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The Lesser-Known Mendel: His Experiments on Hieracium

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The year 2006 is the 140th anniversary of Mendel's pathbreaking article. It is appropriate that a journal devoted to genetics begin the year with an article about Mendel and his work. Much has been written about his deep insights and the failure of the biological community to recognize his work. Here, on this anniversary, instead of extolling his success, we present a scholarly account of Mendel's frustrating attempts to repeat his findings in another species, which, unbeknownst to him, reproduced apomictically.

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MENDEL hoped that the highly polymorphic genus Hieracium would be particularly promising for verifying the laws of inheritance that he had discovered while working on Pisum. But all his incredibly painstaking emasculation and crossing experiments on Hieracium led to results that, to his consternation, seemingly stood in direct contradiction to his laws:

1. The F_1 hybrids from crossings between, as he thought, "true breeding" strains were not uniform, as in Pisum; rather they varied in every conceivable way.
2. The putative F_2 generations, on the contrary, were uniform and did not segregate for any characters, as he would have expected.

These puzzling results caused Mendel (1869 and in his letters to Nägeli in 1866–1873; see Correns 1905) to consider how much Pisum and Hieracium might represent divergent laws of inheritance. Such a hypothetical existence of two different types of inheritance—a "Pisum type" and a "Hieracium type"—was a view shared even by de Vries, Correns, and Bateson in the first years after the rediscovery of Mendel's laws.

Only years after the pioneering embryological investigations of parthenogenesis by Juel (1898) was it eventually realized that the genetic basis underlying the reproduction of Pisum and Hieracium is exactly the same! In fact, the two "types" differ from each other only regarding their modes of reproduction, or more precisely, their embryo formation. Pisum is the paradigm of a plant with a normal sexual reproduction: embryos are derived, after fertilization, from meiotically formed, reduced egg cells with n chromosomes. Hieracium, on the other hand, is one of the comparatively few angiosperms in which embryos develop asexually; *i.e.*, they derive from the parthenogenetic development of apomeiotically formed, unreduced eggs with $2n$ chromosomes. Seeds with such embryos give rise to clones, *i.e.*, exact copies of their respective mother plants. Asexual reproduction by seeds, today termed apomixis (earlier synonym: apogamy), occurs in most species of Hieracium used by Mendel, and this simple fact explains the second of the above-mentioned contradictions that he noticed. The other contradiction to the results that Mendel had expected is due to the fact that apomicts may, exceptionally, also produce reduced egg cells. If, in one of these rare cases, the egg cell is fertilized, the apomict in question reproduces for once sexually, and the hybrid offspring will of course segregate according to Mendel's law.

Years before Mendel published his famous article on Pisum (in 1866), he had already begun to search for new suitable plants in an attempt to corroborate the genetic laws that he had discovered. As is well known, he started preliminary experiments with ~20 species from different and sometimes distant taxonomic genera, including some of our classical genetic subjects, such as Antirrhinum, Melandrium/Lychnis (Silene), Mirabilis, and *Zea mays*. Mendel's great hope, however, was Hieracium (hawkweeds). This huge, extremely polymorphic genus was, already at that time, notorious for its richness—and for the problems inherent in its hybridization.

In Hieracium, too, Mendel carried out preliminary experiments aiming to select true breeding parents, which would be homozygous for the morphological traits

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to be studied. Mendel's great demands in these respects seemed to be met by several Hieracium species from the two main subgenera Pilosella and Archieracium (Euhieracium). They appeared to be constant in their traits, and he therefore considered them to be homozygous and suitable as experimental plants. He set up his first series of Hieracium crossings during the summer of 1866, while Brünn—and Mendel's monastery—were occupied by the Prussian army (Iltis 1924, p. 113). On New Year's Eve of 1866, *after* he had obtained the first seeds and ascertained that they had germinated well, Mendel addressed himself to Carl Nägeli, renowned botanist and specialist on Hieracium. Mendel's most informative correspondence with Nägeli was edited by Correns in 1905—although in a somewhat obscure journal—and was, unfortunately, reprinted only once, in Correns' collected papers as an appendix (Correns 1924, pp. 1233–1297). These 10 fascinating letters have, incomprehensibly, never been included in the widespread, often reedited volume dedicated to Mendel in "Ostwalds Klassiker der exakten Wissenschaften."

