraries. Appreciation is particularly due the libraries of the University of Chicago, Harvard, the Crerar Library of Chicago, and the library of the Missouri Botanical Garden, for liberal access to works of reference. Especial thanks are due the library of the University of Manitoba for affording every possible means for obtaining material, and for securing the loan of important books.

The writer desires to express especial thanks to Dr. Geo. H. Shull and Dr. E. G. Conklin of Princeton University, for most thorough editorial reading given the manuscript in an earlier draft. Their many constructive suggestions have been largely utilized. For the manuscript in its present form, however, together with any imperfections that may appear, the author is solely responsible.

The subject-matter of portions of the first four chapters has appeared in past issues of the Journal of Heredity, to which acknowledgments are due for the privilege of their reproduction in their present form, and for the use of the accompanying illustrations. The Gärtner material has appeared in part in the American Naturalist. The portrait of Darwin is reproduced by permission of the Cambridge University Press, from Volume I of Professor Karl Pearson's "Life, Letters and Labours of Francis Galton." The portraits of Mendel and of Bateson, and the illustration of the Königskloster in Brünn, are reproduced from the Report of the Royal Horticultural Conference on Genetics, 1906, by permission of the President and Council of the Royal Horticultural Society. The portraits of MM. Louis and Henry de Vilmorin are furnished by the courtesy of Messrs. Vilmorin & Co. of Paris. The portrait of Galton is reproduced by permission from Vol. II of Biometrika. A copy of Sir Thomas Millington's portrait was obtained by consent from the original in the Royal College of Physicians in London. The copies of the Assyrian bas-reliefs in Plates VIII, IX, and X, are photographed from the originals in the British Museum, Nimrud Gallery, Nos. 24, 40, and 2. The portrait of Linnaeus (Plate XV) is from Plate VIII, opp. p. 36, of the collection entitled "Linnéporträtt vid Uppsala Å Universitets Vägnar af Tycho Tullberg, Stockholm, 1907." The younger portrait of Camerarius (Plate XII) is furnished by Professor E. Lehmann of the University of Tübingen, from the oil painting in the library of the University. The portrait of Naudin was kindly obtained by Professor Georges Poirault, of the Villa Thuret, Cap d'Antibes, France, and that of Godron by the Doyen of the Faculté des Sciences of the University of Nancy. To Professor E. Baur of Berlin, acknowledgments are due for valuable biographical material on Sprengel and Focke, and to Professor Correns for a portrait of Wichura. To Professors De Vries, Correns and von Tschermak are due especial thanks for kindly furnishing full accounts of their individual discoveries of the Mendel papers and the Mendelian theory. In conclusion, with regard to the form of the present book, which may be criticized for its considerable volume of quoted material, it should be said that two ways were open;—simply to digest the material and present it without quotation except in very significant instances; or to give liberal extracts from the works themselves, in order to subserve the purposes of research to those desiring access to the actual corpus of material embodied in the works of the early hybridists. In some of the Nägeli and Kölreuter material, for example, the former method was followed, but in general the latter was chosen, even at the risk of creating in part a volume of extracts. It was thought that the real ends of science would be best served in a book of this kind by making it available directly as research material, rather than by sacrificing those ends to the aims of authorship. Hence the resulting rather cumbrous form of the material, which could have been otherwise displayed if the former method had been exclusively followed. It is hoped, however, that the purpose of the book may be allowed to apologize for its resultant form.

H. F. Roberts.

University of Manitoba.
August 2, 1928.

CONTENTS

CHAPTER I

CHAPTER II

CHAPTER III

CHAPTER IV

CHAPTER V

CHAPTER VI

CHAPTER VII

CHAPTER VIII

CHAPTER IX

CHAPTER X

CHAPTER XI

CHAPTER XII

ILLUSTRATIONS

PLANT HYBRIDIZATION BEFORE MENDEL

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PLATE I. Date palms in Mesopotamia.

CHAPTER I

THE EARLIEST DISCOVERIES REGARDING SEX IN PLANTS

1. *Early Experiments in Plant Breeding.*

A FULL discussion of the history of the views, opinions, and discoveries regarding sex in plants is reserved for a later publication. On this account, therefore, the present references to the subject will be necessarily brief.

Exactly where or when man first began to practise the cultivation of plants and to bring them into domestication is not known.

It is certain however, that one of the earliest homes of civilized man was in the lower basin of the Tigris and Euphrates rivers in southwestern Asia, today known as Iraq, the site of the traditional "Garden of Eden."

From four to six thousand years before the present era, and at least fifteen hundred years before the days of the Jewish patriarch Abraham, this region was occupied by an already ancient, orderly and settled people, possessing both cultivated plants and domestic animals. Indeed, there is little reason to doubt that the low alluvial plain fed by the "waters of Babylon" was the scene of one of the first of civilized man's attempts at the improvement of plants, for it is known that the cultivation of the date palm was being carried on in this region during the very earliest times.

2. *Date Culture in Ancient Babylonia and Assyria.*

The history of the date palm typifies better than that of almost any other plant, man's relation to the plant world as a moulder of its cultivated forms.

The fact of the culture of dates in Mesopotamia in ancient times is demonstrated by Babylonian and Assyrian monuments, and was recorded by several of the early Greek historians; the monuments show not only the fact of the culture of the date, but even plainly represent the process of hand-pollination.

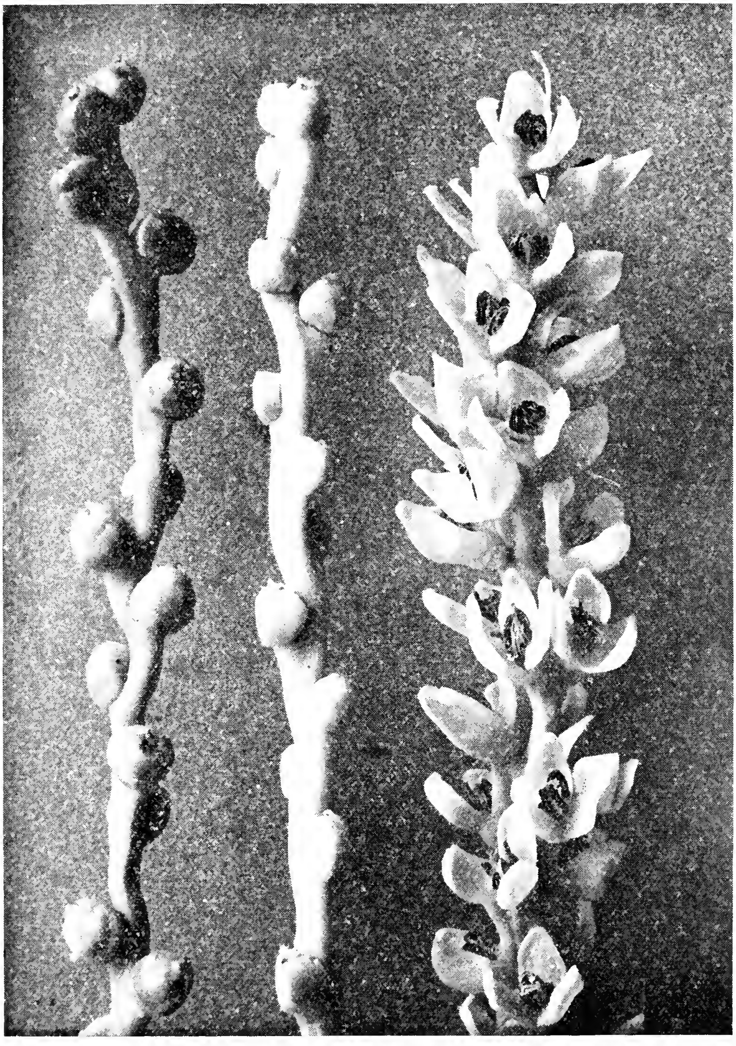

PLATE II. Flowers of the date. *Right* (open cluster), staminate; *left*, pistillate. From U.S. Department of Agriculture, Bureau of Plant Industry, Bull. 53, Plate 7, Fig. 3.

In an Assyrian bas-relief, Ashurbanipal, the Sardanapalus of the Greeks (*circa* 650 B.C.), is represented in his garden, with fruiting garlands of the grape overhead, while to the rear a date palm is represented laden with fruit.

The tremendous economic value of this remarkable tree, even in early times, was attested by a Persian hymn, referred to by Strabo (13),[1] which is reported as having mentioned three hundred and sixty uses for the plant. Later, in the thirteenth century, the celebrated traveller, Marco Polo, speaks of a "city called Bastra (modern Busreh), surrounded by woods in which are grown the best dates in the world."

PLATE III. Date inflorescences. *Left*, staminate inflorescence just emerging from the sheath; *right* (3 figures), pistillate inflorescence in different stages. From U.S. Department of Agriculture, Bureau of Plant Industry, Bull. 53, Plate 7, Figs. 1 and 2.

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[1] Numbers in parentheses refer to the bibliographical list to be found at the end of each chapter.

3. *The Relation of the Date Palm to Plant Breeding.*

It had probably always been recognized, since animals were first extensively domesticated, that the fact of sex lay at the basis of whatever improvement in their characters man could bring about, for the reason that, in animals, "breeding" has always meant the use of superior breeding animals (usually superior males) in crossing. In plants, however, the fact of sex is less evident than in animals, partly because in most plants the sexes are not separated. In the date palm we have at the same time a plant of great economic value in certain regions, and one in which the sexes exist separately as in the higher animals. It therefore

PLATE IV. A young date tree in fruit. U.S. Department of Agriculture, Bureau of Plant Industry, Bull. 271, Plate 9, Fig. 2.

came to be recognized, from very early times, that the date trees were of two kinds, sterile and fruit-bearing, in other words, "male" and "female," and that the product of a sterile "male" tree was needed in order to ensure the bearing of fruit by a fertile "female" tree.

PLATE V. Fruiting branch of the date: Deglet Nur variety, showing the fruiting stalk or peduncle (Arabic "*Sobata*"), and the individual bearing-strands or pedicels, known collectively (Arabic) as the "*Shamrokh*." U.S. Department of Agriculture, Bureau of Plant Industry, Bull. 223, Fig. 12.

Kazwini (6), an Arabic writer on natural history, says of the date: "It is created out of the same substance as Adam, and is the only tree that is artificially fertilized."

The seeds of the date palm produce in about equal numbers male and female trees. The female trees are wind-pollinated, and therefore under natural wild conditions there would easily be enough male trees to fertilize them. Under cultivation, however, the growing of such a large proportion of non-fruiting or sterile trees would be a very wasteful use of the land, and we find that quite early (probably as early as Babylonian and Assyrian times) it was discovered that the pollen from a small number of male trees could be employed to fertilize a considerable number of female trees, by substituting hand-pollination for the natural method. At the present time, according to Swingle (14), the proportion used in planting is about one male to one hundred female trees.

PLATE VI. Demonstration by Arabs of the pollination of the date. Insertion of a sprig of the staminate flowers in the midst of the pistillate cluster. U.S. Department of Agriculture, Bureau of Plant Industry, Bull. 53, Plate 8, Fig. 3.

4. *Variation and Selection of the Date.*

It was soon learned that, when the seeds from the fruits thus obtained by fertilization were planted, the offspring could no more be depended upon to bear fruits like the original, than can the seedlings of budded peaches, apples or pears. As a matter of fact,

Plate VII. Demonstration by Arabs of the pollination of the date. Clusters of the pistillate flowers being tied together to hold the staminate flowers in place. U.S. Department of Agriculture, Bureau of Plant Industry, Bull. 53, Plate 8, Fig. 4.

the seedlings coming from any given variety of date show a very wide range of variation, and it is said that the original parent type seldom re-appears among the seedlings (14).

This diversity of type among seedling dates has led to the establishment of a great number of varieties in cultivation. From four oases in the Sahara alone over four hundred distinct varieties of dates are reported, which differ greatly from one another in many cases, in the size, shape, and flavor of the fruits.

PLATE VIII. Figure of Ashur-nasir-pal, King of Assyria, 883-859 B.C., attended by a winged mythological being carrying pollination basket in left hand, and in the right the staminate inflorescence of the date palm—a ceremonial act. Slab 24, Nimrud Gallery, British Museum.

It is possible to see, therefore, that through the medium of the date palm, at a very early period, the fact was learned of the existence of variation in cultivated plants, a fact which renders selection possible, and in a manner also there was learned the fact of the existence of sex in plants, upon which "plant breeding" is based.

5. *The Discovery of Sex in Plants.*

We have seen that the Assyrians and Babylonians understood

PLATE IX. Assyrian bas-relief. Priest wearing winged apparel and a bird-headed mask, with pollination basket in left hand and staminate inflorescence of date palm in the right. Slab 40, Nimrud Gallery, British Museum.

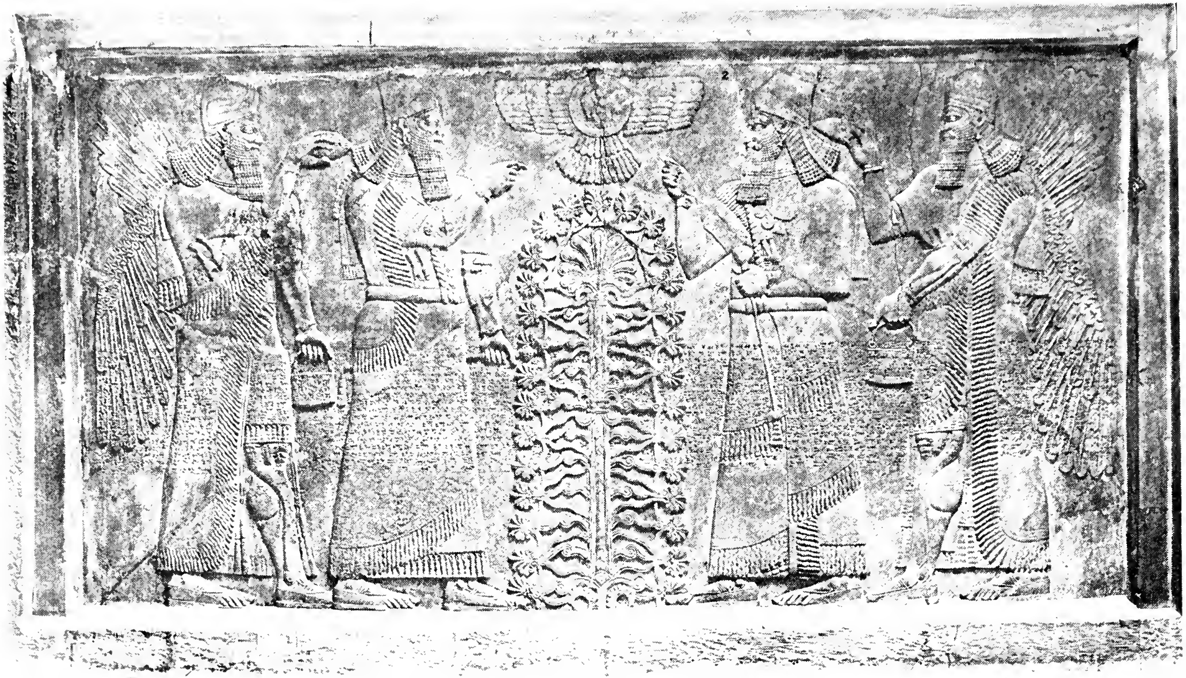


PLATE X. Assyrian bas-relief. Two figures of Ashur-nasir-pal, attended by priests in ceremonial attire, assisting at the pollination rite before a conventionalized pistillate date tree (center). The right hand of each of the priests carries the staminate inflorescence of the date, the left hand holds the pollination tray or basket. Slab 2, Nimrud Gallery, British Museum.

that date palms were of two sorts, male and female, and that they apparently utilized this knowledge in a practical way, by resorting to the artificial pollination of the female trees, in order to make them bear more abundantly. This would naturally give rise to some sort of a conception of sex in the plant as a kind of analogy, but in the absence of evidence of the means and processes of fecundation the conception of plant-sex would be apt to remain long a poetic idea rather than a scientific conclusion. The Arabs, at all events, have continued the practice of the pollination of the palm uninterruptedly down to the present (12b) and, indeed, they seem to have had an idea that the date palm possessed sex somewhat in the same sense in which it exists in the animal kingdom. The Arabic writer Kazwini (*circa* A.D. 1283), to whom reference has already been made, says plainly in the book entitled "Of the Marvels of Nature, and of the Singularities of Created Things":

> "The date has a striking resemblance to man, through the beauty of its erect and slender figure, its division into two distinct sexes, and the property, which is peculiar to it, of being fecundated by a sort of union."

However, the lesson which the date palm might have been supposed to teach, namely, that plants possess sex and that breeding can be conducted with them as with animals, appears to have been lost sight of. Even in those regions where the date was habitually grown, the idea which the long-continued practice of artificial pollination might have suggested—that it was possible to breed and improve other plants in like manner—appears never to have arisen. It would perhaps be thought that the ancient Babylonians, having learned the art of artificial crossing in the case of one plant, would have applied the same process to others. The reason for their failure to do so, however, is explainable. No other economic plants with which they came into contact in their fields were similarly dioecious. They did not, for example, chance to possess an annual species like Indian corn, in which, on one and the same plant, the male and female flowers are in separate inflorescences, in which the pollination is a conspicuous fact, and in which crossing not only can be seen to be continually taking place in nature, but likewise can easily be carried out by artificial means. It is to be remembered that the artificial pollination of the date was practised solely for the production of the fruit and not for the production of seeds or for the purpose of breeding the plant. The breeding of new plants remained a mere matter of chance and was due to the selection of superior bearing trees where they occurred. It is otherwise possible that, if annual grain-plants of the dioecious type had been accessible, further advance might have been made in plant breeding, even at an early period. As a matter of fact however, no lesson was learned from the example of the date palm. The book was closed—and the land of Babylonia, where those whom we may call the first plant breeders lived, became the desert which it remains to this day. Literally, in the words of the Prophet Jeremiah, "Her cities are a desolation, a dry land, and a wilderness."

6. *The First European Investigations on Plant Sex. Camerarius* (1665-1721).

On the 25th of August, 1694, Rudolph Jakob Camerer, Professor of Natural Philosophy in the University of Tübingen, better known under the Latinized name of Camerarius, published a memoir in the form of a letter to a colleague, Professor Michael Bernard Valentin, of the University of Giessen.

This extraordinary "letter" is entitled "De Sexu Plantarum Epistola" (2). It recounts at length the knowledge, slender enough though it was, on the subject which existed up to his time, gives a description of Camerarius' own experimental work, and constitutes the first contribution in the form of an actual scientific investigation into the question of the existence of sex in plants.

The Greek and Roman writers on natural history, Aristotle (1), Herodotus (5), Pliny (11), Theophrastus (15), and others, had commented on the supposed existence of the sexes in plants, even definitely citing the case of the date palm; but the texts report no actual experiments for determining the facts. This latter, therefore, was the contribution of Camerarius.

Camerarius appears to have been the first botanist to discover, by actual experimentation, that the pollen is indispensable to fertilization, and that the pollen-producing flowers or plants are therefore male, and the seed-bearing plants female. The experiments were conducted with *Mercurialis*, spinach, and hemp, all of which are dioecious, and with Indian corn or maize. Camerarius was likewise the first investigator to discover, in the case of maize, two hundred years after its introduction into Europe, the fact that on removing the pollen-bearing flowers from the staminate inflorescence of an isolated plant the seeds remained unfertilized.

PLATE XI. Rudolph Jacob Camerarius, 1665-1721. From Ostwald's "Klassiker der exakten Wissenschaften." No. 105.

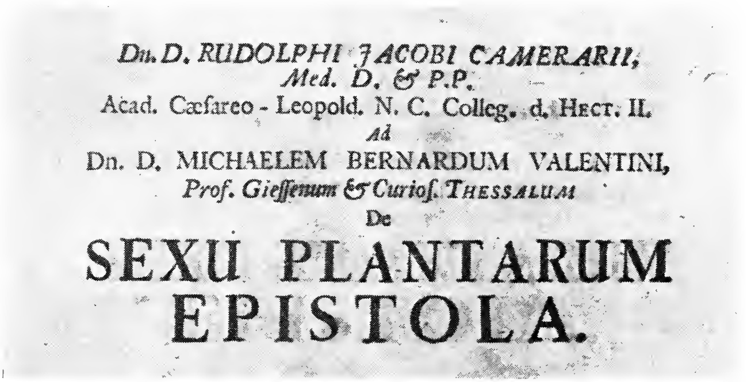
The results obtained by Camerarius with the species mentioned enabled him to deduce the following conclusion regarding sex in plants:

> "They behave indeed to each other as male and female, and are otherwise not different from one another. They are thus distinguished with respect to sex, and this is not to be understood as it is ordinarily done, as a sort of comparison, analogy, or figure of speech, but it is to be taken actually and literally as such." (2c, p. 28.)

PLATE XII. R. J. Camerarius. Younger portrait. From an oil painting in the library of the University of Tübingen.

Camerarius himself did not fail to sense the possibilities latent in the field of hybridization, as the following comment indicates (2c, p. 49):

> "The difficult question, which is also a new one, is whether a female plant can be fertilized by a male of another kind, the female hemp by the male hops; the castor bean from which one has removed the staminate flowers, through pollination with the pollen of Turkish wheat (maize); and whether, and in what degree altered, a seedling will arise therefrom."



Dn. D. RUDOLPHI JACOBI CAMERARII,
Med. D. & P.P.
Acad. Cæſareo-Leopold. N. C. Colleg. d. HECT. II.
Ad
Dn. D. MICHAELEM BERNARDUM VALENTINI,
Prof. Gieſſenum & Curioſ. THESSALUM
De
SEXU PLANTARUM
EPISTOLA.

PLATE XIII. Title-page of the extract from Camerarius' "De Sexu Plantarum Epistola," as printed by Valentin in the Appendix to the "Ephemerides" of the "Academia Caesareo-Leopoldina," 1696.

In this sentence is embodied, though in somewhat odd fashion, an actual scientific conception in the matter, although no experiments on the subject seem to have been attempted by the writer. In this brief paragraph is perhaps revealed, however, the suggestion of a new era of scientific investigation.

It was, nevertheless, more than fifty years before Camerarius' investigations upon sex in plants received substantial recognition, and before the first recorded instance of an actual experiment in hybridization.

7. *Linnaeus.* (1707-1778.)

The relation of Linnaeus to hybridization and the question of sex in plants deserves to be discussed for the sake of the point of view which he expresses regarding the work of Camerarius, as well as for his own contribution to the subject.

In 1759, the Imperial Academy of Sciences at St. Petersburg published an offer of a prize for the determination of the problem of sex in the plant kingdom, as follows:

"Sexum plantarum argumentis et experimentis novis, praeter adhuc jam cognita, vel corroborare, vel impugnare, praemissa expositione historica et physica omnium plantae partium, quae aliquid ad foecundationem et perfectionem seminis et fructus conferre creduntur."

Dn. D. MICHAELIS BERNHARDI
VALENTINI
RESPONSORIA
Ad
Dn. D. RUDOLPHI JACOBI
CAMERARII
EPISTOLAM
De
SEXU PLANTARUM.

PLATE XIV. Title-page of the "Responsoria" of Valentin to the Camerarius Epistola. Appendix to the "Ephemerides" of the "Academia Caesareo-Leopoldina," 1696.

The essay of Linnaeus, entitled "Disquisitio de sexu plantarum," was awarded the prize on September 6, 1760.

Concerning this work, it is stated, in the Praefatio to the "Fundamenta Botanica" published under the editorship of J. E. Gilibert in 1786 (p. viii):

"egregius autor Linnaeus vere novis, variisque experimentis potentiam antherarum seu testiculorum plantae pro foecundatione germinum stabilavit, addit quaedam de hybridis, plurima de motibus voluntariis partium floris."

"To say exactly," Linnaeus remarks, "who first came upon the sex of plants, would be a thing of great difficulty, and of no use." (8c, p. 102.)

The growth of the concept is taken as analogous to the growth of a river, by small, insensible degrees. The fact is alluded to, that the ancient cultivators of palms, figs, and the pistacio (dioecious plants) attained to a certain knowledge of the fact, to the extent that it was found necessary to suspend the male flowers over the females, if fruit was to be obtained. It is noted by Linnaeus, that after the Renaissance, and even in the seventeenth century, botanists in general adhered to the "pristine ignorance"

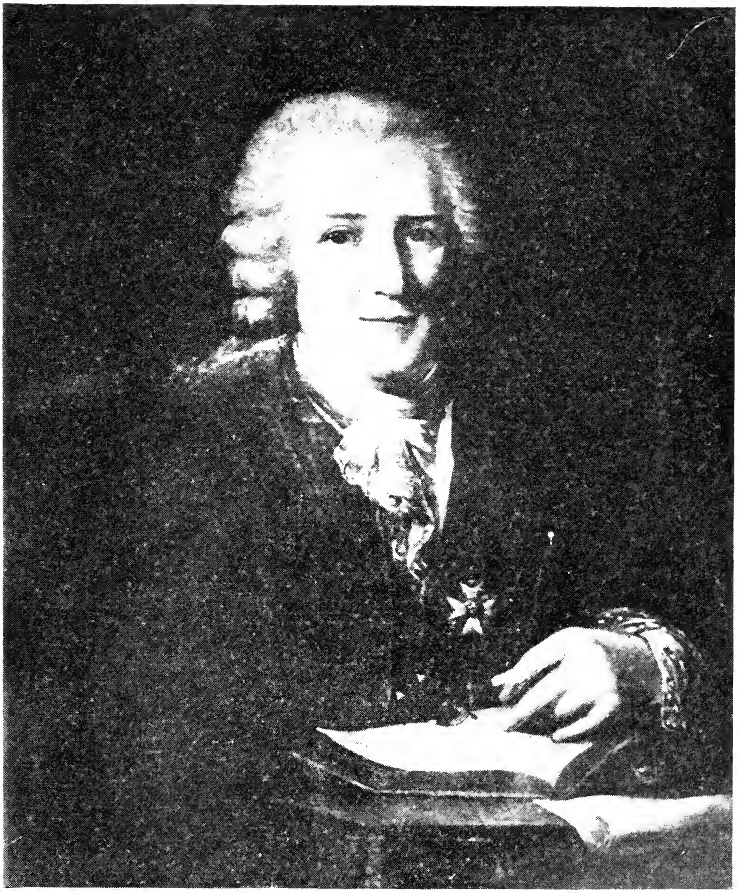


PLATE XV. Carl von Linné, 1707-1778.

IX.

CAR. LINNÆI

Equ. & Archiatr. Reg. &c.

DISQUISITIO
DE
SEXU PLANTARUM

ab Academia Imperiali Scientiarum Petropolitana
præmio (*) ornata
an. 1760. d. 6. Septembr.

CUM ANNOTATIONIBUS

D. JACOBI EDUARDI SMITII
ET
P. M. AUG. BROUSSONET.

Famam extendere factis.

Sexus plantarum antiquiſſimos jam naturæ ſcrutatores latere non potuit, ab hujus vero ævi philoſophis palpari etiam poſſit, oportet. Hoc enim phænomenon adeo in omnibus plantis natura ſpectandum præbet, ut nullum prorſus vegetabile eo carere patiatur.

Ab

(*) Quæ problema: *Sexum plantarum argumentis & experimentis novis, præter adhuc jam cognita, vel corroborare, vel impugnare, præmiſſa expoſitione hiſtorica & phyſica omnium plantæ partium, quæ aliquid ad fœcundationem & perfectionem ſeminis & fructus conferre creduntur*, in ann. 1759. pro præmio propoſuerat.

PLATE XVI. Title-page of the "Disquisitio de Sexu Plantarum of Linnaeus. Prize essay of the Imperial Academy of the Sciences at St. Petersburg, 1760.

regarding sex in plants, although Ray recognized the different sexes in such dioecious plants as *Cannabis*, *Urtica*, *Mercurialis*, *Humulus*, etc., while Tournefort, on the contrary, followed the error of the ancients. Millington is referred to, in the words:

> "they report him to have been the first true discoverer of this doctrine, if indeed it is permissible to call him the discoverer, who perceived something, but did not teach it in public writing." (8c, p. 103.)

It is of especial interest to note Linnaeus' opinion of Camerarius' work, briefly expressed as follows:

> "Rud. Jac. Camerarius and others explained very many things, but no one better than Vaillant, that great botanist of the French, who, in an academic address, edited by Boerhaave, showed himself to have accurately known the matter, although he did not demonstrate it with arguments." (*ib*., p. 103.)

It is of interest to note parenthetically, in the "Sponsalia Plantarum" of Wahlbom (8a), one of the pupils of Linnaeus, the following statement, also made with regard to Camerarius:

> "1695, Rudolphus Jacobus Camerarius, in the 'Epistola de sexu plantarum,' Tübingen, first clearly demonstrated sex and generation, although he was himself not devoid of doubt concerning this truth, which moved him to the experiments which he made with *Cannabis*." (p. 219.)

Of Vaillant, Wahlbom also states, in the same connection, as follows:

> "1718. Sebastianus Vaillantius; discourse concerning the structure of flowers (Lugdun. Batav.). He first truly discerned the sexes of plants, and by many observations placed beyond doubt this mystery of nature, which seemed to all before paradoxical and absurd."

It is, indeed, surprising to find the preference accorded, by a mind like that of Linnaeus, or rather, speaking literally, by Linnaeus and one of his pupils, to the rhetorical discussion of Vaillant over the scientific experimentation of Camerarius. Wahlbom, as a pupil of Linnaeus, probably reflects the latter's view in the matter.

Returning to Linnaeus' "De sexu plantarum":

> "There is," he says, "in certain plants a true difference of sex; these proceed from the seeds of one mother; but certain ones in their flowers show stamens without pistils, and so are rightly called males; others, pistils without stamens, and by right are called females; and this by so constant a law, that never any plant is seen to have borne female flowers, unless other staminiferous flowers were found, either in the same plant, or in different plants of the same species, and versa vice." (*ib*., p. 112.)

Linnaeus contends against the view of Morland and others that the pollen itself enters the stigma, descends through the style, and enters the ovary. This concludes the theoretical portion of the dissertation.

The first experiment which Linnaeus records consisted in removing, "circa vesperam mense Augusti," all the stamens from three flowers of *Mirabilis longiflora*, the other flowers having been destroyed. The flowers emasculated were pollinated with pollen from *Mirabilis jalapa*. The ovules grew but did not mature. (p. 114.)

> "Another evening," he says, "I instituted the same experiment, but pollinated (irrorabam) with the anthers of its own species, and all the seeds matured." (8c, p. 114.)

The next experiment is reported as follows:

> "In the month of January of this year *Antholyza cunonia* bloomed in the window of my room, in an earthen pot, but bore no fruit, because the air, enclosed within the walls, was unable to carry the pollen to the stigma. On a certain day about noon, seeing the stigma absolutely moist, I removed an anther with slender forceps, and lightly rubbed it over one of the expanded portions of the stigmas. The spike of flowers remained for eight or ten days, a fruit developing in that flower from which I had previously removed the anther, and swelling to the magnitude of a bean. This therefore I opened, and saw, in but one of the three cavities, many seeds developing, while the remaining two loculi were absolutely void." (*ib.*, p. 115.)

In the following April, Linnaeus sowed seeds of *Cannabis* in two vessels grown by the window in two different rooms. In one of the vessels, the male and female plants were allowed to grow flowers and bear fruit, which matured in July. The seeds obtained, on being planted, germinated in twelve days. In the other of the vessels, all the male plants were removed, at the age when it was possible to distinguish "the antheriferous males" from the "pistilliferous females." The female plants put forth flowers, the pistils of which lasted unfertilized as long as was required in the other vessel for the fruits to come to maturity, when the pistils, in a quite different manner, immediately withered, after the males had entirely shed their pollen. The unfertilized plants retained their pistils in a green, vegetative condition, and did not wither until when,

> "after a long time, they were exposed to the afflatus of the male pollen. Although the virgin plants produced large calices, these were empty of living seeds. . . . From which I am quite sure that for the hemp deprived

of the male to have borne seeds afterwards, as authors have reported to us, was not effected except by the aid of pollen brought by the wind from somewhere. For no experiment is easier than this; none can be more decisive for demonstrating the generation of plants." (*ib.*, p. 116.)

Datisca cannabina, which had grown for ten years in Linnaeus' botanical garden and had been propagated by perennial roots, produced many flowers, but all females, and hence abortive. (p. 48.)

New seeds were obtained from Paris, and a few tested. These again gave only females, producing flowers without fruits. Finally, in 1757, seeds were again obtained, from which some of the plants came males, flowering in 1758. These were transported to a place as remote as possible from the female plants. When the male flowers were at the point of discharging their pollen, the inflorescence was shaken over a sheet of paper "until the sheet was nearly covered with the yellow pollen." This was placed inverted over the blossoming female flowers. A nocturnal frost in this year injured the *Datiscas* along with other plants; but investigation of the plant, on the flowers of which the pollen had been scattered, showed the rudiments of seeds, whereas in the others not pollinated there appeared no vestiges of seeds. (*ib.*, p. 119.)

Jatropha urens is reported upon as follows: This plant is dioecious. The two sexes flowered annually in the hothouse, but the females preceded the males, dropping their petals or their flowers, eight days before the appearance of the male flowers. Thus, up to the year 1752, no fruit of *Jatropha* was obtained. In this year the male flowers were in a flourishing condition on a taller tree, when another small *Jatropha* set in a pot in the garden began to produce female flowers. This female plant was then set under the staminate tree. This pistillate tree consequently bore seeds which, on being sowed, germinated. On another occasion, pollen of *Jatropha* which had been kept for four to six weeks was used for pollinating three pistillate flowers which had expanded in the meantime. "These three females turned out to be fruit-bearing, but all the rest in the same corymb became abortive." (*ib.*, p. 120.)

This practically concludes the record of Linnaeus' own direct experimental contribution to the matter of sex in plants.

The pollination of the Gleditsch palm in Berlin with the pollen from Leipzig is evidently referred to on page 124, although the species is wrongly given as *Phoenix dactylifera*. Kaempfer's report upon the custom of hand pollination of the date in eastern countries is referred to in the following words:

> "Kaempfer recently reported that it is necessary that oriental peoples, subsisting upon the yield of the palms and the true Lotophagi, transport the male trees to the neighborhood of the females, if they look for fruit." (p. 125.)

Linnaeus concludes by giving an account of four hybrid plants known to have originated in his time:

> "Tres ego, vel quatuor, veras, plantas hybridas meo primum extitisse tempore his oculis vidi, quas ordine enumerabo." (p. 125.)

The *Veronica maritima* ♀ × *Verbena officinalis* ♂ (see p. 27 below) is referred to as resembling the female parent in the fructification, the male parent in the leaves ("fructificatione matrem tota quanta refert, foliis patrem"). (p. 126.)

Omitting the references to a *Delphinium* and a *Hieracium* hybrid, both of which occurred spontaneously, the case should be noted of the hybrid *Tragopogon*, resulting from a cross made by Linnaeus between *Tragopogon pratense* ♀ × *Tragopogon porrifolius* ♂. The history of this hybrid, of which seeds were sent to the St. Petersburg Academy at the same time as the dissertation, is as follows:

Linnaeus states that he made the cross mentioned above in 1757, "in areola horti," where he had planted the two species.

> "I obtained *Tragopogon hybridum* two years ago about autumn, in a small enclosure of the garden, where I had planted *Tragopogon pratense* and *Tragopogon porrifolius*, but the winter supervening destroyed the seeds. Early the following year, when *Tragopogon pratense* flowered, I rubbed off the pollen early in the morning, and at about eight in the morning I sprinkled the pistils with pollen from *Tragopogon porrifolius* and marked the calices with a thread bound around them. From these, towards autumn, I collected the mature seeds, and sowed them in a separate place, where they germinated, and in this year 1759, gave purple flowers with yellow bases, the seeds of which I now send." (pp. 126-7.)

Linnaeus finally concludes with the naïve observation:

> "I do not know whether any other experiment would show generation more certainly than this one itself." (p. 127.)

Hybrid fertilization thus appears to Linnaeus as a new field opened up to botanists,

> "in which, with the pollen of diverse plants upon diverse females . . . they may attempt to effect new species of vegetables. And if I observe this to be not displeasing, the more will my mind be aroused, for that period of life which is left to me, to be consecrated to these experiments, which recommend themselves both in virtue of their attractiveness and by their great usefulness. For, led by many reasons, I am of the opinion that the many and prominent varieties of plants in use in the kitchen have been produced by that kind of generation, such as the numerous *Brassicas*, *Lactucas*, etc., and therefore have not been changed by their location. Wherefore I am unable to have confidence in that rule which holds that all varieties arise from the diverse nature of the soil; for if it were true, plants indeed, when they are changed to new places, would recover their pristine aspect." (p.129.)
>
> "It is impossible to doubt that there are new species produced by hybrid generation. From all these things, we learn that the hybrid is brought forth, as to the medullary substance or the internal plant or fructification as the exact image of the mother, but as to its leaves and other external parts it is as that of the father. These considerations, therefore, lay down a new foundation for the students of nature, to which many things contribute. For thence it appears to follow, that the many species of plants in the same genus in the beginning could not have been otherwise than one plant, and have arisen from this hybrid generation." (pp. 127-8.)

In a dissertation entitled "Fundamentum fructificationis," October 16, 1762, appearing as No. 8, in the "Fundamenta Botanica" (Vol. 1, pp. 169-214) 1786, (8d), by Johannes Mart. Gråberg, one of Linnaeus' pupils, appears the following:

> "That in the vegetable kingdom it is admitted that hybrid generations exist, although rarely, see, from the 'Amoenitates Acad.' (t. 3, p. 28) of our President, his solution of the St. Petersburg question concerning the sex of plants, Petrop. 1760. A most satisfactory example of this fact we have seen this summer in the Academic Garden; here for several years in the same bed grew *Verbascum thapsus*, and *Verbascum lychnitis*."

The origin of the presumed hybrid between these two species appears to have been spontaneous, since the plant in question seems to have come from naturally fertilized seeds of *V. Lychnitis*, and was identified by Linnaeus with the specimen which Agerius, one hundred or more years previously, had sent to Joh. Bauhin, who gave the plant the name of "*Verbascum angustifolium ramosum, flore aureo, folio crassiori*," in his "Historia" (p. 856). Linnaeus' plant is described as being similar to the female parent in the branched stem, the filaments of the flowers, and in the other parts of the inflorescence, but resembling the pollen parent in size, in the calices, and in the somewhat decurrent leaves, which were yet not so much so as in the male parent. Gråberg concludes that:

> "All the observations concerning the generation of hybrid plants, which we have hitherto instituted, show manifestly the interior plant or fructification, to be similar to the mother, the exterior plant, however, or 'mask,' to repeat the image of the father." (8d, p. 293.)

Again it is stated:

> "It is indeed true that numerous hybrid plants do not propagate the species through the seeds, but it nevertheless does not follow that all hybrids are sterile. For that new Tragopogon which our President produced and described in the St. Petersburg discussion, is propagated annually from the seeds." (*ib.*, pp. 293-4.)

The general conclusion regarding hybrids follows:

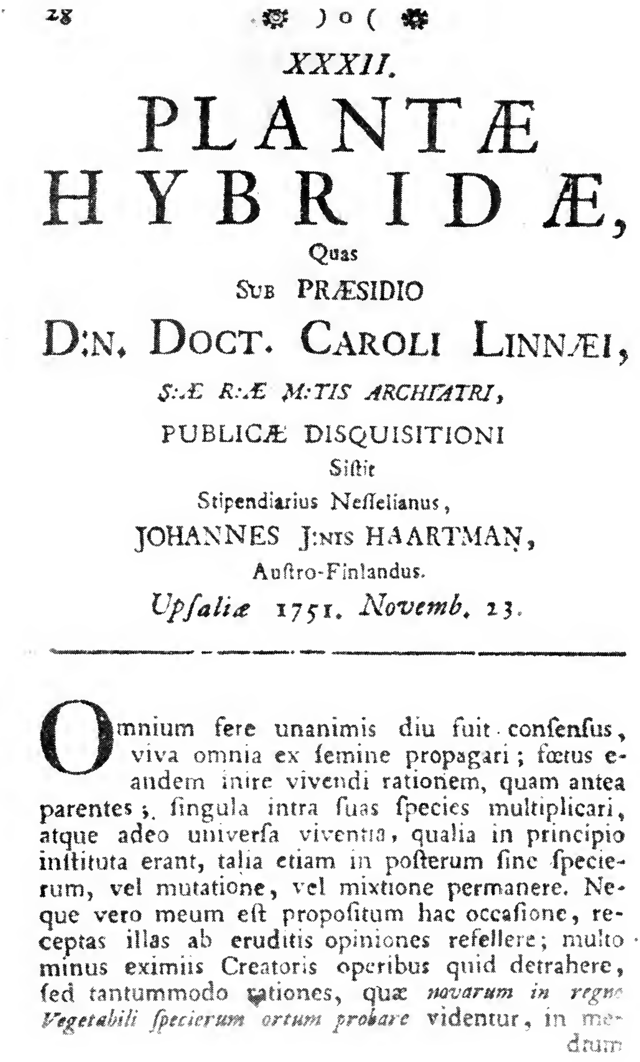
> "In a word, when the stigmas of any plant are sprinkled with foreign pollen, in some cases nothing occurs; where such fecundation succeeds, there proceed from these seeds when sown, plants called hybrids, which, in the fructification, re-image the mother; in the plant, however, most strongly the father. These hybrids, thus born, are either fertile, as *Delphinium aconiti*, *Tragopogon hybridum*, etc., or persist simply sterile like mules, and if they flower they nevertheless produce no seeds, as *Verbascum Thapsus*, *Veronica Verbenae*, etc. The flowers of these sterile plants being examined, the anthers are observed to be sterile, destitute of any pollen." (*ib.*, p. 294.)

An interesting experiment of Linnaeus upon the banana is then recounted as follows:

> "*Musa Paradisiaca*, from its spadix, produces first female flowers; then at length the males; the fruits of this *Musa*, before they flower, have almost attained their proper size, and thereafter they are matured without any seed contained within the fruit. Hence it was said that *Musa* is the only plant known, which is destitute of seeds, and is multiplied by human means by dividing the roots. Accordingly, the President hoped at some time to obtain two *Musa* plants flowering at about the same time, so that he might fecundate the precocious female flowers of the one with the pollen of the male flowers of the other, which he did three years ago. When indeed he removed the anthers from the male flowers for pollinating the pistils of the other, he observed all these anthers in the male flowers to be altogether destitute of pollen. Hence he concluded *Musa Paradisiaca* to be purely a hybrid plant, sprung perchance from *Musa Bihai* as the mother, and from an undeterminable Indian father." (*ib.*, p. 294.)

On November 23, 1751, appeared a discussion, included in the "Amoenitates Academicae" (vol. 3, pp. 28-52, 1764) by another of Linnaeus' pupils, Johannes Haartman, entitled "Plantae Hybridae." (8b.)

This discussion upon hybrid plants is to be noted, insofar as it reflects the views of Linnaeus and his school on the subject.



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XXXII.

PLANTÆ HYBRIDÆ,

Quas
SUB PRÆSIDIO
D:N. DOCT. CAROLI LINNÆI,
S:Æ R:Æ M:TIS ARCHIATRI,
PUBLICÆ DISQUISITIONI
Siſtit
Stipendiarius Neſſelianus,
JOHANNES J:NIS HAARTMAN,
Auſtro-Finlandus.
Upſaliæ 1751. *Novemb.* 23.

Omnium fere unanimis diu fuit conſenſus, viva omnia ex ſemine propagari; fœtus eandem inire vivendi rationem, quam antea parentes; ſingula intra ſuas ſpecies multiplicari, atque adeo univerſa viventia, qualia in principio inſtituta erant, talia etiam in poſterum ſine ſpecierum, vel mutatione, vel mixtione permanere. Neque vero meum eſt propoſitum hac occaſione, receptas illas ab eruditis opiniones refellere; multo minus eximiis Creatoris operibus quid detrahere, ſed tantummodo rationes, quæ *novarum in regno Vegetabili ſpecierum ortum probare* videntur, in me-

dium

PLATE XVII. Title-page of the "Plantae Hybridae" of Johannes Haartman, 1751.

The dissertation (Latin) opens with a somewhat brief philosophical discussion of hybrids, particularly from the viewpoint of whether or not "new species" could arise from genera. Cases are given of 17 bigeneric crosses, 17 congeneric, 6 where congeneric crosses gave rise to aberrations, such as crisping of the leaves, etc., and 7 in the case of genera where the parentage is uncertain.

Veronica maritima ♀ × *Verbena officinalis* ♂ is described in the greatest detail (p. 35), and is illustrated. (8b, pl. 11.) This natural hybrid is reported as having been produced in the Botanical Garden at Upsala in 1750. The statement is made "neque longe ab his lecta est haec nostra planta ♂, quae antea nulli Botanico visa est." (p. 35.) The vegetative and flower characters are described in some detail. The hybrid was perennial, bloomed annually, and was multiplied easily by the roots, but had no fruit ("nullos vero fructus maturat"). (p. 35.)

This particular hybrid appears to have been derived from a but slightly related parentage, viz., from the families Scrophulariaceae and Verbenaceae, respectively, belonging to the different subgroups Solaninae and Verbeninae of the Tubiflorae. Since its occurrence was made a subject for description, and since the date of its appearance, and the observation of its characters (1750) precedes by ten years the hybrid *Nicotiana paniculata* ♀ × *N. rustica* ♂ produced by Kölreuter in 1760, it is of interest to publish the historical account, although as a matter of scientific fact the Kölreuter hybrid marks the actual beginning of the genetics investigation series.

The description of the plant is as follows:

In height, hoary color of the stem and leaves, smoothness of the stem, structure of the spike, and color of the corolla, the plant is stated to resemble the *Veronica* ♀ parent. If the flowers and their color and the roundness of the stem were omitted, "the most acute botanist would have considered it to be *Verbena* itself" (p. 35); the leaves of the hybrid are said to have had "exactly the same singular division, with deeply furrowed lobes" (p. 35). The flowers are stated to have been smaller than those of the female parent, and not larger than the flowers of *Verbena*; the leaves "sometimes in threes, as in the ♀ but more often oppo-

PLATE XVIII. Linnaeus' hybrid, *Veronica maritima* x *Verbena officinalis.*

site as the ♂." Although the plant flowered annually, it was sterile, and bore no fruit, but was perennial and multiplied by the roots.

> "Floruit quidem haec planta omni anno felicissime, in annum quo haec edimus, 1755, et vivis radicibus facillime immutata multiplicatur, nullos vero fructus maturavit." (p. 35.)

It thus appears that Linnaeus' hybrid *Veronica*, originating in 1750, was still alive in 1755.

Another hybrid, between *Verbena hastata* ♀ and *Verbena spuria* ♂ is stated to have originated naturally in the Botanical Garden in 1748, perishing two years later. It is recorded as arising in the same bed with the two species named above,

> "but not through dissemination, considering that no one had the seeds here hitherto, nor through a planting of it, since it had not previously been seen within the country." (p. 43.)

The first description of the hybrid between *Trifolium repens* ♀ and *T. pratense* ♂, the now so well-known and widely-grown "alsike clover" (*T. hybridum*) is given by Haartman (p. 44). This hybrid is stated to have originated not only near Upsala, but also near Aboa, "where I gathered it the past summer" (1751). The description states:

> "The white flower likewise commonly displays a purplish color, in which it approximates to the father by as much as it recedes from the mother. Besides, it bears the fructification of *Trifolium album* ♀ with all its properties."

The account concludes:

> "Paucis locis obvia est haec planta, nec veteribus nota, quod videtur esse signum illam haud ita pridem generam fuisse." (p. 44.)

Perhaps the first exact description, aside from Kölreuter, of intermediate characters in a hybrid, is also given by Haartman (p. 48), in the description of a hybrid *Thalictrum* referred to as a "new plant recently seen in the academic garden." The number of the stamens is given as 40, and of the pistils, 8; those of the female parent being 60 and 16, and of the male parent, 16 and 7, stamens and pistils, respectively; the hybrid was therefore intermediate.

A hybrid, *Helianthus multiflorus*, between *Helianthus annuus* ♀ and *H. tuberosus* ♂, is described as having fibrous roots like the ♀ parent.

In all, Haartman gives a list of 100 hybrid plants, of which descriptions are given in the case of 59. The cases most noteworthy from the historical standpoint have been cited.

On June 11, 1746, appeared, as Dissertation 9, in the "Fundamenta Botanica," the "Sponsalia Plantarum" (8a) of Johan. Gustav Wahlbom, one of Linnaeus' pupils, which undoubtedly also represents the ideas of Linnaeus himself. Since this essay consists entirely of a general discussion upon the sex of plants, it will not be necessary to take it into consideration here.

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"	2,	Holmiae (Holm), Salvius,	1762
"	3,	" " "	1764
"	4,	" " "	1759
"	5,	" " "	1760
"	6,	" " "	1763
"	7,	" " "	1769
"	8,	Erlangae (Erlangen), Schreber,	1785
"	9,	" " "	1785
"	10,	" " "	1790

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CHAPTER II

8. *Kölreuter* (1733-1806).

CAMERARIUS' memoir fell on sterile, or rather on unprepared soil. Over half a century elapsed before one was found to speak his praise as follows:

> "Rudolph Jacob Camerarius is indisputably the first who proved the sex of plants through his own experiments instituted from this point of view. He, my fellow countryman, it is whom the learned world has principally to thank for this great truth, which is so general, and of such great influence upon the physical and economic sciences. Camerarius it was, who criticised in the most fundamental way everything of this material, as well that which was found in the oldest as in the newest writings of his time; compared them with one another and, together with a quantity of his own observations and useful applications, whereby the theory of this truth has now been strengthened, laid the matter before the learned world in a letter to Mich. Bernard Valentin."

These were the words of Joseph Gottlieb Kölreuter. From the 25th of August, 1694, the date of Camerarius' letter concerning his experiments upon sex in plants, until September 1, 1761, there was made no fundamental progress in the real scientific knowledge of the phenomena of inheritance. On this latter date appeared Kölreuter's "Preliminary Report of some Experiments and Observations concerning Sex in Plants." This report was followed in 1763, 1764, and 1766, by three supplementary papers on the same subject, which record the results of 136 distinct experiments in the crossing of plants.

If Camerarius made the actual scientific discovery concerning sex in plants, Kölreuter was the first to give to this discovery scientific application. He was born April 27, 1733, in the Swabian village of Sulz, in the valley of the Neckar, in the Black Forest region of Southwest Germany. From 1760 to 1764, he conducted his experiments, partly in his native village, partly in the garden of a physician, Achatius Gärtner, in the town of Calw in Würtemberg, and partly in St. Petersburg, Berlin, and Leipzig. From 1764 until his death in 1806, he was Professor of Natural His-

Plate XIX. J. G. Kölreuter, 1733-1806.

tory in the University of Karlsruhe. At Sulz, in 1760, Kölreuter produced the first plant hybrid obtained in a scientific experiment.

Kölreuter's most important papers, his "Vorläufige Nachricht," and its three "Fortsetzungen" (1), cover a reported period from 1760 to 1766. In the former year, Kölreuter secured his first hybrid, *Nicotiana paniculata* ♀ × *N. rustica* ♂. The experiments during the following six years, numbering 65 definitely described, covered crosses involving 13 genera and 54 species. Before taking up these experiments in detail, and especially those of genetic interest, it will be well to deal with Kölreuter's views or conclusions with respect to the fertilization process and hybridization. In the first place, it will be understood that Kölreuter worked with the microscope. Sprengel indeed remarks, regarding the former's study of pollination in *Asclepias*, that some of the observations therein he himself had not been able to make. "Da ich kein so gutes Vergrösserungsglas zur Hand gehabt habe, als Kölreuter." (2, 1 : 165.) It is desirable also to remember that Kölreuter not only carried on his investigations upon hybrids, but made extensive observations upon pollination. Indeed it is possible that Sprengel's title for his work "Das entdeckte Geheimniss der Natur," (1793) may have been suggested by Kölreuter's remark, "Gewiss ein jeder anderer, der vor mir diese Betrachtungen angestellet hätte, würde sie längst entdeckt, und sich und allen Naturforschern von diesem Geheimnisse der Natur den Vorhang längst weggezogen haben." (p. 21.) Kölreuter himself alludes to his use of a "Vergrösserungsglas," in his search for the stigmatic surfaces in *Iris* (1, p. 22), and in the examination of the pollen in his first *Nicotiana* hybrid. (p. 31.)

Kölreuter considers that the pollen is a collection of organic particles, which have a definite form in every plant. In structure, the pollen grain consists of an outer thick membrane or rather of a hard and elastic shell, upon which, at equal distances apart, are found the "excretion-canals" and openings for escape of the male fertilizing material. In the species in which the pollen grains are beset with projections, these excretion-canals are in the projections themselves, being found at their apices. Within the elastic shell, there is stated to be a netlike mass of vascular fibres which, in some species, is arranged in almost regular hexagonal fashion; in others, in some other more or less regular way.

> "Through the substance of this elastic shell," says Kölreuter, "one sees an extended net of vascular fibres which, in a few species of pollens, is divided off into almost regular six-sided eyes, in others in another more or less regular way." (p. 7.)

Each such division or "eye" serves as the point of location for one of the elevations or projections, in which an excretion-canal terminates. Immediately beneath the outer shell is a thinner, weaker, white membrane, beneath which is

> "an apparently cellular tissue, which fills the entire cavity of the pollen grain and is, as it were, the nucleus (Kern) of the latter." (p. 8.)

It is probable that the Kölreuter idea would be better translated by the word "kernel" than by the word "nucleus," with its modern connotations. This material or substance which, in the unripe condition, is described as granular, firm and half-transparent, finally at maturity passes over into a uniform, fluid, and transparent material, which comes out of the "cellular tissue." The words "cellular tissue" (zellenförmiges Gewebe) must likewise not be taken in the sense of "tissue-cells," but in the sense of a body or mass of something, enclosed in a cell-like envelope. Nothing more definite than this could possibly have been seen by Kölreuter. The tube and generative cells, the only "structures," visible within the pollen grain through the walls of the exine, that could possibly be taken in any sense as "cellular," may have been visible to Kölreuter's microscope. In this "tissue," at all events, is said to be found the entire mass of the male fertilizing material.

The divisions or "eyes," thought by Kölreuter to be *within* the "elastic shell," are evidently the more or less geometrical reticulations on the outer surface of the exine of the pollen grain in many species. The escape of the contents of the pollen grains is considered to be brought about by the contraction and pressure of its thick outer coat. In consequence of this pressure, the contents are expelled through the "excretion canals" on all sides at once. The swelling of the pollen grain is presumed to take place through the absorption of water. With the beginning of maturity of the contents of the pollen grain, the inner coat acquires firmness and elasticity and, by virtue of this, presses from all sides upon the fertilizing material within, which has now become fluid, and forces it into the place of least resistance, the open excretion canals.

(p. 8.) This is the character of the pollen grain and the manner of its germination as Kölreuter conceived it.

The male fertilizing material, as well as the secretion upon the stigmas, is considered to be of an oily nature. These two secretions commingle with one another, when they come together, in the most intimate manner and make, after commingling, a uniform mass, which, when fertilization ensues, is sucked in by the stigma, and must be conducted through the style to the ovules,—the so-called "seed-eggs" (Saameneyern) or unfertilized "germs" (Keimen). Kölreuter recognizes that a certain number of pollen grains are required for fertilization in every flower, but this number, in comparison with the number produced, is very small. Kölreuter remarks that, in a *Ketmia* flower of average size, 4,863 pollen grains are produced, but that, for the fertilization of the 30-odd seeds in a single capsule, not more than 50-60 pollen grains are required. He found that, the more the number of pollen grains fell below this number, proportionately fewer were the number of seeds produced. If as few as 15 or 20 pollen grains were used, only 10-16 seeds were fertilized. (p. 12.) It was found, moreover, that with this small number of pollen grains the seed capsule after a time began to wilt, and finally fell off. If fewer than 10 pollen grains were used, "then it was just as though I had taken none at all." No trace of fertilization followed, and the ovary degenerated and fell off, in still less time. This experiment tallies closely with the preceding one, in demonstrating that, in the species in question, about two pollen grains are required on the average per ovule, making allowances for the failure of some grains to germinate, and for the failure of the pollen tubes of others to reach the ovary. These latter details were entirely unknown to Kölreuter, who believed he was dealing with a mass effect. In the common *Mirabilis jalapa* the number of pollen grains reached 293, and in a Peruvian species, 121; but of this number but one, or at most two or three, were required for fertilization. Kölreuter found by experiment that in a plant with 2-5 stigmas, by abscission of all but one, and pollinating that one "with a sufficient quantity of pollen" (p. 13), ripe seeds developed in all the cells of the ovary. He states this was found even to be the case in plants in which the stigmas were separated to the base, as in *Paris*. This was so also in *Hypericum* he says, in which each of the five separate stigmas is directed outward toward its own cell of the ovary. Kölreuter made rather extensive examinations of the pollen grains of several hundred genera, and comments on their form and relative sizes. He remarks on the fact that, in almost all grasses, the stigmas are self-pollinated within the closed flower. He comments at some considerable length upon the manner of pollination of a number of species, and especially upon the fact of pollination by insects. Regarding the activity of insects in fertilization, the only example thus far known, he says, is the fig tree:

> "Is it then," he continues (p. 19), "something so wholly exceptional, if Nature, for the maintenance of certain creatures, makes use of others which have no resemblance with them. Experience has taught me precisely the truth of this, that has long been maintained for the fig tree, and for the case of many other and in part very common plants. In all the Cucurbitaceae, in all the Iridaceae, and with not a few plants from the order of Mallows (Malvaceae), fertilization of the female flowers and stigmas occurs only through insects."

In speaking of the fact that cucumbers and melons, confined within hot-beds, do not set fruit, he says:

> "Up to the present day one has ascribed to the wind the pollination of the female flowers; but one would necessarily have had to come to other ideas, if one had only brought the location of the male and female flowers, their form, and the structure of the pollen into closer observation." (p. 20.)

He then continues:

> "And how can one do this, without immediately finding the cause of the pollination in those busy creatures (i.e., the insects). Certainly, any other one, who before me had instituted these observations, would have long since discerned them, and have drawn aside the curtain of this secret of Nature for himself and all investigators of Nature." (p. 20.)

Kölreuter investigated the pollination of the *Iris* (pp. 22-4), and describes with scientific and minute exactness the details of his discoveries. He was apparently the first to discern the actual location of the stigmatic surfaces, in the triangular area toward the apices of the leaf-like so-called stigmas, the inner surfaces of which he found to be covered "over and over with pointed papillae" smeared with a moist secretion.

> "I did not let the matter rest there," he says, "but instituted very many experiments thereupon, which finally completely convinced me that this small part is the true stigma in these plants." (p. 23.)

The opening of the flower, and the relations of the several parts, are described at some length, and the pollination discovered to be by means of humble-bees.

From his experiments with the Iridaceae and Malvaceae, Kölreuter concludes:

> "I have instituted very many and various experiments and observations, which have completely convinced me that the pollination of the stigmas (in the two groups mentioned) is not to be ascribed either to the location which the parts of the flower have to one another, nor to the wind, but simply to the insects alone." (p. 25.)

Kölreuter also comments on the fact that:

> "If one takes away at the same time from a certain number of flowers their still closed anthers, yet their stigmas will always be covered over with a sufficient quantity of pollen, which the insects carry thither from other flowers standing in the neighborhood." (p. 27.)

Thus concludes the general botanical discussion in Kölreuter's first Nachricht, which occupies a space in the Oswald edition of 28 pages, and which has been discussed at length because it is seldom commented upon, and because it shows the preliminary preparation for his hybridization experiments which Kölreuter obtained through natural history investigations at first hand.

The development of the pollen tube was not known in Kölreuter's time, having been first observed by Amici in *Portulaca* in 1823; the penetration of each pollen tube into the ovary and to the micropyle of the ovule, by the same investigator in 1830; and the development of the embryo from an egg cell already present in the embryo-sac before the arrival of the pollen-tube, which stimulates it to further development, also by Amici in 1846. (Sachs, "Hist. of Bot.," 432.) The number of 50-60 pollen grains, found by Kölreuter by experiment to be the minimum number requisite for the fertilization of the 30 or so seeds in a capsule, represented to Kölreuter's mind in a manner the mass amount of the "exudate" required. This latter was supposed, as stated, to be excreted by compression from the maturing pollen grain upon the stigma, there absorbed, and drawn through special conduction or secretion canals into the interior of the ovary.

One can, Kölreuter continues (p. 21), by exposing the female flowers to the wind, while excluding the approach of insects, convince himself, through the immediately succeeding death of the ovary, that pollination in such plants could not occur by means of the wind. Kölreuter then describes, in very considerable detail, the pollination process in *Iris*, in the mallows, and in the water-lilies. In *Argemonè*, *Hypericum*, *Oenothera*, *Epilobium*, *Polemonium*, *Echium*, *Hyoscyamus*, *Nicotiana*, *Antirrhinum*, *Scrophularia* and others, certain details of the pollination process are more briefly remarked upon. The general discussion of pollination concludes as follows:

> "Everywhere, insects are always involved, in the case of plants in which pollination does not ordinarily occur through direct contact; and they have the most to do with their pollination, and consequently also with their fertilization, and probably they furnish, if not to all plants, at least to a very great part of them, this uncommonly great service: for almost all flowers belonging here carry something with them that is agreeable to insects, and one will not easily find one of them with which they are not to be found in quantity." (p. 28.)

Kölreuter now begins his discussion of hybrids. Many so-called hybrids are probably products of the imagination. There are perhaps scarcely any among them which might rightly deserve this name.

> "How can one give them out with certainty as such," he says, "before one has produced them through art and, indeed, through the most unremitting experiments." (p. 29.)

The First "Mule Plant."

In rather naïve fashion Kölreuter describes the reasons which led him to experiment upon the breeding of plants. He calls attention to the fact that man has brought together, in botanical and zoölogical gardens, plants and animals from all quarters of the earth. With animals, this has given rise to the possibility of making hybrids. The history of Kölreuter's first hybridization experiment is given as follows:

> "As improbable as it is, that of two different kinds of animals, which have lived in their natural freedom, a hybrid should ever have been produced, so improbable is it also that, in the orderly arrangement that nature has made in the plant kingdom, a hybrid plant should have arisen. Nature, which always, even in the greatest apparent disorder, adheres to the most beautiful order, has precluded this confusion, in the case of wandering animals, aside from other means, through the natural instincts, and in the case of plants, in which their all too close proximity, the wind, and insects, give a daily opportunity for an unnatural intermixture, she will without doubt have known, through just as certain means, how to take away their force from the operations to be feared therefrom. Presumably, aside from the natural instincts, they are just the same as occur with animals. Perhaps it has also been one of her designs to preclude such a disarrangement to be feared therefrom, that

she has transferred one plant to Africa, and assigned to another its place in America. Perhaps in part for this reason it has happened, that she has enclosed within the boundaries of a certain region only such plants as, in regard to structure, have the least resemblance amongst themselves, and which, consequently, are also least qualified to cause a confusion amongst themselves. If these conjectures have their foundation, as I almost believe, then, in the botanical gardens, where plants of all kinds and from all parts of the world, are together in a narrow space, hybrid plants will probably be able to originate, especially if one puts them together according to a systematic arrangement, and consequently those which have the greatest resemblance to one another. Man at least here gives to plants, in a certain manner, the opportunity which he gives to his animals brought from parts of the world lying far distant from one another, which he keeps confined, contrary to nature, in a zoölogical garden, or in a still narrower space. Would indeed a goldfinch ever have mated with a canary bird, and have produced hybrid offspring, if man had not provided for them the opportunity of coming to know one another more closely? Should not, therefore, hybrid plants have already arisen in botanical gardens? Precisely the reasons, which to me made their production under natural conditions suspicious, move me to admit it under this unnatural one. Because I had already been long convinced of the sex of plants, and had never doubted the possibility of such an unnatural procreation, yet I still allowed myself to be deterred by nothing from instituting experiments on this subject, in the good hope that I might perhaps be indeed so fortunate as to procure a hybrid plant. I have finally in fact, after many experiments instituted in vain with many kinds of plants, in the past year of 1760, in the case of two different species of a natural genus (bey zwoen verschiedenen Gattungen eines natürlichen Geschlechts), namely, in the case of *Nicotiana* (*paniculata*) [Linn. Sp. Pl., p. 180, n. 2], and *Nicotiana* (*rustica*) [Linn. Sp. Pl., p. 180, n. 3], gotten so far that I have fertilized with the pollen-dust (Saamenstaube) of the former, the ovary of the other, obtained perfect seeds, and from these, still in the same year, have raised young plants." (1a, pp. 29-30.)

Regarding the nature of his experiment, Kölreuter says:

"Since I have made this experiment with many flowers, at different times and with all possible precaution, and have thereby every time obtained normal fertilization and perfect seeds, I could not in the least believe that perchance an oversight might have occurred in the experiment, and that the plants already produced from the seeds, of which seventy-eight had come from a hundred and ten seeds, should be only ordinary mother plants. Although I could not immediately quite discern much in them that was unusual and strange, yet I had already found a noticeable difference between the natural seeds and those produced artificially, which let me doubt so much the less of the young plants grown therefrom not being true hybrids. I was finally completely convinced of it, when more than twenty of them which I had kept over winter, partly in the room and partly in a cold green-house, came into flower in the month of March just past. I was with much satisfaction aware, that not alone in the spread of the branches, in the position and color of the flowers throughout, they held precisely the mean between the two natural species, but that with them especially also all the parts belonging to the flower, the anthers alone excepted, taken in comparison with those of the two natural plants, showed an almost geometrical proportion." (*ib.*, pp. 30-1.)

The anthers of the hybrid *Nicotiana* contained less pollen than those of the parents, and instead of having their regular elliptical form

> "they were in comparison quite irregular, shrivelled as though rubbed to pieces; they contained almost nothing of a fluid material, and were, in a word, simply empty husks." (*ib.*, p. 31.)

Kölreuter then goes on to say:

> "The fertility of this new plant appeared to me, therefore, extremely questionable, and the results confirmed my suspicion completely; for among the almost innumerable quantity of flowers there was not one to be found which had borne even a single seed, even though they had been immediately covered with a large quantity of their own pollen dust; while on the other hand, with the two natural species, every capsule is accustomed to bear four or five hundred seeds. This plant is thus in the real sense a true, and, so far as it is known to me, the first botanical mule which has been produced by art." (*ib.*, p. 31.)

In this connection Kölreuter refers as follows to the supposed hybrid *Tragopogon*, reported by Linnaeus to the Imperial Academy of Sciences at St. Petersburg, and which bloomed in the botanical garden at St. Petersburg in the spring of 1761, as being in his expression "only half a hybrid."

> "For the hybrid goat's-beard, which the celebrated Linnaeus considers in his new prize essay, is not a hybrid plant in the real sense, but at most only a half hybrid, and indeed in different degrees, as I will clearly and plainly demonstrate at another opportunity, with many reasons which appear in part from the nature and peculiarity of the composite flowers, and from certain experiments instituted upon the time of fertilization of the same; in part from the structure of the above-mentioned presumed hybrid itself, which had been raised by me from seeds which Linnaeus had sent, together with his prize essay, to the Honorable Russian Imperial Academy of Sciences, and which have bloomed the past spring in the Academy's garden at St. Petersburg." (*ib.*, p. 32.)

The hybrid *Nicotiana paniculata* × *rustica* obtained by *Kölreuter*, he pollinated, in part with the pollen of *paniculata* and in part with that of *rustica*, and obtained fertile seeds in both cases, but in lesser numbers than with the self-fertilized parents. Kölreuter's conceptions regarding hybrid fertilization, and the production of what he refers to as a half hybrid appear in the next following pages. His conception is that from any plant, from which, through fertilization with another, a complete hybrid can be produced, a mere "tincture," as it were, may likewise be transmitted, in the proportion in which its own pollen stands to that of the other that is also purporting to function as the male parent in the fertilization process. This "tincture," or supposed partial contribution of the female parent, through the agency of its own pollen, is presumed by Kölreuter to be (p. 34) the cause of the production of "half-hybrids." This conception of the effect of the pollen as a mass-effect, brought about through the secretion of fertilizing substance by the pollen grains, which was the more effective the greater the quantity of it, was the prevailing theory for some time after Kölreuter's day. Kölreuter's first "Vorläufige Nachricht" closes with a brief discussion of six experiments which he conducted with regard to nectar-producing plants (pp. 34-7), and which need not be referred to here.

The first "Fortsetzung" to the preceding appeared in 1763. The "Vorläufige Nachricht" was dated September 1, 1761, the place of publication not appearing. The first "Fortsetzung" is dated at Calw, December 10, 1762. At this time Kölreuter appears in the publication as Professor of Natural History at Würtemberg. The preface opens with Kölreuter's expression of conviction, that from the experiments in the preceding report the sex of plants was most completely proved, as well as the theory that reproduction in plants resulted from the production of two kinds of fertilizing material. The "Fortsetzung" therefore begins with the statement:

> "To the production of every natural plant two similar fluid materials of different sort are demanded. The one of these is the male, the other the female."

Since these materials are of different sort, or are different from each other in their nature, it is therefore easy to understand that the force or strength of the one must be different from that of the other.

> "From the union and commingling of these two materials, which occurs most intimately and in an orderly manner according to a definite relationship, there arises another of an intermediate sort, and which consequently also possesses an intermediate composite force, arisen from those two simple forces, just as through the union of an acid and an alkaline substance a third or intermediate salt originates." (p. 42.)

It is worthy of mention that Kölreuter records, regarding his first *Nicotiana* hybrid, its much more rapid growth, whereby it was distinguishable from its two parents, as he says, "from the germinating seed on to its complete flowering." (p. 32.)

Kölreuter seems to have interpreted the phenomenon of the hybrid in a completely teleological way. The hybrid plant proceeds in its development normally like any other plant.

> "Even in the case of the most completely infertile hybrid the keenest eye can discern no incompleteness, from the embryo up to flower formation, and yet the most important character, fertility, is lacking, a circumstance that would not be suspected from observation. But instead of an expected number of some 50,000 seeds, none are obtained, and more than a thousand flowers, one after another, are seen to fall, without leaving a single capsule behind." (*ib.*, pp. 43-4.)
>
> "Certainly," he says, "this event is, for a scientific investigator, one of the most deserving of astonishment that has ever occurred upon the wide field of nature." (*ib.*, p. 44.)

The wonderful and unexpected thing, however, to Kölreuter's mind, lay not in the union of two materials,

> "which indeed were not destined for each other by the wise Creator," but rather in the fact "that precisely this plant, when it has reached the highest pitch of its completion, is not in condition to fulfill the final object toward which otherwise all the operations demanded for development appear to be directed, and, in all its apparent completeness, betrays the greatest incompletion that a plant can ever happen upon. This incompleteness consists chiefly in the total lack of good male and female fertilizing material (Saamen), and in the infertility naturally arising therefrom." (*ib.*, p. 44.)

Kölreuter's mind, however, reaches out into the conceived preexisting harmony of nature, which must be preserved at any cost, and this apparent incompleteness becomes resolved into the completeness of an orderly-minded creative agency which abhors confusion of any kind, at least not of its own originating. He proceeds further:

> "If one regards this event, however, from the point of view of its consequences, then one will recognize with pleasure that this actual incompleteness is real completeness. What an astonishing confusion would not the peculiar and unchanged hybrid characters, and the continually retained fertility of such plants give rise to in Nature." (p. 44.) . . . "What evil and unavoidable consequences must these not draw after them?" (*ib.*, p. 44.)

Kölreuter turns from the contemplation of this embarrassing picture, to raise what seemed to him a serious scientific question that appeared to be involved.

> "Experience teaches us," he says, "that from the union of two like-formed fluid fertilizing materials of different sorts a firm and organic body originates, and that every natural plant itself provides those two fertilizing materials required for a new procreation, and especially the one of them, namely, the male, apparently in much larger measure than was necessary for its reproduction." (*ib.*, p. 44.)

On the other hand, according to Kölreuter's view, an artificial process seems to be quite impotent for fertilization purposes, or else it brings it about only in a very limited and incomplete way. This circumstance he holds to be one of the most complicated knots in the whole doctrine of reproduction,

> "to the solution of which all human understanding taken together might still perhaps be too weak." He concludes that: "I will hence not in the least break my head on it, but simply lay it down as a fundamental experience when, later on, the question arises of the explanation of various remarkable characters of a few of the plants obtained from my experiments." (p. 45.)

Thus concludes the theoretical or introductory portion of the "Fortsetzung." Of the experiments which follow, 18 are with species of *Nicotiana*, one with *Dianthus*, one with *Ketmia*, one with *Leucojum*, and one with *Hyoscyamus.*

Of the *Nicotiana* crosses, five are too complicated to be of genetic value, consisting either of crosses of one F_1 hybrid with a different one, or of an F_1 with a cross between a species and another F_1. Nine of the crosses might be considered interesting from the genetic standpoint, being either crosses between species, selfing of F_1's or back crosses on an F_1 by one of the parents and *vice versa.*

Kölreuter made, besides other crosses between species of *Nicotiana*, crosses between species of *Ketmia*, pink (*Dianthus*), stocks (*Matthiola*), dogbane (*Hyoscyamus*), and mullein (*Verbascum*). He ascertained the fact that, in general, only nearly related plants, and not always even these, can be crossed. He determined experimentally the fact that, if the stigmas of flowers are pollinated at the same time by their own pollen and by pollen from another species, fertilization is effected by the former, which would account for the comparative rarity of "species hybrids" in nature.

The cross *Nicotiana rustica* × *paniculata* was repeated, 24 plants resulting, which resembled in behavior those of the first experiment. These, as well as the hybrids in the former case, were found, after most careful experimentation, to be in a slight degree fertile as to the egg-cells, but completely sterile as to the pollen. Kölreuter comments regarding this cross that, in size of the plants and number of flowers, the hybrids far exceed the *rustica* parent. Whether they exceed the *paniculata* parent in these respects, he was not prepared to state.

In case of *Nicotiana paniculata* × *rustica* and its reciprocal, the F_1 hybrids resembled each other completely. In the case of the back-cross of *rustica* upon *rustica* × *paniculata*, all the progeny are reported to have approached the type of the maternal parent, i.e., the F_1 hybrid; a few more, others less. The cross, *N. rustica* × *paniculata*, is reported as furnishing progeny more nearly resembling *paniculata* than in the original cross. It was found possible to cross *N. rustica* × *paniculata* with *N. perennis*, although the cross of *perennis* with either *rustica* or *paniculata* failed.

Kölreuter concludes that the continued self-pollination of hybrids finally results in the re-appearance of the original parental forms.

His ideas regarding fertilization are interesting. He thought, as has been stated, that a plant was formed by the fusion of two fluid materials of different sorts.

"Since these materials are of different sorts, or in their essence are different from each other, it is easy to comprehend that the strength of one must be different from the strength of the other. From the union and commingling of these two materials, which occurs in the most intimate and orderly manner, according to a definite relationship, there originates another, which is of an intermediate sort, and which consequently also possesses an intermediate, compounded force, sprung from those two simple forces. . . . Upon this basis and its operative force, which, according to the different kinds of its twofold fertilizing material (Saamenstoff), must necessarily be different in the case of every different kind of living machine, rests the gradual, progressive formation of the future plant, its particular organic structure, its specific nature whereby it is distinguished from all others, and the proportion of the fertilizing material demanded for a similar new reproduction and, in a word, all those completed conditions (products) which are required for the object to which it is designed." (1, p. 42.) . . . "All the movements and changes, which from the embryo to the time of flowering, take place in every such masterpiece of nature, appear to be directed simply to the great work of reproduction. They all aim at gradually liberating that compound material upon which they are based, and at dividing it again into the two original ground materials; or,

> to speak more properly, to bring these latter themselves into a complete, and, especially from the one side, into masses of unlike size than were demonstrated from the preceding reproduction." (1, p. 43.)

Kölreuter's "Zweite Fortsetzung" to the "Vorläufige Nachricht," published in Leipzig in 1764, gives an account of 49 experiments, of which 29 were distinctly crossing experiments, the remainder being experiments involving the use of the plant's own pollen, simultaneously with that of another species. The species used in the crosses were as follows:

Species	*Number of crosses*
Verbascum	4
Nicotiana	12
Dianthus	7
Hibiscus	2
Datisca	2
Mirabilis	1
Leucojum	1

Of the twelve *Nicotiana* crosses seven, and of the seven *Dianthus* crosses four are compound.

Of the four *Verbascum* crosses, each with the same female, but with different male parents, it is reported that all were intermediate, neither the one nor the other of the parents having the preponderance.

Concluding in his own mind that the five tobacco forms *rustica*, *major*, *paniculata*, *glutinosa*, and *perennis*, were simply varieties of the same species, these, he says:

> "I pollinated the past year (1762) reciprocally together, and obtained through this manifold combination always the most complete capsules," and the plants obtained from these seeds, "held in all parts the mean between their parents, and were just as fruitful as those could ever have been." (p. 118.)

This fact was evidence to Kölreuter's mind that the five supposed "species" were merely varieties of the same natural species.

Regarding crosses between (*Nicotiana glutinosa* × *N. perennis*) and (*Nicotiana glutinosa* × *N. major fl. alb.*) Kölreuter found that the plants were identical in type with those of the reciprocal cross. Of the former he says (p. 120):

> "They did not come into full bloom, but one saw from their whole appearance otherwise that they were as like those of the reciprocal experiment, as one egg like another."

Of the second cross he remarks:

> "So far as its resemblance is concerned, there was not the least differ-

ence to be found between it and those of the reciprocal experiment." (p. 120.)

Pursuing his conception that the activity of the pollen produced a quantitative effect depending upon the amount and character of the pollen employed in fertilization, Kölreuter instituted a series of experiments with *Nicotiana* species. He found that *N. perennis*, pollinated with a small quantity of its own pollen, and a much larger amount of *glutinosa* produced plants wholly *perennis*, which had no character from *glutinosa*. Similarly *N. rustica*, pollinated in part with its own pollen, and also with pollen of *paniculata* and *perennis*, in equal proportions, produced plants which were all ordinary *rustica*, and had taken nothing from the other two. Another flower of *N. rustica*, pollinated with equal portions of its own pollen and pollen of *N. perennis*, gave plants which were ordinary *rustica*, without any trace of *perennis*. A flower of *N. rustica*, pollinated with

> "a very small quantity of its own pollen, and a much greater amount of the pollen of *paniculata*," produced "six true hybrids, of precisely the sort that one is accustomed to get from *rustica* ♀ and *paniculata* ♂." (p. 122.)

Kölreuter investigated the probable nature of the stigmatic secretion, whether it were the female fertilizing substance or not. Removing the secretion from the stigmas of *Nicotiana rustica* with a piece of blotting paper, he pollinated the surface with its own pollen, and added the stigmatic secretion of *N. paniculata*, getting as a result six plants simply *rustica*. From another flower of the same plant, pollinated with its own pollen, to which the secretion from *N. mai. vulg.* was added, he obtained four plants of ordinary *rustica*, with none of the characters of the other species. A flower of *N. paniculata*, pollinated with its own pollen, to which the secretion of *rustica* had been applied, gave four ordinary *paniculata* plants. Upon the stigmas of a hybrid *paniculata* ♀ × *rustica* ♂ and another of *rustica* ♀ × *paniculata* ♂, pollinated with its own pollen, with the addition of the stigmatic secretion of *paniculata*, he obtained plants which all in appearance approached more the *paniculata* parent.

The result of all these experiments led Kölreuter to conclude:

> "That one would almost sooner have reason to hold the female secretion to be a mere innocuous conduction medium, than as a true fertilizing material." (p. 128.)

And again:

> "Hence I believed myself, by virtue of the contrary outcome of my experiments, to be justified rather in holding the oft-mentioned oily secretion for a conduction medium, than to set it up as a true fertilization substance (Saamen)."

