"An Analysis of the Work of Joseph Gottlieb Kölreuter and its Relation to Gregor Mendel's Work"

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1. Introduction

Joseph Gottlieb Kölreuter (1733-1806) is considered one of the most important biologists of the nineteenth century, thanks to the following contributions: 1) his work contributed crucially to decide the largely sustained dispute around the sexuality of plants; 2) the description of the flowers carried out by him was as complete and detailed as there was not at that time of any other part of the plant; 3) his study of the mechanisms of pollination of the flowers (specially of the role of insects on it); 4) through his experiments with hybrids, he laid the foundations for constructive later investigations. In connection with this last point is that he is usually associated with Gregor Mendel (1822-1884), pointing out that he – together with Carl Friedrich von Gärtner (1772-1850) – was one of Mendel's most important precursors. In fact, Mendel considers – in the work that supposedly gave rise to genetics (Mendel, 1865) – that Gärtner and Kölreuter were "the two authorities in the specialty [hybridization]". While it is known that Mendel read (and re-read) carefully Gärtner's book *Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich* (1849) ("Experiments and Observations on Hybrid Production in the Vegetable Kingdom") – being conserved his copy, broadly underlined and marked –, the books of Kölreuter are neither in the library of the old monastery nor in the library of the University of Brno – where the volumes of the scientific institutions of Mendel's time have been moved –. However, Kölreuter is the author with more references and more frequently mentioned in Gärtner (1849). And in fact, when Mendel mentions Kölreuter, he makes it according to Gärtner and not in accordance with the original texts.

The aim of this communication is to present an analysis of Kölreuter's work and of its relation to the work of Mendel, through the examination of the references to him which are found in Mendel (1865).

2. Context and aims of Kölreuter's work

The work of Kölreuter on hybrids has been done with the problem of plant sexuality in the background. Even when already in the antiquity there are references to the distinction between male and female in plants, for example in the Assyrian and Babylonian, as well as in Aristotle, his pupil Theofrast, Herodotus and Plinio when speaking of the dates and the figs, it was accepted a lot of time after that not only the animals but the plants also possess male and female sex. Rudolf Jakob Camerer (1665-1721) (Camerarius) is usually considered the founder of the theory of plant sexuality. However, in spite of the series of experiments carried out by him and referred in his work *De sexu plantarum epistola* ["Letter on the Sex of Plants"] (1694) in support of plant sexuality, it wasn't accepted for a

long time, even after Kölreuter's professor, Johann Georg Gmelin, reissued this letter in 1749 during Kölreuter's days as student in Tübingen.

The Imperial Academy of Sciences of Saint Petersburg offers in 1759 a prize asking "to strengthen or to combat the sexuality of the plants by means of new arguments and experiments." Kölreuter, who was Fellow of the Academy, begins that year his experiments with hybrid plants. This prize is granted to the work of Carl von Linné (1707-1778) (Linnaeus) *Disquisitio de sexu plantarum* ["Investigations on the Sex of Plants"], in 1760, being Kölreuter one of the judges, who doubts about the authenticity of the hybrid described there. In that same year Kölreuter achieves the first successful hybrid crossing with two species of tobacco (*Nicotiana rustica* ♀ & *Nicotiana paniculata* ♂) – which after him (1761, § 16) was the very first true hybrid artificially produced –, and in 1761 the bloom of the first hybrid plant. Back in Germany he continues his hybrids experiments not only with *Nicotiana*, but also with other plant species, such as *Mirabilis*, *Dianthus*, *Verbascum* and *Malvaceen*, in Leipzig, Sulz and Calw first, and in Karlsruhe later, where he get in 1763 an appointment as Professor of Natural History and Director of the Gardens of the Margrave of Baden, Karl Friedrich (1749-1811). In 1786 Kölreuter loses his charge of Director of the Gardens but remains living in Karlsruhe as Professor of Natural History. His main work appears under the title *Vorläufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen* ["Provisory Inform of Some Experiments and Observations Referred to the Sex of Plants"], in four parts, during the years 1761, 1763, 1764, 1766, respectively, where he reports the successful hybridization of a great number of vegetable species.

