Punnett squares and hybrid crosses: how Mendelians learned their trade by the book

Supplementary material to article in BJHS Themes 2020 **(Appendix I and II)**

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Appendix I: List of genetics "manuals" we consulted for annotations and reading marks

Versuche über Pflanzen-Hybriden (Tschermak's edition)
Author: Mendel, Gregor
Publisher: Engelmann/Akademische Verlagsgesellschaft (Leipzig); Friedrich Vieweg and Sohn (Braunschweig)
Edition/Year/Pages: 1/1901/62 pp.; 2/1911/68 pp.; 3/1913/68 pp.; 4/1923/68 pp.; 5/1933/68 pp.; 6/1940/71 pp.; enlarged edition/1970/112 pp.
Translation/Year: *Experiments in Plant Hybridisation* (Bateson's English translation published in the *Journal of the Royal Horticultural Society*)/1910; *Experiments in Plant Hybridisation* (Bateson's revised translation published in Castle's *Genetics and Eugenics*)/1916; *Experiments in Plant Hybridisation* (Bateson's revised translation published by Harvard University Press)/1925 (reprinted until the 1970s)

Mendel's Principles of Heredity
Author: Bateson, William
Publisher: Cambridge University Press (Cambridge, UK)
Edition/Year/Pages: 1/1902/212 pp.; 2/1909/396 pp.; 3/1913/413 pp.; 4/1930/413 pp.
Translation/Year: *Mendels Vererbungstheorien* (German)/1914

Mendelism
Author: Punnett, Reginald E.
Publisher: Bowes (Cambridge, UK), Macmillan (London, UK and New York, US)
Edition/Year/Pages: 1/1905/63 pp.; 2/1907/84 pp.; 3/1911/176 pp.; 4/1912/180 pp.; 5/1919/219 pp.; 6/1922/219 pp.; 7/1927/236 pp.
Translation/Year: *Mendelismus* (German)/1910; *Menderizumu* (Japanese)/1919; *Az Átöröklés* (Hungarian)/1928

The Methods and Scope of Genetics
Author: Bateson, William
Publisher: Cambridge University Press (Cambridge, UK)
Edition/Year/Pages: 1/1908/49 pp.; 1(reprinted)/1912/47 pp.
Translation/Year: ----

Elemente der exakten Erblichkeitslehre
Author: Johannsen, Wilhelm
Publisher: Fischer (Jena)
Edition/Year/Pages: 1/1909/515 pp.; 2/1913/723 pp.; 3/1926/735 pp.
Translation/Year: ------

Einführung in die experimentelle Vererbungslehre
Author: Baur, Erwin
Publisher: Gebrüder Borntraeger (Berlin)
Edition/Year/Pages: 1/1911/293 pp.; 2/1914/401 pp.; 3-4/1919/410 pp.; 5-6/1922/436 pp.; 7-11/1930/478 pp.
Translation/Year: *Vvedenie v ėksperimental'noe izučenie naslědstvennosti* (Russian)/1913

