# FUNDAMENTA GENETICA

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THE REVISED EDITION OF MENDEL'S CLASSIC PAPER WITH A COLLECTION OF 27 ORIGINAL PAPERS PUBLISHED DURING THE REDISCOVERY ERA.

Selection and Commentary by
JAROSLAV KŘÍŽENECKÝ
with Introduction by
BOHUMIL NĚMEC

*Published for the Celebration of the centenary of the publication of Mendel's discoveries in Brno in 1865*

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# BEFORE MENDEL

*Academician B. Němec*

We do not know whether the social and legal concept of heredity is, or is not older than the knowledge of heredity as a natural phenomenon. As early as in the prehistoric times, man must have realized that the characters of animals and plants are usually inherited, otherwise he would not have sown grain if he had not been sure that he would yield grain again and he would not have selected different varieties of domestic animals, particularly of the domestic dog, if he had not been sure that their offspring would possess analogous qualities. Nevertheless, he must have noticed the variability of the cultured plants and animals, no matter what its cause might have been. At a much later date he found that at least some plants multiply also sexually. This recognition concerned first the date-palm whose dioecious character was known to man as early as 5.000 years B.C., and whose male blossom became even a commercial article. From the date-palm and perhaps also from hemp grew the dim concept of the sexuality of plants though this knowledge included still many misty facts. However, for a few thousand years the problem of the sexuality of plants remained a mysterious secret in botany. The superstitions concerning the date-palm were handed down as a tradition and were carried over throughout Middle Age up to the botanists of the New Age.

How these questions were manifested in the antique literature, was described in detail by Ferd. Stiebitz (Antiquitatis de hereditate opinionum fundamenta biologica, Brno 1937). In this work the author treated likewise the antique panspermic (pangenic) theories. In the following I cite the results of his studies into hypotheses concerning the sexuality of plants: "The ancient world had no firm knowledge of the sexuality of plants. On a closer examination, all documents that would seem to suggest a closer knowledge of the sexuality of plants are disclosed as vain. It is true that the ancients called some plants males and others females but they did not mean by this a real sexuality of plants. These terms were purely metaphorical:*) by using them the ancients designated plants

*) Aristoteles Gen. an. I 1. compares the crustaceans with plants and says that the male and female sex is missing even in them and that the terms used here on the basis of some insignificant differences are employed from mere habit.

either similar or of the same species if they differed in appearance or fertility. Theophrastus compared at many occasions male and female plants of the same species and it can be seen that in doing so he means—apart from fertility or sterility—primarily differences in appearance, odour or quality, hence — as one would say at present time—varieties. Meyer (E. H. F. Meyer: Gesch. der Botanik, Königsberg 1854) believes on good reasons that the knowledge of the truth would have hardly escaped to the ancients if they had had—like Orientals—the date-palm or another purely dioecious culture plant daily before their eyes. But the truth is that even Theophrastus who advanced most closely to the true recognition has not solved the problem of the sexuality of plants for the date-palm. In general, he did not surmount the apparently popular theory of male and female plants."

In the ancient Greek science there was too much philosophy and relatively little progressive observation. Had it been otherwise, the theories of the abiogenetic origin of fish, amphibians and mammals as encountered even in Aristotle would not have been possible. It was not until W. Harwey (1578—1657) critically opposed the theory of abiogenesis that his words "ex ovo omne animal" slowly spread to cover all organisms. Harwey was a true investigator and it is remarkable that even a non-biologist could arrive—probably on the basis of observations of the daily life—at the conviction of the continuity of life. Before Harwey, Jan Rokycana, the Czech-brethren archbishop of Prague (1397—1471) admitted in his Postilla that the first organisms were created but all the subsequent ones develop from one another.

The antique concepts of the sexuality of plants remained unchanged throughout the Middle Age up to the Renaissance of natural sciences in the 16th century; towards the end of the 16th century they are found in a very exact formulation in the work of Adam Zalužanský from Zalužany (Zaluzanius †1613) Methodi herbariae libri tres, Prague 1592 (New edition Prague 1940). This work can be duly called the text-book of general botany. In it we read for the first time that it is necessary to cultivate theoretical and applied (medicinal) botany separately. At frequent occasions comments were made to Zalužanský's words concerning the sexuality of plants and this is why they will be cited here in extenso in original version:

"Sexus est foetationis pars. Estque duplex, masculinus et femininus, quorum alter agendi, alter patiendi quidem maiores, uterque tamen utrasque partes obtinet. Plantas autem imo potius omnia, quae terra gignuntur, utrumque sexum habere diligentissimi naturae tradiderunt. Quarum aliis confusus, aliis divisim inest.

Quaedam enim singulae, et per se aliud generandi facultatem habent permistis maris et feminae principiis atque optimo naturae consilio. Cum eium generatio proficiscatur ab agente in patientem, natura operi suo plantarum cui motum negasset actionis huius et passionis primordia proportionalia conjunctum

indidit, ut se foetent et concipiant. Quot et in animalibus quibusdam ut Erythinis et hominum androgynis conspicitur. Hoc modo maxima plantarum pars gignit.