The hybridization experiments in plants was considered important in that context because if the progeny showed paternal and maternal features, or if hybrid plants could be generated and analogies could be shown between them and the hybrids of animals, a powerful support would be provided in favor of the theory of plant sexuality. Kölreuter, who didn't have doubts that those hybrids could be generated artificially, was sure that the nature possessed her own means to prevent their formation in a natural way (1761, § 16; 1766, § 20), as well as of avoiding the propagation like new species of those hybrids that had been obtained by means of experiments (1763, § 1; 1766, § 20). In this way, he supported the so-called "doctrine of special creation" – which claims that all existent species are an immediate creation of God, and that species are constant, in the same way as Linné did in his early writings –, rejecting the "*new* doctrine of special creation" – propounded by Linné later on and according to which certain hybrids that appear in the nature but can also be artificially produced, are fertile and reach the status of new species –. Kölreuter's professor, J.G. Gmelin, proposes to decide experimentally between both doctrines of special creation – the old one and the new one –. Kölreuter accepts the challenge and carries out a series of experiments with hybrids in a greater number than those carried out until that moment, with the additional aim of finding the hidden measures imposed by nature, to produce new species by means of hybridization of species already present.

3. Results of his experiments with hybrids

In order to be able to determine what hinder the production of hybrid plants in nature and the constant reproduction of those artificially obtained, he examined carefully the fertility of his hybrid plants, and observed a remarkable contrast between the *fertility* of pure species and the *sterility* of hybrids. In general, he found that the sterility came "from the male side", i.e., from the pollen. However, in order to see whether the hybrids were also sterile "from the female side", i.e., "from both sides" (or "in maximum degree"), he tried to fecundate some of the hybrids with pollen from the paternal plant and others with pollen from the maternal plant. In some cases he found sterility "in maximum degree"; but in other cases he raised a second generation of hybrids ("back-crossed", in later terminology, or "in ascending degree", if fecundated with paternal pollen, and "in descending degree", if fecundated with maternal pollen, according to the terminology used by Kölreuter). He was successful even in creating a second generation of true hybrids from the self-pollination of these tobacco hybrids, finding a *slight degree of fertility* that was even higher in hybrids of other species. Thanks to the work of Kölreuter were available for the first time in the history of biology reliable and definite descriptions of the hybrids and their offspring. The hybrids from the first generation were in general all *alike* and in most of their characters they were *intermediate* between the two parental species (he observed occasionally a "greater vegetative force" of the hybrid, even in sterile ones). On the other hand, "reversed experiments" ("reciprocal crosses") provided *identical* results, i.e., the hybrid offspring were identical, independently of which of them was the parental species fecundated and which one did fecundate. The hybrids from the back-crosses and from the second generation were all *different* and they tended to be less like their parental hybrids and *more like* one or another of the *originating species* – depending of which of them was the species that contributed with the pollen. This fecundation process of hybrid offspring through the pollen of one of the original species could be continued along successive generations until it was obtained as a result the "return" to the original species from which the pollen came, in a phenomenon that Kölreuter denominates "transmutation" of one species into another, in analogy with the alchemist theory of the "transmutation" of metals. In some cases of self-pollination of the hybrids from the first generation he found that their offspring was of three types: it was either like the original maternal species, or like the hybrid parents from first generation, or like the original paternal species. However, sooner or later the hybrid offspring "return" to one or another of the original species instead of reproducing itself as hybrid, in a well-known phenomenon called "reversion."

Kölreuter explains the obtained results by means of his fecundation theory (Campbell, 1981), developed in analogy with the chemical process of salt formation. It establishes the following:

> To the production of every natural two similar materials of different sorts are demanded. The one of this is male, the other female […]. 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. (Kölreuter (1763), § 1.)

In the usual case, where the hybrids had an intermediate appearance, the union and mixture of the male and female materials occurred in equal proportions. While in the exceptional cases, where the hybrid offspring was varied, the combination occurred in unequal proportions.

On the other hand – and due to what Kölreuter denominates the "law of the nearest affinity" that possesses "a great reach in the nature and in which find its foundation a quantity of phenomena well-known for a long time ago that appear daily so much in the chemistry as in the physics" (1766, § 20) –, it never takes place a fecundation by means of foreign pollen, when a plant receives, at the same time, pollen of its own species, and the pollen of a hybrid plant doesn't fertilize, when it is present the pollen from one of the parental species.