In all, 49 experiments are detailed in Kölreuter's "Zweite Fortsetzung," distributed over seven different genera, as follows:

Nicotiana	30	Datura	2
Dianthus	8	Mirabilis	2
Verbascum	4	Leucojum	1
Hibiscus	2		

Of the 30 *Nicotiana* experiments, eight were species-crosses; nine, experiments with one or more kinds of pollen; seven, experiments to determine the nature of the stigmatic secretion; two were F_1's back-crossed with one of the parents, and four were compound crosses. The pollen and stigma experiments have been described in detail. The species-crosses involved the species *paniculata*, *glutinosa*, *rustica*, *transylvanica*, and *major fl. albo*. There is nothing distinctly interesting in these crosses *per se*. In the case of *paniculata* × *glutinosa* it is stated that the hybrid combined the characters of the two parents in the most exact manner. ("Zeigte nebst den übrigen Merkmalen offenbar an, dass sich die Natur der ♀ mit der Natur der ♂ auf's genaueste vereinigt haben musste.") (p. 110.) Of the back-crosses on the F_1, of which two are reported, in neither case is the number of the progeny sufficient for generalization; being one, in the case of (*N. paniculata* × *rustica*) × *paniculata*, and seven in the case of (*N. paniculata* × *rustica*) × *rustica*. The former cross is stated to have resembled the original *paniculata* parent. In the latter case, all seven more or less completely resembled the *rustica* parent, in this respect resembling the behavior of the ten offspring of the cross in Experiment 2 of the "Nachricht," (*N. rustica* × *paniculata*) × *rustica*, all of which throughout approached the *rustica* parent, some more, some less. The compound crosses are not of essential genetic interest.

Kölreuter reports the results of a curious experiment to determine the possible neutral character of the stigmatic secretion. In 1760, he placed upon the still clean stigmas of a *Ketmia* species, "drops of different natural and artificial oils," deposited the pollen therein, and awaited the result; the flowers all fell off unfertilized.

(p. 140.) In the spring of 1763 the experiment was repeated with a few other plants. When the stigmas of *Nicotiana rustica* showed here and there drops of the secretion, he spread almond oil over the surface with a fine brush, mixing it with the stigmatic secretion, and spreading the whole over the entire surface, then applying a more than sufficient quantity of pollen. Pollination took place successfully. Upon four other flowers, he used hazel-nut oil, upon two, oil of jasmine, and upon four, linseed oil, with the same result. With "distilled or artificial oils" no fertilization took place, as also with animal fats and oils. The use of oil of both sweet and bitter almonds, in the case of *Verbascum blattaria*, resulted in fertilization. With pumpkins, however, the experiment failed, although, as he says: "the oil of almond had penetrated the ovary to over its half." (p. 142.) Kölreuter concludes, on the basis of these experiments, that the essential fertilizing material, issuing from the pollen grain, is the homogeneous fluid oily substance, and not the granular material. The fact that this portion of the pollen material, in his opinion, mingled freely with the added vegetable oils, and still penetrated to the ovary, fertilization following, was evidence, in his view, that both the fluid portion of the pollen exudate and the stigmatic secretion were alike oily substances, mixing freely with other oils of a vegetable nature. Kölreuter's assumption of an exudation under pressure from the pollen grains of their contents lay of course at the basis of this conclusion. He knew nothing of the growth of the pollen tube, the character of which precluded any admixture of the contents of the pollen grains with the stigmatic secretion or anything else. However, considering the lack of morphological knowledge, Kölreuter's experiment may well be regarded as in every sense scientific in spirit, and in the manner in which the conclusions were drawn.

Of the eight experiments in crossing species of *Dianthus*, three were species or variety-crosses, three were back-crosses upon F_1 hybrids, one a self-fertilized F_1, and one a compound cross. From the variations in type obtained in two back-crosses—(*Dianthus chinensis* × *carthusianorum*), and (*D. chinensis* × *carthusianorum*) × *carthusianorum*—Kölreuter concludes that:

> "The union of the fertilizing materials in the production of hybrids in the first descending or ascending degree *does not take place by far*

with the same regularity and uniformity, as in natural plants and the first hybrid originally produced therefrom." (p. 144.) (Italics inserted.)

This sentence is quoted in order to give as clear a picture as possible of the attitude of a scientific mind of that time upon the subject of the so-called "increase in variability" in hybrid generations after the first.

Kölreuter found that although the Chinese pink and the Carthusian could be successfully crossed, it was extremely difficult to cross the Chinese with the garden pink.

> "One will, among a hundred flowers, often scarcely find ten, which are actually fertilized, and which contain one, or at most two to three perfect seeds." (p. 150.)

An interesting genetic fact was ascertained in a cross between *Dianthus chinensis* × *D. hortensis*, in which the latter had "double" flowers, and in *Dianthus chinensis fl. simpl.* × *D. chinensis fl. quadrupl.*, the result being the dominance of the multiple-petalled corolla in the F_1. The statement is briefly made regarding the former cross (p. 152), with respect to the hybrid:

> "Its flowers were all reduplicate, and consisted commonly of 15-20 quite carmine-red leaves; from which one plainly sees, that the pollen of doubled flowers possesses the character of reduplicating simple ones which are pollinated with it."

This statement is extremely interesting because of the germ of genetic thought which it manifests in the mind of Kölreuter. From the second cross above mentioned, he obtained nine plants, among which the most bore quadrupled—i.e., twenty-petalled flowers. (p. 157.) Kölreuter remarks, "this experiment thus confirms that one which has already been noticed above, p. 28, XL Expt."

The thing that immediately suggests itself to Kölreuter's mind through these experiments is the opportunity offered for improving poor single flowers by crossing with doubles.

In the case of a wild plant growing in the neighborhood of Calw, *Dianthus plumarius*, Kölreuter remarks upon an extraordinary condition found by him in the pollen of occasional plants of the species, in which the pollen was of a dark-brown to purple-red color, the grains being much smaller than natural. On pollinating a Chinese pink with this pollen he obtained no seeds, the flower remaining open for ten days. But on pollinating with the ordinary whitish-grey pollen, the plants closed in twenty-four hours, and he got as perfect seed-capsules and seeds as if he had pollinated with the plant's own pollen.

Inasmuch as Kölreuter reports this type of pollen also as being present in *Saponaria officinalis* and in *Gypsophila fastigiata*, it seems probable that he was dealing with a pathological condition, due possibly to a fungus infection. At all events he reports that the shedding of this pollen took place at the same time and in the same manner as in these plants generally. It is interesting to note his comparison of the abnormal pollen grains in question, in respect to color, form and size with the smut of oats, and of other grains. The second "Fortsetzung" closes with brief accounts of crosses of *Hibiscus manihot* with *H. vitifolius* and its reciprocal; *Datura stramonium* with *D. tatula* and its reciprocal; *Mirabilis jalapa* red-flowered × yellow-flowered and reciprocal; and *Leucojum* red-flowered × a white-flowered variety.

With respect to the *Hibiscus* cross, it is only of interest to note the intermediacy of the four plants from each cross and their complete resemblance to one another. In the *Datura* cross between *stramonium* with white flowers, and *tatula* with violet flowers, the hybrids from the two reciprocals, five and three, respectively, were completely alike. The purple color did not dominate. Kölreuter says:

> "Their flowers had a whitish color playing a little into the violet; the flower-tubes marked with five violet stripes, and the others sky-blue." (p. 161.)

In the *Mirabilis* reciprocals, the color

> "in the case of both the hybrid varieties was of mixed red and yellow. The flowers played into orange-yellow." (p. 161.)

In the *Leucojum* red × white cross, the six hybrid plants all had whitish-violet flowers.

Kölreuter's "Dritte Fortsetzung" is dated from Karlsruhe, December 26, 1765. The memoir opens with a brief statement to the effect that, after his success in 1762 at Sulz on the Neckar, in the production of various hybrid plants, he had experienced still greater success in 1763 at Calw, in obtaining, in addition to fertile crosses with four species of *Verbascum*, several other fertile combinations in the same genus, involving chiefly the reciprocal crossing of the species native to the locality. The seeds from these crosses were grown at Karlsruhe in 1764, and came into flower in the same year. Out of the 65 crosses reported in the third "Fortsetzung," the *Verbascum* crosses numbered 18, and involved the species *phoeniceum*, *Thapsus*, *lychnites*, *nigrum*, *blattaria* and *phlomoides*.

All of the *Verbascum* crosses proved sterile. The crosses *Lychnites fl. alb.* × *phoeniceum*, *Blattaria fl. flav.* × *nigrum*, *Blattaria fl. flav.* × *phoeniceum*, *Blattaria fl. flav.* × *Lychnites fl. alb.*, *Thapsus* × *nigrum*, *Lychnites fl. alb.* × *Thapsus*, were carried on reciprocally, and are interesting as being identical in the reciprocal crosses, although their sterility showed them to be species-hybrids rather than variety-crosses.

In describing the cross *Verbascum blattaria fl. flav.* × *Verbascum lychnites fl. flav.*, Kölreuter discusses the question, why one or the other of the previously described hybrid plants should not have sometimes arisen in the wild state, or, if such have not arisen, wherein the obstacle lay for their production, in the case of plants, which, for so many thousands of years, had lived in proximity to one another. He remarks upon the fact that neither in the older nor the later botanical writings is there a description of any hybrid plant of this genus having arisen in the wild. The essential reason, Kölreuter concludes, for the absence of such hybrids, lies in their total or very marked infertility. Concerning Linnaeus' hybrid of *Verbascum Lychnites* × *Thapsus*, he expresses no doubt as to the actual hybrid origin of the plant, in view of the sterility of the plant, and the fact that the parents had grown for years together in the same plot.

Kölreuter concludes then that the principle still holds, which was laid down in the "Vorläufige Nachricht," that, in the natural state of things and under the ordinary set of circumstances, hybrid plants are with difficulty produced or can be produced in nature. Admitting, he says, that a botanist should have the fortune to find a true hybrid plant in the field, the question yet remained whether such an accident could have arisen in a region where the natural conditions had remained entirely undisturbed directly or indirectly. For, he says,

> "true wilderness as it comes from the hand of Nature is one thing; a field, free, but in respect to a hundred things often very much altered by the hand of man, is another." (p. 193.)

Kölreuter goes on to remark upon the apparent fact that the more rapid growth, the accelerated, earlier, and prolonged time of flowering, the development of young shoots in autumn from the roots, as well as from the stem, and a longer duration of the plant, are to be reckoned among the general characteristics of hybrids. (p. 193.)

> "It is very difficult," he says, "to assume a valid reason for the enhanced vegetative vigor before flowering. The continuation of the same after flowering, on the other hand, might be explained from the fact that these plants cannot, like the natural ones, be exhausted and impoverished through the development of the seed." (p. 194.)

With respect to the matter of increased rate of growth in hybrids, Kölreuter makes the following interesting and rather surprising remark:

> "I would wish that I or another were so fortunate as to obtain a hybrid of trees, which, in respect to the utilization of their wood, might have a great economic influence. Perhaps such trees among other good characteristics would also have these, that, if the natural ones required for their full growth, for example, a hundred years, they would reach it in half this time. At least I do not see why they should behave differently in this respect from other hybrid plants." (p. 194.)

Ten further crosses of *Nicotiana* are reported in the third "Fortsetzung," but inasmuch as all but two are compound crosses, they furnish no data of importance. The two remaining are (*N. paniculata* × *rustica*) × *rustica* and (*N. rustica* × *paniculata*) × *rustica*, i.e., back-crosses upon an F_1, as they would now be designated, or, in Kölreuter's terminology, hybrids in the descending degree, i.e., hybrids on the way toward a return to one of the parents. However, no data are given of present genetic value.

Of the remaining crosses described, 29 are *Dianthus* crosses, the species used being *barbatus*, *chinensis*, *brabensis*, *carthusianorum*, *superbus*, *deltoides*, *armeria*, *plumarius*, *glaucus* and various forms of the garden pink, presumably also *plumarius*, but referred to here as "*hortensis*." The *Dianthus* crosses are distributed as follows:

Species and variety-crosses	12	F_1 back crosses	5
Compound crosses	10	F_1 selfs	2

Kölreuter remarks as to the cross *Dianthus barbatus* × *chinensis* that, between the eighteen plants from this cross and those from the reverse cross ("Fortsetz. der Vorläuf. Nachr.," p. 44), there was to be found no noticeable difference. Reference to the page in question, however, gives the cross there reported as *Dian-*

thus chinensis ×*carthusianorum*, so that Kölreuter is apparently in error in his citation. Of the cross *Dianthus hortensis* × *chinensis*, three plants were produced. Kölreuter states:

> "Throughout, there was, between all these plants and those of the reverse cross, both in what pertained to the whole external structure, as well as also in respect to their inner characteristics, no essential difference to be found." (p. 209.)

The reciprocal cross is reported, not in the third "Fortsetzung," but as Experiment 40 in the second. In regard to a cross of *Dianthus chinensis* × *D. superbus*, a carmine-red form with double flowers, it is stated of the hybrids, twenty in number, that:

> "Throughout, these plants held in all details the mean between the female and male, except that they had bloomed earlier and longer." (p. 212.)

Most of the hybrids were infertile as to their pollen, even when abundantly close-pollinated. The egg-cells showed on the other hand a limited amount of fertility, giving, when open-pollinated from other species in the neighborhood, not seldom capsules with generally two to four seeds, and when hand-pollinated from these, six to eight seeds. So far as the doubling of the petals is concerned, it may be assumed that the hybrids were on the whole intermediate, since, as Kölreuter says:

> "One sees plainly that the female contribution in respect to this circumstance is of a like activity and character with the male." (p. 213.)

Of a cross *Dianthus hortensis* × *barbatus* it is stated (p. 216),

> "it showed quite plainly, that it had taken an equal share from both natures."

From a cross between a double *Dianthus chinensis* and a native wild species, *D. armeria*, Kölreuter obtained ten plants, of which he says:

> "Among all these hybrids, there was not a single one with simple flowers, but all either with double, even more strongly reduplicated, or quite doubled very decorative flowers; a circumstance which again places out of all doubt the activity of the female in respect to this point." (p. 222.)

These hybrids were in the highest degree infertile as to the egg-cells, although exposed throughout the summer to pollination from various other natural species in the neighborhood, and even when pollinated most carefully by hand, with pollen from the male or the female parent or from other pinks, setting not a single capsule. Of a cross between a *Dianthus plumarius*, which Gmelin had brought from Siberia, a plant with snow-white fringed petals, and *D. chinensis*, a plant with single flowers, unfringed, scarlet-red, with black-red circle, it is stated:

> "In size, as generally in all details, they showed exactly the mean between those of the male and female." (p. 224.)

From a cross between *Dianthus barbatus* and *chinensis* selfed, three plants were produced, all different from one another. To Kölreuter's mind the matter is regarded thus:

> "So much in the meantime is quite clear, that the self-fertilization of such hybrids must go on dissimilarly, and not in an orderly manner, since it even appears as though thereby sometimes a basis were laid for misbirths, as is manifested by the dwarf stature of the second plant of the present, and of the two hybrids of the thirty-seventh experiment." (p. 233.)

Kölreuter states that a no less amount of difference showed itself among a few plants of the reciprocal cross, to which he refers as being reported in the second "Fortsetzung," Sec. 26, p. 106. The reference cited, however, is to the selfing of a cross between *Dianthus chinensis* × *carthusianorum.*

Kölreuter also states (p. 236) that he had previously taken the complete similarity of hybrids in reciprocal crosses, as an infallible indication of the equilibrium existing between the two fertilization elements, but that one must take this principle in a limited sense. The similarity of reciprocal crosses proves incontrovertibly, that in both cases throughout, the same proportion existed in the mixture of the fertilization elements, but not at all that in every particular case, in respect to mass or activity, an equal amount of each is used in fertilization. As for example, in crossing a blue with a yellow color, a third or green color is produced in a certain definite degree, whether the blue is mixed with the yellow or the yellow with the blue.

> "This green color," he says, "will not exactly, however, on this account, hold completely the mean between the two ground colors, and consequently be distinguishable from that which comes out when one has mixed ten parts of each with the other. In this connection one must, however, pre-suppose that both ground colors are of like activity, for if, for example, the yellow were by one-tenth more active than the blue, yet nevertheless in the given case, irrespective of the unlike proportion in the mass, a medium color would come out, to which each of these ground colors according to its activity contributed equally much." (p. 237.)

The remainder of the crossing experiments reported upon in Kölreuter's third "Fortsetzung" are as follows: A cross between *Datura ferox fl. alb.* and *D. tatula fl. viol.*, a back-cross of *Mirabilis jalapa* (yellow), upon *M. jalapa* red × yellow. A reciprocal cross is reported between *Cheiranthus* (*Matthiola*) *incana* and *Ch. annuus*, between *Sida cristata minor* × *major; Cucurbita* of a small round variety with few, small seeds, by a large *Cucurbita pepo*, and a cross between *Aquilegia vulgaris* × *canadensis* and its reciprocal.

In the *Datura* cross, involving purple flower-color in *D. tatula*, the flowers of the hybrid are reported as being "whitish-violet." The *Mirabilis* back-cross is reported as giving the yellow color in a stronger degree than in the F_1. The *Cheiranthus* (*Matthiola*) cross is interesting because of the genuine genetic purpose for which it was undertaken.

Kölreuter remarks:

> "Since the essential difference which one believes to exist between winter and summer stocks always seemed to me suspicious; I therefore concluded to completely decide this hitherto doubtful matter through the experiment of crossing." (p. 200.)

From these crosses, he raised in 1764, twelve plants from the first, and six from the reciprocal cross. These were in all respects like one another. Their intermediate character showed itself especially in the fact that they began to bloom earlier and more vigorously than the winter stocks are accustomed to do in the first year, and on the other hand brought their flowers out later, and not in the complete numbers that the summer stocks are accustomed to do.

The *Sida* cross is reported as giving a hybrid intermediate in color, form, and size of all the parts, between the two parents. The *Cucurbita* cross likewise gave a complete intermediate.

An interesting discussion follows of the sensitivity of the stamens in flowers of *Opuntia*, *Berberis*, and *Cistus*. The last pages of the third "Fortsetzung" (252-63) are taken up with a discussion of further experiments on the pollination and fertilization process.

> "Since there are some people," he says, "who have brought into doubt the organic structure of the pollen, assumed by me in the 'Vorläuf. Nachr.' Sec. 5, I therefore hold it as my duty to help them out of their dream in this respect, and to give a somewhat closer explanation of this matter." (p. 252.)

Kölreuter then proceeds again to a detailed description of what is now known to be the exine. The fire-lily (*Lilium bulbiferum*) is taken as the type for discussion. The pollen grains of this species, under "moderate magnification," appear, as he says, to have a shagreen-like surface, as though covered with small papillae. With a "stronger magnification, one sees, instead of the papillae, a net-like structure." By pressing the dry pollen grains gently together between two thin sheets of mica, so that the material contained in them is expelled, and bringing them under the microscope, he says:

> "One will see their empty and transparent skins entirely interwoven with vascular or nerve-like threads, which are bound together, and represent an irregular net with unlike angular 'eyes.' These fibres, however, never cut through one another, but make, even where they come together, no knots, but anastomose as it were amongst one another; and therein is this net-like structure wholly different from an actual net." (p. 253.)

Such is Kölreuter's final description of the ridges and reticulations on the exine, which he took for a sort of fibres penetrating its tissue.

If these fibres therefore, he says, represent sap or air-vessels, the sap or air must have free access or passage from one branch to another. Other species of *Lilium* are stated to have the same structure, as also the pollen of *Agave americana* and many species of *Orchis*. From observation of these and others he concluded that, in a very large number of species, on the pollen, which on account of its small size and other characteristics showed scarcely a trace of "organic structure," there were still present similar structures to those in the species indicated. The inner coat of the pollen grain is described so far as it shows itself in the form of the pollen tubes emerging through the germination pores. The germination of the pollen grains, so far as Kölreuter observed it, or was able to follow it, is described as follows. In the case of *Scabiosa succisa*, he gives the following account: The white, smooth, roundish pollen grains, as soon as they are placed in water, give off a great quantity of a pale, sulphur-yellow oil, gradually swell with the absorbed water, and soon thereafter, from three equidistant weaker places in the wall, send out, ordinarily, three conical, membranous plugs, which are immediately to be distinguished from the outer, hard, and opaque shell of the pollen grain by their transparency, and their uncommonly thin and uniform substance. As these plugs or horns gradually arise, one sees also the absorbed water, together with a part of the granular material, press into them and stretch them to bursting. They scarcely reach a length amounting to the small diameter of the pollen grain, before a slit appears at one side of the base, and in a moment the mixed material, which has already entered the plug, pours forcibly out of the slit, the pollen grain noticeably shrinks together, and the remaining two plugs withdraw almost wholly into the pollen grain, or at least noticeably diminish in size. Sometimes, instead of the three horns or plugs, only two or even only one makes its appearance. The process is similarly described for the pollen grains of *Dipsacus fullonum*, *Knautia orientalis*, *Linnaea borealis*, as also for species of *Geranium*. Kölreuter accurately describes the germination-pores of the pollen grains as thin places in the coat. If his observations require correction, it is nevertheless well to note their accuracy within their own category, and within the observational limits then possible.

The third "Fortsetzung" concludes with an extremely careful and interesting natural history account of the sequence of events in the pollination of the stigmas of *Hibiscus manihot.*

> "At about nine in the morning on a clear, warm day," (of July 1759), he says, "a flower of the species named opened. Its four carmine-red pistils stood upright but close together. The whitish anthers opened gradually, and showed in part their pale, sulphur-yellow and still opaque pollen grains. The knobby dark-red stigmas, which hitherto had remained still quite dry, began, from their long, fine and pointed papillae, to secrete the female moisture, and acquired thereby a glistening, as though they had been painted over with a varnish, or had been saturated with a fine oil. I thereupon placed upon them by means of a delicate brush a limited quantity of the still opaque pollen grains. Soon thereafter these acquired also a glistening appearance, and together with this, a transparency which they had previously not yet had, beneath their dull appearance. The glistening of the stigmas increased ever more and more, from the moisture which heaped itself upon them; and the pollen grains borne upon them became, finally, one after the other, so clear and transparent, that the purple-red color of the papillae lying beneath them appeared very plainly through them. During the time, however, when they reached the highest degree of ripeness, they already began to diminish a little in size. Gradually they lost also their transparency again, became ever smaller, and appeared imperceptibly to acquire wrinkles. At last they became very small, shrunk gradually together, lost all transparency and dried out. All these changes took place also at the same time with the other pollen grains remaining

upon the knobs of the stigmas. In the meanwhile, the stigmas had gradually withdrawn from one another, drawn outward, and finally turned back on their outer halves against the base of the flower. Their glistening effect disappeared again gradually with their moisture, and they became finally covered by the closing and wilting petals." (p. 262.)

The above is given in full for the sake of its natural history interest, as a type of observation none too common, and for the sake of showing what Kölreuter's spirit was at its best. The graphic, narrative, and even poetic style of the account should render it a classic among natural history observations. This closes an attempt, extensive and somewhat detailed, to give as complete and exact a presentation of the Kölreuter material as possible. If the account is somewhat disproportionately extended, it is nevertheless desirable to have the data from Kölreuter's slightly difficult and sometimes a trifle obscure German rendered as accessible as possible in English.

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NOTE: From 1770-1775, thirty-one articles by Kölreuter, chiefly on zoological subjects, appeared in the "Novi Commentarii Academiae Scientiarum Imperialis Petropolitanae" (Vols. XV-XX, inc.). Of these, one only (in Vol. XX) was upon hybrid plants. In the "Acta Academiae Scientiarum Imperialis Petropolitanae," 1777-1782, appeared seven articles by Kölreuter on hybrid plants, and in the "Nova Acta" of the same Academy, 1783-1796 (Vols. I, III, XI, XII, XIII), five further papers were published on the subject of plant hybrids. Unfortunately, it has been impossible to secure access to the St. Petersburg papers of Kölreuter in time for their inclusion in the present volume.

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CHAPTER III

9. *Miscellaneous Experiments Regarding Sex in Plants.*

CAMERARIUS and Kölreuter represent the two chief landmarks in the history of plant breeding and genetics up to 1766. While these were the only investigators whose direct contributions to our knowledge of sex in plants, or of heredity in the plant organism, were extensive or fundamental, it is of interest to know that the first person who is reported to have actually crossed plants artificially, was an Englishman named Thomas Fairchild, who, according to Richard Bradley, Professor of Botany in Cambridge University, 1724-1732, (1) in 1719 crossed *Dianthus barbatus L.* (Sweet-William), with pollen of the Carnation (*Dianthus caryophyllus L.*). The cross in question was still known in gardens one hundred years later as "Fairchild's Sweet-William." Nevertheless, as Focke says (2, p. 430):

> "This success in artificial fertilization was never utilized for science, nor does it appear to have given gardeners any stimulus to further investigations."

It is possible that the first conception of the function of the stamens of the flowers as the source of the male fertilizing material is ascribable to an Englishman, Sir Thomas Millington (1628-1704). Millington was a physician by education, B.A., Cambridge, 1649; M.A., 1657; Fellow of All Souls College, Oxford, 1659. He is known as having taken part in the scientific meetings which gave rise to the Royal Society, of which he was an original member. He became Fellow of the College of Physicians in 1672, and was Sedleian Professor of Natural Philosophy at Oxford from 1675 to his death in 1704.

In a lecture on the anatomy of flowers, said to have been read by Nehemiah Grew before the Royal Society, November 6, 1676, the latter is quoted as follows:

PLATE XX. Sir Thomas Millington, 1628-1704. Sedleian Professor of Natural History of Oxford (1675-1704).

> "In discourse hereof with our Learned Savilian (Sedleian), Professor Sir Thomas Millington, he told me, he conceived, That the Attire (Stammens) doth serve, as the Male, for the Generation of the Seed. I immediately reply'd That I was of the same Opinion."

The date of this supposed lecture was six years earlier than Grew's "Anatomy of Plants" in 1682, in which the statement is repeated (4b, 171) in almost identical words, and eighteen years before the publication of Camerarius' "De Sexu Plantarum Epistola."[1] However, the lack of experimental data to support the conclusion gives the incident historical rather than scientific value, except for whatever influence it may have had upon later investigations in the subject.

Richard Bradley's conceptions on the subject of sexuality in plants seem, according to his own statement in his "New Improvements of Planting and Gardening," to have been derived from a certain Robert Balle, likewise a member of the Royal Society. It appears from Bradley's account, that he derived further suggestions in the matter from Moreland's communication to the Royal Society in 1703. (8.) Bradley's account follows:

> "The first hint of this secret [that every plant contains in itself male and female powers] was communicated to me several years ago by a worthy member of the Royal Society, Robert Balle, Esq.; who had this notion for above thirty years, that plants had a mode of generation

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[1] The statement that Grew delivered an address before the Royal Society, November 6, 1676, or, according to Logan, November 9 (p. 64), requires modification. A search through the volumes of the Philosophical Transactions of the Royal Society for the years 1676-77 reveals no address by Grew on the subject, or containing the quotation referred to. An inquiry of the office of the Royal Society was responded to by a letter from the Assistant-Secretary (October 31, 1927) as follows:

"The supposed quotation from a paper by Grew seems certainly at fault. We trace no such paper in the Philosophical Transactions. There was no meeting on November 6, 1676. There was a meeting on November 9, and at that meeting Grew gave a Lecture on Flowers. This seems never to have appeared in print before the publication of his 'Anatomy of Plants' in 1682. But the lecture was ordered to be 'registered' and we have it copied in MS in vol. 5 of our 'Register Book' series. We have glanced through the copy page by page (there are 10 pages of it) but we failed to trace the statement you quote: 'In discourse with . . .' On the face of it we should say that that statement appeared only in the published volume of the 'Anatomy of Plants,' 1682."

In a previous letter (October 8, 1926), from the office of the Royal Society, it is stated: "All the Society did in the present case of Grew's communications was to desire him 'to cause them to be printed together in one volume.'" The first authentic reference, therefore, to the matter, must be taken to be Grew's publication in his "Anatomy of Plants," published in 1682.

somewhat analogous to that of animals. The light which I received from this gentleman was afterward further explained by another learned gentleman of that Society, Mr. Samuel Moreland, who in 'Philos. Trans.,' Number 287, Anno 1703, has given us to understand how the dust of the Apices in flowers [i.e., the male sperm] is conveyed into the uterus or vasculum seminalis of a plant, by which means the seeds therein contained are impregnated. I then made it my business to search after this truth, and have had good fortune enough to bring it to demonstration by several experiments; since which, a gentleman of Paris had printed something of the same nature, in the 'Hist. de l'Acad. des Sciences,' for the year 1711 and 1712, which were published about two years ago."

Bradley's account of the Fairchild crossing experiment is as follows:

"Moreover, a Curious Person may, by this knowledge, produce such rare Kinds of *Plants* as have not yet been heard of, by making choice of two *plants* for his *Purpose* as are near alike in their parts, but chiefly in their *Flowers* or *Seed Vessels;* for example the Carnation and Sweet-William are in some respects alike, the Farina of the one will impregnate the other, and the Seed so enliven'd will produce a Plant differing from either, as may now be seen in the Garden of *Mr. Thomas Fairchild of Hoxton*, a plant neither *Sweet-William* nor *Carnation*, but resembling both equally, which was raised from the Seed of a *Carnation* that had been impregnated by the Farina of the *Sweet-William*." (pp. 20-3.)

Two years earlier, Bradley himself (1. pp. 20-5), had removed the anthers from the flowers of twelve tulips which he had planted in a remote place in his garden, and had discovered that they produced no seeds, while some four hundred tulips, planted elsewhere in the garden and left intact, produced seeds freely.

The account of the experiment is given as follows:

"I shall now proceed to what I call the Demonstrative Part of this *System*. I made my first Experiment upon the *Tulip*, which I chose rather than any other Plant because it seldom misses to produce Seed. Several years ago I had the Conveniency of a large Garden, wherein there was a considerable Bed of Tulips in one Part, containing about 400 Roots; in another Part of it very remote from the former, were Twelve Tulips in perfect Health. At the first opening of the twelve, which I was very careful to observe, I cautiously took out of them all their *Apices*, before the *Farina Fecundans* was ripe or any ways appear'd. These Tulips, being thus castrated, bare no Seed that Summer, while on the other hand every one of the 400 *Plants* which I had let alone produced seed. . . .

"'Tis from this accidental Coupling that proceeds the Numberless Varieties of *Fruits* and *Flowers* which are raised every Day from Seed. The yellow and black Auricula's which were the first we had in England, coupling with one another, produced *Seed* which gave us other varieties, which again mixing their qualities, in like manner, has afforded us by little and little the numberless Variations which we see

> at this Day in every curious *Flower Garden;* for I have saved the Seeds of near an hundred plain *Auricula's,* whose *flowers* were of one Colour, and stood remote from others, and the *Seed* I remember to have produced no Variety; but on the other hand, where I have saved the Seed of such plain Auricula's as have stood together and were differing in their colours, that *Seed* has furnished me with great Varieties, different from the Mother Plants."

In 1731, Philip Miller, in the first edition of his "Gardeners' Dictionary" (7), reported upon a repetition of Bradley's experiment with tulips, and also upon an experiment with spinach, in which plants of the two sexes, grown apart, resulted in the production of seeds devoid of embryos.

Miller (1692-1771), was Governor to the Apothecaries' Company, from 1722 to 1770, at the Chelsea Gardens near London. In 1724, he published "The Gardeners' and Florists' Dictionary, or a Complete System of Horticulture," of which Linnaeus said, "non erit lexicon hortulanorum sed botanicorum." The work went through eight editions during his lifetime. It is said of it that while before its appearance not more than a thousand species of plants were in cultivation, at his death there were more than five thousand. He was a correspondent of Linnaeus, who visited the Chelsea Garden several times, when in England in 1736. The seventh edition of "The Gardeners' Dictionary," in 1759, contained twice as many plants as the first edition, and adopted the nomenclature of Linnaeus. The account here given of Miller's experiment is taken from the 1759 edition, from the chapter (unpaged) entitled "Generation."

> "I shall therefore conclude with mentioning a few Experiments of my own, which I communicated to *Dr. Patrick Blair,* which he improved as Proof of his opinion of *Effluvia,* and *Mr. Bradley* also, as a Proof of the *Farina* entering the Uterus in Substance, and leave the curious Enquirer to determine on that Side of the Question, to which Reasoning and Experiment shall influence him.
>
> "I separated the male Plants of a Bed of Spinach from the female; and the Consequence was that the Seed did swell to the usual Bigness, but when sown it did not grow afterwards; and searching into the Seed I found it wanted the Punctum Vitae (or what Geoffrey calls the Germen).
>
> "I set twelve Tulips by themselves, about six or seven yards from any other and, as soon as they blew, I took out the Stamina (with their Summits) so very carefully, that I scattered none of the male Dust; and about two days afterwards I saw Bees working on a bed of tulips, where I did not take out the stamina; and when they came out they were loaded with the farina or male dust on their legs and bodies; and I saw them fly into the tulips where I had taken out the stamina,

PLATE XXI. Philip Miller, 1691-1771.

and when they came out, I found they had left behind them sufficient to impregnate those flowers, for they bore good ripe seeds which afterwards grew."

In 1739 appeared a small memoir of thirteen pages, by James Logan, "Supreme Justice and President of the Provincial Council of Pennsylvania in America." This memoir, published in Latin at Leiden and entitled "De Plantarum Generatione Experimenta et Meletemata," contains an account of the author's experiments on the fertilization of Indian corn, and his conclusions on the subject of plant fertilization in general. After a description of the plant, and its manner of flowering, he says:

> "On the ear appear very beautiful ranks of grains, generally eight, often even ten, and more rarely indeed twelve, and even sixteen I have seen. In any such row, the grains are 40 more or less, which in their rudimentary stage, when the spike is still tender, may rightly be called ova, and upon each ovum arises a slender, delicate, white filament which is also hollow, and is like a silken thread. These individual threads break through seriatim, between the rows, from the beginning to the ulterior extremity, where, protruding themselves from the leaves which protect the whole ear in a bundle, they appear prominently in the air, in color more often in this prominent part whitish, sometimes indeed, according to the various kind of plant, yellowish, reddish, or purplish; and these filaments, as I suspected, are presently to be understood as the true styles of the ova."

The experiment in fertilization is described as follows:

> "Therefore, setting about experiments with this plant, in my urban garden, 40 feet in width and about 80 feet in length, from the different corners, having heaped up little hills, according to the method of sowing, in the latter part of the month of April, I planted four or five grains of seed (in each). At the beginning of August when the plants had grown to their proper size, and the tassels (cirri) on the summit, and the ears (spicae) on the stalk, had fully appeared, I cut off from one hill all these tassels from within: in others, however, the tassels being intact, I cut off the whole bundle of filaments or styles from certain ears, having gently freed them from the enclosing leaves, and covered them again, and from others cut one-fourth, and others left intact. Another ear, before the bundle (of styles) should get to the light, I gently wrapped in a light, soft cloth of Indian or Chinese linen, called by us 'muslin,' and so loosely that not the least injury should happen to the vegetation, so that, on account of the lightness of the cloth, the ear should enjoy the benefit of the sun, the air and the showers, but that on account of the woolly cloth it would be exposed to no approach of the pollen. Four hills I left whole and intact, and as many of the others also as possible, in that condition which I have stated, I permitted to come to the time of maturity. (pp. 8-9.)
>
> "Towards October, it was seen that in the first hill, which had been completely detasselled, although the ears were satisfactory to the eye, not a single grain was matured, except in a single ear of greater size,

which projected higher up, upon a stalk facing the adjoining hill, on the side toward the prevailing winds. On this ear some twenty grains matured.

"In those (ears) from which I had removed the styles," he states, "exactly as many seeds were found, as I had left styles intact; in those I had wrapped in cloth, not a single one. In the void or empty ova nothing except a dry skin was seen." (p. 9.)

PLATE XXII. James Logan, 1674-1751.

Logan therefore concludes:

> "From these experiments, instituted and carried out by me with the utmost accuracy, as also from several by others, it holds that this pollen, evolved from the anthers, is the true masculine semen, and is most clearly entirely necessary to the fecundation of the uterus and seeds, which fact nevertheless all the centuries concealed up to ours." (p. 9.)

The care with which the experiments were carried out, is sufficiently attested by the remark (p. 16):

> "After these experiments were undertaken, I scarcely permitted myself to be absent from these investigations, either through the state of my health or by business."

Millington is referred to in the following words:

> "Worthy is therefore that Discoverer of this Arcana of Nature, whose memory should be perpetually celebrated. He seems to have been Thomas Millington, an English Knight, Savillian professor in his time before or about the year 1676. For thus reported Grew in an address before the Royal Society, held the 9th of November of that year. Malpighius indeed, so far as I know, nowhere thinks of any use for it (i.e., the pollen). Grew himself suspected the pollen to be necessary for fecundation, but not that it entered the uterus; but twenty or more years after him, Samuel Moreland, also an Englishman, affirmed that it descended to the uterus itself, through the canaliculi of the style." (p. 6.) (See *ante*, pp. 62-64.)

10. *Gleditsch's Pollination Experiments with the Palm.*

In 1751, Johann Gottlieb Gleditsch, Director of the Berlin Botanical Garden, published an account of an experiment in the crossing of a species of palm (*Chamaerops humilis*), of which Sachs says in his "History of Botany":

> "This treatise, in point of its scientific tone and learned handling of the question, is the best that appeared between the time of Camerarius and that of Kölreuter." (9.)

Gleditsch's account, as reported in the "Histoire de l'Académie des Sciences et Belles Lettres," 1749, begins as follows:

> "The theory of sex of plants, which," he says, "has been so long and vigorously debated by modern naturalists, is at present supported upon incontestable foundations, which are experience and reason. Things which the greater number of physicians regarded formerly as ridiculous and imaginary are proved today by the most simple experiments, and with so much evidence that there no longer remains the least place for all the objections capable of being formed against this system, or for all the jests with which it could be loaded." (5a, p. 103.)

It is not, he adds, that there are not more who still doubt the existence of true sex in plants, "but their number is very small, and their arguments do not appear to merit any response."

> "Leaving all these disputes to one side," he continues, "I have only been interested in acquiring a full proof of this theory; and to this end, for several years, I have made experiments on plants of every sort, and I have had the pleasure of seeing the truth discover itself to my researches, and especially in later years, with perennial plants, trees of the same natural species (the sexualists call them vulgarly *dioecious*), of which one carries the male flowers, while the other, its companion, which is quite a different one, carries only the female flowers." (5a, p. 103.)

Of these he mentions, (p. 104) the genera *Ceratonia*, *Pistacia*, *Terebinthus* and *Lentiscus*, and "cette espèce de *Palmier dactylifère* qu'on nomme vulgairement *Chamaerops*, *Chameriphes*."

In the garden of the Academy of Sciences in Berlin, he comments, the difference in sex in the flowers of trees had long been noticed, the gardener himself having remarked it for more than twenty years. The latter was, however, unable to discern the cause of sterility in the plants. The simplicity of mind obtaining in regard to the matter at the time is evidenced by Gleditsch's remark, that the gardener was greatly surprised at the appearance of the perfect fruits of the terebinth (*Pistacia terebinthus*), because he had not thought of this, that the simple sprinkling of the powder of the anthers was sufficient to effect its production. His surprise doubled especially, when, from these fruits, either planted of themselves in the ground or planted expressly with care, he saw arise, a little afterwards, the finest plants in the world. (p. 104.)

The attempt is mentioned of Prince Eugène of Austria, during the last years of his life, to secure the artificial pollination of the palm, a matter of which he had read descriptions. To this end, he had palm trees of the different sexes and of considerable size, sent to his garden at Vienna, but the palms perished in the space of a year, without flowering.

The palm at Berlin upon which Gleditsch determined for his experiments, was a pistillate tree, which was, as he says, possibly more than eighty years old, "and certainly the largest of all those of its species which are found today in the gardens of Germany." According to the testimony of a man said to be of note, and then in his sixty-sixth year, the tree in question was formerly in the Royal Garden at Berlin, and had been seen by the person referred to in its earliest days. During this entire time the tree had borne no fruits, nor later in the Botanical Garden, according to the gardener,

> "and for my part," Gleditsch adds, "I have never remarked, among the flowers which fall every year from this palm, any perfect fruit; still less have I been able to observe any which encloses a fertile seed." (p. 106.)

In the spring of 1749, Gleditsch (p. 106) was able to obtain, from the botanists Ludwig and Boehmer at Leipzig, flowers of a male plant growing there in the garden of a certain Caspar Bose. Gleditsch states as follows:

> "I received them in the spring of 1749, during the days which were already very warm. The heat of the sun had completely withered and spoiled the packets of stamens, and the greater part of the powder had escaped from the seminal vesicles. I collected in a small spoon a part of this powder, which was spread for the time on the paper with which the box was lined on the interior." (p. 106.)

The journey from Leipzig had taken nine days, during which time the pistillate palm at Berlin, on account of the heat, had entirely finished flowering, so that there remained only a very small number of flowers at the tips of the branches; in addition to which, however, unexpectedly, a small cluster of new flowers bloomed late. The pollen, which had escaped from the anthers and adhered to the paper, was spread upon the pistillate flowers, and the packet of already mouldy stamens was applied to the flower cluster that had bloomed late.

> "This sprinkling of the fecundation powder having been done, the fecundation had the success I would have expected; the vegetation-bladders swelled in great number, and became filled with a fertile setting of seed, suitable for further propagation: these became veritable little eggs." (p. 107.)
>
> "These little eggs or seeds ripened in the fruits the last winter, and having been planted in the ground at the beginning of the spring of 1750, plants have come from them conformable to their origin, that is to say, little palms, which testify in an incontestable manner that vegetable fecundation has been fully accomplished." (p. 107.)

Another pollination experiment was made in 1750. Another packet of male flowers was obtained from Leipzig. Of this experiment, Gleditsch states:

> "Its particles have promptly penetrated the stigmas of our female palm, and have the efficacy of fecundating a great quantity of fruits or dates, of which I have presented the clusters to the Academy in order to submit them to its examination." (p. 107.)
>
> "This so simple attempt at the artificial fecundation of our palm makes

> it evident that the greater part of the difficulties which the botanists make a display of in their theories, which very often they invent, in relation to the fecundation of vegetables, have almost no reality, and, if they had, it would necessarily require that the greater number of plants remained sterile." (p. 108.)

A third experiment in the fertilization of the palm, was again undertaken in 1767. The species of palm used in the experiments was, according to Gleditsch's statement, the same individual as used in the two previous ones. (p. 7.)

> "The female palm which we preserve in the Royal Botanical Garden is very old, and of fine appearance, without having ever borne dates up to the years 1749 and 1750, when I fertilized it for the first and second times with the powder of the flowers which I had let come from Leipzig by post. I made report at the same time to the Academy of these two experiments, and I produced by means of the dates, perfectly ripe, young palms, which exist still in the garden." (p. 7.)

After describing the pollination of the palm by means of the transportation of the pollen by air currents, and the hand-pollination of the date in oriental countries, which, he says, "has taken place in these countries since men inhabit them and cultivate them," he remarks:

> "This does not prevent the savants from putting the question nowadays of whether the thing is possible, and the fact is real." (p. 6.)
>
> "Let one separate the male palms from these female ones," he continues, "of which I have said above that the proximity of the males was absolutely necessary for them for fertilization; one will infallibly see happen what took place at Berlin with respect to our female palm, since the time of the late King Frederick I, to wit, that this tree, deprived of its male, had remained in perfect sterility since, and that its fruits have not reached maturity." (p. 6.)
>
> "No one indeed," he says, "will ever confound the unfertilized débris which our palm produced, every year, and which I place here by the side of the effect of fecundation, with these perfect fruits, and especially with that which has served to produce a young palm which derives its extraction from the first." (p. 7.)

The pollen for the third pollination experiments was sent from Karlsruhe, a distance of eighty miles. Referring to the custom in the orient, of hunting for the male trees, from which the inhabitants bring in clusters of the staminate flowers to hang beside the female flowers, he makes the statement that the male flowers remain sometimes fifteen days or three weeks on the road before being used for pollination.

Before undertaking the first two experiments in fertilizing the palm, Gleditsch states that he made other preliminary ones in the

Royal Botanical Garden, upon a mastic tree (*Pistacia lentiscus*), and on a terebinth (*Pistacia terebinthus*), both of which were successful, especially so in the case of the latter, from which he was able to collect nearly half a "Metze"—nearly two liters—of seed.

After the two experiments mentioned, Gleditsch remarks that he allowed the palm to remain eighteen years, without securing another fertilization, not, however, without having taken much pains to procure pollen from other places. At the end of the time referred to, he addressed himself to Kölreuter, who was at the time medical adviser to the Margrave of Bade-Bourlach, and to whom he refers as:

> "One of the most diligent naturalists of our times, who sent me, in the month of May, some of this powder of the flowers, which I had searched for since so long in vain, with a little quantity of the same powder which he had already kept for a year." (p. 9.)

The latter, he states, had no fertilizing effect, but the former was entirely effective. The details of the experiment are not uninteresting. The palm put out successively eleven clusters of flowers between the ninth and twenty-sixth of May. The tree was thoroughly rid of all débris and of all clusters of dried flowers. On account of the height of the tree, it was necessary to erect a scaffold around its crown, so that the flowers could be readily pollinated, and subsequently be observed as long as necessary. Of the eleven flower clusters, three were chosen for pollination, which were the nearest to the glass of the greenhouse and hence the most exposed to the sun.

One of these, the smallest, was pollinated with the pollen which had been kept for a year, "but," he says, "it did not produce any effect, as I was able from the first to observe at the end of fifteen days." (p. 10.) The second and third clusters were pollinated with the fresh pollen.

> "Having been obliged to keep for eight days the fertilizing powder which had been sent me from Carlsruhe, I proceeded to the second fecundation, in the manner which I have already related, in the last days of the month of May." (p. 10.)
>
> "When I afterwards examined," he continues, "what had been the effect of the powder on the flowers, I found that the edge of the flower with the blunt anthers had fallen, or at least had suffered some change, the little ovaries had become softened, had taken on a little growth, their color had become modified, and they had become brilliant." (p. 11.)

In his first two pollination experiments with this tree, Gleditsch relates that he had simply sprinkled the pollen over the flowers without more ado. On this third occasion, he pollinated the pistillate flowers with a camel's-hair brush and, as he states, he did not omit a flower. At the end of the seventh month, the large cluster fertilized produced ripe and perfect fruits, those of the first flowers being the largest, the later ones being of different sizes, by reason of the diminishing amount of light and heat from the sun. The form of the fruits is described as resembling olives, and their color, nut-brown, and in the best specimens, chestnut-brown. The outer coat of the fruit is described as being fine and very brilliant, the interior thick, filamentous and grayish. Under this was the fleshy soft envelope of the seed, which is described as having the color of fresh mace. The odor of the flesh of the fruits is described as disagreeable, resembling at maturity the odor of old butter, whence the name in Germany "Butter-palm." The taste of the fruits is stated to be sharp, corresponding, in certain respects, to the odor. As the result of his experiment, Gleditsch concludes that:

> "The action which is required to produce a rather considerable change has not taken and does not take place without an actual contact, immediate or mediate, of the two palms, as is required in male and female animals, conformably with the general laws of nature, and with the manifest testimony of experience. The contact takes place in fact in plants, but, so far as we are informed at present, the sole way consists in the powder of the flowers of the male plant, where, following the distinct idea which science can furnish us, is found contained that which serves for the fecundation of the plant." (p. 13.)

It is important to note that at no time does Gleditsch appear to have had a clear idea as to the manner of the germination of the pollen grains. The substance in their interior, he says:

> "When it is perfected, and when its time for escaping has arrived, does so little by little, without the vesicles breaking for this effect." (p. 15.)

The character of the contents of the pollen grains is taken to be of the nature of an oil, since, on macerating a quantity of pine pollen in a mortar with mercury, he obtained a substance resembling wax, which could be kneaded between the fingers, but which was not quite wax, he says, for, when placed in an envelope of paper, it was found that "it penetrates all the paper with its subtle oil."

This oil is apparently, in Gleditsch's mind, the material agent of fertilization. The pollen grains fall upon the stigma, which is covered with fine "warty projections" (verrues déliées), "between which the powder of the plants is carried externally, and spreads its oil." (p. 16.) The stigma exudes also a secretion, which Gleditsch considers to represent the contribution of the pistillate plant to fecundation, as the "huile" from the pollen grains constitutes the corresponding contribution of the staminate plant.

> "These two singular sorts of humidity, which are particularly filtered in the flowers, and of which one exudes from the powder of the male flowers, the other from the tube of the ovary, or from the style of the female flower, unite and mingle together, whereby the one alters the properties of the other and produces a substance of a third nature, which participates in those of the two preceding, and which manifests itself more or less in the young plants, after fecundation and propagation." (p. 17.)

The actual process of fertilization, by means of this united substance, is stated by Gleditsch to be as follows:

The most refined of these two fluid substances thus united, is carried by suction into the ovary, where it enters the newly-formed and undeveloped seeds, in a short time causing there, by means of its proper force, a great change in the "pithy center" (point moelleux) found there, i.e., within the ovules; furnishing it (the point moelleux) its nourishment, and laying the foundations for the final development of the young plant newly formed there. It appears, therefore, according to the view here represented (p. 17), that an undifferentiated central point of some kind is assumed to exist in the ovules; that an oily fertilizing material, exuding by degrees from the pollen grains, penetrates to the ovary, generally by means of "canaliculi" often extremely minute, enters the ovules, and reaches the "pithy center" referred to as:

> "That part of the marrow or pith, which, coming from the plant, has terminated in the ovary of the flowers."

The fertilizing substance furnishes to this special "marrow" the addition of a living fluid, which puts it in condition to extend, and which is at the same time its first aliment. (p. 17.) We have at the present time, he says, only a confused idea of the process.

> "We are not able to venture to judge it, except after the visible result of expansion and development, of which we have just spoken." (p. 17.)

This concludes the account of one of the most notable confirmatory experiments in pollination, conducted expressly for the purpose of verifying the theory of the sexuality of plants, and carried out with scientific thoroughness and accuracy.

This outlines the history of the more important experiments known to have been performed in connection with the investigation of sex in plants, to the days of Kölreuter.

By the middle of the eighteenth century, therefore, little doubt should have remained in scientific minds regarding the existence of sex in plants, or as to the necessity of the pollen as a fertilizing agent. As Kölreuter himself says:

> "The pollen is a collection of organic particles, which in every plant have a definite form; it is the true instrument in which the male fertilizing material (Saamen) is produced, disengaged, and made suited for dissemination." ("Vorläufige Nachricht," p. 7.)

Actual experiments in fertilization, many of them between plants of different species, had been successfully carried out in more than twenty important groups of plants, from many different families. We have also in Kölreuter's work a careful study of the characteristics of hybrids, obtained in sixty-five different hybridization experiments, conducted with species from a dozen different genera, belonging to diverse families, together with an accurate comparison of the characters of the hybrid plants of the first generation with those of their parents.

A scientific foundation had therefore been laid for genetic work in the breeding of plants. The value of Kölreuter's own experimental work was doubted, however, by influential contemporary critics, although Sageret (10), whose opinion should have carried weight, said of it:

> "Having several times repeated his experiments, I have occasion to convince myself more and more of his exactitude and of his veracity; I believe then that he merits all confidence."

Kölreuter began with perfectly settled convictions regarding sexuality in the plant kingdom. In the preface to his "Vorläufige Nachricht" of September 1, 1761, he states that he would have accompanied his manuscript material with special proof concerning sex in plants, if he had not considered it in his present view (bey gegenwärtiger Absicht) as in the highest degree superfluous.

> "The most important of these [e.g., the proofs in question] anyone can deduce therefrom, who has only to a tolerable degree a conception of this subject. I flatter myself in the meanwhile with the good hope that, if not through the already propounded propositions alone, yet at least

> through the whole of the plan of my observations and experiments, which will appear in the above-mentioned treatise, and of which the ones here presented are only a small part, I shall completely convince everyone, even the most stiff-necked doubter, of the truth of the sex of plants. If, contrary to all suppositions, such an one should still be found, who, after a close examination, still maintained the contrary, it would be as greatly a surprise to me, as though I heard anyone maintain at clear midday that it is night." ("Vorläufige Nachricht," Vorrede, p. 5.)

Despite the fact that Kölreuter had demonstrated conclusively the possibility of crossing plants, even "species," artificially, and had even laid the foundations for a knowledge of the laws governing hybrids, much doubt still remained in the minds of botanists, regarding the facts which Camerarius' and Kölreuter's experiments demonstrated. As Sachs remarks (9, p. 413):

> "The plant collectors of the Linnaean school, as well as the true systematists at the end of the eighteenth century, had little understanding for such labors as Kölreuter's, and incorrect ideas on hybrids and their power of maintaining themselves prevailed in spite of them in botanical literature."

Gärtner says of Kölreuter's work, writing in 1849 (3 c, p. 5):

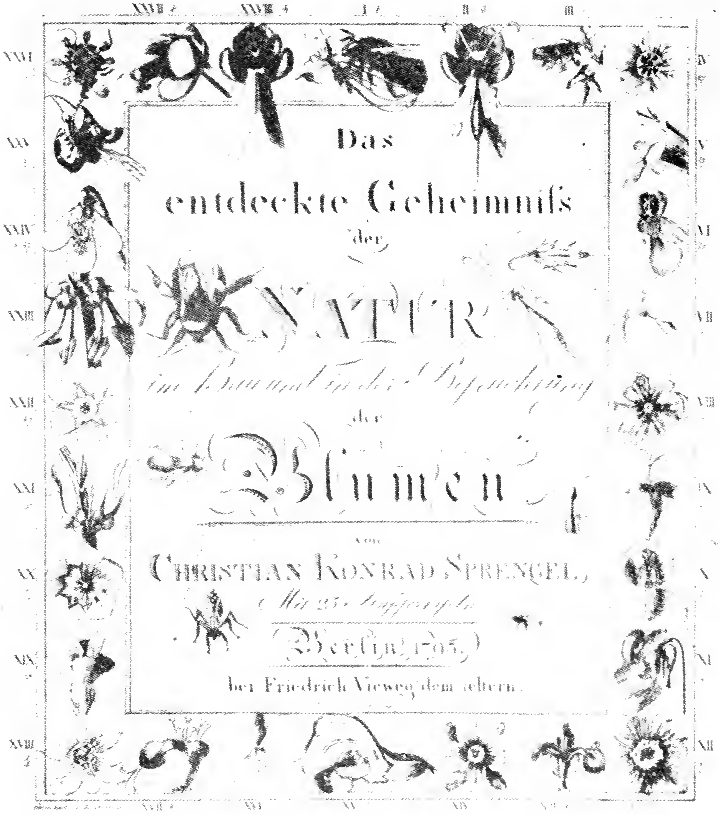
> "Hybridization in its scientific significance was so little thought of, and at the most regarded merely as a proof of the sexuality of plants, that the many important suggestions and actual data which this diligent and exact observer recorded in various treatises have found but little acceptance in plant physiological papers up to the most recent time. On the other hand, even in respect to the sexuality of plants, they were attacked to such a degree that their genuineness was doubted and strenuously contradicted, or else they were regarded as a sort of inoculation phenomenon belonging to gardening."

11. *Christian Konrad Sprengel.*

Christian Konrad Sprengel was born in Brandenburg a H. in 1750, as the fifteenth son of a clergyman. He studied theology and philology at Halle, and in 1774 became instructor in the school of the King Frederick Hospital, and at the Royal Military School in Berlin.

After six years of service, he was appointed (1780) to the position of Head (Rector) of the large Lutheran city school at Spandau, where his teaching was largely in the ancient languages, a position which he held until 1794. In this year he was retired on a pension, and spent his remaining years in Berlin, living in quite simple circumstances, until his death, which occurred April 7, 1816.

At the suggestion of a Dr. Heim, then a practising physician in Spandau, and afterwards a celebrated physician in Berlin, he was led to take up botanical studies as a relief from hypochrondria. It was thus that Sprengel became interested in the biology of the flower, and hence finally, in 1793, published the results of



Das
entdeckte Geheimniſs
der
NATUR
im Bau und in der Befruchtung
der
Blumen
von
Christian Konrad Sprengel.
Mit 25 Kupfertafeln.
Berlin, 1793.
bey Friedrich Vieweg dem ältern.

PLATE XXIII. Title-page of Sprengel's "Das entdeckte Geheimniss der Natur."

five years of minute and extensive observations and studies, in a folio volume with twenty-five plates, which contained hundreds of detailed and accurate illustrations of flowers and their parts. This famous work, "Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen," was based upon the thoroughgoing observation and investigation of nearly five hundred species.

Through lack of funds Sprengel was prevented from publishing the second part of his work, which led him, toward the end of his life, to give up botany altogether, and devote himself to classical studies. During his years of retirement in Berlin, he gave lessons in the classics and in botany for recreation, and on Sundays conducted botanical excursions in the neighborhood of Berlin for small fees.

On account of the dry and formal character of the botanical science of his time, Sprengel's work remained unnoticed for forty-three years after his death.

The first serious mention of it in scientific literature appears to have been that made by Darwin, in the "Origin of Species" in 1859. (6th ed. 1895, p. 119.)

Sprengel is described as a man averse to the conventional flatteries of life, and of a rather recklessly open type of character. In his Berlin excursions he is described as awakening attention through the wealth of his knowledge and his inwardly spiritual character, and as arousing interest alike in all the objects of nature,—an inscription on a gravestone, the construction of a windmill, the course of the stars, and the body of a plant. During Sprengel's Spandau period, it is stated, a large portion of his thirteen years of official duty was filled with an almost unbroken chain of events involving insubordination, quarrels with the authorities, and friction with the parents of the pupils, which circumstances led him to be described by a local chronicler as "inhuman in his punishments, arbitrary in his teaching, stubborn, and little religious." The whole truth appears to have been that Sprengel was a man of a large and powerful nature, with considerable intellectual gifts, rich knowledge, and aware of his own state of advancement, but uncompromising, and, from having been forced into too confined and narrow an environment in which his ideas and prepossessions found little opportunity for expression, his nature consequently spent itself in intractable and dictatorial contentions.

Of his botanical knowledge, gained during his Spandau studies, his contemporary, Willdenow, afterward the first professor of botany in the University of Berlin, made use in his "Prodromus Florae Berolinensis," 1787, and praised the self-taught botanist as "a thoroughly keen-minded plant investigator."

The discoveries of Christian Konrad Sprengel should have called attention to Kölreuter's antecedent discovery of the relation between insects and flowers. While Camerarius had demonstrated the fact that plants possess sex, and Kölreuter had shown that fertile hybrids could be produced between plants of different kinds, the further fact, that crossing in nature, at least among different individuals of the same species, is a common and ordinary phenomenon in the plant kingdom, was not at all known. Aware, as we are today, that the improvement of cultivated plants, due to the appearance of new strains and varieties, is to be accredited largely at the outset to the natural crossing of individuals standing in fairly close genetic relationship to one another, we can see the great importance, in the history of plant breeding, of Sprengel's discovery that flowers are commonly pollinated by insects, and that there is an intimate interrelationship between the plant and the insect worlds.

Sprengel's epoch-making book "The Newly-revealed Secret of Nature in the Structure and Fertilization of Flowers" (11) constitutes a third great landmark in plant breeding, after the original discovery of the possibility of artificial pollination by the Mesopotamian date growers. Such a wealth of accurate first-hand observations on the adaptations of flowers to cross-pollination had never before been made. To Sprengel also is due the discovery of dichogamy, i.e., the maturing of the stamens and the pistils of flowers at different times. His conclusion, that nature in most cases intended that flowers should not be fertilized by their own pollen, and that the peculiarities of flower structure can only be understood when studied in relation to the insect, was revolutionary for his time.

Sprengel's work has been well described by Sachs, as "the first attempt to explain the origin of organic forms from definite relation to their environment." (9, p. 415.)

Conceding the fact that plants actually have sex, it is plain that some kind of breeding must be possible. Granting that hybrids even between different species can be produced, it is further plain that new kinds of plants can be originated. But what of the additional fact, the contribution of Sprengel, that in general nearly all flowering plants with definite floral envelopes are naturally cross-fertilized. It signified that the bringing together of combinations of parental characters is the rule rather than the exception in nature, and that, therefore, the breeding of new types in the plant world may be said to be going on all the time. It remained for Darwin to show how the results from such perpetual crossings are limited and held in check by the operation of natural selection. At all events, Sprengel's discoveries at once disclosed at least an important reason for diversity, for so many variations in nature, upon which fact man had unconsciously depended for the selection of "superior" types of plants, and hence for the "improvement" of races.

Unfortunately, the discoveries and disclosures of Sprengel awakened little interest at the time. Like the work of Camerarius and Kölreuter, the investigations of Sprengel, in turn, suffered comparative obscurity. Biologists of his day believed in the dogma of the fixity of species, upon which Kölreuter's and Sprengel's experiments and discoveries regarding cross-pollination by means of insects tended to cast doubt, and to require the substitution, for the doctrine of the fixity of species, of the principle of the comparative stability of organic forms.

Although the scientific world traces a continuity of thought and investigation from Gärtner back to Camerarius, the fact must not be lost sight of that each of the three chief investigators who laid the early foundations of plant genetics, Camerarius, Kölreuter, and Sprengel, was considerably ignored by the biological science of his own time.

Two generations elapsed from the time of Camerarius to that of Kölreuter, and another from Kölreuter's time to that of Sprengel. It is more than a fourth generation from Sprengel's publication to the time of the work of William Herbert (1837); a third of a generation more to the appearance of Gärtner's memoir (1849), and about half of another generation again, before the appearance of Mendel's celebrated papers (1866), and finally,

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more than another generation until the date of the rediscovery of Mendel's work (1900), the beginning of the scientific period properly speaking.

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CHAPTER IV

THE EARLY ENGLISH HYBRIDISTS

AT the beginning of the nineteenth century there began to appear in England the first signs of the application of the science of hybridization to the practical art of breeding, in the work of Thomas Andrew Knight, and of William Herbert.

12. *Thomas Andrew Knight.*

Thomas Andrew Knight was a country gentleman by occupation. Born Angust 12, 1759, he was educated at Oxford, and early began to interest himself on his estate at Elton in Herefordshire in experiments in the raising of new varieties of fruits and vegetables. In 1795, his work as a horticulturist first became known through some papers read at the sessions of the Royal Society. He was an organizer of the Horticultural Society of London, founded 1804, of which he was president from 1811 until his death in 1838. He was an annual contributor to its "Transactions," and was the author of upwards of one hundred papers. In 1841, three years after his death, a collection of eighty-two of his papers was published by the botanists Bentham and Lindley. Of Knight's published papers, forty-six are enumerated in the Royal Society's Catalogue. Knight was not a scientific man, but a practical horticulturist with scientific instincts, who proceeded on the principle that the improvement of plants depended upon the same scientific laws as the improvement of animals, and that cross-breeding was the key to the origination of new and improved sorts. His principal work of crossing was carried out with currants, grapes, apples, pears, and peaches, to the end of producing hardier and superior fruits. One of his discoveries of genetic interest was that in crosses of varieties of red upon white currant, by far the greater number of the hybrids produced red fruit, in other words demonstrating the dominance of red. A con-

PLATE XXIV. Thomas Andrew Knight, 1759-1838.

clusion formulated by Knight, on the basis of his experience, afterwards confirmed by Darwin, and since called the Knight-Darwin law, was that:

> "New varieties of every species of fruit will generally be better· obtained by introducing the farina (pollen) of one variety of fruit into the blossom of another, than by propagating from one single kind." (3f, p. 38.)

However, the work of Knight which attracts the most attention from the standpoint of genetics is his experiment with peas. The paper in question, read before the Horticultural Society, June 3, 1823, was entitled "Some Remarks on the Supposed Influences of the Pollen, in Cross-breeding, on the Color of the Seed-coats of Plants and the qualities of Their Fruits."

This paper is really, in part, a reply to certain phases of the experiments of John Goss upon the same plant. Knight's introductory statement, which follows, is a curious reminder in point of form of Mendel's own introduction to his report upon his experiments with peas nearly half a century later. Knight says:

> "The numerous varieties of strictly permanent habits of the pea, its annual life, and the distinct character in form, size and color to many of its varieties, induced me, many years ago, to select it for the purpose of ascertaining, by a long course of experiments, the effects of introducing the pollen of one variety into the prepared blossoms of another. My chief object in these experiments was to obtain such information as would enable me to calculate the probable effects of similar operations upon other species of plants, and I believe it would not be easy to suggest an experiment of cross-breeding upon this plant, of which I have not seen the result, through many successive generations." (3f, p. 378.)

In the particular experiment in question Knight determined that, in crossing a pea with grey seed-coats upon one with white seed-coats, no immediate change in color took place, but that the resulting hybrid seeds produced plants the next year which uniformly bore grey seeds, as well as having the purple-colored stems and the flowers of the male parent. He further discovered the fact that by crossing plants grown from these (heterozygous) grey seeds, with pollen from what he calls a "permanent" white variety, plants of two types appeared, one bearing grey and the other white seeds—in other words, in modern terms, the result of the cross of a recessive white upon a hybrid dominant grey. No numbers are reported, so that a scientific basis of ratios, as later found by Mendel, was not laid.

Twenty-five years earlier, in 1799, Knight undertook experiments with plants to test the theory of "superfoetation," that is to say, the possibility of two males combining in the fecundation of a female. At the time, the behavior of the fertilizing cells was absolutely unknown, as was the fact that but one sperm cell was required to fertilize the egg. In fact, cells as such, and their function, were not as yet discovered. It was quite commonly supposed, for instance, that an excess of pollen in pollination produced an excess effect amounting to a preponderating evidence of the male characters in the offspring.

Peas were chosen for the purpose of the experiment in question. The principal object was to obtain new and improved varieties of apples, but inasmuch as years must elapse before the results would become known, it was resolved, in the interval, to experiment with annual plants.

> "Among these," he says, "none appeared so well adapted to answer my purpose as the common pea; not only because I could obtain many varieties of this plant, of different forms, sizes and colors; but also because the structure of its blossoms, by preventing the ingress of insects and adventitious fauna, has rendered its varieties remarkably permanent." (3a, p. 196.)

Having a variety in his garden which appeared to him, from having been long grown in the same soil, to have lost its vigor, he emasculated a dozen flowers upon it in 1787, pollinating half of them with the pollen from "a large and luxuriant grey pea," leaving the other half dozen as they were. The ovules in the pods of the unfertilized flowers, withered, of course.

> "Those in the other pods attained maturity, but were not in any sensible degree different from those afforded by other plants of the same variety, owing, I imagine, to the external covering of the seed (as I have found in other plants) being furnished entirely by the female." (*ib.*, p. 197.)

Knight was thus induced to take up garden peas for his experiments, for the same reason, as stated, that led Mendel later to do likewise. His reflections upon the reason for the act of fertilization by pollen from the grey-seeded pea (i.e., with grey seed-coats) not affecting the fertilized ovules in respect to their seed-coats, show the mind of an acute observer.

> "In the succeeding spring the difference, however, became extremely obvious; for the plants from them rose with excessive luxuriance, and the color of their leaves and stems clearly indicated that they had all

exchanged their whiteness for the color of the male parent; the seeds produced in autumn were dark gray." (*ib.*, p. 197.)

Here, then, is the *first recorded instance of color-dominance in peas.* Knight, however, did not follow out the results to the next generation from the selfed hybrids, but re-pollinated the hybrids with pollen from a white variety, as the result of which, he says, there were produced a variety of new kinds,

> "Many of which were, in size and in every respect, much superior to the original white kind, and grew with excessive luxuriance, some of them attaining the height of more than twelve feet. I had frequent occasion to observe, in this plant, a stronger tendency to produce purple blossoms and colored seeds than white ones; for, when I introduced the farina of a purple blossom into a white one, the whole of the seeds in the succeeding year became colored." (*ib.*, p. 197.)

Here again is an early observation of the fact of dominance, and possibly of heterosis. Knight proceeds to the conclusion that, by mixing the pollen of the two kinds of peas, he could, through the behavior of the seeds, readily determine whether "superfoetation" had taken place or not. In view of the non-existence of "superfoetation," except in the rare cases of dispermy, the experiment itself is not of importance, but it brought forth the following remark, which is interesting as showing Knight's knowledge of the fact of dominance of grey seed-coat color.

> "For as the offspring of a white pea is always white, unless the farina of a colored kind be introduced into the blossom, and as the color of the gray one is always transferred to its offspring, although the female be white, it readily occurred to me, that if the farina of both were mingled or applied at the same moment, the offspring of each could be easily distinguished." (*ib.*, p. 198.)

Pollinating the flowers of some of the hybrids with the pollen from a white-seeded pea, he says, "The second year I obtained white seeds." Here, he should have obtained gray and white, half and half, but he makes no mention of numbers, since the numerical relations of the seeds did not occur to him as being significant.

It is interesting to note the results of Knight's experiment in reciprocal crossing.

> "By introducing the farina of the largest and most luxuriant kinds into the blossoms of the most diminutive, and by reversing this process, I found that the powers of the male and female, in their effects upon the offspring, are exactly equal." (*ib.*, p. 200.)

The vigor of growth, the size of the seeds procured, and the season of maturity were the same, although the one was a very early and the other a very late variety.

> "I had in this experiment, a striking instance of the stimulative effects of crossing the breeds; for the smallest variety, whose height rarely exceeded two feet, was increased to six feet, whilst the height of the large and luxuriant kind was very little diminished." (*ib.*, p. 200.)

Despite the fact that Focke says (Pflanzenmischlinge, p. 436) "he has contributed more to our knowledge of hybrids than any other writer during the first half of the nineteenth century"—a statement which may, of course, perhaps be seriously disputed—it is nevertheless true that Knight was the first experimenter to apply the science of plant hybridization to plant improvement. Although endowed with scientific insight of no mean order, his chief claim to recognition as a plant breeder lies in the fact that he possessed a practical instinct for getting improved orchard fruits into existence. Knight remarked upon the fact that it had long since been ascertained by physiologists that, since the seed-coats, or membranes which cover the cotyledons of the seed, together with the receptacles which contain them, are visible for some time before the blossoms reach their full growth, therefore the existence of such structures is independent of the influence of the pollen. The fact is also that the seed-coats and the fruit of some species reach nearly if not completely their full growth, when the pollen has been entirely withheld; therefore, from these and other observations, he concludes:

> "It has been inferred that neither the external cover of the seeds, nor the form, taste or flavor of fruits, are affected by the influence of the pollen of a plant of a different variety or species." (3f, p. 377.)

There exists, however, he continues, some difference of opinion in this regard, the experiments of Goss appearing to support the opinion that:

> "The color of the seed-coat, at least, may be changed by the influence of the pollen of a variety of different character." (*ib.*, p. 378.)

The account which Knight then gives of his experiments is as follows:

> When the pollen of a grey-seeded pea was used to fertilize the flowers of a white variety, "no change whatever took place in the form, or color, or size of the seed; all were white, and externally quite similar to others which had been produced by the unmutilated blossoms of the same plant." (*ib.*, p. 379.)

These seeds, however, sown the following year,

> "uniformly afforded plants with colored leaves and stems, and purple flowers; and these produced gray peas only." (*ib.*, p. 379.)

In the case of Goss's "Blue Prussian" Pea, Knight continues, the cotyledons being blue in color, and this color being perceptible through the semi-transparent seed-coats, caused the latter to appear blue, although they were really white. He concludes:

> "The color of the cotyledons only was, I therefore conceive, changed, whilst the seed-coats retained their primary degree of whiteness." (*ib.*, p. 379.)

Knight therefore finally holds that the opinions that neither the color of the seed-coats, nor the form, taste, or flavor of fruits, are ever affected by the immediate influence of the pollen of a plant of another variety or species, are well-founded (*ib.*, p. 380.)

Knight thus built up an opinion of a general character regarding the fruits of plants, based upon his experiments involving the seed-coats alone. However insufficient such a conclusion seems at the present time, drawn from such partial premises, it is explainable by the fact that the morphology of seed-development was, at that time, little understood, so that the factors affecting any one part of the fruit, such as the seed-coats, might easily be conceived of as similarly affecting other parts.

The following examples will serve to illustrate the nature of his results. Of his currant crosses, he says:

> "Five varieties, three red and two white, out of about two hundred, appeared to me to possess considerably greater merits than either of their parents, and one of the red will, I believe, prove larger than any red currant now in cultivation."

By crossing the "Noblesse" peach (female) by "Nutmeg" (male), he obtained about twenty seedlings, of which three:

> "Appeared better peaches than I previously possessed." Of one of these he says: "Its fruit has attained a more uniform degree of perfection than I have ever witnessed in any other variety. The trees have also been free from every vestige of mildew, in a situation where the disease is very prevalent, and have entirely escaped the attacks of insects."

In 1809, Knight gave a paper before the Royal Society, entitled: "On the comparative influence of male and female parents on their offspring." (3c.)

Prompted by the conception of Linnaeus, "that the character of the male parent predominated in the exterior parts of both plants and animals," Knight undertook some experiments with the different species of fruit trees, but most extensively with the apple. He makes the general statement:

> "I have observed that seedling plants, when propagated from male and female parents of distinct characters and permanent habits, generally, though with some few exceptions, inherit much more of the character of the female, than of the male parent." (p. 393.)

Without commenting upon this generalization, the experiments themselves may be briefly noticed. Crosses were made between the British and the Siberian crab-apple, which as, he says,

> ". . . however dissimilar in habit and character, appear to constitute a single species only, in which much variation has been effected by the influence of climate on successive generations." (p. 395.)

Knight reports a reciprocal cross between apple and Siberian crab. Both trees were trained to walls, where they blossomed earlier than ordinarily. All the flowers on the two trees except those used were removed and the stamens carefully removed from the remaining ones. Of the plants produced by cross-pollination, Knight says:

> "There was a very considerable degree of dissimilarity in the appearance of the offspring; and the leaves, and general habits of each, presented an obvious prevalence of the character of the female parent." (p. 393.)

Where the British crab-apple was used as the female parent, the buds did not unfold quite so early in the spring, and their fruits generally exceeded very considerably in size those which were produced by the trees which derived their existence from the seeds of the Siberian crab.

> "There was also a prevalence of the character of the female parent in the form of the fruit." (3c, p. 394.)

The greater portion of the article is taken up with a discussion of similar cases in animal breeding. One observation is not without interest.

> "In several species of domesticated or cultivated animals (I believe in all), particular females are found to produce a very large majority, and sometimes all their offspring, of the same sex; and I have proved repeatedly that, by dividing a herd of thirty cows into three equal parts, I could calculate, with confidence, upon a large majority of females from one part, of males from another, and upon nearly an equal number of males and females from the remainder. I have frequently endeavored to

> change these habits by changing the male; but always without success, and I have, in some instances, observed the offspring of the one sex, though obtained from different males, to exceed those of the other in the proportion of five or six and even seven to one. When on the contrary, I have attended to the numerous offspring of a single bull, or ram, or horse, I have never seen any considerable difference in the number of offspring of either sex." (3c, pp. 397-8.)

This interesting empirical observation is quoted as being of historical interest, and the observation regarding the difference in the reciprocal apple crosses is worth preservation.

Knight sums up his practical views upon the relation of the science of botany to the breeding of plants in the following words:

> "I cannot dismiss the subject, without expressing my regret, that those who have made the science of botany their study, should have considered the improvement of those vegetables which, in their cultivated state, afford the largest portion of subsistence to mankind, and other animals, as little connected with the subject of their pursuit. Hence it has happened that whilst much attention has been paid to the improvement of every species of useful animals, the most valuable esculent plants have been almost wholly neglected. But when the extent of the benefit which would arise to the plants, which, with the same extent of soil and labor, would afford even a small increase of produce, is considered, this subject appears of no inconsiderable importance. . . . The improvement of animals is attained with much expense, and the improved kinds necessarily extend themselves slowly; but a single bushel of improved wheat or peas may in ten years be made to afford seed enough to supply the whole island." (3a, p. 204.)

Focke, in his Pflanzenmischlinge," pp. 432-3, gives the following summary of Knight's services to the science and practice of hybridization:

> "Toward the end of the eighteenth century, a man appeared, whose works have been of particular significance for the knowledge of fertilization and crossing, Thomas Andrew Knight, the celebrated fruit and vegetable breeder. Starting with the successful efforts of the animal breeders, he came upon the thought whether it was not possible to improve domestic animals through crossing the races, to obtain more admirable sorts of economic plants. Without knowing anything of Kölreuter, he began his experiments with fruit trees, and from 1787 on, with peas, with which he was naturally able much earlier to turn out definite results. The progeny of his crossed races of peas gained extraordinarily in vigor and yield. Already in 1799 ('Phil. Trans.,' 1799, Part I, p. 202), Knight was able to express the principle, that nature intended that a sexual intercourse should take place between neighboring plants of the same species. He laid down this principle through his results in individual and race crosses, especially in the genus *Pisum*."

13. *William Herbert.*

The work of William Herbert was to a considerable extent contemporary with that of Knight. Born January 12, 1778, son of the Earl of Carnarvon, educated at Eton and Oxford, he was trained for the bar, which he finally left for the Church, entering orders, and finally becoming Dean of Manchester. Fond of out-door life and sport, he possessed also, in addition to literary talent, an instinct for plant studies. Herbert worked largely on the improvement of florists' flowers but also conducted experiments with some agricultural plants. He was engaged for a considerable time upon his own experiments, before he came upon the work of Kölreuter, some fifty or more years before his day, which he immediately assimilated, and estimated at its true value, as the following comment indicates:

> "The first experiments, with a view to ascertain the possibility of producing hybrid vegetables, appear to have been made in Germany, by Kölreuter, who published reports of his proceedings in the Acts of the Petersburgh Academy between fifty and sixty years ago. *Lycium*, *Digitalis*, *Nicotiana*, *Datura* and *Lobelia* were the chief plants with which he worked successfully, and as I have found nothing in his reports to the best of my recollection opposed to my own general observations, it is unnecessary to state more concerning his mules than the fact that he was the father of such experiments. They do not seem to have been at all followed up by others, or to have attracted the attention of cultivators or botanists as they ought to have done; and nothing else material on the subject has fallen under my notice of earlier date than Mr. Knight's report of his crosses of fruit trees, and my own of ornamental flowers, in the Transactions of the Horticultural Society of London. Those papers attracted the public notice, and appear to have excited many persons, both in this country and abroad, to similar experiments." (2c, p. 335.)

In the year 1819, after having paid attention for some years to the production of hybrid plants, but then unaware of the work of Kölreuter, Herbert brought his views on the subject of hybrids before the Horticultural Society, and they were published in the "Transactions" of that body. He comments upon the matter as follows:

> "It is, however, satisfactory to find at the present day, after the attention of botanists and cultivators has been fully called to the subject during the space of many years, and a multitude of experiments carried on by a variety of persons, that, although our knowledge of its mysteries is still very limited, my general views have been fully verified, and my anticipations confirmed in a manner which I was scarcely sanguine enough to have expected." (2c, p. 336.)

The view then quite generally prevalent among botanists concerning hybridization was that a fertile cross was of itself proof that the two parents were of the same species, while sterile offspring constituted conclusive evidence that they were of different species. This view was held, as Herbert says:

> "Without suggesting any alteration in the definition of the term 'species,' but leaving it to imply what it had before universally signified in the language of botanists."

Again he says:

> "Having, in fact, the same fundamental opinion, that the production of a fertile intermixture designated the common origin of the parents, I held also, what experience has in a great measure confirmed, that the production of any intermixture amongst vegetables, whether fertile or not, gave reason to suspect that the parents were descended from one common stock, and showed that they were referable to one genus; but that there was no substantial and natural difference between what botanists had called species, and what they had termed varieties, the distinction being merely in degree, and not absolute; so that, without first reforming the terms used in botany, and ascertaining more precisely what was meant by a species, those who argued on the subject were fighting the air." (2c, p. 337.)

Herbert's entire freedom from any slavish adhesion to the species idea with respect to hybrids is plainly stated.

> "Further experiments have shown," he says, "that the sterility or fertility of the offspring does not depend upon original diversity of stock; and that, if two species are to be united in a scientific arrangement on account of a fertile issue, the botanist must give up his specific distinctions generally, and entrench himself within the general." (2c, p. 337.)
>
> "In fact there is no real or natural line of difference between species and permanent or descendible variety, as the terms have been applied by all botanists; nor do there exist any features on which reliance can be placed to pronounce whether two plants are distinguishable as species or varieties. Any person, who attends to the subject, will perceive that no botanist has laid down any precise rules by which that point of inquiry can be solved, and that the most variable, contradictory and unsubstantial features have been taken by different persons, and by the same person on different occasions, to uphold the distinctions they proposed to establish; the truth being that such distinctions are quite arbitrary, and that, if two plants are found capable of inter-breeding, when approached by the hand of man, they are as much one as if they were made to intermix more readily and frequently by the mere agency of the wind, or assiduity of insects, and are not separable with more truth by any positive difference, than the varieties which cannot be prevented from crossing with each other when in the same vicinity." (2c, p. 341.)