In aliorum genere non nisi binae simul generant, quae dividuntur in marem et feminam ut nullae manifestus quam palmae; neque eium sine mare gignunt feminae, et si sit excisus, viduae postae sterilescunt, quas erectis hispidus comis afflatu, visuque ipso et pulvere etiam maritat, circa se nutantes et se pronas blandioribus comis. Adjuvat hunc Veneris intelectum ars ingeniumque hominis, coitu excogitato, ex maribus flore ac lanugine, interim vero tantum pulvere feminis insperso."

Zalužanský presents a description of flowers according to the Pemptades of Dodonaeus (1580). As to the problem of the sexuality of plants, he refers to Aristotle, Theophrastus and Pliny. Caesalpinus, in most probability, escaped him. The latter did not admit sexuality in plants and Zalužanský would have hardly omitted to react to the negative attitude of this author. He had, however, no own concrete observations or findings and Čelakovský (1878) said properly that Zalužanský was rather a natural philosopher than a natural scientist; furthermore, he says that Julius Sachs, in his History of botany, appreciated duly the merits of Zalužanský, saying that Zalužanský tried to concentrate all existing and inherited knowledge into a kind of theory without adding his own observations."

Nevertheless, it should be appreciated that, up to the epoch of Grew, Zalužanský was the first to express clearly the opinion that not only animals but also plants must have sexuality. It is only true to cite again his own words: "Plantas autem imo potius omnia, quae terra gignuntur, sexum habere diligentissimi naturae tradiderunt." He referred to other botanists but did not know by himself—or at least did not write to know it—which of the flower organs are male or female. He had not—or simply did not present—any experimental or descriptive data on behalf of his statements.

These data were presented first by N. Grew (1628—1711). In his Anatomy of plants published in 1682 he was the first to say that the anthers are most likely to be the male organs of plants which fertilize the pericarp by means of pollendust. He writes that the sacs of anthers resemble small testicles while the globules and flower-dust in the anthers and on the pistil represent vegetable sperms.

Grew, for himself, did not see the significance of the anthers of phanerogamous plants to the sexual reproduction. He refers to a discussion conducted by professor Sir Thomas Millington, a person otherwise entirely unknown in botany, in which this man declared the stamina to be the fertilizing organ of the flower. Grew considered them originally to be a mere ornament of the flower and an organ serving for the elimination of noxious juices.

In his Historia plantarum (1686), John Ray completes what has been suggested by Grew. He likewise accepts the idea of the possible fertilization of the flower

from distance. It is said that the female date-palms may be fertilized by wind even in the desert.

Like the recognition of the sexuality of plants was important to the knowledge of the problems of heredity—and one might even say that it was more important than the recognition of the sexuality in animals—so was also important the establishment of the term of the species. The theories of abiogenesis and palinogenesis, accepted unscrupulously since antiquity up to that time, gave evidence against biology as an independent science and could not admit heredity as a manifestation of the continuity of life. In 1686, however, John Ray determined the characters of the species—or, properly speaking, the characters of the taxone of the systematic unit—in a way which remained as yet unsurpassed: "Nulla certior occurrit quam distincta propagatio ex semine." Ahltough the taxonomists did not consider the use of this method as determining, the method is becoming in recent years topical.

A fundamental advance in the knowledge of the sexuality of plants was achieved by R. J. Camerarius (1665—1721). He separated female plants of the dioecious species Mercurialis annua from male individuals and obtained no seeds. In all probability, and also fortunately, male flowers did not develop on female flowers which remained unfertilized for a long time. Camerarius cut off early the male flowers on the ricinus plant and seeds did not develop either in this case. His observations were published in 1694 in a small treatise under the title "De sexu plantarum epistola". In this book Camerarius repeatedly emphasized that plants—like animals—need combine the sex products of both sexes to produce an embryo. That his pioneering work has not fallen into oblivion, is proved by the fact that his treatise, published originally in 1694, was re-edited by J. Chr. Mikan in 1797 in Prague.

The progress in genetics was braked for some time by the preformation hypothesis which assumed that the sperm or egg contains a ready embryo which develops after fertilization simply as a result of the magnifying growth. The epigeneticists, convinced that the embryonic development consists in the new-formation of organs and differentiation of the structure, were in minority. The renowned preformist Albr. v. Haller (1708—1778) proclaimed categorically "nulla est epigenesis". Although the existence of hybrids which possessed some characters from the mother and others from the father contradicted the preformation hypothesis, it was not until in 1759 that is was refuted by C. Fr. Wolff in his dissertation Theoria generationis, completed in 1768 by a further treatise "De formatione intestinorum". In these treatises he proved that the plants develop by the new-formation of organs (leaves) similarly as the chick develops in the egg in the same way. He proved the untenability of the preformation doctrine and opened new pathways to the research of ontogeny and heredity.