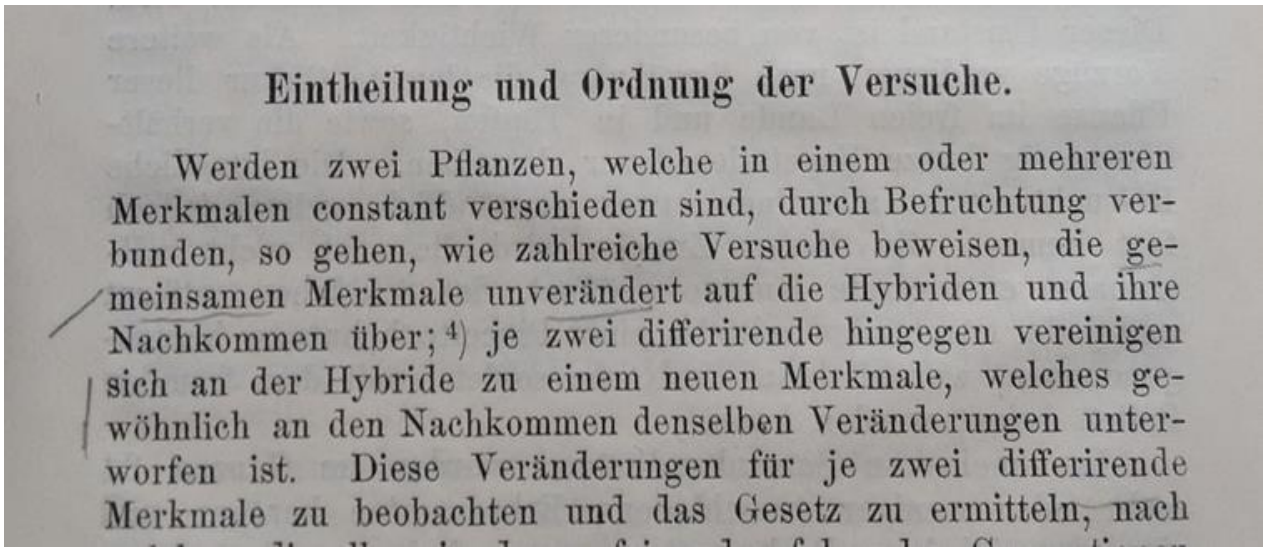
Die wissenschaftlichen Grundlagen der Pflanzenzüchtung: Ein Lehrbuch für Landwirte, Gärtner und Forstleute
Author: Baur, Erwin
Publisher: Gebrüder Borntraeger (Berlin)
Edition/Year/Pages:1-2/1921/115 pp.; 3-5/1924/108 pp.
Translation/Year: *Nauchnye osnovy selektsii; rukovodstvo dlia sel'skikh khoziaev, sadovodov i lesovodov* (Russian)/1924

Genetics and Eugenics: A Textbook for Students of Biology and a Reference Book for Animal and Plant Breeders
Author: Castle, William E.
Publisher: Harvard University Press (Cambridge, MA)
Edition/Year/Pages: 1/1916/353 pp.; 2/1920/395 pp.; 3/1924/434 pp.; 4/1930/ 474 pp.
Translation/Year: ----

Statistical Methods for Research Workers
Author: Fisher, Ronald A.
Publisher: Oliver and Boyd (Edinburgh, UK) and Hafner (US)
Edition/Year/Pages: 1/1925/239 pp. + pull-out tables; 2/1928/269 pp. + pull-out tables; 3/1930/283 pp. + pull-out tables; 4/1932/307 pp.; 5/1934/319 pp.; 6/1936/339 pp.; 7/1938/356 pp.; 8/1941/354 pp.; 9/1944/350 pp.; 10/1946/354 pp. [also reprinted]; 11/1950/354 pp.; 12/1954/356 pp.; 13/1958/356 pp. [also reprinted]; 14/1970/362 pp. [also reprinted].
Translation/Year: *Méthodes statistiques adaptées à la recherche scientifique* (French)/1947; *Metodi statistici ad uso dei ricercatori* (Italian)/1948; *Metodos estadisticos para investigadores* (Spanish)/1949; *Kenkyuusyano tameno toukeiteki houhou* (Japanese)/1952; *Statistische Methoden für die Wissenschaft* (German)/1956; *Statisticheskie metody dlya issledovatelei* (Russian)/1958