In his first letter to Nägeli (Correns 1905, pp. 195–198; Correns 1924, pp. 1238–1240), Mendel wrote that Hieracium, Cirsium, and Geum had been chosen for further experiments to test the conformity with Pisum ("Um die Uibereinstimmung mit *Pisum* zu erproben. . ."; "Für weitere Versuche wurden *Hieracium*, *Cirsium* und *Geum* gewählt"), and he points to first results. The initiative to work on Hieracium was thus clearly taken by Mendel. Contrary to a widespread belief, Nägeli did not press Mendel to choose Hieracium, nor did he impose this baffling genus on him. Of course, Nägeli was delighted by Mendel's plan, as his first, detailed response clearly shows (Iltis 1924, p. 130): "It is an excellent idea of yours to include also other plants [than Pisum] in the project of your investigations, and I am sure that you will arrive at quite different results (concerning the inherited traits) if you pursue your investigations working with other plants. It would be particularly desirable if you succeeded to make hybrid crosses in *Hieracium*." ("Ihr Vorhaben, noch andere Pflanzen in den Kreis Ihrer Versuche zu ziehen, ist vortrefflich und ich bin überzeugt, das Sie bei weiteren verschiedenen Formen wesentlich andere Resultate (rücksichtlich der vererbten Merkmale) erhalten werden. Besonders erwünscht wäre es, wenn es Ihnen gelänge, hybride Befruchtungen bei Hieracien auszuführen . . ."). He also provided advice and pointed out difficulties and problems. Although questions concerning natural and artificial interspecific hybridization in complex genera such as Hieracium were of predominant interest to Nägeli, one may really wonder whether he would have devoted more attention to Mendel's pioneer work, had he not seen the unexpected opportunity of finding in Mendel a gifted collaborator for his own research work. Generally speaking, in those days theories of the formation and origin of species were at the center of scientific interest—not yet the arithmetic and statistic subtleties dealing with segregation of inherited traits. The time had obviously not yet come for quantitative analyses, since the qualitative aspects were still in need of clarification. This should be kept in mind when the meager attention to Mendel's discoveries is deplored.

All emasculations of Hieracium were done by Mendel himself by hand—in Compositae an almost unimaginable task! (For details of his methods, see Mendel 1869, p. 27; Correns 1905, pp. 212 and 229–1930; and Correns 1924, pp. 1252 and 1266–1967.) Mendel's first successful cross, *Hieracium praealtum* × *H. stoloniferum*, completed in the summer of 1866 (Correns 1905, p. 212; Correns 1924, p. 1252), gave rise to just four seeds, from which he obtained four flowering plants. But only one of them was a true hybrid. Evidently, Mendel's method of emasculation, extremely laborious as it was, nevertheless seems to have been quite efficient. The other three plants were mother-like, and Mendel assumed that they had issued from unintended self-fertilizations. Therefore, in the following years, he subsequently emasculated younger and younger stages, albeit always with equally unsatisfactory results. Not only these, but also most of the later crossing combinations, led generally to mother-like, and only very rarely to hybrid, offspring. We do not know, even roughly, how many mother-like offspring turned up; but it must have been an extremely large number. According to Correns, in all the years (1866–1871) that Mendel devoted to these investigations (Correns 1905, pp. 190–191; Correns 1924, p. 1234), he did obtain—apart from numerous mother-like plants—hundreds of true hybrids from 21 crossing combinations. Taking these data as indicative of the total number, Mendel must have made many thousands of emasculations by hand! All the crossing combinations that Mendel meticulously performed on Hieracium led to the most perplexing results: Whenever he, rarely enough, succeeded in raising more than one hybrid from a given combination, the offspring were—quite contrary to the uniform F_1 hybrids that he had obtained in his experiments on Pisum—not uniform at all; rather, they varied in all characters observed (Mendel 1869; Correns 1905, pp. 231–232; Correns 1924, p. 1268). Later on, Mendel obtained a somewhat larger number of seedlings from the cross between a variety he termed "*H.*XII" [and which Nägeli identified as "*H. cymigerum* Rchb.(?)"] and *H. pilosella*. Both parents were collected by Mendel near Brünn, and he took them to be real "species" since, in preliminary experiments, he had found them to be true breeding. However, in the following summer (1870) he ascertained that the 29 hybrids issued from this cross were not uniform F_1 hybrids, as he had expected; rather, they showed a continuous series of variations between the traits of both their parents (Correns 1905, p. 232; Correns 1924, p. 1268).

