A Cytological Basis
for the Mendelian Laws

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A CYTOLOGICAL BASIS

FOR THE MENDELIAN LAWS

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IN THE DECADE FOLLOWING THE YEAR 1860, Gregor Mendel, an abbot
of the Roman Church, experimented in the garden of his abbey in
Brünn with plant hybrids. This experience led him to results and con-
clusions now believed by students of heredity to be of great impor-
tance. These were published in the *Verhandlung des Naturforschenden*
Vereins of Brünn and were lost to the view of scientists until their re-
discovery about two years ago by de Vries, Correns, and Tschermak.
The plants experimented with by Mendel were mainly species of
Pisum, Phaseolus, and *Hieracium,* and, although the results were in a
measure contradictory, those founded upon his pea experiments were
uniform, and constituted the basis for his conclusions, namely, those
expressed by the "Mendelian Laws". The essential conception of Men-
del may be briefly stated as follows:

When one pure form (*A*) is crossed with another pure form (*a*) the
hybrid of the primary cross shows the *A* characters only. When, how-
ever, the hybrid plants of this generation are fertilized among them-
selves and produce offspring the *a* characters are first seen, and in a
definite proportion to the form bearing the *A* characters. These consti-
tute the hybrids of the second generation. If now the hybrids of the sec-
ond generation are fertilized in such a manner that plants with a
characters are crossed with those bearing the same characters, and

likewise plants bearing the opposing characters with forms like themselves, the resulting hybrids will behave in a manner characteristic of the respective cross. That is (1) The plants with a characters will be found to transmit those characters only, i. e., they are "fixed"; and (2) When the plants with *A* characters are fertilized with other plants with the same characters, that is to say, if inbred, two sorts of hybrids will result: one portion will bear only the *A* characters, which may be demonstrated by inbreeding as before, and one portion, apparently also with *A* characters only, will he found to vary just as the hybrids of the primary cross varied, i. e., this portion is really mixed or hybrid. The hybrids that bear the *a* characters are known as the "recessives"; they do not appear in the first generation, and those with the *A* characters are called the "dominants", and they mask in the first generation the recessives. This general scheme may be better understood if tabulated as follows:
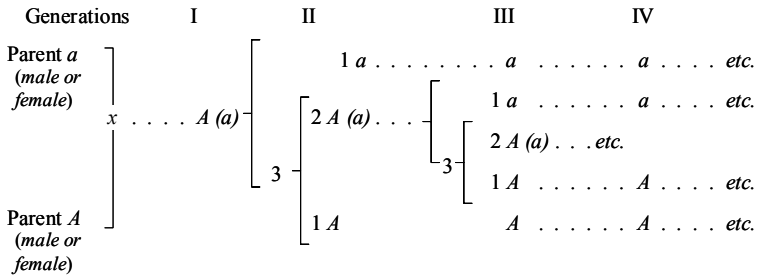

Fig. 1. Explanation: *A*: dominant character; *a*: recessive character; *A(a)*: a hybrid having both characters of which (*a*) is masked by *A*.

Not only do the hybrids vary thus in a regular manner but there is also a definite proportion of recessives (*a*), and dominants (*A*), as the table indicates. That is, referring to the table, in the second generation one fourth of the offspring is recessive (*a*), and three fourths apparently dominant (*A*) only, but really composed of the two sorts [*A(a)*] one third of these being dominant (pure), and two thirds mixed [*A(a)*]. The latter continue in the succeeding generation to vary just as the hybrids of the primary cross varied, i. e., one fourth of their offspring bearing recessive, one fourth bearing dominant characters, and one half being both dominant and recessive.

The regularity in the variation as just described in the second and later generations is accounted for by supposing that the hybrids of the first generation organize germ cells which are of pure descent, and that these unite in fertilization according to the laws of chance. Taking a specific case by way of illustration, we can imagine the following to

take place when the sex cells *A(a)* of say the second generation meet each other in fecundation.