Appendix II: Additional Images

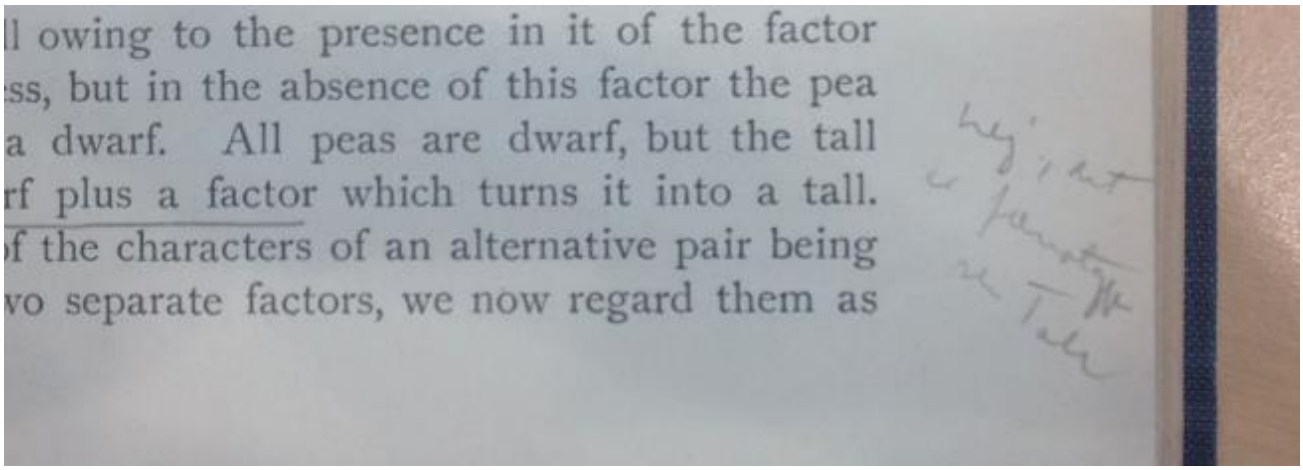
We could not include as many images as we would have liked in the final version of our manuscript. The following had to be left out, but are reproduced here, since there is a risk that the annotated print copies we consulted may be lost or destroyed.



Eintheilung und Ordnung der Versuche.

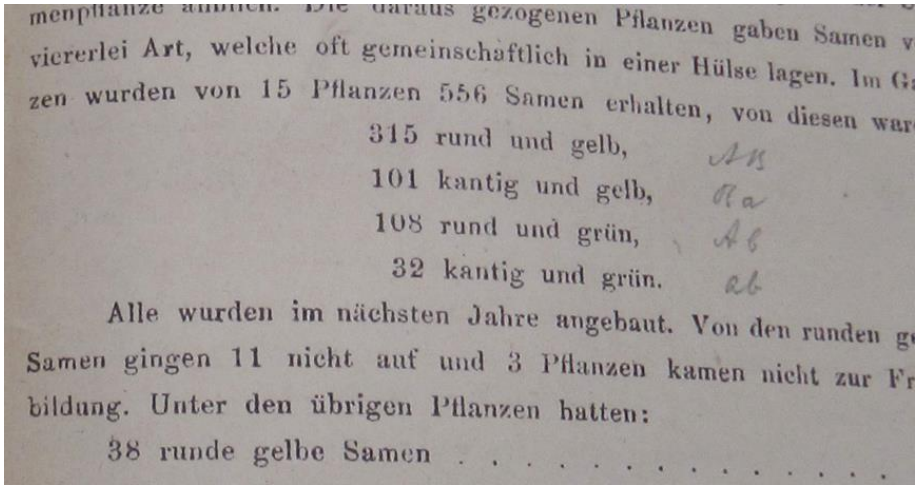
Werden zwei Pflanzen, welche in einem oder mehreren Merkmalen constant verschieden sind, durch Befruchtung verbunden, so gehen, wie zahlreiche Versuche beweisen, die gemeinsamen Merkmale unverändert auf die Hybriden und ihre Nachkommen über;[4]) je zwei differirende hingegen vereinigen sich an der Hybride zu einem neuen Merkmale, welches gewöhnlich an den Nachkommen denselben Veränderungen unterworfen ist. Diese Veränderungen für je zwei differirende Merkmale zu beobachten und das Gesetz zu ermitteln, nach

Fig. 1: Reading marks from a copy of Tschermak's 1901 edition of Mendel's paper that is preserved in the Library of the Botanic Garden and Botanical Museum Berlin. The reader highlighted Mendel's statements about the appearance of hybrids, in essence comprising the law of uniformity. Gregor Mendel, *Versuche über Pflanzenhybriden: Zwei Abhandlungen, 1865 und 1869*, (eds.) Erich Tschermak, Ostwalds Klassiker der exakten Wissenschaften, Nr. 121, Leipzig: Wilhelm Engelmann, 1901, Library of the Botanic Garden and Botanical Museum Berlin, Call no. GE 20, p. 6.