In contrast to other Hieracia, *H. auricula* was found by Mendel to be "a completely reliable experimental plant

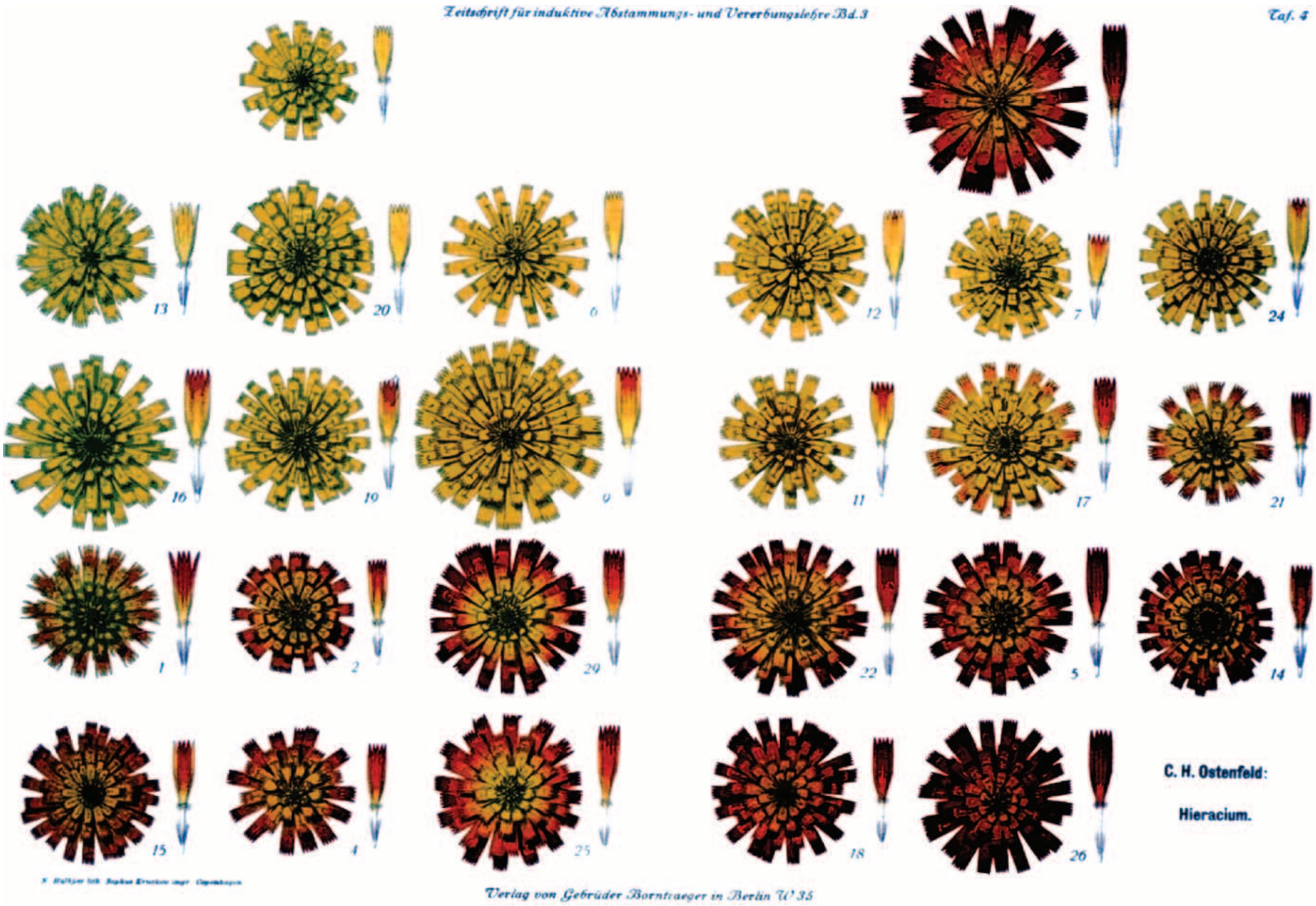

FIGURE 1.—Hybrids resulting from a cross between *H. auricula* × *H. aurantiacum*. *H. auricula* × *H. aurantiacum* was only one of many crossing combinations effectuated by Mendel, although it was the one with by far the largest progeny. Since Mendel, in preliminary experiments, ascertained that both parents were "true breeding," he considered them to be "constant species." But instead of an expected uniform F_1, he obtained, to his consternation, segregating offspring covering the whole palette of transitions, as illustrated here by a figure from OSTENFELD (1910), who repeated the same cross. Mendel could not have known at that time that the pollen parent *H. aurantiacum* is, in reality, a highly heterozygous hybrid, genetically fixed thanks only to apomictic reproduction, and thus feigning a true-breeding "species."

when working with due care" ("...bei einiger Vorsicht eine vollkommen verläsliche Versuchspflanze," CORRENS 1905, p. 230; CORRENS 1924, p. 1267). (Today we know why: *H. auricula* is a normal, purely sexual species!) Mendel used it—most carefully emasculated—as a mother plant in different crossing combinations. The most successful of these, *i.e.