It was the view of Herbert that fertility in hybrids depended much upon circumstances of climate, soil and situation. He finally concludes that experiments had made it almost certain

> "that the fertility of the hybrid or mixed offspring *depends more upon*

the constitutional than the closer botanical affinities of the parents." (2c, p. 342.)

As to whether there was a real fundamental difference between plants which could produce fertile and those which could produce only sterile offspring by crossing, Herbert says further:

> "It was my opinion that fertility depended much upon circumstances of climate, soil and situation, and that there did not exist any decided line of absolute sterility in hybrid vegetables, though from reasons which I did not pretend to be able to develop, but undoubtedly depending upon certain affinities either of structure or constitution, there was a greater disposition to fertility in some than in others. Subsequent experiments have confirmed this view to such a degree as to make it almost certain—that the fertility of the hybrid or mixed offspring depends more upon the constitutional than the closer botanical affinities of the parents." (2c, p. 342.)

He holds that it obtains as a general fact throughout the plant kingdom, that species which have close botanical affinity, if they have widely different soil or climatic requirements, are apt to produce sterile offspring as the result of a cross, while, if they have the same constitutional habit, they tend to give rise to fertile offspring.

From the standpoint, then, of a practical plant hybridizer and horticulturist, Herbert holds that:

> "Any discrimination between species and permanent varieties of plants is artificial, capricious, and insignificant; that the question which is perpetually agitated, whether such a wild plant is a new species, or a variety of a known species, is waste of intellect on a point which is capable of no precise definition." (2c, p. 346.)
>
> "The effect, therefore, of the system of crossing, as pursued by the cultivator, instead of confusing the labors of the botanist, will be to force him to study the truth, and take care that his arrangement and subdivisions are conformable to the secret laws of nature; and will only confound him when his views shall appear to have been superficial and inaccurate; while on the other hand it will furnish him an irrefragable confirmation when they are based upon reality." (2c, p. 346.)

The attitude of Herbert with regard to the production of hybrids was not, however, so much the attitude of the scientist as that of the horticulturist and florist. His point of view is well stated in the following:

> "To the cultivators of ornamental plants, the facility of raising hybrid varieties affords an endless source of interest and amusement. He sees in the several species of each genus that he possesses, the materials with which he must work, and he considers in what manner he can blend them to the best advantage, looking to the several gifts in which each excels, whether of hardiness to endure our seasons, or brilliancy in its colors,

> of delicacy in its markings, of fragrance, or stature, or profusion of blossom, and he may anticipate with tolerable accuracy the probable aspect of the intermediate plant which he is permitted to create; for that term may be figuratively applied to the introduction into the world of a natural form which has probably never before existed in it." (2c, p. 346.)

With regard to the matter of inheritance of winter-hardiness, Herbert did some experimentation, as the result of which he found that the hybrid offspring held an intermediate position, being:

> ". . . less hardy than the one of its parents which bears the greatest exposure, and not so delicate as the other; but if one of the parents is quite hardy and the other not quite able to support our winters, the probability is that the offspring will support them, though it may suffer from a very unusual depression of the thermometer or excess of moisture which would not destroy its hardier parent." (2c, p. 347.)

Regarding the matter of acclimatization, he held substantially the same view which generally obtains among plant physiologists of the present day, that:

> "It does not appear that in reality any plant becomes acclimated under our observation, except by crossing with a hardier variety, or by the accidental alteration of constitution in some particular seedling; nor that any period of time does in fact work an alteration in the constitution of an individual plant, so as to make it endure a climate which it was originally unable to bear." (2c, p. 347.)

Entering into details regarding hybrids of his acquaintance, Herbert notes in fact that the first hybrid among liliaceous plants appearing in English gardens was the cross between *Hippeastrum vittatum* and *H. regium.* The next being the cross between *Crinum capense*, and *Crinum zeylanicum* in the greenhouse of the Earl of Carnarvon in 1813.

> "It is to be observed," he remarks, "that in some cases, the seminal varieties of plants preserve themselves almost as distinct in their generations as if they were separate species" (2c, p. 366),

and instances the cases of the orange, yellow, white, black, red, and pink hollyhocks, which come true from the seeds, although planted adjacent in the garden. He speaks also of the tendency among carnation seedlings to follow the color of the parent plant.

> "I have had greater success," he says, "than any other person in raising from seed double camellias of various tints and appearance, and some of the best have been produced either from single flowers, or plants raised from single ones, impregnated by the pollen of double flowers, preferring, where it can be got, the pollen that is borne on a petal." (2c, p. 367.)

He notices the curious fact that the striped sorts of camellias have usually more white in their flowers when they flower early in the spring, and that the earliest ripening seed of the year is most apt to yield white or particolored seedlings.

Herbert carried on some experiments with double flowers and, in 1834, undertook an experiment in the improvement of agricultural plants, pollinating the Swedish turnip (rutabaga) with pollen of the white, and flowers on another branch of the same plant with pollen of the red-rooted turnip, which he speaks of as producing

> ". . . perhaps a greater tonnage than the white, bearing both frosts and unfavorable summers better, and thriving in soils where the white does not succeed." (2c, p. 370.)

The seeds sown, produced good roots the same season:

> "The leaves differed in appearance from those of the Swedes, and did not, like them, retain the rain-water on their surface." (2c, p. 370.)

In the following spring, the hybrids came into flower, the flowers of the hybrids being, for the most part, bright yellow like those of the male, a smaller number bearing straw-colored flowers like the Swedish turnip, but there were no intermediates.

In a paper entitled "On hybridization amongst vegetables," Jour. Hort. Soc. of London, 2:1-28; 81-107 (1847), Herbert discusses quite at length the species question, and shows how firm the allegiance still remained to the conception that fertile offspring produced from a cross, constituted *prima facie* evidence that the parents were within the same species. He says:

> "And that is the use of hybridizing experiments, which I have invariably suggested; for, if I can produce a fertile offspring between two plants that botanists have reckoned fundamentally distinct, I consider that I have shown them to be one kind; and indeed I am inclined to think that, if a well-formed and healthy offspring proceeds at all from their union, it would be rash to hold them of distinct origin." (2d, p. 7.)

Herbert states (*ib.*, p. 8), that he had had:

> ". . . no opportunities, by the help of a powerful microscope, of pursuing any investigation into the process by which the pollen fertilizes the ovules,"

and goes on to say that, although he could not therefore undertake to contradict those who asserted that the pollen grains,

> "from their own bulk, emitted tubes which reached from the surface of the stigma to ovules in the germen"—a distance, as in certain species of *Hymenocallis*, amounting to sometimes 12-13 inches—it did not appear

possible to him that "such a minute body should emit a tube of such length, through which its contents were passed into the ovary, as asserted." (p. 8.)

Later on (p. 8) he alludes to the matter again:

> ". . . it is utterly impossible that such a minute body should emit such a pipe and its contents, that is, emit it of its own substance," and adds that he apprehends the truth to be "that by contact with the juices of the cognate plant it acquires that which enables it to gain bulk for such an elongation."

Herbert noticed the fact that in species crosses (e.g., *Passiflora coerulea* × *onychina*) the ovaries may develop as the result of the fertilization stimulus (in this case forming "two fine plump fruits, two inches long"), the interior remaining empty as a bladder, "the outer coat of the fruit only having been fertilized in consequence of the weakness of the cross-bred pollen." (*ib.*, p. 9.) In other cases, he comments, one may find a perfect ovary, and seeds grown to full size, although "containing a perishable lymph, and no sound kernel." It appears to Herbert that the fertilization-process is one which may consist of gradual degrees, and that "it follows therefore that a continued operation of the pollen must be necessary to produce all these requisites for the formation of a good seed." (*ib.*, p. 9.) He speaks of the "fertilization" of the seed-coats and of the "albumen" as a process independent of the fertilization of the ovules, since the result of such fertilization may cause the seeds to grow, although without developing an embryo. He finally concludes (p. 10):

> "If, therefore, as I apprehend, the pollen tubes cannot reach the ovules without deriving substance from the cognate juices of the style through which they descend, it becomes easy to understand how there may be sufficient affinity between them to carry on the process to the degree necessary for quickening the capsule, but not to carry it on to the point requisite and with the excitement and irritability necessary for reaching the ovules, etc."

Again, he continues, where adaptation of the two types is perfect, a perfect offspring is produced; where it is not perfect, an inadequate or weak fertilization occurs, and, "it is further to be observed that there is frequently an imperfect hybrid fertilization which can give life, but not sustain it well." Among these he mentions *Hibiscus palustris* × *speciosus*, of which the seeds always sprouted, but of which only one was saved to the third leaf, when it perished. He states that of *Rhododendron ponti-*

cum × an orange *Azalea* he had never raised seedlings beyond the third or fourth leaf. From *Rhododendron canadense* × *Azalea pontica*, he succeeded in saving "only one out of more than a hundred seedlings, and that became a vigorous plant." (*ib.*, p. 11.)

He says further:

> "In these cases I apprehend that, although the affinity of the juices is sufficient to enable the pollen to fertilize the ovule, the stimulus is insufficient, the operation languid, and the fertilization weak and inadequate to give a healthy constitution. It has been generally observed that hybrid fertilization is slower than natural fertilization, and that often a much smaller number of ovules are vivified." (p. 11.)

Herbert comments shrewdly on Knight's report as to having "given at the same time the curl of one cabbage and the red color of another to a third variety." (p. 12.) This Herbert considers to have been impossible, if it was supposed to have been effected by one fertilization.

> "He might easily have obtained the twofold features by two successive crosses, but I believe not in one generation by simultaneous application of different pollens: for I do not think that two grains even of the same pollen can get effectual access to the foramen of one and the same ovule." (*ib.*, p. 12.)

Herbert did much work, both of a systematic sort and by way of crossing, upon the Amaryllidaceae, the species chiefly utilized belonging to the genera *Hippeastrum*, *Crinum* and *Hymenocallis*, the genus *Narcissus* being also rather extensively dealt with. In December, 1819, Herbert made a communication to the Horticultural Society of London (Vol. 4, pp. 15-50), entitled "On the production of hybrid vegetables; with the result of experiments made in the investigation of the subject," in which a number of observations are made of some genetic value. For the most part, the article consists of an account of various interesting crosses with a number of genera of ornamental bulbous plants, together with some discussion of the species question, and of the fact of sterility in certain crosses. The case is reported of a cross by Knight, between a smooth cabbage (female) and a curled and red cabbage (male), in which the curled leaf character and the red color both appeared in the seedlings. The state of knowledge concerning fertilization is indicated by Herbert's discussion of the subject. Seeds originally exist in the "germen." During the maturation of the stigma, the germen and seeds grow until the stigma reaches maturity, when the "germen" generally ceases to grow, and unless it receives the "congenial dust" it fails. Herbert then raises the question, how it is that a seed can draw from the plant the nourishment necessary for its growth up to a certain point, and yet be unable to obtain the further support necessary to bring it to maturity. His opinion follows:

> "I suspect the fact to be," he says, "that as long as the style remains fresh the seed receives a portion of its nourishment by a return of the sap from the style and stigma; and thus continues to advance rapidly in growth without any fecundation: but I apprehend that, during that period, it is only that part of the seed, which is to form the cotyledon, or seedling leaf, that grows, and that the actual germ of the young plant does not exist completely till after the fecundation of the stigma, when I conceive it to be actually formed by an union of the substance transmitted through the vessels of the style, and that which was already with the cotyledon, and thus partake of the type of both parents." (2a, p. 29.)

"If," Herbert further comments, "the fecundation only gave the embryo a stimulus to excite it to draw nourishment," then, the male type would not be evident in the offspring. He further decides upon the necessity of the pollen as the source of the male contribution, on the basis of the fact which he had observed that, in the case of seeds apparently perfect, where the stigma had not been pollinated, or had been pollinated with pollen from a plant not sufficiently related,

> "on opening such seeds, there is a total deficiency of the germ, the seed being an inert lump, which cannot vegetate." (2a, p. 29.)

Herbert alludes to the idea, which he says was somewhat prevalent, that if plant hybrids are fertile, their progeny will revert to the type of the female parent. (2a, p. 40.) This he holds to be extremely improbable, and, if true, almost inexplicable, the reason being that, if fertile, they can be fecundated by pollen from either parent.

The careful perusal of the entire body of William Herbert's contributions shows the operation of a careful, logical, strong, and able mind, which, within the entire limit of its opportunity, made thorough and conscientious efforts in the breeding of plants, and secured considerable results of much interest, and made many acute and shrewd observations of a botanical nature.

The services which Dean Herbert rendered plant breeding, consisted notably in the clear and intelligent manner in which he contended, contrary to Knight and many others, that species and varieties were but arbitrary and artificial distinctions in the plant kingdom, so far as hybridization was concerned, and that the idea of determining whether "species" were such, or only "varieties," through the relative fertility of their hybrid offspring, was an error, since

> ". . . species and varieties are but intergrading types. The species of botanists and the permanent local varieties are not essentially different in their nature, but are variations induced by causes more or less remote in the period of their operation, though the features of their diversity may be severally more or less important, and they differ from accidental varieties in the permanent habit of similar reproduction, which they have acquired from soil and climate, and that after a long succession of ages."

He was a close and keen observer, inclining toward experimentation with ornamental flowers, as did Knight toward experiments with horticultural fruits. He also calls for mention as the first English-speaking investigator to notice the work of Kölreuter.

14. *John Goss and Alexander Seton.*

Besides the work of Knight and Herbert, an experiment with garden peas from the first half of the nineteenth century, which has elicited considerable interest, also because of its suggestion of the later discoveries of Mendel, is that of John Goss, of Hatherleigh, in Devonshire, England.

In the summer of 1820, Goss pollinated flowers of the "Blue Prussian" variety with pollen of a dwarf pea known as "Dwarf Spanish," obtaining, as the result of the cross, three pods of hybrid seeds. In the spring of 1821, when he opened these pods for planting, he was surprised to find that the color of the seeds (i.e., of the cotyledons), instead of being a deep blue like those of the female parent, was yellowish-white like that of the male. Here was evidently a case of complete dominance of yellow-white over blue cotyledons. However, the plants growing from these seeds "produced some pods with all blue, some with all white, and many with both blue and white seeds in the same pod." Here was evidently a plain discovery of the fact of segregation, according to what later became known as Mendel's law. The following spring (1822) he separated the blue peas from the white, sowing the seeds of each color in separate rows. He found the blue seeds, which would now be called the recessives, produced in turn only blue seeds, while the white seeds, or dominants, "yielded some pods with all white, and some with both blue and white peas intermixed." Here, then, is the typical case of the segregation from the heterozygotes of hybrid dominants, without of course statistical data.

Although Goss, in this experiment, undoubtedly made evident the facts of dominance and segregation, he did not recognize them as such, nor did he apparently, sow the seeds of his different plants separately, or make counts as did Mendel, of the numbers of seeds of the two colors found on each separate plant. Goss was chiefly interested in the question of the possibility of the "new variety" having superior value as an edible pea, and remarked that, in case it possessed no superior merit, there might yet be "something in its history that will emit a ray of physiological light." However, the "physiological light" did not appear until after the rediscovery of Mendel's papers in 1900. The paper of John Goss was read before the Horticultural Society, October 15, 1822. (1.)

At the meeting of the 20th of August preceding, a communication was read on the same subject from Alexander Seton. Seton had pollinated the flowers of the "Dwarf Imperial," a green-seeded pea, with the pollen of a tall white-seeded variety. One pod with four peas was produced, all of which were green, possibly the dominance of green cotyledon color over its absence (white). The plants growing from the four peas (F_1 seeds) were intermediate in size between the two parents; and the pods, on ripening,

> ". . . instead of their containing peas like those of either parent, or of an appearance between the two, almost every one of them had some peas of the full green color of the Dwarf Imperial, and others of the whitish color of that with which it had been impregnated, mixed indiscriminately, and in undefined numbers; *they were all completely either of one color or of the other, none of them having an intermediate tint.*" (5, p. 237.)

Here again are recorded the phenomena of dominance and of segregation, but owing to the fact that the numbers of the seeds were not counted, the results were not available for scientific purposes, nor would they have aroused attention, any more than those of Goss, except for Mendel's work later.

15. *The Experiments of Thomas Laxton.*

In 1872, Thomas Laxton published, in the Journal of the Royal Horticultural Society, results of hybridization experiments, entitled "Notes on Some Changes and Variations in the Offspring of Cross-fertilized Peas" (4b), which have several points of distinct interest: first, in that the fact of dominance in color and form of the seeds was brought out; second, from the fact that, to a certain limited extent, a statement of numerical results was attempted. The results in neither of these were sufficient to constitute a scientific experiment, but the work as a whole gives evidence of care, close observation, and some thought. Among the several reported pieces of experimental work with peas before Mendel, Laxton's is perhaps to be commended as being more nearly of an exact nature, and is also interesting from the fact that it constitutes the last experimental work in the hybridization of peas, published before the final re-appearance of Mendel's papers themselves. Laxton says:

> "Since the year 1858, I have been carrying on continued and successive courses of experiments in cross-fertilizing the cultivated varieties of the Pea, partly with a view to produce improved characters, and partly for the purpose of noting the results of artificial impregnation on a genus of plants, which, although not absolutely beyond the reach of accidental cross-fertilization, is, for most practical purposes, sufficiently free from it to make the changes produced by artificial impregnation approximately reliable, at all events more so than in the majority of genera." (4b, p. 10.)

Laxton, at the time of his experiments, was not aware of the work of Knight with peas some fifty years previously.

In 1866, a cross was made upon an early, white-flowered variety, known as "Ringleader," with round, white seeds, and growing to a height of about 2½ feet, by a purple-flowered variety known as "Maple," with slightly indented seeds, and taller than the preceding. This produced one pod, containing five round, white peas like those of the female parent, the ordinary result. The seeds of the parent variety known as "Maple" are not described, but the results leave it to be inferred that the seed-coat color was grayish-purple, whence the name. In 1867, the five seeds of the F_1 generation produced "tall, purple-flowered, purplish-stemmed" plants, and the seeds, "with few exceptions," had "maple or brownish-streaked seed-coats." The remainder are reported with "entirely violet or deep purple-colored envelopes" (the ordinary dominant for seed-coat color in the F_1). The dominance of roundness in the first generation was followed in the second (the F_1 for the seed-coats) by segregation, which is recorded by Laxton, to the effect that "in shape, the peas were partly indented; but a few were round." (4b, p. 11.)

The lack of a proper ratio in this case, of 3 round to 1 indented, was probably due to the small number of plants involved.

In 1868 (the F_2 for flower and seed-coat color), Laxton says:

> "Some of the plants had light-colored stems and leaves; these all showed white flowers and produced round white seeds. Others had purple flowers, showed the purple on the stems and at the axils of the stipules, and produced seeds with maple, grey, purple-streaked, or mottled, and a few only, again, with violet-colored envelopes." (4b, p. 11.)

It is further stated that:

> "The pods on each plant, in the majority of instances, contained peas of like characters; but in a few cases the peas in the same pod varied slightly, and in some instances a pod or two on the same plant contained seeds all distinct from the remainder." (4b, p. 11.)

It is reported that the white-flowered plants of the F_2 were

> "generally dwarfish, of about the height of 'Ringleader,' but the colored-flowered sorts varied altogether as to height, period of ripening, and color and shape of seed." (p. 11.)

There would appear to be here some evidence of partial linkage of height with white flower and seed-coat color.

The outline of the results of Laxton's cross, stated in modern terms, is as follows:

1866 *Parents*

"Ringleader"	*"Maple"*
Flowers—white	Flowers—purple
Seed-coats—white	Seed-coats—"maple"
Cotyledons—round	Cotyledons—indented
Height—2½ feet	Height—taller than "Ringleader"

Progeny

1866. F_1 (for cotyledons)
Cotyledons—round

1867. F_1 (for flower color and seed-coat color)
Flowers—purple
Seed-coats

(1)	(2) ("a few")
Maple or brownish-streaked	Violet or deep purple

Cotyledons—partly indented; a few round
Height—tall

1868. F_2

(1)	(2) ("a few only")
Flowers—purple	Flowers—purple
Seed-coats—maple-grey, purple-streaked, or mottled	Seed-coats—violet
Cotyledons—round or partially indented	Cotyledons—round or partially indented
Height—variable	Height—variable

(3)
Flowers—white
Seed-coats—white
Cotyledons—round
Height—same as "Ringleader"

(4) (on some of the purple-flowered plants)

(4—1)	(4—2)
Seeds not described; presumably shades of maple, etc.	(A few pods on each plant) Seed-coats all white (some pods) Seed-coats black (others) Seed-coats violet (a few)

1869. F_3

Progeny of (1)

(1—1) ("majority")	(1—2) (minority)
Flowers—purple	Flowers—purple
Seed-coats—purple or grey	Seed-coats—maple or brown-streaked
Cotyledons—round or only partially indented	Cotyledons—round or only partially indented

Progeny of (2)

(2—1) ("almost invariably")	(2—2) ("now and then")
Flowers—purple	Flowers—purple
Seed-coats—purplish-grey, or maple	Seed-coats — clear violet ("either wholly in one pod, or only a single pea in a pod")
Cotyledons—round or only partially indented	Cotyledons—round or only partially indented

Progeny of (3) (all)
Flowers—white
Seed-coats—white
Cotyledons—round

As the seeds of the F_2 generation (reported as a "few only"), with "violet-colored envelopes," as distinguished from the majority having maple-grey and mottled seed-coats, these, when again sown, are reported as producing "nearly all maple or particolored seeds, and only here and there one with a violet-colored envelope." The violet seed-coat color is also reported as having "appeared only incidentally, and in a like degree in the produce of the maple-colored seeds." (4b, p. 11.)

In the following year, 1869, the seeds of the different types of the preceding year were again sown separately. The white-seeded peas again produced only plants with white flowers and round white seeds. Some of the colored seeds, which Laxton said he had expected would produce purple-flowered plants, produced plants with white flowers, and round, white seeds only (in other words recessives). The majority of the colored seeds, however, produced plants with purple flowers, and seeds "principally marked with purple or grey, the maple or brown-streaked being in the minority." (*ib.*, p. 11.)

It is stated that in some pods the seeds were all white, in others all black, and in a few all violet, and again that:

> ". . . those plants which bore maple-colored seeds seemed the most constant and fixed in character of the purple-flowered seedlings; and the purplish and grey peas, being of intermediate characters, appeared to vary most. The violet-colored seeds produced almost invariably purplish, grey or maple peas, the clear, violet color only now and then appearing, either wholly in one pod, or a single pea or two in a pod." The purple-flowered plants are stated to produce from the 1869 sowing, seeds that were "either round or only partly indented," the plants varying as to height and time of maturity. (*ib.*, *p.* 12.)

Laxton also records the important fact that

> "in no case, however, does there seem to have been an intermediate-colored flower . . . I have never noticed a single tinted white flower nor an indented white seed in either of the three years' produce." (*ib.*, p. 12.)

The quantities of the different colors produced in the seeds of the 1869 plants, are reported as being, in order of their amounts, as follows:

> "First, white, about half; second, purplish, grey, and violet (intermediate colors) about three-eighths; third, maple, about one-eighth." (p. 12.)

True ratios are, of course, not derivable, on account of the small numbers involved. Laxton's own conclusion as to the parental types is as follows:

> That the white-flowered, white-seeded pea is "an original variety, well fixed and distinct entirely from the maple, that the maple is a cross-bred variety which has become somewhat permanent and would seem to include amongst its ancestors one or more bearing seeds either altogether or partly violet- or purple-colored." (*ib.*, p. 12.)

From Laxton's cross of 1866, it appears that dominance of round form for cotyledons was evident in the cross, since he says:

> "This cross produced a pod containing five round, white peas, exactly like the ordinary 'Ringleader' seeds." (*ib.*, p. 10.)

Purple flower color, and color in the seed-coats, was dominant in the 1867-grown plants.

The seed-coat color of the F_1, however, which was "maple" in the male parent, split into maple (the majority), and violet or deep-purple (a few), in the following generation, grown in 1868.

The F_2 progeny, in 1868, split up into plants with purple flowers and colored seed-coats, and a recessive with white flowers and white seed-coats, which latter bred true in 1868 and 1869. Of the purple-flowered progeny of the F_2, the seed-coats were mostly maple or some modification of it. A few had violet seed-coats. The former, in 1869, split into a majority with seed-coats purple or grey, and only a minority maple or brown-streaked. The "few" in the F_2 with violet seed-coats, split, in the F_3, into (almost entirely) purplish-grey or maple, with occasional ones violet again. Without further speculation as to the probabilities in respect to the original maple seed-coat color, which Laxton was dealing with in the male parent of the cross, the facts above are given for whatever interest they may have. It should be mentioned that the seeds, in what we know as the F_2 generation, are described as being "partly indented, a few round." It is not clear whether Laxton meant by "partly indented," the same thing as in the description "slightly indented," by which the seeds of the original "Maple" parent are described. It may be taken to mean simply that a part of the seeds were indented; a few round. The expectation would have been, "mostly round, a few indented," to use Laxton's manner of describing.

The dominance of tallness in the F_1 is shown, and the clear segregation out of dwarf with white flower color and white seed-coats in the F_2.

Laxton adds that he had derived from his experiments the same conclusion as Knight and others:

> "That the colors of the envelopes of the seeds of peas immediately resulting from a cross are never changed." (p. 12.) He states also: "I find, however, that the color and probably the substance of the cotyledons are sometimes, but not always, changed by the cross-fertilization of two different varieties." (p. 12.)

One of the most striking features of Laxton's paper is the following remarkable, detailed observation, distinctly Mendelian in character, and one which should entitle the paper to especial interest.

He says:

> "I have also noticed that a cross between a round white and a blue wrinkled pea, will in the third and fourth generations (second and third year's produce) at times bring forth blue round, blue wrinkled, white round, and white wrinkled peas in the same pod, that the white round seeds when again sown, will produce only white round seeds, that the white wrinkled seeds will, up to the fourth or fifth generation, produce both blue and white wrinkled and round peas, that the blue round peas will produce blue wrinkled and round peas, but that the blue wrinkled peas will bear only blue wrinkled seeds." (p. 13.)

There does not exist anywhere, in the pre-Mendelian literature, any other similar, clear, distinct, or detailed statement of an observation of segregation involving two pairs of characters. So far as it has come to the knowledge of the writer, there exists no similar observation, or one of equal value, or so closely approximating an analytical statement, preceding Mendel's account.

It is interesting to trace, in Laxton's conclusions from the above, the manner in which the logic of the situation appealed to his mind.

"This would seem to indicate," he says, "that the white round and the blue wrinkled peas, are distinct varieties derived from ancestors respectively possessing only one of these marked qualities." (p. 13.)

This in itself is a genetic conclusion. In Mendel's case, such a fact pointed to the purity of the gametes. To Laxton's mind, it indicated a pure line of similar ancestors—the same thing in principle, but less analytically stated. Laxton is interested more in the ancestors than in the manner of transmission; Mendel in the mechanism of the transmission itself. Thus Laxton says:

> "In my opinion the white round peas trace their origin to a dwarfish pea having white flowers and round white seeds, and the blue wrinkled varieties to a tall variety having also white flowers, but blue wrinkled seeds." (p. 13.)

One of the principal objectives of the early breeders was to ascertain when and how a "variety" could be "fixed." Laxton concludes that three or four years is

> ". . . the shortest time which I have ascertained it takes to attain the

climax of variation in the produce of cross-fertilized peas, and until which time it would seem useless to expect a fixed seedling variety to be produced, although a reversion to the characters of either parent, or any one of the ancestors, may take place at an earlier period." (p. 13.)

Laxton's purely botanical attitude toward the matter is well brought out in his final statement:

> ". . . in conclusion I may, perhaps, in furtherance of the objects of this paper, be permitted to inquire whether any light can, from these observations or other means, be thrown upon the origin of the cultivated kinds of peas, especially the 'maple' variety, and also as to the source whence the violet and other colors, which appear at intervals on the seeds and in the offspring of the cross-fertilized purple-flowered peas, are derived." (p. 14.)

16. *The Experiments of Patrick Shirreff.*

Before closing an account of the early English hybridizers, it is proper to add an account of the work carried on in the breeding of wheat by Patrick Shirreff of Scotland, recorded in his brief memoir, "Improvement of the cereals and an essay on the wheat-fly," published at Edinburgh and London, in 1873. These experiments began in 1819, with a series of pure line selections of wheat and oats, and concluded with hybridization experiments.

The fact that Shirreff appears not only to have been the first experimenter of any consequence with the cereals to follow the principle of selecting only pure lines, and the fact that he was the first considerable hybridizer of wheat, make it desirable to include an account of his series of experiments for the sake of their historical value, as well as because of their not inconsiderable practical success. The circumstance that dominance in certain cases was reported, even if not further commented upon, is interesting as a matter of record.

In the spring of 1819, when walking over a field of wheat, on the farm of Mungoswells, in the County of Haddington, Scotland, Shirreff noticed "a green spreading plant" which attracted his notice, "the crop then looking miserable from the effects of a severe winter." At harvest time 63 heads were harvested, yielding 2,473 grains. These were dibbled in, the following autumn, at wide intervals. For two succeeding seasons, the seed was sown broadcast, and the first harvest of the progeny of the original plant amounted to 336 bushels.

In the summer of 1824, "a tall oat plant was observed on a

PLATE XXV. Patrick Shirreff.

field of the cereal, on the farm of Mungoswells." (6, p. 2.) The seeds from this plant were grown in a collection of named varieties. At harvest, the crop from the plant proved to be the tallest in the collection. The variety was then raised, and introduced under the name of Hopetoun oat.

In the fall of 1832 "a fine ear of wheat was found on the farm of Drum, which adjoins Mungoswells. This ear originally contained one hundred and two grains." The progeny from the head became the Hopetoun wheat.

> "The grain is rather large, white and heavy, the ear is handsome and its chaff white." . . . (6, p. 4.)
>
> "This variety found its way into many of the wheat-growing districts of Britain, and over a wide range of country and climate. It succeeded better than some of the white varieties originated in Scotland, which became so high colored when grown in the south of England, as not to be classed in that country as white wheat." (*ib.*, p. 4.)
>
> "The next cereal," Shirreff says, "which I selected, raised and introduced into full practice, was the Shirreff oat, which ripens early, and is reported to be very prolific." (*ib.*, p. 5.)
>
> "Hitherto," he remarks, "I had followed the improvement of the cereals by fits and starts, on the spur of the moment; but in 1856, something like a continued and systematic investigation of the subject was begun." (p. 5.)

He proceeded to examine the wheat fields on both sides of the Tweed, especially in East Lothian, and selected many heads which differed from the general crop.

> "My experimental plot of wheat for 1857," he says, "contained plants from the seeds of more than seventy ears, which had been selected during the previous years." (*ib.*, p. 6.)

From the many strains originating from the first year's selections, three kinds only were propagated. The names given to them were "Shirreff's Bearded Red," "Shirreff's Bearded White," and "Pringles."

Shirreff now found that the limitations of time and space made it necessary to restrict the number of strains experimented with. The following interesting account is given of what is probably the first systematic planting of plots for the experimental growing of pure strains of wheat.

> "My comparative trial-plot of wheat might be described thus: On a field cropped with wheat, named and unnamed varieties were grown in parallel pairs, from twelve to fifteen feet long, and from nine to twelve inches broad, with a foot-path a yard wide, surrounding the whole plot. . . . From time to time, notes were made regarding each kind,

> such as their time of ripening, length of stem, etc. By such means, the new varieties could be more readily distinguished from the old, and twice-naming detected, as the effects of soil and seasons upon the different kinds approximated. . . . Then, commencing on one side, the seeds were placed by the hand at a given thickness, and each variety covered with earth before another was planted. By proceeding in this manner, the seeds were placed in the soil at nearly equal depths and distances, and the different varieties kept from intermixing in the process of sowing." (*ib.*, pp. 8-9.)

By 1860, "Shirreff's Bearded Red" had increased until it amounted to twelve acres.

In 1860, the trial wheat plots contained seed from eighty-four heads. By this time, Shirreff had become well known, so that heads of wheat were being sent to him by many persons from different places, the seeds of which found their way into his experimental plots.

"In 1862, an attempt was made to improve oats." (p. 12.) From fields in the neighborhood of Haddington selected heads were taken. In 1864, the more promising kinds were included in this trial plot along with eighteen named varieties. Ultimately, four of the selections were propagated, under the names of "Early Fellow," "Fine Fellow," "Long Fellow," and "Early Angus."

Shirreff had by this time come to the following conclusion:

> "Many people believe that some plants can be altered by skilful treatment, but my experience had tended to show that there is no way of permanently improving a species but by a new variety. In support of the view of plant improving, gardeners can point to hosts of new and improved varieties of fruits, vegetables, and flowers, while, to corroborate, farmers can bring forward the Chevalier Barley, Swede Turnip, Italian rye-grass and the Alsike Clover. To this principle of improvement the cereals form no exception; and the small amelioration which they have undergone in this age of progress, may fitly be attributed to the apathy of corn growers in this department of agriculture." (*ib.*, pp. 14-18.)
>
> "New varieties of the cereals," Shirreff says, "can annually be obtained from three sources—from crossing, from natural sports, and from foreign countries." (*ib.*, p. 18.)

Shirreff's technique in the crossing of wheat may be of interest to breeders of this cereal.

> "Before commencing to cross," he says, "consider what properties the new variety is wished to inherit; and fix upon such kinds as possess in the highest degree the desired properties." (*ib.*, p. 22.)

A day or two after the head emerged from the sheath, the head was shortened, every alternate spikelet was removed, and only the two lateral or outside flowers of each spikelet were allowed to grow. Such a head would consist of four to six spikelets with eight to twelve flowers. The head of the plant intended to be used as the pollen parent was then brought, the anthers removed from the flowers of the proposed female parent, and the anthers from the head of wheat intended for the male parent were removed and placed within the glumes of the emasculated flower. It was recommended that two persons work in cooperation, one to hold open the chaff-scales or glumes, the other to remove and replace the anthers with a pair of forceps. The head thus pollinated was then fastened to a stake and enveloped in wire gauze as protection against being rubbed against by other heads, and against birds. It is interesting to note the subsequent care with which the hybrid seeds were treated:

> "As soon as the grains obtained by crossing become dry, place them in thumb pots in a garden, protecting them from birds and insects by sprigs of furze spread on the surface, and by a few coal ashes in the bottom, and afterwards remove the plants to where they were intended to be grown. This plan prevents the intermixing of kinds, and generally the attacks of insects residing in the soil, or frequenting the air, in the early stages of the plants' growth." (*ib.*, p. 24.)
>
> "The inflorescence of oats and barley being wintered with wheat, the crossing of these cereals can be effected in like manner as with wheat." (*ib.*, p. 24.)

Knight's experiments in the crossing of wheat are quoted by Shirreff as follows (*ib.*, p. 27):

> "I readily obtained as many varieties as I wished, by merely sowing the different kinds together; for the structure of the blossom of this plant, unlike that of the pea, freely admits of adventitious farina, and is thereby very liable to sport varieties. Some of those I obtained were excellent, others very bad, and none of them permanent. By separating the first varieties, a most abundant crop was produced, but in quality was not equal to the quantity; and all the discarded varieties again and again made their appearance. It appeared to me an extraordinary circumstance, that in the years of 1795 and 1796, when almost all the whole corn of the island was blighted, the varieties thus obtained only escaped in this neighborhood when sown on different soils and situations."

Knight is referred to by Shirreff as "the first individual in Britain known to have crossed wheat." (*ib.*, p. 26.)

A Mr. Raynbird, who competed for a medal given by the Highland Society of Scotland with a wheat obtained by hybridization, known as "Raynbird's Hybrid," was, as Shirreff says,

> ". . . perhaps the first person who offered a hybrid or cross-bred wheat to the notice of the British farmers." (*ib.*, p. 8.)

Regarding his own crossing Shirreff says:

> "One of my first attempts at crossing was made with April and Talavera varieties, the latter being the pollen parent."

Regarding the hybrid he says:

> "The plant from cross-fecundation appeared to be an intermediate between the breeders." (*ib.*, p. 28.)

Between Shirreff's first and second attempts at the crossing of wheat a period of nearly twenty years intervened.

The technique developed by Shirreff in his wheat crossing experiments is further described as follows:

> "The valves of the chaff were opened, and the anthers removed one by one with the point of a needle. Three or four days afterwards, according to the state of the weather, the valves of the chaff were again opened, and the stigma touched with a camel's-hair brush covered with pollen from the anthers of the male breeder. From the opening and closing of the chaff valves," Shirreff says, "they frequently dropped off after fecundation had been effected; and scarcely one attempt in ten ended successfully until the method described at page 21 was adopted, which so changed matters that three attempts out of four proved successful." (*ib.*, pp. 29-30.)
>
> "For some time," Shirreff says, "my cross-fecundations produced nothing very striking, until a variety in my comparative trial-plot attracted notice, from the size of ear, and the length and strength of the straw. When ripe, the grains were found to be fine in quality, and it was decided to raise a stock from it for field practice." (*ib.*, p. 31.)

The variety in question was produced by crossing "Shirreff's Bearded White" with pollen from "Talavera," with a view to enlarging the seeds of the Bearded White, which were small and round. The hybrid was called "King Richard," and was found to be intermediate between the parents in form of ear, while approaching the Talavera in size and form. In tillering habit it was intermediate.

Shirreff, of course, knew nothing of the laws of segregation, and a hybrid once obtained was for him always a hybrid. The "mixed ears," spoken of as appearing in the progeny, were probably the segregating forms. Shirreff says:

> "These mixed ears in all probability are owing to the hybridous origin of King Richard, and are not likely to be got rid of without raising a stock again from a single grain, and when necessary doing so again and again." (*ib.*, p. 31.)

By such selection he originated a new strain called "King Red Chaff White," which was exhibited in bulk for the first time in 1870. Regarding it he says:

> "Altogether, I am at present disposed to regard King Red Chaff White as perhaps one of the best wheats I have sowed." (*ib.*, p. 3.)

Shirreff also crossed Talavera, which has white chaff, with a variety with small white seeds and red chaff. In this hybrid he makes perhaps the first reference to color dominance in the chaff of wheat.

> "The plant from the seed, in form of ear and seed, closely resembled Talavera, *but the color of the chaff was red.*" (*ib.*, p. 33.)

The dominance of downy chaff over smooth chaff, was also recorded as follows:

> "A downy-chaffed variety with tall straw, which had been selected from Hopetoun, was fecundated with pollen from Talavera, and the result was a constant variety with the *downy chaff* and fine straw of the seed parent." (*ib.*, p. 33.)

Shirreff records (pp. 34-5) his observations on the natural crossing of wheat in the field.

> "Having satisfied myself of the possibility of changing the seeds and external characteristics of the wheat plant by crossing, I resolved to attempt altering the habit of ripening." (*ib.*, p. 36.)

For this purpose he used a spring wheat known as Tuscany, brought originally from New Zealand. Tuscany wheat was found to ripen eight or ten days earlier than other kinds grown by him. In 1869, he crossed Tuscany with King Richard and with Talavera, with the object of improving the straw and grain of the former variety, but of introducing its earlier ripening. From the cross with King Richard he obtained earlier seeds, which were planted in thumb pots. These were taken to the field, and six plants finally came to harvest. The cross from Tuscany with Talavera produced one plant. In 1811, these first-generation hybrids were harvested. Shirreff, of course, assumed that the new types thus appearing were as likely to be fixed in type as the parents.

Shirreff records, that of the seven first-generation hybrids, five were summer and two winter wheat. Out of over eighty wheat plants resulting from hybridization, he reports that he grew, in 1872, upwards of forty.

As to the seldom occurrence of natural crossing, Shirreff notes:

> "If varieties growing contiguous are always instrumental in fecundaing one another, my experimental plots must have long since become a

heterogeneous mass, when between one and two hundred sets have been grown within a foot of each other for nearly fourteen years."

Shirreff remarks pointedly upon the necessity for the final test of the product, as the criterion of science in the improvement of wheat.

> "One of the chief difficulties which an individual experiences when improving the plant, is to ascertain the quality of the grain or the flour produced from it. . . . In an inquiry of this nature, the aid of the chemist is thought to be of little avail, and the baker's bread, taking color, quality, and quantity into consideration, is a more satisfactory test to the farmer." (p. 62.)
>
> "In carrying out the improvement of cereals, the selecting of varieties may be considered an important step; and the object in all probability, will be sooner accomplished and better controlled, by first creating a diversity, which can easily be effected by crossing. . . . Crossing tends to produce variation in kinds not given to sporting, and in this respect it has much advantage over the system of improvement by merely selecting from the crops of the farm. A new and important source of variation is opened up by crossing, but a judicious improver of the cereals will never overlook this interesting proceeding. Always cross with the seedlings which inherit in the greatest degree the properties you wish a cereal to possess, and by persevering for a series of years to select, and by crossing in this manner, success in all probability will be ultimately attained." (p. 95.)

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CHAPTER V

THE WORK OF THE FRENCH HYBRIDISTS

17. *The Experiments of Sageret.*

DURING the time of the prosecution of the work of Knight and Herbert there appeared the results in hybridization obtained by Sageret in France.

Augustin Sageret was born at Paris, July 27, 1763. He was a naturalist and practical agronomist, was one of the founders of the Society of Horticulture of Paris, and a member of the Royal Society of Agriculture, afterwards called the Academy of Agriculture. He was author of an agronomic survey of the canton of Lorris, where he settled at the age of fifty-six, to take up and bring into condition an agricultural domain of 750 acres. He had the honor of having the genus *Sageretia* named after him by Brogniart. His death occurred in 1851.

Sageret's experiments in crossing were largely confined to the Cucurbitaceae, and his results were published in a memoir, entitled "Considérations sur la production des hybrides, des variantes et des variétés en général, et sur celles de la famille des Cucurbitacées en particulier," which appeared in 1826, in the Annales des Sciences Naturelles, Vol. 8. (5.)

Sageret made some discoveries that clearly anticipate our modern knowledge of segregation, and he was able to furnish what was, for the time, a fairly satisfactory scientific explanation for the reappearance of ancestral characters. The experiment upon which his conclusions were primarily based was a cross, in which a muskmelon was the female, and a cantaloupe the male parent. Each plant was regarded as a relatively pure type-representative of its kind. In stating the results of the cross, Sageret for the first time, so far as the writer knows, in the history of plant hybridization, aligned the characters of the parents in opposing or contrasting pairs, after Mendel's fashion forty years later.

Following is the list of contrasting parental characters, as Sageret gives them:

Muskmelon (*Female*)	*Cantaloupe* (*Male*)
1. flesh white	1. flesh yellow
2. seeds white	2. seeds yellow
3. skin smooth	3. skin netted
4. ribs slightly evident	4. ribs strongly pronounced
5. flavor sugary, and very acid at the same time	5. flavor sweet

Sageret remarks:

> "The assumed product of the crosses made ought to have been intermediate: 1—flesh very pale yellow; 2—seeds very pale yellow; 3—netting light; 4—ribs slightly marked; 5—flavor at once sweet and sprightly: but the contrary was the case." (5, p. 303.)

As a matter of fact, in the two hybrid fruits reported upon, the *characters were not blended or intermediate at all, but were clearly and distinctly those of the one or the other parent.*

first hybrid	*second hybrid*
1. flesh yellow	1. flesh yellowish
2. seeds white	2. seeds white
3. skin netted	3. skin smooth
4. ribs rather pronounced	4. ribs wanting
5. flavor acid	5. flavor sweet

In the further support of his conclusions regarding the descent of characters in unitary fashion, he remarks upon the inheritance of human hair and eye-color, in the mating of a brunette with a blonde type.

Sageret remarks upon the fact that such hybrids are types, of which he had "several times obtained the analogues or their equivalent." While there is fusion here and there, he says, "one sees here a much more marked distribution of their different characters without any mixture between them." (5, p. 303.) He even uses for the first time in the literature of plant hybridization, the word "dominate" with reference to characters in crossing, in the following words. Speaking of the inheritance of flavor in various melon crosses, he says:

> "The acid flavor of the muskmelon is encountered in the form of the cantaloupe and the snake-melon; in others, the form of the cantaloupe dominated." (5, p. 307.)

Summing up the results of his experiments in a general conclusion, he says, with regard to the natural expectation that in a hybrid there will be a complete or partial fusion of the parental characters, that:

> "This fusion of characters may take place in certain cases; but it has appeared to me that, in general, things did not take place in this way," and again: "It has appeared to me that, in general, the resemblance of the hybrid to its two ascendants consisted, not in an intimate fusion of the diverse characters peculiar to each one of them in particular, *but rather in a distribution, equal, or unequal, of the same characters.*" (5, p. 302.)

Here we meet, for the first time in the literature of hybridization, the phrase "distribution of characters" now so familiar. "These facts," Sageret remarks, "have been confirmed by a multitude of my experiments."

It is evident, from the following statement, that Sageret appraised his discovery of the dominance of characters in crossing at its proper value:

> "The ideas which I present," he says, "have appeared remarkable to me; they seem to me to be of a very great importance." (5, p. 302.)

In addition to his melon crosses, Sageret secured a hybrid between a black radish and a cabbage, of which he writes:

> "Some of the fruits, instead of being intermediate, were like either cabbage or radish on the same inflorescence." (5, p. 297.)

Each silique bore a single seed, analogous to its pod, to which he makes reference in a further comment upon "the distribution among hybrids of the characters of their ascendants without fusion of these characters" (5, p. 304)—a point of view with regard to the results of hybridization that needs little to make it modern.

It is a matter of additional interest that Sageret was further able to derive a natural scientific conclusion from the facts of unit-character inheritance as he found them, with respect to the reappearance of old or the appearance of new "species."

The hybrids "often reproduced for me," he says, "varieties which had long ago disappeared." (5, p. 304.)

He finally concludes:

> "To what, then, does this faculty belong, which nature has of reproducing upon the descendants such or such a character, which had belonged to their ancestors? We do not know: we are able, however, to suspect that it depends upon a type, upon a primitive mould, which contains the germ which sleeps and awakens, which develops or not according to circumstances, and possibly that which we call a new

species is only an old species in which develop organs ancient but forgotten, or new organs, of which the germ existed, but of which the development had not yet been favored." (5, pp. 304-5.)

The clear manner in which Sageret's mind rather instinctively seized the conception of the independent descent of characters is exemplified in a sentence in which he says that all plants, and possibly still more, hybrid plants,

> ". . . having the ability to recall, so to speak at will, without measure and indifferently, and independently of one another, the qualities of their ascendants, it is possible that some among them, illy assorted, should have left out all there was of good and have taken all there was of ill." (5:308.)

18. *Godron and Naudin on Hybridization.*

In 1861, the Paris Academy of Sciences proposed the following problem to receive the grand prize in the physical sciences:

> "To study plant hybrids from the point of view of their fecundity, and of the perpetuity or non-perpetuity of their characters.
>
> "The production of hybrids amongst plants of different species of the same genus is a fact determined long since, but many precise researches still remain to be made in order to solve the following questions, which have an interest equally from the point of view of general physiology, and of the determination of the limits of species, of the extent of their variations.
>
> 1. "In what cases of hybrids are they self-fertile? Does this fecundity of hybrids stand in relation to the external resemblances of the species from which they come, or does it testify to a special affinity from the point of view of fertilization, as has been remarked regarding the ease of production of the hybrids themselves?
> 2. "Do self-sterile hybrids always owe their sterility to the imperfection of the pollen? Are the pistil and the ovules always suspectible of being fecundated by a foreign pollen, properly selected? Is an appreciably imperfect condition sometimes observed in the pistil and the ovules?
> 3. "Do hybrids, which reproduce themselves by their own fecundation, sometimes preserve invariable characters for several generations, and are they able to become the type of constant races, or do they always return, on the contrary, to the forms of their ancestors, after several generations, as recent observations seem to indicate?"

The two chief competitors under the Academy's offer were Charles Naudin, of the Museum of Natural History at Paris, and D. A. Godron, of the University of Nancy, the prize being awarded to the former. The papers of both appeared in Vol. 19 of the Annales des Sciences Naturelles (Botanique), 4me Série, 1863. (2c, 4c.)

The title of Godron's thesis was, "Des hybrides végétaux, considérées au point de vue de leur fécondité, et la perpétuité de leurs charactères."

Godron.

Godron's paper is chiefly devoted to the solution of the question

> ". . . whether hybrids reproducing by self-fertilization sometimes keep their characters invariable during several generations, and whether they are able to become the types of constant races, or whether, on the contrary, they always return to the form of their ancestors at the end of several generations, as recent observations seem to indicate."

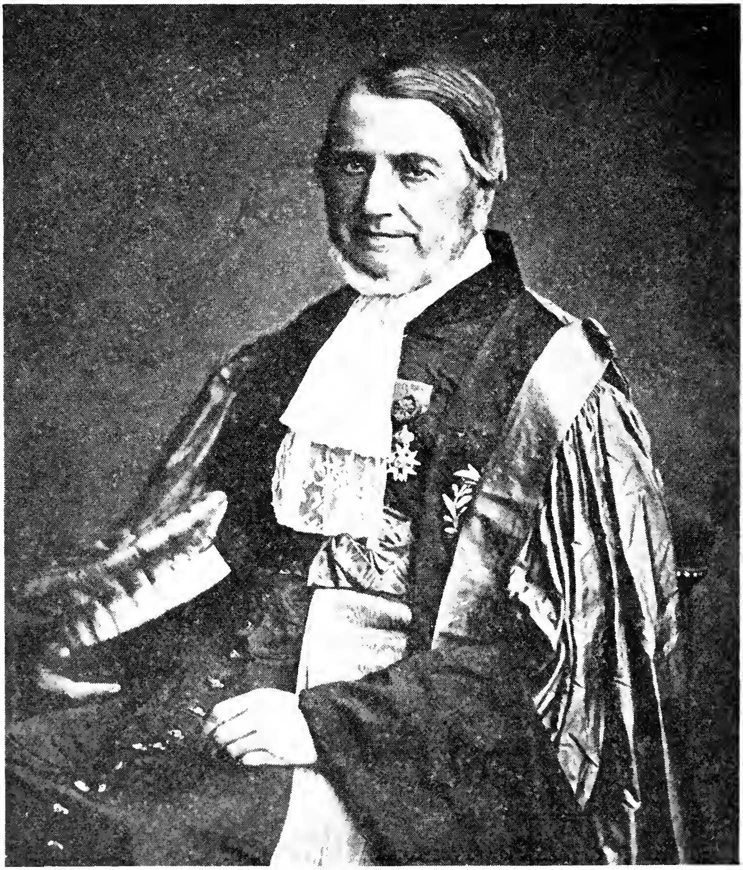

PLATE XXVI. D. A. Godron, 1807-1880, Professor at the University at Nancy.

In answer to this query, he says:

"We have determined, upon hybrids of *Linaria*, that the hybrid forms may become very fertile, and that a certain number of individuals from the second generation return respectively to the two primitive types,

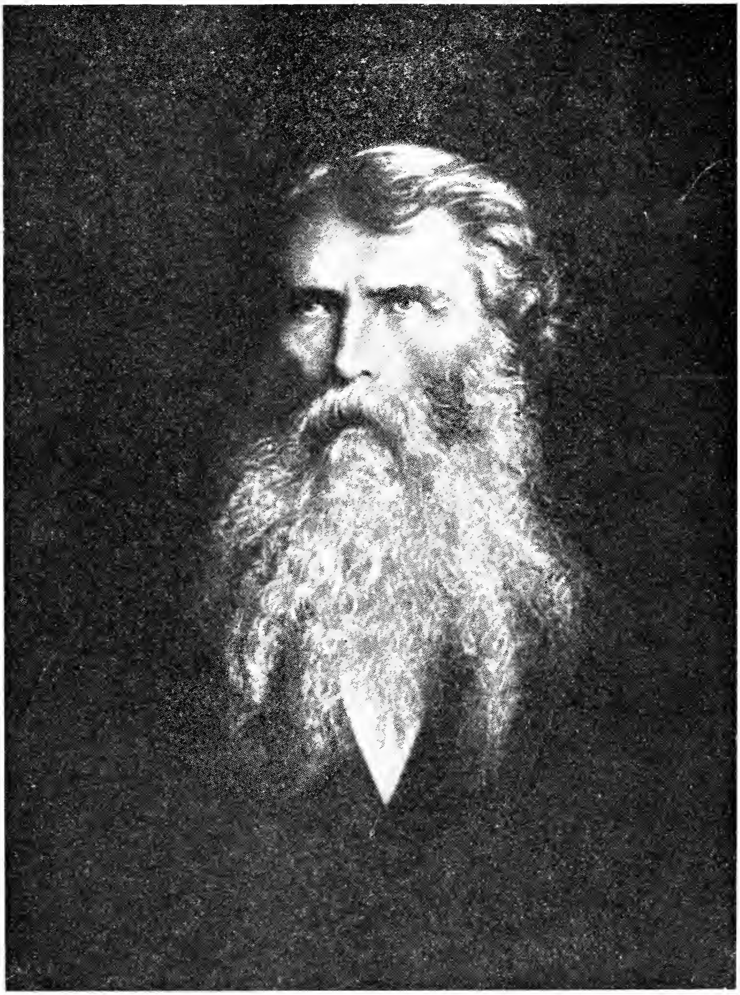

PLATE XXVII. Charles Naudin, 1815-1899.

when they grow in company with their parents, and this return movement manifests itself much more in the following generations." (2c, p. 174).

Godron remarks that the same fact has been observed by Lecoq in the fertile hybrids of *Mirabilis*, by Naudin in the fertile hybrids of *Nicotiana*, and by several observers in *Primula* and in *Petunia.*

From these experiments, then, he considers the proof of the final return of fertile hybrids to their parental forms to be established.

Godron was a victim of the rigid idea of species, which held that, because so many hybrids between different "species," so-called, were sterile, therefore any hybrid which turned out to be fertile must necessarily, *ipso facto*, prove the parents not to be of different species, but to be merely varieties of the same species.

To the vain purpose of settling this verbal controversy, whether such and such plants were to be regarded as separate "species," or merely as "varieties" of the same species, many of the most ardent endeavors of hybridists, both before and since Mendel's time, have been conscientiously and duly devoted. A sample of this method of reasoning in a circle, so vigorously combatted by Herbert, and characterized by him as "fighting the air," is exemplified in a sentence of Godron's which typifies the general view at that time. He speaks of a

"*law* which has its sanction in the numerous experiments which, for a century past, have been made by Kölreuter, Wiegmann, C. F. Gärtner, etc., and by M. Naudin himself, *that simple hybrids are sterile or but little fertile.*" (2c, p. 139.)

Considering the fact, however, that the hybrids between confessedly distinct species are so frequently sterile, it is not surprising that, in view of the then greater interest in the species question itself, hybridizers should have turned systematic botanists, and have made the sterility of the hybrid offspring a criterion of species distinction.

Besides his competing memoir before the Paris Academy, Godron was the author of several other contributions to the literature of plant hybridization, including that of the celebrated question as to the possible origin of cultivated wheat from the wild plant *Aegilops ovata.*

In 1863, Godron (2) reported a series of observations upon the fecundity of hybrids. He investigated the question whether this fecundity, in succeeding generations, bore any relation to the ease with which the original hybridization was effected. From experiments with *Verbascum* hybrids he came to the conclusion that the fertility of hybrids does not always have any relation to the ease with which the cross is effected in the first instance. From investigations which Godron made upon the cause of sterility, he discovered that in some cases deformed and aborted pollen was not, as frequently, the cause, but that perfectly formed pollen may be inactive. He raised the question whether

> ". . . the very great development which the organs of vegetation take on in simple hybrids of *Verbascum*, the numerous branches and the immense quantity of flowers which originate on these branches, would not exhaust the vegetative juices at the expense of the organs of reproduction. Would there not be there a fact which the law of the balance of organs would explain, the force of which one so frequently determines as well in the plant as in the animal kingdom." (2c, p. 172.)

Godron concludes, in general, that crosses of two races or varieties of the same species are characterized by absolute fertility, that the sterility of the simple hybrids is proof that they come from distinct species, and that crossing between two species of different "genera" is impossible. We thus see the trend of Godron's mind—to establish by experiments in crossing the question of what constitutes a species, a point of view that has entirely disappeared today. At the present time, of course, no especial account is necessarily taken in crossing as to the precise systematic position of the organisms which it is intended to cross. They may be different "varieties," or different "species," or even belong to different so-called "genera." Attention is necessarily directed primarily to the nature of the characters which it is desired to involve in the cross, the behavior of which it is sought to investigate.

In his brief memoir, "Recherches expérimentales sur l'hybridité dans la règne végétale" (2b), Godron discusses the question of the fecundity of hybrids and the perpetuity or non-perpetuity of their characters. He states that, from crossing experiments of his own on species of the genera *Verbascum*, *Primula*, *Nicotiana*, *Digitalis*, *Antirrhinum*, *Linaria*, and *Aegilops*, "when two species, incontestably distinct, are fecundated, the one by the other, they give products constantly sterile." (p. 228.) On the other hand, he further comments (p. 254):

> "Crosses between two races or two varieties give, on the contrary, as Kölreuter has established, and as all those have recognized who have followed in his footsteps, products as fertile as legitimate species."

Godron's point of view as to the value attaching to hybrid studies, is shown by his remark:

> "This fecundity then, equal to that of the parents, characterizes crosses (métis) and offers us a criterion to distinguish what is a race or a variety from that which is a species." (p. 255.)

As to the fertility of hybrids and the perpetuity of their characters, he cites especially the case of *Aegilops triticoides* pollinated with pollen of wheat, and giving as a result *Aegilops speltaeformis*, which, he says "at first fertile to a mediocre degree, like all hybrids of the second generation, produces, in the following years, as many seeds as any *Aegilops* or *Triticum* known. (p. 272.) The fact that the fecundity of the hybrids does not always bear a relation to the facility with which the cross is effected in the first place, is illustrated by Godron from *Verbascum* crosses, especially *Verbascum austriaco-nigrum* × *phoeniceum*. (p. 283.) This sterility he recognizes as being due to one or several possible operating causes: The complete absence of pollen, defective pollen—deformed, etc.—or physiological sterility, as in the case of *Antirrhinum majus. A Barrelieri*, which, although having an abundance of pollen, apparently completely normal, yet remained entirely infertile.

Godron again comments on the very great vegetative development in hybrids of *Verbascum*:

> "The numerous branches, and the immense quantity of flowers which arise on these branches, would they not exhaust the vegetable juices at the expense of the organs of reproduction?" (p. 287.)

With regard to the question (p. 289) whether hybrids, self-fertilized, sometimes retain their characters unchanged for several generations, and thus become the type of constant races, or whether, on the contrary, they always return to the forms of one of their parents after several generations, Godron gives his case of *Linaria* hybrids, stating that:

> "these hybrid forms may become very fertile, and a certain number of individuals return, after the second generation, to the one and the other

> of their two primitive types, when they grow in company with their parents; and that this return movement manifests itself still more in the succeeding generations." (p. 289.)

He notes that the same fact was observed by Lecoq in fertile hybrids of *Mirabilis*, by Naudin in fertile hybrids of *Nicotiana*, and by himself in hybrids of *Petunia violacea* × *nyctaginaeflora.*

> "These facts," he says, "seem to militate in favor of this opinion, that hybrids are not able, contrary to the opinion of Linnaeus, to form new permanent types, or, in a word, new species." (p. 290.)

He then cites at full length the exception already noted, of *Aegilops speltaeformis*:

> ". . . which seems to constitute a permanent hybrid race, and appears to comport itself like a veritable species." (p. 290.)

However, after a careful review of the results of his own experiments with *Aegilops* and those of Fabre, he decided that *Aegilops speltaeformis* does not behave like a true species, even though it is fertile, that its propagation and permanence remain dependent upon the care of man, and that, abandoned to itself, it is destined to perish. Hence, Godron concludes (p. 296.):

> "Hybridity remains thus no less one of the most precious means of recognizing what is a species, and of distinguishing it from that which is not."

Nothing could show more clearly than Godron's small memoir of 1862 the point of view of his time regarding the hybrid question. Hybrids in many cases, well experimented upon, were seen to "return" gradually to the parental types. In what manner or to what degree, statistically speaking, such "reversion" occurred, was not made the subject of inquiry. Infertility of hybrids of "true species," or fertility of crosses of "varieties," was a determined fact, accepted as relatively certain, and valued as a sort of criterion or means of ascertaining what organisms were "species," and what were "varieties."

Naudin.

With regard to the paper of Naudin (4c), the general conclusions of importance for his time, at which he arrived, are as follows, in the language of the Committee of Award of the Academy, which is quoted verbatim to show the point of view in the science then prevailing:

> "The first and the most important of all is that the singular beings which result from the cross-fertilization of two different types, far from being condemned to absolute sterility, are frequently endowed with the faculty of producing seeds capable of germination." (1, p. 129.)

An essential feature in Naudin's paper, of high importance from our present standpoint, is the independent behavior of characters in a cross, referred to by the Academy committee as follows:

> "Not content with responding by numerous experiments to the questions propounded by the Academy, the author . . . has sought to throw light upon several points, some obscure, others not yet studied, in the history of hybrids. He has confirmed that which Sageret already knew, that in a hybrid the characters of the two parents are often shown, not blended but approximated, in such fashion that the fruit of a *Datura* hybrid, born of two species, the one with a smooth, and the other with a spiny capsule, presents smooth surfaces in the midst of a surface generally spiny. This 'disjunction,' as it is called, is explained according to him by the presence in the hybrid of two specific essences, which tend to be separated more or less rapidly the one from the other. He even sees in this disjunction the true cause of the return of fertile hybrids to the specific types from which they came." (*ib.*, p. 131.)

It is further of great interest to note that the seeds gathered from the smooth side of the capsule reproduced only the smooth-capsule form, *Datura laevis*, while those taken from the spiny side gave rise only to the spiny form, *Datura stramonium.* In Verlot's paper, yet to be discussed, further instances of this type of segregation will be found.

Naudin stated more clearly and definitely than others had hitherto done the fact of the general uniformity of the hybrid offspring of the first generation, and the diversity of form, with partial reversion to, or, as we would now put it, the reappearance of, the parental types, in the second hybrid or F_2 generation. His language is as follows:

> "Finally, one may say that the hybrids of the same cross resemble one another in the first generation as much, or almost as much, as the individuals which come from a single legitimate species." (4c, p. 188; Comptes Rendus, 4d, p. 839.)

In contradiction to the results derived by Sageret from his particular set of experiments, Naudin asserts the generally intermediate nature of the first generation hybrid condition:

> "All the hybridologists are in accord in recognizing that the hybrids (and it is always a question of the hybrids of the first generation) are mixed forms, intermediate between those of the two parent species. This is, in fact, what takes place in the immense majority of cases; but it

> does not follow therefrom that these intermediate forms are always at an equal distance from those of the two species." (4c, p. 189.)

He goes on to remark upon the vagueness with which this relative approximation is determined, resting as it does largely upon a basis of opinion. He also calls attention to the fact, that sometimes hybrids resemble one of the two parents in certain parts, and the other in other parts.

Regarding segregation in the second hybrid generation, he says:

> "Very often, to the so perfect uniformity of the first generation, there succeeds an extreme medley of forms, some approaching the specific type of the father, the others that of the mother. . . . (4c, p. 190.)
>
> "It is, as a matter of fact, in the second generation that this dissolution of the hybrid forms commences in the great majority of cases. . . . (4c, p. 190.)
>
> "Among several of these hybrids of the second generation, there is a complete return to one or the other of the two parental species, or to both, and diverse degrees of approach to these species." (4c, p. 191.)

Naudin now comes to what he regards as the philosophical explanation of these facts.

> "All these facts are *naturally explained by the disjunction of the two specific essences, in the pollen and in the ovules of the hybrid. A hybrid plant is an individual in which are found united two different essences, having their respective modes of development and final direction, which mutually counter one another, and which are incessantly in a struggle to disengage themselves from one another.*" (4c, p. 191.)

The above is Naudin's statement of the "law of disjunction." It is essentially a statement of the principle operating in what is known as Mendel's Law, but must be regarded rather as a philosophical inference, or divination of the truth, than as a scientific conclusion derived from the data of specific experiment.

> "The hybrid," says Naudin, "in this hypothesis, would be a living mosaic, in which the eye would not discern the discordant elements as long as they remained intermingled; but if, in consequence of their affinities, the elements of the same species, mutually approximating one another, agglomerate in rather considerable masses, there may result therefrom parts discernible to the eye, sometimes entire organs, etc." (4c, p. 192.)

Naudin concludes that the pollen and the ovules, and the pollen especially, "are the parts of the plant where the specific disjunction takes place with the most energy." (4c, p. 193.)

He goes on to suppose (and here, perhaps, he comes close to a statement of Mendel's view), viz.:

> "That, in the hybrids of the first generation, the disjunction takes place at the same time in the anther and in the contents of the ovary; that some of the grains of pollen belong totally to the species of the father, and others to the species of the mother; that in others again the disjunction has not occurred or has just commenced: let us grant again that the ovules are, in the same degree, segregated toward the side of the father and toward the side of the mother. . . . If the tube from a grain of pollen approximated to the species of the male parent encounters an ovule segregated in the same direction, there will be produced a plant entirely reverted to the paternal species. The same combination being accomplished between a grain of pollen and an ovule, both separated in the direction of the female parent of the hybrid, the product will return in the same way to the species of the latter; if, on the contrary, the combination is effected between an ovule, and a grain of pollen, segregated in a direction contrary the one to the other, there will result a true cross-fertilization, like that which has given birth to the hybrid itself, and there will result therefrom a form intermediate between the two specific types." (4c, p. 193.)

In 1864, Naudin communicated a second report to the Academy, in which he confirmed his previous results as to uniformity in the first generation crosses, the identity of reciprocal crosses, and the "disorderly variation," as he calls it, of the hybrids of the second and succeeding generations. In neither of the two papers is there any numerical classification of the hybrid types.

Naudin's memoir is often referred to as amounting virtually to a statement of Mendel's law of the disjunction of hybrids. In Naudin's case, however, the statement was of a speculative nature, and consisted in the propounding of a scientific hypothesis; in Mendel's case, his "law" was a scientific conclusion derived as the result of experiment.

Reviewing this list of statements in the light of present knowledge, we can see that they constitute a more or less correct, nonscientific formulation of the truth.

For example, the more or less rapid return of hybrids, that is to say of heterozygotes, to the parental forms, is a now sufficiently well-established fact of segregation according to Mendelian ratios, which, if there be a single pair of allelomorphs in question, takes place on a 1 : 2 : 1 basis in each successive self-fertilized generation. The more or less rapid return to its parents of the hybrid fertilized by its parent, means, of course, the splitting of 50 per cent dominants, or recessives, as the case may be, which are like the parental types in the case in question.

Naudin propounded, in 1863, a well-reasoned theory of probable truth; Mendel, however, in 186~~8~~5, formulated a statement of ascertained fact.

In 1865, Naudin, who had won so much credit for his memoir on hybridization in 1863, published a paper on what he termed "disordered variation" in hybrid plants, occurring as the result of crosses he had made between a variety of cultivated lettuce and a wild species (*Lactuca virosa*). Of the cross he says:

> "The hybrid of the first generation was very fertile, and from the seeds sprang a multitude of young plants, very varied in aspect, which intermingled in all degrees the characters of the two species."

Of these F_2 plants, twenty were preserved, concerning which he remarks that they presented as a whole "all the phenomena of the most disordered variation."

No two individuals of the twenty in the second generation were alike, and yet, so far as the characters were concerned, nothing new was seen to appear that had not already existed in the one or the other parent.

> "One essential point to bring forward here," Naudin adds, "is that, in this overlapping of the characters of the two different species, one does not see anything new appear, anything which does not appertain to the one or to the other. Variation, as disorderly as it may be, moves between limits which it does not transgress. The two specific natures are engaged in a struggle in the hybrid, to which each one brings its contingent; but from this conflict there do not really issue new forms; that which is produced is never but an amalgamation of forms already existing in the parent types. The hybrid is but a composition of borrowed pieces, a sort of living mosaic, of which each piece, discernible or not, is ascribable to one or the other of the producing species."

Naudin concludes that not the surrounding medium, but the nature of the ancestry, is the cause of all the variations seen in plants. He calls attention to the fact that seeds of the same sowing, although exposed to the same environment, do not vary in the same manner.

> "We see the variation without any rule, by the sowing of their seeds, of plants subjected since time immemorial to our cultivation, such for example as the vine and the greater number of our fruit trees; it all brings us to think that they owe it to crosses, probably very ancient and possibly anterior to all domestication, between neighboring species."

Naudin then answers the question, "Whence comes heredity and what is it," as follows:

> "It is always the passage from one equilibrium to the other, and always along the line of least resistance."

The term "disordered variation" (*variation désordonnée*) is probably employed by Naudin for the first time in his paper of November 21, 1864, "De l'hybridité considérée comme cause de variabilité dans les végétaux." (4d, p. 157.) The use of the term arose from experiments in crossing, reciprocally, *Datura laevis* and *ferox*. In 1863, sixty individuals were grown of the cross *laevis* × *ferox*, and seventy of *ferox* × *laevis*. Of these plants, all of which came to full development, he says,

> ". . . they have been so perfectly like one another that the two lots would have been easily taken for a single one." (p. 155.)

This result he considers a new confirmation of the conclusion already announced in his memoir presented to the Academy in 1863, (4c):

> ". . . that there is no sensible difference between the reciprocal hybrids of two species, and that in the first generation the hybrids of the same derivation resemble one another as much as do the individuals of the same pure species, issuing from the same sowing." (4d, p. 155.)
>
> "In this first generation," he adds, "the entire collection of the hybrid individuals of the same origin, however numerous they may be, is as homogeneous and as uniform as a group of individuals would be of an invariable species, or of a pure and clearly characterized race." (*ib.*, p. 155.)

According to Naudin's statement, although both the parents had white flowers and green stems, the hybrids of the first generation were all characterized by violet flowers and brown stems, and with spiny fruits. This development Naudin ascribes to an extension, over the whole plant of the hybrid, of a character which was found to appear in a rudimentary way in the stems of the seedlings of *D. ferox*, which, at the time of germination, are stated to be of a deep violet-purple, extending from the root to the cotyledons, where it suddenly stops, giving way to a clear green tint. In the hybrids of the first generation:

> ". . . it takes on an enormous increase, reaching all parts of the plant, and manifesting its action especially upon the flower." (p. 156.)

In 1864 the second generation of plants of the two reciprocals was grown. Nineteen plants were raised of *D. ferox* × *laevis*, and twenty-six of *D. laevis* × *ferox*.

> "To the great uniformity [i.e., of the first generation] there succeeded the most astonishing diversity of forms, a diversity which is such that, of the forty-five plants which compose the two lots, one would not find two which exactly resembled each other." (p. 157.)

The plants differed from one another in height, habit, form of the foliage, coloration of the stems and flowers, degree of fertility, size of the fruits and their degree of spinescence. The various vegetative characters are given in a descriptive manner and in some detail, but without classification.

> "To sum up," he says, "the forty-five plants of the two lots, constitute, so to speak, as many individual varieties as if, the bond which attached them to the specific types being broken, their vegetation had wandered in all directions. This it is that I câll 'disordered variation' [variation désordonnée], in opposition to another very different manner of varying of which I shall speak farther on." (p. 157.)

The idea seems not to have suggested itself to Naudin that there could necessarily be any ascertainable law underlying the confusion which the variations in question represented, or that any quantitative study of the characters of the plants of the second generation was therefore necessary.

In an article, "Sur les plantes hybrides," published in the Revue Horticole for 1861, Naudin had already arrived from his experiments at certain conclusions regarding the hybrid condition. The hybrid, he says (4b, p. 397), may have characters of two orders: The first, to which in general the most attention is given, is the mixture in diverse proportions of the characters peculiar to each of the parental forms, and which constitutes the hybrid a form intermediate between the two. This mixture of characters may be an equal distribution of the characters of the two parents, but more often it is very unequal, in which case the hybrid more or less sensibly approaches one of the two species. In general, this fusion of characters is seen in all the parts of the hybrid, but there are cases, more rare, as Naudin states:

> ". . . Where the characters dissociate [se dissocient] to occupy separately and exclusively certain organs, so that the hybrid appears to be formed of heterogeneous parts, borrowed from the two species, and as it were, soldered to one another." (p. 397.)

The hybrid orange, in which the fruit is lemon in certain portions and orange in others, is cited as "one of the best known examples of this form of disjunctive hybridity."

Often the two orders of characters exist simultaneously in the same hybrid plant, but is it not rare, says Naudin, for one of them to appear alone.

> "It is a rare case where a hybrid resembles exclusively one of the two

> parents; that is to say reproduces identically one of the two specific forms." (p. 397.)

In the same article Naudin reports upon an experiment in crossing *Petunia nyctaginaeflora*, with white corolla and yellowish pollen, by *Petunia violacea*, with purple corolla and violet-blue pollen. Naudin says:

> "Our experiments have taught us that the hybrids in the first generation are very uniform in most of the species." (p. 398.)

Of thirty-six plants derived from the above cross, thirty-five were very much alike, with lilac flowers and bluish pollen. The second generation is recorded in some detail. Ten plants resembled *P. violacea* in form and color, so that it was impossible to distinguish them from the type. Nineteen plants had flowers white or very feebly rose-colored, with violet throat and with grey-blue pollen. Sixteen plants had flowers more or less lilac. One only had white flowers. In the third generation 116 plants were grown (in 1856), concerning which it is not necessary to go into detail.

The conclusion which Naudin drew from his *Petunia* experiments, repeated, as he says, several times, was to the effect that at least in the genus in question:

> ". . . the hybrids have no constancy, and that one is not able to count upon the sowing of their seeds to reproduce and preserve the varieties which crossing has caused to arise." (p. 398.)

19. *Verlot's Memoir on the Breeding of Plants.*

In 1865, B. Verlot of the Jardin des Plantes at Paris published a brief memoir, which in 1862 had received a prize from the Imperial and Central Horticultural Society, the thesis of which was as follows:

> "To demonstrate the circumstances which determine the production and fixation of varieties in ornamental plants."

The memoir is of interest as thoroughly and typically embodying the general point of view of the day concerning hybridization and the origin of new varieties, while affording at the same time much matter of interest from the standpoint of practical horticulture.

Verlot presented the view that, while the causes of variation are unknown, they arise under definable circumstances, chief among which he enumerates prolonged cultivation, removal from one set of climatic and soil conditions to another, and hybridization.

The thought of the time did not clearly distinguish a difference between the nature of the changes brought about by the external environment, and those arising from sexual fertilization. Both were generally assumed to be equally heritable. Cultivation long continued was considered to have been especially potent in bringing about variation. In Verlot's words:

> "It is especially with plants cultivated for a great number of years, with those the introduction of which is so ancient that it is lost in the night of time, that one finds profound and multiplied modifications." (6, p. 4.)

He further voices the then prevailing view regarding the relation between culture and variations:

> "If we compare," he says, "a species in its spontaneous condition with the same species cultivated, transported, that is to say, most often into conditions of climate, soil, etc., completely different from those in which it lived before, we shall be struck by seeing that, in our gardens, this latter will show derivations of type more numerous than in the wild state. We shall infer from this fact the consequence that the faculty of varying, which is proper to the plant, augments with culture. If we observe then that the plants cultivated in our gardens which have varied the most, as for example the dahlias, the roses, the camellias, the rhododendrons, the potato, etc., are not borrowed for the most part from our flora, nor from one of the neighboring floras, but on the contrary come from distant countries, where they grow under conditions often absolutely different from those in which we cultivate them, we shall conclude that, the more a species is depatriated, the more easily it will vary." (6, p. 30.) And again, "the more plants are cultivated, the greater their variations are and, by the same token, the easier they are to fix. We will possibly be contradicted, but we do not hesitate to consider, once more, long practised culture as one of the most favorable antecedents to the rapid fixation of variations." (6, p. 38.)

It now seems probable that the increased variation manifested by wild plants, when brought into cultivation, is due to the removal of the restrictive influences of competition, rather than to any actual increase in the range of heritable variability itself.

Verlot cites, as examples of the changes supposedly wrought by culture, the changes brought about in the roots of such plants as beet and parsnip; in the production of dwarf plants; in various modifications of general habit, such as fastigiate, pyramidal and weeping variations in trees; in the appearance of variations with laciniate or otherwise modified leaves; in the varieties with leaves colored white, yellow, red, or brown; in the arrangement of the leaves, as in the sudden appearance, on an ordinary alternate-leaved plant of *Rosa alba*, of a shoot with opposite leaves, propagated as *Rosa cannabifolia.* From the evidence he concludes that cultivation sets up within the plant a condition of instability, which gives rise not only to seed variation, but to variation within the plant itself—what we would call bud-variation or "somatic segregation," as in the case just cited; the case of a chrysanthemum reported, which bore at the same time yellow- and rose-colored flowers; and of a citrus fruit half-and-half orange and lemon. Another case cited by Verlot is that of a variegated *Camellia imperialis*, which for twelve years had constantly given brilliant white flowers set off with rose-colored striations and variegations, and upon which a small branch appeared one year, bearing three flowers in a group, of a uniform color, the same tint as that of the striations and variegations of the other flowers.

> "It is evident in these cases," says Verlot, "that the colorations disjoin, and that this variation returns by disjunction to its colored parent for certain plants of hybrid origin." (6, p. 67.)
>
> "As we see," he says, "by the sole fact that a plant is cultivated it is forced to vary. The instability of a cultivated plant is even evident in certain cases, in such a way that it does not only manifest itself in the direct descendants of the plant, but also in the plant itself. Thus, while the generality of the branches of a plant bear leaves, flowers and fruits of definite forms or colors, a branch is sometimes produced, in which the leaves, flowers, and fruits present completely different characters.
>
> "We recognize that culture has been, and is still, the essential cause of the variation of plants, and that thereby man has, so to speak, compelled them to re-clothe themselves with new forms appropriate to his needs or to his caprices." (6, p. 5.)

The above statement excellently presents the older point of view regarding variation. Such cases as the rose, chrysanthemum and orange, and the famous chimaera, *Cytisus adami* (*C. purpureus* × *Laburnum*), Verlot accounts for under the guise of Naudin's conception of "disjunction."

> "It is by disjunction that, in these last cases, the specific forms thus appear in hybrid plants, and it is with woody plants, it will be noticed, that this fact achieves all the phases of existence of a hybrid plant, an existence of which this disjunction would be the last term." (6, p. 14.)

He then refers to Naudin's case of disjunction in *Datura*, which is elsewhere discussed.

Verlot's expression of view on the matter of methods of selection is so thoroughly typical of the thought of his time, viz., that variation is in consequence of the "breaking up" of the "type," and that selection *ipso facto*, intensifies the variation in the direction selected for, that it is a matter of interest to present here the view expressed.

> "If a variation is produced in a direction other than that toward which one tends, it ought not to be abandoned for that; one will have more chance to obtain new variations in sowing a deviation from the type, even in a diametrically opposite direction, than in sowing anew the type itself. In the deviation there is already a tendency toward perturbation, and toward the beginning of the destruction of atavism." (6, p. 31.)

Another interesting example of the older point of view regarding plant improvement is Vilmorin's opinion, quoted by Verlot, which is here reproduced to show how thoroughly the primary idea concerning the "breaking up of the type" in order to bring about "variation" entered into the thought and operations of pre-Mendelian breeders.

> "To obtain from a plant not yet modified varieties of a kind determined in advance, I will first set myself to making it vary in some direction or other, choosing for the reproducing factor, not that one of the accidental varieties which would most nearly approach the form which I have proposed to myself to obtain, but simply that which would most differ from the type. In the second generation, the same care would make me choose a deviation, the greatest possible at first, the one most different, in a word, from that which I would have chosen in the first place. Following this direction for several generations, there necessarily ought to result, in the products obtained, an extreme tendency to vary; there then results again, and that is the principal point according to me, that the force of atavism, asserting itself counter to very divergent influences, will have lost a great part of its power, or, if one ventures to make use of this comparison, it will exert it always in a broken line." (6, p. 28.)

Man's relation to the fixation of characters in new races of plants is stated by Verlot in the usual manner prevalent in the days before Mendelian analysis:

> "In brief, gardeners have remarked, with reason, that a plant newly introduced is very susceptible to vary. This fact, it is conceived, has nothing surprising about it. It confirms that which we have previously said, that a variety, whatever it might be, had need, in order to become fixed, of being cultivated for a greater or less length of time, until one had finally come to maintain with it the tendency not to depart from being that which he had made it." (6, p. 70.)

In other words, the idea then prevalent and more or less imperfectly expressed was that, in some unknown manner, man, by continued selection, succeeds in impressing upon a "variety" the stamp of a certain type and, through repeated and continuous selection in the same direction, finally "fixes" it, so that the variety becomes, as it were, stabilized.