4. Reception of his hybridization work

The register of the experiments carried out by Kölreuter didn't have much repercussion among his contemporaries. In addition, many of his experiments finished prematurely, some suffering for a lack of facilities and good equipment, and he was never able to carry out his intention of hybridizing finches to demonstrate that his conclusions on plants were also applicable to animals. The sense of frustration grew in his last life years, even when he continues with his experiments up to 1805, dying in 1806.

Although the Swiss biologist Johann Hedwig (1730-1799) repeated just one of Kölreuter's hybridization experiments in 1798, it was Augustin Sageret (1763-1861) the first one in reproducing his experiments with plant hybrids fifty years after the publication of his main work and twenty years after his death, but he didn't give details of his experiments; Arend Joachim Friedrich Wiegmann (1770-1853) and Carl Friedrich von Gärtner followed him. They all testified the accuracy of Kölreuter's work. But he has also critics – particularly Franz Joseph Schelver (1778-1832) and his student August Wilhelm Eduard Theodor Henschel (1790-1856) – who still denied the plant sexuality and questioned the content and meaning of his experiments. With the aim to silence those critics it was that Gärtner repeated and extended his work and in this way laid the foundations on which Mendel built (Lorenzano 1995, 2001).

5. Mendel's references to Kölreuter

It is probable that Mendel had heard of Gärtner's book *Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich* from his professor of vegetable physiology, Franz Unger (1800-1870), during his stance in Vienna, in 1852; maybe he read it carefully in the years 1853-1854, before he has chosen the 34 varieties of peas with those that worked (Olby, 1985); he commented and underlined that book, among other places, where Kölreuter, William Herbert (1778-1847) and Henri Lecoq (1802-1871) were mentioned; they are, besides to Max Wichura (1817-1866) (another reading of Mendel), the only authors that Mendel mentions in his *Versuche über Pflanzen-Hybriden*.

In Mendel (1865), Kölreuter is mentioned in five opportunities. The first of them occurs at the beginning of the "Introductory Remarks" ("*Einleitende Bemerkungen*").

Mendel establishes there the aim of his experiments – "to follow up the development of the hybrids in their progeny" –, considered as having shared with his predecessors, inside those that stands out Kölreuter, intending to find "a generally applicable law governing the formation and development of hybrids", so that "we can finally reach the solution of a question the importance of which cannot be overestimated in connection with the history of the evolution of organic forms"; also, he criticizes his predecessors – Kölreuter included – not to have proceeded by means of a statistical analysis:

"Introductory Remarks"

> Experience of artificial fertilization, such as is effected with ornamental plants in order to obtain new variations in color, has led to the experiments which will here be discussed. 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[1] of the hybrids in their progeny.
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> To this object numerous careful observers, such as Kölreuter, Gärtner, Herbert, Lecoq, Wichura and others, have devoted a part of their lives with inexhaustible perseverance. Gärtner especially in his work "die Bastarderzeugung im Pflanzenreiche", has recorded very valuable observations; and quite recently Wichura published the results of some profound investigations into the hybrids of the Willow. 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* make on plants belonging to the most diverse orders. 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 the hybrids appear, or to arrange these forms with certainty according to their separate generations, or definitely to ascertain their statistical relations. It requires indeed some courage to undertake a labor of such far-reaching extent; this appears, however, to be the only right way by which we can finally reach the solution of a question the importance of which cannot be overestimated in connection with the history of the evolution of organic forms. (Mendel, 1865, pp. 3-4; Mendel's emphasis.)

In the second mention to Kölreuter, Mendel refers to the phenomenon known as "reversion" – in the believe also that it could be described and explained, under the

[1] The term „Entwicklung" that in German current usage means "development" seems to have been used then to refer so much to the ontogenetic development as to the filogenetic, that is, so much to the embryological development as to the evolution.

suppositions of validity for the following generations of hybrids of "law of simple combination of characters",[2] and same fecundity on the average for each generation –:

> The observation made by Gärtner, Kölreuter, and others, that hybrids are inclined to revert to the parental forms, is also confirmed by the experiments described. It is seen that the number of the hybrids which arise from one fertilization, as compared with the number of forms which become constant, and their progeny from generation to generation, is continually diminishing, but that nevertheless they could not entirely disappear. (Mendel, 1865, p. 17.)