The eighteenth century became an age in which the sexuality of plants was not only confirmed by experimental research, investigation of phanerogamous

plants and hybridisation experiments beyond any doubt but also used in taxonomy as the basis of the systematics; this immense work was achieved due to Carolus Linné (1707—1778). In 1759, the Academy of St. Petersburg offered a prize for the solution of the theme "Sexum plantarum argumentis et experimentis novis adhuc jam cognita vel corroborare vel impugnare". Linné presented his dissertation "Disquisitio de sexu plantarum" and was awarded the prize July 6, 1760. The most important result of his investigation was the observation that it is possible, by the hybridisation of two species such as Tragopogon pratensis and perrifolius, to obtain fertile intermediary bastards; this result was confirmed in modern time by Ö. Winge. This is of particular importance since the reliability of the results of Linné's experiments was doubted in the past even by the classicist of the bastardisation of plant species, J. G. Kölreuter (1733—1806).

To tell the truth, the hybrids between the taxones of plants had been known since a longer time (C. Zirkle 1935, The beginnings of plant hybridisation, Philadelphia). Cotton Mather (1963—1720), in his treatise Religio philosophica or the Christian Philosopher (1721), described hybrids between the varieties of maize (Zea mays) with grains of differing colour and the varieties of the genus Cucurbita. These hybrids developed by spontaneous fertilization. Cotton Mather was a mystic (Max. Perty, Mystische Erscheinungen 1872, Zürich) but his observations were confirmed soon after by other authors. Th. Fairchild (1667 to 1729) obtained, not long before 1717, the first intentional hybrid between the species Dianthus caryophyllus and D. barbatus.

Kölreuter was the first to conduct hybridisation experiments on a larger scale intentionally. The hybrids between the species Nicotiana rustica and paniculata, obtained in 1761, exhibited properties standing amidst their parents. By backcrossing Kölreuter made the hybrids return to the paternal species N. paniculata. Although the transfer of pollen by insects and wind has been known at that time, it was not until in 1793 that Ch. K. Sprengel showed in his book Das entdeckte Geheimnis der Natur how many mechanisms of the flower are responsible for the fact that flowers are fertilized mostly by foreign pollen and not by their own flower-dust. The mass of facts concerning the sexuality of plants was so great that the attacks directed against the Linnéists (e.g. the publication of P. J. Schelver 1812) had to cease and hybridisation proved true also in practice. Among the practicians should be mentioned the names of Th. A. Knight (1759 to 1835), William Herbert (1778—1848), Th. Laxton (1866—1872), and L. de Vilmorin (1816—1860). The hypothesis that the hybridisation between individual representants of various genera and species was responsible for the rise of new species was formulated already by Linné who recommended the use of the method of hybridisation as a tool of research in botany.

As mentioned above, the sexuality was known in animals long since but parthenogenesis was accepted as well, though mostly in an erroneous way.

Aristotle admitted the existence of parthenogenesis in some fish and bees. Experimental evidence for the parthenogenesis in bees was presented by parson Antonín Janiš in his treatise "On Apiculture" published in 1789 (Prague).

Yet, besides the hybrids which showed in many cases the characters of new species, sudden appearance of stable and new taxones was observed even without hybridisation and these taxones had the character of novelty. As early as in 1590, Sprenger, an apothecary in Heildelberg found in his experimental garden common celandine (Chelidonium maius foliis et floribus incisis) with narrow-cut leaves and flowers which showed to be a stable taxone. After Linné's peloria there appeared numerous sudden variations of this type (single variations, sports) which cast doubt on the stability of the characters of the species.

Knight was both a theoretician and practician and tried to obtain new woods, grave vine, plum-trees, cherry-trees, apple-trees and pear-trees similarly as J. E. Proche attempted later (1822—1908) in Bohemia. Knight worked also on pea and obtained by crossing its varieties remarkable results. It is of interest how early many experimental workers used in their experiments numerous species employed up to the present time: pea was worked upon by John Glass (1824), Seton (1824), Th. Laxton (1866), H. de Vilmorin (1890), while others used maize, Mirabilis, Datura, Digitalis, Cucumis, Cheiranthus, etc. Cereals were used for experimentation with the selection (P. Sheriff) and hybridisation (K. Rümker). In experiments on pea, some investigators disclosed phenomena (dominance, splitting, independence of the distribution of characters) described later by Gr. Mendel in his research work on the laws of hybridisation. An immense material concerning the bastardisation was processed by C. F. Gärtner (1772 to 1850) who conducted more than 9.000 experiments without ever succeeding in the detection of a commonly valid law of the hereditary transfer of characters by bastardisation. The cause of his failure lies, among others, in that he worked, similarly as Godron and Naudin (1815—1899) with large and not with small species which differed in a small number of characters only.

Since the beginning of the 18. century crossing was used according to Linné's suggestions for the obtainment of new varieties of culture-plants. In many cases the cultivators were not theoretically interested as it was the case, for example, with the Czech pomologist Proche who worked out, on the other hand, a successful method of his own by which he obtained many new varieties (in his comments he described altogether 1520 varieties), particularly apple-trees which gained in Central Europe a considerable spread.

In time and topic, the immediate predecessor of Mendel was Charles Naudin who worked with large species which differed in many characters; but he did not determine the numeric ratios of the different hybrids and could not, therefore, obtain regular results. Some of his findings were confirmed by Mendel, the finding, for example, that the first generation gives rise to identical hybrids exhibiting properties standing between their parents and sharing some char-