It probably usually means that, by continuous selection of some certain type, those individuals are usually isolated, which are more or less homozygous for the character-units thus represented, and which become "fixed" because no heterozygous factors are left to split apart.

We have here, in other words, an unscientific expression, through practical experience, of the fact which the breeder of today would define as the selection of a heterozygote having dominant characters differing from those of the species. Being of hybrid nature, such a plant would break up, and hence yield to selection, whereas the plants resembling the type, being more apt to be homozygous, would be less liable to vary in their progeny. He emphasizes the view just set forth still more emphatically in the following words:

> "If two variations are produced, of which the one differs little from the type, but is placed upon the line which leads in the desired direction, and the other is placed in an opposite direction, but departing considerably from the type, we shall not neglect nevertheless to follow this latter, because with it the breaking-up of atavism is more advanced." (6, p. 31.)

The necessity of fixing upon some single individual plant, as the basis of selection, is referred to by Verlot in the following terms:

> "We ought then to recognize that it is necessary to take account for the choice of the seed-bearers, not only of the external characters, but even of the idiosyncrasy of each one of them. Now, since this does not manifest itself except by its effects, we shall, if a variation seems to present some difficulties in becoming fixed, have to examine separately the products of each of the seed parents, and make our choice bear upon those which present, in the least pronounced degree, atavism or the tendency to return to the primitive type." (6, p. 32.)

Verlot's experience with and observations upon hybrid plants, as coming from an experienced horticulturist, are valuable, especially to the practical plant breeder.

Regarding the now well-understood fact of the gradual disappearance of the hybrid form through segregation, he says:

> "Their fertility is of short duration, through the more or less rapid return of their products to the types which have given them birth." (6, p. 25.)

Regarding the general aspects of plant hybrids, he adds:

> "All their characters, of whatever nature they may be, with the exception of a more considerable development of the organs of vegetation, are in general intermediate between those of the parents, but always limited by them." (6, p. 25.)

Regarding the matter of the bounds or limits of the hybrid characters, he remarks elsewhere:

> "Let us call attention to a circumstance always constant in the hybrids, which we have to consider, that is the absence in the products of colors other than those, or a combination of those, of the parents. We shall insist upon this characteristic, because we shall have occasion to recur to it; it will serve us to establish that, up to now, the facts prove that, by hybrid fecundations, one will obtain, in whatever part of the plant they present themselves, only the variations of color limited to those of the parents." (6, p. 18.)

Since Verlot's view regarding the nature of a "hybrid" was the conventional one, that it consists of a cross between what are commonly called distinct "species," he was led to notice the very common fact of comparative sterility in these cases. Noting the well-known characteristic of augmented vegetative growth in hybrids, he is led to ascribe the frequent seed-sterility to this latter—a conclusion easily if naïvely arrived at, from the well-known inverse relation between undue vegetative luxuriance and seed reproduction. As an instance of intermediacy, Verlot alludes to the matter of height:

> "In crossing an almost dwarf species with the pollen of a taller species, . . . the seeds of this cross will undoubtedly produce individuals taller than was their mother." (6, p. 44.)

Regarding intermediateness in size in flowers, he says:

> "In crossing a species '*parviflora*' by its variety '*grandiflora*' we shall be able . . . to obtain individuals with flowers larger than those of their mother; by crossing, one is able then to create a race or a variety in which the size of the flowers will be augmented." (6, p. 47.)

With regard to the same matter in respect to earliness and lateness, he says:

> "Supposing one crosses a very early plant with its very late variety, or *vice versa*, one will only be able to obtain varieties intermediate between the parents in earliness or lateness." (6, p. 50.)

Regarding fragrance, he mentions the case of a cross between *Rhododendron ciliatum* (odorless), and *R. edgeworthii* (very fragrant), the hybrid being less intensely fragrant than the pollen parent. (6, p. 31.)

In the matter of color intermediateness, he makes the statement:

> "Once obtained, white coloration is able to serve, either by crossing or by hybridization, in the production of new variations ordinarily intermediate between them and the color from which it has proceeded." (*ib.*, p. 59.)

In other words, presumably, dilution through the presence of but a single dose of the color factor.

The most interesting portion of Verlot's memoir is his discussion of the practical results achieved with ornamental plants in the field of hybridization.

Regarding dwarfing, he cites McNab (p. 42) to the effect that the best dwarf varieties of *Rhododendron* are obtained by the use of pollen taken from the small stamens:

> ". . . the products of which," he says, "I am able to certify, are very different from those obtained by the use of the pollen of the large stamens."

Regarding breeding for winter-hardiness, he mentions the case of the cross of *Amaryllis brasiliensis*, a delicate species impossible to winter out of doors, by *Amaryllis vittata*, a much hardier plant, whereby hybrids were produced which, with light covering, would withstand the climate of Paris. Likewise, *Rhododendron arboreum*, which cannot resist more than two to three degrees of cold, gave, when crossed by *R. catawbiense*—a much hardier form, though with inferior inflorescence—hybrids which inherited the hardiness of the female parent.

Verlot did not recognize the phenomenon of dominance as such in the first generation of the hybrids, but he mentions the case of a white *Gloxinia*, crossed by pollen from a blue-flowered variety, in which, out of one thousand seedlings,

> ". . . all bore nothing but perfectly blue flowers, not a single one of them being white nor a single one variegated." (6, p. 65.)

Regarding the inheritance of variegations, it may be of interest to note that the following species are mentioned, in which the variegated form breeds true from the seeds.

Alyssum maritimum
Barbarea vulgaris
Celtis australis
Cheiranthus cheiri

With these are to be included the variegated ferns *Pteris argyraea and P. aspericaulis var. tricolor.*

He remarks upon an interesting fact, that the variegations do not appear upon the first leaves of a variegated variety.

Regarding the heredity of double flowers, he reports no crossings, but simply remarks upon cases of double-flowered peach and apple, which came true from the seed. (6, p. 83.)

Verlot summarizes his views upon hybrids in the following words, which are worth reproducing because they fairly well represent the general knowledge of the time as follows:

(1) "Hybrid fecundation is not able to produce anything but variations which will be able, it is true, to multiply themselves mechanically, but which will not be fixable, and which consequently cannot be brought to constitute races or varieties, the fertility being limited to a few generations, or disappearing, after a certain time, by the disjunction of the types.

(2) "One of the characters of the hybrids is also a great development of the vegetative organs, coincident with less abundant flowering. They are in general intermediate between the species types, but often approach more the father.

(3) "The hybrid, fertilized by a parent, returns also promptly to the parent.

(4) "The hybrid, self-fertilized, returns more or less rapidly to the parents.

(5) "Crossing, that is to say, reciprocal fertilization of varieties of races of the same species, will serve for obtaining new variations, intermediate between the parents, very fertile, and which can be fixed more or less rapidly and constitute new varieties or races." (6.)

20. *The Work of the Vilmorins.*

The eminent services of the Vilmorin family for over two hundred and thirty years to French agriculture, and particularly through the improvement of the sugar-beet and of wheat, cannot be taken up here. It would not, however, do justice to the mental activities of a long succession of the members of this family, and of the distinguished house of Vilmorin-Andrieux & Cie. of Paris, if one omitted to at least mention the fact that, through no less than seven generations of father and son of the family of Vilmorin, there were published by them, in journals and annals of agriculture and horticulture, in proceedings of agricultural and horticultural societies, and in journals of botany and related subjects, more than three hundred and sixty articles dealing with plants, from the various standpoints of agriculture, of horticulture and floriculture, and of botany. Some fourteen of these were contributed to the Bulletin de la Société Botanique de France. It remains in the present instance to discuss the contributions of Louis de Vilmorin (1816-1860), and of his son Henry (1843-1899), to investigations in heredity and in hybridization.

The first experimental effort, since the work of Sageret, to find a definite numerical relation in the transmission of characters from a cross was the work of Louis de Vilmorin, carried on with *Lupinus hirsutus* from 1856-1860, and reported upon by his son in 1879. (7b.) This species affords the advantage of being generally self-fertilized, and has ordinarily blue, but also frequently rose-colored flowers, there being no other color or intermediate shade. The plants used came from seeds of these two varieties, from commercial lots, kept pure by rogueing out all plants not of the desired color. It was Vilmorin's conception that, in a self-fertilized plant such as lupine, there was introduced a great advantage in the study of heredity, since each individual was the descendant of a single plant of the preceding generation, and not of a number of ancestors, doubling itself at each stage, as in the case of plants where two individuals are involved in seed reproduction.

> "It may then be admitted," says Vilmorin, "that the seed sowed the first year of the experiments, in 1856, reckoned a series of at least fifteen ascendants, which have given flowers constantly of the same color, blue for some, rose for the others." (7b, p. 6.)

No crosses were made, but records were kept for four years of the different kinds of plants derived from each sowing. Out of the progeny produced each year, instead of planting all or a considerable number, but one representative of each color was planted, as a rule, so that large numbers are not available. The fact that both the blue and the rose-colored plants for the most part broke up into blue and rose for each year indicates that each strain was in the hybrid or heterozygous condition.

In forty cases during the five years, the rose-flowered plants broke up into blue and rose; in three apparently, and in the other cases possibly, there appeared to be a 3 : 1 ratio of rose to blue. In thirty-six cases in the same period, the blue-flowered plants in turn broke up into blue and rose; in six of these cases, the ratio was close to 3 : 1. It is evident that Vilmorin's experiments need repetition, since a clear breaking-up of *both* blue and rose-flowered plants into blue and rose again would not be expected. A few cases of rose and a few cases of blue bred true. To Vilmorin, it was simply a question of filtering out the progeny until they become true, either rose or blue-flowered. He remarks upon the fact that "the color blue persists more obstinately, becomes fixed more quickly, and once fixed maintains itself better, than the rose color." (7b, p. 8.)

PLATE XXVIII. Louis Lévêque de Vilmorin, 1816-1860.

This experiment is one of the few attempts at obtaining information as to the numerical relations between the progeny of plants in the hybrid condition, although in the present instance, the plants not having been knowingly crossed, they were not regarded by Vilmorin as being in the hybrid condition with respect to flower color. The fact of their breaking-up, however, shows that such was nevertheless the case. This being true, it is probable that the large number of irregular ratios which were obtained was due to crossing by insects. Vilmorin was naturally unable to deduce any precise conclusion from such an array of data. It must be

PLATE XXIX. Henry Lévêque de Vilmorin, 1843-1899.

kept clearly in mind that, from his point of view, a plant was a constant struggle between two opposing forces, the force exerted by its immediate parentage and that exerted by its ancestry.

> "The characters of an individual plant are the result of the action of two distinct, and in a certain measure, opposed forces. The first represents the tendency to individual variation or idiosyncrasy. It causes the individual to present characters different from those of its ancestors, while remaining enclosed within the limits assigned to the species. This force, although probably complex in its nature as in its effects, may, for facility of reasoning, be considered as 'simple.' The other force is that which calls upon the individual to reproduce the character of its ascendants." (7b, p. 41; 8, pp. 33-4.)
>
> "This latter, simple, and insofar as the ancestors are concerned, of the individuals which one considers have presented invariable characters, becomes on the contrary evidently complex, if there have already been some variations. The tendency to assemble a collection of beings dissimilar among themselves cannot be the effect of a single force, but the resultant of several more or less divergent forces. One may call 'atavism' the tendency which, in this case, calls the plant to resemble the totality of ascendants, and 'heredity' that which leads it to reproduce the characters of the individual from which it immediately descends." (7b, p. 4.)

In another place (7d), Henry de Vilmorin quotes his father's viewpoint again as follows:

> "If we consider a seed at the moment when, put into the ground, it gives birth to a new individual, we may regard it as solicited, so far as the characters are concerned which the plant must exhibit to which it is to give birth, by two distinct and opposing forces. These two forces, which act oppositely, and from the equilibrium of which results the fixity of species, may be considered as follows:
>
> "The first, or centripetal force, is the result of the law of the resemblance of children to fathers, or atavism. Its operation has for its results the maintaining, within the limits of variation assigned to the species, of the departures produced by the opposite force.
>
> "The other is the centrifugal force, resultant of the law of differences in individuals or idiosyncrasy, and causes each one of the individuals composing a species, whether one is able to consider it as the progeny of a single individual or of a pair, to present differences which constitute its own physiognomy, and produce that infinite variety in unity which characterizes the works of the Creator." (p. 489.)

Vilmorin thought that the action of these diverse tendencies would be measured by the proportion of plants with blue flowers, and of plants with rose-colored flowers, respectively, which proceed from the seeds of an individual of one of these two colors, and especially since, in his view, there were no intermediates. The inferences, rather than conclusions, which Vilmorin believes he is able to derive from the experiment, are based upon the fact that the majority of the descendants, in his experiments, resembled their immediate parent, and that the power of that which he calls "direct heredity" is altogether preponderant. From the fact that now and again a plant would "take back" to a more remote ancestor, he concluded that "atavism" was also a constant and tenacious force to be reckoned with.

> "It is this force," he observes, "which causes to reappear the characters of the great mass of the ancestors among distant descendants, across numerous generations presenting different characters. The action of this force may appear limited, if one considers only its influence upon a single generation, but, if one reflects that it acts constantly and always in the same direction, it is explained that it suffices to maintain the fixity of plant species." (7b, p. 10.)

Elsewhere, Vilmorin further remarks regarding the forces involved in inheritance:

> "We come first, for the greater simplicity, to consider atavism as constituting a single force, but, if one reflects, one will see that it presents rather a bundle of forces acting almost in the same direction, and composed of the individual call or attraction of all the ancestors. Now, to facilitate the intelligence of action of this force, it will be necessary for us to consider first, and in an abstract manner, the force of the resemblance to the mass of the ancestors, which may be considered as due to the attraction of the type of the species, and to which we shall reserve the name of atavism; then separately, and in a more special manner the attraction of the force of resemblance to the father direct, or heredity, which, less powerful but nearer, will tend to perpetuate in the child the characters proper to the immediate parent."

Another conclusion which Vilmorin draws, is as to

> ". . . the very rapid enfeebling of the influence of heredity beyond the first generation, in other terms, the little tendency which plants show to resemble any ancestor exhibiting characters other than those of the mass of ancestors, if this ancestor is not the immediate author of the plants. We have seen frequent examples of blue plants issued from two or three generations of rose plants, and giving birth nevertheless to a progeny entirely or almost blue."

As to the conclusion which one may draw from these experiments, he says:

> "It will not be a mathematical evaluation of the comparative power of the different forces which act upon the transmission of the characters in the plants. On the other hand, in a word, one knows that the phenomena in which the vital forces intervene do not permit themselves to be reduced to figures, and on the other hand, were it otherwise, that the number of individuals observed in each generation would not be enough to give precise numbers, limited as that was by that of the seeds of the hybrid plants, the seeds being in *Lupinus hirsutus* very large and few."

The only general conclusion which Vilmorin was able to derive from the lupine experiment, which he was able to put into the form of what might be called "rules." are the following:

> 1. "A very marked tendency of plants to reproduce the characters of the immediate ascendants; it is the effect of *direct heredity*.
> 2. "A tendency less strong, but much more persistent, to resemble the mass of the distant ancestors. It is that which has been spoken of under the name of atavism.
> 3. "A rapid enfeebling of the tendency to reproduce the characters of an ascendant which is not the immediate author of the plant, if these characters are not those of the mass of the ancestors." (7d, p. 490.)

Vilmorin summarizes by saying:

> "The experiment already gives indications which, approximated to the results of the experiments made and to be made, will permit, one day without a doubt, to be embraced in a complete and methodical presentation the totality of the laws which regulate the heredity transmission of characters in plants." (7b, p. 11.)

The difficulty with Vilmorin's experiment, as with so many others before that of Mendel, was that it did not undertake to deal with the progeny of plants purposely crossed with the object of determining *the numbers and proportions of individuals of the different kinds*, that appeared in the second and "variable" generation. So far as Vilmorin's experiment itself was concerned, had the plants been covered, to prevent all possibility of crossing, and had the numbers of the progeny planted been large, instead of consisting of single representatives of the blue and rose-colored strains, respectively, results of value to students of breeding might have been definitely revealed.

In another memoir (8) Louis de Vilmorin raises the question whether

> ". . . the qualities or the characters produced in an individual by external and accidental circumstances, such as are peculiar to it and have not affected its ancestry, are in some proportion transmissible sexually." (p. 2.)

Instinct, he says, leads him to a negative conclusion, although, as he admitted, determinative data upon the subject were lacking. In undertaking the study of heredity, Vilmorin remarks upon the necessity of disengaging as much as possible the study of heredity from the circumstances which might characterize its action. The latter he finds complicated by the question of the range of the variations in the plant induced by external conditions.

> "For it is only after having determined the normal amplitude of these variations that one is able to judge if more considerable ones present themselves, which one is able to attribute with certainty to the action of the causes of perturbation which one studies." (8, p. 3.)

Vilmorin's scientific point of view is plainly shown in the following statement:

> "The number of forces which are in play is so considerable, the manner in which they are able to combine is so varied, that it explains to me in part how difficult it is to obtain completely concordant results in an experiment where all the influences, save that which one studies, ought to remain invariable." (8, p. 4.)

In the following, Louis de Vilmorin shows an appreciation, in advance of its scientific demonstration by Johannsen, of the principle of using pure-bred strains or "pure lines" in breeding; of breeding from the individual plant, and not by means of mass selection. Referring to the breeding of the sugar beet, he says:

> "All that I have been able to observe up to the present, on the question of the transmission by heredity of characters in plants, makes me think that it is necessary to individualize the observations as much as possible. So I have adopted the custom, when I had to fashion a race, no matter how little rebellious, of gathering and sowing the seed separately of each one of the individuals which I have marked as my choice, instead of making, as ordinarily, a choice composed of as many individuals as I needed to collect the quantity of grain of which I had need, and I have always remarked that among these individuals there were some which always gave a better return than others, and which I finally adopted as the sole type for amelioration." (8. p. 18.)

In 1890, Henry de Vilmorin reported (7d) an interesting observation with peas, similar in character to that of Goss, which awakens surprise from its not having aroused further investigation. Speaking of the progeny, he says:

> "All the seeds of the same plant are not rigorously alike among themselves. They differ, especially when the plant which has borne them is of a mixed race, and has undergone, or is in the process of undergoing, modifications through the action of the environment in which it lives."

Vilmorin then, in the following words, anticipated the present point of view regarding the distribution of characters.

> "The different characters which enter into the composition impress themselves differently in the different seeds, and are reproduced in diverse combinations in the plants issuing from those seeds."

He proceeds to give as an illustration, precisely the case of the distribution of characters which formed part of Mendel's experiment.

> "It is known that among peas there exist races with white seeds, and others which, even at maturity, have green seeds. Now this year [1889], examining peas obtained by crossing a race with green seeds with a race with white seeds, I have frequently found in the same pod seeds of different colors. This character of color, easily appreciable to the eye, permits the conclusion that all the seeds of the same plant are not necessarily alike among themselves, nor endowed exactly with the same faculty of reproduction." (p. 488.)

No analysis, however, was made of the nature of this phenomenon, by growing separately the green and the white seeds thus produced.

Vilmorin ventures no further view upon the fundamental nature of hybridization than to say that cross-fecundation has this inexplicable but well-determined result, so far as the characters of the plant are concerned, "of grouping them in the different seeds resulting from the cross in very variable combinations and proportions."

It is to be seen that there exists here a recognition of the germ of the idea of the segregation of characters, without, however, furnishing the data for knowing their possible proportions.

Henry de Vilmorin reported to the Société Botanique de France (Sessions of February 27 and December 10, 1880; 7c, pp. 73-4, 356-61), upon the hybridization of wheat. "Several times in the course of recent years," he states, "I have had occasion to make crosses between different varieties of wheat, to the end of obtaining new forms, presenting, from the agricultural point of view, certain qualities which I sought to develop." (p. 73.) These crosses originally made between varieties of *Triticum sativum*, suggested the attempting of crosses also between different forms of wheat, originally regarded as belonging to different species. The characters of the hybrids in the *sativum* crosses were reported as being in general intermediate, now approaching one, now the other parent, or offering characters found in neither. Crossing a pubescent wheat, "Blé à duvet," reciprocally with a reddish, beardless, smooth spelt (*T. spelta*), the products of the cross were intermediate where spelt was the ♀ and "Blé à duvet" the ♂ parent. From the reciprocal cross, eight similar and intermediate plants were obtained. The grain was adherent to the glumes, and the rachis fragile as in spelt, but less so. The important thing, in Vilmorin's opinion, was the ability of two supposed "species" of wheat to

PLATE XXX. Henri Lecoq. Professor of the Natural Sciences at the University of Clermont-Ferrand.

cross, giving a uniform and strictly intermediate progeny. In the more extensive report (7c, 356-61), reciprocal crosses made in 1878 were reported between *T. sativum* and *T. turgidum*, *durum*, *polonicum* and *spelta*. All the possible combinations between *sativum* and the other four were attempted with success, except in the crosses upon *T. polonicum* ♀. The reciprocals with this form as ♂ succeeded. Crosses (reciprocally) with *T. monococcum* failed. In the pubescent, white-chaffed, wheat-spelt crosses, the spelt characters were reported as being the most strongly characterized in the descendants. All combinations of color and pubescence of glumes (except pubescence in the speltoid forms), is reported. Second-generation results are given of crosses between "Chiddam d'automne," a soft, white-chaffed, beardless wheat, by "Ismaël," a pubescent, hard wheat, and between "Blé Seigle," a red, pubescent, beardless variety of *T. sativum*, and "Blé Buisson," a poulard wheat. From the first-named cross, Vilmorin reports the second generation in 1880 as giving the most diverse forms, no two alike, nor a single one reproducing the characters of either of the original parents. Not only were noted soft and hard wheats, but wheats resembling poulard (*T. turgidum*), and more or less the spelts (*T. spelta*), which, he remarks "is surprising in the progeny of a soft and of a hard wheat." Of the cross with "de Beauce," the second generation gave "the most curious mixture of wheats, dwarf and tall as to straw, bearded and beardless, with heads extraordinarily slender or extremely compact." (p. 359.) There also appeared a form resembling *T. durum*, but beardless. The cross involving "Blé Seigle" and "Blé Buisson" is reported as giving rise, in the second generation, to "wheats of all sorts, bearded or beardless," but among which "one notices a very marked tendency to approach forms derived from *T. spelta*." Among these there was "even a branched spelt issued from two wheats with simple heads." These cases appear to Vilmorin to be cases of the "disorderly variation" reported by Naudin. He remarks, "Similarly to Naudin, it is in the second generation that I observe this variation." (p. 359.) Vilmorin further comments upon the appearance, among the progeny of the two wheats, of characters not those of either of the parents, but belonging to other wheat forms. The general conclusion is, "If these forms can be fixed with their present characters, it will be very difficult to doubt that the most of the races of wheat, considered ordinarily as so many species, are in reality but variations of one and the same plant." (p. 359.)

21. *Lecoq's Memoir on Hybridization.*

In 1827 appeared the first edition of a work by Henri Lecoq, entitled "Recherches sur la Réproduction des Végétaux." In 1845 appeared his work on hybridization, published in 1846 in German translation. A second edition of the book was published as late as 1862. Lecoq, who was Professor of the Natural Sciences and Director of the Botanical Garden at Clermont-Ferrand, sought to present the subject in such manner as would be of interest and of tangible concrete value to the practical gardeners of his time. To this end he says:

> "In order to be as clear as possible, I have endeavored not to frighten away every practical gardener and friend of gardening through useless parade of science and erudition." (3b, p. 5.)

His point of view is well stated thus:

> "However limited a flower garden, however small the corner of the earth may be which a garden amateur can command, he is nevertheless in a position to institute a number of useful investigations and noteworthy experiments, to prepare for himself innumerable joyous delights, when he succeeds, through artificial fertilization, in enriching his little garden, his friends, his native region, with a new creation, which owes its existence to his care and his intelligence. What pleasure when he can extend these annually almost entirely at his will, with new shades and colors never seen, obtain larger flowers, or bring about unlimited doubling." (*ib.*, p. 6.)

Lecoq enlarges upon the results that can thus be obtained in fruit and vegetable gardening, and in agriculture:

> "Although we possess already about five hundred sorts of grains, yet we can still always obtain better ones, at least new modifications which are better adapted to this or that soil or climate, or to all the conditions of this or that agriculture." (*ib.*, p. 7.)

The general method to be pursued is laid down simply as follows: according to Lecoq's and the then prevailing point of view, the first thing that one must strive after, in order to bring plants to vary, is "the shattering of their stability, and the breaking up of their habit." For this purpose, it was considered desirable to sow their seeds under different conditions of climate, temperature, soil, moisture, etc. When, after several such sowings, a case occurs where individual seedlings show more or less remarkable changes, varying more or less, showing that stability or habit has been unsettled, the seeds of the varying plants are to be gathered, since from these, new varieties are to be expected. The seeds of such new forms are sown over again and so on continually. Such changes Lecoq considers "purely morphological phenomena, that is to say, changes of the natural form without hybridization."

Once arrived at this point, hybridization of the thus newly-obtained varieties was to continue, and still other new ones thereby again obtained. Such was the simple formula of this genial friend of plants and gardening, for the breeding and improvement of plants. After a brief botanical discussion of natural fertilization, Lecoq devotes the remainder of his book to a discussion of artificial fertilization, first in its general aspects and applications, and then in detail, as applicable to the various more important families of the seed plants, of which he brings into discussion seventy-five, including two hundred and ninety species.

Speaking of the hybrid offspring of the crossing of plants of different genera or different species, Lecoq says:

> "In general, the product of such a fertilization shows at the same time the characters and peculiarities of the father and of the mother; but I have noticed that in a very great number of crosses achieved by myself with all conceivable foresight, the hybrids or products have almost always taken more from the mother plant than from the father." (3b, p. 41.)

The reason for this might possibly be attributed to frequent cases of accidental self-fertilization.

Again Lecoq says:

> "The most difficult thing was and always is the shattering of the stability of the first type, the breaking of its habit; just as soon as an impulse thereto is present, then variation begins to know the limits of which no human eye and no human understanding suffices. With the mighty lever of hybridization in the hand, the power of the gardener is an almost unlimited one." (*ib.*, p. 45.)

Lecoq comes now to the discussion of special objects in the breeding of plants. Speaking of breeding for double flowers, he makes a remark that has genetic value.

> "One has almost the certainty of getting many double flowers, as soon as one of the crossed species has become double, and in no wise was the doubleness of both parents necessary, as many gardeners believe." (*ib.*, p. 45.)
>
> "Two plants with half-double flowers often furnish hybrids with very double or completely double flowers; but extremely seldom does the case occur where two species with single flowers produce in the immediately following progeny hybrids with double flowers." (*ib.*, p. 46.)

With respect to color, Lecoq remarks:

> "Most ordinarily, colors mingle, mix and fuse through hybridization just as though one had put them together in a palette, and there arises therefrom a middle or half tint; but with many genera they do not fuse, but remain separate, and appear as variegations on the corolla, as for example in the morning-glory, tulip, etc.; in stripes as in the aster; in flecks or clouds as in many varieties of *Dahlia;* in peripheral markings or borderings, as in some auriculas, primulas, etc." (*ib.*, p. 47.)

Coming to matters of detail with respect to the crossing of plants in different families, there are a number of interesting remarks which deserve to be noted. In discussing the family of the *Cruciferae*, Lecoq refers to the case of a cross by Sageret between a cabbage and a black radish, the latter serving as the seed parent. This hybrid is reported to have had two types of shoots, one superposed over the other, and both entirely distinguishable through their form, one being like that of the cabbage, and the other resembling the radish. This appears to be an interesting case of factor-mutation in somatic cells. Lecoq mentions the further case of a sectorial chimaera in *Dianthus barbatus*, which sometimes, as he says, shows "variations" in which flowers of different color occur not only on the same plant, but in the same inflorescence, white and red flowers being immediately juxtaposed. His view is as follows:

> "Plants which show these characters are hybrids, and confirm an observation made long since by Sageret, which my experience also verifies, that one frequently gets hybrids which do not stand in the middle between father and mother, but appear to have taken on some organ or other completely from the one and from the other, respectively, and without any modification at all. I should at least scarcely know how to explain the appearance of different colored flowers upon the same plant in any other manner." (p. 117.)

In discussing the Leguminosae, Lecoq speaks of the crossing of alfalfa, and alludes to the undoubted probability of successfully crossing *Medicago sativa*, or ordinary alfalfa, with *Medicago lupulina or* Yellow Trefoil, but remarks:

> "There appears to be no necessity for the creation of new plants, so long as one has not already recognized, in those already present, essential defects or disadvantages, or on the other hand marked advantages." (*ib.*, p. 145.)

It is interesting here to remember that it is undoubtedly to a natural cross of these two species that the Grimm variety of alfalfa is due, which has enabled alfalfa growing to be carried into the northern border states of the western United States, and the western provinces of Canada.

Speaking of the crossing of agricultural plants in general, Lecoq remarks:

> "It certainly remains highly regrettable that thus far there has been so little concern about hybridization of agricultural plants, and that it has been simply left to chance to get varieties, while it would have been so easy [referring here to beets] to institute with discretion crossing experiments which certainly would be a new cause of agricultural riches." (*ib.*, p. 305.)

Lecoq lived before the days of the breeding of the cereals. Alluding to the breeding of wheat, he says:

> "It remains one of the extraordinary human facts, that such a simple operation, exacting neither time nor money, which can have such large results, has thus far not been attempted on a plant upon which so many families of all European lands are fed." (*ib.*, p. 401.)

In conclusion it may be mentioned that Lecoq crossed a variety of corn called *Zea rostrata* (corn with pointed or beaked kernels) with ordinary yellow and red corn, and says:

> "I completely destroyed the beak. Every single variety of this fine plant brings out some kind of a change through hybridization, either in the form of the cobs, or through the variegation of the kernels, or through entire metamorphosis of the color." (*ib.*, p. 398.)

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CHAPTER VI

THE GERMAN HYBRIDIZERS

22. *Wiegmann's Experiments.*

IN 1819, and for a second time in 1822, the Physical Section of the Royal Prussian Academy of the Sciences, had, at Link's proposal, offered a prize for an answer to the question: "Does hybrid fertilization occur in the plant kingdom?" (Gibt es eine Bastarderzeugung im Pflanzenreiche?) and this, despite the fact that as early as 1761, Kölreuter had flattered himself with the hope that now,

> ". . . even the most stubborn doubter of the truth of the sexuality of plants would be completely convinced. If contrary to all conjecture," he says, "there should be such an one, who, after a rigid examination, still maintained the contrary, it would astonish me as greatly as though I heard someone on a clear mid-day maintain that it was night."

Fifty-six years after this utterance however, apparently unconvinced, the Prussian Academy still sought light in the darkness that Kölreuter had congratulated himself to have dispelled.

On the third of July, 1826, the Academy's prize was conferred upon Dr. A. F. Wiegmann, physician, of Braunschweig. Since the investigation did not, however, in the Academy's opinion, furnish a complete solution to the question, only half, instead of the whole of the prize was granted. The award was made in the following language:

> "The author has described the results of his investigations with appropriate brevity. These results are in part completely convincing, and in part not;"

the reason being given, that certain of Wiegmann's hybrid specimens submitted scarcely showed evidence of being of a hybrid character. Since, on the other hand, Wiegmann's results completely confirmed and extended those of Kölreuter, and especially by reason of his determination of the fact that self-fertilized hybrids may bear fertile seeds, it was decided to grant the award.

Wiegmann, through forty years of observation, including the fact of having actually produced two geranium crosses as early as his sixteenth year, was already predisposed toward the affirmative of the question submitted. His investigations, begun in 1822, were finally published in 1828 (7). In order to overcome all possible criticisms from the opponents of the idea of sexuality in plants, which he considered might be directed against what he designates as "an unnatural handling of plants in pots," he conducted his operations in the open ground, in connection with which, he alludes to the several hindrances he was obliged to undergo, "weak sight, a trembling hand, and painful bending and kneeling." (7, p. 2.)

Wiegmann refers to the main failures encountered, including the attempted repetition of a number of Kölreuter's experiments, as being probably due in part to having attempted crosses between different genera.

> "Since many stigmas, according to my numerous experiments, take the pollen of too distant genera either not at all, or with extreme difficulty." (p. 2.)
>
> "Plants which together are to produce hybrids," he says, "must have some relationship with one another, as Kölreuter has already remarked. The nearer the parent plants are related to one another, the more easily will hybrid fertilization succeed; most easily in the case of different sub-species or varieties; then different species of the same genus; less easily in the case of plants of different genera." (*ib.*, p. 26.)

Wiegmann, however, was entirely free from any rigid dogmatic attitude on the species question. His views in this regard are completely modern. Continuing the above, he says:

> "Yet at the same time, one needs indeed pay less attention to differences based on artificial generic characters. Genera like *Pisum* and *Vicia, Ervum* and *Vicia, Lychnis* and *Cucubalus*, are in their nature so related that hybrids can arise from them, as Kölreuter and I have demonstrated." (p. 27.)
>
> "So much the more I dispute his opinion," he says of Kölreuter, "respecting the difference between true 'species' and 'variety' falsely derived from the fertility or infertility of the hybrid plants." (*ib.*, p. 25.)

Wiegmann, in fact, regards chance crossing in nature, between species or sorts of plants, as having given rise to new agricultural races.

> "It appears from my experiments," he says (p. 26), "that many species, or constant subspecies, e.g., *Pisum arvense, Vicia leucosperma, Vicia faba* (red-seeded), as well as the most of the varieties of cabbage and the cereals, whose origin is unknown, possibly are hybrid plants, which

have been produced upon our fields and in our gardens through the proximity of a few related plants, and have remained constant." (p. 26.)

Wiegmann sums up the matter of the bearing of degrees of relationship upon crossing as follows (p. 27):

> "Mainly it rests on the point that the different plants do not vary from one another greatly in their natural constitution, and that their secretions are not too heterogeneous, since otherwise the pollinating substance would not be absorbed by the stigma.
>
> "In general," he says, "foreign pollen takes hold of the stigma with much greater difficulty than does its own, and in order to obtain complete fertilization, one must often deposit it several times, even when the foreign pollen is from a plant of the same species." (p. 3.)

Wiegmann's experiments covered a list of thirty-six crosses, using the following species and cultivated varieties:

Avena, 3 species and varieties
Allium (onion, etc.), 2 species
Brassica (cabbage, etc.) 4 races
Nicotiana (tobacco, etc.), 2 species
Pisum (pea), 1 species
Ervum (lentil), 1 species
Dianthus (pink), 3 species
Phaseolus (bean), 2 varieties
Verbascum (mullein), 9 species
Vicia (vetch), 3 species

The general conclusions Wiegmann draws from his experiments are most interesting. The most important are those which relate to the possible vigor of new species.

> "My experiments sufficiently prove," he says, "that the fertilization of different subspecies, *inter se*, is a source of manifold degenerations of species in the plant kingdom, and that insects, especially bees and bumblebees, as well as little beetles and flies, play a much more important rôle in the fertilization of plants than one has lately been inclined to allow them, but of which I have the indubitable proofs." (p. 3.)
>
> "Even though the structure of the corolla in the case of leguminous plants," he says again (p. 26), "scarcely appears to admit of the access of insects and foreign pollen, yet the plants obtained from the seeds of experimental plants show such a striking alteration in their specific characters, especially in the form of the seed and its envelopes, that an influence of foreign pollen on the ovules will scarcely be able to be denied. I myself have numberless times convinced myself of the fact that bumblebees, bees and small insects from the order of flies and beetles, can fertilize the flowers of the *Leguminosae* in the manner stated by Sprengel. It is therefore necessary in agriculture to give heed to this matter, if one wishes to keep plants that are to be cultivated in their quality and integrity."

With respect to observations of a more special nature, Wiegmann's memoir contains much interest. Regarding the breaking-up of the progeny of hybrids, he says, speaking of Kölreuter's observations:

> "I have found his observations well founded, that the plants produced from seed from one capsule of hybrid plants, often differ from one

another in respect to fertility, and especially in the structure of certain parts, now approximating more to the father, now to the mother." (p. 25.)

Wiegmann's independence of traditional authority is witnessed in his contradiction of the view of "the great Linnaeus," that hybrids resemble the mother in the fertilization apparatus, and the father in foliage and habit. Instead, he says:

> "The change through the foreign fertilizing pollen shows itself in very different parts in different plants; in the anther-filaments, in the inflorescence, in the form, color, and odor of the corolla, in the height of the stem and its divisions, in the form and outside covering of the leaf." (p. 23.)

Referring to the then general assumption that hybrids (of the F_1 generation) occupy a mid-position with respect to their characters between the two parents, he says:

> "In many cases this does not occur, but either the color of the father or that of the mother shows itself alone dominant (herrschend) in the hybrid. The same also obtains among animal hybrids; the two colors may, through mingling, give an intermediate one, but in just as many cases the one only prevails. Plant hybrids therefore unite in themselves in part the peculiarities of the father, in part those of the mother, whereby they approach now the maternal, now the paternal form." (p. 21.)

Regarding the matter of dominance, Wiegmann further incidentally remarks upon the case of the crossing of two species of *Dianthus*, where "the form of the father has almost entirely suppressed that of the mother." (p. 22.)

For present-day genetics, one of the most interesting points in Wiegmann's report is his discussion of the immediate effect of the pollen in the case of leguminous plants. According to his statement:

> "Even immediately after fertilization, an alteration arising in the form and color of the seed, and in the form and size of the pods, is especially unmistakable in the case of the leguminous plants, although otherwise all fruits and seeds of hybrid plants from other families have never shown themselves to me to be different from those of the mother plants." (p. 23.)

And again:

> "The principle expressed by Gärtner, that the influence of foreign pollen changes nothing in the form and external character of the fruits and seeds of the mother plants, should, according to my investigations, undergo a modification in the case of Diadelphia (*Leguminosae*), since, in the case of these, the foreign pollen exerts an immediate effect upon the color and other characters of the fruits and seeds." (p. 29.)

In the case of *Phaseolus*, he says:

> "Previous experiments have taught me that *Phaseoli* of one species, but of two different kinds of flowers and seeds, when placed together, bear differently colored seeds, and, in the second generations, also differently colored flowers." (p. 23.)

Wiegmann carried on some field experiments with beans, vetches, oats, and cabbage, in which adjoining rows of plants were allowed to freely cross-pollinate through the agency of the wind and insects, from which he concluded:

> "It appears further, from the behavior of the *Leguminosae* and of cabbage, that agronomists and gardeners cannot be careful enough in the arrangement of their fields in order not to suffer from the great damage through hybrid fertilization occurring even the first year." (p. 36.)

Speaking generally, he says further:

> "It is not entirely improbable that that which exhibited itself to me thus far, as being peculiar to the *Leguminosae* alone, may take place also among other plant-families, and the clearing up of this matter remains very desirable for botany, as well as for agriculture in particular." (p. 30.)

Wiegmann's work, as a whole, impresses one as the work of a man without scientific prepossessions, willing to investigate for himself, and to dispute freely the authority of other investigators, such as Linnaeus, Kölreuter, and Gärtner, and, withal, a man with a practical bias for and sympathy with agriculture.

23. *The Work of Carl Friedrich von Gärtner.*

In the valley of the Nagold, in the Black Forest region of Würtemberg, some forty miles southeast of Stuttgart, the capital, lies the village of Calw.

Here Kölreuter, whose home was in Sulz, a little way to the south, also in the Neckar valley, lived for a time, and did some of his work in hybridization, in the garden of a local physician. By a curious coincidence, in the same village of Calw in which Kölreuter had previously worked, and but forty miles north of Sulz, where the latter had formerly obtained the first hybrid plant ever produced in a scientific experiment, lived and died Carl Friedrich von Gärtner, who for twenty-five years conducted extensive experimental work in hybridization. He was a physician, and son of the distinguished botanist, Joseph Gärtner, Professor at Tübingen and St. Petersburg, and author of an authoritative work on the seeds and fruits of plants, in which were figured the morphology of more than a thousand species. The introduc-

Plate XXXI. C. F. von Gärtner, 1772-1850.

PLATE XXXII. Village of Calw, in Würtemberg, home of C. F. von Gärtner.

PLATE XXXIII. Marketplace in Calw, Würtemberg.

tion to the volume for 1778 contains, in the words of Sachs, "valuable reflections on sexuality in plants."

In 1830, two years after the appearance of Wiegmann's memoir, the Dutch Academy of Sciences at Haarlem, in turn, propounded anew the riddle of hybridization in the following words:

> "What does experience teach regarding the production of new species and varieties, through the artificial fertilization of flowers of the one with the pollen of the other, and what economic and ornamental plants can be produced and multiplied in this way?"

PLATE XXIV. Present site in Calw of a portion of the former experimental garden of C. F. von Gärtner.

No reply was received (January 1, 1833), and the offer was accordingly renewed for another three years until January 1, 1836.

In October, 1835, Gärtner learned of the prize offer, and was able to present a brief résumé of his work up to that time, which, indeed, prompted a further extension of time on the part of the Academy. Gärtner finally presented the Academy with a memoir of two hundred pages, and with herbarium mounts of one hundred and fifty different sorts of hybrid plants produced by hand pollination. On May 20, 1837, this memoir received the prize, and was later (April 20, 1839) published in revised and extended form, together with an extensive list of the experimental material, and with the obtained results arranged in tabulated form.

An idea of the amount of labor expended by Gärtner during the twenty-five years of his hybridization experiments may be gathered by the statement that he carried out nearly ten thousand separate experiments in crossing, among seven hundred species, belonging to eighty different genera of plants, and obtained in all some three hundred and fifty different hybrid plants, as the total result.

Among the prominent genera worked with were *Althaea*, *Antirrhinum*, *Aquilegia*, *Avena*, *Datura*, *Delphinium*, *Dianthus*, *Digitalis*, *Fuchsia*, *Gladiolus*, *Hypericum*, *Lobelia*, *Lychnis*, *Malva*, *Matthiola*, *Nicotiana*, *Oenothera*, *Papaver*, *Primula*, *Ribes*, *Verbascum*, and *Zea*.

Genus	*Number of species used in crosses*	*Number of attempted combinations*	*Number of hybrid plants obtained*
Nicotiana (Tobacco, etc.)	23	432	85
Dianthus (Pink)	20	349	87
Lychnis (Campion)	1	137	18
Verbascum (Mullein)	14	118	97
Lobelia	4	97	20
Digitalis (Foxglove)	9	59	14
Datura (Jimson Weed, etc.)	8	55	16
Oenothera (Evening Primrose)	19	52	6
Aquilegia (Columbine)	9	33	23
	107	1332	366

Gärtner undertook to classify hybrids for convenience into three types: (1) intermediate, (2) commingled, and (3) definite. The first included those in which "a complete balance occurred of both fertilizing materials, in respect to either mass or activity." (2f, p. 277.)

Commingled types are those in which

> ". . . now this, now that part of the hybrid approaches more to the maternal or to the paternal form, whereby, however, the characters of the parents, in their transference to the new organism, never go over pure, but in which the parental characters always suffer a certain modification." (*ib.*, p. 282.)

Under the third class of hybrids, Gärtner places those

> ". . . among which the resemblance of a hybrid to one of its parents, either to the father or the mother, is so marked and preponderating that the agreement with the one or with the other is unquestioned." (*ib.*, p. 285.)

Gärtner recognized, as did the other hybridists of his day, that there was always a difference between the first and the succeeding generations, the former being uniform, the later ones variously splitting up. He made no distinction between the second and the other following generations, but simply says that the fundamental ground material of which the hybrid is made

> ". . . behaves differently in the second and in the further stages of breeding, where, on account of the different nature of the two factors of the hybrids in the succeeding fertilizations, an altered, shifting, variable direction in type-formation enters into the arising varieties." (*ib.*, p. 572.)

He further says, concerning variability in hybrids of the second and succeeding generations:

> "Other hybrids, and in fact the most of them which are fertile, present from the seeds of the second and further generations, different forms, i.e., varieties varying from the normal types, which in part are unlike the original hybrid mother, or deviate from the same, now more, now less." (p. 422.)

His most definite statement, however, regarding what we call "segregation" is as follows:

> "Among many fertile hybrids, this change in the second and succeeding generations affects not only the flowers but also the entire habit, even to the exclusion of the flowers, whereby the majority of the individuals from a single cross ordinarily retain the form of the hybrid mother, a few others have become more like the original mother parent, and finally, here and there an individual more nearly reverted to the original father." (*ib.*, p. 422.)

Gärtner did not fail to recognize the fact of unusual vigor in hybrids, although he does not distinguish as to the generation.

> "The marked increase in the size of the flowers is a phenomenon not seldom occurring among hybrids [p. 295] and one of the most marked and general characters of plant hybrids is the luxuriance of all their parts, since, among very many of them, an exuberance of growth and development of roots, branches, leaves and flowers manifests itself, which is not encountered among the parents, even under careful cultivation." (*ib.*, p. 526.)

Gärtner recognized at once the possibilities for agriculture in the fact of the increased vigor of hybrids, although, of course, he did not realize the fact that this increased vigor belonged only to a "hybrid" generation, as distinguished from F_2 segregates.

> "Among the characters of hybrids worthy of recommendation for agriculture, their tendency toward luxuriance in the stalks and leaves, and their extraordinary capacity for tillering, is related above. With respect to the raising of forage, agriculture could, without doubt, make great use of this characteristic." (p. 634.)

Gärtner derived, from his long experience, a certain philosophy concerning the nature of hybrids which is noteworthy. He recognized an inequality in the influence of the relative "potency," as he termed it, of one parent over another in a cross; which potency was maintained whichever way the cross was made. As now interpreted it probably means the relative dominance of one or more factors of the respective parents. Gärtner, not having the knowledge which has come in consequence of Mendel's investigations, sought a theoretical explanation for this phenomenon of dominance and gave it the designation "sexual affinity" (*Wahlverwandschaft*) in the crossing of species, the magnitude of which he considered could be measured by the number of viable seeds produced in the cross. He seems to confuse the matter by appearing to indicate that there might possibly be a different number of seeds produced by the reciprocals of reciprocal crosses, thus presumably indicating a possible "prepotency," so called, of one of the parents in the cross. In other cases he seems to mean simply the relative influence, so to speak, of such and such species when crossed with others. This appears to be the meaning in the following:

> "This manifestation of generic types, according to which one species operates in a predominant manner over several other species in hybrid breeding, is a further incontrovertible proof that the relationship of the forces, through which the union of two pure species takes place, must be unlike, and that thereby there can be no question of any balance of factors." (2f, p. 290.)

It will be seen that Gärtner's view of hybridization was that "species" was crossed with "species" as such, each species as a whole exerting its own relative power or "potency" in the cross—the hybrid being regarded as the resultant, so to speak, of the contest for supremacy of the two competing natures in the compound. This view is well enough expressed in the following passages:

> "Thus, just as there are species in a natural genus, which possess a prepotent fertilizing power upon several other species of their genus, so there are also species which exert upon several others such a typical predominating effect, not to an equal extent to be sure, but still of such a

> nature that their operation, in all combinations is to be recognized by a character in common.
>
> "Both of these forces, are, however, of different kinds, and follow different laws." (p. 289.)

Gärtner did not realize, in spite of Sageret's experiments, that some individual characters of a parent might be found to dominate in a cross and others not.

> "The laws of hybrid types orient themselves," he says, "not toward the individual organs of plants—do not apply to a single part, e.g., stems, leaves, etc.—but are applicable rather to the inner natures of species. The organs which determine the types of hybrids must therefore be investigated and compared in their totality and in their natural interrelationship. For the most part, the peculiarity of a hybrid expresses itself in its entire aspect; only in this respect the flower is most frequently and plainly distinguished above other parts of the plant." (p. 251.)

We do come, however, upon a form of utterance that is somewhat singularly Mendelian in character:

> "In the formation of simple hybrids, as in sexual reproduction in general, two factors are active. This unlikeness of activity, flowing from the specific difference of species, expresses itself through the more pronounced or the weaker manifestation of the individual paternal characters in the different parts of the hybrid. Whether the total nature of the species and its formative impulse determines the direction and form of the type, or whether the individual parts of plants have a special influence upon the modifications, may not be determined without further investigation." (p. 257.)

Gärtner made some crosses with corn and with peas, to determine the question of the immediate influence of the pollen upon the character of the seed. In corn he got no results, because of crossing white corn with red, in the case of which latter, the color, being due to the skin or pericarp, does not show itself until the following season. Because of the importance of the later genetic results with *Pisum* and *Zea mays*, it will be of interest to follow in some detail Gärtner's work in the crossing of plants of these two species.

The following comment is made upon Knight's experiment with peas:

> "Th. Andr. Knight, in the year 1787, instituted experiments with *Pisum sativum fructo-albo* (Common White Pea) and *P. sativum fructo-cinereo* (Grey Pea), which were first made public in the year 1799, concerning which he noted that the pods obtained from these artificial fertilizations were not markedly different from those of the ordinary seed capsules of this variety (*Pisum album*); from which he derived the conclusion that it was probably true, that the outer hull of the seed of *Pisum*, as

he had also found with the other plants, was entirely formed by the *female organs*. Of the change in the *color* of the seeds no mention occurs here; yet it is to be expected of Knight that this should not have escaped him, if it had actually taken place in the case of his seeds. In a later appearing report of this celebrated agricultural writer, the alteration in the color of the seeds of peas through artificial pollination is conceived, but in the second generation, however." (p. 80.)

In view of a number of previously reported results with respect to the immediate influence of foreign pollen upon the seed and the fruit, Gärtner undertook, in 1829, a series of experiments of his own to this end. For this investigation he chose the following-named varieties of garden peas:

1. Parisian Wax Pea, tall, with white flowers, designated as *Pisum sativum luteum*
2. Red-flowered Sugar Pea (*Pisum sativum macrospermum*)
3. White-flowered Creeping Pea with yellow seeds (*Pisum sativum nanum repens*)
4. Early Green Brockel Pea (*Pisum sativum viride*).

All of them, as he states, were constant and well-marked varieties. The results may be summarized as follows (3f, pp. 80-6):

I. *P. sativum luteum* × *P. macrospermum*.
The seeds from the four flowers pollinated gave 16 round yellow seeds of the same size and form as the self-fertilized flowers.

II. *P. sativum luteum* × *P. sativum viride*.
From the five flowers pollinated the pods contained as follows:

1. 4 round-oval seeds of the same size as the self-fertilized, of greenish-yellow color
2. 6 round seeds of dirty-yellow color
3. 1 seed, greenish-yellow
4. remaining unfertilized
5. 1 round seed, greenish-yellow.

Gärtner says (p. 82):

"All these seeds in the following year (1830) germinated well, and furnished five sound plants."

Of the color and form of the seeds of these plants, however, he makes no report.

III. *P. sativum macrospermum* (very tall, with purple flowers and greenish-yellow seeds) × *P. sativum nanum repens* (with white flowers and yellow seeds).

From four flowers pollinated fruits were obtained, containing as follows:

1. 4 "somewhat more dirty-yellow seeds than those of the maternal parent, which are more greenish," an evident observation of dominance
2. 4 seeds similar to the above
3. 4 seeds which did not mature
4. 4 seeds similar to (1).

IV. *Pisum sativum nanum repens* × *Pisum sativum viride* (with white flowers and green seeds).

Four pods were produced. The result as to the seeds is reported as follows:

> "On complete ripening and desiccation of the pods and of the seeds, there was, however, no essential difference to be described between those arisen from natural (maternal) fertilization, and those arisen from hybridization; only that the hybrid peas appeared to be somewhat more round and less uneven. The color was not different." (p. 83.)

V. *Pisum sativum nanum repens* (with white flowers and yellow seeds) × *P. sativum viride*. Six flowers were pollinated, producing altogether 22 seeds, which all appear to have been round with greenish-yellow color.

VI. *Pisum sativum viride* (with blue or green seeds) × *P. sativum luteum*.

But one flower was pollinated, producing a single seed

> ". . . which was not decidedly yellow, still less blue or green, but dirty yellow, thus incontrovertibly changed in color, since the flowers left to self-fertilization furnished simply green or blue seeds." (p. 84.)

VII. *Pisum sativum viride* × *P. sativum macrospermum*.

Five flowers pollinated, from which four pods were obtained, containing in all 12 seeds, all round and yellow, with the exception of one that did not come to maturity.

VIII. *Pisum sativum viride* × *P. sativum nanum repens*.

One flower pollinated; five seeds produced, all pale yellow.

Gärtner did not follow out the distribution of form and color in the seeds to the second generation. The statement which most nearly approaches to a conclusion in this regard, is found on p. 326, as follows:

> "The above-mentioned change in color of the seeds of *Pisum sativum* through hybrid fertilization comes out in the second generation more definitely and more decidedly than in the first immediate hybrid product through the immediate influence of the foreign pollen, whereby a quite similar relation as in Mays and other seeds is produced." (p. 326.)

Again (3f, p. 496), speaking of the "running out" of certain *Leguminosae*, he says:

> "Already above [p. 82], several varieties of *Pisum* have been under discussion and exact experiments have been reported, whereby it has been demonstrated that, through fertilization, such an alteration in the seeds is effected, that in the plants deviations from the previous condition come to light."

Gärtner's most general statement, however, regarding the second hybrid generation appears to be as follows (*ib.*, p. 422):

> "In many fertile hybrids, this alteration in the second and further generations affects not only the flowers, but also the entire habit, even to the exclusion of the flowers, whereby the majority of the individuals of a single breeding ordinarily retain the form of the hybrid mother, a few others here become more like the stem-father."

Concerning the influence of foreign pollen upon the immediate form and color of the hybrid seed, Gärtner reports further upon his experiments with *Zea mays.* Having maintained constant a *Zea mays nana* strain with yellow seeds and a *Zea mays major* strain with red-striped seeds, in cultivation in his garden for several years, in 1825, he crossed thirteen ears of the yellow with pollen of the red-striped strain, from which but a single ear with five seeds developed.

> "The five perfect seeds were neither in size or color in the least different from those of the mother, so that immediately after the completed ripening of the seeds, it appeared doubtful whether really a hybrid fertilization had taken place with them; the germination in the following year, however, . . . placed the hybrid fertilization of the plants obtained in a clear light; so that it proceeds uncontradictably therefrom, that with *Zea mays* the pollen of an otherwise colored species or variety only changes the nature of the embryo, not, however, the external quality and color of the seeds." (*ib.*, p. 88.)

Gärtner, of course, was unable to distinguish between the behavior of endosperm and pericarp color in maize crosses.

His investigations on color-inheritance in the seeds of Indian corn, were induced by the facts of color-inheritance in the seeds of peas. He states:

> "There was under discussion [p. 80] the matter of the immediate working of the foreign pollen upon the quality and color of the seeds, and the fact was cited that the genus *Pisum* shows the peculiarity, that the seeds of the different varieties of *Pisum sativum* assume immediately another color through the foreign pollen: therefore arose in our case the presumption, that this would likewise also obtain with the different varieties of *Zea mays*. Earlier experiments with *Zea mays*, by R. J. Camerarius, Logan, Pontedera, and Henschel, which Schelver has assembled, give no information on this point." (*ib.*, p. 322.)

In 1824, as stated above, Gärtner pollinated *Zea mays nana* with small yellow seeds, with pollen of *Zea mays major*, with grey, red, and striped seeds. Of the various pollinations (on thirteen plants), only one of the crossed ears grew; viz., the one pollinated from a plant of the red-striped variety, which produced five seeds.

In 1825, these five seeds were grown, and produced four ears. Two of these had only yellow seeds, somewhat larger than those of the female plant. Of the two others, however, one ear had 64, out of 288 seeds, "more or less reddish and gray"; the other, out of 143 seeds, had 39 which, like the preceding, were more or less colored.

> "It is, however, to be remarked that the yellow color of these intermingled yellow seeds was not pure yellow like that of the maternal parent, but dirty yellow; thus, therefore, as well in size as in color somewhat altered." (*ib.*, p. 323.)

The experiment was carried over to the second generation.

For further determination as to the alteration of the colors of the seeds obtained in the preceding experiment, the seeds from each ear were separated, especially according to the colors, into four parts, and sowed apart, in order to obtain the result, in the second generation, of each color separately. The seeds were divided into:

(a) pure yellow (c) clear grey
(b) dirty yellow (d) dark reddish-grey. (p. 323.)

The pure yellow seeds, (a) above, produced 59 ears, 32 of which bore yellow seeds; several others are reported to have had only a few colored seeds; in the case of several, there were "a number of seeds dissimilarly colored, distributed at random, but by far the greater part of the seeds were yellow."

The dirty yellow seeds, (b), gave 5 ears, on which markedly more colored seeds were found than on the ears from (a), the great majority being yellow. There was no ear with yellow seeds exclusively.

The clear grey seeds, (c), produced two ears, on which the proportions of seeds were reported as follows: pure yellow, ¼; yellow and speckled grey, about ⅛; reddish-grey, 1/12; and dark reddish-grey and brownish-red, ¼.

This is the only instance in Gärtner's maize experiments in which the numbers in the second generation are reported.

The seeds of (d) did not germinate.

While the experiment has not particular genetic value, inasmuch as the parents were not selfed lines, and close-pollination is not reported as having been effected in the case of the F_1, the work is interesting historically.

Gärtner considered the fact noteworthy, as he states (p. 325) that red-and-yellow striped seeds were derived from the grey seeds, and notes that the stripes concentrated about the point of insertion of the style, his actual object of investigation being to determine whether, in the case of *Zea mays*, as in *Pisum*, an immediate effect was produced by foreign pollen. He considered the fact to have been demonstrated in the negative by his experiment.

> "Since it is, however, determined, that the color of the seeds of *Zea mays* do not immediately undergo an alteration through foreign pollination, but that the capacity for the color change indicated is first produced in the germ through hybrid fertilization, and the different colors of the seeds appear for the most part separate and without order on the ears of the second generation; it is therefore to be doubted that the previously mentioned stripes produced in the second generation through the fertilization process with their own pollen proceed from the point of insertion of the pistil (stigma), but that they proceed rather from the base of the seed, run through the outer layer of the testa, and unite at the apex of the seed at the base of the pistil; so that the reason therefor is to be sought, not in the fertilization material, but in the rudiment of the unfertilized egg." (*ib.*, p. 326.)

The remark is of interest as a sort of genetic conclusion, in which morphological reasoning was involved, the fact of the conveyance of the stripes in the seed toward the base of the stigma being assumed by Gärtner to be *prima facie* evidence of the fact that the "influence" of the pollen ("Befruchtungssubstanz") affected the morphology of the seed from the point of entrance of the pollen into the ovary at the base of the stigma. Since this reasoning antedated any knowledge of the manner in which fertilization actually took place, it is not particularly surprising. It is, however, unfortunate in Gärtner's case that he was unable to differentiate between endosperm color and pericarp color, which latter he was actually dealing with. Consequently, his experiments, while proving to his mind the fact that the immediate effect of cross-fertilization did not appear in the case of the seeds of maize, is, of course, wide of the mark, since the appearance of stripes in the presumed "second" generation was the normal F_1 appearance of pericarp color.

Gärtner's work is noteworthy, not only for the remarkable number of species with which he experimented, but for the scrupulous care which he exercised in his operations, if we may judge from his own statements, as for example, the following:

> "For complete assurance of the purity and reliability of the products of hybrid breeding, and for testing the conclusions derived therefrom, we have repeated most of the experiments, especially the doubtful cases, not only once, but several times, and put them to the test through crossing of the same species; for, even with the most scrupulous foresight and precision, individual and rare instances have still occurred in these tedious and wearisome investigations, where the suspicion had made itself felt of a mistake or error having crept in, either in pollination or emasculation, since such results stood in direct contradiction to the usual experiences and, on a repetition of the experiment, made themselves incontrovertibly evident as an error. We believe it possible to attain no higher degree of certainty in this branch of natural science, and to be able to bring the conclusions derived therefrom to no higher proofs, than through the precise coincidence of the forms of the products, by repetition, under the same conditions with the same species, but with different individuals and at different times." (*ib.*, p. 675.)

In closing this account of Gärtner's work, it will be of interest to note Focke's comment in his "Pflanzenmischlinge."

> "Gärtner's 'Versuche und Beobachtungen' contains the essential contents of the prize essay for which an award was offered by the Royal Netherlands Academy of Sciences in 1830, and the contributions contained in his scattered papers." (1, p. 438.)

As Focke says:

> "The work, although rich in contents, is unfortunately of an extraordinary clumsiness, and is therefore, on the one hand, insufficiently known and, on the other hand, frequently overrated." (*ib.*, p. 438.)
>
> "Concerning the reliability of the assertions, one can only with difficulty form a definite judgment, since the book swarms with numberless inaccuracies and contradictions: A careful special study has forced upon me the conviction that the errors in Gärtner's work have proceeded from an extraordinary lack of authorship, and the inability lucidly to arrange the observations and facts." (*ib.*, p. 438.)
>
> "So far as concerns the material which Gärtner worked upon, his in-

vestigations on hybridization move almost exclusively within the previously indicated lines of Kölreuter. He has especially experimented with the same plant genera in which Kölreuter attained success; he has incontestably demonstrated great persistence and restless industry in his numerous experiments, but has scarcely done anything else than to confirm or carry further the Kölreuter investigations. As rich a source of the knowledge of hybrids as the Gärtner work indeed is, one must yet never forget that it must only be used with great caution and critical circumspection." (*ib.*, p. 438.)

Focke's accurate summary is sufficient as a description of the Gärtner memoir. The endeavor has been to present herein the essential facts and observations, as well as the more important conclusions which it contains. In conclusion, however, with due deference to Focke's criticisms, it may be said, attention should be called to what may be considered one of the most fundamental types of expression upon the subject treated.

The physiological nature of a "species" is stated in the following sentence:

> "The essentiality of the species, therefore, consists in the definite relationship of its sexual powers to other species, which relationship, together with specific form in each species, is a peculiar, special and constant one. Form and essence are in this connection one." (2f, p. 163.)

And again:

> "Not the external similarity in the form and habit of species, but the harmony of the inner nature, gives the capacity for hybrid fertilization: both are likewise not always harmoniously bound together." (*ib.*, p. 186.)

In this statement is revealed a real comprehension of the physiological nature of species; which comprises something else than the elementary conception of trying-out the crossing of supposed species for the purpose of determining whether their offspring are or are not sterile; the former case proving the parentage in question as belonging to different "*species*," the latter, as being merely "*varieties*" of the *same* species. Although the process may be the same in both cases, the method of presentation above shows a deeper conception of the process involved.

24. *Wichura and the Hybridization of Willows.*

In 1865 appeared Wichura's memoir on the hybridization of plants (5), based upon experiments in the crossing of willows which had occupied him from 1852 to 1858, inclusive. A brief preliminary report had appeared in "Flora" in 1854, and also within the same year in the report of the Schlesische Gesellschaft.

Taken as a whole, Wichura's work dealt, not with the investigations of individual specific characters, but with species taken entire and treated as such. As was the general custom, he regarded a "species" as an integral whole, that could be crossed in its entirety. With this conception he made what he called "binary,"

PLATE XXXV. Max Ernest Wichura, 1817-1866, Jurist, Botanist, Regierungsrat at Breslau (1859-1866).

"ternary," and "quaternary" crosses, i.e., crosses (1) between two species; (2) between a species and a hybrid; and (3) crosses between two hybrids. Besides the smaller list of Wichura's successful crosses, he published a much longer one of his failures, which stands as evidence both of the considerable amount of crossing-work that was done, and of the scientific integrity of the experimentor.

Of the ordinary, or, as he calls them, "binary" crosses Wichura made in all thirty-five successful crosses and combinations of such (of which ten were strictly "binary," i.e., simply crosses in the ordinary sense), between twenty-one different species of willows.

Although, as has been stated, Wichura, similarly to most of the other hybridists of his day, paid no attention to the crossing of characters taken as units, he remarks upon the evidence of individual characters being inherited as such:

> "It was of interest," he says (6, p. 27), "to observe how the unusual narrowness of the leaves in the experiment, utilizing *Salix purpurea* × *viminalis*, remained still recognizable in the following generation; a proof that even in hybrid fertilization individual characteristics of the parent plants can be inherited."

Wichura noted in willows, as others had done in other plants, the fact of a higher degree of sterility on the part of hybrids obtained between species of more distant specific relationship. The greater amount of vegetative vigor of hybrids was remarked upon by Wichura in the following words (6, p. 40):

> "Not only in the reproductive organs, but also in their vegetative behavior, hybrids show many phenomena whereby they are more or less strikingly distinguished from true species. According to the corroborating observations of Kölreuter and Gärtner, a larger part of the hybrids obtained by them through hand crossing were distinguished by luxuriance of growth. The plants grew to a greater height than the parents, spread out farther laterally by virtue of an increased capacity for sprouting, had a longer life-period, were able to withstand cold longer, and had more abundant, larger, and earlier flowers than the parents. . . . Among the willow hybrids, similar phenomena occur, but the example of luxuriant growth by no means constitutes the rule."

Wichura further observed that:

> "Even the most fertile hybrids fall behind the parents in their productiveness. A certain deficiency in the parts set aside for reproduction must therefore also occur with them. If we associate this in reverse relation with the excess of their vegetative development, it stands in complete harmony with the facts otherwise demonstrated. We shall therefore have

> to say, in order to express the relationship correctly, that in the case of very vigorous hybrids the weakness of the sexual parts brings out an increased development of the vegetative growth, whereas it is not the case with others which are too weak for such reaction [meaning crosses between two distant species]." (6, p. 43.)

Wichura concluded from his observations that hybrids were intermediate in respect to the differing parental characters. Cases of dominance do not seem to have come under his hand.

> "Among the numerous artificial and natural willow hybrids observed by me," he says, "I have throughout verified but one apparent exception to the principle of intermediateness.
>
> ". . . Even the time of flowering of hybrids holds the mean between the times of flowering of the two parents." (*ib.*, p. 47.)
>
> "As rich in species as the genus of the willows is, and as numerous combinations of hybrid fertilizations as it has to show, nevertheless I have never yet verified anything of a preponderant influence in any one of its species, but rather always found that their hybrids hold the mean between the constant characters of the parents." (*ib.*, p. 50.)
>
> "In hybrid fertilization, if unlike factors [Factoren] unite, there arises an intermediate formation, etc." (*ib.*, p. 86.)

The latter passage appears to be the first occasion where the term "factor" has been used in the literature of plant breeding, although here the "factors" referred to are perhaps the parents as a whole which participate in the cross, rather than the character-forming units from those parents.

His general conclusion is (*ib.*, p. 46.):

> "Constant characters, through which the parent species are distinguished from one another . . . go half over to the hybrid, so that it holds the middle position between them."

Two observations of Gärtner's were verified by Wichura—the identity of reciprocal crosses (pp. 51 and 186), and the fact of "variation" in hybrid progeny.

As to the question of the relative importance of the egg or the pollen in the result of fertilization, Wichura says (p. 57):

> "One sees the question is still far removed from having been brought to light, but from Gärtner's and my own observations it appears at least determined, that the products of hybrid pollen in breeding are more various than those of the pollen of true species."

Regarding the generally observed identity of reciprocal crosses, Wichura draws the following conclusion (p. 86):

> "We have found that the products which come from reciprocal crossing, unlike the well-known experiments made in the animal kingdom, completely coincide with each other.
>
> "*From this it must follow, however, with mathematical necessity, that*

the pollen cell must have exactly the same share in the conformation of the fertilization product as the egg."

So far as the writer knows, this is the first complete categorical statement in the literature of plant breeding of such a conclusion as to the behavior of the sex cells in amphimixis.

One is completely impressed, in reading Wichura's work, with the scrupulous care, accuracy and precision with which his hybridization experiments were carried out. One or two passages in point are interesting. Referring to a case of Gärtner's, where exceptional types appeared in the midst of "a greater number of hybrid plants of completely similar types," he says (p. 53):

> "To judge concerning the here-mentioned exceptional types, without myself having seen them, is scarcely possible. From the relatively limited number of my experiments, which have not yielded the like, I cannot, to be sure, deny its possibility; but here likewise, as above in the case of reversions, there is the suspicion of the existence of a complete disturbance of the experiment, whether that the protection had not been complete, or the pollen utilized for fertilization not pure, or the seeds sown not free from foreign admixture. Whoever knows from his own experience how much care must be observed in order to keep an experiment clean, becomes skeptical respecting all results of an experiment which vary from the usual rule, of the correctness of which one has not achieved conviction through his own observations."

Regarding these and other so-called anomalies as the result of crossing, he again says (p. 89):

> "That concerning all these points and many other disputable questions . . . we know so little has indeed its basis in part in the method hitherto of artificial cross-fertilization, which suffers from the double deficiency, that the care requisite to the correctness of the experiment, through the exclusion of foreign pollen, had not been taken in the first place, and secondly that, although many experiments have been instituted in very different families, nevertheless the individual hybrids have not been bred and observed in sufficient numbers. However, this is imperative throughout for attainment of general results. Only when one has at hand the same hybrids in hundreds of cases, partly from the same, partly from different parents, repeated through different years, only then will one be in a position to separate the essential phenomena of hybridization from the more accidental ones."

Finally (p. 92), Wichura remarks, expressing the hope that a learned society or an individual with means might repeat his own experiments on a larger scale:

> "The most scrupulous exactness in such case would be indispensable. Failing this, and especially if the possibility of the access of foreign pollen is not completely excluded, then all experiments, the more extensively they are undertaken, only contribute the more to the confusion of the matter. This must be taken to heart."

Regarding the possibility of securing a cross in any given case, Wichura remarks (p. 84):

> ". . . Only such species can be united in a hybrid, which agree in relatively many characters, and correspondingly in many life conditions. Experience teaches the same thing in the familiar rule, that hybrid combinations only occur between species of the same genus, or different, yet nearly related, genera."

He comes to a generalization of genetic value in the following statement (p. 85):

> "It is known that families die out after a few generations whose members carry in themselves the germ of a disease, and who mate only among themselves; and variety breeders know very well that all diverging characters of animal and plant species may be intensified when, in successive fertilization, the precaution is taken that only similarly divergent individuals mate with one another."

25. *Regel on Hybridization.*

The views of Regel (5) on hybridization, also illustrate in an interesting manner the general attitude of the hybridists of the time on the subject of the products of crossing:

> "The hybrid plant always originates through sexual intermingling of two parent species, actually different from each other. Plant forms which have originated through mutual fertilization of different varieties of one and the same species are not real hybrids, but are frequently falsely regarded as such." (5, p. 59.)

Regel designates the former as "true," and the latter as "false" hybrids.

This point of view has, of course, long since been completely superseded by the point of view expressed by the term "the hybrid condition," with respect to such and such characters possessed by the plant. Regel carried on experiments in 1846, in the crossing of Calceolarias, in which he found that, in respect of the essential characters, the hybrids occupied an intermediate position between the two parents.

26. *Carl Wilhelm von Nägeli and the Hybrid Question.*

In 1865 Carl von Nägeli (4c) presented a survey of the work of the earlier hybridizers. The occasion for the discussion, he says,

> ". . . presented itself to me from an investigation of the signification of the intermediate forms occurring in nature between many species." (4c, p. 187.)

The theme of hybridization, he says, is of importance because

> ". . . it sheds light upon reproduction, in so far as it is the question

PLATE XXXVI. Carl von Nägeli.

1817-1891

concerning the manner in which the characters of the parents are carried over to the offspring." (*ib.*)

Concerning the question whether hybridization could be used to reveal the then much-disputed difference between "species" and "variety," Nägeli concludes that between species and varieties there exists no essential difference, in characters which either the external form, the internal structure, or the chemical composition exhibits, but that there is simply a gradual intergradation between the two.

> "If we compare species and varieties with regard to sexual affinity, we find no boundary which divides them. In general, the relationship is, of course, greater between varieties and lesser between species." (4c, p. 200.)

This being the case, there can be no point in making the behavior of hybrids determine whether the parents of the cross were "species," or "varieties," and yet, as Nägeli remarks:

> "By far the most numerous and the most important investigations on hybridization have been carried on by decided adherents to specific fixity."

Elsewhere Nägeli refers to the origin of species and varieties in the following words:

> "For, when it becomes apparent that varieties are not the consequence of external influences, but are brought about through inner causes, then the difference in principle between specific and varietal, constant and variable characters, is removed. One must then assume, from the tendency to vary in the plant independently from without, that it is the specific nature itself which determines variety formation. Between species and variety there exists then a causal relation, and the relation finds its logical expression in the principle that the species is nothing but a further developed variety." (4a, p. 104.)
>
> "The formation of more or less constant varieties or races is not the consequence and the expression of outer agencies, but is brought about through inner causes." (*ib.*, p. 105.)

After enumerating the list of experimenters and investigators in the field of hybridization, he says:

> "If, in spite of these numerous experiments, no greater agreement with respect to hybrid-formation in the plant kingdom prevails, the reason may reside in various circumstances . . . Proceeding from the unalterableness of species, the endeavor is above all to determine the difference between species-hybrid and variety-hybrid—a difference which in reality does not exist." (4c, p. 89.)

In this paragraph, Nägeli briefly states the unfortunate situation into which the study of hybrids had fallen. In a word, the whole matter of the study of hybridization was largely used as a means for determining degrees of distinction between species.

Nägeli comments truly on the meagre range of information which many investigators possessed, proceeding either from observations of supposed hybrids in nature, or from conclusions derived from their own scanty experiments, which:

> ". . . on account of their incompleteness, and frequently on account of their inexactness, were unavailable for new theory." (4c, p. 190.)

He then pertinently remarks:

> "The knowledge of hybridization would in recent times have made more progress, if many observers, instead of beginning anew, had made use of the results of the first-two-named German investigators [Kölreuter and Gärtner], who applied the labor of their lives to the solution of this problem." (4c, p. 190.)

Here Nägeli strikes at a weak point not only in the science of his own day, but of a later time. Resting upon the experiments of Mendel, investigators have too frequently overlooked the suggestions to be found in the work of the pre-Mendelian students of hybridization. Concerning the then existing state of the knowledge of crossing, he says:

> "No field of knowledge is less complete; and continued, critically conducted experiments are in the highest degree desirable, but they can have scientific value only when they rest upon the knowledge of what has already occurred; when they either verify the already determined laws through new facts, or modify, extend or limit them; in the latter case, however, showing the conditions under which these modifications appear." (4c, p. 190.)

Nägeli indulges in a gleam of wit at the expense of those who felt no quarrel over the species question so far as hybridization was concerned, but who relied upon the rule, that at least only species of the same "genus" could hybridize, and that therefore those species which possessed the capacity to cross must be united in the same "genus." He remarks:

> "If I say that all wines belong to the genus 'liquid' it does not follow therefrom that every liquid has to be a kind of wine, and that everything that is not a wine must on this account also be no liquid." (4c, p. 192.)

In order to assist in obtaining a picture of the status of hybrid theory at the time of the publication of Mendel's paper, it will not be without interest to note the substance of the series of nine conclusions given by Nägeli in his paper "Die Bastardbildung im Pflanzenreiche" (4c), presented before the Akademie der Wissenschaften at Munich, December 15, 1865. It will be noted that most of these so-called "rules" bear generally upon what plants will cross, whether the progeny are likely to be fertile or not, and the general appearance of the hybrid with respect to the parents. Briefly summarized, these are as follows:

> 1. "That plant-forms, which stand systematically near together, can form crosses with one another." (4c, p. 191.)

from which it follows conversely that systematically nearly related plant forms may cross, the limit for crossing in general not exceeding the genus, and very often not going beyond the same section of the genus, and sometimes remaining within the species, different natural orders and genera differing in this regard.

> 2. "Plant-forms cross with much more difficulty and, on reciprocal fertilization, give a much scantier number of fertile seeds, the less they are sexually interrelated. This sexual affinity is not the same in significance as systematic affinity, which makes itself evident through external differences in form, color and habit, nor as that of the inner relationship, which is based upon the chemical and physical constitution." (*ib.*, p. 193.)

Varieties and species cross with the greater difficulty, and in reciprocal crosses produce the smaller number of fertile seeds, the less closely related they are sexually. This "sexual affinity" is taken by Nägeli not to be identical with systematic relationship as determined by morphological characters, color or habit, nor with the inner chemical or physical constitution. Just what "sexual affinity" thus implies is not entirely evident. Nägeli illustrates the fact by the case of two plants, A and B, in which A can be fertilized by B, but not B by A, quoting Gärtner's case of *Nicotiana paniculata* × *N. langsdorfii* in which, out of 79 flowers, 66 set fruit; whereas, of 44 flowers of the reciprocal cross, not one set seed. Nägeli remarks (p. 196), regarding sexual affinity:

> "As pertains to the latter, one knows nothing concerning the nature of it. Possibly it might be conditioned through external (mechanical) causes; more probably it is connected with local chemico-physical constitutions lying in the sex organs.

> 3. "The fertility of hybrids is so much the less, . . . the farther the propagating forms are removed from one another in sexual relationship. Species-hybrids are thus, in general, less fertile than variety-hybrids." (*ib.*, p. 200.)

> 4. "The rule that the sexual affinity is so much the greater the nearer the parental forms are externally and internally related holds good only up to a certain limit, within which the fertility diminishes in both respects." (*ib.*, p. 207.)

The closer the sexual affinity, the easier cross-fertilization occurs, the more seeds are produced, and the hybrids springing from them are the more fertile up to a certain limit, self-fertilization producing, as a rule, plants with less fertility and vegetative vigor than cross-fertilization with a nearly related variety. Crossing within the same variety is, for the most part, less favorable than crossing with a nearly related variety.

5. "If at the same time different kinds of pollen get upon the stigma, only that one becomes operative which has the greater sexual affinity." (*ib.*, p. 210.)

When two kinds of pollen reach the stigma, the one alone is effective that has the greater sexual affinity. Consequently, the presence of pollen of the same species excludes as a rule the possibility of hybrid fertilization through another species. Since fertilization through pollen of weaker affinity takes place more slowly, therefore pollen of stronger affinity which arrives somewhat later may function likewise, and seeds of two kinds be produced in one plant.

6. "The peculiar operation of the male material affects exclusively the germinal vesicle fertilized by it, and makes itself manifest therefore only in the embryo, and in the plant grown out of it." (*ib.*, p. 213.)

The operation of the male fertilizing material affects only the embryo-sac, and makes itself evident only in the embryo and the plant growing therefrom. The later changes are the same, no matter what the source of the pollen may be. (*ib.*)

7. "The hybrid sprung from the commingling of two different parental forms stands between the two in its systematic characters. For the most part, it holds about the middle position; more seldom, it has received from one of them a preponderating share, so that it resembles the one parental form more than the other." (*ib.*, p. 214.)

A cross arising from two different parental forms stands between them in respect to the systematic characters, generally more or less in the middle; more seldom one or the other parent has a preponderant share, so that it resembles it more than the other parental form; this being more strikingly evident in variety- than in species-hybrids. In hybrid breeding, either every character occupies an intermediate position, or a part of the characters approach the one, a part the other parental form. In the latter case, the division often occurs in such manner that the vegetative organs (stems and leaves), more nearly correspond to the one, or the reproductive (flowers and fruits), to the other. In general, the characters go over to the hybrid the more unchanged, the more inessential they are: the more important and constant they are, the more they are intermediate structures. For this reason, parental characters in species-hybrids tend to be fused; in variety-hybrids to be more or less unmodified. Whether the one or the other parental form is used as the pollen parent is of little or no significance, so far as the characters of the hybrid are concerned. Nägeli holds, however, that the exchange of parents in reciprocal crossing brings about a modification of inner characters in the hybrid, which become evident in unlike fertility and in an unlike tendency to vary in the progeny. (*ib.*)

8. "The rule that the characters of the hybrid plant move between the corresponding ones of the parental forms does not hold good in a strict sense." (*ib.*, p. 225.)

Some characters, by virtue of individual variation, may extend over this boundary, which happens the more, the more nearly related to each other the parental forms are; hence, most nearly in the case of little different varieties. The variation from the rule in the case of species-hybrids assumes a general character, through the fact that the hybrids of nearly related species become weakened in the reproductive organs, but luxuriate in the vegetative organs, and that the hybrids of more distantly related species develop feebly in all their parts, and soon die out through lack of vital energy. (*ib.*)

9. "In general, hybrids vary so much the less in the first generation, the farther the parental forms are removed from one another in relationship; thus species-hybrids less than variety-hybrids. The former are often distinguished by great uniformity, the latter by great diversity." (*ib.*, p. 230.)