As indicated by Callender (1988), Mendel here distorts the conceptions of Kölreuter (and of Gärtner), since according to the opinion of these authors the hybrids not only possess the tendency of returning to the original species, but rather this return is something *necessary* and *unavoidable* in all hybrid plants without exception, that is, it constitutes a natural law (as it Gärtner says, 1849, p. 159). For Mendel, on the contrary, the hybrid plants don't disappear completely with time; what happens with the successive generations, according to Mendel, is a constant increase of the absolute number of hybrids together with a growing decrease of their frequency relative to the plants that "return" to their parental forms.

At the beginning of the "Concluding Remarks", in the third reference to Kölreuter, Mendel writes:

"Concluding Remarks"

> It can hardly fail to be of interest to compare the observations made regarding *Pisum* with the results arrived at by the two authorities in this branch of knowledge [hybridization], Kölreuter and Gärtner, in their investigations. According to the opinion of both, the hybrids in outward appearance present either a form intermediate between the original species, or they closely resemble either the one or the other type, and sometimes can hardly be discriminated from it. From their seeds usually arise, if the fertilization was effected by their own pollen, various forms which differ from the normal type. As a rule, the majority of individuals obtained by one fertilization maintain the hybrid form, while some few others come more like the seed parent, and one or

[2] What Mendel calls the "law of simple combination of characters" – "If *A* be taken as denoting one of the two constant characters, for instance the dominant, *a* the recessive, and *Aa* the hybrid form in which both are conjoined, the expression: $A + 2Aa + a$ shows the terms in the series for the progeny of the hybrids of two differentiating characters" (Mendel, 1865, p. 17) – synthesizes a great amount of empirical results in the form of an empiric law. It describes the proportions (relative frequencies) in which each class or form of the progeny are obtained in the total series in monohybrid experiments, that is, in those in which are only considered two different characters. This and the "law of combination of different characters" – which generalizes for several different characters the combinatorial series obtained for the dihybrids and trihybrids – constitute "the law discovered on *Pisum* for the formation and development of the hybrids".

> other individual approaches the pollen parent. This, however, is not the case with hybrids without exception. Sometimes the offspring have more nearly approached, some the one and some the other of the two original stocks, or they all incline more to one or the other side; while in other cases *they remain perfectly like the hybrid* and continue constant in their offspring. The hybrids of varieties behave like hybrids of species, but they possess greater variability of form and more pronounced tendency to revert to the original types.
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> With regard to the *form* of the hybrids and their *development*, as a rule an agreement with the observations made in *Pisum* is unmistakable. It is otherwise with the exceptional cases cited. (Mendel, 1865, p. 38; Mendel's emphasis.)

In this paragraph Mendel intends to compare his results obtained in *Pisum* with that observed by Kölreuter (and Gärtner) in their experiments. Mendel points out there that his results (considered in a qualitative and comparative manner and not quantitatively) agree quite well with those of Kölreuter (and Gärtner), regarding the form of the hybrids and their development, that is, so much of the hybrids appearance and the appearance of their offspring. In relation to the appearance of the hybrids, Mendel doesn't find that this is intermediate in *Pisum* – one of the possibilities pointed out by these authors –, but only similar to one or another to the parental forms – the other of the possibilities –. As for the appearance of hybrids offspring, Mendel observes that in *Pisum* this is *variable*: most preserve the hybrid form, while some are more like one of the parental forms and others more like the other one. However, a difference exists in the consideration of those hybrids (to which *Pisum* doesn't belong) whose offspring is constant, that is, in those hybrids whose offspring conserves the appearance of the hybrid forms and spread without modification. As Mendel accentuates later on in his text:

> We meet with an *essential difference* in those hybrids which remain constant in their progeny and propagate themselves as truly as the pure species. […] For the history of the evolution of plants this circumstance is of special importance, since constant hybrids acquire the status of *new species*. (Mendel, 1865, p. 40; Mendel's emphasis.)