The pollen, which is of pure descent, unites with the egg, which also is of pure descent, and the chances of union may be thus expressed: *A a; A A; a a; a A*. So that it happens, since the anther forms two sorts of germ cells and the ovary also two sorts, that in this way one half of the hybrids of say the third generation will be of mixed descent, and one half of pure, the latter being equally recessive and dominant. The results as calculated by the laws of chance, are thus seen to be precisely the same as what is found empirically to occur.

Such are the more essential facts and conclusions of the discovery by Mendel, and upon them are based the two so-called "laws" of Mendel, namely, the law of dominance and that of the splitting of the hybrid race. The latter alone concerns us at present.

We now arrive at the interesting question, Is there a cytological basis for Mendel's law of the splitting of the hybrid race?

Bateson has recently suggested the idea that the *"essential* part of the discovery (of Mendel—the italics are my own) is the evidence that *the germ cells or gametes produced by cross-bred organisms may in respect of given characters be of the pure parental types and consequently incapable of transmitting the opposite character".* (The italics are in the original.) This notion has also been expressed by others, or may be implied from their conclusions. Assuming such to be the case, how may we account morphologically for the purity of the sex cells?

Do the sex cells, which are thus shown by experiment to be pure, arise by normal maturation mitoses, such as take place in pure races, or are the divisions irregular, abnormal, and peculiar to each hybrid organism? It has, I think, generally been felt by botanists that the variations in the hybrids were, in some manner, connected with that of the formation of the sex cells from which they arose, and this has apparently received cytological support. For instance, both Guyer, from his morphological studies of hybrid pigeons, and Juel, from studies of hybrid *Syringa,* arrive at the conclusion last given, although this must be implied from Juel's results, as for example, his account of how a *Syringa* hybrid pollen grain may become pure as respects the chromosomes of its nucleus. The pigeon hybrid was a fertile one and the *Syringa* infertile; the possibility thus comes up of the variation in the hybrid pigeons being caused and brought about by the normal, rather than the irregular maturation mitoses. I have for two years past been studying the spermatogenesis of a fertile cotton hybrid, and I have attained results similar to those of Guyer. In the case of the cotton, however, the abnormal divisions were so clearly such, that sex cells arising from them would, in all likelihood, not be capable of continuing the

race. It, therefore, seemed to me that, at least in the cotton, variation in the hybrid offspring must come about either because the maturation mitoses were such as would induce them, or quite independently of these nuclear divisions, since, in fertile hybrids the mitoses are normal.

The nuclear divisions from which the pollen grains arise, as commonly understood by botanists to take place, would surely not induce the variation in the hybrids after the regular manner demanded by the law of Mendel, and, believing that this variation does not occur independently of these divisions, I venture to suggest a kind of maturation division which would, I believe, account for the variation as above given, and at the same time agree fully with the present day observations on the divisions if not with the conclusions derived therefrom.

This matter finds and apparently adequate explanation if we accept the results of Rückert and others (Wilson, The Cell, 257 and 273) based on the study of pure forms of both vertebrates and invertebrates. These results may be stated in brief as follows: The chromosomes derived from the father and the mother unite in synapsis and separate in the metaphase of one of the maturation divisions, and also a single longitudinal division occurs, so that the end is attained that the chromatin is distributed in such a way that two of the cells receive pure paternal, and two cells pure maternal chromosomes, and no cells receive chromosomes from both the father and the mother. In this manner *it has been demonstrated that pure races of animals may, and normally do, organize sex cells of pure descent.*

Now since such is shown to he the case in *pure* races of animals, I suggest that the sex cells of *fertile* animal hybrids *are formed in a similar way,* and thus we may have in animals a cytological basis for variation in accord with the Mendelian conception. And I further suggest that this is the case in plants as well. This notion is, I am well aware, squarely opposed to the present conception ,of the nature of the maturation mitoses in plants, but I submit (1) That the optical effect in the dividing sex nuclei would be the same in either case, and (2) That closer study of the early stages in the spermatogenesis of plants would give a result entirely analogous to the results drawn from analogous morphological studies of animals.