If the hybrids are self-fertilized, the variability increases in the second and succeeding generations by so much the more, the more completely it was lacking in the first. The farther apart the parental forms lie, the more certainly the offspring in the second and succeeding generations fall into the three distinct varieties, one which corresponds to the original type, and two others which are more similar to the parental forms (Stammformen). These varieties have, however, at least in the next generation, little constancy; they change easily into one another. An actual reversion to one of the two parent forms (on pure in-breeding) occurs especially when the parental forms are very nearly related; thus with the hybrids of varieties, and of variety-like species. When it occurs with other species-hybrids, it appears to be limited to those cases where one species has exercised a predominant influence in the hybrid fertilization. (*ib.*, p. 231.)

Regarding "variability" in hybrids in general, Nägeli remarks:

> "Variability of the hybrids, that is to say, the diversity of forms which belong to the same generation, and their behavior on propagation once or many times by self-fertilization, form two points in the study of hybridization which are still least ascertained, and which the least appear to be subjected to fast rules." (*ib.*, p. 231.)
>
> "Among the species-hybrids, there are also some which already in the first generation show a noticeable variability. These are especially those which are derived from very nearly related species, as the hybrid of *Lychnis diurna Sibth.* × *Lychnis vespertina Sibth.* The least variability is found as a rule in the hybrids of those parent species which possess a slender mutual relationship." (*ib.*, p. 232.)

In the case of allied species, each of which has similar variety types, according to Nägeli, the mutually similar types cross more readily than the others; e.g., *Verbascum blattaria Linn.* and *Verbascum lychnitis Linn.* have both yellow and white-flowered varieties. The white-flowered *V. blattaria* crosses more readily with the white-flowered *V. lychnitis*, and *vice-versa*, and the same holds good as to the number of hybrid seeds produced.

The following statement appears to be the nearest approach to an observation of anything like a "Mendelian" character to be found in Nägeli's writings:

> "When the hybrids are self-fertilized, the variability increases so much the more in the second and succeeding generations, the more it was lacking in the first, and indeed the farther apart the parental forms lie from one another, the more certainly three different varieties spring up, one which corresponds to the original [i.e., hybrid] type, and the two others which are more like the parental forms." (*ib.*, p. 230.)

Despite the existence of correspondence between Mendel and Nägeli, the latter does not so much as mention Mendel's *Hieracium* crosses, even in the somewhat extensive paper of twenty-nine pages, of March 10, 1866, "Die systematische Behandlung der Hieracien, rücksichtlich der Mittelformen" (4h).

A further epitomization of rules or conclusions regarding hybrids appears, in the form of seven summarized statements and commentaries thereupon, in Nägeli's paper (4f).

1. Nägeli concludes that the hybrid in all its parts is an entirely normal phenomenon, and is distinguished in no manner

from all other plants. A plant can thus not be distinguished immediately as being of hybrid origin.

2. Since species-hybrids are frequently fertile, and the individuals of pure species not seldom infertile, the perfect or imperfect structure of the sex-organs is not decisive concerning the nature of an organism. From the sterility of the male and female organs, nothing can thus be summarily concluded regarding hybridity, or from the fertility of the same regarding their pure origin.

3. Hybrids constitute a regular intermediate formation, since they have inherited their characters from the two parental species in almost equal measure. An extension beyond this occurs only in a very limited and quite definite manner.

Since the capacity for sexual reproduction becomes weakened, and the vegetative activities especially aroused, he therefore concludes:

> "We can hence take a plant into consideration as a hybrid, only when its systematic characters can respond to these demands." (p. 300.)

The total point of view regarding the hybrid, as Nägeli considers it to be, is even more definitely summarized in the next succeeding sentence.

> "When it is a question of the hybrid nature of a plant, the first and most important criterion is that it be a middle form between two definite species. This requirement is often left out of consideration."

And again:

> "For the correct estimation of hybrids, it is especially to be remembered that the most constant and important characters hold most exactly the mean between the parent species, and that, on the other hand, a character can so much the more approach the one species, the more unimportant it is." (4f, p. 300.)

4. Between two forms there exists only one hybrid middle form, indifferently whichever of the parental forms was used as the pollen parent. On the other hand, the hybrid may form varieties, which approach the parents in an irregular manner.

5. Hybrid fertilization takes place through foreign pollen, when its own pollen is kept away from the stigma.

6. Species-hybrids have, as a rule, either quite infertile or weakened reproductive organs. In the latter case they form, on self-fertilization, a limited number of viable seeds, and die out after a few or several generations.

Pollination through one of the two parent species, however, excludes self-fertilization, and the hybrid reverts back to this parental species. The hybrid middle-forms between species have accordingly no constancy, and disappear again after a short time. According to the relationship of the parental forms, they appear in three ways:

(1) In the species with the most limited relationship: as a middle-form, present in an extremely few quite infertile individuals, *without* transition-forms to the parental species.

(2) In species with limited relationship: as a scanty middle-form with restricted fertility, and *with individual* transition-forms to one or the other of the two parent species.

(3) In species with close relationship: as a more or less scanty middle-form with partial fertility, and *with numerous* transition-forms to both the parent species.

7. There are other intermediate forms, which are distinguished through greater individual numbers, and through complete fertility and constancy. They appear in three ways:

(1) As an isolated middle-form; the gaps between it and the two principal species being mostly filled up by scanty hybrid transition-forms.

(2) As two or several isolated middle-forms which lead by degrees from one principal species to another; the gaps between these and between them and the principal forms being filled up through limited hybrid transition stages.

(3) An unnoticeable transition series between the two principal species, in which all the members are represented by numerous and completely fertile individuals. The hybridity of these constant intermediate forms is apparently evidenced by their occurrence solely in company with the parental forms.

In one passage (4c, p. 229), Nägeli remarks upon the fact of heterosis in species-hybrids, i.e., the fact that species-hybrids show, in the whole vegetative sphere in the widest sense,

> ". . . a striking tendency to vegetative luxuriance; in this respect they ordinarily transcend the two parental varieties."

A statement of a rather general character regarding species-crosses is made as follows (4e, p. 260):

> "When two species together form a hybrid, the characters in which the parents differ from one another do not go over to it complete, but

they are united to form intermediate characters, which are only incompletely accommodated."

Farther on (p. 263), he comments on the fact that two hybridizing forms, because they furnish each a single fertilizing cell, share equally in the hybrid product. It is not assumed, he says, that two different plants have their reproductive cells qualitatively and quantitatively similarly fitted out, but it may be assumed on the contrary, that the reproductive cells of different species, varieties, and individuals, are always dissimilarly constituted, and that hence that plant which forms the active material in greatest quantity and of best quality has always the preponderance in the fertilization.

The discussion of the nature of the hybrid in "Die Theorie der Bastardbildung" (4e) is further to be summarized as follows:

Two species of different genera, or of different sections of the same genus, do not ordinarily bring about cell division in the embryo, the fertilization remaining without result. If the hybridizing forms are a little more nearly related, the embryo remains few-celled and dies out. With nearer relationship, the embryo develops but does not germinate; or it germinates, but forms a very weakly plant which soon dies, or else a weakly plant which flowers but does not bear seed. As the relationship of the parental forms becomes closer, the vitality of the hybrid increases, reaching its maximum as a rule, when nearly related varieties mutually cross. He concludes that the unlike viability of the product proceeding from self-fertilization, in-breeding, crossing of varieties, and the hybridization of species, respectively, is due to the greater or lesser degree of disturbances taking place in the individual, and the general initial adaptability of the fertilizing cells. Since vegetative growth and reproduction are two essentially different functions, two types of mutual adaptation must be assumed, the vegetative and the sexual. Neither of these is complete, inasmuch as the one partly excludes the other. The sexual harmony (Concordanz) is much more easily disturbed than the vegetative. Hence, under deleterious influences, a plant usually limits, first its seed reproduction, and long afterward its vegetative activity. The infertility of a hybrid depends upon the disturbance of the sexual adaptation, i.e., upon whether the pollen tube of the one and the germinal vesicle of the other form a union capable of development. It is sometimes the case, that the pollen tubes of A have a greater sexual attraction to the germinal vesicle of B, than the pollen tubes of B to the germinal vesicle of A. Hybrids are stated to possess one character in common, that they are much more inclined to variation than are the pure forms. This variability, according to Nägeli, in the case of variety-hybrids, occurs in the first generation; in the case of species-hybrids, in the second or later generations. Sometimes, Nägeli proceeds, the offspring resemble, not the parents but the grandparents, and characters sometimes come into appearance in a later generation, which were present in a previous generation, but which afterwards disappeared. The organism may, at the same time, harbor several tendencies, of which some attain to development sooner, others later, and others not at all. He continues:

> "It is now comprehensible that pre-eminently two tendencies are located in the hybrid, the one that it should resemble the father, the other that it should resemble the mother. Correspondingly, the changes in the second and following generations consist especially in this, that forms develop which are very similar to the two parent forms." (p. 285.)

The tendency of cultivated plants to vary more than wild plants may, according to Nägeli, have a double cause. On the one hand, through the long operation of partly unnatural conditions, the balance is seriously disturbed, and hence a stimulation is given to inner changes. More important is the circumstance that natural selection does not take place, or only in a direction corresponding to the demands of cultivation. In the wild condition, the incipient new varieties perish, since, in the struggle for existence, only the most advantageous variation persists. In cultivation, on the other hand, all individual variations, so far as they form seeds and do not run counter to the demands of cultivation, reproduce and form new individual modifications through crossing with other variations.

A physiological question discussed by Nägeli, is that of the relative infertility of species-hybrids. For example, according to Gärtner's experiment which Nägeli cites, the hybrids between *Lobelia cardinalis Linn.* and *Lobelia fulgens Willd.* ripened 900 seeds per capsule; the parents, on the other hand, 1,100 to 1,200. *Lychnis-diurna Sibth.* × *L. vespertina Sibth.* produced 90 to 125; the parents 150 to 190 seeds. *Datura stramonium* × *D. tatula*

Linn. gave 220 to 280 seeds; the parents 600 to 800 seeds. There are other hybrids, as Nägeli says, which produce only ¼, 1/6, 1/10, or 1/20 as many seeds as the parent species. This weakening of sexual vigor in species-hybrids, as Nageli says, also

> ". . . shows itself plainly in the fact that all species-hybrids give fewer seeds by self-fertilization than when pollinated by one of the parent species." (4c, p. 202.)

A question of scientific moment, is discussed by Nägeli in respect to the nature of reciprocal crosses. In most of Kölreuter's and Gärtner's crosses, as Nägeli says, the results of the crosses were so much alike that a difference in point of deviation was not to be recognized. In the case of some plants, however, a slight difference showed itself

> ". . . more frequently in the form and color of the flowers, more seldom in the form and substance of the leaves." (4c, p. 217.)

Nägeli calls attention also to the fact brought out by Gärtner's investigations, that in some cases, where reciprocal crosses are identical, yet their progeny derived from self-fertilization show differences. Gärtner's cases are cited, of *Digitalis purpurea* × *D. lutea*, and *Dianthus pulchellus* × *D. arenarius*, as being more "variable" in their progeny than their reciprocals. What this particular mode of variability in the first generation may consist in is not stated.

The general state of knowledge in Nägeli's time of the behavior of plants in crossing, since made clear through Mendel's results, is well exemplified in his statement as follows:

> "If it is certain that in hybrid formation, in individual cases, the one parental form shares more actively than the other, still the question may be reasonably asked, whether the hybrid ever inherits mathematically equally much from its parents; whether the one or the other parental form has not always the preponderance. This is, of course, probable, but facts are still lacking which are able to decide the question in one or the other direction." (4c, p. 222.)

Mendel's work solved in part this very problem, to the extent of showing the presence of so-called "dominant" factors in the one or the other parent. Nägeli's paper (4b), here reviewed, was read before the Royal Bavarian Academy of Sciences at Munich, December 15, 1865. The preceding February 8 and March 8 of the same year witnessed the reading of Mendel's paper on hybridization, before the Natural History Society of Brünn. In other words, less than one year before the question as to the reason for the preponderance of one parental contribution over the other, was stated by Nägeli as lacking facts for its elucidation, Mendel had already presented the facts explaining dominance.

Nägeli, from the then generally existing point of view, stated the mode of transfer of the characters in hybrids as follows:

> "The characters of the parental forms are, as a rule, so carried over to the hybrid that, in every individual one, the mutual influence makes itself felt. One character does not go over as it were unchanged from one, the other unchanged from the other parental form, but there occurs an inter-penetration of the paternal and the maternal character, and an intimacy between their characters." (4c, p. 222.)

Here again we have a statement which has been modified by Mendel's discovery of dominance in variety-crosses. Nägeli remarks, however, that those who have largely or exclusively crossed varieties, or in crosses have given their attention to "varietal characters" so-called, are of the opinion that the characters go over unchanged, quoting the results of Sageret's experiments referred to in a previous article. Despite these cases of what is now known as dominance, Nägeli states the general rule as he saw it, thus:

> "The rule, however, is that the characters of the father and the mother combine and interpenetrate, whereby a new individual character originates which holds more or less the mean. The way and manner in which the union occurs cannot be determined in advance." (*ib.*, p. 224.)

Regarding the vigor of first-generation hybrids, Nägeli remarks as follows:

> "Growth and development of the individual is especially aroused in species-hybrids. These are frequently larger than their two parents. They form more and larger leaves, the stem is raised higher, and branches more vigorously, and effects multiplication more easily through stolons, rhizomes, etc. . . . Hybrids are also distinguished through the fact that they bloom longer and more abundantly than the two parent forms. The hybrid of plants which bloom first in the second year, blooms for the most part in the first; the hybrid of plants which only come to flower formation after a series of years, arrives thereat a few years earlier. Likewise, with regard to the individual vegetative period, the rule holds good that the hybrids begin to bloom earlier in the year and continue to bloom later in the fall. In general, they often form quite a large quantity of flowers, which are especially larger, sometimes also more fragrant and intensely colored, and of which each individual one lasts longer, for example several days; when the flowers of the parent species wilt after the first day." (*ib.*, p. 228.)

This closes the account of Nägeli's contribution to the literature of hybrids—a rather clear, complete, and searching review of the fundamental matters in respect to hybridization, as they were realized and generally understood at that time.

In view of the considerable attention at one time aroused by Nägeli's theory of the idioplasm, and the fact that it is interesting historically as a presentation of a theory thought to be possibly operative in the case of amphimixis, it seems desirable to introduce at this point a presentation of Nägeli's contribution to the theory of the factors in development (Mechanisch-physiologische Theorie der Abstammungslehre). (4i, pp. 822, 1884.) It is hoped that the historical value of the contribution, theoretically speaking, as being one of the last of the unitary theories of descent propounded before the discovery of Mendel's investigations, will make amends for the quantity of the material necessarily introduced.

Nägeli considers that the substance containing the "Anlagen" (the "Plasmasubstanz") consists of different modifications of albumins, the molecules of which are united in molecular groups of crystalline form, which he calls "micellae," soluble and insoluble forms commingled, forming a half-fluid, slime-like mass. This organization he designates as the "stereoplasm," of which he considers that only the smaller portion represents the actual "Anlagen" or factors.

From what Nägeli calls the "Anlage-plasm;" i.e., the gene-protoplasm, there is a definite movement of a developmental character, leading to a cell-complex of greater or less size, such as a certain leaf, root, etc. This protoplasmic series Nägeli designates briefly as the "idioplasm," as distinguished from the remaining "stereoplasm." (4i, p. 23.) Crossing, or rather amphimixis, is considered to be the cause of bringing the factors of lesser strength into development. Crossing especially is supposed to be one of the causes for the development of the "Anlagen" (factor-rudiments) of lesser potency, that is to say, those still in process either of origination, or of disappearance. Latent Anlagen[1] come more easily into development through amphimixis than through sexual modes of propagation. (*ib.*, p. 24.) Differences in

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[1] The German word "Anlagen" being practically untranslatable will be used henceforth without further comment, for "rudiments of factors," etc.

growth, internal organization and external conformation, as well as in the activities of the organism, are conditioned by numberless differences in the chemical and plastic processes of the living material, and by numberless combinations of the operative forces, all of which are due to "the unlike form, size and arrangement of the micellae of the idioplasm." (p. 26.)

This being the case, then equality in respect to the inheritance, is conditioned by the combining cells containing, on fertilization, equal amounts of the idioplasmic material. Cases where a preponderance in the inheritance is on the side of the male or the female parent, respectively,

> ". . . must be explained through the fact that a greater quantity of idioplasm occurs, now in the unfertilized egg cells, now in the spermatozoa uniting with them." (p. 27.)

The difference in potency of the idioplasm is indicated by the fact that the male fertilization-plasma in the spermatozoid may amount, in Nägeli's view, to only one or two parts of the mass of that of the female in the unfertilized egg cell or primordial vesicle, and yet, if it contains an equal number of hereditary units (Anlagen), then these must possess a hundred times more "idioplastic power" than those of the egg. This purely empirical mass theory of the mechanics of heredity preceded the chromosome explanation of the facts.

With regard to the relative total amount of the idioplasm, Nägeli holds that it is probable that only a very small part is to be designated as the idioplasm proper, while the remainder must be regarded as trophoplasm or nutritive plasm.

> "The activity of the idioplasm makes itself everywhere evident where an heritable process of growth or metamorphosis takes place. Its presence in these places may therefore be presumed. When, on the contrary, there are places where neither growth nor metamorphosis can take place, it is presumed that the cause may either be due to lack of the idioplasm or partly to the fact that a proper mixture of idioplasm and trophoplasm is lacking." (p. 29.)

The idioplasm is presumed to be in a continual state of migration toward the places of development, and the growth processes are determined, first by the constitution of the idioplasm, secondly by its quantity, and thirdly by the manner in which it is commingled with the trophoplasm. (p. 29.)

Nägeli holds that either the idioplasm changes continually during the growth process, returning with the formation of the embryo to its original constitution in the initial cell, or else it maintains the same constitution, and the altered conditions of time and place in the individual's life-history affect its potentiality. (p. 30.) Attention is called to the fact that a branch with different characters from those of other branches, may grow out from a tree, a case, manifestly, in which external conditions do not come into play. In such cases, the idioplasm has evidently undergone a phylogenetic metamorphosis. (p. 31.) It is assumed to be possible for the idioplasm to change within definite limits, during individual growth. The idioplasm of each of the different cells of an individual may be considered, for practical purposes, as different, "insofar as it possesses an individual productive capacity." (p. 31.) The development into activity of the Anlagen in the idioplasm is conditioned to some extent by the nutrition, e.g., whether, in the case of certain trees, foliage or flower shoots are formed, or vegetative growth without flower formation at all, under unfavorable climatic conditions. (p. 32.) The variety in the growth processes in the idioplasm is conceived of as possible in the following manner: The idioplasmic structure represents a fixed arrangement, and its parts (the micellae) may be conceived of as lying in rows in several dimensions crossing one another, so that the same particle always belongs to rows of divergent space-dimensions. Growth of the idioplasm is the growth of these rows through the accession of new micellae, uniformly intercalated, or through end-deposition. The idioplasm may increase either through the growth of the rows alone, through the extension in width of the cross-rows, or through the growth of rows in some oblique direction. The growth of the rows in question to some determined dimension results in the development of a definite "Anlage." (p. 34.) This structure of an idioplasmatic system, Nägeli holds, is analogous to that of other organized bodies, which consists of crystalline micellae, comprising a larger or smaller number of molecules.

> "The starch grains give us a presentment of the idioplasm. Both are fixed micellar systems, which lie free in the cell contents, in the cell-sap or in the half-fluid plasm, and which grow through the intercalation of micellae."

The idioplasm, constructed as surmised above, "can be known only in one dimension, namely, in that in which its autogenetic growth takes place." However, the idioplasm in an individual propagating vegetatively may retain its arrangement unchanged to the smallest particular. This fact, it appears, can be explained in no other way than by the fact of the idioplasm being arranged in firmly converging parallel rows, which grow through micellar intercalation, the structural arrangement remaining the same. (p. 38.)

One assumption, which as Nägeli says, "is scarcely to be proved out of hand," is that the idioplasm constitutes a connected net throughout the entire organism.

> "This will assume in the cells, according to their construction, a different form; ordinarily, however, in the longer plant cells. forming a membrane over the surface, frequently also running through the cell cavity and especially crowded together in the nucleus." (p. 41.)

Since all the chemical and plastic processes of an heritable nature are regulated through the idioplasmic fibrils, these must be everywhere present throughout the different parts of the cells, and communication must be supposed to take place between the idioplasms located in the different parts of the organism.

> "The idioplasm-net probably lies at the basis of the so frequently recurring net-like arrangement of the plasma, and the net-like structure of the nuclear substance." (p. 41.)

The idioplasm is conceived as originating the trophoplasm, and thereby the non-albuminous constructive material, and determines the form of the latter. (p. 47.) Nägeli considers that the irritability of the micellar rows of the idioplasm is not to be expressed in terms of periods similar to those of nerve-activity, but that it extends over a longer time—days, weeks, and months, during which time the active idioplasm increases. (p. 47.)

Nägeli considers it improbable that the growth of the micellar row itself determines the development of the corresponding "Anlagen," but rather that both phenomena are brought about by a like cause.

> "The effect, which the idioplasm group, engaged in active growth, exercises upon the surrounding idioplasm, may occur in a manner similar to that exerted by the plasma of the yeast cells upon the fermentation material." (p. 48.)

The process of operation of the micellar rows of the idioplasm Nägeli considers theoretically to be as follows:

The ontogenetic development of the individual begins, during which time the micellar rows in the idioplasm which cause the first developmental stage become active. This induces a passive growth of the other rows, and an increase, perhaps manifold, of the entire idioplasm. A tension arises from inequality in the growth-intensities of the different rows, which sooner or later, according to the number, arrangement, and energy of the active rows, brings the process to a standstill; the tension is felt as a stimulus due to disturbance of equilibrium, and this tension is shifted from one group of Anlagen to another, until all are passed through, and the ontogenetic development arrives again at the original embryonal state, during the reproductive period. (p. 40.)

The effect of nutrition upon the idioplasm is interpreted by Nägeli as follows:

The nutritional stimuli, generally speaking, although they do not alter the idioplasm qualitatively, may still affect the development of the Anlagen, so that Anlagen which might otherwise remain latent now come into development, or, the nutrition being lacking, their development is checked.

Nägeli considers it possible that the idioplasm may only return approximately, during the reproduction stage, to its original constitution, and that a slow phylogenetic metamorphosis may take place. (p. 53.) It is manifest, as he says, that, in order for this to occur, the external influences must either directly or indirectly bring about a metamorphosis of the idioplasm. (p. 54.) In order for the idioplasm undergoing change in some specific part of the organism to bring about alterations in the rest, the result must be achieved in either a material or a dynamic way. By the former method, Nägeli conceives it possible that all the cells communicate with one another and with the nearest sieve tubes by means of very fine pores.

> "The sieve-tubes, however, which represent large canals with laterally large openings in the uninterrupted partition-walls, bring about the exchange between the most different and distant organs." (p. 56.)

According to the dynamic theory, if all plant cells communicated with one another through fine pores, then these pores contain, besides the trophoplasm, also idioplasm, "so that the latter forms a connecting system through the whole organism." The net-like connection then of the idioplasm throughout the organism, from cell to cell through the pore-canals, makes possible the transfer of stimuli in a manner analogous to that of the nerves. (p. 58.) For transmission to a distant point in the organism,

> ". . . there requires to be not merely a single stimulus, but rather a sum of various stimuli to be transmitted, which are able to cause a qualitatively definite process."

This sense-image conduction through the idioplasm is conceived of as being brought about by organized albuminous bodies.

> "This theory of dynamic participation appears to me to solve the question at hand in the simplest manner. The idioplasm of all the cells of a plant exists in immediate contact. Every change which it experiences in any place becomes everywhere recognized, and in a corresponding manner utilized. We must assume that the stimulus that operates locally is immediately telegraphed everywhere, and everywhere has the same effect; for everywhere a continuous and general sensation which the idioplasm experiences explains the otherwise impressive fact, that the idioplasm, despite the so dissimilar conditions of nutrition and stimulus to which it is exposed in the different parts of an organism, yet develops and changes everywhere in completely like manner, as we especially recognize from the fact that the cells of the root, the stem, and the leaf, produce exactly the same individual."

Nägeli now constructs a theory of sex development as follows: A peculiar category of Anlagen may occupy a middle place between stability and instability, formed by the cohesion of two or more Anlagen, of which one must develop to the exclusion of the other. This will depend now upon internal and now upon external causes.

> "Thus, doubtless, it is inner, but still unknown causes which, in the case of organisms in which the sexes are separate, determine whether, in a developing embryo, the male or female organism reaches development." (p. 194.)

We thus have a purely theoretical conception of sex-equilibrium as existing in the groups of Anlagen in the idioplasm, of which external causes of some sort stimulate the development of some rather than that of their partners in the equilibrium.

Nägeli emphasizes the conception that the increase of the idioplasm in ontogenetic development takes place

> ". . . through the longitudinal growth of the rows, namely, through intercalary insertion of micellae in every micellar row, which thereby elongates, without altering their cross-sectional configuration." (p. 531.)

Each row, therefore, is considered to contain all the Anlagen which the individual has inherited in the embryo, and each cell accordingly is entire in respect to its idioplasmic content, and is idioplasmatically capacitated to become the germ of a new individual. (p. 531.)

The evolution process, from the standpoint of the idioplasm, is depicted by Nägeli in the following manner:

> "The idioplasm through accretion [mit der Zunahme] steadily changes its configuration in the successive ontogenies, but relatively slowly; so that from the embryo of one generation to the embryo of the next generation it makes a small amount of progress. The summation of these progress-differentials through a whole line of descent represents the genetic history of an organism, since the latter through its idioplasm alone holds together in unbroken continuity with the unicellular beginning of the stock." (p. 532.)
>
> "Since further, in embryo-formation, the new ontogeny begins as a unicellular individual, so that the Anlagen of the idioplasm come into development which have arisen in the unicellular ancestor, and similarly the successively following development of the Anlagen which have their origin in their analogous ancestors, the two cooperating causes, the phylogenetic configuration of the idioplasm successively following, and the developmental stages of the individual conditioned by these, have, as a necessary consequence, that the ontogeny is the recapitulation of the phylogeny." (p. 533.)

In the idioplasm of an embryo, the micellar rows of Anlagen from the respective parents may in some cases, Nägeli holds, have a medium composition, due apparently to the merging of the micellar rows of the two parents. In such cases, intermediate characters will develop. Or, on the other hand,

> "The paternal and maternal rows lie unaltered in the idioplasm of the child, and in different grouping in relation to one another, and bring about in the organism the characters from the two sides, either unmodified beside one another, or only one of the parental characters, while the other remains latent." (p. 534.)

The relative development or latency of the inherited Anlagen in the child determines the degree of resemblance to the one or the other parent. The theory of descent, then, is concisely stated by Nägeli as follows:

> "Since from one ontogeny to the next following, idioplasm alone is carried over, therefore the phylogenetic development consists only of the continuous formation of the idioplasm, and the entire pedigree, from the primordial drop of plasma to the now living organism (plant or animal), is really nothing else than an individual consisting of idioplasm, which in every ontogeny, forms a new individual body corresponding to its progress." (p. 541.)
>
> "Of heredity as a specific phenomenon, if we hold the internal essence of the organisms in view, there can really be no discussion, since the

line of descent is a continuous individual of idioplasm. In this case it is nothing but the persistence of the organized substance in a changing process of movement or the necessary passing over of one idioplasmatic configuration into the next following. And it is not alone between the ontogenetically different plant- and animal-individuals, but also within these individuals everywhere present, where every individual part (cells, organs) follows another in time. Heritable phenomena are such as of necessity pass over to the following generations, and in general such as have their seat in the idioplasm, since the non-idioplasmic substance is only capable of continuing through a limited number of cell generations." (p. 542.)

27. *Treatise of W. O. Focke.*

The last of the hybridists of the older school who engaged in extensive publication, was Wilhelm Olbers Focke, who published in 1881, his "Pflanzenmischlinge," a work of 569 pages (1), consisting primarily of a systematic arrangement, according to orders, families, and genera, of plant hybrids known to have been produced by various experimenters up to his time, or reported as having been found wild. This arrangement, while it made no pretension to completeness, was yet the most thorough and extensive single compendium of the kind yet published.

"I have," he says, "so far as it was possible, examined the statements met with, have not quoted the least credible at all; others I have accepted as questionable, but, in the case of the most of the information, I have had no reason for doubting the correctness of the observations, even though, on the other hand, I could not regard them as confirmed or sufficiently vouched for." (p. 3.)

"At all events," Focke remarks, "through the present collection of known facts, it will, as I think, be rendered essentially easier to find the objects toward which future investigations concerning plant crosses must be directed." (*ib.*, p. 2.)

In the case of most hybrids, especially those occurring wild, Focke contented himself with brief references concerning their occurrence, but entered into more extended consideration of the more carefully investigated hybrids produced by hand-pollination.

Focke himself was not extensively engaged in investigations in hybridization.

"To my regret," he says, "I have never been in a situation to institute hybridization experiments on a large scale, nevertheless, through crosses and breeding carried on by myself, I have at least gained some practical experience, which should be of decided use for the estimation of the statements of others." (*ib.*, p. 3.)

As to the results of his observations however, Focke came to an important generalization regarding the size of F_1 hybrids; that the characters of crosses are derived from the characters of the parent species; and that *only in size and luxuriance, as well*

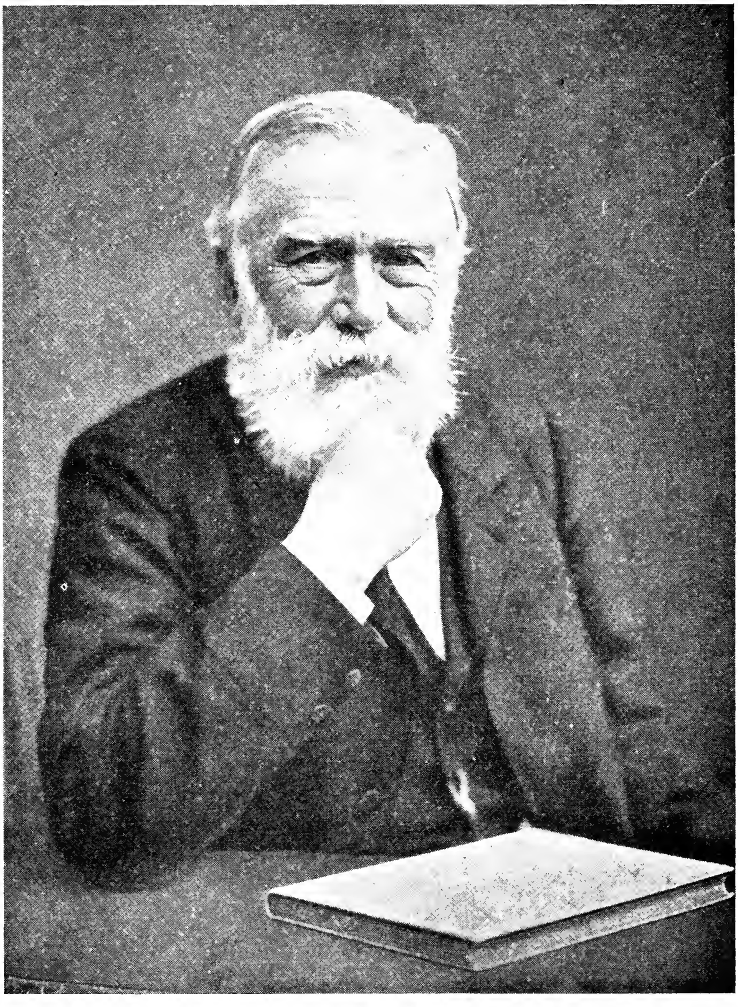

PLATE XXXVII. W. O. Focke, d. 1922.

as in sexual capacity, are hybrids for the most part distinguished from the two parental species.

Crosses between different races and species are distinguished from individuals of a pure race by their vegetative activity.

Hybrids between markedly different races, he remarks, are frequently very tender, especially in youth, so that the rearing of the seedlings takes place with difficulty. *Hybrids between more nearly related species and races, on the other hand, are as a rule thrifty and vigorous; they are distinguished for the most part by size, rapidity of growth, early flowering, abundance of bloom, long duration of life, marked capacity of reproduction, unusual size of individual organs and similar characteristics.*

> "Complete reversions to the parental types, without the operation of the pollen of the parents, occur only in the case of the hybrids of nearly related races."

Focke's own experiments were made in the crossing of species of *Raphanus*, *Melandryum*, *Rubus*, *Anagallis*, *Digitalis*, and *Nicotiana.* While the actual number of crosses made by Focke was few, and the results, as in the case of most other observers of hybrid phenomena, were not analyzed in respect to the generations of the hybrids, yet in the one case of a cross made between *Digitalis purpurea* × *D. ambigua* Focke made measurements of certain organs in the parents and in the hybrids, which, so far as the writer's inquiry has extended, with the exception of those of

	Upper calyx apex		Remaining calyx apex		Length of the corolla		Width of the corolla	Height of the corolla
	length (mm.)	width (mm.)	length (mm.)	width (mm.)	upper	lower		
Digitalis purpurea	22	4	22	10	44	54	20	15
Digitalis ambigua	9	1.5	11	2	31	40	16	13
Digitalis purpurea × ambigua	18	3	20	5	38	45	18	15

Summary of Averages	*Theoretical mm.*	*Found mm.*
Average of length measurements, assuming a mean condition to be the normal	26.3	23.0
Average of width measurements	9.6	7.0

Darwin and Mendel, and the single experiments of Henslow, also with *Digitalis*, and of MacFarlane with a number of other species, constitute the only quantitative measurements made upon hybrid cases prior to 1900. The data are few, but are historically interesting. They show the intermediate condition in the F_1 generation in respect to length and width of the organs measured. (p. 320.)

By Focke's time (1881) the details regarding the behavior of hybrids had sufficiently accumulated so that he was able to say:

> "Our knowledge concerning the fertilization of plants has noticeably extended during recent decades, so that we are no longer in a position to group the facts together, as has been customary, under a few general standpoints. The multifariousness of the phenomena in organic nature is enormously greater than one has thus far been accustomed to assume." (p. 446.)

Focke had distinctly the physiological rather than the morphological point of view regarding hybrids and hybridization, and was not bound by wooden or stereotyped conventions of thought regarding the systematic relations of species.

> "Taken as a whole, it is correct, that the groups of forms do not as a rule very well admit of being delimited according to their sexual behavior. The degrees of morphological and physiological differences correspond to one another frequently somewhat exactly, yet there are examples in which this is absolutely not the case." (p. 448.)

Again he expresses a plastic point of view in this regard, in the following words:

> "One will do well not to judge the morphological relations between two plant forms according to their physiological behavior and vice versa. It is a question in every case of determining the facts, but not to force them into a definite mould.
>
> "Under all circumstances, from the behavior of hybrids, one may only with great care be able to draw conclusions concerning the specific likeness or unlikeness of the parental forms." (p. 449.)

The fact that, as a rule, the nearer the systematic relationship becomes, the more readily what are called "species" cross, was naturally sufficiently recognized by Focke.

> "Two essentially different species can scarcely ever completely mutually fertilize each other." (p. 457.)
>
> "Many hybrids, especially those between unlike parent species, are, as stated, unfruitful; the most show a diminished, a few an almost normal fertility." (p. 457.)
>
> "A delimitation of genera in such a manner that all species which are able to furnish hybrids among one another may be placed in the same genus, would be extremely unnatural. On the other hand, it is not far-

fetched to think of limiting the boundary of a genus to species which are capable of mutual fertilization." (p. 456.)

"We may therefore assert the rule that the races of one and the same species, or of very nearly related species, almost always are capable of mutual fertilization without special difficulty." (p. 450.)

Focke calls attention to the interesting fact that different families and different genera are very unlike in respect to their capacity for cross-fertilization.

"In some families, individual genera show very great differences in their tendency to and their capacity of hybridization." (p. 451.)

However, "whether two species may be crossed with one another or not, can only be determined with certainty through experiment." (p. 451.)

Focke calls attention to the matter of ecological species in relation to crossing, that deserves much further investigation.

"It appears to be difficult to cross plants with one another, which inhabit very different zones, or very different habitats (water and dry places). When it succeeds, the hybrids are sterile." (p. 453.)

However, he calls attention to the fact that:

"The origin of plants from the old or the new world, from the northern or the southern hemisphere, forms in and for itself no hindrance to crossing. Evergreens and deciduous, day-blooming and night-blooming plants may often cross without difficulty." (p. 454.)

"In some genera or groups of species, in which hybrids easily originate, there are individual species which appear to be more inclined than others to enter into hybrid combinations." (p. 454.)

Focke calls attention to the fact that hybrid formation between two species does not always succeed equally easily in both directions, mentioning the case of *Mirabilis jalapa* × *M. longiflora*:

"Many other cases are furnished by breeders of hybrids, in which hybridization has succeeded in only *one* way. If, however, the experiments have not been carried on frequently and in various places, and with different individuals and races of the parents, one can draw no far-reaching conclusions from the failure." (p. 455.)

"It has not seldom been observed that two species are mutually able to effectively pollinate each other, but that A produces more seeds with the pollen of B, then B with the pollen of A." (p. 455.)

According to Focke,

". . . most of these cases come from Gärtner's experience, and require still further confirmation, if indeed the occurrence of this relation may not be completely questioned." (p. 455.)

Focke calls attention to an impression he had gained:

"That genera with more or less zygomorphic flowers, which belong to families in which actinomorphy prevails, show quite an especial inclination toward hybrid formation.

"Whoever is not able to recognize immediately from his own observation the fluidity and mutability of the series of living forms, a few newly-described intermediate forms will certainly not convince him of the correctness of the doctrine of descent. The more earnestly and carefully one proceeds in the exploration of truth, so much the more gain will science and the theory of evolution derive from the investigation." (p. 463.)

Focke disposes of the question whether a plant pollinated from two sources could produce double-pollinated seeds, in the following words:

"By analogy with animal fertilization-phenomena, it is to be regarded as unquestionable, that every single ovule can only be fertilized by a single pollen tube. It is a fact that, in all experiments carried out with scientific precision, no hybrid has ever been obtained, in which the operation of more than one parental species was to be recognized, no matter how many kinds of pollen might be placed upon the stigmas of the maternal flowers." (p. 448.)

On the basis of the available data, Focke undertook to formulate a series of statements or rules, embodying the laws of the behavior of hybrids so far as the then existing information made it possible to do so. This was the first direct attempt after Nägeli, among the hybridizers of the older school, to formulate a complete, coherent statement of principles from the extensive body of data connected with hybridization. The five laws or principles which Focke laid down are as follows:

1. "All individuals derived from the crossing of two pure species or races are, when produced and grown under like conditions, as a rule completely alike, *or are scarcely more different from one another than specimens of one and the same pure species are accustomed to be.*" (p. 469.)

As corollary to this statement, the following is appended:

"Least difficult to answer is the question, concerning which it has been most strenuously contended, namely, that of the greater influence of the one or the other sex on the type of the progeny. The hybrids of the two species or races, A and B, are like each other, indifferently whether A was the male or the female parent-species in the cross. . . . It is determined through numerous experiments rather *that in the plant kingdom in general, in the case of true species, the form-determining power of the male and the female elements in the cross are completely like one another.*" (pp. 469-70.)

Focke modified this statement, however, by saying that:

"Like all other rules of hybridization, so likewise is that of the similarity of both products of crossing not without exceptions. It is nevertheless self-evident that a perchance observed dissimilarity can be regarded as conditioned by the stronger operation of the male or the female element only when the experiments have been instituted in like manner, and when they, by several times repetition, have always led to the same result." (p. 470.)

2. "*The characters of hybrids are derived from the characters of the parents. Only in size and luxuriance, as in sexual power, are they dis-distinguished for the most part from both parents.*" (p. 473.)

With regard to the manner in which the characters are bound together in hybrids, Focke makes the following statement:

"In general a fusion or mutual penetration of the characters takes place, frequently, however, in such manner that in one aspect the one, in another the second parental form appears to prevail. Sometimes, for example, the hybrid recalls in its leaves more the one, in its flowers more the other parental form." (p. 473.)

Focke remarks upon the fact that in the crossing of nearly related races, especially color-varieties, plants frequently are derived, which resemble exactly or nearly so one of the parent races; citing cases of *Brassica rapa*, *Linum*, *Pisum*, *Phaseolus*, *Anagallis*, *Atropa*, and *Datura*.

"Only in the second generation," he says, "does the influence of the older parental race ordinarily betray itself, and in this manner that a part of the seedlings completely or in certain respects revert to it." (p. 474.)

"In later generations of the hybrid plants deviations from the characters of the parents are still more generally observed." (p. 474.)

3. "*Crosses between different races and species are distinguished, as a rule, through their vegetative activity, from the specimens of a pure race. Hybrids between noticeably different species are frequently very tender, especially in youth, so that the rearing of the seedlings succeeds with difficulty. Hybrids between nearly related species and races are, on the other hand, luxuriant and vigorous; they are distinguished for the most part by size, rapidity of growth, early flowering, abundance of flowers, longer life period, vigorous power of reproduction, unusual size of individual organs, and similar characters.*" (p. 475.)

4. "*Hybrids of different species form in their anthers a more limited number of pollen grains, and in their fruits a more limited number of normal seeds than the plants of pure origin. Frequently they produce neither pollen nor seeds. With hybrids of nearly related races this weakening of the capacity for sexual reproduction as a rule is not present. The flowers of the infertile or little fertile hybrids remain fresh as a rule for a long time.*" (pp. 476-7.)

5. "*Abnormalities and structural variations in the flower-parts of hybrid plants are far more abundant, especially, than on individuals of pure origin.*" (p. 481.)

Focke's treatise is often referred to as being noteworthy for containing, with the sole exception of Hoffman's memoir (3), the only references to Mendel's work anterior to 1900. A careful study of Focke's report brings into interesting relief the reason for his having failed to appraise the Mendel paper at its present value. In the first place, Focke was especially interested in the works of those who produced more extended contributions. The works of Kölreuter, Gärtner, Wichura, and Wiegmann, whose works were much more voluminous and pretentious in the field which they occupied, receive appropriate consideration, as do also Naudin's and Godron's prize contributions: but Mendel's paper evidently appeared to Focke simply in the guise of one of the numerous, apparently similar, contributions to the knowledge of the results of crossing within some single group. The works of Kölreuter and Gärtner, for example, are regarded simply and without question as attempts to compass the sphere of hybridization phenomena as a whole, and from a much broader standpoint. It was supposedly not at all conceivable, that the laws of hybrid breeding could be compassed within a series of experiments upon a single plant. Whatever experiments Mendel therefore reported were to be considered, like the experiments of Knight and others, merely for whatever obvious data they seemed conspicuously to present. Focke's work is, however, an excellent compendium of all the experiments in crossing done up to 1881. The details of his data are laborious, exact, well classified and scientifically arranged, comprising 79 families of Dicotyledons, 13 families of Monocotyledons, 2 families of Gymnosperms, 2 of Pteridophytes, 1 of the Musci, and 1 of the Algae.

It is interesting, in view of the fact that Focke's publication constitutes the only actual epitome, in cyclopaedic form, of the hybridization experiments carried on up to his time, to note the relative number of references to the different more important names, as follows: Gärtner, 409; Kölreuter, 214; Herbert, 155; Godron, 102; Naudin, 89; Darwin, 34; Knight, 32; Caspary, 31; Wiegmann, 30; Nägeli, 28; Lecoq, 26; Wichura, 20; Linnaeus, 21; Mendel, 15; Hoffmann, 14; Sageret, 10; Shirreff, 3; Rimpau, 2; Seton and Goss, 1 each.

The fifteen references to Mendel's name occur on the following pages and in the following connections:

p. 110	*Pisum*	1 citation
p. 111	*Phaseolus*	1 citation
p. 215	*Hieracium*	2 citations
p. 216	*Hieracium*	1 citation
p. 218	*Hieracium*	5 citations
p. 483	*Hieracium*	1 citation
p. 444	*Phaseolus* and *Hieracium*	1 citation
p. 459	Theoretical matter	1 citation
p. 492	Theoretical matter	1 citation

The most important reference to Mendel in the above is the often-cited remark under the genus *Pisum*:

> "Mendel's numerous crossings gave results which were quite similar to those of Knight, but Mendel believed that he found constant number-relationships between the types of the crosses." (p. 110.)

This statement manifestly shows a merely superficial understanding of the real significance of Mendel's results. How far short this understanding actually fell is revealed in the statement immediately following:

> "In general, the seeds produced through a hybrid pollination preserve also, with peas, exactly the color which belongs to the mother plant, even when from these seeds themselves plants proceed, which entirely resemble the father plant, and which then also bring forth the seeds of the latter." (p. 110.)

The facts of dominance, and of the difference in the significance of cotyledon-color and seed-coat color, pass unnoticed. We have here plainly the case of the inheritance of seed-coat color taken for the entire case of seed-inheritance in peas, the dominance of roundness of form discovered by Mendel being clearly overlooked.

The next reference is to crossing in *Phaseolus*.

> "*Ph. vulgaris L. var nanus L.* ♀ × *multiflorus Lam. fl. coccin.* ♂ was produced artificially by Mendel." (p. 111.)

Then follows a paragraph of fourteen lines, discussing in a merely conventional manner the inconclusive results of the cross, the color-characters of flowers and seeds alone being noticed.

Mendel's statement with regard to his *Phaseolus* crosses (Bateson, p. 367) was evidently overlooked, to the effect that "the development of the hybrids, with regard to those characters which concern the form of the plants, follows the same laws as in *Pisum*," as well as his further suggestion regarding the matter of color-inheritance in the plant, as follows (p. 367):

> "Even these enigmatical results, however, might probably be explained by the law governing *Pisum*, if we might assume that the color of the flowers and seeds of *Ph. multiflorus* is a combination of two or more entirely independent colors, which individually act like any other constant character in the plant,"

the matter being then discussed analytically at length in Mendel's characteristic form of presentation.

It seems singular that the peculiarity of Mendel's form of statement, and its apparent significance, should have been able to escape Focke's attention.

The remaining passages in which Mendel is referred to, under the discussion of *Hieracium* (pp. 215, 216, 218, and 483) are as follows:

> "That hybrids in this genus [*Hieracium*] are very frequent, is certain; individually, however, many of the views thus far are to be regarded as not sufficiently assured. The hybrids are, according to Mendel's results, polymorphous, but the individual forms as a rule are true from seed [pflegen samenbeständig zu sein]." (p. 215.)
>
> "*H. auricula L.* ♀ × *pilosella L.* ♂ was artificially produced by Fr. Schultz and G. Mendel." (p. 215.)
>
> "Mendel obtained only a single specimen from his artificial cross, *H. auric.* ♀ × *pilos.* ♂, which was somewhat fertile and furnished a constant progeny." (p. 216.)
>
> "G. Mendel produced *H. auric.* ♀ × *H. prat.* ♂ artificially: he obtained 3 specimens, which were markedly different among themselves, and were tolerably fertile; the progeny of each of these cases resembled the mother plant." (p. 218.)
>
> "Mendel obtained *H. auricul.* ♀ × *aurantiacum* ♂, in two materially different specimens, of which one (per-aurant.) was sterile, the other (per-auricula.) produced a single seed." (p. 218.)
>
> "*H. praealtum Vill.* ♀ × *aurantiacum L.* ♂ was obtained by G. Mendel in two different tolerably fertile specimens. The progeny of each of these individuals resembled the mother plant; however, an individual of the second generation had attained completely normal fertility." (p. 218.)
>
> "*H. echioides Linn.* ♀ × *aurantiacum Linn.* ♂ G. Mendel obtained in a single specimen, which was completely fertile and true to seed, and even on pollination with the parent pollen furnished no reversions." (p. 218.)
>
> "*H. praealtum Vill.* ♀ × *flagellare Rchd.* ♂ G. Mendel obtained in a single specimen, whose fertility was nearly normal, and whose progeny was constant." (p. 218.)
>
> "The different primary forms of the *Hieracium* hybrids Mendel found true from seed." (p. 483.)

A general statement on p. 444 shows clearly the relative unimportance of Mendel to Focke's mind, the name being merely that of a person who had made certain experiments calling for mention. It will be noted that the peas experiments are not alluded to at all in Focke's general discussion ("Geschichte der Bastardkunde," 1, pp. 429-45), but merely those with *Phaseolus* and *Hieracium*, as follows:

> "Of the scientific crossing experiments from the most recent time, Rob. Caspary's hybridizations of *Nymphaeaceae*, G. Mendel's with *Phaseolus* and *Hieracium*, D. A. Godron's with *Datura*, *Aegilops* × *Triticum*, and *Papaver*, deserve to be designated as particularly instructive. Godron's series of experiments with *Datura* crosses are to be regarded as the most signal work [als die hervorragendste Leistung]." (1, p. 444.)

We thus have here, succinctly expressed, the relative point of view held by this tolerably keen scrutinizer of the literature on hybridization up to 1881. It is evident that "G. Mendel's" investigations, made very little impression upon the mind of the reviewer.

A further reference to Mendel's name among others appears on p. 459, as follows:

> "The experiments of Kölreuter, Wiegmann, Gärtner, Godron, Naudin, Wichura, Mendel, Caspary, and others, served only scientific ends, while Herbert and Regel united scientific and horticultural ones." (*ib.*, p. 459.)

The point of view expressed above is sufficiently evident. The final reference to Mendel is on p. 492, as follows:

> "To none of the scientific hybrid breeders has it occurred to attach particular species names to his newly-produced plant forms; Kölreuter and Gärtner, Wiegmann and Lehmann, Naudin and Godron, Wichura, Mendel and Caspary, in this respect have proceeded quite uniformly."

We thus have, in closing, final testimony as to the merely formal and conventional impression which Mendel's researches made upon the European mind up to Focke's time and later. In fact we may say that his papers made no more or further impression, as the evidence shows, than any other two contributions of equal length, published during the time under consideration.

It is interesting to note the following extract from Focke's section on "Xenias," (pp. 510-18). The paragraph discusses Goss's, Seton's, and Knight's peas' experiments:

> "J. Goss fertilized flowers of the blue-seeded pea, 'Prolific Blue," with pollen of a white dwarf pea. The pods contained yellowish-white seeds which, when sown, furnished plants whose pods contained in part blue, in part white, in part seeds of both kinds. After selection, the blue sort remained constant, the white produced in part pods with white, in part pods with both kinds of seeds. (Trans. Hort. Soc. of London, V, p. 234.) Knight, in his numerous crosses, never observed an immediate change of the seed-color in consequence of the operation of foreign pollen. Alex. Seton saw peas of two colors in the same pod, but just as in the case of Goss arising in a hybrid (Blendling), not immediately in consequence of foreign pollination. (Transact. Hort. Soc. London, V, pp. 236, 379.) Recently, in the meantime, cases are also reported, in which such pods with two kinds of seeds purport to be produced (erzeugt sein sollen) directly in a blue-seeded sort through foreign pollen. (Deutsche Gartenzeit, 4 Jahrg, p. 71.) Gärtner also obtained seeds a few times in his crossing experiments, the color in which had deviated from the mother plant." (1, p. 514.)

Knight's peas experiments having consisted in the crossing of a white-seeded by a grey-seeded variety, and the dominance of seed-coat color not being evident until the following generation, there would consequently be no xenia effect.

It is surprising, however, that Focke should have so clearly overlooked the actual facts in the Goss experiment. The Blue Prussian variety employed as the seed-parent had seeds with deep "blue" cotyledons, or what would evidently properly be called dark green. The pollen parent had "yellowish-white" seeds (i.e., cotyledons). As the result of the cross, Goss obtained three pods, which contained, when ripe, instead of the "deep blue" seeds of the maternal parent, yellowish-white seeds, like those of the pollen parent. There was thus a perfectly clear case of what is now known as dominance, of the sort referred to by Focke as "xenia." The case of Seton is somewhat similar. A grey-seeded pea (i.e., with grey seed-coats) was crossed with the pollen of a "white-seeded" variety. A pod with four seeds was produced, all of which are stated to have been green. There thus appears, so far as can be judged, to have taken place in the first generation a dominance of green cotyledon color over its absence (white), instead of the usually reported case of the dominance of yellow cotyledon color over green. That such was the case appears from the fact that the seeds of the following year were mingled blue and white in the pods, "mixed indiscriminately and in undefined numbers."

They were all completely either of one color or of the other, none of them having an intermediate tint. It is thus quite evident, that dominance (or "xenia") took place in the first generation, followed by segregation in the second. Gärtner's case should have been noted of a cross of "Early Green Brockel" (*Pisum sativum viride*) with green cotyledons, with "White-flowered creeping pea" (*Pisum sativum nanum repens*) with yellow seeds, in which a pod with five seeds, all yellow, was produced as the result of the cross. (Gärtner, "Versuche und Beobachtungen," pp. 84-5.)

There was thus here a clear case of color dominance ("xenia") in the cotyledons which does not appear to have particularly attracted Focke's attention.

Focke was, until his death in October, 1922, a practising physician of the city of Bremen. His interest in all biological, and especially in botanical questions, was considerable. He was likewise interested in philosophical problems, and was a vigorous supporter of Darwin. Focke was the founder of the Natural History Society in Bremen (1864), and until 1895 remained the editor of its "Transactions." His best-known botanical contribution is his "Pflanzenmischlinge" (1881), besides which he published in 1877 a "Synopsis Ruborum Germaniae" and "Species Ruborum, Monographia, Generis Rubi Prodromus," published in the Bibliotheka Botanica, 1914. He is reported as having contributed greatly as a physician to the development of medical science in Bremen. On his eightieth birthday, a "Festheft" appeared in his honor in the Abhandlungen of the Natural History Society of Bremen, Vol. 23.

28. *The Hoffman Mendel Citations.*

Aside from Focke's the only other reference to Mendel before 1900 is made by Hermann Hoffmann, "Untersuchungen zur Bestimmung des Werthes von Species and Varietät," at Giessen, 1869, referred to by R. C. Punnett, in Nature, Vol. 116, p. 606, October 24, 1925.

Hoffman was Professor of Botany at Giessen, and became engaged, from 1855, upon experiments with varieties of garden beans, the results of which were reported in the Botanische Zeitung for 1862. As a result of these experiments it was found that small variations which appeared in the seeds did not lead to the formation of permanent new forms, but rather, on continued (isolated) culture, reverted every time immediately to the fundamental form. (p. 1.) The experiments were continued in the light of Darwin's "Origin of Species" which appeared in 1859, the object of the experiments being to determine whether new species and varieties continue to originate from natural selection, or through physical and similar influences. Hoffmann's contribution of 1869 is therefore a study chiefly of variation, the question being as to whether "varieties" can be "fixed."

The chief portion of the paper (pp. 47-80), is devoted to the author's selection experiments with varieties of *Phaseolus vulgaris*. Although some crossing was attempted, the experiments are almost entirely in selection for color in the seed-coat. The ultimate aim of the investigation was the determination of the value of species and varieties, and the fixability of varieties. Hoffmann concludes (pp. 169-71) that certain varieties of *Phaseolus vulgaris* are "true species," and that the same is the case for some varieties of peas, and that, in the case of *Phaseolus multiflorus* and several so-called sub-species of *P. vulgaris*, and in most of the white-flowered varieties of blue or red-flowered species, and in a variety of *Pisum sativum*, color is not fixable.

PLATE XXXVIII. Hermann Hoffmann, Professor of Botany at the University of Giessen (1855).

Variation and the results of crossing are briefly discussed in the case of 159 genera. Among these, under "Geum" (No. 71,

p. 112), Mendel's reference to Gärtner's cross of *G. urbanum* × *rivale* is referred to as follows:

> "From *G. urbanum* × *rivale* Gärtner appears to have raised exceedingly fertile and constant hybrids (according to Mendel, Verh. nat. hist. Ver. Brünn. IV, p. 40). I do not find this verified on the reading of the original. (Bast. Erz. 698)."

(The Mendel reference in question is found on p. 373 of Bateson's "Mendel's Principles of Heredity," under the caption "Concluding Remarks," in Mendel's first paper.)

At p. 136 of Hoffmann, No. 118, under the heading of the genus *Pisum*, appears the following:

> "*Pisum* in 6 years' observations by G. Mendel (Verh. Nat. Histor. Ver. zu Brünn, 1865, IV, pp. 6 and 33). Hybrids of *Pisum sativum*, etc., from forms true to seed."

After a considerable discussion of the possibilities in respect to accidental crossing by insects (referring still to Mendel), Hoffmann concludes as follows:

> "Hybrids possess an inclination in the following generation to strike back to the parental species."

It seems extraordinary that, as Punnett remarks, although Hoffmann's somewhat extended experiments were carried on with *Phaseolus*, he should have made no mention of Mendel's experiments with this genus, which should have been easily noticed, since they were reported upon toward the close of the paper on peas. No mention is made of Mendel's paper on *Hieracium* crosses, although a brief paragraph (No. 75, p. 144) is devoted by Hoffmann to *Hieracium* variation studies.

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(h) Die systematische Behandlung der Hieracien, rücksichtlich der Mittelformen. *ibid.*, March 10, 1866. Botanische Mittheilungen, 2 : 340-69.

(i) Mechanisch-physiologische Theorie der Abstammungslehre. Munich, 1884.

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CHAPTER VII

THE WORK OF CHARLES DARWIN

29. *Darwin's Contribution to the Theory of Hybrids.*

THE period from 1859 until the rediscovery of Mendel's papers in 1900 was so strongly colored by the views of Charles Darwin, and so dominated by the magnitude of his work, that it sometimes seems as though originality and initiative during that period had been considerably abandoned, and as though, so far as evolution was concerned, the scientific world had remained content simply to quote the work of Darwin.

It is the purpose of the present chapter to present the contributions of Darwin to the knowledge of hybrids. To this end it seems desirable, so far as possible, to let Darwin's words speak for themselves, and hence, although the text may seem burdened with extracts, yet, for those interested in tracing the history of ideas in genetics, it will perhaps be of service to assemble such a résumé of Darwin's work and thought in the field of hybridization. Brought together in such a way, an author's contribution can be more successfully evaluated at leisure by those who may be interested. The writer has therefore sought to bring together, in somewhat connected and coherent form, the various views, conclusions, and experimental data on the subject of hybrids and hybridization found in Darwin's different writings.

On November 24, 1859, appeared the first edition of "The Origin of Species" (1a), antedating by seven years the appearance of the papers of Mendel.

One of the primary questions concerning crossing that interested Darwin was the matter of sterility and fertility in hybrids. Investigators before Darwin's time had been to a considerable extent obsessed by the species question, which crossing was supposed to solve. If a cross succeeded, or produced fertile offspring, it argued that the parent forms were "varieties." If the cross failed, or if its offspring were sterile, it demonstrated that they were "species." With the sole exception of Sageret (2), none of the earlier hybridists seems to have formed, as the result of experiment, anything like the modern conception of characters as

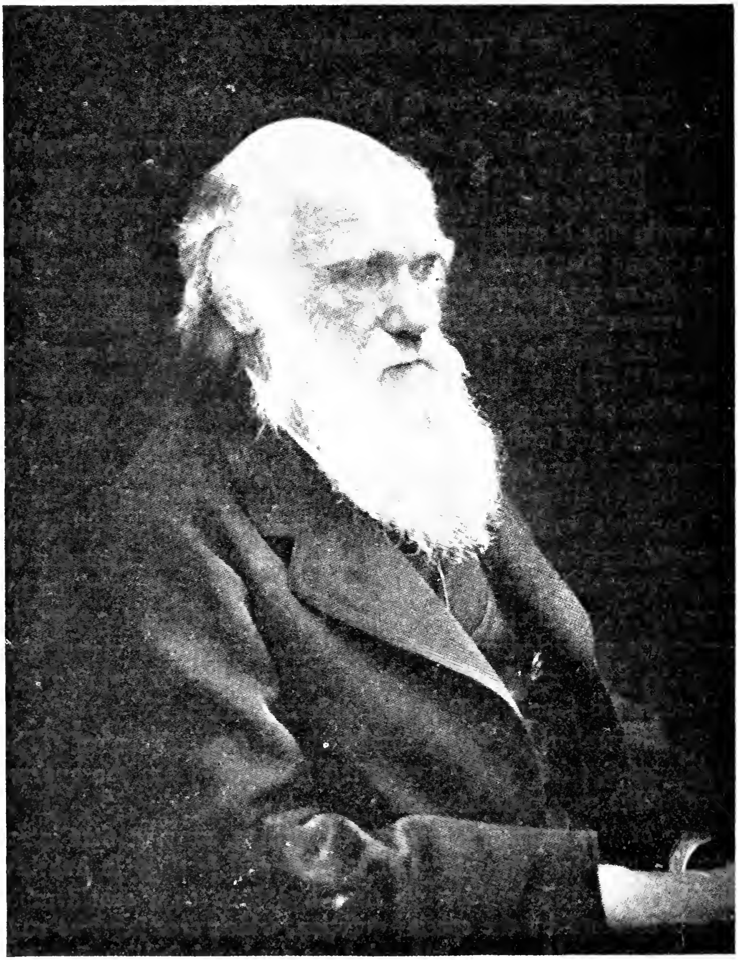

PLATE XXXIX. Charles Darwin, 1809-1882.

biological units, and, with the sole exception of Naudin and Darwin, no scientific theory was even conceived of, which might explain the *modus operandi* of amphimixis in the case of hybrids.

By Darwin the question of hybridization, while indeed for the most part taken up more or less conventionally, received nevertheless broader treatment. To begin with, Darwin held that the inability of species to cross

> ". . . is often completely independent of their systematic affinity, that is of any difference in their structure or constitution, excepting in their reproductive systems." (1a, 2: 14.)

So that, even as early as the writing of the "Origin of Species," Darwin is seen to maintain that the susceptibility of plants to crossing stood in no necessary relation to the degree of their resemblance, and that

> ". . . facility of making a first cross between any two species is not always governed by their systematic affinity or degree of resemblance to each other." (1a, 2: 16.)

This fact, he adds, is demonstrated by the case of reciprocal crosses, alluding here to the relative facility of making the cross, according as the one or the other species is used as the male or the female.

> "Occasionally," he says, there is "the widest possible difference, in the facility of effecting a union. The hybrids, moreover, produced from reciprocal crosses, often differ in fertility." (*ib.*)

Darwin again later, in "Animals and Plants under Domestication," refers to the matter as follows:

> "Why should some species cross with facility, and yet produce very sterile hybrids; and other species cross with extreme difficulty, and yet produce fairly fertile hybrids? Why should there often be so great a difference in the result of a reciprocal cross between the same two species?" (*ib.*, *p.* 217.)

Darwin comments frequently, in the "Origin of Species," upon the fact that the hybrids produced from reciprocal crosses often differ in fertility, and that, while two species may be difficult to cross, there is no strict parallelism between the difficulty of effecting the cross, and the degree of sterility of the hybrids resulting therefrom.

As Darwin observes, difference in the results, in respect to the relative ease of making reciprocal crosses, had been previously noted by Kölreuter, who found, after two hundred trials continued over a period of eight years, that, while *Mirabilis jalapa* could easily be fertilized by *M. longiflora*, the reverse cross could not be effected. With regard to the difference in the facility with which reciprocal crosses can be made, there may be some fundamental resemblance between this fact and the ease with which reciprocal grafts can be made, wherein Darwin instances the fact that the currant can, although with difficulty, be grafted upon the gooseberry, while the reciprocal graft cannot be made. Certainly the well-established truth of factorial mutations in vegetative cells, followed by germinal differences to correspond, should sufficiently indicate that the behavior of the somatic and of the reproductive cells ought not to be regarded as being so sharply separated as is usually done. At all events, the problem of the reason for the relative difference in the respective facility of making reciprocal crosses, as well as the further one of such differences as exist, in the case of mule and hinny, between the respective products of reciprocal crosses, are questions that have been too little investigated since Darwin's time, and require explanation.

Since the advent of Mendelian studies in 1900, it has been rather conventionally assumed that reciprocal crosses are more or less identical in type. That such is not necessarily the case, Darwin's early observations should suffice to indicate.

The problem of the fertility of selfed and crossed plants engaged Darwin's close interest. In forty-one cases, belonging to twenty-three species, the ratio of the fertility of the crossed to that of the self-fertilized plants, was found to be as 100:60. In another experiment to determine the relative fertility of flowers when crossed or selfed, the ratio in thirty cases, belonging to twenty-seven species, was as 100:55.

There is no evidence, Darwin finds,

> ". . . that the fertility of plants goes on diminishing in successive self-fertilized generations," and "no close correspondence, either in the parent plants or in the successive generations, between the relative number of seeds produced by the crossed and self-fertilized flowers, and the relative powers of growth of the seedlings raised from such seeds." (1b, p. 327.)

Darwin's investigations were directed quite extensively to the question of self-sterility in plants, a field which bears strongly upon our knowledge of heredity, but in which likewise, until recently, comparatively little experimental work had been done since his time. As the result of his own studies, supplemented by those of Hildebrand and Fritz Müller, he was able to say:

> "We may therefore confidently assert, that a self-sterile plant can be fertilized by the pollen of any one of a thousand or ten thousand individuals of the same species, but not by its own." (*ib.*, p. 347.)

Regarding all the causes of sterility, or inability to accept fertilization, we are still somewhat at a loss for a complete explanation, although recent chromosome discoveries are throwing light upon the subject. Darwin states the situation in his time:

> "The veil of secrecy is as yet far from lifted; nor will it be until we can say why it is beneficial that the sexual elements should be differentiated to a certain extent, and why, if the differentiation be carried still further, injury follows. It is an extraordinary fact, that, with many species, flowers fertilized with their own pollen are either absolutely or in some degree sterile; if fertilized with pollen from another flower on the same plant, they are sometimes, though rarely, a little more fertile; if fertilized with pollen from another individual or variety of the same species, they are fully fertile; but if with pollen from a distant species they are sterile in all possible degrees, until utter sterility is reached. Thus we have a long series with absolute sterility at the two ends; at one end due to the sexual elements not having been differentiated, and at the other end to their having been differentiated in too great a degree, or in some peculiar manner." (*ib.*, pp. 460-1.)

The questions which Darwin raises in this connection are as follows (p. 458):

1. Why the individuals of some species profit greatly, others very little, by being crossed.
2. Why the advantages from crossing seem to accrue exclusively now to the vegetative and now to the reproductive system, although generally to both.
3. Why some members of a species should be sterile, while others are entirely fertile with their own pollen.
4. Why a change of environment or of climate should affect the sterility of self-sterile species.
5. Why the members of some species should be more fertile with the pollen from another species than with their own.

Regarding the general matter of sterility in hybrids, Darwin comments as follows:

> "It is notorious that, when distinct species of plants are crossed, they produce, with the rarest exceptions, fewer seeds than the normal num-

ber. This unproductiveness varies in different species up to sterility so complete that not even an empty capsule is formed." (1b, p. 468.)

"It is also notorious that not only the parent species, but the hybrids raised from them, are more or less sterile, and that their pollen is often in a more or less aborted condition. The degree of sterility of various hybrids does not always strictly correspond with the degree of difficulty in uniting the parent forms. When hybrids are capable of breeding *inter se*, their descendants are more or less sterile, and they often become still more sterile in the later generations." (*ib.*, p. 469.)

"With the majority of species, flowers fertilized with their own pollen yield fewer, sometimes much fewer seeds, than those fertilized with pollen from another individual or variety." (*ib.*, p. 469.)

As the result of his investigations regarding sterility of pollen, Darwin was able to render at least one service, that of removing the obsession which had so long afflicted the study of the hybrid question, viz., the variety-species discussion. He says:

> "It can thus be shown that neither sterility nor fertility affords any certain distinction between species and varieties. The evidence from this source graduates away, and is doubtful in the same degree as is the evidence derived from other constitutional and structural differences." (1a, 2:4.)

The question of the chemical and cytological basis for sterility or non-receptivity to pollen remains still in part a field for the investigator.

One of the most important questions from the present-day viewpoint which Darwin investigated was that of heterosis, the relative vigor of the first generation hybrids as compared with that of their parents. The following allusions occur in the "Origin of Species."

Darwin comments on the fact that crosses between individuals of the same species, where they differ to a certain extent, give increased vigor and fertility, while close-fertilization long continued almost always leads to physical degeneracy, and remarks:

> "We know also that a cross between distinct individuals of the same variety, and between distinct varieties, increases the number of the offspring, and certainly gives to them increased size and vigour." (1a, 2:269.)

Darwin thoroughly investigated, as is well known, the comparative relation of the offspring of crossed to those of selfed plants with respect to vigor.

> "I have made so many experiments, and collected so many facts, showing on the one hand that an occasional cross with a distinct individual

or variety increases the vigour and fertility of the offspring, and on the other hand that very close interbreeding lessens their vigour and fertility, that I cannot doubt the correctness of this conclusion." (2a, 2:5.)

"Again, both with plants and animals, there is the clearest evidence that a cross between individuals of the same species, which differ to a certain extent, gives vigour and fertility to the offspring; and that close interbreeding continued during several generations between the nearest relations, if these be kept under the same conditions of life, almost always leads to decreased size, weakness, or sterility." (1a, 2:27-8.)

In "Cross and Self-Fertilization," Darwin again discusses the effects of crossing as follows, expressing the view:

"Firstly, that the advantages of cross-fertilization do not follow from some mysterious virtue in the mere union of two distinct individuals, but from such individuals having been subjected during previous generations to different conditions, or to their having varied in a manner commonly called spontaneous, so that in either case their sexual elements have been in some degree differentiated; and secondly, that the injury from self-fertilization follows from the want of such differentiation in the sexual elements." (1b, p. 448.)

"After plants have been propagated by self-fertilization for several generations, a single cross with a fresh stock restores their pristine vigour and we have a strictly analogous result with our domestic animals." (1b, p. 444.)

"A cross with a fresh stock, or with another variety, seems to be always beneficial whether or not the mother plants have been intercrossed or self-fertilized for several previous generations." (1b, p. 449.)

Darwin also remarks upon the greater power of the cross-fertilized plants in his experiments to stand exposure, the crossed plants enduring sudden removal from greenhouse to out-of-doors conditions better than did the self-fertilized, and also resisting cold, and intemperate weather conditions more successfully. This was the case with morning-glory and with *Mimulus*.

"The offspring of plants of the eighth self-fertilized generation of *Mimulus*, crossed by a fresh stock, survived a frost which killed every single self-fertilized and intercrossed plant of the old stock." (1b, p. 289.)

"Independently of any external cause which could be detected, the self-fertilized plants were more liable to premature death than the crossed." (*ib.*, p. 290.)

Out of several hundred plants in all, involved in the experiment, only seven of the crossed plants died, while at least twenty-nine of the self-fertilized were thus lost.

With regard to time of flowering, in four out of fifty-eight cases a crossed, in nine cases a selfed, plant flowered first.

Darwin broached the view that the increased vigor of first generation hybrids was chiefly due to the forms used in the cross having been exposed to somewhat different conditions of life. He also contended that his experiments proved that:

> "If all the individuals of the same variety can be subjected during several generations to the same conditions, the good derived from crossing is often much diminished or wholly disappears." (1a, 2:270.)

This statement appears to be an *obiter dictum* of Darwin's, to the support of which he does not adduce direct experimental evidence.

Again he says:

> "Anyhow my experiments indicate that crossing plants, which have been long subjected to almost though not quite the same conditions, is the most powerful of all the means for retaining some degree of differentiation in the sexual elements, as shown by the superiority in the later generations of the intercrossed over the self-fertilized seedlings." (1b, pp. 454-5.)
>
> "We know," he says. "that a plant propagated for some generations in another garden in the same district serves as a first stock, and has high fertilizing powers." (*ib.*, p. 455.)

The importance of this view has yet, so far as the writer knows, to be re-investigated under controlled conditions.

It was Darwin's view, as the result of his experiments, that the increased vigor of intercrossed plants is due to the constitution or nature of the sexual elements, which conditions he took to be of the general nature of differentiation due to the action of environment.

> "It is certain," he says, "that the differences are not of an external nature, for two plants which resemble each other as closely as the individuals of the same species ever do, profit in the plainest manner when intercrossed, if their progenitors have been exposed during several generations to different conditions." (1b, p. 270.)

Darwin asserts that there is not a single case in his experiments

> ". . . which affords decisive evidence against the rule that a cross between plants, the progenitors of which have been subjected to somewhat diversified conditions, is beneficial to the offspring." (*ib.*, p. 281.)

The fact that increased vegetative vigor in first generation hybrids was also sometimes accompanied by diminished fertility was likewise observed by Darwin.

> "For it deserves especial attention that mongrel animals and plants,

> which are so far from being sterile that their fertility is often actually augmented, have, as previously shown, their size, hardiness, and constitutional vigour generally increased. It is not a little remarkable that an accession of vigour and size should thus arise under the opposite contingencies of increased and diminished fertility." (1c, 2: 108.)

In the case of Darwin's experiments to determine the relative effects upon vigor of selfing and crossing, respectively, the data were determined chiefly with respect to height and weight of the plants, which were grown on opposite sides of the same pot in all instances.

Regarding the relative heights and weights of 292 plants derived from a cross with a fresh stock, and of 305 plants either selfed or intercrossed between plants of the same stock, and belonging to thirteen species and twelve genera, Darwin says:

> "Considering all the cases . . . there can be no doubt that plants profit immensely, though in different ways, by a cross with a fresh stock, or with a distinct sub-variety." He emphasizes further, "it cannot be maintained that the benefit thus derived is due merely to the plants of the fresh stock being perfectly healthy, whilst those which had been long intercrossed or self-fertilized had become unhealthy; for in most cases there was no appearance of such unhealthiness." (*ib.*, p. 269.)

Experiments were also made with plants belonging to five genera in four different families. One of the most interesting cases was that of a plant of marjoram (*Origanum vulgare*). The height of the crossed was to that of the selfed as 100:86.

> "They differed also to a wonderful degree in constitutional vigour. The crossed plants flowered first, and produced twice as many flower-stems; and they afterwards increased by stolons to such an extent as almost to overwhelm the self-fertilized plants." (1b, p. 302.)

Darwin holds that the inferiority of the selfed seedlings in height can have been in no way due to any morbidity or disease in the mother plants; certainly, he maintains, no such theory of a diseased condition would in anywise hold, in the case of

> ". . . intercrossing the individuals of the same variety or distinct varieties, if these have been subjected during some generations to different conditions." (1b, p. 450.)

In four out of the five cases experimented with, the intercrossing of flowers upon the same plant did not differ in effect from the strictest self-fertilization. He says:

> "On the whole, the results here arrived at . . . agree well with our general conclusion that the advantage of a cross depends on the progenitors of the crossed plants possessing somewhat different constitutions,

either from having been exposed to different conditions, or to their having varied from unknown causes in a manner which we in our ignorance are forced to speak of as spontaneous." (1b, pp. 302-3.)

Darwin's experiments indicated, as in the case of heartsease and sweet peas, that

> ". . . the advantage derived from a cross between two plants was not confined to the offspring of the first generation." (1b, p. 305.)
>
> "Laxton's varieties [of sweet peas] produced by artificial crosses," as Darwin says, "have retained their astonishing vigour and luxuriance for a considerable number of generations." (*ib.*, p. 305.)

Darwin concludes:

> "As the advantage from a cross depends on the plants which are crossed differing somewhat in constitution, it may be inferred as probable that under similar conditions a cross between the nearest relations would not benefit the offspring so much as one between non-related plants." (*ib.*, p. 305.)

Darwin finally also remarks in general:

> "It is interesting to observe . . . the graduated series from plants which, when fertilized by their own pollen, yield the full number of seeds, but with the seedlings a little dwarfed in stature, to plants which, when self-fertilized, yield few seeds, to those which yield none, but have their ovaria somewhat developed, and, lastly, to those in which the plant's own pollen and stigma mutually act on one another like poison." (1c, 2:119.)

The relative weight and germinative energy of seeds from crossed and from self-fertilized plants, was investigated by Darwin in the case of sixteen species, with the result that the weight of the seeds of the former to that of the latter was found on the average to be as 100:96. In ten out of the sixteen cases, the self-fertilized seeds were either equal or superior to the crossed in weight, and in six out of these ten, the plants raised from these selfed seeds were greatly superior in height and in other respects to those from the crossed seeds. In the matter of the germination of selfed and crossed seeds, the results were conflicting. Darwin, however, discovered that, in general, seedlings of greater constitutional vigor are obtained when crossed by other individuals of the same stock than when pollinated by their own pollen.

In plants of fifty-seven different species belonging in all to fifty-two genera and to thirty different families, Darwin carried out the most extensive experiment yet on record, conducted for the purpose of determining the difference in size between the offspring of cross-fertilized and of close-fertilized plants.

The total number of the crossed plants amounted to 1,101, and of the selfed plants to 1,076. As a result, Darwin found that the plants derived from crosses between different strains of the same species were taller on the average, than plants derived from crosses within the same strain, and taller in the latter case than in the case of the offspring of self-fertilized plants. The average ratio of 620 crossed to 607 selfed plants in respect to height, derived from Darwin's tables, was as 100:86.

From the fact that flower buds are in a sense distinct individual plant units, which sometimes vary and differ widely from one another, and yet, when on the same plant, owing to the fact that the whole plant has come from the same fertilized cell, rarely are widely differentiated, Darwin reasons that the effects of intercrossing can be explained. He says:

> "The fact that a cross between two flowers on the same plant does no good or very little good, is likewise a strong corroboration of our conclusion; for the sexual elements in the flowers on the same plant can rarely have been differentiated, though this is possible, as flower buds are in one sense distinct individuals, sometimes varying and differing from one another in structure and constitution." (1b, p. 449.)
>
> "Thus," he concludes, "the proposition that the benefit from cross fertilization depends on the plants which are crossed having been subjected during previous generations to somewhat different conditions, or to their having varied from some unknown cause as if they had been thus subjected, is securely fortified from all sides." (1b, p. 449.)

Darwin comments also on the reversed situation, where changes in the external conditions result in sterility, for which he seeks to find a logical connection with the condition induced by crossing.

> "For as, on the one hand, slight changes in the conditions of life are favourable to plants and animals, and the crossing of varieties adds to the size, vigour, and fertility of their offspring, so, on the other hand, certain other changes in the conditions of life cause sterility; and as this likewise ensues from crossing much modified forms or species, we have a parallel and a double series of facts which apparently stand in close relation to each other." (1c, 2:126.)

Darwin appears to hold the ill effects of close fertilization to be due to the fact that the sexual elements in the different flowers on the same plant have not differentiated, while in his conclusion he appears to consider the benefits of cross-fertilization to be due to the individuals involved in the cross having been differentiated through being exposed to different conditions.

Darwin frequently emphasizes the same view regarding the differentiating effects of a new environment.

> "But hardly any cases afford more striking evidence how powerfully a change in the conditions of life acts on the sexual elements, than those already given, of plants which are completely self-sterile in one country, and when brought to another, yield, even in the first generation, a fair supply of self-fertilized seeds." (1b, p. 452.) And again, ". . . We know that a plant propagated for some generations in another garden in the same district serves as a fresh stock and has high fertilizing powers. The curious cases of plants which can fertilize and be fertilized by any other individual of the same species, but are altogether sterile with their own pollen, become intelligible, if the view here propounded is correct, namely, that the individuals of the same species growing in a state of nature near together have not really been subjected during several previous generations to quite the same conditions." (1b, pp. 455-6.)
>
> "When two varieties which present well-marked differences are crossed, their descendants in the later generations differ greatly from one another in external characters; and this is due to the augmentation or obliteration of some of these characters, and to the reappearance of former ones through reversion; and so it will be, as we may feel almost sure, with any slight differences in the constitution of their sexual elements." (1b, p. 454.)

With regard to the ill effects derived from self-fertilization, Darwin says:

> "Whether with plants the evil from self-fertilization goes on increasing during successive generations is not as yet known; but we may infer from my experiments that the increase, if any, is far from rapid. After plants have been propagated by self-fertilization for several generations, a single cross with a fresh stock restores their pristine vigour, and we have a strictly analogous result with the domestic animals. The good effects of cross-fertilization are transmitted by plants to the next generation; and, judging from the varieties of the common pea, to many succeeding generations. But this may merely be that crossed plants of the first generation are extremely vigorous, and transmit their vigour, like any other character, to their successors." (1b, p. 444.)

In this paragraph, Darwin calls attention to a fact already referred to, that attracted little attention for a generation, viz., the immediate improvement due to a cross, known as "heterosis." Darwin was thus, if not the first to call sharply to attention the matter of the relatively increased size and vigor of first generation hybrids, at least the first to subject the question to experimental analysis.