*, *H. auricula* × *H. aurantiacum* (see Figure 1), resulted in 98 seedlings, from which Mendel obtained 84 flowering plants in 1870 (CORRENS 1905, pp. 230 and 238; CORRENS 1924, pp. 1267 and 1274; *nota bene:* in Mendel's article of 1869 (p. 29), only 2 flowering plants were mentioned). But these 84 sister hybrids were—again unlike what Mendel thought according to the uniformity expected in the F_1 generation—by no means uniform; rather they showed manifold variations in every imaginable respect, even regarding fertility (CORRENS 1905, p. 239; CORRENS 1924, p. 1274). (Today, we know why: *H. aurantiacum* is, in reality, highly heterozygous!) In 1906 and 1907, the same cross was repeated by OSTENFELD (1910, pp. 259–260) using a radically simplified method (RAUNKIÆR 1903; OSTENFELD 1903) and, again, it did not give rise to a uniform F_1 generation, as expected, but to the amazing variety of hybrids shown in the superb colored lithograph reproduced as Figure 1. It provides a hint of what the cross realized by Mendel four decades earlier may have looked like—not forgetting that Mendel had obtained nearly three times as many hybrids as Ostenfeld refers to! Perhaps Mendel felt even more perplexed when he was confronted with the assumed F_2 offspring of such putative F_1 hybrids—as far as these were fertile at all. When he either self-fertilized them or crossed them *inter se*, or after open pollinations, he chiefly obtained uniform, mother-like offspring instead of segregating F_2 hybrids. Nevertheless, he still considered them to be true F_2 generation plants (MENDEL 1869, p. 30). Just as uniform were the progeny of such plants in up to four subsequent generations (CORRENS 1905, pp. 222, 233; CORRENS 1924, pp. 1261, 1270).