So Mendel believes he have found an essential difference between the hybrids of *Pisum* and those, which he denominates "constant", and which spread pure and acquire the status of new species. That means that new species can be originated through hybridization of species already present. In this way, and against Kölreuter (and Gärtner), Mendel supports the "new doctrine of special creation" proposed by Linné.

We would like to point out another discrepancy between the thought of Mendel and that of Kölreuter. For the last one there is an essential difference between varieties and species, as well as there is a difference between the hybrids of varieties and the hybrids of species, and believes that this can be established by means of the different behavior of the hybrids of varieties and of the hybrids of species with respect to their fertility: the first ones are fertile, as well as their offspring, while the last ones are sterile. Mendel, on the other hand, considers that there is not a sharp difference between the hybrids of varieties and the hybrids of species, and that the difference between them is just a gradual one, and he believes that there is not a sharp difference between species and varieties – in a similar manner as conceived by Knight and Herbert –. In this sense Mendel had previously written

in the text: “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” (Mendel, 1865, p. 24).

The two last mentions to Kölreuter appear at the end of Mendel’s paper, when he discusses the transformation (or transmutation) experiments and its significance:

> In conclusion, the experiments carried out by Kölreuter, Gärtner, and others with respect to the *transformation of one species into another by artificial fertilization* merit special mention. Particular importance has been attached to these experiments and Gärtner reckons them “among the most difficult of all in hybridization”. (Mendel, 1865, p. 43; Mendel’s emphasis.)

And in the very last reference to Kölreuter, talking about the differences in the time required for the transformation, depending on what sex is chosen, Mendel states:

> Gärtner found by repeated experiments that the *respective* period of transformation varies in many species, so that frequently a species *A* can be transformed into a species *B* a generation sooner than can species *B* into species *A*. He deduces therefrom that Kölreuter’s opinion can hardly be maintained that “the two natures in hybrids are perfectly in *equilibrium*”. It seems however that Kölreuter does not deserve this reproach but rather that Gärtner has overlooked an important point, to which he himself draws attention elsewhere, namely that it “depends on which individual is chosen for further transformation”. (Mendel, 1865, p. 45; Mendel’s emphasis.)

One of the interesting aspects of this reference is that Mendel doesn’t quote Kölreuter directly from the original writing (Kölreuter, 1763, § 6) – where it is literally read “that the two types of natures maintain in the hybrids the most complete balance” –, but rather he does it from the slightly modified quotation from Gärtner (1849, p. 472), without mentioning the page. The other interesting aspect is that Mendel rejects the critical observation of Gärtner to Kölreuter – about the differences in the time required for the reciprocal transmutation of one species into another – and that he defends Kölreuter using Gärtner’s words, through a modified quotation from Gärtner (1849) without mentioning the page (p. 459).

6. Conclusions

In this communication we exposed and analyze, in first term, the work of Joseph Gottlieb Kölreuter. From it we emphasize the context in which he carried out his experiments with hybrids – trying to support the theory of plant sexuality by means of the production of hybrids, but being opposed to the “new doctrine of special creation” proposed by Linné, and in total agreement with the belief in the constancy of the species and in their sharp differentiation of the varieties –, as well as his more important results and conclusions: the *sterility* of the hybrids, the *nearest affinity* of the pollen, the *reversion* of the hybrids, their *intermediate* character, the *identity of the hybrids* obtained by reciprocal

crosses, and the *transformation of one species into another* by means of successive reciprocal pollinations.

In second term we saw the relationship between the work of Kölreuter and that of Mendel, through the references to Kölreuter made by Mendel, even when it doesn't seem that he had had a direct knowledge of his work but only through Gärtner (1849). Mendel belongs to the *tradition of the hybridists*, like Kölreuter did. Mendel, contrary to his predecessors, had a mathematical treatment of the topic, *carrying out a statistical analysis* of his experiments, *proposing a "law of the formation and development of the hybrids*"; he declares himself *against the necessity of the intermediate character* of the hybrids, and – when accepting the existence of *constant hybrids* – also against their *sterility*, the *constancy of the species* (and their *sharp differentiation from the varieties*), and *in favor of* the idea of *the origin of new species by means of hybridization of species already present*, that is, in favor of Linné's "*new doctrine of special creation*".

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