Darwin supposed that what occurred in the case of hybridization was a general breaking-up of the plant's characters, hybridization being understood to operate in about the same way upon the plant's organization as do changes in the external conditions.

> "Thus," Darwin says, "when organic beings are placed during several generations under conditions not natural to them, they are extremely liable to vary, which seems to be partly due to their reproductive systems having been specially affected, though in a lesser degree than when sterility ensues. So it is with hybrids, for their offspring in successive generations are eminently liable to vary, as every experimentalist knows." (1a, 2:26.)

And further:

> "Now hybrids in the first generation are descended from species (excluding those long cultivated) which have not had their reproductive systems seriously affected, and their descendants are highly variable." (1a, 2:41.)

Darwin deserves credit for stoutly contesting the point of view then widely current that the longer a character is handed down by a breed, the more force *per se* it will carry in the transmission. Discussing some of the cases, he says:

> "In none of these, nor in the following cases, does there appear to be any relation between the force with which a character is transmitted and the length of time during which it has been transmitted." (1c, 2:37.)

The basis for such a view, that the longer a strain is grown, and the more it is selected, the more uniform, i.e., the more homozygous, it becomes, was not scientifically known in Darwin's time, but Darwin acutely perceived that the mere repeated act of selection itself, whatever else might be involved, would not necessarily increase the "potency" of transmission.

Darwin's view as to the reason for the good effects of crossing was based upon the long prevalent opinion that, since animals, and hence presumably plants, profit from changes in their conditions, probably such changes operate to affect the germ cells, or that in some way the germ cells receive an extra stimulation on that account which redounds to the benefit of the offspring. (1c, 2:155.)

So far as variability is concerned, Darwin holds:

> "That variability of every kind is directly or indirectly caused by changed conditions of life. Or, to put the case from another point of view, if it were possible to expose all the individuals of a species during many generations to absolutely uniform conditions of life, there would be no variability." (1c, 2:234.)

Darwin quotes Pallas to the effect that all variation is due to crossing, to which view, however, he opposed the facts of bud-variation. It remained Darwin's view, as it was that of practically all of the older school of breeders, that it was probable that crossing in and of itself, when one or both the parents have been long under cultivation, increases the "variability" of the offspring, independently of the fact of the commingling of the parental characters themselves. (1c, 2:243-4.)

The fundamental cause underlying variation Darwin considered to be the food supply.

> "Of all the causes which induce variability," he says, "excess of food whether or not changed in nature, is probably the most powerful." (1c, 2:236.)

However, in face of the fact of the bud variation of the peach to form the nectarine, Darwin concluded that there must have been some cause, internal or external, to stimulate a bud to change its character. He says:

> "I cannot imagine a class of facts better adapted to force on our minds the conviction that what we call the external conditions of life are in many cases quite insignificant in relation to the particular variation, in comparison with the organization or constitution of the being which varies." (1c, 2:269.)

So, from the case of the red *Magnum Bonum* plum, which appeared on a forty-year old tree of the yellow *Magnum Bonum* variety, Darwin also concludes:

> "When we reflect on these facts, we become deeply impressed with the conviction that in such cases the nature of the variation depends but little on the conditions to which the plant has been exposed, and not in any special manner on its individual character, but much more on the inherited nature or constitution of the whole group of allied beings to which the plant in question belongs. We are thus driven to conclude that in most cases the conditions of life play a subordinate part in causing any particular modification; like that which a spark plays, when a mass of combustibles bursts into flame, the nature of the flame depending on the combustible matter, and not on the spark." (1c, 2:272.)

In general, regarding the character of hybrids, Darwin held that while in the majority of cases, the hybrid offspring are intermediate between their parents, yet that certain characters are incapable of fusion.

> "When two breeds are crossed, their characters usually become intimately fused together; but some characters refuse to blend, and are transmitted in an unmodified state, either from both parents or from one." (1c, 2:67.)

As cases in point, Darwin cites the crossing of gray and white mice, the offspring of which are pure white or gray, but not intermediate, and the crossing of white, black, and fawn-colored angora rabbits, in which the colors are separately inherited, and not combined in the same animal. The non-intermediate character of the inheritance in the case of turnspit dogs and ancon sheep is referred to, as is also the inheritance in the case of tailless, hornless breeds. Similar results in the case of stocks, toad-flax, and sweet peas are cited. (1c, 2:68.)

Darwin (1c, 2:44-45; 68-69), in discussing what he called "prepotency," is dealing in very many cases with that which we now recognize as simple dominance. For example, in the crossing of snap-dragons Darwin found that when the normal or irregular-flowered (zygomorphic) type is crossed reciprocally with the peloric or regular-flowered (actinomorphic) type, the former prevails in the first generation to the exclusion of the latter. The 127 hybrid plants, self-fertilized, yielded in the second generation irregular to regular plants in the ratio of 88 to 37. This is evidently an approximation to the 3:1 ratio, its defectiveness being undoubtedly due to the limited numbers.

Darwin, however, regards it simply as a

> ". . . good instance of the wide difference between the inheritance of a character and the power of transmitting it to crossed offspring." (1c, 2:45.)

Darwin was thus quite unable, with the information then available, to frame a satisfactory explanation for the various phenomena passing under the name of "prepotency."

He makes one remark relative to prepotency, however, which slightly grazes the recent presence-and-absence theory of Mendelian inheritance.

> "We can seldom tell what makes one race or species prepotent over another; but it sometimes depends on the same character being present and visible in one parent, and latent or potentially present in the other." (1c, 2:58.)

The fact that certain characters are bound up with sex, or "sex-linked," did not escape Darwin's observation. He alludes to cases where a son does not inherit a character directly from his father, or transmit it directly to his son, but receives it by transmission from a mother who does not show it herself, and where he transmits it in turn through the medium of a daughter, who also does not show the character, but who acts as a carrier.

> "Characters may first appear in either sex, but oftener in the male than in the female, and afterwards be transmitted to the offspring of the same sex. In this case, we may feel confident that the peculiarity in question is really present, though latent, in the opposite sex. Hence the father may transmit through his daughter any character to his grandson; and the mother conversely to her granddaughter. We thus learn, and the fact is an important one, that transmission and development are distinct powers. Occasionally these two powers seem to be antagonistic, or incapable of combination in the same individual; for several cases have been recorded in which the son has not directly inherited a character from his father, or directly transmitted it to his son, but has received it by transmission through his non-affected mother, and transmitted it though his non-affected daughter. Owing to inheritance being limited by sex, we see how secondary sexual characters may have arisen under nature; their preservation and accumulation being dependent on their service to either sex." (1c, 2:58-9.)

Darwin's mind was chiefly occupied, not with the question of the fundamental nature of hybridity, but, as we have seen, with the question of the relative sterility of selfed and crossed plants, and their relative vigor. However, among the interesting matters from the genetic standpoint, are his recognition of the general fact of the intermediacy of first-generation hybrids, and the occasional dominance of one or the other set of parental characters, and the phenomenon called "reversion."

It is in connection with the question of reversion that we find the greatest theoretical interest in Darwin's writings on the subject of hybridization. On this subject of "reversion," Darwin's utterances are remarkable, especially in "Animals and Plants under Domestication." In most cases he regards "reversion" as the coming to light of a "latent" character, as e.g.:

> ". . . hornless breeds of cattle possess a latent capacity to produce horns, yet when crossed with horned breeds, they do not invariably produce offspring bearing horns." (1c, 2:44.)

Darwin considered it doubtful whether, as was then popularly supposed, the length of time during which a character had been inherited had any influence on its fixedness, and concludes, from the fact that, when wild species which had remained so for ages are brought into cultivation, they immediately begin to vary, that no character can be considered as absolutely fixed by long inheritance. (1c, 2:56.)

As previously stated, one of the problems that primarily interested Darwin was the question of sterility and fertility in hybrids, the fact of sterility being relied upon to prove that the parents belonged to different "species," whereas fertility indicated that the parents were varieties of the same species. At present, while it is recognized that organisms more distantly related—frequently different so-called "species"—do not ordinarily cross, or, if they do, the progeny are quite frequently sexually sterile, yet the attitude has quite changed from the strictly systematic point of view formerly adhered to. Darwin recognized in general that:

> "There is often the widest possible difference in the facility of making reciprocal crosses. Such cases are highly important, for they prove that the capacity in any two species to cross is often completely independent of their systematic affinity, that is of any difference in their structure or constitution, excepting in their reproductive systems." (1a, 2:14.)

Darwin's relation to the study of hybridization is, as already stated, chiefly known through his extensive and classical experiments on self and cross-fertilization in plants.

In forty cases, belonging to twenty-three species, the ratio of the fertility of the crossed to that of the self-fertilized plants was found to be as 100:50 (*ib.*, pp. 314-17); in another case, the ratio, in thirty cases, belonging to twenty-eight species, was as 100:75. (*ib.*, pp. 322-3.)

Darwin, at the outset, merely comments on the results of crossing as follows:

> "In considering the final result of the commingling of two or more breeds, we must not forget that the act of crossing in itself tends to bring back long-lost characters not proper to the immediate parent-forms." (1c, 2:64.)

It was noticed that from three to eight generations were usually required before a breed derived from a cross comes to be considered free from danger of "reversion." What constituted the machinery to bring about reversion remained, but for Mendel's as yet undiscovered researches, unknown. The state of knowledge in this regard is exemplified by Darwin's remark:

> "That the act of crossing in itself gives an impulse towards reversion, as shown by the re-appearance of long-lost characters, has never, I believe, been hitherto proved." (1c, 2:13.)

Darwin recognized, as did most of the breeders before Mendel, that:

> "As a general rule, crossed offspring in the first generation are nearly

> intermediate between their parents, but the grandchildren and succeeding generations continually revert, in a greater or lesser degree, to one or both of their progenitors." (1c, 2:22.)

From cases of intermediacy, Darwin proceeds to discuss what we should call cases of dominance, and finally cases in which the offspring in the first generation are neither intermediate nor uniparental in type, but in which there is vegetative splitting, or mutation:

> "In which differently coloured flowers borne on the same root resemble both parents, . . . and those in which the same flower or fruit is striped or blotched with the two parental colours, or bears a single stripe of the colour or other characteristic quality of one of the parent-forms." (1c, 2:69.)

It is interesting to see how Darwin now undertook, in the absence of experimental evidence, to devise a scientific solution for the re-appearance of parental characters in the second generation of the offspring. Taking Naudin's idea of segregation or "disjunction" of the elements of the species, he concludes as follows:

> "If . . . pollen which included the elements of one species happened to unite with ovules including the elements of the other species the *intermediate or hybrid state would still be retained, and there would be no reversion. But it would, as I suspect, be more correct to say that the elements of both parent-species exist in every hybrid in a double state*, namely, blended together and completely separate." (Italics inserted.) (1c, 2:23)

The above comes very near to being a scientific statement of the actual condition of things in a hybrid plant or animal. It is, in fact, the closest to a correct expression of the true condition in the heterozygote, of anything outside of Mendel's own writings.

According to Darwin's theory of "pangenesis," every cell in the body was supposed to throw off small particles known as "gemmules," which carried the characters to the reproductive cells. In a hybrid, Darwin assumes that there are two kinds of "gemmules" or character-carriers, pure gemmules coming from each of the two parents, and combined or hybridized gemmules as well. In the following statements Darwin then proceeds to give, from his standpoint, as clear an account as could be demanded of the cause for the re-appearance of the original parental characters.

> "*When two hybrids pair, the combination of pure gemmules derived from the one hybrid with the pure gemmules of the same parts derived*

> *from the other would necessarily lead to complete reversion of character; and it is perhaps not too bold a supposition that unmodified and undeteriorated gemmules of the same nature would be especially apt to combine.*" (1c, 2:383.) (Italics inserted.)

This statement approximates toward an explanation of what is understood to occur when two F_1 hybrids are mated. The reunion of, say, character-unit or determiner D from the male with D from the female gives DD, which reconstitutes one of the original parents with respect to a character which breeds true; and this is what we now understand "reversion" to be—the restoration in stable form of characters disunited and scattered or "segregated" in the offspring of a cross.

Continuing, Darwin says:

> "Pure gemmules in combination with hybridized gemmules would lead to partial reversion. And lastly, *hybridized gemmules derived from both parent-hybrids would simply reproduce the original hybrid form.* All these cases and degrees of reversion incessantly occur. 1c, 2:383.) (Italics inserted.)

The above is an attempt at a statement of the conditions of things in the heterozygous or hybrid condition except that "hybrid gemmules," or their equivalents, are not believed to exist as such, and the crossing of the F_1 with itself yields, of course, not all "hybrids" as Darwin supposed, but leaves only one-half the offspring in the hybrid condition. In the simple Mendelian hybrid it has been found, to be sure, that, in addition to the parental character-types being reproduced pure—i.e., 25 per cent of each—one-half, or 50 per cent, of the individuals in the second generation reproduce again the hybrid form, owing to the factors not being united with their like, but with, as it were, unlike factors, or as it may be the absence of the factor in the opposite parent. However, there are often modifying factors which do come in from the other parent; at all events, the result is oftentimes a dilution of the original character. Assuming the "hybridized" gemmules to represent the "Dr" condition, we have in Darwin's statement what is an approximation towards genetic language. In other words, Darwin's theoretical statement comes rather close to representing the Mendelian point of view in regard to the mating of hybrid organisms of the F_1 generation.

It seems strange indeed that with Darwin's instinct for detail, and the acuteness and accuracy of his sense of observation, it did not occur to him to study the nature of hybrids in the same manner that Mendel adopted, viz., by finding out the numerical relations of the different kinds of character-types among the progeny, and by formulating some law or principle to explain their ratios. However, it is a matter of interest that Darwin, in the absence of actual experiments in point, should have come as close as he actually did to finding an approximation toward a correct theoretical explanation of what occurs in the cells of hybrids.

Darwin's theory was a natural corollary to his doctrine of pangenesis. It is perhaps strange that, after the publication of Naudin's idea of disjunction, and especially after the phenomenon of segregation in peas had been noticed by five observers, all of whose experiments Darwin remarks upon, Darwin himself did not anticipate, in part at least, Mendel's actual experiment. However, it is a matter of special interest that *a priori*, in the absence of experimental data, he should have come as close to the principle of the Mendelian explanation as the above passages seem to indicate.

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CHAPTER VIII

THE WORK OF FRANCIS GALTON

30. *Sir Francis Galton's Investigations in Heredity.*

DURING the period from 1865 to 1900, one of the greatest contributors to the theory of heredity was Sir Francis Galton, and his investigations deserve to be reported with clearness and in some detail, partly because the nature of his experiments and their results are not always entirely understood, and partly also because of a popular misconception of the nature and applicability of his "law."

In 1889 appeared Galton's famous book on "Natural Inheritance" (2a), which should be specially noted, inasmuch as it constituted the first deliberate attempt since Quetelet's publications (1832-1846-1848-1871), dealing with anthropometric measurements, to marshal vital statistics into a series in such a form as to show the laws governing heredity in populations, in respect to such matters as stature, eye-color, artistic faculty, and disease, since these involve Galton's well-known "Law of Regression," and consist in the application of mathematical principles to the statistical data of inheritance. Inasmuch as this was the most thorough and extensive attempt at the development of a law of heredity upon a mathematical basis appearing prior to the re-discovery of Mendel's papers in 1900, it calls for consideration herein.

Galton calls attention to the fact that the faculties of men may be roughly sorted into those that are natural and those that are acquired, and proposes dealing with the former class.

Galton is noteworthy, in his day, for calling attention to the particulate nature of inheritance. It is interesting to quote his words:

> "All living beings are individuals in one aspect, and composite in another. They are stable fabrics of an inconceivably large number of cells, each of which has, in some sense, a separate life of its own, and

which have been combined under influences that are the subjects of much speculation, but are as yet little understood. We seem to inherit bit by bit, this element from one progenitor, that from another, under conditions that will be more clearly expressed as we proceed, while the several

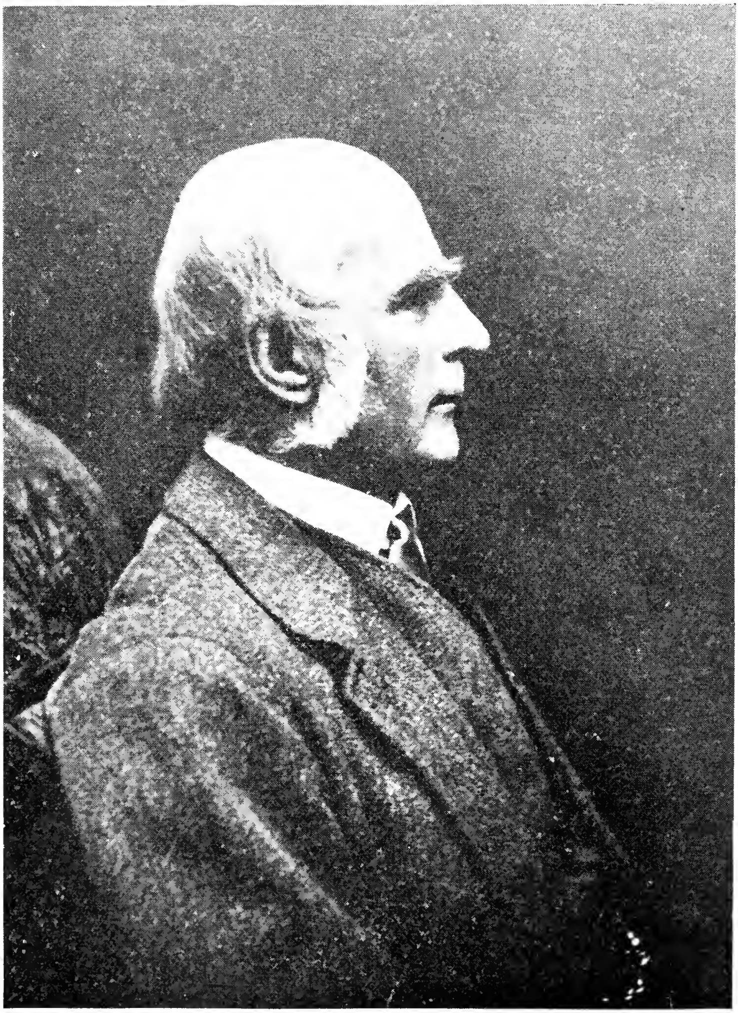

PLATE XL. Sir Francis Galton, 1822-1911.

bits are themselves liable to some small change during the process of transmission. Inheritance may therefore be described as largely if not wholly 'particulate,' and as such it will be treated in these pages." (2a, p. 7.)

"We appear, then, to be severally built up out of a host of minute particles, of whose nature we know nothing, any one of which may be derived from any one progenitor, but which are usually transmitted in aggregates, considerable groups being derived from the same progenitor. It would seem that while the embryo is developing itself, the particles, more or less qualified for each new post, wait as it were in competition to obtain it. Also that the particle that succeeds must owe its success partly to accident of position and partly to being better qualified than any equally well-placed competitor to gain a lodgment." (2a, p. 9.)

It is the latter conception that was concretely exemplified in Mendel's principle of dominance, to which it appears that Galton offered no corresponding hypothesis. Galton, however, recognized the existence of "heritages that blend," and "heritages that are mutually exclusive." For the former he cites the case of human skin color, referring to crosses between the white and the negro, adding:

"It need be none the less 'particulate' in its origin, but the result may be regarded as a fine mosaic too minute for its elements to be distinguished in a general view." (*ib.*, p. 12.)

It appears that the conception of "particulate inheritance" interested Galton, since the quality of his mind was such as to demand concrete expressions for the interpretation of inheritance phenomena. The facts indeed increasingly appear to show that much so-called "blended inheritance" is actually particulate in character.

As an example of "heritages that come altogether from one progenitor to the exclusion of the rest," he cites eye-color.

"Eye-colour," he says, "is a fairly good illustration of this, the children of a light-eyed and of a dark-eyed parent being much more apt to take their eye-colours after the one or the other than to have intermediate and blended tints." (*ib.*, p. 12.)

Galton recognized the existence of "latent" characters.

"The total heritage of each man must include greater variety of material than was utilized in forming his personal structure. [2a, p. 18.] The existence in some latent form," he says, "of an unused portion is proved by his power already alluded to, of transmitting ancestral characters that he did not personally exhibit. Therefore the organized structure of each individual should be viewed as the fulfillment of only one out of an indefinite number of mutually exclusive possibilities. His structure is the coherent and more or less stable development of what is no more than an imperfect sample of a large variety of elements." (*ib.*, p. 18.)

Galton, in the absence of the chromosome theory of the inheritance of what he calls the "elements" or "particles" of the potential heritage, undertakes to classify the "imperfect sample of a large variety of elements," under three possible categories: first, the conception embodied in Darwin's theory of pangenesis; secondly, "that of a more or less general co-ordination of the influences exerted on each element, not only by its immediate neighbours, but by many or most of the others as well," and finally, that of "accident or chance, under which name a group of agencies are to be comprehended, diverse in character and alike only in the fact that their influence on the settlement of each particle was not immediately directed towards that end." (*ib.*, p. 19.)

Galton proposes the idea that the particulate nature of inheritance makes it appear that there is really

> ". . . no direct hereditary relation between the personal parents and the personal child," but "that the main line of hereditary connection unites the sets of elements out of which the personal parents had been evolved with the set out of which the personal child was evolved. The main line may be rudely likened to the chain of a necklace, and the personalities to pendants attached to its links. We are unable to see the particles and watch their grouping, and we know nothing directly about them, but we may gain some idea of the various possible results by noting the differences between the brothers in any large fraternity . . . whose total heritages must have been much alike, but whose personal structures are often very dissimilar." (*ib.*, pp. 19-20.)

In a discussion which follows as to the nature of stability in the inheritance of the organism, Galton makes a hypothetical suggestion as to the behavior in inheritance, or the nature of the hereditary factors concerned.

> "The changes," he says, "in the substance of the newly fertilized ova of all animals . . . indicate segregations as well as aggregations, and it is reasonable to suppose that repulsions concur with affinities in producing them. We know nothing as yet of the nature of these affinities and repulsions, but we may expect them to act in great numbers and on all sides in a space of three dimensions. . . . Every particle must have many immediate neighbours. . . . We may therefore feel assured that the particles which are still unfixed must be affected by very numerous influences acting from all sides and varying with slight changes of place, and that they must occupy many positions of temporary and unsteady equilibrium, and be subject to repeated unsettlement, before they finally assume the positions in which they severally remain at rest." (*ib.*, pp. 20-1.)

Galton effectively combats the very general view that natural selection proceeds only through small steps,

> ". . . for which," he says, "it is difficult to see either the need or the justification, namely, that the course of evolution always proceeds by steps that are severally minute, and that become effective only through accumulation." (*ib.*, p. 32.)
>
> "That the steps *may* be small and that they *must* be small are very different views; it is only to the latter that I object, and only that the indefinite word 'small' is used in the sense of 'barely discernible,' or as small compared with such large sports as are known to have been the origins of new races." (*ib.*, p. 32.)

Galton then points out that an apparent ground for this common belief lies in the fact that when intergrading forms are looked for, whether in the case of plants, animals, language-forms, weapons, utensils, or any other evolutionary product:

> "A long and orderly series can usually be made out, each member of which differs in an almost imperceptible degree from the adjacent specimens [p. 32]. But," he says, "it does not at all follow, because these intermediate forms have been found to exist, that they are the very stages that were passed through in the course of evolution. Counter-evidence exists in abundance, not only of the appearance of considerable sports, but of their remarkable stability in hereditary transmission." (*ib.*, p. 32.)

Galton's ruling conception in dealing with the question of heredity was, as is well known, to proceed by the method of deduction from the law of averages, as demonstrated by populations. Herein we see the prevalent misconception of his day, so far as the investigation of individual inheritance is concerned—that of predicting the behavior of the individual upon the basis of the law of probability, as demonstrated by the outcome or product of generations of like populations.

> "The science of heredity," he says, "is concerned with Fraternities and large Populations rather than with individuals, and must treat them as units." (p. 35.)

The greater portion of Galton's "Natural Inheritance" is devoted to the discussion of anthropometric data collected upon the subject of stature, eye-color, artistic faculty, and disease. His biometric observations were, however, originally made upon sweet peas. He states:

> "I had to collect all my data for myself, as nothing existed, so far as I know, that would satisfy even my primary requirement. This was to obtain records of at least two successive generations of some population of considerable size. They must have lived under conditions that were

> of a usual kind, and in which no great varieties of nature were to be found. Natural selection must have had little influence on the characteristics that were to be examined. These must be measurable, variable, and fairly constant in the same individual. The result of numerous inquiries, made of the most competent persons, was that I began my experiments many years ago on the seeds of sweet peas. . . ." (p. 71.)

At first both size and weight were determined but, after becoming assured of the equivalence of the two methods, Galton confined himself to the weights, in that they were more easily ascertained than the measurements.

> "It is more than 10 years (from 1889) since I procured these data. They were the result of an extensive series of experiments on the produce of seeds of different sizes, but of the same species, conducted for the following reasons. I had endeavoured to find a population possessed of some measurable characteristic that was suitable for investigating the causes of the statistical similarity between successive generations of a people." (p. 80.)

As to the selection of sweet peas, Galton says:

> "They do not cross-fertilize, which is a very exceptional condition among plants; they are hardy, prolific, of a convenient size to handle, and nearly spherical; their weight does not alter perceptibly when the air changes from damp to dry, and the little pea at the end of the pod, so characteristic of ordinary peas, is absent in sweet peas." (p. 80.)

Seven sets were selected for planting, containing ten seeds each, graduating in weight from the heaviest to the lightest.

After speaking of the immense amount of labor involved in the details of the experiment, Galton says:

> "The results were most satisfactory. They gave me two data, which were all that I wanted in order to understand, in its simplest approximate form, the way in which one generation of a people is descended from a previous one; and thus I got at the heart of the problem at once." (p. 82.)

The tabulated results of this work upon the weights of seeds in two succeeding generations of sweet peas were such as to demonstrate what Galton called the fact of filial regression.

> "It will be seen," he says, "that for each increase of one unit on the part of the parent seed, there is a mean increase of only one-third of a unit in the filial seed; and again that the mean filial seed resembles the parental when the latter is about 15.5 hundredths of an inch in diameter. Taking 15.5 as the point towards which Filial Regression points, whatever may be the parental deviation from that point, the mean Filial Deviation will be in the same direction, but only one-third as much." (p. 225.)

In the investigation of the inheritance of human stature. Galton states his reasons for selecting it as a subject for the investigation of heredity.

> "Some of its merits are obvious enough, such as the ease and frequency with which it may be measured, its practical constancy during thirty-five or forty years of middle life, its comparatively small dependence upon differences of bringing up, and its inconsiderable influence on the rate of mortality." (p. 83.)
>
> "Other advantages not equally obvious are equally great. One of these is the fact that human stature is not a simple element but a sum of the accumulated lengths or thicknesses of more than a hundred bodily parts." (pp. 83-4.)
>
> "The beautiful regularity in the Statures of a population, whenever they are statistically marshalled in the order of their heights, is due to the number of variable and quasi-independent elements of which Stature is the sum." (p. 85.)

The data for stature and the other human characters observed were obtained from the "Records of Family Faculties," amounting to 150 families in all, from which Galton extracted data as to the stature of 205 couples of parents, as compared with a total of 930 of their adult children of both sexes. For purposes of calculation, Galton introduced the theoretical "mid-parent,"

> ". . . an ideal person of composite sex, whose Stature is halfway between the Stature of the father and the transmuted Stature of the mother." (p. 87.)

The transmutation for female stature was stated as follows:

> "The artifice is never to deal with female measures as they are observed, but always to employ their male equivalent in the place of them. I transmute all the observations of females before taking them in hand, and thenceforth am able to deal with them on equal terms with the observed male values. For example: the statures of women bear to those of men the proportion of about twelve to thirteen. Consequently by adding to each observed female stature at the rate of one inch for every foot, we are enabled to compare their statures, so increased and transmuted, with the observed statures of males on equal terms." (*ib.*, p. 6.)

As a result of these data, Galton concluded that:

> "The filial deviation from P (the mid-stature of the population, 68½ inches), is, on the average, only two-thirds as wide as the Mid-Parental Deviation. I call this ratio of 2 to 3 the ratio of 'Filial Regression.' It is the proportion in which the Son is, on the average, less exceptional than his Mid-Parent." (p. 97.)
>
> "This value of two-thirds will therefore be accepted as the amount of regression, on the average in many cases, from the mid-parental to the mid-filial stature whatever the mid-parental stature may be." (p. 98.)

Galton discusses the practical effects of the law of regression thus:

"The law of regression tells heavily against the full hereditary transmission of any gift. Only a few out of many children would be likely to differ from mediocrity so widely as their mid-parent, and still fewer would differ as widely as the more exceptional of the two parents. . . ." (p. 106.)

"It must be clearly understood that there is nothing in these statements to invalidate the general doctrine that the children of a gifted pair are much more likely to be gifted than the children of a mediocre pair. They merely express the fact that the ablest of all the children of a few gifted pairs is not likely to be as gifted as the ablest of all the children of a very great many mediocre pairs." (p. 106.)

From the data obtained, Galton undertook to calculate the value of the respective contributions of the successively ascending ancestors to the inheritance.

"If D is the stature of the mid-parent, then mid-parents whose stature is P D have children whose average stature is P 2/3 D. In other words, a character in a man implies a character of 1/3 of that amount in his mid-parent. Likewise the character in the mid-parent of the man being D, the same character in the mid-parent of the mid-parent would be 1/3 D, that of the mid-great-grandparents 1/9 D, and so on. Hence the total inheritance would be represented by D (1+1/3+1/9+&c.)=D 3/2." (p. 134.)

By theoretical calculations (p. 135) Galton arrives, from two different directions, at the figures 4/9 and 6/11, respectively, as representative values for the extent to which the mid-parents' characters are represented in, or, as he says, "influence" the offspring. These values, 44/99 and 54/99, as he says, "differ but slightly from 1/2, so we may fairly accept that as the result."

"Hence the influence, pure and simple, of the mid-parent may be taken as 1/2, and that of the mid-grandparent as 1/4, and of the individual grandparent 1/16, and so on. It would, however, be hazardous, on the present basis, to extend this sequence with confidence to more distant generations." (p. 136.)

With respect to the inheritance of eye-color, Galton makes comment as follows:

"Stature and eye-colour are not only different as qualities, but they are more contrasted in hereditary behaviour than perhaps any other common qualities. Parents of different statures usually transmit a blended inheritance to their children, but parents of different eye-colours usually transmit an alternative heritage. If one parent is as much taller than the average of his or her sex as the other parent is shorter, the stature of their children will be distributed, as we have already seen, in nearly the same way as if the parents had both been of medium height. But if one parent has a light eye-colour, and the other a dark eye-colour, some of the children will, as a rule, be light and the rest dark; they will

> seldom be medium eye-coloured, like the children of medium eye-coloured parents." (p. 139.)
>
> "If notwithstanding this two-fold difference between the qualities of stature and eye-colour, the shares of hereditary contribution from the various ancestors are alike in two cases, as I shall expect to show that they are, we may with some confidence expect that the law by which those hereditary contributions are found to be governed may be widely and perhaps universally applicable." (p. 139.)

The data for eye-color were drawn from the same collection of family records referred to for the data for statures. Taking the fraternities in which the eye-color is known for the two parents and the four grandparents, there are 211 of such groups, with a total of 1,023 children. Letting S stand for the individual subject of the investigation, F for the parent of the individual, G_1 for his grandparent, G_2 for his great-grandparent, etc., the transmission to the individual is F, 1/4; G_1, 1/16; G_2, 1/64; etc.

Supposing that the amount of any peculiarity possessed by F is equal to D, then, as Galton has shown, each of the immediate ancestors of F, who stand in the relation of G_1 to S, will on the average possess 1/3 D. Similarly, each of the four grandparents of F (who stand in the order of G_2 to S) will, on the average, possess 1/9 D and so on. Now F transmits to S only 1/4 of his inherited peculiarity; G_1 transmits only 1/16; G_2 only 1/64 and so on. Hence the aggregate total of the inheritance of any peculiarity in the heritage that may be expected in S is as follows:

$$D\left\{ 1/4+2(1/3\times 1/2^4)+4(1/9\times 1/2^6)+\&c. \right\} = D(1/2^2+1/2^3.3+1/2^4.3^2+\&c.)=D\times 0.30$$

where the eye-colors of the two parents are given.

This means that each parent must contribute 0.30 to the heritage of the offspring in question, or the two parents taken together, 0.60, leaving a residue of 0.40 due to the influence of ancestry about which nothing is known or implied.

By a similar calculation Galton shows that the aggregate of the probable heritages from G_1 are expressed by D×0.16 (0.1583), where the eye-colors are given of the four grandparents. Similarly, where the eye-colors are given of the two parents and four grandparents, the aggregate contribution of each grandparent is D×3/40=D×0.075, taken as 0.08.

In Tables 19 and 20 (pp. 215-16), the observed and the calculated eye-colors are given for 16 groups of families, in which

> ". . . those families are grouped together in whom the distribution of light, hazel, and dark eye-colour among the parents and grandparents is alike. Each group contains at least twenty brothers or sisters." (p. 215.)

The correctness of the calculations, as compared with the observed data, are well shown, as Galton remarks, by the totals in Table 19, in which the aggregate calculated number of light-eyed children, under Groups I, II, III, are given as 623, 601, and 614, respectively, while the observed numbers were 629, being correct, therefore, in the ratio of 99, 96, and 98 to 100.

Galton concludes his observations on the subject of eye-color as follows:

> "My returns are insufficiently numerous and too subject to uncertainty of observation, to make it worth while to submit them to a more rigorous analysis, but the broad conclusion to which the present results irresistibly lead is that the same peculiar hereditary relation, that was shown to subsist between a man and each of his ancestors in respect to the quality of stature, also subsists in respect to that of eye-colour." (p. 153.)

No attempt will be made to discuss the data and calculations with respect to inheritance of artistic faculty and of disease.

Sufficient has been presented to show the mode of operation of Galton's mind in respect to the matter of inheritance. It suffices to say, that Galton's work constituted the first considerable attempt at an exact analysis of hereditary data upon a mathematical basis, during the pre-Mendelian period. The fact that his data do not constitute a genetic analysis, but a statistical statement of the general result in respect to populations, does not detract from their absolute value, or from their correctness from the standpoint of the operation of the law of averages upon populations, where the data for several generations are properly grouped and classified as a whole.

In 1897 (2b) Galton contributed to the Proceedings of the Royal Society (Vol. 61, pp. 401-13, June 3, 1897), a brief memoir constituting the continuation of his investigation upon the law of ancestral inheritance reported in his "Natural Inheritance" of 1869, the material from which the memoir was derived being the pedigree records of the well-known Basset hounds of Sir Everett Millais. The paper in question is entitled, "The average contribution of each several ancestor to the total heritage of the offspring."

In this contribution Galton remarks that the truth of the statistical law of heredity, which had been stated "briefly and with hesitation" in his "Natural Inheritance," because "it was then unsupported by sufficient evidence," having been now found to hold for a particular case, there are, as he says, "strong grounds for believing it to be a general law of heredity." (p. 401). Galton at first in this connection, began "a somewhat extensive series of experiments with moths," which, however, failed owing to the diminishing fertility of successive broods, and the disturbing effects of differences in food and environment. Consequently, as he says, "no statistical results of any consistency or value could be obtained from them." (p. 402.) While engaged in planning another extensive experiment with small, fast-breeding mammals, Galton

> ". . . became acquainted with the existence of a long series of records, preserved by Sir Everett Millais, of the colours during many successive generations of a large pedigree stock of Basset hounds, that he originated some twenty years ago, having purchased ninety-three of them on the continent for the purpose. These records afford the foundation upon which this memoir rests." (p. 402.)

The "law," as briefly stated is,

> ". . . that the two parents contribute between them on the average, one-half or (0.5) of the total heritage of the offspring; the four grandparents, one-quarter or $(0.5)^2$, the eight great-grandparents one-eighth or $(0.5)^3$, etc., which being equal to 1, accounts for the whole heritage." (p. 402.)
>
> "The same statement may be put into a different form, in which a parent, grandparent, etc., is spoken of without reference to sex, by saying that each parent contributes on an average, one-quarter or $(0.5)^2$, each grandparent one-sixteenth or $(0.5)^4$, and so on, and that generally the occupier of each ancestral place in the *n*th degree, whatever be the value of n, contributes $(0.5)^{2n}$ of the heritage." (p. 402.)

Galton refers to sex-limited inheritance, although not precisely in the manner now current, in the following statement:

> "The neglect of individual prepotencies is justified in a law that avowedly relates to average results; they must, of course, be taken into account when applying the general law to individual cases. No difficulty arises in dealing with characters that are limited by sex, when their equivalents in the opposite sex are known, for instance in the statures of men and women." (p. 402.)

That Galton undertook in a way to conceive of the genotype as the object of his research, is shown by the following statement:

> "It should be noted that nothing in this statistical law contradicts the generally accepted view that the chief, if not the sole, line of descent runs from germ to germ and not from person to person. The person may be accepted on the whole as a fair representative of the germ, and, that being so, the statistical laws which apply to the persons would apply to the germs also, though with less precision in individual cases." (p. 403.)

As an *a priori* argument for reasonableness of the law, Galton says:

> ". . . there is such a thing as an average contribution appropriate to each ancestral place, which admits of statistical valuation, however minute it may be. It is also well known that the more distant stages of ancestry contribute considerably less than the nearer ones. Further, it is reasonable to believe that the contributions of parents to children are in the same proportion as those of the grandparents to the parents, of the great-grandparents to the grandparents, and so on; in short, that their total amount is to be expressed by the sum of the terms in an infinite geometric series diminishing to zero. Lastly, it is an essential condition that their total amount should be equal to 1, in order to account for the whole of the heritage. All these conditions are fulfilled by the series of $\frac{1}{2}$, $\frac{1}{2}^2$, $\frac{1}{2}^3$, etc., and by no other. These and the foregoing considerations were referred to when saying that the law might be inferred with considerable assurance *a priori*: consequently, being found true in the particular case about to be stated, there is good reason to accept the law in a general sense." (p. 403.)

As to the material of the investigation—the Basset hounds referred to—they were dwarf blood-hounds, showing but two color variations; one white with large blotches ranging between red and yellow, registered as "lemon and white"; another with the above coloration plus more or less black, called "tricolour." Galton says:

> "Tricolour is, in fact, the introduction of melanism, so I shall treat the colours simply as being 'tricolour' or 'non-tricolour'; more briefly as T or N. I am assured that transitional cases between T and N are very rare, and that experts would hardly ever disagree about the class to which any particular hound should be assigned." (p. 403.)

For his purposes, Galton made use of "The Basset Hound Club Rules and Stud Book," compiled by Sir Everett Millais, comprising the pedigree records of the hounds in question from 1874 to 1896, and containing the names of nearly 1,000 animals.

Out of these, Galton obtained a series of 817 hounds of known color, descended from parents of known color. In 567 cases out of the 817, the colors of all four of the grandparents were also known.

> "The upshot is," he says, "that I have had the good fortune to discuss a total of 817 hounds of known colour, all descended from parents of known colour. In 567 out of the 817, the colours of all four of the grandparents are also known; in 188 of the latter, in turn, the colours of all eight great-grandparents were also known." (p. 404.)

Galton's remarks with reference to his effort to find a rule that would apply with respect to what might be presumed to be sex-linked inheritance, or as it was then called sex-prepotency, are interesting as showing the manner in which it was possible to arrive at conclusions upon this point by means of the statistical method.

> "Our first inquiry then must be, 'is or is not one sex so markedly prepotent over the other in transmitting colour, that a disregard of sex would introduce statistical error?' In answering this, we should bear in mind a common experience, that statistical questions relating to sex are very difficult to deal with." Large and unknown disturbing causes appear often to exist, that make data that are commonly homogeneous very heterogeneous in reality. "Some of these are undoubtedly present here, especially such as may be due to individual prepotencies combined with close interbreeding. . . ."

The results were derived from two classes of data; one, derived from individuals of which all the grandparents were known, amounting to 567 individuals; the other, of which all the grandparents were not known, amounting to 250 individuals. These data, as Galton states,

> ". . . will be seen to disagree widely, concurring only in showing that the dam is prepotent over the sire in transmitting colour."

Taking the data from the two respective classes separately, the former, called the "A" data, gave relative prepotency as 58 : 51, or 114 : 100. The second set, or the "B" data, gave a relative ratio of prepotency as 47 : 32 or 147 : 100. Taken together, the data give a combined ratio of 54 : 45 or of 120:100, i.e., as 6 is to 5. (pp. 404-5.)

It was found that a certain amount of preferential activity took place, exhibited by the tendency to use tricolors as sires, so that reciprocal matings were not equally numerous. "Still," Galton remarks, "on the application of a general test, the error feared is too insignificant to be observed." (p. 405.)

It is interesting to note that Galton endeavors by means of his statistical method to arrive at a conclusion concerning what he termed sex-prepotency, and that he recognized the fact that some single character, color in this case, might operate in a special manner in the inheritance.

Galton's manner of calculating the influence of the tricolor factor is interesting. He found from the data that 79 per cent of the parents of tricolor hounds were tricolor also, and that 56 per cent of the parents of non-tricolor hounds were tricolor. Supposing all the four grandparents, A_2, to be tricolor, then only 0.79 per cent of A_3 will be tricolor also; $(0.79)^2$ of A_4 and so on. The several degrees of ancestry will respectively contribute an average of tricolor to each a_0, amounting to $(0.5)^3 \times (0.79) + (1 + (0.5) \times (0.79) + (0.5)^2 \times (0.79)^2 + \text{etc.}) = 0.1632$. His conclusion therefore is that the average tricolor contribution from the ancestry of *each* of the four tricolor grandparents will be equal to one-fourth of this, viz., 0.0408.

Similarly, the average tricolor contribution from the ancestry of each *non-tricolor* grandparent is found to be 0.0243. When the furthest generation known is that of the great-grandparents, the formula differs from the preceding only by substituting $(0.5)^4 \times (0.79)$ for $(0.5)^3 \times (0.79)$. Thus the average tricolor contribution from the total of the eight tricolor great-grandparents is found to be 0.0816, and the contribution from each of them 0.0102. Similarly the contribution from each non-tricolor great-grandparent is found to be 0.0061.

On the same basis of these calculations, and taking the number of tricolors in the parents in the classes of 2, 1, and 0, respectively, and the number of tricolors in the grandparents as 4, 3, 2, and 1, respectively, Galton was able to calculate coefficients for tricolor occurrence in the offspring. Thus, taking the case of tricolor in both the parents, combined with tricolors in 4, 3, 2, and 1 of the grandparents, respectively, the multiplying coefficients are found to be as follows: 0.91, 0.83, 0.76, and 0.68. Multiplying the number of cases, 119, 119, 28, and 11 in the four categories, by the four respective coefficients, gives the calculated numbers of the tricolor offspring as 108, 99, 21, and 8, respectively. How closely this calculation fitted the actual cases, is proved by the fact that the observed tricolor cases in the offspring in question, for the four categories of 4, 3, 2, and 1 tricolor grandparents with both parents tricolor, was 106, 101, 24, and 8, respectively. The correspondence between the calculated result and the observed numbers, in the case where one parent only was tricolor, and where neither was tricolor, was equally close. The calculations made in a similar manner, where the number of tricolors in the great-grandparents was 8, 7, 6, 5, and 4, respectively; in the grandparents, 4, 3, and 2, respectively, and in the parents 2 and 1, respectively, showed an equally remarkable close correspondence between the calculated results and the observed facts.

For example, where the tricolors in the great-grandparents were, 7, 6, 5, and 4, respectively, the number of tricolors in grandparents 3, and the number in the parents 2, the relation between the calculated and the observed facts in the four cases was found to be 16:17, 18:19, 13:14, and 5:6, respectively. The summary of all cases gave the relation of calculated to observed tricolor in the offspring as 180:181.

It would thus appear that the contribution of the immediate ancestors to the color-inheritance, theoretically and experimentally, would be as follows:

Parents	each	0.2500
Grandparents (tricolor, calculated)	each	0.0625
Grandparents (tricolor, experimental)	each	0.0408
Grandparents (non-tricolor, experimental)	each	0.0243

Using these particular coefficients as components of value, Galton constructed a general coefficient to express each set of combinations of tricolor and non-tricolor, found in the hounds' ancestry. The cases are as follows, using "T" for tricolor and "N" for non-tricolor.

The letters represent all possible combinations of tricolor "T," and non-tricolor "N," according as they occur in the different cases, each pair of letters representing a pair of grandparents, paternal and maternal.

Case I

TT-TT

Here all four of the grandparents of the tricolor animals were tricolor also. The condition of the ancestry then, in terms of the partial values of the ancestor's contribution is:

2 parents	each	0.2500	0.5000
4 grandparents (tricolor, calculated)	each	0.0625	0.2500
4 grandparents (tricolor, experimental)	each	0.0408	0.1632
			0.9132

Case II

TT.TN TN.TT TT.NT NT.TT

2 parents	each	0.2500	0.5000
3 grandparents (tricolor, calculated)	each	0.0625	0.1875
3 grandparents (tricolor, experimental)	each	0.0408	0.1224
1 grandparent (non-tricolor, experimental)	each	0.0243	0.0243
			0.8342

Case III

TN.TN TT.NN TN.NT NT.TN NN.TT NT.NT

2 parents	each	0.2500	0.2000
2 grandparents (tricolor, calculated)	each	0.0625	0.1250
2 grandparents (tricolor, experimental)	each	0.0408	0.0816
2 grandparents (non-tricolor, experimental)	each	0.0243	0.0486
			0.7552

Case IV

TN.NN NN.TN NT.NN NN.NT

2 parents	each	0.2500	0.5000
1 grandparent (tricolor, calculated)	each	0.0625	0.0625
1 grandparent (tricolor, experimental)	each	0.0408	0.0408
3 grandparents (non-tricolor, experimental)	each	0.0243	0.0729
			0.6761

Thus, taking the total number of tricolor cases up to the second descending generation, and multiplying by the respective coefficients of each, the relation of the total sum number of tricolor offspring calculated, to those observed, was as 391:387. The data are given in detail in the following table, somewhat rearranged from Galton. In each instance, the coefficient, multiplied by the number of cases, gives the theoretical or calculated number of tricolor animals out of the total (the underscored number). Beneath the figure of each case, is given the actual observed number of tricolors.

NO. OF TRICOLORS IN PARENTS		NO. OF TRICOLORS IN GRANDPARENTS				TOTAL TRICOLOR OFFSPRING	
		4	3	2	1		
		CASE I	CASE II	CASE III	CASE IV	CAL.	OBS.
2	No. of cases	119	119	28	11		
	Coefficient	0.91	0.83	0.76	0.68		
	Tricolor (cal.)	108	99	21	8		
	Tricolor (observed)	106	101	24	8	236	239
1	No. of cases	37	158	60	6		
	Coefficient	0.66	0.58	0.51	0.43		
	Tricolor (cal.)	24	92	30	3		
	Tricolor (observed)	20	79	36	4	149	139
0	No. of cases			18	6		
	Coefficient			0.26	0.18		
	Tricolor (cal.)			5	1		
	Tricolor (observed)			7	2		
						6	9
						391	387

In like manner, where the pedigree reached up to the *third* ascending generation, the total number of tricolor cases in the offspring calculated, to those observed, was as 180 to 181. Thus in both instances there was an almost perfect coincidence of the observed data with the mathematical law.

Galton did not rest content with the obtained results:

> "In order to satisfy myself," he says, "that the correspondence between calculated and observed values was a sharp test of the correctness of the coefficients, I made many experiments by altering them slightly, and re-calculating. In every case there was a notable diminution in the accuracy of the results. The test that the theory has successfully undergone appeared on that account to be even more searching and severe than I had anticipated." (p. 408.)

Galton was thus able to demonstrate the possibility of calculating, on a statistical basis, the probable number of offspring in a given case of color-inheritance, in a manner that satisfied the requirements of a statistical law of descent. The fact that Galton's constituted the only attempt during the pre-Mendelian period, to arrive at a fully exact and quantitative scientific method of attacking the question of inheritance, renders it noteworthy, even although the method is statistical rather than genetic in character.

Galton well sums up his views in words that are probably little widely known, but that should be read, in order to realize that the author of "Galton's Law" was not a mere mathematical machine, but a man of broad humanistic as well as utilitarian views.

> "It is hardly necessary to insist on the importance of possessing a correct law of heredity. Vast sums of money are spent in rearing pedigree stock of the most varied kinds, as horses, cattle, sheep, pigs, dogs, and other animals, besides flowers and fruits. The current views of the breeders and horticulturists on heredity are contradictory in important respects, and therefore *must* be more or less erroneous. Certainly no popular view at all resembles that which is justified by the present memoir. A correct law of heredity would also be of service in discussing actuarial problems relating to hereditary longevity and disease, and it might throw light on many questions connected with the theory of evolution."

As Goldschmidt says:

> "Of course the significance of a biological law disappears for the law of ancestral heredity. All that it shows is that it can be taken as a statistical consequence of Mendelian number-ratios when, in a mixed population, the members of which propagate among themselves, average values are regarded." (2, p. 62.)

Galton's Law has been thus fully treated because of its fundamental character as a law of evolution, describing the average trend of circumstances when a large number of individuals are taken together without reference to sex. It is an expression of the law of bodily appearances, and only pretends to describe the condition in the germ cells, as Galton himself observes, insofar as the bodily characteristics are the outward expression of an internal germinal condition, which Galton assumed, reasoning reversely, must be the case, else why should there be an average inheritance of the color-characters of the nature described. However, Galton's expectation that his discovery might be available for practical breeding purposes has not been entirely justified. It has indeed proved the value of pedigree records for live stock, and the general truth of the axiom that "like begets like." In a word, in the light of our present understanding, "Galton's Law" is largely an average mathematical expression for the operation of the law of dominance. It is the most important effort, however, during what may be called the "Darwinian period," at obtaining an exact statistical expression of the law of inheritance in populations.

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CHAPTER IX

31. *Miscellaneous Investigations on the Histological Structure of Hybrids*

THE contributions here under consideration, of Macfarlane, Henslow, Wilson, and Darbishire, are devoted largely to the study of the details of the histological characters of a considerable number of plants and of their hybrids in the first generation. Although the work of the last-named investigator came after the rediscovery of Mendel, the work of Darbishire on peas is included because of the interest attaching to work with this plant, and its relation to the general subject of Mendelism.

a. *Henslow.*

The paper of J. S. Henslow (5), "On the Examination of a hybrid Digitalis," read November 14, 1831, and published in the Transactions of the Cambridge Philosophical Society, 4:257-78 (1833), while minor in extent, was perhaps the first paper on hybrids, since the publications of Sageret, which attempted to deal with characters of the hybrid and of its parents from the comparative standpoint, and, to some extent, in terms of measurement. It is certainly the first paper of the sort to appear in English.

Henslow, while Professor of Botany at Cambridge University, states that:

> "Chance having favored me with a hybrid Digitalis during the past summer [1831], in my own garden, I employed myself, whilst it continued to flower, which was from June 19 to July 22, in daily examining its character, and anatomizing its parts of fructification. I was careful to compare my observations, with as much patience and accuracy as I can command, with the structure of its two parents. It seemed to me not unlikely that something interesting might result from a rigorous examination of this kind, or at least that its recorded details might serve as a point of departure for future observations." (p. 257.)

The plant, according to Henslow (5), was a natural garden cross between *Digitalis lutea* and *D. purpurea.* The seeds of each

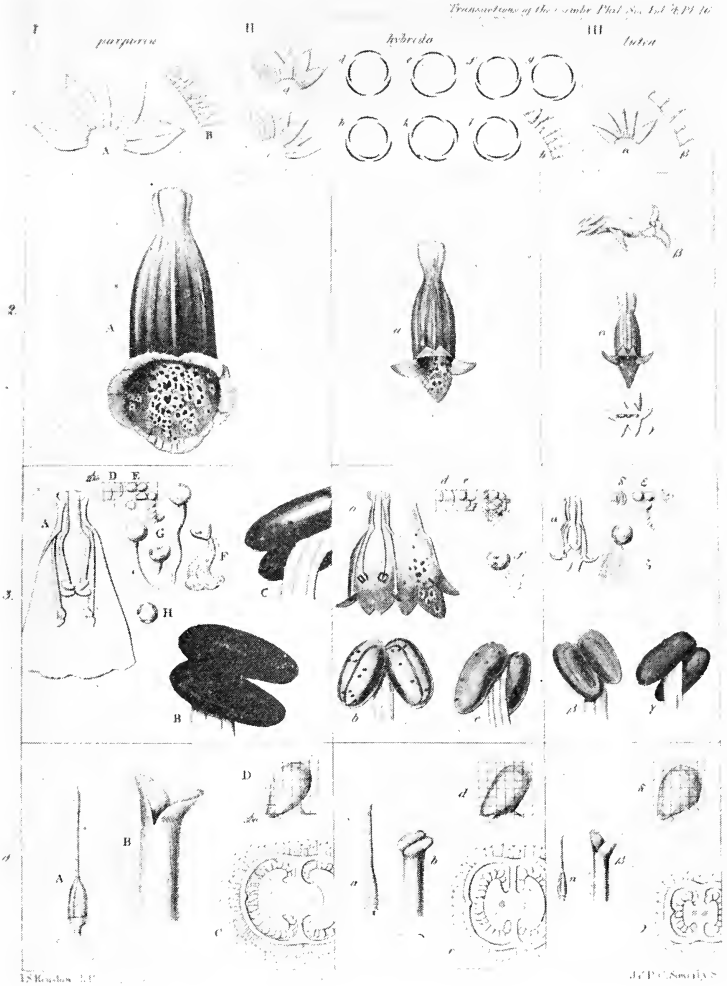

PLATE XLI. *Digitalis lutea* x *purpurea*: flowering organs and tissues of parents and F_1 hybrid, by J. S. Henslow.

had been allowed to scatter, and the seedlings to grow wherever they chanced to appear.

> "I had already," he says, "remarked a singularity in the general appearance of one of these, and was watching the expansion of its flowers, when I was agreeably surprised to find it a decided hybrid, obviously having most of its characters exactly intermediate between those of *purpurea* and *lutea.* [p. 258.] . . . My plant exactly agrees in most particulars with a hybrid procured by Kölreuter in 1768, from seeds of *lutea* fertilized by the pollen of *purpurea.* (Acad. Petropol. Anno. 1777.)"

In general habit, Henslow's hybrid is stated to have approached "much nearer *lutea* than *purpurea.*" (p. 258.)

> "It is, however," he continues, "decidedly taller and more robust than any specimens of the former species which my garden ever produced. Kölreuter indeed asserts that the specimens raised by him were taller than either of their parents, but he assigns a lower limit to the height of *purpurea* than that to which many plants of this species have attained with me."

On p. 258, Henslow gives an analysis of twenty-five characters in root, stem, leaf, inflorescence, flower, stamens, and pistil, with illustrative plates.

> "A single glance of the eye," he says, "will thus be sufficient to show how totally intermediate most of its organs are, both in size and form, and in some cases also in colour, to those of the two parents." (p. 259.)

Attempts to fertilize the hybrid with its own pollen, as well as with pollen of the two parents, failed, and the comment is made that Kölreuter was similarly unsuccessful in his case. Some discussion is given as to whether hybrids are self-fertile or not. The paper merits mention by reason of the fact that, if not the first, it is one of the first attempts to present, in systematic detailed form, a comparative study, in part microscopic, of the structures in a hybrid and its two parents. A satisfactory scale is not given. A few of the principal characters noted are given in the following table:

External Characters

	D. purpurea	*D. lutea*	*Hybrid lutea × purpurea*
Root	Biennial	Bi-triennial	Apparently perennial
Height of stem	3 to 5 ft.	2 ft.	About 3½ ft.
Length of raceme	1½ in. to 3 ft.	¾ to 1¼ ft.	About 1½ ft.
Leaves	Woolly	Glabrous	Nearly smooth above, quite woolly below

	D. purpurea	*D. lutea*	*Hybrid lutea × purpurea*
Flowers	Large, cernuous	Small, more drooping	Medium size, nearly horizontal
Corolla	Purple	Yellow	Yellow ground, tinted with red
Spots on corolla	Numerous, deep purple	No spots	A few dark purplish red spots
Anthers	Deeper orange-yellow, with numerous spots, often confluent	Lighter yellow, no spots	Yellow, inclining to orange, with a few small, scattered purplish red spots

b. *Marfarlane.*

In the 90's of the last century, J. M. Macfarlane (6) published considerable work based upon a histological study of the characters of hybrids and of their parents, which did much to throw light upon the ultimate character of the hybrid condition in the F_1 generation. As the result of these investigations upon the histological details of many hybrids and of their parents, Macfarlane was able to take a much more exact point of view regarding the structural characters in hybrids than most of his contemporaries, one indeed for which few data then existed, and in which investigation seems not to have been continued until the post-Mendelian work of Darbishire (1), on the structure of the starch grains in crosses of peas.

Macfarlane's work was first presented at the meeting of the Edinburgh Botanical Society, March 1890, the first published contribution being an article in the Gardeners' Chronicle for May 3 (6a). In this article he says:

> "During the last few years I have studied minutely the general and microscopic structure of pitchered and insectivorous plants. At an early stage in my investigations, I was struck by the perfect blendings in certain well-known hybrids of the appearance presented by their parents, and this, not merely in habit, consistence, shape and color, but even in such minute details as the relative number of stomata in a given area, the size and shape of the cell hairs, and of the cells from which these sprung, and the mode of disposition of thickening substance on their primary cell wall." (p. 543.)

A series of seventeen hybrid *Sarracenias* formed the first principal material. It is stated:

> "As one after another of these was passed under the microscope, I was gradually inclined to believe that a hybrid plant may exhibit blending

of parent peculiarities in every cell. This was easily demonstrated in the case of epidermal tissues, which are apparently the most plastic of all." (p. 543.)

Being unwilling to rest upon conclusions derived from such highly specialized forms, he examined other known hybrids, belonging to various orders, including *Dianthus lindsayi*, *Philageria veitchii*, *Saxifraga andrewsii* and *churchillii*, and *Hedychium sadlerianum*. "These," he says, "not only verified my previous conclusions, but enabled me to extend them in a convincing way." (p. 544.)

It is interesting to note certain characters among those investigated by Macfarlane, in evidence of his conclusions on the intermediacy of hybrids. In the case of *Dianthus lindsayi*, a cross between *Dianthus barbatus* and *Dianthus alpinus*, the former parent has 900 stomata on the lower, and 100-400 on the upper epidermis; the latter, 600 on the lower, and 460 on the upper epidermis. The hybrid has 750 stomata on the lower, and 290 on the upper surface. The epidermal cells of the hybrid were also found to be intermediate. In the rhizome of the cross between *Hedychium coronarium* and *H. gardnerianum*, it was found, that while the starch granules of the former were large, flat, oval plates, and those of the latter small triangular shells, those of the hybrid were shaped as though half of the granule in *H. coronarium* had been gradually fused with a reduced one of *H. gardnerianum*. Investigations of the starch grains in *H. coronarium* and *H. elatum* gave similar results. In the orchid-hybrid known as *Masdevallia chelsoni*, compared with one of its parents, some investigations were made on the inheritance of flower color. This hybrid has purplish-red sepals, the color effect being the combined result of large yellow chromoplasts in the epidermal cells, and epidermal hairs filled with purple pigment. In *M. chelsoni* the size of the chromoplasts was found to be from one-third to one-half the size of those found in the parent examined. In *Bryanthus erectus*, a bigeneric hybrid of the Ericaceae (a cross between *Rhododendron chamaecistus* and *Menziesia empetriformis* var. *Drummondii*), in the relative size of the pith cells; in the structure of the phloem; in the shape and disposition of the leaf cells in transverse section; and in the structure of the floral parts, the hybrid was found to be intermediate between the parents.

In *Erica watsoni*, a natural hybrid between *E. ciliaris* and *E. tetralix*, the hybrid was found to be very evenly balanced. Details are given of the anthers only. (p. 544.) In a cross between *Rhododendron ciliatum* and *R. edgeworthii*, the hybrid is said greatly to resemble the former parent, and scarcely at all the latter in its gross morphology. In the histological details of leaf structure, however, "the minute features of both parents were strongly traceable in the hybrid." (p. 544.)

In a cross between *Cypripedium insigne* and *C. villosum*, the number of the stomata was found to be as follows, for the magnification used:

C. insigne	11-12
C. villosum	21-23
Hybrid	16-17

In a cross between *Cypripedium barbatum* and *C. insigne*, the relationship was as follows, in respect to the distribution of the stomata:

C. barbatum	3-4	
C. insigne	11-12	
C. ashburtonae (hybrid)	6-7	(p. 544.)

In a rather brief contribution to the Gardeners' Chronicle for June 20, 1891 (6c), the matter of color, flowering period, and constitutional vigor of hybrids is discussed. The article in question seems to have been contributed in view of Henslow's paper before the Royal Horticultural Society, May 12, 1891, and reviewed in the Gardeners' Chronicle for May 16, on color inheritance in "greenhouse Rhododendrons." Macfarlane holds that the evidence from Henslow's examination, to the effect that color-inheritance was more or less a variable matter, should probably be modified. His statement is interesting, in that it shows an approach of mind toward a stricter scientific use of the materials in crossing. He remarks:

> "I feel that it will eventually be possible, in the great majority of cases, to predict the exact color which the hybrid will show, especially if the color in each parent be due to the presence of one pigment only" (6c); the examples chosen by Henslow being complicated by the frequent presence of two pigments, a dissolved red and a granular yellow, in at least one of the parents.
>
> "If we compare parents which each develop one pigment, or one of which only is white, i.e., devoid of colour, it may be laid down as a broad general rule, that the hybrid will be intermediate between the two, having regard to the size of the floral parts of each."

Macfarlane then cites four cases of *Rhododendron* crosses which are color-intermediates between their parents, as follows:

Rhododendron atrovirens	purple-crimson
" *ciliatum*	pink-white
" *praecox* (hybrid)	intermediate
" *arboreum*	scarlet
" *caucasicum*	white
" *nobleanum* (hybrid)	cerise
" *ciliatum*	pink-white
" *glaucum*	dull-pink
" *grievei* (hybrid)	pale whitish-pink
" *chamaecistus*	pale pink
Menziesia empetriformis, var. *drummondii*	rose-pink
Bryanthus erectus (hybrid)	intermediate

This intermediacy of flower color in hybrids Macfarlane considered to be best exemplified by cases where yellow is involved, due to the presence of yellow chromoplasts in the cells. The case of hybrid Oxlips, crosses between Primrose and Cowslip, are cited, as also cases of hybrid *Hedychiums* (fam. Zingiberaceae), as follows:

	Hedychium gardnerianum	orange
×	*Hedychium coronarium*	white
gave	*Hedychium sadlerianum* (hybrid)	intermediate
	and	
	Hedychium sadlerianum	
×	*Hedychium coronarium*	
gave	*Hedychium lindsayi*	pale, maize-white in bud, becoming white in blossom

In cases where yellow, red or blue occur in the same or neighboring cells of a tissue, "the hybrid product may take after one or the other of the parents in an apparently arbitrary way." As to a possible theoretical explanation, Macfarlane says:

> "Suffice it to say that I regard many of the unequal blendings in hybrid colour and structure to be due to incompatibility in chemical or molecular union, and the resulting predominance of that colour which is the more stable or readily evolved of the two." (6c.)

A brief note is given upon inheritance of time of flowering. From the time of flowering of numerous species, and of hybrids, at the Edinburgh Botanic Garden, including a record since 1889, of 800 plants in the rock garden, including also several hybrids and their parents, it is concluded that:

> "These, supplemented by limited observations of my own, all point distinctly to a flowering period in hybrids closely intermediate between the parents." (6c.)

On the matter of the constitutional vigor of hybrids, the case is cited of *Montbretia crocosmaeflora*, a hybrid between *Montbretia pottsii* and *Tritonia aurea*.[1]

During the winter of 1890-91 the corms of *M. pottsii* were scarcely injured; those of *Tritonia aurea* only survived where planted against the outer side of a hothouse. The corms of the hybrid survived to the extent of 60 per cent.

In 1892, Macfarlane published the final results of his studies on the microscopic structure of hybrids, in the Transactions of the Royal Society of Edinburgh. (6e.)

This memoir was published as the conclusion of a series of studies of the microscopic structure of upwards of sixty hybrids, in comparison with that of their parents. The details are given with respect to nine hybrids and their parents, as follows:

Philageria veitchii (*Lapageria rosea* × *Philesia buxifolia*) (species from southern Chile)
Dianthus grievei (*D. alpinus* × *D. barbatus*)
Geum intermedium (*G. rivale* × *G. urbanum*)
Ribes culverwellii (*R. grossularia* × *R. nigrum*)
Saxifraga andrewsii (*S. aizoon* × *S. geum*)
Erica watsoni (*E. ciliaris* × *E. tetralix*)
Bryanthus erectus (*Menziesia empetriformis, var. drummondii* × *Rhododendron Chamaecistus*)
Masdevallia chelsoni (*M. amabilis* × *M. veitchiana*)
Cypripedium leeanum (*C. insigne* × *C. spicerianum*)

In addition, he says, "about sixty-five hybrids and their parents have been examined in some of their parts," to which partial reference is made as to special particulars. An elaborate study is also given of the well-known graft-hybrid *Cytisus adami*, the accidental result of a case of the budding of *Cytisus purpureus* upon the stock of *Cytisus laburnum* (*Laburnum vulgare*), a type for which no equivalent sexual hybrid exists, all attempts to cross the two species sexually having failed. *Cytisus purpureus* is a low, creeping, and *C. laburnum* an upright shrub. *C. purpureus* grows, when grafted upon *C. laburnum*, as well as, or better than upon its own roots. Thousands of grafted plants give only normal, upright-growing forms of *purpureus*. In M. Adam's

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[1] *Montbretia* is a synonym of *Tritonia*, a group of thirty South African bulbous plants of the Iridaceae, belonging to the Gladioleae, of the sub.-fam. Ixiodeae.

particular case, originating in 1829, the shoot arising from the bud was manifestly a vegetative hybrid in its characters, and has since been multiplied, and introduced into botanical gardens and elsewhere. For a long time, until the experiments of H. Winkler (1907-10) on "graft-hybrids" (chimaeras), *Cytisus adami* was almost the sole type-representative of the class. Macfarlane devotes eleven pages to the discussion of the anatomical details of the plant and its stock-scion parentage.

No summary of the whole of Macfarlane's investigation can be given, except to state that in general the hybrid forms studied gave almost complete intermediacy in most of the principal details of structure. The case of *Philageria veitchii*, produced in the nurseries of Messrs. Veitch at Exeter, was first described fully in its gross morphological characters by Dr. M. T. Masters in the Gardeners' Chronicle for 1872. The two parents differ widely in habit, *Lapageria rosea* being a twining plant, 25 to 30 ft. in length, inhabiting the forests along the lower levels of the Andes, from Valdivia to Concepcion; *Philesia buxifolia* being a "low-growing, dense, tufted shrub, attaining a height of ten to fifteen inches," inhabiting "the swampy, unproductive wind and rain-swept region extending from Chile southwards to Tierra del Fuego." The hybrid, which is called a "scrambling shrub," is described by Masters as being in habit more nearly akin to the female parent (*Lapageria*); the foliage intermediate, but nearest like *Philesia;* flower stalk, calyx and corolla more like *Philesia;* stamens and pistil resembling more the *Lapageria* parent.

The anatomical characters of the hybrid and of its parents may be briefly summarized from Macfarlane's details as follows: (Diameters in μ.)

LAPAGERIA	PHILESIA	PHILAGERIA (F_1 HYBRID)
	Outer cortex cells	
60	20	32-35
	Inner cortex cells (av.)	
100-120	45-50	70-75
	Bundle-sheath cells	
48-50 (radially) 35-40 (tangentially)	18-20 (isodiametric)	35 (radially) 20-22 (tangentially)
	Cells of stem *Epidermal cells*	
100x30x25	80x30x35	60x30x40

	Vascular bundle cells	
	Xylem	
180-200	250	400
	Phloem (sieve-tubes)	
20-25	25-28	40-45
	Phloem (companion cells)	
5-8	7-9	8-10
	Cells of leaf palisade layer	
2 layers	2-3 layers	3-4 layers
110x30 (upper)	70—80x35 (upper)	35x35
75x35 (lower)	50—60x35 (second)	
	Median vascular bundle of petiole	
37-40	30-32	20

The structural details of cells from *Cytisus adami* and its stock-graft parents are as follows:

CYTISUS LABURNUM (STOCK)	CYTISUS ADAMI (GRAFT-HYBRID)	CYTISUS PURPUREUS (SCION)
	Cortex	
13-15 layers	13-15 layers	7-10 thin-walled layers
sclerenchyma cells, none	sclerenchyma cells, none	5 longitudinal masses of sclerenchyma cells
	Leaf	
epidermis covered with spindle-shaped hairs	epidermis, glabrous	epidermis, glabrous
	Vascular bundle of petiole	
	Phloem (sieve-tubes)	
6	4-4.5	3-4
	Xylem (tracheids)	
20	14-15	8
	Epidermis (stomata in field) (× 400)	
0 (upper)	12-14 (upper)	27-30 (upper)
40 (lower)	17-20 (lower)	30 (lower)
	Flower, *Petals.* *Standard.*	
glabrous	marginal fringe of 60-65 hairs	marginal fringe of 125-130 hairs
	Wings	
glabrous	marginal fringe of (av.) 90 hairs	marginal fringe of 160-170 hairs
	Keel	
glabrous	marginal fringe of 48-50 hairs	marginal fringe of 100-110 hairs
	Stamens	
	Pollen-cells (diam.)	
21-23 μ	23-25 μ	25-26 μ

Further details from Macfarlane's rather exhaustive anatomical studies cannot be given, but the above will suffice to show the manner of the investigations, and the general type of the results.

Some general conclusions which Macfarlane derives are interesting. In e.g., the production of epidermal hairs, it is stated:

> "If the parents possess one or more kinds that are fundamentally similar, but which differ in size, number and position, the hybrid reproduces them in an intermediate way. . . . If the hairs of two parents are pretty dissimilar, instead of a blending of these in one, the hybrid reproduces each, though reduced in size and number by half." (p. 270 6e.)
>
> "The distribution of stomata over any epidermal area has been proved to be a mean between the extremes of the parents, if the stomata of the parents occur over one surface or both, and if the leaves are similar in consistence, but . . . if the stomatic distribution and leaf consistence differ in the parents, this may give rise to correspondingly different results in the hybrid." (*ib.*, p. 271.)
>
> ". . . every hybrid has yielded a large series of examples which prove the size, outline, amount of thickening, and localization and growth of cell walls, is, as a rule, intermediate between those of the parents." (*ib.*, p. 271.)

Interesting is the account of the laying down of secondary cell-wall thickenings, which, whether of a cuticularized, lignified, or colloid nature, in the hybrid constitute a mean in amount and mode of deposition between the extremes of the two parents. The most striking illustration is that of the bundle-sheath cells of *Philageria* and its parents, where 5 lignified cell-lamellae are found in *Lapageria*, 11-12 in *Philesia*, and 8-9 in *Philageria*.

In leaves of the same age and like position, the chloroplasts, in depth of color and size, are found to be intermediate in the hybrid. (*Saxifraga*, *ib.*, p. 272.)

As the result of his histological investigations, Macfarlane came to the conclusion that the male and female elements in the fertilization, act complementarily to a degree amounting to half, for each of the two sexes, in the fertilization product. The principal comment is as follows:

> "No matter what tissue or set of tissues is chosen, if the cells composing such are tolerably diverse in the parents, one can trace with ease the modifying action which both sex elements have had on them, while these clearly prove that each sex element, after union with its complementary element, represents potentially half its former individuality, or retains half its former hereditary properties." (*ib.*, p. 273.)

Macfarlane uses the term "unisexual heredity" to designate the cases in which

> ". . . structures found only in one parent, and with no corresponding counterpart in the other, are handed down, though reduced by half." (*ib.*, p. 273.)

In this connection he makes a rather interesting comment:

> "Now it has been repeatedly noticed that when a species varies from the normal, it seldom does so in only one point or structural detail, but a certain variation-wave, so to speak travels through the entire organism, giving it that combined set of characters which make it rank as a subspecies." (*ib.*, p. 274.)

As what he terms "bisexual heredity," Macfarlane designates such cases as *Ribes culverwellii*,

> ". . . in which the simple hairs of *R. grossularia* and the oil-secreting peltate hairs of *R. nigrum* are both separately reproduced, though about half as large as those of the parents." (p. 274.)

The case of the similar inheritance of epidermal hairs in *Saxifraga* and *Carduus* hybrids is also cited. It is interesting to note that Macfarlane reports that he knows of no cases

> ". . . where internal elements or tissue-masses are thus separately reproduced" (p. 274), and he further notes that "all the hybrids in which the above has been observed are derived from parents considerably removed in systematic relationship, and the incompatibility of blending the diverse types of hairs probably explains their appearance as separate growths." (*ib.*, p. 274.)

He says further:

> "But the general principle here illustrated on an exaggerated scale is that the offspring of two parents may inherit from each diverse peculiarities which, instead of blending evenly, retain their separate individuality. Future experiment and observation alone will decide for us whether these can be passed down through two, three, or more generations, and till we have the evidence it would be impossible to generalize." (*ib.*, p. 274.)

A theoretical attempt at the resolution of the behavior of the characters in a hybrid into their factorial components is further enunciated:

> "If we view a fertilized egg of any plant, which is about to segment to form an embryo, as being not merely a chemically complex nucleated mass of protoplasm, but as a microcosm in which the orderly-arranged molecules of the conjugated male elements have so exactly fitted into and become united with corresponding molecules of the female element, that after conjugation, coordinated groups of molecules are set apart as stem-producers, root-producers, leaf-producers, and hair-producers, we will have done much to clear away obstacles. But physically there is

no reason why we may not assume that each cell of the future plant has representative molecules in the apparently simple egg." (*ib.*, p. 276.)

The general matter of fertility or sterility in the case of crosses is briefly epitomized in the following statement:

> "To sum up present-day experiences, it may be said that crosses between species that are nearly related in structure and habit can readily be effected, and the offspring may be largely fertile, at least among certain genera. Crosses between species that differ considerably in form, flower color, and habit, are more difficult to perform, and the hybrids are largely sterile, while crosses between such divergent species or genera as *Dianthus alpinus* and *barbatus*, *Saxifraga geum* and *Aizoon*, *Lapageria* and *Philesia* are almost wholly sterile." (*ib.*, p. 277.)

And again:

> "If we return now to hybrid production of the more extreme types, though in virtue of the attraction which exists between sexual elements, the original male and female cells from parents of different species—in the absence of cells from the same species—may be capable of uniting, and, in the process, of overcoming the repulsion due to dissimilar corelative molecules in each, when the attempt is made by all the hermaphrodite cells of the resulting hybrid organism to concentrate representative hermaphrodite groups of molecules, many cases will occur in which these will blend imperfectly, owing to difference in the composition and amount of chemical substances present, or interference and cancelling effects due to unequal propagation of waves of motion between the molecules. Thus many groups of molecules will break down or fail to reach their destination, so that gaps or vacancies will occur in the organic completeness of the pollen or egg cell. It will then have the shrivelled half-empty look so characteristic of hybrid sex-cells that are sterile. In hybrids from more nearly related species the interfering or cancelling effects will be reduced in proportion, and a larger number of sex cells will have a chance to mature." (*ib.*, p. 281.)

The last paper of Macfarlane's dealing with the histological details of plant hybrids, is entitled "Observations on some hybrids between *Drosera filiformis* and *D. intermedia*," published in 1899. (6g.)

The investigation was conducted upon a natural hybrid between the above species, discovered near Atco, New Jersey. A group of eleven plants was found, intermediate in form and color between the two above local species. These were removed to the greenhouses of the Botanical Garden of the University of Pennsylvania, where a histological examination was made of the two parent species and of the hybrid. The comment is made that

> "The phenomenon which the writer terms 'bisexual heredity' receives several striking exemplifications. Where two more or less diverse growths have occurred, one on either parent, these have been shown to be re-

produced, not in blended fashion, but as distinct structures reduced either in size or number or both." (p. 98.)

Following are the details of measurements in the parents and the first generation hybrid, for the principal characters studied.

Tissue			
Leaves	*D. filiformis*	*D. intermedia*	*Hybrid*
	8 in. long; 1/2 in. wide. Petiole, 3/8 in.-5 in. long, non-glandular	Av. 1 1/2 in. long. Blade 1/5 in. wide. Sharp difference between petiole and lamina. Base of the petiole has a quadrangular area also	Typical summer leaves may be 10-11 in. and greatly attenuated at tips, but average 3 1/2 in., of which 1/2 in. may be petiole. No basal quadrangular area: intermediate in size and shape
	Upper epidermal cells of this area average 250x38μ. Chloroplasts few, scattered and small; each 2.5 to 3μ diam. Stomata not present on this area	Upper epidermal cells of this area, 225x28μ, and contain a very few small chloroplasts	Upper epidermal cells, 188-200x32μ. Chloroplasts small and few
	Lower epidermis of this area has cells longer and narrower, 185x20μ, well filled with large chloroplasts, each 7.5-8μ across	Lower epidermis has elongated narrow cells, 200-225x15μ	Lower epidermal cells average 186-195x21μ and chloroplasts measure 2.5μ
Presence of stomata	A few stomata, each 40x23-25μ. 2-celled sessile glands of stoma-like character	No stomata, and instead of the 2-celled glands, there are glandular bifid hairs	Numerous 2-celled glands, and also bifid hairs, but of reduced size
2-celled glandular hairs	28x18μ, slightly elevated above surface	45-50μ high x 37μ across	33μ high x 32μ across

Stomata (lower surface)	36μ long x 24μ wide	26x25μ	32μ diam.
Chloroplasts of guard cells	20-22, and measure 2μ diam.	12-14, and measure 1.8μ diam.	15-17, and measure 2.5μ diam.
Tentacles	Pigment confined to the oval or elliptical head of each tentacle. Hair-stalk green	Pigment richest in the head-cells, but distributed in the cells of each stalk for 2/3 its length	Pigment less pronounced, and extends 1/3 to nearly 1/2 the length of the stalk
Head of tentacle	22x165μ	220x105μ	210x125μ
Stomata of lamina (upper epidermis)	40x30μ; 9 in an area. 300μ across	27x22μ; 7 in an area. 300μ across	34x25μ; 8 in an area. 300μ across
Axis of inflorescence	9 3/4 in.	5 1/2 in.	6 3/4 in.
Cortex	4-5 rows of thin-walled parenchyma cells, with abundant chloroplasts. 5-6 layers of sclerenchyma tissue	1-2 layers of parenchyma. 3-4 layers of slightly sclerenchyma tissue	2-3 layers of parenchyma cells. 4-5 layers of sclerenchyma tissue
No. of flowers in inflorescence	14	8	10
Size of flowers	7/8 in. across; purple and pink	1/4 in. across; pure white	3/8 in. across; faintly pink
Pollen grains	56μ diam.	44μ diam.	48-50μ diam.

Macfarlane deserves to be remembered, therefore, among those who have contributed to build up a substantial knowledge of the hybridization process, because of the exact character of his investigations, and his anticipation of the discoveries made only after the publication of Mendel's papers. His contribution, fundamentally speaking, may be summed up in his own words as follows:

> "From extended observations that the writer has made, alike on living plants, and on their minute tissues, he adheres to the view that an average hybrid is nearly intermediate between the parents." (6f.) And that:
>
> "Every cell of a plant inherits the peculiarities of both parents, at times in a perfectly balanced way, so far as our limited powers of study can carry us, at times with an evident leaning or bias to one parent." (6a.)

c. *Wilson.*

In a paper entitled "The structure of certain new hybrids (*Passiflora*, *Albuca*, *Ribes*, *Begonia*, *etc.*)," John H. Wilson reported, to the meeting of the Hybrid Conference in London in 1899, the following data regarding the structural character of hybrids in species of the above genera. Inasmuch as this constitutes another one of the few pre-Mendelian attempts at the measurement of the characters involved in hybridization, the results are given in some of the principal cases, as follows:

Passiflora buonapartea × *P. coerulea*

Branches	♀ Stout, tetragonal-winged, light green	♂ Almost cylindrical; 5-6 well defined angles; glaucous-green with reddish purple	F_1 *hybrid*, Stouter than the ♀ and more angular; about 5 angles. Much purple coloration.
Leaf-blades	Large, ovate-cordate, somewhat acuminate; dorsal, dark green; ventral, lighter green; 8 5/8 in. long; 7 1/4 in. broad; entire	5-, often 7-lobed, by branching of the two lower lobes; occasionally 3-lobed; dorsal, deep green; ventral, glaucous. Minute marginal glands at leaf notches, near base of lobes; 5 in. long; 7 3/8 in. broad	Invariably 3-lobed, 7 1/2 in. long, 10 3/4 in. wide at tips of lobes. Average length, 5 1/4 in. x 7 1/2 in.