In 1869, Mendel summarized the following in his short article: "In *Pisum*, the hybrids (. . .) have the same appearance in every instance; their progeny, however, are variable and segregate according to a distinctive law. In Hieracium, the direct opposite seems to reveal itself, based on the experiments conducted to date." ("Bei *Pisum* haben die Bastarde (. . .) in allen Fällen den gleichen Typus, ihre Nachkommen dagegen sind veränderlich und variiren nach einem bestimmten Gesetze. Bei *Hieracium* scheint sich nach den bisherigen Versuchen das gerade Gegentheil davon herausstellen zu wollen.") In July 1870, Mendel confirmed this conjecture (Correns 1905, p. 233; Correns 1924, p. 1270): "At this point, I cannot hold back remarking that it must be noticed that the hybrids of *Hieracium* show an almost opposite behavior when compared with those of *Pisum*. We are here, obviously, confronted with only isolated phenomena, which are the emanation of a higher general law." ("Ich kann bei dieser Gelegenheit die Bemerkung nicht unterdrücken, wie sehr es auffallen mus, das die Bastarde von *Hieracium* im Vergleich mit jenen von *Pisum* ein geradezu entgegengesetztes Verhalten beobachten. Wir haben es hier offenbar nur mit einzelnen Erscheinungen zu thun, die der Ausflus eines höheren allgemeinen Gesetzes sind.")

Since Mendel was confident of being on the track of a "higher general law," it is inconceivable that his disappointments and discouragements with Hieracium really were the cause for abandoning his experimental research on genetics. There is little doubt that the true reason rather has to be sought in his serious health problems, especially his overstrained eyes—likely a consequence of his exhaustive, lens-aided emasculations for his crossing experiments—and in his overexertion as abbot (from April 1868 onward). The famous Augustinian "Stift St. Thomas (Königinkloster) zu Alt-Brünn" (Brno) was culturally one of the most eminent monasteries in the realm of the ancient Habsburg monarchy. The high position as abbot meant for him anything but a sinecure. For the sake of his prosperous monastery, he engaged, with growing irritation, in a long, wearisome, and exhausting fight against the state and the treasury. Eventually, he was successful, but paid for his victory with the deterioration of his health.

In November 1873, in his last letter to Nägeli (Correns 1905, p. 242; Correns 1924, p. 1277), Mendel wrote in a state of resignation: "I feel truly unhappy that I have to neglect my plants and bees so completely." ("Ich fühle mich wahrhaft unglücklich, das ich meine Pflanzen und Bienen so gänzlich vernachlässigen mus.") Mendel carried out his last crossing experiment on the poorly fertile hybrid individual *H. praealtum* × *H. aurantiacum* (already mentioned in 1868: see Mendel 1869 and Correns 1905, p. 223, and Correns 1924, p. 1261). After "self-pollination" with its own poorly fertile pollen, this plant set seed in only one-quarter to one-third of the florets. However, when abundantly and repeatedly cross-pollinated, *e.g.*, with the quite good pollen of the male parent *H. aurantiacum*, the seed set increased dramatically: The hybrid in question became fully fertile! At first, Mendel (1869, p. 30) suspected that the reason for this striking difference was "that after natural self-fertilization one part of the ovules capable of conception were (in fact) not fertilized due to the poor quality of its own pollen" ("dass bei dem natürlichen Verlaufe der Selbstbefruchtung ein Theil der conceptionsfähigen Eichen [ovules] wegen schlechter Beschaffenheit des eigenen Pollens nicht befruchtet wird"). In the following year, however, while analyzing the progeny, Mendel (Correns 1905, p. 245; Correns 1924, p. 1279) detected that the "self-pollinated" floral clusters had led to mother-like offspring, whereas the cross-pollinated ones issued not only mother-like offspring (in comparably low proportions) but also a significant number of hybrid offspring, obviously corresponding to all those ovules that would have remained sterile without cross-pollination (unfortunately, Mendel did not communicate the exact quantitative data to Nägeli). Mendel, quite perplexed, tentatively drew the following conclusion: "The [rather good] pollen of *H. aurantiacum* was effective only in those florets which would have remained sterile, had it not intervened; however, it could not dislodge the hybrid pollen" [*i.e.*, the poor pollen of the hybrid mother plant]. ("Der Pollen von *H. aurantiacum* war demnach nur in solchen Blüthchen wirksam, die ohne seine Dazwischenkunft steril geblieben wären, den Bastard-Pollen konnte er jedoch nicht verdrängen" (Correns 1905, p. 245; Correns 1924, p. 1279).

