CONCERNING THE LAW OF SEGREGATION OF HYBRIDS

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First published in English as: De Vries, H.. 1950. Concerning the law of segregation of hybrids. *Genetics*, 35(5, pt 2): 30-32. Originally published as: De Vries, H. 1900. Sur la loi de disjonction des hybrides. *Comptes Rendus de l'Academie des Sciences (Paris)*, 130: 845-847.

Electronic Scholarly Publishing Project

Foundations Series: Classical Genetics

Series Editor: Robert J. Robbins

The ESP Foundations of Classical Genetics project has received support from the ELSI component of the United States Department of Energy Human Genome Project. ESP also welcomes help from volunteers and collaborators, who recommend works for publication, provide access to original materials, and assist with technical and production work. If you are interested in volunteering, or are otherwise interested in the project, contact the series editor: rrobbins@fhcrc.org.

Bibliographical Note

This ESP publication is a newly typeset, unabridged version, based on the original 1950 edition published by the Genetics Society of America in a special supplement to the journal *Genetics*. All footnotes and endnotes are as they appeared in the original work.

Production Credits

Scanning of originals:	ESP staff
OCRing of originals:	ESP staff
Typesetting:	ESP staff
Proofreading/Copyediting:	ESP staff
Graphics work:	ESP staff
Copyfitting/Final production:	ESP staff

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ACCORDING TO THE PRINCIPLES which I have expressed elsewhere (*Intracelluläre Pangenesis*, 1889), the specific characters of organisms are composed of separate units. One is able to study, experimentally, these units either by the phenomena of variability and mutability or by the production of hybrids. In the latter case one chooses in preference hybrids from parents which are distinguishable from each other by only a single character (the monohybrids) or by a small number of well delimitated characters, and for which one considers only one or two of the units and leaves the others aside.

Ordinarily the hybrids are described as exhibiting simultaneously the characters of the father and the mother. In my opinion, one must admit, in order to understand this result, that the hybrids have some of the simple characters from the father and other equally simple characters from the mother. But when the father and the mother are distinguishable only by a single point, the hybrid could not be in the middle, since the simple character must be considered as one non-divisible unit.

Otherwise the study of simple characters of the hybrids can furnish the most direct evidence of the stated principle. The hybrid always shows the character of one of the two parents and that in all of its force. The character of one parent is always separated from the other, it is not present reduced by one half.

The table which follows gives some examples. Ordinarily it is the character of the species which prevails over that of the variety, or the most ancient character prevails over that which is the younger. But I observed diverse exceptions to this rule.

In the hybrid the simple differential character from one of the parents is accordingly visible or *dominant* while the antagonistic character is in the latent condition or *recessive*.[1]

The antagonistic characters ordinarily remain combined during all of the vegetative life, one dominant, the other latent. But in the generative period, they are segregated. Each grain of pollen and each oosphere receives only one of the two.

For the monohybrids, one has therefore the thesis *that their pollen and their ovules are no longer hybrid*, so that they have the pure character of one of the parents. And the same proposition can be supported for the others (di- and polyhybrids), when one considers only a single character at a time.

By this principle one is able to deduce almost all of the rules which govern the distribution of characters in the descendents of hybrids. I have tested a portion by experiment, but shall restrict myself here to summarizing the experiments which establish the principle of the laws.

Having cultivated several hundreds of individuals from seeds of different hybrids, with which I took care in assuring a pure cross pollination, I have found for the products the following proportion of individuals presenting the recessive character:

Parent having the dominant character	Parent having the recessive character	Proportion of hybrids with the recessive character
Agrostemma Githago	*A. nicaeensis*	24 per 100
Chelidonium majus	*C. laciniatum*	26 " "
Coreopis tinctoria	*C. brunea*	25 " "
Datura Tabula	*D. Stramonium*	28 " "
Hyoscyamus niger	*H. pallidus*	26 " "
Lychnis diurna (red)	*L. vespertina* (white)	27 " "
Lychnis vespertina (hairy)	*L. glabra*	28 " "
Oenothera Lamarckiana	*Oe. Brevistylis*	22 " "
Solanum nigrum	*S. chlorocarpum*	24 " "
Trifolium pratense	*T. album*	25 " "
Veronica longifolia	*V. alba*	22 " "

1 In this article I was only concerned with the true hybrids and omitted the *false hybrids* of Millardet.

One sees that the proportion of the hybrids with the recessive character is always close to 25 per 100.

The culture of a further generation permits the study of a distinction among the 75 per 100 individuals presenting the dominant character. I cite as an example a cross of a poppy having basal black spots on the petals with one having white spots.

If one grows the hybrid seeds from the two varieties, calling N the plants with black spots, and B the plants with white spots, one obtains as for the preceding:

75 per 100 N and 25 per 100 B

But a second culture of seeds contributed by the self pollinated N plants, the seeds arising from each plant grown in a separate plot, gives for 25 of the 75 plants a pure progeny with black petals and for the 50 others a mixture of plants with black petals and plants with white petals in the proportion of 37.5 N to 12.5 B.

One has therefore, in short, by assembling the results of the two successive cultures:

100 hybrid seeds of N and of B

75 N		25 B
25 N	50 B	25 B
25 N	37.5 N + 12.5 B	25 B

I have also studied two other successive generations of these same hybrids. Each time they have repeated the same phenomena of segregation.

I have obtained the same results with the hybrids of sugary corn and starchy corn, within which the endosperms are visibly hybrid at the same time as the embryo.

One can unify the whole of these results by supposing that the two antagonistic qualities, dominant and recessive, are distributed [mutually exclusively] in equal parts to the pollen just as to 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 can represent the number and the nature of the hybrids by the following representative formula in which the numbers of D and R are equal:

$$(D+R)(D+R) = D^2 + 2DR + R^2$$

This repeats the statement that there will be 25 per 100 of D, 50 per 100 of DR and 25 per 100 of R.

The D individuals will have the pure dominant character, having inherited it from father and mother. In the same fashion the R

individuals will have the pure recessive character, while DR will be the hybrids. The latter bear the dominant visible character and the recessive latent character.

One will only be able to distinguish the 25 per 100 D, from the 50 per 100 DR by a second culture.

The totality of these experiments establishes the law of segregation of hybrids and confirms the principles that I have expressed concerning the specific characters considered as being distinct units.