Passiflora alba × *P. buonapartea*

Leaf	Lamina, 3-lobed, 6 in. long, 6 1/2 in. wide. Petiole 3 1/4 in. or more	Long-ovate, cordate, somewhat acuminate; entire. 8 5/8 in. long, 7 1/4 in. wide	3-lobed, 6 in. long, 7 in. wide

Ribes nigrum × *R. grossularia*

No. of flowers in inflorescence	7-8-13	1-2	Av. 3
Ovarian glands	Sessile, 0.15-0.17 mm. diam.	0.1 mm. diam.; stalks 1.2 mm. long	0.1-0.13 mm. diam., length of stalk. 0.03-0.13 mm.

d. *Darbishire.*

Darbishire, in 1908 (1), appears to have been the first, since the re-discovery of Mendel's papers, to demonstrate further the facts brought out by Macfarlane's earliest investigations. Darbishire's experiments involved the crossing of a variety of peas in which the cotyledons were green and round (Eclipse), with one in which the cotyledons were yellow and wrinkled (British Queen). In the (F_1), out of 579 starch grains in the cells of the cotyledons, 356 were single and 223 compound. The singles were more nearly round than in the Eclipse parent, the single starch grains (av. of 102 grains), as compared with an index of 66:14 in the length-breadth index, being 92:19 in the Eclipse parent (av. of 232 grains). In the compound grains, the commonest types were those with 4, 5, or 6 component parts (7 and 8 being rarer), 2 and 3 being intermediate in frequency between those with 4, and 5 and 6 on the one hand, and 7 and 8 on the other. Grains with 7 and 8 component parts were not much larger than those with 4, 5, and 6, while grains with 2 or 3 were always found to be conspicuously smaller than those with 4, 5, and 6. In the British Queen parent, the grains (all compound, an occasional one only entire), have 2-8 component parts.

32. *Spillman. Mendelian Results with Wheat, prior to* 1900.

In 1901 appeared a brief but interesting and somewhat noteworthy paper on inheritance of characters in wheat hybrids, by W. J. Spillman, then of the Washington State Experiment Station, now of the United States Department of Agriculture. The paper, read before the Fifteenth Annual Convention of the Association of American Agricultural Colleges and Experiment Stations, November 12-14, 1901, represented a definite effort to obtain results of a quantitative character. The results, so far as they were attained, are stated in somewhat Mendelian fashion, although a knowledge of the then just published reports of Mendel's investigations had not yet reached the author. Nägeli, Sachs, and Darwin are quoted.

The study was based upon an undertaking to obtain a winter wheat for Eastern Washington. Some 150 varieties were tried, but none were found satisfactory, the worst common defects being shattering of the grain, lodging, susceptibility to smut (bunt), and unsatisfactory milling qualities. Having failed to find suitable varieties, it was undertaken to produce them by crossing the most promising winter varieties with the leading spring varieties known to be locally adapted.

Beginning with 1899, 14 crosses were made between parents of spring "Club" wheat (*Triticum compactum*), and the ordinary *vulgare* types of winter wheat. From these crosses 215 plants were harvested in 1900. Of these, 149 proved to be hybrids, being intermediate in type between the parents. The remainder were identical with the female parent, thus showing that the flowers had been self-fertilized. The following remarkable statement occurs:

> "No important variations occurred in the first generation, except as noted below, but when the heads appeared on the second generation, a remarkable state of affairs was seen to exist. At first glance it appeared that each of the hybrids had split up into all sorts of types, but closer inspection showed that in every case but one, which is noticed later, the forms in each plot were simply combinations of the characters of the parent forms. Further inspection revealed the fact that, in plots of similar breeding, exactly the same types were present. This suggested the idea that perhaps a hybrid tended to produce certain definite types, and possibly in definite proportions." (p. 88.)

All of the hybrid plots were accordingly assorted into types, and the proportions of each type determined. The results confirmed the idea that definite types and proportions existed in the progeny. The statement follows:

> "If similar results are shown to follow the crossing of other groups of wheat, it seems entirely possible to predict, in the main, what types will result from crossing any two established varieties, and approximately the proportion of each type that will appear in the second generation." (p. 88.)

The statement is then made:

> "With the exception already referred to, the second generation consisted of the two parent types, and of all the intermediate types possible between them." (p. 88.)

The instance is given where one parent had long, bearded heads, and the other short, beardless heads; six types could be distinguished:

> ". . . 2 of these had long heads like one of the parents, 2 others short heads like the other parent, and 2 were intermediate; and one of each of these 3 groups had beards, while the other had none." (p. 88.)

In crosses involving pubescent chaff but no beards, a similar set of 6 types appeared. Where one of the parents had pubescent chaff of dark brown color, 12 types were theoretically possible and were actually found. The remark follows:

> "It was stated above that the first generation tends to be the same in similarly bred hybrids and is intermediate between the parents." (p. 89.)

This was found to be the case in 11 out of 14 crosses. In a case involving "velvet" (pubescent) chaff, there were 12 types in the second generation, 6 with velvet, and 6 without. In the first generation, 1 out of 9 plants differed from the rest only in having no "velvet" or pubescence on the chaff. Such plants of the first generation produced only the 6 types without "velvet" in the second generation.

A general statement, also quite remarkable in character, is made to the effect that:

> "It has been stated by nearly all investigators that there is a tendency in the second and later generations, to revert to the parent form. It seems possible that there is a more accurate way of stating this. *The types that tend to occur in the second generation, as indicated by our results, include all possible combinations of the characters of the two parents. This of course includes the parent forms themselves, and we find the parent forms repeated in the second generation, constituting apparently certain definite portions of this generation.*" (Italics inserted.) (p. 89.)

Another interesting statement then follows:

> "Another important fact, that is clearly revealed by the tables of percentages, is that *the type that is most abundant in the second generation is the same as the first generation type, whether the latter is of the usual intermediate type or otherwise.* The exceptions to this are so rare as to render them doubtful." (Italics inserted.) (p. 89.)

So far as the writer knows, this constitutes the first and, indeed, the sole observation from the time of Kölreuter, with the exception of Mendel's own investigation, to take note of the fact that, in the second generation, *the most abundant type to appear is the type of the first generation itself.* This is an observation of the fact which Mendel definitely worked out, of the appearance in the second generation of 2 Dr to one each of the DD and rr types, the Dr type being the reappearance of the original Dr combination of the first generation.

Spillman goes on to comment upon the work of hybridization done since the time of Kölreuter, having special reference to the work of the various breeders of the cereals, Garton Brothers, Rimpau, Farrer, Vilmorin, and others. The statement follows:

> "Sachs remarks that Kölreuter, the first man to produce plant hybrids, covered the ground so completely that subsequent investigators have added little to his results."

The comment is then made:

> "But quantitative investigations have been too seldom undertaken. It seems to me that they are not unimportant." (p. 93.)

The quantitative results in question follow in very accurately arranged detail, in 14 tables, covering the quantitative distribution of the types of the second generation. The characters of the heads involved are, long and short, bearded and beardless; velvet (pubescent) chaff, and glabrous chaff; brown-colored and light-colored chaff. The investigator had no conception at the outset, as had Mendel, of consciously crossing contrasting character-pairs as such, and unfortunately did not take note of the fact of dominance in the case of the bearded-beardless, and pubescent-glabrous crosses. This was unquestionably due to the fact that length of head, the most salient character, did not show F_1 dominance for long × short crosses, but intermediacy.

In all the tables, the numbers which reproduce the characters of the first generation are printed in heavy type, so that there is statistical evidence of the dominance of characters involved, although no reference is made to it as such.

The individual columns give, in exactness and detail, the distribution of the plants in classes, according to the head-characters, but there is no summary of the proportionate numbers of these types. With the total available data obtained, it would have been possible for Spillman to have not only verified F_1 dominance for beardlessness over beardedness, pubescent chaff over glabrous chaff, and brown pubescence over light pubescence, but also to have determined the ratios of the distribution of those characters in the second generation. A few of the numerical results follow, summarized from some of the tables.

The data comprising Spillman's results are given in fourteen tables (pp. 94-98 of the memoir). The principal data from these tables which may be taken as examples of his Mendelian ratios, are those dealing with the inheritance of length of spike, awns, pubescence of the glumes, and color of glumes. In all of the tables, the progeny are classified in percentages, first, as to long, semi-long and short (head-length character); as to pubescent and glabrous chaff, beardless and bearded heads, brown and light-colored glumes. The varieties used in the crosses are as follows:

Compactum-vulgare Crosses	*Table*
Little Club (*compactum*) ♀ × Emporium (*vulgare*) ♂	I
Little Club (*compactum*) ♀ × Jones' Winter Fife (*vulgare*) ♂	II
White Track (*vulgare*) ♀ × Little Club (*compactum*) ♂	III
Little Club (*compactum*) ♀ × Valley (*vulgare*) ♂	IV
Emporium (*vulgare*) ♀ × Little Club (*compactum*) ♂	IX
Little Club (*compactum*) ♀ × Farquhar (*vulgare*) ♂	XI
Farquhar (*vulgare*) ♀ × Little Club (*compactum*) ♂	XII
Valley (*vulgare*) ♀ × Little Club (*compactum*) ♂	XIII
Little Club (*compactum*) ♀ × Turkey (*vulgare*) ♂	XIV

Inter-vulgare Crosses	
Red Chaff ♀ × White Track ♂	V
Red Chaff ♀ × McPherson ♂	VI
Red Chaff ♀ × Jones' Winter Fife ♂	VII
Red Chaff ♀ × Farquhar ♂	VIII
Red Chaff ♀ × Lehigh ♂	X

Summarizing the results in the tables for Spillman's fourteen crosses, the data of F_2 inheritance for the characters investigated are as follows:

Compactum-vulgare Crosses		*Table*
Long	2546.1	
Semi-long	3754.4	
Short	1967.1	

A ratio of $1 : \left\{ \begin{matrix} 1.4 \\ 1.9 \end{matrix} \right\} : 1$, or approximately 1 : 2 : 1.

Awns

Heads awnless	4770.3
Heads awned	880.8

A ratio of 5.4 : 1, instead of the expected one of 3 : 1. However, if individual tables are taken (omitting Table XII) normal ratios exist.

Pubescence of Glumes

Glumes pubescent	4224.7
Glumes glabrous	1371.8

A ratio of 3.1 : 1

Color of Glumes

Glumes brown in color	3143.7
Glumes light	1061.8

A ratio of 2.9 : 1

Referring to the results from individual tables, the following may be cited in illustration, from the *compactum-vulgare* crosses:

A *Awnless-awned (glumes)*

Table XIII (Valley ♀ × Little Club ♂)

	Awnless	*Awned*	*Ratio*
Types I and II (heads long)	197.0	68.8	2.8 : 1
Types III and IV (heads intermediate)	405.9	136.6	2.9 : 1
Types V and VI (heads short)	219.8	72.1	3 : 1

Table XIV (Little Club ♀ × Turkey ♂)

	Awnless	*Awned*	*Ratio*
Types I and II (heads long)	130.5	44.0	2.9 : 1
Types III and IV (heads intermediate)	222.0	125.9	1.7 : 1
Types V and VI (heads short)	120.6	46.0	2.6 : 1

Table IX (Emporium ♀ × Little Club ♂)

Awnless	*Awned*	*Ratio*
434.1	145.1	2.9 : 1

B *Pubescent-glabrous (glumes)*

Table II (Little Club ♀ × Jones' Winter Fife ♂)

	Pubescent	*Glabrous*	*Ratio*
Types I and II (heads long)	444.1	148.4	2.9 : 1
Types III and IV (heads intermediate)	769.4	274.2	2.8 : 1
Types V and VI (heads short)	409.8	155.5	2.6 : 1

Table XII (Farquhar ♀ × Little Club ♂)

	Pubescent	*Glabrous*	*Ratio*
Types V and VI (heads long, glumes brown)	582.3	149.7	3.8 : 1
Types VII and VIII (heads long, glumes light)	206.3	324.0	no ratio
Types IX and X (heads intermediate, glumes brown)	700.2	165.1	4.2 : 1
Types XI & XII (heads intermediate, glumes light)	185.5	54.3	3.4 : 1
Types XIII and XIV (heads short, glumes brown)	243.7	92.9	2.6 : 1
Types XV and XVI (heads short; glumes light)	160.8	17.4	5 : 1

It thus appears that Mendelian results for length of head (in *compactum-vulgare* crosses), inheritance of awns, pubescence of glumes and color of glumes were reported in November, 1901, in complete statistical form, although not analyzed with reference to the ratios.

Exact data do not seem to be obtainable as to inheritance of length of spike in *compactum-vulgare* crosses, but in crosses between *spelta* and *compactum* (Malinowski, 1921), the length of heads and the structure of the spikelets were reported as being controlled each by a single gene. The F_2 is reported as splitting according to the ratio 1 : 2 : 1 (*Triticum spelta*, *vulgare* and *compactum* all have 42 chromosomes as the diploid number).

Dicoccum-vulgare crosses by the same investigator gave likewise a 1 : 2 : 1 ratio for inheritance of length of spike, *dicoccum* having 28 chromosomes as the diploid number.

The fact that results for awn-inheritance are, F_1 awnless; F_2 awnless-awned, 3 : 1, was first determined by Biffen (1905), and has since been repeatedly confirmed by the work of some fourteen investigators.

The dominance of pubescence over glabrousness in the glumes was also first determined by Biffen in 1905, in *vulgare* crosses. Results for similar inheritance in other *Triticum* crosses has likewise been determined. Exact investigations in inheritance of brown glume color were first carried out by Nilsson-Ehle in 1909, the F_2 ratio being found for the most part to be 3 : 1 but sometimes 15 : 1. Similarly Love and Craig (1919) found a 15 : 1 ratio between a brown *vulgare* and a yellow *durum*, thus indicating the presence of two genes for brown glume color.

This will suffice for a brief review of the present genetic status of the characters investigated by Spillman.

The writer concludes, as a result of his investigation:

> "While the results here reported are not sufficient to justify the positive assertion that certain quantitative laws govern the transmission of parental characters to hybrid offspring, yet they point so strongly in this direction, that we may state some of these laws provisionally, looking to future investigation for their confirmation, modification, or rejection." (p. 93.)

These provisional laws are stated as follows:

> "That similarly bred hybrids tend to be alike in the first generation, and to be intermediate between the parent forms, and that rarely an individual resembles one parent more or less closely, has been stated by others. We may add to this, provisionally at least, the following:
>
> (1) "In the second generation of hybrids of similar breeding (with close fertilization), the same types tend to occur and in definite proportions; 2 of these types are like the parents, the others include all possible intermediate forms.
>
> (2) "With few exceptions, the most abundant type in the second generation is the same as the type found in the first generation, whether the first generation was strictly intermediate between the parents or not." (p. 93.)

It is a matter of some interest to record such a succinct and definitely scientific attempt at a statement of the conditions governing the second generation of hybrids, based on the results of a carefully planned experiment, considerable in extent, and with the data definitely classified in a statistical, and to that extent a quantitative manner.

A rather interesting statement of a more or less Mendelian type is made in the concluding portion of the paper.

> "We have begun investigations with a view to ascertaining whether these quantitative laws extend to hybrids between other groups of wheat varieties, and whether, when a composite is formed from several varieties, all the types will appear that could be formed by combination of parent characters. It is interesting to note the possibilities that are open to the breeder should this prove to be the case. We could then produce anything we desire if we can find varieties possessing the characters we wish to combine." (p. 94.)

The concluding statement is:

> "In work of this character, the larger the number of individuals, the greater the probability of finding any desired combination of characters. It is therefore desirable to secure as many grains of each cross as possible, and to raise all their progeny. Those who are familiar with the details of such work, will realize that this entails an enormous amount of labor, and one can hardly hope for success without both patience and enthusiasm, coupled with some training." (p. 94.)

This concludes the discussion of a paper that has been perhaps considerably overlooked, but which represents a very definite attempt to analyze the data of heredity upon a rational and indeed almost a Mendelian basis.

This closes the survey of the work of the students of hybridization, from the date of the appearance of Mendel's papers in 1865 until their reappearance to the scientific world in 1900. This period, while important for the imposing names of Darwin and Galton, was also important for the propounding of the law of the disjunction of hybrids by Naudin, which, as we have seen, led Darwin to theoretical conclusions regarding the behavior of the characters in the sexual cells in the case of hybrids, similar in general character to the conclusion which Mendel's investigation established.

To the modern student of breeding, it seems exceedingly strange that to none of those who carried on the earlier experiments in hybridization it should have occurred to determine, whether the second or "variable" generation of hybrids was anything other than a disorderly congeries of forms; whether, beneath this apparent disorder, there might not be concealed some law.

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CHAPTER X

33. *The Discovery of Gregor Mendel.*

THE year 1900 marks the beginning of the modern period in the study of heredity. Despite the fact that there had been some development of the idea that a living organism is an aggregation of characters in the form of units of some description, there had been no attempts to ascertain by experiment, how such supposed units might behave in the offspring of a cross. In the year above mentioned the papers of Gregor Mendel came to light (5), being quoted almost simultaneously in the scientific contributions of three European botanists, De Vries in Holland (3), Correns in Germany (2), and Von Tschermak in Austria (6). Of Mendel's two papers, the important one in this connection, entitled "Experiments in Plant Hybridization," was read at the meetings of the Natural History Society of Brünn in Bohemia (Czecho-Slovakia) at the sessions of February 8 and March 8, 1865. This paper had passed entirely unnoticed by the scientific circles of Europe, although it appeared in 1866 in the Transactions of the Society. From its publication until 1900, Mendel's paper appears to have been completely overlooked, except for the citations in Focke's "Pflanzenmischlinge," and the single citation of Hoffmann, elsewhere referred to.

Gregor Johann Mendel, a monk of the Augustinian order in the Catholic Church, was the son of a small peasant farmer, and his education was what he was able to secure at the village school, supplemented by a course at the gymnasium at Tropau, finishing with a year at Olmutz. After completing the course at the gymnasium, Mendel applied for admission to the Augustinian order of the monastery of St. Thomas in Brünn, generally referred to as the Königskloster. In the school and in the gymnasium Mendel had won distinction as a student, and on entering the monastery was chosen to assist in the educational work of the religious order.

PLATE XLII. Gregor Mendel, 1822-1884.

In 1847 he was ordained priest, and in 1851, at the expense of the establishment, he was sent to the University of Vienna, remaining there until 1853 as a student of mathematics, physics, and biology. On returning to Brünn, he became a teacher, chiefly of physics, in the local Technische Hochschule. It is reported that he was unusually successful as a teacher. In 1868 he was chosen Abbot of the monastery at Brünn. The famous scientific investigations connected with his name were conducted in the monastery garden during the eight years preceding 1865. After his election as Abbot in 1868, his scientific work ceased, and he became involved in 1872 in a quarrel with the Austrian government, over a law imposing a special tax upon the property of religious corporations. This controversy, and others in which he became involved, made the last ten years of his life a period of bitterness and disappointment. On January 6, 1884, Mendel died at the age of 62. In addition to his work with plants, Mendel conducted experiments in the breeding of bees, securing queens of various

PLATE XLIII. The Augustinian Cloister at Brünn.

races, and using some fifty hives for his experiments. Of these experiments, no written record has survived.

Mendel was a man of keen scientific instincts in general. He was interested in meteorology, and made a study of sun spots with reference to their relation to meteorological phenomena on the earth. He kept meteorological records for many years, and practically until his death. At least some of these records are published in the Transactions of the Brünn Society. He served one term as president of the Natural History Society of Brünn. That Mendel possessed unusual business and administrative ability is evidenced by the fact that he rose to the station of Abbot in his order, a position which placed him in charge of the business affairs of the organization; and by the interesting fact that he was chosen chairman of the Moravian Hypotheken-Bank of his city. A curious report exists as to his ability as a chess player, and his love for chess seems to be well established by statements of his associates in the St. Thomas Cloister. Mendel was also good at bowling, and had an alley, on the walls of which some of his scores are still pointed out. That Mendel throughout his life possessed the spirit of a leader and organizer is very clear. A minor circumstance bearing upon this fact is the incident that in his native village of Heinzendorf he is recalled as the organizer of a fire brigade. The erection of a new fire station in the town, after Mendel's name became famous, was the occasion for the placing of a memorial tablet in the building.

Gregor Mendel, however, died in 1884—sixteen years before his work of 1868 5 became known to the scientific world.

At the time when Mendel's paper on hybridization appeared, scientific circles, and the intellectual world generally, were full in the midst of the discussions and debates precipitated by the publication in 1859 of Darwin's "Origin of Species," and of the first edition of his "Variation of Animals and Plants under Domestication" in 1868. It is clear that Darwin had never seen Mendel's paper, although Mendel was familiar with Darwin's work. Indeed the only biologist of note with whom Mendel appears to have been in correspondence was Nägeli. The correspondence between them is published, but there is no evidence that Nägeli grasped the significance of Mendel's discovery. The only references to Mendel's paper in scientific literature before 1900, as already remarked, are the statements referred to above in Focke and Hoffmann.

Mendel was led to undertake his investigations through a realization *that some law must underlie the fact of the regular reappearance of the same types of hybrids whenever the same two species are crossed.*

He says:

> "The striking regularity with which the same hybrid forms always reappeared whenever fertilization took place between the same species induced further experiments to be undertaken, the object of which was to follow up the development of the hybrids in their progeny." (5d, p. 335.)
>
> ". . . That so far no generally applicable law governing the formation and development of hybrids has been successfully formulated can hardly be wondered at by anyone who is acquainted with the extent of the task, and can appreciate the difficulties with which experiments of this class have to contend. A final decision can only be arrived at when we shall have before us the results of detailed experiments made on plants belonging to the most diverse orders." (*ib.*, pp. 335-6.)

The kernel of Mendel's method, and the revelation of his scientific insight, which so far outstripped that of all previous investigators in the field of hybridization, appears in the following paragraph:

> "Those who survey the work done in this department will arrive at the conviction that, among all the numerous experiments made, not one has been carried out to such an extent and in such a way as to make it possible to determine the number of different forms under which the offspring of hybrids appear, or to arrange these forms with certainty according to their separate generations, or definitely to ascertain their statistical relations." (*ib.*, p. 336.)

As Bateson says:

> "It is to the clear conception of these three primary necessities that the whole success of Mendel's work is due. So far as I know this conception was absolutely new in his day." (*ib.*, p. 336, note.)

In the first place Mendel devoted great care to the selection of a plant for his experiments, the requisites being, as he says, the possession of constant differentiating characters, freedom from accidental crossing by foreign pollen, and fertility of the hybrids. No one before Mendel had apparently grasped the necessity for the employment of the following method as outlined by him:

> "In order to discover the relations in which the hybrid forms stand toward each other, and also toward their progenitors, it appears to be necessary that all members of the series developed in each successive generation should be, *without exception*, subjected to observation." (*ib.*, p. 337.)

Mendel's attention was called to the Leguminosae as a possible group for experimentation, because "of their peculiar floral structure." (p. 337.) After making experiments with several members of this family, he came to the conclusion that the genus *Pisum* (pea) fulfilled his requirements. He investigated, during two years, thirty-four more or less distinct varieties of peas obtained from seedsmen. Twenty-two of these varieties "were selected and cultivated during the whole period of the experiments. They remained constant without an exception." (p. 338.)

Mendel concerned himself little with the supposed systematic classification of his varieties of peas. The majority of them he assigns to *Pisum sativum*, others to sub-species of this, and still others to distinct species.

> "The positions, however, which may be assigned for them in a classificatory system are quite immaterial for the purpose of the experiments in question. It has so far been found to be just as impossible to draw a sharp line between the hybrids of species and varieties, as between species and varieties themselves." (p. 338.)

The earlier hybridizers of plants, for the most part, made a distinction between "hybrids" so-called, between "species," and "crosses" between "varieties." Mendel discards this terminology, recognizing that the distinction is one of degree and not of kind, a distinction essentially artificial when closely applied.

The fundamental difference between Mendel's hybridization experiments and all others stands out most clearly in the following statement:

> "If two plants which differ constantly in one or several characters be crossed, numerous experiments have demonstrated that the common characters are transmitted unchanged to the hybrids and their progeny; but each pair of differentiating characters, on the other hand, unite in the hybrid to form a new character, which in the progeny of the hybrid is usually variable. The object of the experiment was to observe these variations in the case of each pair of differentiating characters, and to deduce the law according to which they appear in the successive generations. The experiment resolves itself therefore into just as many separate experiments as there are constantly differentiating characters presented in the experimental plants." (pp. 338-9.)

The "characters" which Mendel, after careful consideration, finally selected for his work were the following:

1. *The form of the ripe seeds* (i.e., of the ripe cotyledons), whether (a) *round*, or (b) *wrinkled.*
2. *The color of the ripe seeds* (i.e., of the ripe cotyledons within the transparent seed coats), whether (a) *yellow*, or (b) *green.*
3. *The color of the seed coat*, whether (a) *gray* or *brown*, with *violet-red flowers*, or (b) *white* with *white flowers.*
4. *The form of the ripe pods*, whether (a) *inflated*, or (b) *constricted, between the seeds.*
5. *The color of the unripe pods*, whether (a) *green* or (b) *yellow.*
6. *The difference in the position of the flowers*, whether (a) *distributed along the main axis*, or (b) *bunched at the top of the stem in a false umbel.*
7. *The difference in length of stem*, whether (a) 6-7 ft. *in length*, or (b) ¾-½ ft.

Each two "differentiating characters" as they are called, in the seven pairs, were tested by crossing. It may be interesting to notice how many crosses were actually made.

1st	character-pair	—60 crosses on	15 plants
2nd	"	—58 crosses on	10 plants
3rd	"	—35 crosses on	10 plants
4th	"	—40 crosses on	10 plants
5th	"	—23 crosses on	6 plants
6th	"	—34 crosses on	10 plants
7th	"	—37 crosses on	10 plants

In all the seven classes of cases, reciprocal crosses were made.

Mendel calls attention to the fact that previous experiments with hybrids showed that, as a rule, hybrids were not exactly intermediate between their two parents, and that, with respect to some of the cases,

> ". . . One of the two parental characters is so preponderant that it is difficult, or quite impossible, to detect the other in the hybrid." (p. 342.)
>
> "This," he adds, "is precisely the case with the pea hybrids. In the case of each of the seven crosses, the hybrid character resembles that of one of the parental forms so closely that the other either escapes observation completely or cannot be detected with certainty." (p. 342.)

The character which became evident in the hybrid, Mendel called the *dominant*, and the character that remained latent, the *recessive*. He calls attention to the fact that the dominant character is unaffected by the direction of the cross—that it makes no difference whether the parent bearing the character that becomes dominant in the hybrid is used as the pollen parent or as the seed parent. This interesting fact, as Mendel states, had already been observed by Gärtner (4), whose statement it may be worth while to reproduce.

> "This most important and most interesting phenomenon in the crossing of plants for the production of hybrids is the complete similarity of the two products; in that seeds which come from the one as well as from the other fertilization give rise to plants of the most complete similarity; so that the dissimilar origin and derivation of the two kinds of hybrids, after the most careful investigation with respect to their form and type, does not admit of the slightest distinction between them, and even the most practised expert with a hybrid species is not in a position to distinguish the origin of the hybrid with respect to the sex of the parents. . . . This is the general rule with almost all plants." (p. 223.)

Here it is well to call attention to the fact that Mendel never for a moment considered, as did all the older hybridizers, that he was crossing one *individual* as a whole with another as a whole, but that he was pitting one character in an individual against a single *contrasting character* in another individual. Herein is revealed Mendel's scientific genius and analytical insight.

In the seven classes of "character-crosses," if we may so designate them, that Mendel made with peas, he found that in the first generation, the following characters were dominant.

	Dominant		*Recessive*
1.	round seeds	over	wrinkled seeds
2.	yellow seeds	"	green seeds
3.	grey or brown seed-coats	"	white (i.e., colorless) seed-coats
4.	inflated ripe pods	"	constricted ripe pods
5.	immature green pods	"	immature yellow pods
6.	axial arrangement of flowers	"	bunched or terminal arrangement of flowers
7.	tall stems	"	dwarf stems

Of these "characters," those relating to the shape and color of the seeds (i.e., of the cotyledons within the seed-coats) can, of course, be seen at once after the flowers have been fertilized, and the seeds grown. All of the other characters, of seed coats, pods, flowers and stems, can only, of course, become apparent when the hybrid seedlings grow up and produce stems, flowers, pods, and seeds themselves.

Mendel now proceeds with the study of the second generation (F_2). Of the self-fertilized hybrid he says:

> "In this generation there re-appear, together with the dominant characters, also the recessive ones with their peculiarities fully developed, *and this occurs in the definitely expressed average proportion of three to one*, so that among each four plants of this generation three display the dominant character, and one the recessive. This relates without exception to all the characters which were investigated in the experiments. The angular, wrinkled form of seeds, the green color of the albumen, the white color of the seed-coats and the flowers, the constrictions of the pods, the yellow color of the unripe pod, of the stalk, of the calyx, and of the leaf venation; the umbel-like form of the inflorescence, and the dwarfed stem, all re-appear in the numerical proportions given without any essential alterations. Transitional forms were not observed in any experiment." (Italics inserted.) (p. 344.)

It will be interesting to give in this connection, the actual data of the experiments themselves.

It is seen from the table on page 295, that the ratios throughout are nearly or quite 3:1. In the two seed experiments, each pod usually produced both kinds of seed. As Mendel says:

> "In well-developed pods which contained on the average six to nine seeds, it often happened that all the seeds were round or all yellow; on the other hand there were never observed more than five wrinkled or five green ones in one pod." (1, p. 344.)

The net result of Mendel's investigation of the F_2 and the F_3 generations is expressed as follows:

> "The ratio of 3 to 1, in accordance with which the distribution of the dominant and recessive characters results in the first generation, resolves itself therefore in all experiments, into the ratio of 1 pure dominant; 2 hybrids; 1 recessive, if the dominant character be differentiated according to its significance as a hybrid character or as a parental one." (*ib.*, p. 349.)

In other words, the 75 per cent of plants which show the dominant form in the F_2 generation were found by Mendel's analysis (i.e., by growing them another year) really to consist of two parts hybrids, which go on splitting in the original ratio of 3:1; and one part pure dominants, which continue to breed true as such.

Mendel summarizes the matter in the following significant sentence:

> "Since the members of the first generation (F_2) spring directly from the seed of *the hybrids* (F_1), *it is now clear that the hybrids form seeds having one or the other of the two differentiating characters, and of these, one-half develop again the hybrid form, while the other half yields plants which remain constant, and receive the dominant or the recessive characters respectively in equal numbers*." (Italics as in original.) (p. 349.)

EXPERIMENT NO.	SUBJECT OF THE EXPERIMENT; F_2 GENERATION	NO. OF PLANTS	SEEDS		PLANTS		TOTAL NO.		RATIO
			DOMINANT	RECESSIVE	DOMINANT	RECESSIVE	DOMINANT	RECESSIVE	
1	Form of seed	253	round 5,474	wrinkled 1,850	....	....	5,474	1,850	2.96 : 1
2	Color of cotyledons	258	yellow 6,022	green 2,001	....	....	6,022	2,001	3.01 : 1
3	Color of seed-coats	929	grey 705	white 224	....	....	705	224	3.15 : 1
4	Form of pods	1,181	....	....	inflated 882	constricted 299	882	299	2.95 : 1
5	Color of unripe pods	580	....	....	green 428	yellow 152	428	152	2.82 : 1
6	Position of flowers	858	....	....	axial 651	terminal 207	651	207	3.14 : 1
7	Length of stem	1,064	....	....	long 787	short 277	787	277	2.84 : 1
						Total	14,949	5,010	2.98 : 1

The matter may be simply outlined by the usual familiar diagram. Supposing the case of plants bearing round, and plants bearing wrinkled seeds; the dominant parent (round) being expressed by R and the recessive parent (wrinkled) by W, then:

(1)	R	×	W	Parents
		‖		
(2)		RW		F_1 generation
(3)	R	RW	W	F_2 generation
	25%	50%	25%	
(4)	R	RW	W	F_3 generation
	25%	50%	25%	
		etc.		

In the above diagram it is assumed (and so it occurred in Mendel's case) that the R's and RW's in (3) will all look alike—i.e., that they will all appear round, and hence will make up 75 per cent of the total, while the other 25 per cent will be pure W's or wrinkled's, and will appear as such. Now by growing self-fertilized plants of the combined R's and RW's in (3) it will come out in the F_3 generation (4) that one-third of the combined lot of R's and RW's of (3), i.e., 25 per cent of the whole number, will breed true as R's, while the other two-thirds (50 per cent of the entire number) will turn out to split up again in the ratio of three R's, or rather of apparent R's, to one W—in other words, the ratio that indicates their hybrid composition.

We can say, therefore, that in any case of simple Mendelian hybrids, i.e., where one character-pair only is concerned, *the hybrid or F_1 generation has always internally the following invisible composition, which can be revealed by breeding.*

25%	50%	25%
pure dominant	dominant-recessive or hybrid (appearing dominant)	pure recessive

All these are bound together in the F_1 generation under the apparent uniformity which the dominant character imposes. Generalizing, and expressing the dominant by D and recessive by R, we have:

$$\begin{array}{l} D \times R = DR \\ DR \times DR = 1DD : 2DR : 1RR \end{array}$$

Thus far we have followed, in considerable detail, Mendel's original experiments themselves. It is plain that these exhaustive and laboriously detailed experiments leave no doubt as to the central facts of what we know as the "Mendelian" factor-analysis, viz., that each germ cell or gamete carries what Mendel called the dominant or the recessive character as the case may be, in pure form; that, in the hybrids, the gametes carry the dominant and the recessive characters respectively in equal numbers, so that when they unite at random according to the law of chance, they will produce all possible combinations in equal numbers as follows:

Male gamete		*Female gamete*	*Zygote*
1. D	×	D	DD
2. D	×	R	DR
3. R	×	D	RD
4. R	×	R	RR

This means that in any hybrid there exist equal numbers of these four combinations, when a single opposing pair of characters is involved, so that the result of all the four possible combinations will be:

25%	25%	25%	25%
DD	DR	RD	RR

as the condition of things existing in any Mendelian monohybrid (i.e., in which a single pair of characters only is considered), or, as commonly expressed:

25%	50%	25%
DD	DR	RR

We have seen that, with an increase in the number of character-pairs, we simply increase the number of terms in the series, by the formation of a combination series, in which each kind of character-combination of the one unites with each kind of character-combination of the other series—a process which can be represented by the algebraic multiplication of

$$\begin{aligned} &A + 2\,Aa + a \\ \text{by } &B + 2\,Bb + b \end{aligned}$$

We can do this, because $A+2Aa+a$ is, as we have seen, the series of segregated types which the F_1 or hybrid generation, Dr (expressing the recessive by a small letter), algebraically actually can and does form on self-fertilization. Likewise, with the series $B+2Bb+b$, into which the hybrid Bb segregates on self-fertilization. The algebraic multiplication of these two series simply represents the fact that both B and b unite with A, 2Aa and a and so on.

Since the segregation of the offspring of a self-fertilized hybrid involving one pair of characters, a dominant D and recessive r, gives us a total of 3 apparent D's to 1 r, or the familiar ratio of 3 : 1, then two pairs of opposing characters, thus segregating, would give a ratio of 9:3:3:1, which is plainly the result of the combination of two 3 : 1 ratios, this being the result obtained by multiplying together the ratios in which each of the character-combinations separately occurs. Taking, for example, the characters round (D) and wrinkled (r) : and yellow (D) and green (r) :

In the F_2 generation, there are 3 yellows to 1 green in every 4, and there are 3 round to 1 wrinkled in every 4.

Where both of these two sets of character-pairs are united in the same hybrid, the numerical proportions of the character-combinations, so far as appearances go, will necessarily then be as follows:

Yellow and round	3 × 3 = 9
Yellow and wrinkled	3 × 1 = 3
Green and round	1 × 3 = 3
Green and wrinkled	1 × 1 = 1

In the detailed analysis we will have:

1. *Yellow round*	
(1) pure as to color and form	1
(2) pure as to color but not as to form	2
(3) pure as to form but not as to color	2
(4) hybrid in both respects	4
	9
2. *Yellow wrinkled*	
(1) pure as to color and form	1
(2) pure as to form but not as to color	2
	3
3. *Green round*	
(1) pure as to both color and form	1
(2) pure as to color but not as to form	2
	3

4. *Green wrinkled*	
(1) pure as to both color and form	1
	1
Total number of types	16

We may now use the customary table of squares to represent the possible number of zygote forms that are derived from a given number of characters carried by the gametes.

Let us continue to take round and wrinkled, and yellow and green as the character-pairs. We may then represent the F_1 generation as being formed in the following way, where a plant bearing the characters green and wrinkled is fertilized by pollen from a plant bearing the yellow and round characters in its germ cells.

	Male gametes AB
Female gametes ab	AaBb

Likewise, let us suppose the reciprocal cross, where a plant bearing yellow and round characters, is fertilized by pollen from a plant bearing the characters green and wrinkled. We then have:

	Male gametes ab
Female gametes AB	AaBb

In both cases, as is plain, the zygote will theoretically have the same character and appearance, AaBb. If we wish to show the actual condition of things in the zygote, we may use the customary four-square table, indicating the dominant and recessive characters by D and r.

TABLE I

Male gametes

		D	r
Female Gametes	D	DD	Dr
	r	rD	rr

In this table we therefore see four kinds of gametes formed in the hybrid zygote of the F_1 generation. Let this hybrid be self-fertilized, and we have, of course, each of the four types of male gametes uniting with each of the same four types of female gametes. The process may then be reproduced by a sixteen-square table as follows:

TABLE II

Male gametes

		AB	aB	Ab	ab
Female gametes	AB	AA.BB	Aa.BB	AA.Bb	Aa.Bb
	aB	Aa.BB	aa.BB	Aa.Bb	aa.Bb
	Ab	AA.Bb	Aa.Bb	AA.bb	Aa.bb
	ab	Aa.Bb	aa.Bb	Aa.bb	aa.bb

So far as appearances go, the plants resulting from these sixteen combinations would be as follows:

TABLE III

YELLOW ROUND	YELLOW ROUND	YELLOW ROUND	YELLOW ROUND
YELLOW ROUND	GREEN ROUND	YELLOW ROUND	GREEN ROUND
YELLOW ROUND	YELLOW ROUND	YELLOW WRINKLED	YELLOW WRINKLED
YELLOW ROUND	GREEN ROUND	YELLOW WRINKLED	GREEN WRINKLED

We have here 9 YELLOW ROUND, 3 YELLOW WRINKLED, 3 GREEN ROUND, and 1 GREEN WRINKLED. This is, to be sure, a table of appearances only, or what are known as the "phenotypes." This, then, is the way in which the plants or zygotes, formed by the gametic union of one *AaBb* hybrid with another *AaBb* hybrid, actually look. *What they actually are* is expressed in Table II. We have in Table II a zygote AA.BB, produced by the combination of a gamete bearing the combination AB with a gamete bearing the character-combination AB. Such an organism has been called homozygous, the gametes forming it being alike for both characters. At the end of the same row we find a zygote whose constitution is AaBb, produced by a combination of a gamete AB with a gamete ab, which combination is called *heterozygous*, the gametes forming it being *unlike for both characters* of the two pairs. We have also in the same rows, zygotes AABb, and AaBB, which are heterozygous for color (Bb), in the first case, and for form (Aa), in the second case. We may then have organisms that are homozygous (i.e., alike) for both pairs of characters (DDrr); homozygous for a single pair of characters (DD) and heterozygous (i.e., unlike) for another pair (Dr); or heterozygous for both pairs (DrDr). If the combinations in Table III, representing the behavior of two character-pairs in fertilization, be compared with Mendel's way of stating the combinations, using A and a for round and wrinkled, and B and b for yellow and green, respectively, differences will appear which should be explained. According to Mendel's form of statement for example, wrinkled yellow in the zygote is represented by Mendel as aBb. Plainly this comes about as the result of the combination of a wrinkled yellow gamete (aB), with a wrinkled green gamete (ab) using the letter "a" but once for the character represented. Such a combination at the end of the second row in Table II as is now represented by *aa.Bb* Mendel represented by aBb, because, since the "a" characters in the two gametes were alike, he felt no need of representing the character in the zygote by double letters. But since the "B" character, uniting with the "b" character, gave a zygote character of double composition, he represents it by "Bb." At present, it is of course the practice to represent the actual gametic condition in the zygote by giving the letters representing the full gametic composition. So that A×B is represented by AA.BB, not simply by AB as in Mendel's terminology, and so on. Following the expression introduced by Bateson in 1901, each member of an opposing pair of characters is spoken of as an "allelomorph," from the Greek *allelon* (reciprocal) and *morphé* (form). Round and wrinkled are then *"allelomorphs,"* and such character-pairs are referred to as *"allelomorphic"* pairs. This terminology has, of course, become practically universal.

It was Mendel's belief, and this belief has been confirmed by the discoveries since made, that all fertilizations are of the same character, and that the phenomena which we call "Mendelian" are really the general phenomena which occur in all unions whatsoever of sexual cells, whether of plants or of animals, including man, where independently operating factors are concerned; in other words, that the phenomenon called "Mendelian" is the universal condition in amphimixis. It is extremely interesting to note the signally significant insight of Mendel's comment as follows:

> "Whether the variable hybrids of other plant species observe an entire *agreement must also be decided experimentally. In the meantime we may assume that in material points an essential difference can scarcely occur, since unity in the developmental plan of organized life is beyond dispute.*" (5d, p. 375.) (Italics inserted.)

Mendel himself, in his later experiments of crossing the dwarf Lima Bean (*Phaseolus nanus*) "with small white seeds," with the Scarlet Runner Bean (*Phaseolus multiflorus*) with "large seeds which bore black flecks and splashes on a peach-blossom-red ground," found that the color combination in the seeds appeared not to follow his law. Anticipating modern work, which has confirmed his hypothetical conclusion, he says:

> "Even these enigmatical results, however, might probably be explained by the law governing *Pisum*, if we might assume that the color of the flower and seeds of *Phaseolus multiflorus is a combination of two or more entirely independent colors, which individually act like any other constant character in the plant.*" (Italics inserted.) (p. 367.)

Mendel concludes with a further significant statement (p. 370), which is perhaps one of the most striking illustrations of anticipatory analysis to be found in the entire paper, and which was first actually and fully demonstrated by the work of Bateson with Sweet Peas in 1905 and 1906.

> "Whoever studies the coloration which results in ornamental plants from similar fertilization can hardly escape the conviction that here also the development follows a definite law which possibly finds its expression *in the combination of several independent color characters.*" (p. 370.)

This leads to a reference to the matter of what are commonly known as "unit characters." Whatever these unit character-determinants or genes may be, they are probably of the nature of factors, the release of the operation of which sets in train a series of physiological changes, which ultimately wind up by producing the visible structural characters in question, and which are seen to function as units in the cross. This conception was, as a matter of fact, Mendel's own. The fact, furthermore, that in the production of many complex characters several factorial units may share, Mendel himself also surmised.

Mendel's conclusion, then, from his peas hybrids is as follows (1):

> "It is now clear that the hybrids form seeds having one or other of the two differentiating characters, and of these one-half develop again the hybrid form, while the other half yield plants which remain constant, and receive the dominant or the recessive characters (respectively) in equal numbers." (p. 349.)

Since the offspring of hybrids split off or segregate to the extent of one-half in each succeeding generation, an example of the result in respect to the seeds is given by Mendel as follows:

Generation	*D*	*Dr*	*r*	*Ratios*
1	1	2	1	1 : 2 : 1
2	6	4	6	3 : 2 : 3
3	28	8	28	7 : 2 : 7
4	120	16	120	15 : 2 : 15
5	496	32	496	31 : 2 : 31
				$2^r-1 : 2 : 2^r-1$

> "In the tenth generation, for instance, $2^r-1=1023$. There results, therefore, in each 2,048 plants which are in this generation, 1,023 with the constant dominant character, 1,023 with the recessive character, and only two hybrids." (p. 350.)

Mendel thus demonstrated that the hybrid character originally brought together by crossing cannot be "fixed" as a whole by selection. Each succeeding generation of the close-fertilized progeny will undergo a constant diminution of the number of the hybrids, according to a fixed and unalterable ratio, with the result that by the tenth generation, there will be a practical elimination of the hybrid condition in most cases, all of the progeny having been segregated into various combinations of dominants and recessives.

Hybrids in which two pairs of characters are concerned: results of Mendel's experiments.

Mendel next undertook to determine the behavior of hybrids in which more than one differentiating pair of characters was concerned. To determine what would happen in such a case, he undertook two experiments; in the one, the parents differed in the form and in the color of the seed (i.e., of the cotyledons within the seed coat), involving therefore *two* differentiating characters in each cross. In the second experiment, the seeds of the two parents differed *in form*, *in color*, *and in the color of the seed coats*: thus involving *three* pairs of differentiating characters in each cross.

For convenience' sake, in the first experiment, Mendel used the following symbols:

A. round seed form	a. wrinkled seed form
B. yellow seed color	b. green seed color

In the F_1 generation all the seeds produced were round and yellow, as would have been expected from the fact that round when taken singly is dominant over wrinkled, and yellow when taken singly is dominant over green.

The fifteen plants raised from these yellow round seeds, yielded, however, *four kinds of seeds*, 556 in all, distributed in the following way:

			Ratio (approximate)
315	round and yellow	AB	9
101	wrinkled and yellow	aB	3
108	round and green	Ab	3
32	wrinkled and green	ab	1

All of these 556 seeds were sown in the following year. The plants that came to maturity, were distributed with regard to the kinds of seeds they bore, as follows:

1. Sowing all the round yellow seeds mentioned above, 301 plants resulted, which bore seeds in the following ways:

38 plants had round yellow seeds	AABB
65 plants had round yellow and round green seeds	AABB and AAbb
60 plants had round yellow and wrinkled yellow seeds	AABB and aaBB
138 plants had round yellow, round green, wrinkled yellow, and wrinkled green seeds	AABB, AAbb, aaBB and aabb

2. Sowing all the wrinkled yellow seeds above, 96 plants resulted, which bore seeds in the following ways:

28 plants had wrinkled yellow seeds	aaBB
68 plants had wrinkled yellow and wrinkled green seeds	aaBB and aabb

3. Sowing all the round green seeds above, 102 plants bore seeds in the following ways:

35 plants had round green seeds	AAbb
67 plants had round green seeds and wrinkled green seeds	AAbb and aabb

4. Sowing all the wrinkled green seeds, 30 plants resulted which bore seeds as follows:

30 plants had all wrinkled green seeds	aabb

Combining all these results into a common table we find:

CLASS I

GROUP	NO. OF PLANTS	FORMULA	APPEARANCE OF SEEDS	ACTUAL COMPOSITION OF SEEDS	BEHAVIOR
1	38	AABB	round yellow	round yellow	constant
2	35	AAbb	round green	round green	constant
3	28	aaBB	wrinkled yellow	wrinkled yellow	constant
4	30	aabb	wrinkled green	wrinkled green	constant
Av.	32				

CLASS II

GROUP	NO. OF PLANTS	FORMULA	APPEARANCE OF SEEDS	ACTUAL COMPOSITION OF SEEDS	BEHAVIOR
5	65	AABb	round yellow	round yellow (green)	hybrid
6	68	aaBb	wrinkled yellow	wrinkled yellow (green)	hybrid
7	60	AaBB	round yellow	round (wrinkled) yellow	hybrid
8	67	Aabb	round green	round (wrinkled) green	hybrid
Av.	65				

CLASS III

GROUP	NO. OF PLANTS	FORMULA	APPEARANCE OF SEEDS	ACTUAL COMPOSITION OF SEEDS	BEHAVIOR
9	138	AaBb	round yellow	round (wrinkled) yellow (green)	hybrid
Av.	138				

The character enclosed in parentheses, according to Mendel's original conception, is the latent one in the hybrid.

Mendel then observed that the whole of these different groups of plants could be arranged into three different classes, as follows:

1. The first class included only groups 1, 2, 3, and 4, with the signs AB, Ab, aB, and ab. It is evident that round yellow seeds (AB) will come true, as both the characters are dominants of different character-pairs; likewise with wrinkled green seeds (ab), since both of these characters are recessives of different character-pairs. So also round green seeds (AAbb) and wrinkled yellow (aaBB) will also come true and be constant, since they combine the dominant of one character-pair with the recessive of another.

2. The second class of plants includes groups Nos. 5, 6, 7, and 8, AABb, aaBb, AaBB, and Aabb.

The above groups, as Mendel puts it, "are constant in one character and hybrid in another, and vary in the next generation only in the hybrid character." (p. 352.)

This means, for example, that the plants in group No. 5, which bears the sign AABb, are round (A) and yellow (B) in appearance, but since they bear also the hidden recessive character (b), they are hybrid with respect to color.

Likewise with the plants in group 6, which bear seeds that all appear wrinkled yellow, but which are hybrid (Bb) as to color, since the B and the b occur together.

3. Finally, the third class includes only group 9, in which 138 plants bear round yellow seeds so far as appearances go, but, since Aa and Bb are confined together, it is apparent that these seeds are not pure round, but hybrid round, and that the yellows are not pure yellow but hybrid yellow.

Now, by comparing the average number of plants of the groups in the three classes, we get a very close ratio of 1:2:4, since the actual ratios of 32:65:138, approximate almost exactly to the theoretical ratio of 33:65:132.

It therefore appears from the above analysis that there are, in all, nine sorts of forms, as follows, and in the following proportions:

AABB AAbb, aaBB aabb, 2AABb 2aaBb, 2AaBB, 2Aabb, 4AaBb

This expression is evidently a combination series, representing the product of the algebraic expression

$$(AA+2Aa+aa) \times (BB+2Bb+bb),$$

and expresses the full number of possible combinations of germ cells in the hybrids.

After having determined the behavior of the offspring of hybrids in which two pairs of characters were involved, Mendel proceeded to investigate the behavior of hybrids where three character-pairs are introduced, e.g.:

1. Form of seeds, whether round or wrinkled,
2. Color of seeds, whether yellow or green,
3. Color of seed-coats, whether grey-brown or white.

As Mendel says (p. 353), "among all the experiments it demanded the most time and trouble."

From the 24 crosses made, 687 seeds were produced. From these, in the succeeding year, he raised 639 plants which bore fruit. The characters are indicated as before:

Dominant	*Recessive*
A—round seeds	a—wrinkled seeds
B—yellow seeds	b—green seeds
C—grey-brown seed-coats	c—white seed-coats

The character of the seeds borne by these plants was as follows:

CLASS I

			Formula	*Appearance of the seeds*
Group 1	8	plants	AABBCC	round yellow grey
Group 2	14	"	AABBcc	round yellow white
Group 3	9	"	AAbbCC	round green grey
Group 4	11	"	AAbbcc	round green white
Group 5	8	"	aaBBCC	wrinkled yellow grey
Group 6	10	"	aaBBcc	wrinkled yellow white
Group 7	10	"	aabbCC	wrinkled green grey
Group 8	7	"	aabbcc	wrinkled green white
Average	10			

CLASS II

		Formula	Appearance of the seeds
Group 9	22 plants	AABBCc	round yellow grey
Group 10	47 "	AAbbCc	round green grey
Group 11	25 "	aaBBCc	wrinkled yellow grey
Group 12	20 "	aabbCc	wrinkled green grey
Group 13	15 "	AABbCC	round yellow grey
Group 14	18 "	AABbcc	round yellow white
Group 15	19 "	aaBbCC	wrinkled yellow grey
Group 16	24 "	aaBbcc	wrinkled yellow white
Group 17	14 "	AaBBCC	round yellow grey
Group 18	18 "	AaBBcc	round yellow white
Group 19	20 "	AabbCC	round green grey
Group 20	16 "	Aabbcc	round green white
Average	19		

CLASS III

		Formula	Appearance of the seeds
Group 21	45 plants	AABbCc	round yellow grey
Group 22	36 "	aaBbCc	wrinkled yellow grey
Group 23	38 "	AaBBCc	round yellow grey
Group 24	40 "	AabbCc	round green grey
Group 25	49 "	AaBbCC	round yellow grey
Group 26	48 "	AaBbcc	round yellow white
Average	43		

CLASS IV

		Formula	Appearance of the seeds
Group 27	78 plants	AaBbCc	round yellow grey

CLASS I

	Actual conditions as determined by breeding	
Group 1	round yellow grey	Constant
Group 2	round yellow white	"
Group 3	round green grey	"
Group 4	round green white	"
Group 5	wrinkled yellow grey	"
Group 6	wrinkled yellow white	"
Group 7	wrinkled green grey	"
Group 8	wrinkled green white	"

CLASS II

Group 9	round yellow grey (white)	Hybrid
Group 10	round green grey (white)	"
Group 11	wrinkled yellow grey (white)	"
Group 12	wrinkled green grey (white)	"
Group 13	round yellow (green) grey	"
Group 14	round yellow (green) white	"
Group 15	wrinkled yellow (green) grey	"
Group 16	wrinkled yellow (green) white	"
Group 17	round (wrinkled) yellow grey	"
Group 18	round (wrinkled) yellow white	"
Group 19	round (wrinkled) green grey	"
Group 20	round (wrinkled) green white	"

CLASS III

Group 21	round yellow (green) grey (white)	Hybrid
Group 22	wrinkled yellow (green) grey (white)	"
Group 23	round (wrinkled) yellow grey (white)	"
Group 24	round (wrinkled) green grey (white)	"
Group 25	round (wrinkled) yellow (green) grey	"
Group 26	round (wrinkled) yellow (green) white	"

CLASS IV

Group 27	round (wrinkled) yellow (green) grey (white)	Hybrid

We have thus an expression with 27 terms or character-combinations, the members of which manifestly fall into four classes.

Class I, of 8 terms, contains plants that are *constant in all their characters*, as can be seen by inspection, since they all contain the pure dominant or pure recessive of one character, united with a pure dominant or a pure recessive of each of the other two. Each of the character-combinations in Class I occurs on the average in 10 plants.

Class II has 12 terms or character-combinations, each of which is constant for two characters, but inconstant or hybrid in the third. This is illustrated by the combination AABBCc. The symbols indicate that the seeds in this combination are round (AA), yellow (BB), and grey-brown in the seed-coats (Cc). But the fact that c is combined with C indicates that we have here not a pure dominant (CC), but a hybrid (Cc). In other words, AABBCc is *constant for form and seed-color*, but hybrid as to seed-coat color alone (Cc). It will be noticed that the average number of plants per character-combination in Class II is 19.

Class III has 6 terms or character-combinations, with an average of 43 plants to each such combination. All the groups in this class are constant as to one character and hybrid as to the other two. For example, Group 21 bears the sign AABbCc. This means that the seeds of each of the 45 plants in this group had the following appearance: they were all round (AA), yellow (Bb), and grey-brown (as to seed-coat) (Cc). But since B is hybrid as to color of the cotyledons, and since C is accompanied by c it is hybrid as to seed-color and seed-coat color also.

Finally, Class IV has one term with 78 plants, each of which is hybrid with respect to *all three* of the character-pairs.

The ratios in which the average of the plants in each class stand to one another, of 10:19:43:78, are so close to 10:20:40:80, or 1 : 2 : 4 : 8, that there is no doubt whatsoever that this is the actual ratio.

It then appears that the actual condition of things in a hybrid, in which *three* pairs of characters are in question, is a combination obtained by multiplying together the following expressions:

$$\begin{aligned} & AA + 2Aa + aa, \\ & BB + 2Bb + bb, \\ \text{and}\qquad & CC + 2Cc + cc. \end{aligned}$$

The result is that we get all the possible combinations of these various terms (or character-combinations), to the number of 27, as follows:

1 AABBCC
2 AABBcc
3 AAbbCC
4 AAbbcc
5 aaBBCC
6 aaBBcc
7 aabbCC
8 aabbcc
9 2AABBCc
10 2AAbbCc
11 2aaBBCc
12 2aabbCc
13 2AABbCC
14 2AABbcc
15 2aaBbCC
16 2aaBbcc
17 2AaBBCC
18 2AaBBcc
19 2AabbCC
20 2Aabbcc
21 4AABbCc
22 4aaBbCc
23 4AaBBCc
24 4AabbCc
25 4AaBbCC
26 4AaBbcc
27 8AaBbCc

Mendel did not stop here, however, but carried on further experiments in which the remaining characters, i.e., pod-characters, height, etc., were also combined by twos and threes, which he says all gave approximately the same results. From these experiments he concludes that:

"There is therefore no doubt that, for the whole of the characters involved in the experiments, the principle applied that the *offspring of the hybrid in which several essentially different characters are combined exhibit the terms of a series of combinations, in which the developmental series for each pair of differentiating* characters are united. It is demonstrated at the same time that the relation of each pair of different characters in hybrid union is independent of the other differences in the two original parental stocks." (p. 354.)

The last sentence in the above is characteristic of Mendel's type of experimental work, and demonstrates in small compass the difference between his method of attack upon the problem of heredity, and that of all of his predecessors.

Mendel concludes that, where two or more characters are combined in a cross, the offspring of the resulting hybrids form the terms of a series of combinations, in which each pair of differentiating characters is present, either as a pure dominant, or a pure recessive, or a hybrid dominant. Moreover, if there is:

One differentiating pair of characters in the parents, the number of character-combinations, i.e., the number of terms of the series, will be: $3^1 = 3$.

If there are:

Two differentiating pairs of characters in the parents, the number of combinations will be: $3^2 = 9$.

If there are:

Three differentiating pairs of characters in the parents, the number of combinations will be: $3^3 = 27$.

Hence, generalizing, where "n" differentiating pairs of characters are present in the parents, the number of combinations will be 3^n.

Moreover, the total number of individuals which constitute the series will be 4^n, and the number of constant combinations will be 2^n.

To apply this rule to the case which Mendel worked upon, with three differentiating pairs of characters, we have:

$3^n = 3^3 = 27$ (No. of possible character-combinations)
$4^n = 4^3 = 64$ (Individuals in the entire series)
$2^n = 2^3 = 8$ (Constant character-combinations)

"All constant combinations," Mendel says, "which in peas are possible by the combination of the said seven differentiating characters, were actually obtained by repeated crossing. Their number is given by $2^7 = 128$. Thereby is simultaneously given the practical proof *that the* *constant characters which appear in the several varieties of a group of plants, may be obtained in all the associations which are possible according to the mathematical laws of combination, by means of repeated artificial fertilization.*" (p. 355.)

Mendel now undertook to draw conclusions from his data. As we have seen:

> "The offspring of the hybrids of each pair of differentiating characters are, one-half, hybrid again, while the other half are constant in equal proportions having the characters of the seed and pollen parents respectively. If several differentiating characters are combined by cross-fertilization in a hybrid, the resulting offspring form the terms of a combination-series in which the combination series for each pair of differentiating characters are united." (p. 356.)

Mendel then comes finally to these fundamental conclusions:

> "So far as experience goes, we find it in every case confirmed, that constant progeny can only be formed when the egg cells and the fertilizing pollen are of like character, so that both are provided with the material for creating quite similar individuals, as is the case with the normal fertilization of pure species. We must therefore regard it as certain that exactly similar factors must be at work also in the production of the constant forms in the hybrid plants. Since the various constant forms are produced in one plant or even in one flower of a plant, *the conclusion appears logical that in the ovaries of the hybrid, there are formed as many sorts of egg cells, and in the anthers as many sorts of pollen cells, as there are possible constant combination forms, and that these egg and pollen cells agree in their internal composition with those of the separate forms.* (p. 356.)
>
> "In point of fact it is possible to demonstrate theoretically that this hypothesis would fully suffice to account for the development of the hybrids in the separate generations, *if we might at the same time assume that the various kinds of egg and pollen cells were formed in the hybrids on the average in equal numbers.*" (Italics inserted.) (p. 357.)

It was necessary, however, to put these last conclusions to experimental proof.

We have seen from Mendel's results, that in any F_2 generation of a hybrid, the ratio of the "impure" or hybrid type to either of the pure types is as 2 : 1.

We have also seen that the whole of any F_2 generation produced by self-fertilization of the originally formed hybrids of the F_1 generation, consisted of:

$$\underbrace{\begin{array}{lcl}25\% & + & 50\% \\ \text{pure} & & \text{impure} \\ \text{dominants} & & \text{dominants} \\ \text{DD} & & \text{Dr}\end{array}}_{\substack{\text{i.e., } 75\% \\ \text{apparent D}}} \quad + \quad \underset{\substack{25\% \\ \text{pure r}}}{\begin{array}{l}25\% \\ \text{pure} \\ \text{recessives} \\ \text{rr}\end{array}}$$

If now both the male and the female germ cells bear the characters of either the dominant or the recessive in equal numbers, and cross at random, then

$$D \times r = Dr$$
and
$$r \times D = rD$$

Then, when the F_1 hybrid, which we have been calling Dr, but which is also rD, produces its offspring by self-fertilization, we should get four kinds of combinations of germ cells in equal numbers as follows:

1. $D \times D = DD$
2. $D \times r = Dr$
3. $r \times D = rD$
4. $r \times r = rr$

i.e.	25%	25%	25%	25%
	DD	Dr	rD	rr

It is plain that this combination would be a germ-cell analysis of the actual visible result already stated in the ordinary form of a ratio.

25%		50%		25%
DD	:	Dr	:	rr

In order to prove his assumption, "that the various kinds of egg and pollen cells were formed in the hybrids on the average in equal numbers," Mendel carried out the following experiment.

He crossed two forms of peas which were different in both the form and in the color of the seeds. Hence, following the symbols previously used:

A	round seeds	a	wrinkled seeds
B	yellow seeds	b	green seeds

The F_1 hybrids thus produced were sown, and there were also sown seeds of both of the two parental types. AB and ab crosses were then made as follows:

1. The F_1 hybrids were crossed with pollen of AB (round yellow)
2. The F_1 hybrids were crossed with pollen of ab (wrinkled green)
3. AB (round yellow) were crossed with pollen of F_1 hybrids.
4. ab (wrinkled green) were crossed with pollen of F_1 hybrids.

All of the flowers on each of three plants were pollinated for the purpose of this experiment.

We have seen that, on the basis of the theory already stated, the offspring of an F_1 hybrid, when one character-pair is involved, should be: AB, Ab, aB, and ab, in equal numbers.

In the crossing experiment just undertaken, there would then be the following combinations:

Series
1. Egg cells AB, Ab, aB, ab, × pollen cells AB
2. Egg cells AB, Ab, aB, ab, × pollen cells ab
3. Egg cells AB, × pollen cells AB, Ab, aB, ab
4. Egg cells ab, × pollen cells AB, Ab, aB, ab

There would then result combinations as follows:

Series				
1.	AABB	AABb	AaBB	AaBb
2.	AaBb	Aabb	aaBb	aabb
3.	AABB	AABb	AaBB	AaBb
4.	AaBb	Aabb	aaBb	aabb

The appearance of the seeds and their actual composition would be then as follows:

SERIES I

Formula	*Appearance*	*Actual Composition*	*Behavior*
AABB	round yellow	round yellow	constant
AABb	round yellow	round yellow (green)	hybrid
AaBB	round yellow	round (wrinkled) yellow	hybrid
AaBb	round yellow	round (wrinkled) yellow (green)	hybrid

SERIES II

Formula	*Appearance*	*Actual Composition*	*Behavior*
AaBb	round yellow	round (wrinkled) yellow (green)	hybrid
Aabb	round green	round (wrinkled) green	hybrid
aaBb	wrinkled yellow	wrinkled yellow (green)	hybrid
aabb	wrinkled green	wrinkled green	constant

SERIES III

Formula	*Appearance*	*Actual Composition*	*Behavior*
AABB	round yellow	round yellow	constant
AABb	round yellow	round yellow (green)	hybrid
AaBB	round yellow	round (wrinkled) yellow	hybrid
AaBb	round yellow	round (wrinkled) yellow (green)	hybrid

SERIES IV

Formula	*Appearance*	*Actual Composition*	*Behavior*
AaBb	round yellow	round (wrinkled) yellow (green)	hybrid
Aabb	round green	round (wrinkled) green	hybrid
aaBb	wrinkled yellow	wrinkled yellow (green)	hybrid
aabb	wrinkled green	wrinkled green	constant

If, as Mendel assumed, the egg and pollen cells bore the different characters of dominant and recessive in equal numbers, then we would expect in each experiment, that the four combinations would be produced in equal numbers.

It is plain, that in the *first* and *third* series all the seeds *appear round* and yellow.

In the *second* and *fourth* series, one lot would appear *round yellow*, another *round green*, another *wrinkled yellow*, and a fourth *wrinkled green.*

The actual experiment bore out the theoretical expectation.

No. of seeds	*Appearance of seeds*
Series 1 yielded 98	round yellow
Series 2 yielded 31	round yellow
26	round green
27	wrinkled yellow
26	wrinkled green
Series 3 yielded 94	round yellow
Series 4 yielded 24	round yellow
25	round green
22	wrinkled yellow
27	wrinkled green

It is clear thus far, as to the outcome in series 2 and 4. In both cases, the four different possible combinations were produced in equal numbers. It now remained to determine the actual composition of the 98 and 94 seeds in the first and third series, respectively. All of the seeds of each of these two series were sown. From the 98 seeds of Series I, 90 plants resulted, and from the 94 seeds of the second series, came 87 plants.

These all yielded as follows:

	No. of seeds	*Composition*	*Formula*
Series I yielded	20	round yellow	AABB
	23	round yellow (green)	AABb
	25	round (wrinkled) yellow	AaBB
	22	round (wrinkled) yellow (green)	AaBb
Series III yielded	25	round yellow	AABB
	19	round yellow (green)	AABb
	22	round (wrinkled) yellow	AaBB
	21	round (wrinkled) yellow (green)	AaBb

This means that, when all of the 90 plants in Series I ran to seed, 20 of them yielded *all round yellow* seeds; 23 plants yielded *yellow and green* seeds in a ratio of 3 : 1, and thereby showed that, *although looking round yellow*, their actual composition was round yellow (*green*) *AABb*. Likewise, there were 25 that yielded *round yellow and wrinkled yellow* in the ratio of 3 : 1, thereby proving that their original composition, although they also all *looked round yellow*, was actually *round* (*wrinkled*) *yellow*, *AaBB*. The same hybrid condition (*for both character-pairs*) was also shown to exist for the 22 seeds of the 90 plants in Series I, which split up into plants bearing partly wrinkled and green seeds as recessives, thus revealing the original composition of these 22 seeds sown to be AaBb.

The analysis having been made clear for Series I and III, let us turn back to Series II and IV, and see what their actual composition turned out to be. Mendel found as follows:

SERIES II

The 31 round yellow seeds yielded plants with round (wrinkled) yellow (green) seeds—AaBb

The 26 round green seeds yielded plants with round (wrinkled) green seeds—Aabb

The 27 wrinkled yellow seeds yielded plants with wrinkled yellow (green) seeds—aaBb

The 26 wrinkled green seeds yielded plants with wrinkled green seeds —aabb

SERIES IV

The 24 round yellow seeds yielded plants with round (wrinkled) yellow (green) seeds—AaBb

The 25 round green seeds yielded plants with round (wrinkled) green seeds—Aabb

The 22 wrinkled yellow seeds yielded plants with wrinkled yellow (green) seeds—aaBb

The 27 wrinkled green seeds yielded plants with wrinkled green seeds —aabb

From all of which it appears that the actual composition of the seeds of the four series was as follows, summarizing:

Series I	20	AABB	Series III	25	AABB
	23	AABb		19	AABb
	25	AaBB		22	AaBB
	22	AaBb		21	AaBb
Series II	31	AaBb	Series IV	24	AaBb
	26	Aabb		25	Aabb
	27	aaBb		22	aaBb
	26	aabb		27	aabb

It is now perfectly plain that the crossed plants in the four series gave, *in each series*, *all four* of the theoretically possible combinations for the series, and in equal numbers throughout.

It is also plain that Series I and III, which are reciprocals, are alike, and that Series II and IV, which are also reciprocals, are also alike in the composition of their seeds.

This would have seemed sufficient to prove the correctness of Mendel's theory, *that the pollen and egg cells of the hybrids carry the dominant and the recessive characters in equal numbers, and that consequently, in self-fertilized hybrids, all the possible combinations of the unitary characters called "dominant" and "recessive" are to be found in the pollen and egg cells in equal numbers.*

Mendel did not rest content, however, with the demonstration which the experiment with the seed characters alone afforded. He likewise experimented with the characters of flower-color and length of stem, conducting the experiment so that, in the third year of the investigation, each character ought to appear in half of the plants, if the theory were correct.

Using *violet-red* flower color as against *white*, and *long* stem as against *short*, he had 166 plants to flower in the third year, distributed as follows:

Class	*Color of flower*	*Stem*	*No. of plants*
1	violet-red	long	47
2	white	long	40
3	violet-red	short	38
4	white	short	41

It is plain that the result is the same in kind as Mendel obtained with the seed-characters. Even in addition to the experiments already carried out, Mendel further says:

> "For the characters of form of pod, color of pod, and position of flowers, experiments were also made on a small scale, and results obtained in perfect agreement. All the differentiating characters duly appeared, and in nearly equal numbers." (p. 361.)

It is therefore evident that Mendel was justified in arriving at the conclusions:

> "Experimentally, therefore, the theory is confirmed, that the pea hybrids form egg and pollen cells which, in their constitution, represent in equal numbers all constant forms which result from the combination of the characters united in fertilization." (p. 361.)
>
> "The law of combination of different characters which governs the development of the hybrids finds therefore its foundation and explanation in the principle enunciated, that the hybrids produce egg cells and pollen cells which in equal numbers represent all constant forms which result from the combination of the characters brought together in fertilization." (p. 364.)

Mendel finally concludes this memorable paper with a brief account of crossing experiments with a Pole Garden Bean, *Phaseolus vulgaris*, growing 10 to 12 feet in height, and *Phaseolus nanus*, a dwarf variety. *Phaseolus vulgaris* had yellow pods constricted when ripe, and *Phaseolus nanus* green pods inflated when ripe. Mendel found that tall stems, green pod-color, and inflated pod-form were dominant over short stems, yellow color, and constricted pod-form.

This concludes a rather full account and analysis of Mendel's celebrated report on the behavior of hybrids. Nothing in any wise approaching this masterpiece of investigation had ever appeared in the field of hybridization. For far-reaching and searching analysis, for clear thinking-out of the fundamental principles involved, and for deliberate, painstaking, and accurate following-up of elaborate details, no single piece of investigation in this field before his time will at all compare with it, especially when we consider the absolute absence of precedent and initiative for the work. In a way, Darwin's experimental work in the crossing of plants resembles it. Indeed, when we regard Mendel's work in the light of its pioneer quality, exhaustive mastery of details, marshalled throughout with reference to a fundamental motive that was never lost sight of, we may well find no comparison for Mendel's work than with that of Darwin.

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CHAPTER XI

34. *The Discovery of Mendel's Papers.*

THE re-discovery of Mendel's papers was announced in the three following contributions; during the months of March and April, 1900:

De Vries, Hugo.

1. Das Spaltungsgesetz der Bastarde (Vorläufige Mittheilung). Article No. 11, in Berichte der deutschen botanischen Gesellschaft, Vol. 18, pp. 83-90. (Received for publication, March 14, 1900.)
2. Sur la loi de disjonction des hybrides. Note de M. Hugo De Vries, présentée par M. Gaston Bonnier, Comptes Rendus de l'Académie des Sciences, Paris, Vol. 130, pp. 845-7. (Received for publication March 26, 1900, but appearing in publication before the preceding.)

   A further paper of significance is the following:
3. Über erbungleiche Kreuzungen (Vorläufige Mittheilung). Article No. 53, in Berichte der deutschen botanischen Gesellschaft, Vol. 18, pp. 435-43. (Received for publication November 21, 1900.)

Correns, C.

G. Mendels Regel über das Verhalten der Nachkommenschaft der Rassenbastarde. Article No. 19 in the Berichte der deutschen botanischen Gesellschaft, Vol. 18, pp. 158-68. (Received for publication, April 24, 1900. Dated Tübingen, April 22, 1900.)

Tschermak, E. von.

1. Über künstliche Kreuzung bei *Pisum sativum*, Article no. 26. Berichte der deutschen botanischen Gesellschaft, Vol. 18, pp. 232-9. (Received for publication, June 2, 1900.)

2. Über künstliche Kreuzung bei *Pisum sativum*, Zeitschrift für das landwirtschaftliche Versuchswesen in Oesterreich. 3 Jahrgang, Heft. 5, pp. 465-555, 1900.

Of the three authors, priority in respect of publication of results lies with Hugo De Vries, then Professor of Botany at the University of Amsterdam (now retired), in his paper, "Das Spaltungsgesetz der Bastarde," constituting Article No. 11 of Vol. 18, of the Berichte der deutschen botanischen Gesellschaft. (Received for publication March 14, 1900.)

The second in order of publication was that of Professor Carl Correns, then Professor of Botany at the University of Tübingen, now Director of the Kaiser Wilhelm Institut für Biologie, Berlin-Dahlem, in Article 19, of Vol. 18 of the Berichte der deutschen botanischen Gesellschaft. (Received for publication, April 24, 1900.)

Third in publication was the paper of Dr. Erich von Tschermak, now Professor in charge of the Lehr-Kanzel für Pflanzenzüchtung, at the Hochschule für Bodenkultur at Vienna; published in Vol. 18, pp. 232-9, of the Berichte der deutschen botanischen Gesellschaft. Received for publication June 2, 1900, and followed by a paper of the same title as above, given in the Zeitschrift für das landwirtschaftliche Versuchswesen in Oesterreich, 3 Jahrgang, Heft. 5, pp. 465-555.

Following are the statements by the three discoverers of Mendel's epoch-making paper of investigation, as to the manner of its discovery by them individually. These reports are in the form of letters to the author, written on request, for inclusion herein. The communication of De Vries is in English; those of Correns and von Tschermak are in German, and are translated for publication. A portion of the Correns report is taken from the article entitled "Etwas über Gregor Mendel's Leben und Wirken" in Die Naturwissenschaften, Jahrgang 10, Heft 29 (July 21, 1922), pp. 629-31, kindly also sent by Professor Correns. Further data are supplied from letters to the author.

PLATE XLIV. Professor Hugo De Vries, University of Amsterdam (retired).

1848 - 1935

De Vries (letter of December 18, 1924)*:*

> "When preparing my book on the Mutation Theory, I worked on the basis of Darwin's Hypothesis of Pangenesis, and of the version of it proposed in my Intracellular Pangenesis. The main principle of Pangenesis is the conception of unit characters. This led on the one side to the theory of the origin of species by means of mutations, and on the other to the description of the phenomena of hybridization as recombinations of these units. In 1893, I crossed *Oenothera lamarckiana* with *O. lam. brevistylis*, and found their progeny to be uniform, and true to the specific parent in 1894, but splitting in the second generation 1895, giving 17-26 individuals with the recessive character (Mut. The. 11, p. 157). Many other species were tried with the same result, and dihybrid crosses showed the laws of chance to be valid for them also. After finishing most of these experiments, I happened to read L. H. Bailey's 'Plant Breeding' of 1895.[1] In the list of literature of this book, I found the first mention of Mendel's now celebrated paper, and accordingly looked it up and studied it. Thereupon I published in March 1900 the results of my own investigations in the Comptes Rendus de l'Académie des Sciences, T. CXXX, p. 845, under the title of 'Sur la loi de disjonction des hybrides,' and shortly afterwards, in the same year, in the Berichte der deutschen botanischen Gesellschaft, T. XVIII, p. 83, (March 14, 1900). A full account of my experiments was given in the second volume of the German edition of my Mutation Theory, 1903."

The paper of De Vries, "Sur la loi de disjonction des hybrides," appearing in the Comptes Rendus for March 26, 1900, states quite briefly results similar to those of Mendel, but obtained anterior to the author's re-discovery of the Mendel paper.

Although from the printed volumes of the Comptes Rendus and of the Berichte d. d. bot. Gesellschaft it appears that the longer and fuller article, in German, in the latter, was received

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[1] Professor Bailey's account of the manner in which the reference to Mendel's paper came to be included in his book on "Plant Breeding," is found in a footnote to "Plant Breeding" by L. H. Bailey, 4th ed., 1908, p. 155, as follows:

"The following extract from a recent letter from Professor De Vries (printed here by permission) will explain the reference in the text. 'Many years ago you had the kindness to send me your article on Cross-Breeding and Hybridization, of 1892; and I hope it will interest you to know that it was by means of your bibliography therein that I learnt some years afterwards of the existence of Mendel's papers, which now are coming to so high credit. Without your aid I fear I should not have found them at all.'" Professor Baily concludes:

"My reference to Mendel in the bibliography referred to was taken from Focke's writing. I had not seen Mendel's paper. The essay, 'Cross-Breeding and Hybridization,' forms Chapter II of the present book; but the bibliography that accompanies it was not printed until the second edition of the book."

for publication first, March 14, 1900, yet the brief two-page article in French in the Comptes Rendus, dated March 26, 1900, was the first actually to appear.

In the Comptes Rendus article, no mention is made of Mendel's paper, but the author's own results are given. In the article in the Berichte, however, Mendel's paper is discussed, and the author's own results in harmony therewith are given in detail.

Following are abstracts of the three principal papers of De Vries concerned with the Mendelian discovery:

a. *De Vries, Hugo.*

Sur la loi de disjonction des hybrides.

Comptes Rendus, T. 130, pp. 845-7, 1900. (1b.)

The author cites from his Intracellular Pangenesis, 1889, the principle enunciated that the

> ". . . specific characters of organisms are composed of very distinct units. One is able to study experimentally these units, either in the phenomena of variability, of mutability, or by the production of hybrids. In the latter case, one chooses by preference hybrids whose parents are not distinguished among themselves except by a single character (mono-hybrids), or by a small number of characters, well delimited, and from which one does not consider but one or two of these units, while leaving the others to one side." (*ib.*, p. 845.)
>
> "Ordinarily hybrids are described as participating at the same time in the characters of the father and of the mother. In my opinion one ought to admit, in order to understand this fact, that the hybrids have, some of them, the simple characters of the father, and others characters equally simple of the mother. But when the father and the mother are not distinguished except in a single point, the hybrid could not hold the mean between them; because the simple character should be considered as a non-divisible unit." (*ib.*, p. 845.)
>
> "The hybrid shows always the character of one of the two parents, and that always in all its force; never is the character of one parent, which to the other is lacking, found reduced by half." (*ib.*, p. 845.)
>
> "Ordinarily," De Vries comments, "it is the character of the species which supervenes over that of the variety, or the older character over the younger. . . . But," he adds, "I have observed diverse exceptions to these rules." (*ib.*, p. 845.)

De Vries then adds:

> "In the hybrid, the simple differentiating character of one of the parents is then visible or dominant; while the antagonistic character is in a latent or recessive state." (*ib.*, p. 845.)
>
> "The antagonistic characters remain ordinarily combined during the vegetative life, these dominant, the others latent. But in the generation period they are disjoined. Each grain of pollen and each oosphere receives but one of the two." (*ib.*, p. 845.)

The important statement then follows:

> "For monohybrids, one has then the *proposition that their pollen and their ovules are no longer hybrids*, that they have the character pure of one of the parents, and the same proposition may be sustained for the others (di- and polyhybrids), when one considers each time but a single simple character." (*ib.*, p. 846.)

> "From this principle one is able to deduce nearly all the laws which govern the distribution of characters of hybrids." (*ib.*, p. 846.)

De Vries then gives a table of eleven species, from which, when cross-fertilized, he found:

> ". . . for the products, the following proportion of individuals presenting the recessive characters." (*ib.*, p. 846.)