No doubt, the results of his last experiment (1870–1871) supported Mendel in his presumption that, as far as true breeding hybrids in cases like Hieracium were concerned, the same laws of inheritance in cases like Pisum were not valid. These assumptions, as well as the fact that Mendel did not answer Nägeli's last two letters (1874 and 1875; see Correns 1905, pp. 190 and 247; Correns 1924, pp. 1234 and 1281), may have had a decisive influence on Nägeli, justifying his temporizing and his skeptical attitude toward Mendel's results. One should always remember that Nägeli's main concerns were neither peas nor details regarding the inheritance of single traits, but the huge Hieracium species complex, which, in those days, seemed to be an almost ideal model for studying processes of hybridization, speciation, and microevolution.

In the following decades, the presumption that in certain instances divergent genetic laws might be valid received further support: on one hand by Focke, a renowned Rubus specialist who, in his celebrated compilation, "Die Pflanzen-Mischlinge" (1881), mentioned several "true breeding" ("constant") hybrids in different genera, and on the other hand by Millardet, who unfortunately died before he could publish the results on false hybrids ("faux hybrides") in Rubus, which he had announced in 1894 (Millardet 1894, p. 362; see Correns 1903, p. 488; Bateson 1906, p. 400). But what is more, in the first years after the rediscovery of Mendel's laws, even de Vries, Correns, and Bateson were evidently convinced of the fundamentally different behavior of plants with a "Pisum type of inheritance" standing "in sharpest contrast" ("in schroffstem Gegensatz," Correns 1901b, p. 74) to plants with a "Hieracium type of inheritance." Commenting in his English translation of Mendel's two publications, Bateson (1902, p. 34; reprint 1928, p. 27) states that, in Hieracium, the [F_1] "hybrids, if they are fertile at all, produce offspring like themselves, not like their parents. ... To these cases the Mendelian principle will in nowise apply." But in the second edition, Bateson (1909, p. 247) admits: "In the earlier discussions which followed the rediscovery of these papers we all were inclined to follow Mendel in supposing that Hieracium illustrated a distinct kind of sexual inheritance in which segregation was absent, and it seemed natural to suspect that the association of this phenomenon with partial sterility was not accidental."

At the turn of the century, new theories and new terminology were advanced in a rush. In 1900 de Vries (p. 436) stated: "In *Hieracium* Mendel had found a case of non-segregating hybrids ... but Mendel did not have the opportunity [!] to expand his investigations and, thus, it remained unknown to him whether one of the two types—*Hieracium* or peas—would have a more general validity in the plant kingdom. Accordingly, his results, until recently, were looked upon as referring to special cases lacking fundamental relevance —and were consigned to oblivion." ("Einen solchen Fall sich nicht spaltender Bastarde hatte Mendel bei *Hieracium* gefunden ... Mendel hatte aber nicht die Gelegenheit, seine Untersuchungen weiter auszudehnen, und so blieb es ihm unbekannt, ob eine von diesen beiden Typen—*Hieracium* oder Erbsen—für das Pflanzenreich eine allgemeinere Gültigkeit haben würde. Dementsprechend sind seine Ergebnisse bis vor Kurzem als Einzelfälle ohne principielle Bedeutung betrachtet worden und in Vergessenheit gerathen.") Adapting Millardet's (1894) terms, but using them in a slightly different sense, de Vries distinguished between (1) normally segregating hybrids ("hybrides normaux") and (2) false hybrids ("faux hybrides"), the offspring of which either do not segregate at all (as usually happens in Hieracium and Rubus) or segregate according to other rules (like those valid in Oenothera, de Vries' main laboratory plant). To characterize these two types, de Vries (1900, p. 437) proposed the terms "isogon" ("erbgleich") *vs.* "anisogon" ("erbungleich"). Correns (1901a, p. 212, and 1901b, p. 80), asserting that this terminology was misleading, coined instead the new terms "schizogon" *vs.* "homöogon" and postulated different types of inheritance. But Bateson and Saunders (1902, p. 126, reprint 1928, p. 30) thought it sufficient to outline the phenomena simply as "true breeding" *vs.* "not true breeding." Nevertheless, they too (in a "Note, added March, 1902", p. 155, reprint 1928, p. 62) were unable to stand aloof from introducing the new terms "amphilepsis" *vs.* "monolepsis" to characterize the "Pisum type" and the "Hieracium type" of inheritance, respectively. Correns (1903), for his part, felt misunderstood, reacted a bit piqued, and stuck to his terminology and typology.