Parent having the dominant character	*Parent having the recessive character*	*Proportion of hybrid with the recessive character*
Agrostemma githago	A. nicaeensis	24
Chelidonium majus	C. laciniatum	26
Coreopsis tinctoria	C. brunnea	25
Datura tatula	D. stramonium	28
Hyoscyamus niger	H. pallidus	26
Lychnis diurna (red)	L. vespertina (white)	27
Lychnis vespertina (pubescent)	L. glabra (smooth)	28
Oenothera lamarckiana	O. brevistylis	22
Solanum nigrum	S. chlorocarpum	24
Trifolium pratense	T. album	25
Veronica longifolia	V. alba	22

From these results he deduced the conclusion:

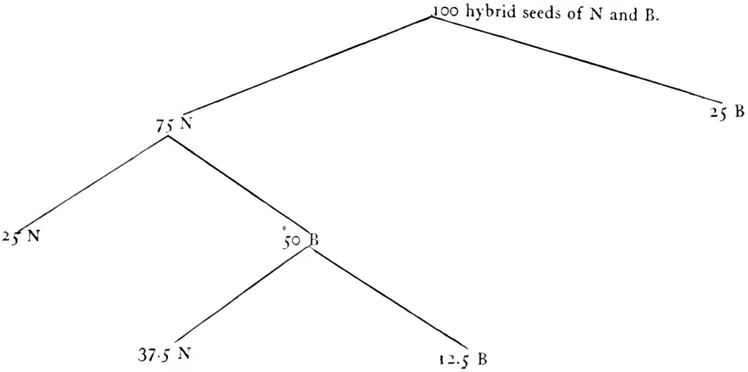
> "We see the recessive character is always near 25 per 100." (*ib.*, p. 846.)

The author then goes on to state that:

> "The cultivation of a further generation permits making a distinction among the 75 per 100 individuals presenting the dominant character."

He then cites the results with a poppy having a black basal spot upon the petals, with one having a white spot. Calling the former N, and the latter B, he obtained, as for the preceding, 75 per cent N and 25 per cent B, in the hybrids of the first generation. From the seeds of these hybrid plants, self-fertilized and sowing the seeds from each plant in a separate plot, he obtained for 25 out of the 75 plants bearing N, a pure progeny with black petals, and for the 50 others, a mixture of plants with black petals, and of plants with white petals, in the proportion of 37.5 N to 12.5 B. He concludes:

"We then have, summarizing the results of the two successive cultures:



(Diagram inserted.)

De Vries further adds:

"I have, thus far, studied two other successive generations of these same hybrids. They have repeated each time the same phenomenon of disjunction.

"I have obtained the same results with the hybrids of sugar maize and of starchy maize, in which the endosperms are visibly hybrid at the same time as the embryo." (*ib.*, p. 847.)

He then states a general conclusion as follows:

"One may condense the ensemble of these results by supposing that the two antagonistic qualities, dominant and recessive, are disposed in equal parts, in the pollen as in the ovules.

"If one calls D the grains of pollen or the ovules having a dominant character, and R those which have the recessive character, one may represent the number and nature of the hybrids by the following representative formula in which the numbers D and R are equal:

$$(D + R) \times (D + R) = D^2 + 2DR + R^2$$

"This amounts to saying that there will be 25 per 100 of D, 50 per 100 of DR and 25 per 100 of R.

"The individuals D will have the dominant character pure, having inherited it from the father and from the mother. In the same manner, the individuals R will have the recessive character pure, while DR will be hybrids. These will carry the dominant character apparent and the recessive character latent.

"One will not be able to distinguish the 25 per 100 D from the 50 per 100 DR, except by a second culture." (*ib.*, p. 847.)

De Vries' final conclusion is:

"The *ensemble* of these experiments puts then in evidence the law of the disjunction of hybrids, and confirms the principle I have enunciated upon the specific characters considered as distinct units." (*ib.*, p. 847.)

The next paper to be considered is:

De Vries:

Das Spaltungsgesetz der Bastarde.

Ber. d. d. bot. Ges., Vol. 18, pp. 83-90. (1a).

In this communication, De Vries again cites his Intracellular Pangenesis (pp. 60-75) for his original thesis, that:

> "The whole character of the plant is built up of definite units. These so-called elements of the species, or elementary characters, one thinks of as bound to material carriers. To each individual character there corresponds a special form of material carrier. Transitions between these elements are as little found as between the molecules of chemistry." (1a, p. 83.)

De Vries then goes on to say:

> "In this latter domain [i.e., that of hybrids], it demands a complete changing about of the views from which investigation has to proceed.
>
> "Nowhere as clearly as here [i.e., in the experiments on crossing and hybridization] does the image of the species appear in contra-distinction to its composition out of independent factors in the background." (Intracellular Pangenesis, German ed., 1889, p. 25.)

De Vries then comments on the fact that the then existing doctrine regarding hybrids regards species, sub-species, and varieties, as the units, the combination of which form hybrids, a distinction being made between crosses of varieties, and the true hybrids of species. (1a, p. 84.)

This attitude is, according to his views, to be given up for physiological investigation. (1a, p. 84.)

> "In its stead is to be placed the principle of the crossing of species-characters. The units of species-characters are accordingly to be regarded and studied as sharply separated magnitudes. They are to be treated as being independent of one another everywhere, and as long as no grounds for the contrary are apparent. In every crossing experiment, there is accordingly only one character, or a definite number of such, to be taken into observation: the remainder may, for the time, be left out of consideration. Or rather it is indifferent whether the parents differ from one another in still other points. For the experiments, however, manifestly the hybrids, both of whose parents differ only in the one character, form the simplest cases [monohybrids in contrast to di- and polyhybrids]."

If the parents of a hybrid diverge from one another in only one point, or if one takes one or a few of their points of difference into consideration, then they are in these characters antagonistic, in all others alike, or, for the calculation, indifferent; the crossing experiment will therefore be limited to the antagonistic characters.

"My experiments," he says, "have led me to the following principles:

1. "*Of the two antagonistic characters, the hybrid carries only the one and, indeed, in complete expression.* It is accordingly in this point not to be distinguished from one of the two parents. Intermediates do not occur.

2. "*On the formation of the pollen and egg cells the two antagonistic characters separate.* They follow accordingly, in the majority of cases, simple laws of probability. These two principles, in the most essential points, have already been propounded a long time since by Mendel, for a special case (peas). They passed, however, again into oblivion, and were misunderstood. They obtain generally according to my experiments, for true hybrids.

"The lack of intermediates, between any two simple antagonistic characters in the hybrids, is perhaps the best proof that such characters are indeed delimited units. (1a, pp. 84-5.)

"That polyhybrids so often represent intermediate forms, rests manifestly upon the fact that they have inherited a part of their characters from the father, another part from the mother. With monohybrids, such, however, is not possible.

"Of the two antagonistic characters, that visible in the hybrid is the *dominating*, the latent is the recessive." (*ib.*, p. 85.)

In regard to Mendel's paper, De Vries remarks further in a footnote (1a, p. 85):

"This important treatise is so seldom cited, that I myself for the first time came to know about it *after I had closed the majority of my experiments, and had derived therefrom the principles contributed in the text.*"

The italics are inserted, in order to call more definite attention to this very important fact, in view of the almost parallel nature of the conclusions of De Vries with those arrived at by Mendel himself.

In the following section of his paper, De Vries goes on to state (p. 85):

"In the hybrid, the two antagonistic characters lie near one another as primordia. In vegetative life only, the dominating one is ordinarily visible. Exceptions are seldom." (*ib.*, p. 86.)

As such De Vries cites the case of *Veronica longifolia* (*blue*) × *V. longifolia* (*alba*), in which inflorescences occur, the flowers of which are white on the one side, and blue on the other. Such cases De Vries calls sectional splittings (sectionale Spaltungen).

Continuing, it is stated as to the primordia of the antagonistic characters:

"On the formation of the pollen grains and egg cells, they separate. The individual pairs of antagonistic characters behave at that time independently of one another."

From this separation results the law:

> "The pollen grains and egg cells of the monohybrids are not hybrids, but belong purely to the one or the other of the two parental types. For di-polyhybrids the same holds good, in relation to every character regarded by itself." (*ib.*, p. 86.)

De Vries then proceeds to the now well-known statement of the situation in a hybrid, as regards the pollen and egg cells, in the representation of the dominant and the recessive characters, which is substantially as previously stated by the author in the Comptes Rendus, except for the addition of the following general statement:

> "In the simplest case, the splitting manifestly occurs in equal halves, and one gets:
> 50% dom. + 50% rec. pollen grains,
> 50% dom. + 50% rec. egg cells." (p. 86.)

For the existence of 75 per cent with the dominant and 25 per cent with the recessive character among the progeny of a monohybrid, De Vries adduces data from his own experiments with a considerable number of species. He says:

> "This composition I found to be verified in very many experiments." (*ib.*, p. 87.)

In addition to the crosses reported in the Comptes Rendus, De Vries cites the following ratios, giving in each case the year of the cross. Some of these were also given in the brief note in the Comptes Rendus.

1. A. BY ARTIFICIAL CROSSING

Dominating	*Recessive*	*Rec. %*	*year of the cross*
Agrostemma githago	A. nicaeensis	24	1898
Chelidonium majus	C. laciniatum	26	1898
Hyoscyamus niger	H. pallidus	26	1898
Lychnis diurna (red)	L. vespertina (white)	27	1892
Lychnis vespertina (pubescent)	L. glabra (smooth)	28	1892
Oenothera lamarckiana	O. brevistylis	22	1898
Papaver somniferum (Mephisto)	P. (Danebrog)	28	1893
Papaver somniferum nanum (single)	P. somniferum nanum (double)	24	1894
Zea mays (starchy)	Zea mays saccharata	25	1898
Aster tripolium	A. album	27	1897
Chrysanthemum roxburghi (yellow)	C. album	23	1893
Coreopsis tinctoria	C. brunnea	25	1896
Solanum nigrum	S. chlorocarpum	24	1894
Veronica longifolia	V. alba	22	1894
Viola cornuta	V. alba	23	1899

The mean for all the experiments is given as 24.93 per cent. De Vries adds further:

> "The experiments comprise ordinarily a few hundred, sometimes about 1.000 individuals. With many other species I obtained corresponding results." (1a, p. 87.)

The analysis of the 75 per cent apparently dominant follows:

> "The distinguishing of the remaining 75% in the two groups cited is much more troublesome. It requires that a number of individuals with the dominating character be fertilized with their own pollen, and that, in the next year, for every plant, the progeny be cultivated and counted. This was carried out in 1896 for *Papaver somniferum* (*Mephisto*) × *Danebrog*. From the first generation of 1895, the progeny of the succeeding year were found to be as follows:

Dominating (Mephisto)	24%
Hybrids (with 25% Danebrog)	51%
Recessive (Danebrog)	25%" (*ib.*, p. 87.)

De Vries states (*ib.*, p. 88.):

> "This result corresponds to the above assumed formula. Or, more correctly, out of these figures I first derived the formula.
>
> "The dominating and the recessive characters show themselves accordingly constant in the progeny, as far as they were isolated through segregation. The hybrids, however, split again according to the same law. They furnished, in this experiment, on the average, 77% with the dominating, and 23% with the recessive character.
>
> "This behavior remains, in the course of the years, the same. I have continued this experiment through two still further generations. The 50% hybrids split; the 25% dominating remain constant." (*ib.*, p. 88.)

De Vries also confirms the principle that the hybrid, crossed with either of the two parents, gives the progeny which, for the character in question, are 50 per cent: 50 per cent. The cases are:

	%	*Year*
Clarkia pulchella × *white*	50	1896
Oenothera lamarkiana × *brevistylis*	55	1895
Silene armeria (*red*) × *white*	50	1895

Crosses were also made (1897), between the prickly *Datura tatula* and the smooth *D. stramonium inermis*. The plants of the first generation were blue with prickly fruits, as follows:

Flowers	%
blue (dom. + hybrid)	72
white (recessive)	28

Fruits	%
Smooth blue	26.8
Smooth white	28.0
Av.	27.4 (*ib.*, p. 89.)

A cross was made between *Trifolium pratense album* and *T. pratense quinquefolium*, with the following results:

			Expt.	*Calc.*
1. red,	3	leaflets	13	19
2. white,	5	"	21	19
3. red,	5	"	61	56
4. white,	3	"	5	6

These were for about 220 plants.

De Vries closes with the important statement (p. 89):

> "It is frequently possible, through the segregation experiments, to separate simple characters into several factors. Thus, the color of flowers is frequently composite and, after crossing, one obtains the individual factors, in part separated, in part in different mixtures."

Experiments with *Antirrhinum majus*, *Silene armeria*, and *Prunella vulgaris*, are stated as confirming the above.

De Vries' final statement is (*ib.*, p. 90):

> "From these, and numerous further experiments, I conclude that the law of segregation (Spaltungsgesetz), found by Mendel for peas, finds a very general application, and that, for the study of the units out of which the species-character is composed, it has a quite fundamental significance." (*ib.*, p. 90.)

One of the most striking features of the above paper is the anticipation by De Vries of the multiple factor explanation for certain characters such as flower color, first reported upon experimentally by Bateson for the crossing of two white sweet peas of the Emily Henderson variety, which gave purple in the F_1.

The next paper in the series to be considered is the third paper of De Vries on "Erbungleiche Kreuzungen (Vorläufige Mittheilung)," constituting No. 53, in the Ber. d. d. Bot. Gesell., November 21, 1900. (1c.)

De Vries in this article, briefly begins by summarizing the Mendelian discovery.

> "In a paper published in these 'Berichte' concerning the *Law of Segregation* of hybrids, I have shown that this law which Mendel had derived from his investigations with peas, finds a very general application in the plant kingdom, and is of capital importance for the theory of hybridization. The since published important extensive investigations of Correns, Tschermak, Webber and others, have established in part the correctness of Mendel's results [Erfahrungen], and in part the justification of this generalization.
>
> "Mendel had demonstrated for his peas-crosses, that their results could be derived in simple manner from certain principles. In the first place

he found that, in the vegetative development of the hybrid individuals, the one character of every character-pair is dominant (dominierend), and the other recessive. On the formation of the sex organs, however, the antagonistic characters, united in the hybrid, separate in such manner that, in respect to each individual pair, the egg cells and pollen grains are no longer hybrids. This splitting occurs in equal parts, in that 50% of the sexual cells contain the one, and 50% the other character of each pair. In respect to this splitting, the two antagonistic characters are of *equal value*, independently of the question as to whether they are dominating or recessive in the vegetative life." (1c, pp. 435-6.)

The remainder of the paper is a discussion of an apparent exception to the law of equal splitting, as demonstrated by certain *Oenothera* crosses.

This concludes the contributions of De Vries to the Mendelian discovery.

It would not do full justice to the work of De Vries in this connection, if adequate cognizance were not taken of his point of view in certain fundamental matters bearing upon the unit-factor hypothesis, already propounded in his "Intracellular Pangenesis," originally published in German in 1889. (1e.) The following extracts are taken from the English translation of 1910 (1d), which renders the original without revision. (Italics, where used, are inserted throughout.)

Referring to the nature of specific characters, De Vries says:

"*But, if the specific characters are regarded in the light of the theory of descent, it soon becomes evident that they are composed of single factors more or less independent of each other. One finds almost every one of these factors in numerous species, and their varying groupings and combinations with less common factors cause the extraordinary diversity in the organic world.*

"Even the most cursory comparison of the various organisms *leads, in this light, to the conviction of the composite nature of specific characters.*" (ed. 1910, p. 11; ed. 1889, p. 8.)

Again, "the variation of the individual hereditary characters independently of one another" ["Das Variiren der einzelnen erblichen Eigenschaften unabhängig von einander"] (ed. 1910, p. 19; ed. 1889, p. 16), constituted the subject of a not inconsiderable discussion, in which it is stated:

"A comparative consideration of the organic world convinces us that *the hereditary characters of a species, even if connected with one another in various ways, are yet essentially independent entities, from the union of which the specific characters originate.*"

The fact is emphasized that, in both the plant and the animal kingdoms:

> "The independent varying of single characteristics forms the rule, while the combined variation of them is the exception." (ed. 1910, p. 21; 1889, p. 17.)

De Vries then asserts, in a significant and for the time rather remarkable sentence, that:

> "In most cases it cannot be decided whether the germ attribute is determined by a single hereditary character or by a small group of them."

The section closes with a significant comment upon one phenomenon, which, he says,

> "greatly complicates the study of hereditary characters," viz., the fact "of their being commonly united in smaller or larger groups which behave like units, the single members of the groups usually appearing together."

De Vries remarks upon the fact that different authors, such as Darwin and Nägeli, have also strongly emphasized this point, but, he adds, the working-out of the theory in detail is rendered difficult by the fact that:

> "In many cases it will obviously be extremely difficult to decide whether one is dealing with a single hereditary character, or with a small group of them." (ed. 1810, pp. 23-4; ed. 1889, pp. 21-2.)

It will be especially interesting to quote rather fully from the discussion on the matter of unit-characters in hybrids:

> "In summarizing briefly what has been said, we see that experiments and observations on the origin and fixing of variations teach us to recognize hereditary characters as units with which we can experiment. They teach us further that these units are miscible in almost every proportion, most experiments really amounting merely to a change in this proportion." (ed. 1910, p. 27; ed. 1889, p. 24.)
>
> "The above considerations are verified in a striking manner by experiments in hybridization and crossing. In no other connection does the conception of a species as a unit made up of independent factors stand forth so clearly. Everyone knows that the hereditary character of two parents may be mixed in a hybrid. And the excellent experiments of many investigators have taught us how, in the descendants of hybrids, an almost endless variation can be observed, which is essentially due to a mixing of the characteristics of the parents in a most varied manner." (ed. 1900, p. 27; ed. 1889, p. 25.)
>
> "The hybrids of the first generation have quite definite characteristics for each pair of species. If one produces a hybrid of two species, which previous investigators have already succeeded in crossing, he can, as a rule, rely on the description given of it tallying exactly with the newly produced intermediate form. If the hybrid is fertile without the help of its parents, and if its progeny are grown through a few generations

in thousands of specimens, one can almost always observe that hardly any two are alike. Some revert to the form of the pollen-parent, others to that of the pistil-parent, a third group occupies a central position. Between these are placed the others, in the most motley variety of staminate and pistillate characteristics and in almost every graduation of mutual intermixture." (ed. 1910, p. 27; ed. 1889, p. 25.)

"Many and prominent authors have pointed out the significance of hybrids for establishing the nature of fertilization. With the same right, we may use them in trying to penetrate into the mystery of specific character. And then they clearly prove to us that this character is fundamentally not an indivisible entity. *The characteristics of a hybrid* (*of the first generation*) *are as sharply defined and as constant, and on the whole of the same order, as those of the pure species, and the frequent specific name,* 'hybridus,' might go to prove that even the best systematists felt this agreement." (ed. 1910, p. 28; ed. 1889, p. 26.)

De Vries remarks, with considerable acumen, that the combination in a hybrid, of two, three, or more species, is not in itself a matter of importance. The species entity concept was discarded by him for the unit-character concept, already as early as 1889. There is no reason other than a purely practical one, why any limit need be put to the number of species entering into the hybrid composition; why,

". . . in fact, there should not be combined in one hybrid characteristics which have been taken from an unlimited series of allied species. But this is of small importance, the chief point being the proposition that the *character of a pure species, like that of hybrids is of a compound nature.*" (ed. 1910, pp. 27-8; ed. 1889, pp. 24-6.)

Further on he says:

"The process of fertilization, in its essence, does not consist therefore in the union of two sexes, but in the mixing of the hereditary characters of two individuals of different origin, or at least such as have been subjected to different external conditions." (ed. 1910, p. 31; ed. 1889, p. 29.)

Further comment on the subject of the existence of hereditary characters as factorial units or unit factors is as follows:

"*Let us regard the individual hereditary factors as independent units, which can be combined with each other in different proportions into the individual character of a plant.*" (ed. 1910, p. 31; ed. 1889, p. 29.)

"*In the preceding paragraphs we have seen how the single hereditary characters occur as independent units in the experiments of hybridization and crossing, and how they can be attained in almost every degree. In the same way evidently, we must think of those units as independent in the ordinary process of fertilization as well.*" (ed. 1910, p. 33; ed. 1889, p. 31.)

"Seemingly elementary, the specific character is actually an exceedingly complex whole. It is built up of numerous individual factors, the hereditary characters. *The more highly differentiated the species, the higher is the number of the component units.* By far the most of these units recur in numerous, many of them in numberless, organisms, and in allied species the common part of the character is built up of the same units." (ed. 1910, p. 33; ed. 1889, pp. 31-2.)

The following statement is, perhaps, especially important as indicating De Vries' attitude at a period considerably antecedent to his experimental investigations upon unit-factors of the Mendelian type:

"*The hereditary factors, of which the hereditary characters are the visible signs, are independent units which may have originated separately as to time, and can also be lost independently of one another.*" (ed. 1910, pp. 33-4; ed. 1889, pp. 31-2.)

The fact is called attention to that, although the factors are independent to such a degree that each may of itself become weaker and even disappear completely, yet they are, as a rule, united into smaller or larger groups, in which they act at least in co-ordinate fashion, so that:

"When external influences, such as a stimulus to gall-formation, bring a definite character into dominance, the entire group to which it belongs is usually set into increased activity." (ed. 1910, p. 34; ed. 1889, p. 32.)

b. *Correns, C.*

Regarding his discovery of Mendel's paper, and the inception of his work with *Pisum*, Professor Correns reports as follows; (letter of January 23, 1925):

"You ask further concerning the re-discovery of the Mendelian Laws. I cannot add much to what I have contributed in the Mendel issue of the 'Naturwissenschaften.' It will, in the meantime, certainly have reached your hands. The operation of a principle was soon found in the case of peas and maize. I was able accordingly soon to proceed systematically in the experiments, as the two genealogies for peas in my first contribution show. I did not come at first upon the explanation of the regular relationship [Gesetzmässigkeit], but I likewise, however, did not seek intensively after it. For I wished, for various reasons, to first finish an extensive book upon the sexual propagation of the foliose mosses, upon which I had worked for years. I then wished first to push intensively the elaboration of the investigations on xenias and hybrids, which had been carried on at the same time since 1894. The printing of the book lasted until in August 1899; then I was able to devote myself earnestly to the genetics researches. The date of the day upon which, in the autumn (October) of 1899, I found the explanation, I no longer know; I do not make note of such matters. I only know that it came to me at once 'like a flash,' as I lay toward morning awake in bed, and let the results again run through my head. Even as little do I know now the date upon which I read Mendel's memoir for the first time; it was at all events a few weeks later. I then first made ready for the press the contribution on xenias in maize. In it, it is already pointed

PLATE XLV. Professor C. Correns, Director, Kaiser-Wilhelm Institut für Biologie, Berlin.

1864-

out, that in crosses between maize races I had found very interesting but very complicated relationships. That other investigators also worked in the same direction I naturally did not know, otherwise I would have hastened more with the preparation of the publication.

"On the morning of the 21st of April, 1900, I received a separate 'Sur la loi de disjonction des hybrides,' of De Vries, and by the evening of the 22nd of April, my contribution, 'G. Mendels Regel über das Verhalten der Nachkommenschaft der Bastarde,' was ready. I sent it to the German Botanical Society in Berlin, where it was received April 24, and was reported in the session of April 27. The issue in question of the 'Berichte' appeared at the end of May, about the 25th. The contribution has been again printed in the volume in which the German Society for the Science of Heredity has recently collected my genetic works, insofar as they have not appeared independently anew.

"For that matter, I do not lay too much weight upon the re-discovery itself. According to my opinion, it was important that the Mendelian laws should finally be known and verified. Whether it happened by their being independently found anew, or through the fact that someone first read the memoir of Mendel, and then repeated the experiments, is, however, at bottom, an indifferent matter *for science*. It was accordingly only a confirmation of what had been discovered more than 30 years before. And through all that in the meantime had been discovered and thought (I think above all of Weismann), the intellectual labor of finding out the laws anew for oneself was so lightened, that it stands far behind the work of Mendel. I myself should prefer, for my part, to lay more weight upon my later works, e.g., the *Bryonia* experiments."

In response to further inquiry, Professor Correns' reply is as follows (letter of January 30, 1925):

"I did not discover the constant relationship [Gesetzmässigkeit] in *Pisum* alone but in *Zea* and *Pisum* simultaneously. In the publication, I placed *Pisum* in the foreground on Mendel's account, and out of didactic considerations. That I, however, also experimented with *Pisum* almost from the beginning, is explained from the way in which, as a matter of fact, I arrived at my genetic investigations. Originally I started out to solve the xenia question. To this end I wished to test experimentally all the assertions known in the literature. I began (1894) with *Phaseolus vulgaris nanus* (with which, however, cross-fertilization did not succeed at all for me), then with *Zea*, *Pisum*, *Lilium* and *Matthiola*. This is all related in my 'Crosses between maize races, with particular reference to xenias,' Bibliotheca Botanica, Heft 53 (1902), where the results are also mentioned; those upon *Matthiola* were also published previously in another place. For *Pisum* there are different pertinent assumptions. One only needs refer, for example, to Darwin, 'The variation of animals and plants under domestication,' and to Focke. Unfortunately Focke here, in the case of xenias, does not mention Mendel, otherwise I should have probably read his work immediately at the beginning of my investigations. After I had carried on cross-fertilizations with *Pisum* likewise on account of the xenia question (there exist, indeed, assumptions on the influence of the seed-coat), it was I suppose, quite natural to grow the crosses themselves, as I did not only with *Pisum*, but also with *Zea* and *Matthiola*, and finally also with *Lilium*. In this connection the advantages of *Pisum* naturally made themselves at once noticeable, especially the great convenience of the investigations, which, indeed, I could only carry on accessorily.

"To one of my most fruitful objects of research, *Mirabilis jalapa*, I also first came indirectly, when I investigated (1907) the influence which the number of pollen grains used for pollination has upon the progeny. I had originally, indeed, not at all overlooked the matter of studying the behavior of the progeny in further generations, but had proceeded from other bases of inquiry.

"Besides through Focke's book, I had been made cognizant of Mendel's investigations through my teacher Nägeli. And I believe also to remember that he told me of Mendel, but certainly only of the *Hieracium* investigations, in which alone he was permanently interested. Something of them was known to me also from the theoretical introduction to the first volume of the Hieracium monograph of Nägeli and Peter, and from Nägeli's introduction to the *Primula* monograph of E. Widmer. The memoir of Mendel on his Hieracium hybrids I first read, however, with that on the peas hybrids, in the autumn of 1899. Nägeli was, at the time when I became his pupil, already in ill health, read none of his colleagues' works any longer, and likewise no longer conducted his practicum any more. He interested me in the structure and growth of the vegetable cell membrane. When I began the genetic researches (1891), he was already dead. The above-cited references to Mendel, and indeed also the recollection of the verbal mention of Mendel, prompted me to ask Nägeli's family for possible letters received. His scientific correspondence was, however, not to be found at that time. It first came to light through an accident in 1904. The letters of Mendel were sent to me by the family, and were published by me; the remaining scientific correspondence the family then destroyed."

In Die Naturwissenschaften, 10th Jahrgang, Heft 29, pp. 623-31 (July 21, 1922), a number devoted to papers in memory of Gregor Mendel, on the one hundredth anniversary of his birth, Professor Correns contributed an article entitled, "Etwas über Gregor Mendels Leben und Wirken." In the course of this article (p. 630), Correns reports as follows. His comments are herewith introduced as supplementary to the letters quoted above:

"Through experiments in xenia formation, I have had my attention directed to the behavior of hybrids in maize and peas races. The investigations, however, could only be carried on slowly, in a certain degree as side issues, through years, together with the other work, so that I was already able to propound, in the first contribution on *Pisum sativum*, a genealogical tree up to the fourth generation inclusive. I had soon come to the counting-out stage, and also to the correct explanation, when for the first time I looked through the literature, and found that my results were not new. Focke says on the subject of *Pisum* in his 'Pflanzenmischlinge' (1881) that Mendel's numerous peas crosses gave results which were quite like those of Knight, 'but Mendel believed that he found constant numerical relationships between the types of the hybrids.'

"It has occurred no differently with De Vries and von Tschermak. De Vries especially, in the lecture given on July 11, 1899, at the first 'Hybrid Conference in London,' on 'Hybridizing of Monstrosities,' and which first appeared in April 1900 (Journ. Roy. Hort. Soc. 24:69), described, although quite without the precise Mendelian formulation, the hybrid between the smooth *Melandrium album glabrum* (*M. preslii Opiz*) and the typically hairy race of *Melandrium rubrum*, which, with respect to the hairiness, typically Mendelizes."

Following is the paper of Correns entitled, "G. Mendels Regel über das Verhalten der Nachkommenschaft der Rassenbastarde," Ber. d. d. bot. Ges. Vol. 18, published April 24, 1900 (2a).

The paper opens as follows:

"The latest publication of Hugo De Vries, 'Sur la loi de disjonction des hybrides' [Comptes Rendus de L'Acad. des Sci., Paris, March 26, 1900], which I came into possession of yesterday, through the generosity of the author, prompts me to the following contribution:

"I also, in my hybridization experiments with races of maize and peas, had arrived at the same result as De Vries, who experimented with races of very different sorts of plants, among them also with two maize races. When I had found the orderly behavior, and the explanation therefor—to which I shall immediately return—it happened in my case, as it manifestly now does with De Vries, that I held it all as being something new. *I then, however, was obliged to convince myself that the Abbot Gregor Mendel in Brünn in the* 60*'s, through long years of and very extended experiments with peas, not only had come to the same result as De Vries and I, but that he had also exactly the same explanation, so far as it was at all possible in* 1866." (2a, p. 158.)

". . . The work of Mendel's, which is indeed mentioned in Focke's 'Pflanzenmischlinge,' but has not been adequately appreciated, and which has otherwise scarcely found attention, belongs to the best that has been ever written upon hybrids, in spite of numerous demonstrations which no one can make in incidental matters, for example, in what pertains to their terminology.

"I have then not held it to be necessary to assure myself the priority for this 'post-discovery,' through a preliminary contribution, but decided to continue the experiments still further. I confine myself in the following to a few statements concerning the results with races of peas." (*ib.*, p. 159.)

"The races of peas are, as Mendel correctly emphasizes, precisely invaluable for the questions interesting us here, because the flowers are not only autogamous, but also are exceedingly seldom crossed by insects. I came upon these circumstances through my experiments on the formation of xenias—which here gave only negative results—and followed the observations further, when I found that here the 'regularity' is much more evident than with maize, in which it had first come to hand with me.

> "The characters through which the races of peas are distinguished, one can, as generally, arrange together in pairs, in which every member of a pair relates to the same point, the one with the one, the other with the other race, e.g., to the color of the cotyledons, of the flower, of the seed-coat, of the hilum on the seeds, etc. In many pairs, the one character, or as the case may be the primordium [Anlage] of it, is so much 'stronger' than the other, or e.g., the primordium, that only it alone comes to light in the hybrid plant, while the other throughout does not show. One can call the one the dominating and the other the recessive, as Mendel did in his time and, through a remarkable accident, De Vries does also now. Dominating, is, for example, the yellow color of the cotyledons as opposed to green, the red of the flower as opposed to white." (p. 159.)
>
> "It is, however, quite incomprehensible to me, as De Vries is able to assume, that in all character-pairs in which the two races differ there is one dominating pair-member in the hybrid." [The author here quotes from De Vries, as follows: Comptes Rendus, 1900, p. 845: "*Per contra*, the study of the simple characters of hybrids is able to furnish the most direct proof of the principle enunciated—*the hybrid shows always the character of one of the two parents, and that always in all its force; never is the character of the parent, which is lacking to the other one, found reduced by half*."]
>
> "Even in the races of peas, in which several character-pairs correspond exactly to the scheme, there are others in which no character dominates; thus the color of the seed-coat, whether red-orange, or greenish-hyaline. Then again, the hybrid can show all transitions, even in the seed-coat of peas, or it shows always more of one than of another character, as Stocks hybrids, in which, for example, a given hybrid can still be distinguished from the one parental race by the markedly weaker pubescence, but always, after some examination; while with the other, the smooth parental race, it extraordinarily contrasts." (p. 160.)

For some two pages and a half, Correns then outlines Mendel's general results with a single pair of allelomorphs, and follows with a tabular statement of his individual results.

Experiment I

Cross between late Erfurt green "Folgeerbse" with green cotyledons, and "purple-violet" (Schlesien) "Kneifelerbse," with yellow cotyledons.

Generations

F_1 51 yellow (19 planted)

F_2 619 yellow (25 planted) 260 green (25%) (11 planted)
7 yellow (28%)

F_3:

251 yellow (7 planted)	550 yellow (18 planted)	195 green (26.2%) (14 planted)	538 green (10 planted)

F_4:	224 yellow	216 yellow	225 yellow	70 green (23.89%)	307 green

Experiment II

Late green Erfurt "Folgeerbse" with green cotyledons, and "Bohnenerbse" with yellow cotyledons.

F_1	31 yellow (12 planted)			
F_2	775 yellow (21 planted)	247 green (20 planted)		
F_3:	292 green	462 yellow	149 green (23.6%)	670 green

Correns holds (p. 164) that the separation of dominant and recessive factors (Anlagen) takes place at the earliest, on the laying down of the primordia of the ovules and stamens, and at the latest, on the first nuclear division in the pollen grain, and in the division at which the primary embryo-sac nucleus is formed.

As to the fact that, when the hybrid in the F_1 generation, instead of being self-pollinated, is pollinated with pollen from the dominant parent, its progeny is half dominant pure, and half dominant, but giving progeny 3:1 dominant and recessive; and that when an F_1 hybrid is pollinated by the recessive parent, it gives a progeny one half of which is recessive, the other half dominant, but producing progeny 3:1 dominant and recessive; Correns states (p. 165):

> "This theoretically derived rule I find realized in my maize crosses."

Correns shows in this first paper a full insight into the significance of the following rule of Mendel:

> "It is thereby proven at the time, *that the behavior of every two differing characters in hybrid combination is independent of the differences otherwise* in the two parent plants,"

by the statement in a note (p. 166) that,

> "Even this rule does not hold in general; there are races with *coupled* characters."

This is, for the time, knowledge in advance of the then state of investigation with respect to Mendelian behavior.

Moreover the later work of Bateson on hybrids of sweet peas, involving pollen grains of different shapes, is already forecast by Correns in the statement (footnote, pp. 166-7):

> "If the pollen grains differ externally in the parent races, then one may expect that the hybrid may form two kinds of pollen cells, externally distinguishable among themselves, in case Mendel's rule holds good. This is in fact true, as Focke first observed."

Correns appears to have been the first to comprehend so thoroughly the fundamental nature of the Mendel experiments, as to give the general result the designation of "Mendel's Law."

> "The hybrid forms sexual nuclei which unite with the primordia [Anlagen] for the individual characters of the parents in all possible combinations, but not those of the same pair of characters. Every combination appears about equally often.
>
> "If the parent races differ only in *one* pair of characters (two characters, Aa), then the hybrid forms *two kinds* of sexual nuclei (A,a), which are like those of the parents: of each sort, 50% of the total number. If they differ in *two* pairs of characters (four characters, Aa, Bb), then there are *four kinds* of sexual nuclei (AB, Ab, aB, ab); of each sort 25% of the total number. If they differ in three pairs of characters (six characters, Aa, Bb, Cc), then there exist *eight kinds* of sexual nuclei (ABC, ABc, AbC, Abc, aBC, aBc, abC, abc); of each sort 12.5% of the total number; etc." (p. 166.)

Immediately following this illustration, the statement is made:

> "I call this the Mendelian Rule: it includes also De Vries' 'Loi de disjonction.' Everything further may be derived from it." (p. 167.)

We thus have here the first completely definite analysis of the Mendelian paper itself, of Mendel's own results, and the first use of the term, "The Mendelian Rule" or "Law."

However, Correns was not at the time at all of the opinion that Mendel's Law was a universal one in its character. He held that it obtained for a certain number of cases, and presumably for those where a single member of the character-pair dominates, and for the most part only in the case of race- or variety-hybrids.

Correns holds that the view:

> "That all parts of hybrids follow it, is quite out of the question."

To this point he cites his cases of crosses between two races of peas with colorless and with orange-red seed-coats becoming brown on ripening, in which, in the first generation, different stages of intermediates are found. In the second generation, the extremes of yellow and colorless gave again the same extremes, united by a series of transition-stages. The same is stated to hold for the character of the seeds, and their form and size. (p. 167.)

We thus have in this paper an analysis of the work of Mendel, and one which already itself constitutes a preliminary investigation into the more complete understanding of the supposed exceptions, which latter formed a few years later one of the main fields of inquiry, until the functioning of several possible factors or "genes," operating for the same single phenotypic "character," was more fully demonstrated. This was probably first achieved, as already stated, by the work of Professor William Bateson for sweet peas ("Reports to the Evolution Committee of the Royal Society." Report II, pp. 88-90; "Experiments carried out by W. Bateson, E. R. Saunders, and R. C. Punnett in 1904," pp. 80-99).

Regarding this matter, however, Professor Bateson writes as follows (letter of February 2, 1925):

> "I am not sure whether the color of the sweet peas should be regarded as the first compound character demonstrated. Perhaps it should, but the walnut comb and the hoariness of stocks were made out about the same time."

c. *E. von Tschermak.*

Regarding his discovery of Mendel's paper, and his initial research in relation thereto, Professor von Tschermak reports as follows (letter of January 7, 1925):

> "After the taking of my doctorate at the University of Halle a. S. (1895), at the instigation of my teachers Maercker and Rümker, I became occupied for two years as volunteer in the horticultural business of the firms Chr. Bertram, in Stendal (1896), and of Sachs, Dippe and Metter, in Quedlinburg (1897). This sojourn, as well as a visit to the renowned grain-breeding stations in the Province of Saxony, especially to Amtsrat Dr. Rimpau in Schlanstedt, awakened my interest in practical questions. My address [1] 'Concerning methods of improvement and breeding of agricultural and horticultural plants in Germany' at the Club der Land-und-Forstwirthe in Vienna, January 7, 1898, brought me into relations with the 'Hochschule für Bodenkultur' in Vienna. Prof. Dr. A. Liebenberg placed in prospect for me the assistant's place in his department, which, however, at that time was not vacant. Following the suggestion of a pupil of my father, the mineralogist, Professor Renard, at the University of Ghent, to extend my practical horticultural knowledge among some well-known horticultural enterprises of Belgium, Holland and France, I betook myself in the spring of 1898 to Ghent. The circumstance, that I there found only the opportunity to get acquainted with hot-house management, but not with the breeding of vegetables and garden flowers as I expected, was the inducement to strive to apply the abundant time remaining available to experimental work in the botanical garden, which interested me so exceedingly that I devoted myself exclusively to my

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[1] Wiener landwirtschaftliche Zeitung, 1898.

PLATE XLVI. Professor E. von Tschermak, Landwirtschaftliche Hochschule, Vienna.

investigational activity. Professor MacLeod, Director of the Botanical Garden in Ghent, discussed quite briefly with me a program of work to carry out pollination experiments with plants to be selected, which should determine, whether perchance, in individual cases, with respect to development of the fruit, differences existed as the result of autogamous, geitonogamous and xenogamous fertilization of like or dissimilar species. I had in the beginning the good fortune, quite by chance, to choose for these investigations the Wallflowers, in which xenogamy increased the growth in length of the shoot by about twofold, as compared with autogamy and geitonogamy. These experiments were later continued and extended in Vienna.[2] Since I remained in Ghent only until July, it was a question of looking out for a plant which could bring its vegetation-period to a close by this time. I selected peas, impelled by the reading of Darwin on the effects of cross- and self-fertilization. I was also urged by the incompleteness of the observation-material in the case of this plant with Darwin (only four pairs of plants were measured and compared to complete these experiments). The yield-results from my experiments I took with me to Vienna. From these, together with other questions to be answered, since green-cotyledonous peas had been crossed with yellow-cotyledonous, wrinkled-seeded with round-seeded, I had already been able to determine the method of operation of the xenia effect. Since the prospective assistant's position was still not yet open in 1899, I volunteered for a year on the estate of the Imperial family's foundation in Esslingen, near Vienna, because the setting apart of 50 hectares from this management for the purpose of the founding of an experimental establishment for our Hochschule was in prospect.

"There, in the garden of a neighboring estate owner, my experiments with peas, begun in Ghent, were continued, and at the same time, new crosses instituted with grain and garden beans. The working up of the F_2 of my peas hybrids, followed in the fall of 1899. In this I was struck especially by the different value of the characters of the individual races with respect to their structure, cotyledon-color and form (see conclusion III of my first paper, in which I emphasized besides that, instead of 'dominieren' [dominate], one should say rather 'prävalieren' [predominate], at least in certain cases [see conclusion VIII]). In counting out the seed-characters, the ever-recurring number relationship of 3:1 could naturally not escape me, any more than the number-relation of 1:1 on back-crossing of green-seeded peas with hybrid pollen of the F_1 generation. The rules of inheritance, quite intentionally, I expressed at first purely descriptively or phenomenologically, in order not at once to anchor the newly-beginning experimental phase of the doctrine of heredity—as had happened inexpediently with Darwinism—to definite theoretical terms. From this standpoint, I designated the regularities found by Mendel and myself, as those of the regularly varying values of the characters for the inheritance, under which I comprehended not only the rule of dominance, but mass-value (dominance-recessiveness, or equivalence of value); quantities-value (the relation of segregation), and inheritance-value, or splitting *per se*.

"Later likewise, I have remained consistently faithful to that stand-

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[2] Beihefte der deutschen botanischen Gesellschaft, 1902, Heft 1.

point which separates the permanent good of the exact facts of observation clearly and distinctly from the naturally and necessarily changing expression of theoretical explanations, especially of fertile working hypotheses.

"In the autumn of 1899, I received from Prof. A. v. Liebenberg the permission to volunteer in his department, and to make use of the library. The first work I seized upon was the well-known book of Focke: 'Pflanzenmischlinge,' of 1881. There I found, in the chapter on 'Peas,' the familiar obscure expression of Focke's concerning Mendel's treatise, as well as the views on Mendel's experiments with beans and Hieraceae. Since Mendel's work was not on hand in the library of the Hochschule für Bodenkultur, I had on the same day of this 'discovery' the 'Transactions of the Natural History Society of Brünn,' hunted out of the University library, which now gave me the information, to my greatest surprise, that the regular relationships discovered by me, had already been discovered by Mendel much earlier. Still, I believed myself to be at this time the only one who had made this discovery anew. By Christmas, my paper was finished, ready for publication, and on the 17th of January, 1900, it was delivered at the rectorate of the Hochschule für Bodenkultur, as an inaugural dissertation. In the beginning of April 1900, I received from Hugo De Vries, whom I had visited from Ghent in the year 1898, the article 'Sur la loi de disjonction des hybrides' (March 26, 1900), in which De Vries, on pages 1-2 says: 'In the hybrid the simple differential character of one of the parents is then visible or *dominant*, while the antagonistic character is in the latent or *recessive* state.' I read this sentence with the greatest interest, but also, frankly stated, with consternation, for it was now quite clear to me that De Vries must also know the work of Mendel, although it was not cited in this paper. For me it was naturally, as a beginning docent, not indifferent that my work should be anticipated, wherefore I immediately sought from the rectorate the permission to let my already censored work be taken out and printed.

"I have my friend Dr. Bersch to thank that my work was accepted for the Zeitschrift für das landwirtschaftliche Versuchswesen in Oesterreich, and the printing of it immediately undertaken. In the meantime there appeared soon thereafter the extensive work of De Vries in the Reports of the German Botanical Society (Heft 3). I was able to utilize it already as early as during the correction of my proofs. On the reading of the second proof I was surprised anew by the work of Correns (Ber. d. d. Bot. Gesell. Heft 4, April 24). I was therefore able to take it into consideration only in the footnote to my first paper. As may readily be conceived, I now made every effort to induce the publisher of the journal before-mentioned, as well as the printing office, to publish the separates of my work before the appearance of the number in question, which, fortunately, likewise succeeded (May, 1900). In the meantime, I wrote quickly an abstract of my paper, for the Berichte der deutschen botanischen Gesellschaft (received for publication June 2, Heft 6), which, however, appeared somewhat later than the separates of my complete paper, which I immediately sent out.

"The classical significance of the Mendel work was at once clear to me, for which reason, already in the year 1900, I made application for its acceptance in Ostwald's 'Klassiker der exakten Wissenschaften,' provided with notes of my own. They delayed, however, so long with the

> printing, that I very impatiently wrote to the editor, that in the meanwhile the works of Mendel had been printed by Goebel in Flora (1901). Now at length Mendel's works were found worthy of being enrolled in the 'Klassiker der exakten Wissenschaften.' "

For the younger Tschermak, as he states, it was not easily effected to bring his re-discovery of Mendel, simultaneously made with De Vries and Correns, into general recognition. Thus, in the early years after the re-discovery of the Mendelian Laws, in references to the discoveries the mention of his name was omitted altogether, as in the "Lehrbuch" of Strasburger and Wettstein. Nevertheless, this oversight was soon made good. Continuing, he states:

> "The practical significance of Mendelism for plant and animal breeding was first immediately recognized by myself, and always emphasized; as also the great part of my publications even today, with theoretical conclusions, always place the practical side in the foreground. Through my visit in the year 1901 at Svalöf, the method of breeding hitherto obtaining there was directed to quite new, modern, 'Mendelian' lines, which is now recognized ungrudgingly in Sweden by Nilsson-Ehle."

The preliminary paper of von Tschermak's, referred to in the letter above, contributed to the Berichte der deutschen botanischen Gesellschaft, and entitled "Über künstliche Kreuzung bei *Pisum sativum*," was printed as Contribution 26, pp. 232-9 of volume 18, and received by that journal for publication on June 2, 1900. This paper, although in a sense an abstract of the much fuller contribution to the Zeitschrift für das landwirtschaftliche Versuchswesen in Oesterreich, Heft 5, 1900, is nevertheless of special interest, since it renders the first account of the author's experiments appearing in the issues of a botanical journal.

The author states:

> "Prompted by the experiments of Darwin on the effects of cross- and self-fertilization in the plant kingdom, I began in the year 1898 to institute crossing experiments with *Pisum sativum*, because especially the cases of exceptions from the principle generally expressed, concerning the advantageous effect of the crossing of different individuals and different varieties in contrast to self-fertilization, interested me—a group to which *Pisum sativum* also belongs." (3a, p. 232.)

The author then gives a brief summary of Darwin's experiments, and states that, in view of the small amount of the latter's experimental material, it appeared to be called for, especially since Darwin did not emasculate the flowers, to repeat these experiments on a larger scale and with greater exactness. (*ib.*, p. 232.)

The central point of the paper, so far as the Mendelian discussion is concerned, follows:

> "I also carried out artificial crosses between different varieties of *Pisum sativum*, which had as the objective the study of the immediate influence of the foreign pollen upon the constitution (form and color) of the seeds produced thereby, as well as to follow in the following generations of the hybrids the inheritance of constant differing characters of the two parent sorts used for crossing.
>
> "In the second year of the experiment, the behavior of the hybrids in respect to their growth (especially with respect to their height), their seed-production, and the change in color and form of the seeds and pods, when placed in comparison with the corresponding characters of the descendants obtained from self-fertilization of the parents." (*ib.*, p. 233.)
>
> "On nine different varieties of peas, crosses were carried out between flowers of the same plant (geitonogamy), between flowers of the same variety but of other individuals (isomorphic xenogamy), and between flowers of different varieties, the seeds of which are distinguished from one another either through their form, or color, or through both characters (heteromorphic xenogamy)." (pp. 233-4.)

The results of the experimental work then briefly follow (*ib.*, pp. 234-9):

The crossing-for-height experiment confirmed Darwin's results, so far as the comparison of self-fertilized plants with geitonogamous crosses was concerned. With respect, however, to crosses in the ordinary sense (heteromorphic xenogamy), i.e., those between varieties called by the author "Mischlinge" (hybrids), only certain of the hybrid forms showed increased growth in height over the selfed plants.

> "With other combinations, on the other hand, such an 'advantage' of crossing as against self-fertilization was lacking, and a plus increment of the hybrid as compared with the self-fertilized maternal variety, for example in the case of a hybrid from a relatively dwarf variety, with a relatively tall one, is primarily indeed simply to be taken as an inheritance from the father, and is not to signify an 'advantage' from crossing *per se* in contrast to self-fertilization.
>
> "For an interpretation in the latter sense, only such cases are justifiable in which the hybrid exceeds in height the derivations of self-fertilization not only of the maternal variety, but also of the paternal one." (*ib.*, p. 234.)

There follows hereupon the statement of the significant results of von Tschermak's own experiments, so far as F_1 dominance is concerned:

"The taller type has always the greater influence, indifferently as to whether it is due to the maternal or the paternal variety. The derivatives of a relatively dwarf sort appear, after pollination with the pollen of a relatively tall one, as Andrew Knight has already observed, relatively strongly increased in height; in the reverse case, the hybrids, if generally so, are yet only a little dwarfed." (*ib.*, p. 234.)

The author's account follows of the results obtained in respect to form and color inheritance in the seeds:

"In certain cases of artificial crossing of different varieties of peas, a direct influence of the foreign pollen upon the seeds could be determined. Quite definite combinations led with regularity to this effect. The characters, which were taken into consideration for the recognition of such an influence, related to the form of the seeds, and the color of the storage tissue. The seeds of the varieties used were either round, and at the same time smooth or only slightly wrinkled, or they were more or less cubical (*Pisum quadratum*), and at the same time deeply wrinkled. The color of the storage tissues was either yellow, or green in many shades. My experiments gave as a result that the selected differences in the same structure, and hence the characteristic 'characters' of the individual varieties, showed themselves in respect to their inheritance as not of equal value. Regularly the one character in question of the paternal or maternal plant comes exclusively to development (dominating character according to Mendel), in contrast to the recessive character of the other parent plant, which, however, in the seeds of the hybrid plants is accustomed in part to come again to light. In harmony with the statements of Mendel, the round, smooth form manifested itself as dominating, in contrast to the cubical, deeply wrinkled one; the yellow coloration of the storage tissue in contrast to the green color, and indifferently indeed whether the seed- or the pollen-parent possessed this character (as also Mendel)." (p. 235.)

Von Tschermak calls attention to a fact not mentioned in Mendel's paper, that:

"The appearance of the dominating and the recessive character is not a purely exclusive one. In individual cases I was able further to determine with certainty a simultaneous appearance of both, that is to say, of transition stages. The principle founded by the investigator named of the regular inequality of the characters for the inheritance, receives full confirmation through my experiments with *Pisum sativum*, as well as through the observations of Körnicke, Correns, and De Vries upon *Zea mays*, and further by De Vries in his species crosses, and shows itself to be highly significant for the doctrine of inheritance generally." (*ib.*, p. 235.)

A fact of considerable interest, likewise not noted by Mendel, is cited as follows:

"In certain cases of form and, in part, of color-difference of the parent varieties, and of indicated character-fusion in the products, each of the parent sorts showed relatively more influence upon the structure (especially form) of the crossed product, when it furnished the ovary, than when it furnished the pollen." (p. 236.)

The obtaining of a 3:1 ratio in the F_2 from his own results is stated by von Tschermak as follows:

> "In the seeds of the hybrids (in the first generation), obtained through self-fertilization, the characters yellow and smooth showed themselves, exactly as in the cross-pollinated seeds of the mother plant, as of higher value or hereditary potency than the characters green and wrinkled. While, however, in the artificial breeding of products of heteromorphic xenogamy, the first named characters are almost without exception dominating, while the latter, 'recessive,' only in individual cases come to light pure or as admixture, the former characters in the seeds of the first hybrid generation only in the majority of cases get into expression pure: in the minority, the recessive characters come out pure. In the first case there thus exists an almost absolute dominance, in the second mere superiority ['Prävalenz'] (in a certain relationship). Mixtures of both character groups are here also seldom, but perhaps less seldom than there. The number of the bearers of the dominating or prevailing character, to that of the bearers of the recessive, is related about as 3:1. The comparison of the derivatives from reciprocal crossing of different varieties showed, analogously to the results given above for the products of reciprocal pollination, that in certain experimental cases the egg cell appears to be a more operative bearer of the dominating color-character, than the pollen cell. But for the proposition of a statement in this regard further investigations are needed. The combination of two dominating or recessive characters in one parental form carries with it the same behavior in the seed production of the hybrids, as the characters in question do when isolated. An alteration in the value, such as an increase of the dominance [Prävalenz], does not thereby enter in." (*ib.*, p. 236.)

This closes the essentially Mendelian portion of the above paper, "Über künstliche Kreuzung bei *Pisum sativum*." The Zeitschrift für das landwirtschaftliche Versuchswesen in Oesterreich, III Jahrgang, 1900, pp. 465-555. (3b contains the complete report, of which the article in the Ber. d. d. bot. Ges. 18:232-9 was a preliminary account.) The complete account follows:

The experiments in question were begun in the Botanical Garden at Ghent in Belgium in the spring of 1898. Von Tschermak says (letter to the author of January 7, 1925):

> "The principal incentive to the experimental work lay in the results of Darwin's experiments on 'The Effects of Cross and Self Fertilization in the Vegetable Kingdom.' (1877). The experiments prove that seedlings from a cross between individuals of the same species almost always exceed in height, weight, vigor of growth and frequently also in fertility, the corresponding individuals produced by self-fertilization." (3b, p. 465.)
>
> "The result," says von Tschermak, "formed the first instigation to my researches, which, on the one hand, on account of the significance of this question for the science of plant breeding, on the other hand, on account

of the incompleteness of the observation-material in Darwin's case, calculated upon a larger scale (on the basis of an exact numerical test) were intended for the investigation of this exceptional case. As I became acquainted with the further literature in question upon experiments carried out with peas, I introduced in addition a series of other experiments, which deal with the inheritance of the characters of unequal value, dominant or recessive (Mendel), and which should especially determine exactly the results of the immediate influence of foreign pollen upon the structure of the fruit produced thereby, or the simultaneous operation of two pollen species in many-seeded fruits. The experiments were begun in the year 1898, in the Botanical Garden in Ghent, the Director of which, Professor MacLeod, has bound me in gratitude through the active interest which he manifested toward my researches."

The writer proceeds to comment on the fact that, in recent times, methods for the artificial crossing of grain varieties had been published in large measure, but for peas in lesser detail.

"Concerning the process of the artificial crossing of peas there exist only scanty statements." (3b, p. 468.)

Mendel's work is thus alluded to (*ib.*, p. 468):

"Crossing experiments with peas for purely scientific purposes, have been carried out by Gärtner ('Bastardierung im Pflanzenreiche,' 1849, pp. 71ff.); Darwin ('Variation,' Chaps. 9, 11; 'Cross- and Self-fertilization,' p. 151); and Gr. Mendel ('Verhandlung der Naturforscher Verein,' Brünn, 1865, IV Bd., pp. 3 ff.)."

The experiments of von Tschermak in 1898 comprised ten pots for each variety used, each with 4-5 seeds, the two most vigorous being left to grow to maturity. In this experiment, the results of close and self-fertilization were also considered.

"The experiments pursued primarily the same end, of obtaining materials for evidence regarding self-fertilization and crossing, in order to be able to repeat in the following year, the test experiments of Darwin." (3b, p. 476.)

"The continuation of the experiment was carried out in the spring of 1899, in a walled garden in Esslingen [Lower Austria]." (*ib.*, p. 477.)

Since this portion of the experiment does not touch the Mendelian question, it need be no further noticed.

Later in the course of the same experiment, the following statement occurs:

"My experiments showed first, that frequently, and indeed under different conditions, even in the constitution of the seeds the influence of the pollen originating from the other variety could be recognized." (*ib.*, p. 505.)

Commenting further, it is stated:

> "*The previously listed differences of the same structure, in other words, the characteristic 'characters' of the individual varieties, manifested themselves in respect to inheritance, as not being equivalent.* Regularly, the character in question, of the father or mother plant, comes exclusively into expression (dominating characters according to Mendel), *in contradistinction to the recessive character of the other parent plant, which, however, is accustomed to come again to light in part in the seeds of the hybrid plant. As dominating, in harmony with the statements of Mendel, the round, smooth form as opposed to the cubical and deeply wrinkled one; the yellow color of the storage tissue as opposed to the green color, and indifferently, whether the seed of the pollen parent possessed this character* (*as likewise Mendel*)." (*ib.*, pp. 505-6.)

The author notes that:

> "In individual cases of artificial crossing of different varieties of peas, a direct influence of the foreign pollen upon the seeds could be determined. To these effects quite definite combinations led with regularity. The characters which were taken into consideration for the recognition of such an influence concerned the form of the seeds and the color of the storage tissue. The seeds of the varieties used were either round, and at the same time smooth, or only gently wrinkled, mostly somewhat oblong through close packing in the pods, or else they were more or less cubical (*Pisum quadratum*), and at the same time deeply wrinkled. The color of the storage tissues is either yellow, or green in various shades; the pod is mostly dirty-to-yellowish white, or it shows a more or less marked yellowish-green to green shimmer, which proceeds from tannin-like pigments which appear partly in the hard layer, and partly in the parenchyma layer, or in both together. With the colors mentioned of the seed-coat white flower-color is always correlated. Gray, gray-brown, leather-brown, often dotted with violet, as well as green with violet spots, is combined with flowers which show a violet-colored standard, and purple wings, with red markings in the leaf axils." (p. 505.)

The first distinct mention in the paper of Mendelian results is in connection with the height experiment (*ib.*, p. 476):

> "The products of crossing further afford opportunity to study the direct influence of the pollen upon their color and form. *Such an influence showed itself in crosses between differently colored and differently formed peas, for definite combinations, with the greatest regularity.*"

The above experiment, having been planned for the different purposes hitherto named, was not followed up from the Mendelian standpoint.

The author finds (*ib.*, p. 507):

> "The appearance of the dominating and of the recessive character *is not a purely exclusive one.* In individual cases, I could, on the contrary, detect with certainty a simultaneous appearance of both intermediates.

> "In respect to color, Telephone No. 2, with cotyledons yellowish or whitish-green, sometimes also completely clear yellow, × Pois d'Auvergne No. 9, with cotyledons pure yellow; the F_1 hybrid seeds were found to be in general yellow, but with plainly visible green spots. [*ib.*, p. 507.] In like manner, the crossing of Couturier No. 6, with orange-yellow cotyledons, with Express No. 14, with light green cotyledons, instead of giving pure yellow, gave a transition tone between yellow and green. Pois d'Auvergne, No. 9, cotyledons dodder-yellow-orange, with Telephone No. 2, yellowish or whitish-green, gave instead of pure yellow, a green spotting on the otherwise yellow cotyledons." (*ib.*, p. 507.)
>
> "Likewise in respect to form, cases are not lacking in which the ordinarily dominating compared with the ordinarily recessive in a certain relationship." (*ib.*, p. 508.)

The cases, however, do not appear to have been quite so clearly defined as the preceding.

After an extended further discussion of the relation of the pollen to the character of the pod in the seed parent, von Tschermak remarks as follows, citing the older literature of Darwin, Gärtner, Knight and Laxton:

> "My experiments have most points of resemblance to the observations of Gregor Mendel, who worked with 34 varieties of peas. *From his is derived the above adopted and strengthened conception of dominating and recessive characters.* In seeds obtained through artificial pollination, he observed the former (yellow) coloration, and roundness. His results with respect to the crossed plants, studied through several generations, will have to be entered into later.
>
> "*It must be cited, as the especial service of this observer, that he recognized the regularly unlike value of the different characters for inheritance, and demonstrated it clearly, for the especially adopted species, Pisum sativum.*" (pp. 513-14.)

This is the first extended reference to Mendel in this paper. One of von Tschermak's observations referred to a phenomenon under the name used by Gärtner, of Prävalenz (prepotency).

Twelve crosses, with reciprocal crosses, constituted the experiment. Quoting:

> "In the last four cases, of form, and in part color-difference of the parent sorts, and of indicated commingling of characters in the product, each of the parent sorts showed (relatively) more influence upon the constitution of the crossed product, when it furnished the seed-pod, than when it furnished the pollen." (*ib.*, p. 514.)

The last thirty-four pages of the memoir, constituting Part IV of the von Tschermak paper, are devoted to the subject, "Beobachtungen an den durch künstliche Kreuzung erzeugten Mischlingen." (Observations on hybrids produced through artificial crossing.)

In the whole of the paper, the author by preference uses the word "Mischling" for crosses made between varieties of the same species.

> "Since the forms of peas used by me, according to the general view at present, represent varieties of one and the same species, *Pisum sativum L.*, I designate the products of their crossing (heteromorphic xenogamy) as 'Mischlinge,' not as hybrids ['Bastarde']." (*ib.*, p. 521.)

This paragraph clearly shows the transition state of mind between the earlier point of view regarding "hybrids," in which the product was regarded as a whole, and from the *a priori* standpoint of the degree of closeness of relationship of the two parents, and demonstrates that the idea of the crossing of competitive characters, i.e., of what has been later denominated the contending of two members of an "allelomorphic" pair, as being a universal phenomenon no matter what the degree of relationship of the parents, had not yet gained a certain foothold. In von Tschermak's paper of 1900, we still see that the crossed plant product was being thought of as a whole, rather than in terms of its individual character-factors regarded singly.

Considerable experimental work follows in the von Tschermak paper on the relative height, etc., of self-fertilized individuals, individuals from crosses upon the same plant, and on different plants of the same variety, in the case of peas. The following conclusion was arrived at:

> "From the whole of my experiments it results that, in the sorts of *Pisum sativum* used, a cross between different flowers of the same individual, as between flowers of different individuals of the same variety, brings no advantage to the descendants, in comparison to the plants proceeding from self-fertilization." (*ib.*, p. 522.)

In this conclusion the writer confirms wholly Darwin's experiments.

A further conclusion from the series of experiments is arrived at in general, that:

> "*Among the twelve hybrid forms* [*Mischlingsformen*] *cited, there accordingly results in probability a simple taking-over of the paternal height-character, but no proof of a height excess through crossing in itself, in contrast to self-fertilization. The hybrids in question stand in height either between the parents, and indeed nearer the higher member, or resemble them.*" (*ib.*, p. 530.)

From further cases of exceptions, he concludes:

> "The hybrids accordingly appear, on the crossing of certain varieties of *Pisum sativum, to gain an access of height, in comparison with the paternal and maternal variety grown from self-fertilized products; with other combinations, on the other hand, such an advantage of crossing, as compared with self-fertilization, is lacking, and there is merely to be found an influence of the paternal variety on the height of the hybrid.*" (*ib.*, p. 531.)

Further, it is stated:

> "With respect to the *relative influence* (or the relative weight) *of a difference in the height-character* of the paternal and the maternal variety, my conclusions furnish the following:
>
> "*The higher type prevails, indifferently as to whether it is due to the father or the mother.* The derivatives of a relatively low variety, after pollination with the pollen of a relatively high one, appear, as Andrew Knight already observed, relatively strongly increased in height. In the reverse case, the hybrids are generally little, if at all, lowered in height." (*ib.*, p. 532.)

The attitude of mind prevailing at the time of the discovery of Mendel's paper, is singularly brought out even in the paper of von Tschermak, in the following form of statement:

> "In the seeds of the hybrids [Mischlinge], obtainable in the first generation from self-fertilization, the characters yellow and smooth, evidenced themselves precisely as in the case of the cross-pollinated seeds of the mother plant, as being of higher value or hereditary potency, than the characters green and wrinkled, while in the case of the artificial breeding of products of heteromorphic xenogamy the first-named characters *are almost exclusively dominant; the latter, 'recessive' ones, only come to light pure* in individual cases (or as admixture); those characters in the seeds of the first hybrid generation attain, only in the *majority of cases*, to development pure; in the minority of cases, the 'recessive' characters appear.
>
> "In the first case, there exists an almost absolute dominance; in the second a mere prevalence (in certain relationships)." (*ib.*, pp. 534-5.)

This statement appears to show that, in the investigator's mind at that time, the old idea of a sort of "prevalence of potency" existed, which, in what we now call the F_1 generation, gave almost exclusive dominance ("bei der künstlichen Erzeugung von Produkte hetermorpher Xenogamie, die erstgenannten Merkmale fast *ausnahmlos dominierend* sind, die letzteren, 'rezessiven,' nur in Einzelfällen rein, [oder als Beimischung] zur Tage treten," etc.). (*ib.*, p. 535.)

However, in what is now known as the F_2 generation, referred to by von Tschermak as "an den aus Selbstbefruchtung erhaltenen Samen der Mischlinge in erster Generation" (p. 535), it is stated, not that an absolute ratio exists, but that "the characters yellow and smooth," are "of higher value or hereditary potency than the characters green and wrinkled (die Merkmale gelb und glatt als von höheren Werthigkeit oder Vererbungspotenz wie die Merkmale grün und runzelig)." (*ib.*, p. 534.)

However, in an immediately following statement of the numerical results with these characters, the writer reports as follows:

(1) *Pot-grown hybrid plants*

Yellow	*Green*	*Ratio*
61	29	2.06 : 1
Green smooth	*Green wrinkled*	*Ratio*
15	5	3.00 : 1

(2) *Field-grown hybrid plants*

No. of plants	*Yellow*	*Green*	*Ratio*
1	79	30	2.70 : 1
1	52	23	2.70 : 1
2	203	68	3.00 : 1

In another case reported from six plants, the ratio of two characters was found as follows:

Yellow smooth	435
Green smooth	148
Yellow wrinkled	116
Green wrinkled	49

or a ratio of 9:3:3:1. (*ib.*, pp. 526-8.)

The conclusion is then stated (3b, p. 535) as follows:

"*The number of the bearers of the dominating or as the case may be prevailing characters is thus related to the bearers of the recessive about as* 3 : 1."

We thus find, at the beginning of the period of Mendelian investigation, the use of the concept "dominating" or "prevailing" instead of "dominant," reflecting in this respect the influence of the preceding generations of the older hybridizers rather than the direct influence of Mendel himself.

For "the products of those hybrids, whose parents were different in two seed-characters" (3b, p. 535), the following experimental results are further given:

	(1) *Pot-grown plants*		(2) *Field-grown plants*	
Characters	*Numbers*	*Ratios*	*Numbers*	*Ratios*
Yellow smooth	28	9.3	504	8.3
Green smooth	12	4.0	180	3.0
Yellow wrinkled	20	6.6	145	2.4
Green wrinkled	3	1.0	61	1.0

Von Tschermak's final conclusion agrees with Mendel's results, and is stated as follows:

> "From this essential approach to the average value, there results, in my judgment, the conclusion, that the combination of two dominating (or recessive) characters in the one parent form results in the same relationship in the seed product of the hybrids, as the characters in question do when isolated. An alteration of the value, or an increase of the prevalence, does not thereby enter in." (3b, p. 536.)

This concludes the account, rather extended in detail, of the three remarkable, practically simultaneous, discoveries of Mendel's celebrated papers published in the year 1900. Without regard to the actual precedence in respect to dates of publication, the entirely independent and practically equal merit of the contributions of the three separate investigators leaves little room for contention from the standpoint of the contributions themselves. The remarkable fact for science of the nearly simultaneous triple rediscovery of Mendel's Law dwarfs into insignificance the matter of precedence therein.

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CHAPTER XII

35. *The Contribution of William Bateson.*

A HISTORICAL survey of the circumstances surrounding the discovery of Mendel's paper in 1900 would be incomplete without including the contribution of Professor William Bateson (now deceased), formerly of Cambridge University, then director of the John Innes Horticultural Institution of Merton—the first translator and editor of Mendel's papers into English.

For a considerable time Bateson had worked upon the phenomena of variation, and particularly upon what was designated "discontinuous variation," as a means of evolution. In this particular field Professor Bateson was the most conspicuous investigator in the English-speaking world, in a somewhat similar manner as, under the thesis of the Mutation Theory, De Vries remained upon the Continent. In this connection, Bateson had published a considerable volume of material in his "Materials for the Study of Variation, treated with Especial Regard to Discontinuity in the Origin of Species." (593 pp., London, 1894.)

At the sessions of the International Conference on Hybridization (the Cross-breeding of Species), and on the Cross-breeding of Varieties, called at the invitation of the Council of the Royal Horticultural Society, and held at Chiswick and London (July 11 and 12, 1899), Bateson presented a paper entitled "Hybridization and cross-breeding as a method of scientific investigation," read July 11, 1899, and published in the Hybrid Conference Report (Jour. Roy. Hort. Soc., Vol. 24, pp. 59-66).

In this paper it is interesting to note Bateson's attitude of mind during this transition period. Bateson says:

> "The first question was: How large are the integral steps by which varieties arise? The second question is: How, when they have arisen, are

PLATE XLVII. Professor William Bateson, Director of John Innes Horticultural Institution, (deceased).

> such variations perpetuated? It is here especially that we appeal to the work of the cross-breeder. He, and he only, can answer this question: Why do not nascent varieties become obliterated by crossing with the type form?" (p. 62.)

It is interesting to note how completely Bateson's attitude toward the phenomenon then known as "discontinuous variation" had prepared him, as in like manner also De Vries was prepared, to take the analytical point of view toward the hybridization process, even before the publication of Mendel's results, as the following quite remarkable passage clearly indicates:

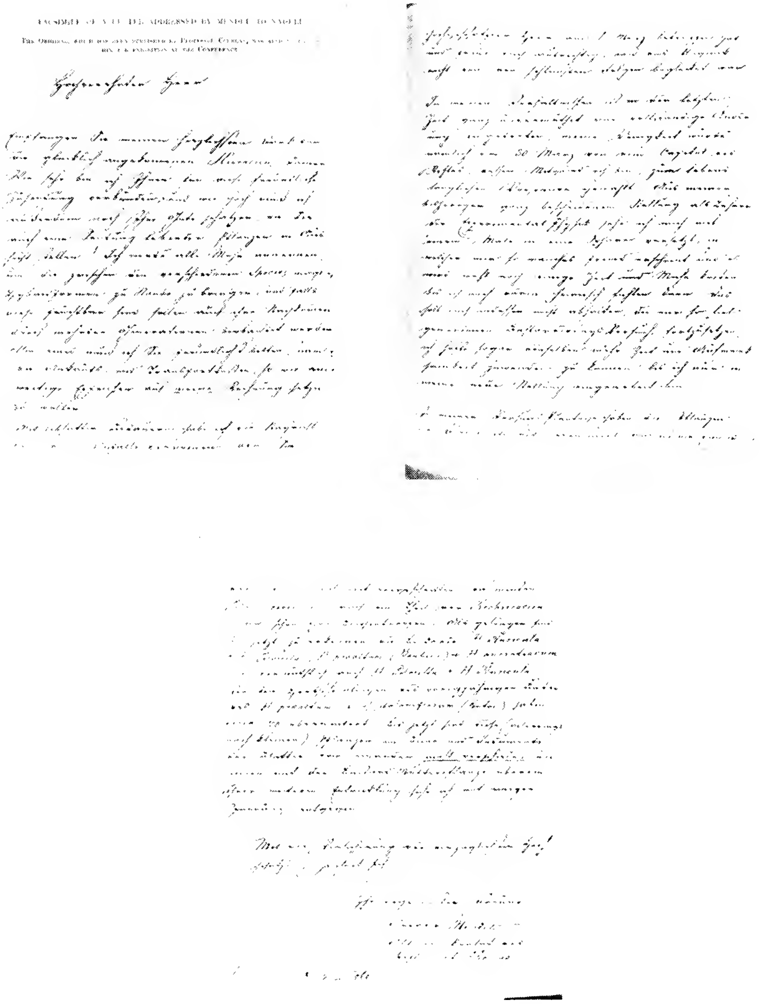
> "The recognition of the existence of discontinuity in variation, and of the possibility of complete or integral inheritance when the variety is crossed with the type, is, I believe, destined to simplify to us the phenomenon of evolution perhaps beyond anything that we can foresee. At this time we need no more *general* ideas about evolution. We need *particular* knowledge of the evolution of *particular* forms. What we first require is to know what happens when a variety is crossed with its *nearest allies*. If the result is to have a scientific value, it is almost absolutely necessary that the offspring of such crossing should then be examined *statistically*. It must be recorded how many of the offspring resembled each parent, and how many showed characters intermediate between those of the parents. *If the parents differ in several characters, the offspring must be examined statistically, and marshalled, as it is called, in respect to each of those characters separately.* . . . All that is really necessary is that *some* approximate numerical statement of the result should be kept." (Italics inserted.) (p. 63.)

If Mendel's paper had never come to light, it is more than probable that investigation would have ultimately been directed to the *crux* of the method of inquiry, by this utterance of Bateson's, remarkable for the time, and noteworthy as being the first, and indeed the only clear postulation of the terms of a scientific basis for an investigation of the descent of characters, in all the literature antecedent to the re-discovery of Mendel, viz:

> "*That if the parents differ in several characters, the offspring must be examined statistically, and marshalled, as it is called, in respect of each of those characters separately.*" (Italics inserted.) (p. 63.)

This remarkable statement progressed beyond any point of view theretofore expressed, and should be preserved as a memorial to the prescience of Professor Bateson, the first champion of Mendelism in the English-speaking scientific world.

Bateson's standpoint is further illustrated by the following statement:



FACSIMILE OF A LETTER ADDRESSED BY MENDEL TO NÄGELI

The Original, which has been furnished by Professor Correns, was [illegible] exhibition at the Conference

Hochverehrter Herr!

PLATE XLVIII. Facsimile of letter of Mendel to Nägeli, with signature. Furnished by Professor Correns.

> "Cross-breeding, then, is a method of investigating *particular* cases of evolution one by one, and determining which variations are discontinuous and which are not, which characters are capable of blending to produce a mean form and which are not. It has sometimes been urged against this method of investigation that the results are often conflicting. It has been said that such work will only lead to accumulations of contradictory evidence. It is, however, in this very fact of the variety of results that the great promise of the method lies." (p. 64.)

From the whole of the above, it appears that to Bateson's mind, at that time, one of the principal purposes of hybridization was to determine in what cases blending occurred, and in what cases characters were discontinuous in their descent, which was the first prerequisite to an actual experiment to determine the facts, and the credit for which, as a prolegomenon, unquestionably belongs to Bateson alone.

As illustrations of "discontinuous" inheritance after crossing, Bateson cites the case of the crossing of *Matthiola incana*, a hairy species, and its smooth variety, crossed by Trevor Clarke, reporting the fact observed that:

> "On crossing these two varieties the offspring consisted entirely of completely hoary and completely glabrous individuals, no intermediate being present." (p. 64.)

The case of *Lychnis diurna* (hairy), crossed with its glabrous variety by De Vries, is also cited.

> "All of the first generation of cross-breds inherited the hairiness in its complete form: when, however, these plants were crossed again with the smooth form, the result was a mixed progeny, of which some were hairy, and others smooth." (p. 64.)

A third case was given as that of *Biscutella laevigata*, reported from the investigations of Miss E. R. Saunders, one of Bateson's pupils. The species type is a hairy plant of the Alps, with a local variety having the *leaf surfaces* smooth; the smooth form is found to occur abundantly with the hairy types, intermediates seldom occurring.

> "The result of artificial cross-breeding went to show that of the young seedlings of mixed parentage some were hairy, some smooth, and a good many intermediate. But as these seedlings grew, the hairy and the smooth retained their original characters, while the intermediate ones gradually became smooth. The transition was not effected by actual loss of hairs, but, after the first few leaves of intermediate character, the leaves subsequently produced were smooth." (p. 65.)

Bateson goes on to say:

> "In all these three cases there is discontinuity, the intermediates between the varieties being absent or relatively scarce. Nevertheless, on examination, it is found that the discontinuity is not maintained in the same way in the different cases. The transmitting powers of the one variety in respect of the other are quite different in each case, and it must, I think, be admitted that we have here a fact of great physiological significance. In each of the three cases enumerated, the two varieties are seen to stand towards each other in a different relation, and in each the mechanism of inheritance works differently." (p. 65.)

Bateson finally closes with the following significant comment upon the contention that the results of crossing are uncertain, sometimes one result occurring, and sometimes another:

> "This, of course, merely means that *the problem must be studied on a scale sufficiently large to give a statistical result.* There is here an almost untouched ground on which the properties of specific characters can be investigated." (Italics inserted.) (p. 66.)

On May 8, 1900, not quite a year after the address referred to above, and almost immediately after the appearance of the papers from Holland, Germany, and Austria on the subject of the Mendelian investigations, Professor Bateson presented to the Royal Horticultural Society, the results of the then recently published reports of De Vries, Correns, and von Tschermak, together with an outline of Mendel's results, in a lecture entitled "Problems of heredity as a subject for horticultural investigation," published in the Journal of the Society, Vol. 25, pp. 54-61, in which he concludes as follows regarding the Mendelian results:

> "The numbers with which Mendel worked, though large, were not large enough to give really smooth results; but, with a few rather marked exceptions, the observations are remarkably consistent, and the approximation to the numbers demanded by the law is greatest in those cases where the largest numbers were used. When we consider, besides, that Tschermak and Correns announce confirmation in the case of *Pisum,* and De Vries adds the evidence of his long series of observations on other species and orders, there can be no doubt that Mendel's law is a substantial reality; though whether some of the cases that depart most widely from it can be brought within the terms of the same principle or not can only be decided by further experiments." (p. 59.)

This address may be said to constitute the first public introduction of Mendel's results to English-speaking workers by an investigator of standing. Bateson followed soon after with a complete translation of Mendel's paper (Jour. Roy. Hort. Soc., 1901, Vol. 26, pp. 1-32[1]), and later (1902) by its publication in the

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[1] Mendel's paper, "Experiments in Plant Hybridization," appears on

form of a small octavo volume entitled "Mendel's Principles of Heredity; A Defence," now out of print. Concerning these publications he says later, in the preface to his "Mendel's Principles of Heredity":

> "The translation of the first of Mendel's two papers, based on a draft prepared for the society by Mr. C. T. Druery, was printed in the Royal Horticultural Society's Journal, 1901. With modifications I published it separately in 1902, giving a brief summary of Mendelism as then developed, under the title 'Mendel's Principles of Heredity; a Defence.' The object of that publication was to put Mendel's work before the English-speaking peoples, and to repel the attack which the late Professor Weldon had recently made on Mendelian methods and the conclusions drawn from them. The edition was at once sold out, but I did not reprint the book. As a defence it had served its purpose."

In 1909, under the title "Mendel's Principles of Heredity," Bateson published, in a volume of about four hundred pages, the results of the Mendelian investigations made by himself and his fellow-workers, together with results from the general field, already very considerable. In the second part of this volume there appeared a biographical notice of Mendel, and translations of Mendel's papers "Experiments in Plant-Hybridization" and "On Hieracium-Hybrids obtained by Artificial Fertilization." This work was reprinted with appendixes in 1913. It is only justice to Professor Bateson to say that the general recognition of Mendel's work and its fundamental significance in England and this country is largely due, in its inception, to his clear-sighted comprehension of the requirements for an investigation of the problem of heredity, and his immediate and ready appreciation of the importance of Mendel's results, based upon his own prolegomenon of opinion, and as confirmed by the work of Mendel's three discoverers. To Bateson's prompt and courageous championship of the then comparatively obscure matter of the Mendelian Law, the first progress in English-speaking quarters of the principles involved is therefore chiefly to be accredited.

pp. 1-32 of Vol. 26 for 1901-02. The paper is prefaced by a two-page introductory note by W. Bateson. The name of the translator does not itself appear. In the first paragraph of his note Bateson writes:

"It will consequently be a matter for satisfaction that the Royal Horticultural Society has undertaken to publish a translation of this extraordinarily valuable contribution to biological science."

Finally, it is to Professor Bateson, that the initiation of the first definite Mendelian terminology after 1900 is due, the words "allelomorph," "homozygote" and "heterozygote" having been proposed by him as early as 1901, in the First Report to the Evolution Committee of the Royal Society, presented for publication December 17 of that year. In this report, appearing less than two years after the rediscovery of the Mendel papers, Bateson made the following statement (p. 126):

> "We thus reach the conception of unit-characters existing in antagonistic pairs. Such characters we propose to call *allelomorphs*, and the zygote formed by the union of a pair of opposite allelomorphic gametes, we call a *heterozygote*. Similarly the zygote formed by the union of gametes having similar allelomorphs, may be spoken of as a *homozygote*. Upon a wide survey, we now recognize that this first principle has an extensive application in nature. We cannot as yet determine the limits of its applicability, and it is possible that many characters may really be allelomorphic, which we now suppose to be 'transmissible' in any degree of intensity."

This concludes the discussion, made purposely as complete as possible, of the facts and documents surrounding the discovery and bringing to light of Mendel's celebrated paper in 1900. It is believed that this should form a fitting conclusion to the attempt to give as complete an historical account as possible of the data upon hybridization in plants during what may be called the pre-Mendelian period—the period from Kölreuter's first publication in 1763 to 1900.

INDEX

LIST OF HYBRIDS BY GENERA OF THEIR PARENTAGES, AND OF GENERA MADE THE SUBJECT OF EXPERIMENT