To my knowledge, Ostenfeld (1904, p. 540) was the first to interpret the outcome of Mendel's crossing experiments on Hieracium (as far as they were known to him from Mendel's short communication in 1869) as simply a result of parthenogenesis. Meanwhile, Juel (1898, 1900) had, indeed, finally established that the embryos of *Antennaria alpina* develop parthenogenetically from unreduced ($2n$) egg cells containing the complete chromosome sets of a somatic cell. Since fertilization is omitted, the results are mother-like offspring (clones). This asexual mode of reproduction by seeds—today termed apomixis (formerly apogamy)—is typical of most "species" of Hieracium. Hence, Mendel had by no means emasculated carelessly!

On this basis, even the enigmatic results of Mendel's last experiment, dealt with above, could easily have been explained: In the hybrid plant *H. praealtum* × *H. aurantiacum* only a minor portion of the egg cells are able to develop parthenogenetically, leading to mother-like offspring. The major portion of its egg cells need to be fertilized, but since the pollen of the same plant is not fertile, many florets do not set seeds. However, if pollinated with alien, fertile pollen, hybrids may develop in addition to the mother-like offspring. If, at that time, due notice had been taken of this prototypical example of both sexual and apomictic reproduction occurring simultaneously in the same plant, this finding might have prevented the rise of the tenaciously passed-on misconception of regarding apomixis as a loss of sexuality!

In 1905, while writing the accompanying text to his edition of Mendel's letters to Nägeli, Correns had also come to realize that in Hieracium seeds are formed parthenogenetically. He thus tacitly skipped over the superfluous terminology, merely observing incidentally in a footnote (Correns 1905, p. 246; 1924, p. 1280): "Parthenogenesis (sensu lato) was at that time, albeit established (for *Caelebogyne*, *Chara crinita* [a stonewort]), nevertheless so rare a phenomenon that it seems understandable that neither Mendel nor Nägeli had taken it into consideration." ("Zu damaliger Zeit war eben die Parthenogenesis (sens.lat.) eine zwar sichergestellte (*Caelebogyne*, *Chara crinita*), aber so seltene Erscheinung, das es begreiflich erscheint, das weder Mendel noch Nägeli an sie dachten.") But it should be added that, for a span of several years, the same reasoning must be applied to Correns himself, too—as well as to de Vries and to Bateson! The basic question as to whether parthenogenesis occurs at all in seed plants had been passionately discussed since 1839 (Smith 1841). In any case, the phenomenon was taken into consideration only for purely female plants; and this in itself would have already given Mendel—who had been accustomed to finding pollen of quite good quality in several Hieracia that he used as experimental plants—reason enough to regard the mere idea of parthenogenesis (which was well known to him from his honeybees) as being really absurd.

The controversy over parthenogenesis in seed plants remained open for decades. As late as 1898, Dangeard (p. 270) argued that in pteridophytes and angiosperms parthenogenesis was "theoretically almost impossible" (". . . que la parthénogénèse soit théoriquement à peu près impossible"). And when Juel, in the very same year of 1898, finally had established beyond a doubt that true parthenogenesis *does* occur in angiosperms, his crucial article on embryology, although published at a prominent place in an authoritative reference journal, escaped his colleagues' notice for years! In a few words, the rediscovery of Mendel's laws did not immediately lead to a recognition of their universal validity. This was achieved only after detours.

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LITERATURE CITED

Bateson, B., 1928 *Collected Scientific Papers of W. Bateson, FRS.* pp. 29–68. Cambridge University Press, Cambridge, UK.

Bateson, W., 1902 *Mendel's Principles of Heredity: A Defense*, pp. xvi and 212. Cambridge University Press, Cambridge, UK.

Bateson, W., 1906 The progress of genetics since the rediscovery of Mendel's papers. Progr. Res. Bot. **1:** 368–418.

Bateson, W., 1909 *Mendel's Principles of Heredity*, pp. xiv and 396. Cambridge University Press, Cambridge, UK.

Bateson, W., and E. R. Saunders, 1902 Experimental studies in the physiology of heredity. The facts of heredity in the light of Mendel's discovery. Rep. Evol. Comm. R. Soc. **1:** 125–160 (reprinted in B. Bateson, 1928, Collected scientific papers of W. Bateson. FRS **2:** 29–68.)

Correns, C., 1901a Ueber Bastarde zwischen Rassen von Zea Mays, nebst einer Bemerkung über die "faux hybrides" Millardet's und die "unechten Bastarde" de Vries. Ber. Dt. Bot. Ges. **19:** 211–220.

Correns, C., 1901b Die Ergebnisse der neuesten Bastardforschungen für die Vererbungslehre. Sammelreferat. Ber. Dt. Bot. Ges. **19:** 71–94.

Correns, C., 1903 Neue Untersuchungen auf dem Gebiet der Bastardirungslehre. Herbst 1901 bis Herbst 1902. Sammelreferat. Bot. Zeitung 61 (8): 114–126 and Bot. Centralblatt **92**(21): 481–488.

Correns, C., 1905 Gregor Mendel's Briefe an Carl Nägeli 1866–1873. Ein Nachtrag zu den veröffentlichten Bastardierungsversuchen Mendels. Abh. Math.-Phys. Classe Kgl. Sächs. Ges. Wiss. **29**(3): 189–265.

Correns, C., 1924 Reprint in *Gesammelte Abhandlungen*, pp. 1233–1297. Springer, Berlin.

Dangeard, P.-A., 1898 Théorie de la sexualité. Le Botaniste **6:** 261–288.

de Vries, H., 1900 Ueber erbungleiche Kreuzungen. Ber. Dt. Bot. Ges. **18:** 435–443.

Focke, W. O., 1881 Die Pflanzen-Mischlinge. Ein Beitrag zur Biologie der Gewächse. 569 S. Borntaeger, Berlin.

Iltis, H., 1924 *Gregor Johann Mendel: Leben, Werk und Wirkung*. Springer, Berlin.

Juel, H. O., 1898 Parthenogenesis bei *Antennaria alpina* (L.). R. Br. Bot. Centralblatt **74**(13): 369–372.

Juel, H. O., 1900 Vergleichende Untersuchungen über typische und parthenogenetische Fortpflanzung bei der Gattung *Antennaria*. Kgl. Svenska Vetenskapsakad. Handl. **33**(5): 1–59.

Mendel, G., 1869 Ueber einige aus künstlicher Befruchtung gewonnenen Hieracium-Bastarde. Verh. Naturf. Ver. Brünn **8** (Abhandlungen): 26–31 (English translation: "On Hieracium hybrids obtained by artificial fertilisation." See W. Bateson, 1902, pp. 96–103, and W. Bateson, 1909, pp. 362–368).

Millardet, A., 1894 Note sur l'hybridation sans croisement ou fausse hybridization. Mém. Soc. Sci. Phys. Nat. Bordeaux. 4e Série **4:** 347–372.

Ostenfeld, C. H., 1903 English abstract on Raunkiær (1903). Bot. Centralblatt **93:** 81–83.

Ostenfeld, C. H., 1904 Weitere Beiträge zur Kenntnis der Fruchtentwicklung bei der Gattung Hieracium. Ber. Dt. Bot. Ges. **22:** 537–541.

Ostenfeld, C. H., 1910 Further studies on the apogamy and hybridization of the Hieracia. Zeitschrift für induktive Abstammungs- und Vererbungslehre **3:** 241–285.

Raunkiaer, C., 1903 Kimdannelse uden Befrugtning hos Mælkebøtte (*Taraxacum*). [Parthenogenesis in the dandelion (*Taraxacum*), Danish] Bot. Tidsskr. **25:** 109–140.

Smith, J., 1841 Notice of a plant which produces perfect seeds without any apparent action of pollen. Trans. Linn. Soc. Lond. **18:** 509–512.