ll owing to the presence in it of the factor
ss, but in the absence of this factor the pea
a dwarf. All peas are dwarf, but the tall
rf plus a factor which turns it into a tall.
f the characters of an alternative pair being
vo separate factors, we now regard them as

Fig. 2: Marginal comment by Wilhelm Johannsen in Reginald C. Punnett's *Mendelism* (third edition, 1911). The comment reads 'Nej, det er phenotyp ren Tall'. Reginald C. Punnett, *Mendelism*, third edition, London: MacMillan, 1911. With kind permission of the Royal Danish Library, Copenhagen, Call no. 8° N. hist. 20481, p. 31.



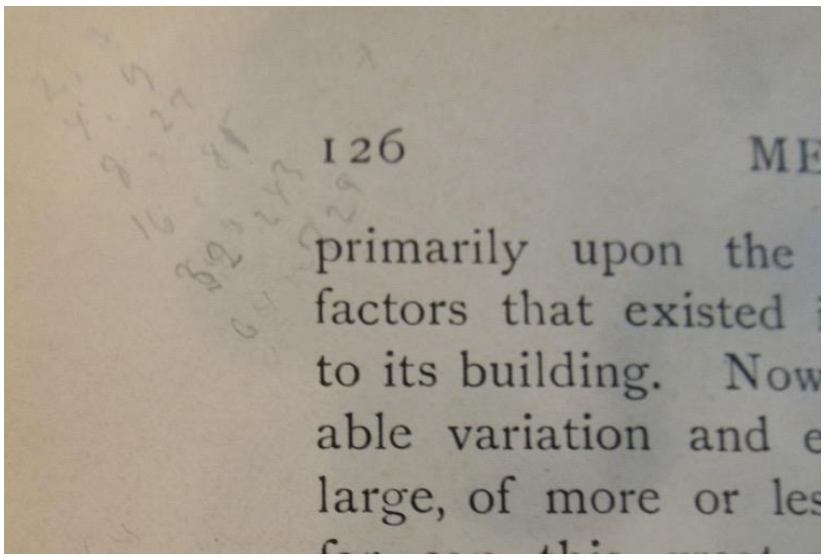
menpflanze ähnlich. Die daraus gezogenen Pflanzen gaben Samen v
viererlei Art, welche oft gemeinschaftlich in einer Hülse lagen. Im G
zen wurden von 15 Pflanzen 556 Samen erhalten, von diesen war

315 rund und gelb, AB
101 kantig und gelb, Ba
108 rund und grün, Ab
32 kantig und grün. ab

Alle wurden im nächsten Jahre angebaut. Von den runden g
Samen gingen 11 nicht auf und 3 Pflanzen kamen nicht zur Fr
bildung. Unter den übrigen Pflanzen hatten:

38 runde gelbe Samen . . . . . .

Fig. 3: Annotation of an anonymous reader in Mendel's original paper (from a facsimile copy held at the Staatsbibliothek in Berlin). Next to each combination of traits, the reader noted down the combinations for dominant and recessive characters (A = rund/round; B = gelb/yellow; a = kantig/angular; b = grün/green; cf. Fig. 5). On the second line the algebraic letters are Ba, not aB as one would expect considering the notation used by Mendel throughout the paper. Evidently, the reader had not yet internalised Mendel's conventions and there were still slips of the pen, here probably due to the "dominance" of B, which suggests placing it first. Gregor Mendel, *Versuche über Pflanzen-Hybriden. Brünn 1866*, Facsimile-Edition, Ed. W. Junk, No. 20, Berlin: W. Junk, 1917, p. 42. With kind permission of Staatsbibliothek zu Berlin – Preußischer Kulturbesitz, Call no. Ag 213-20.



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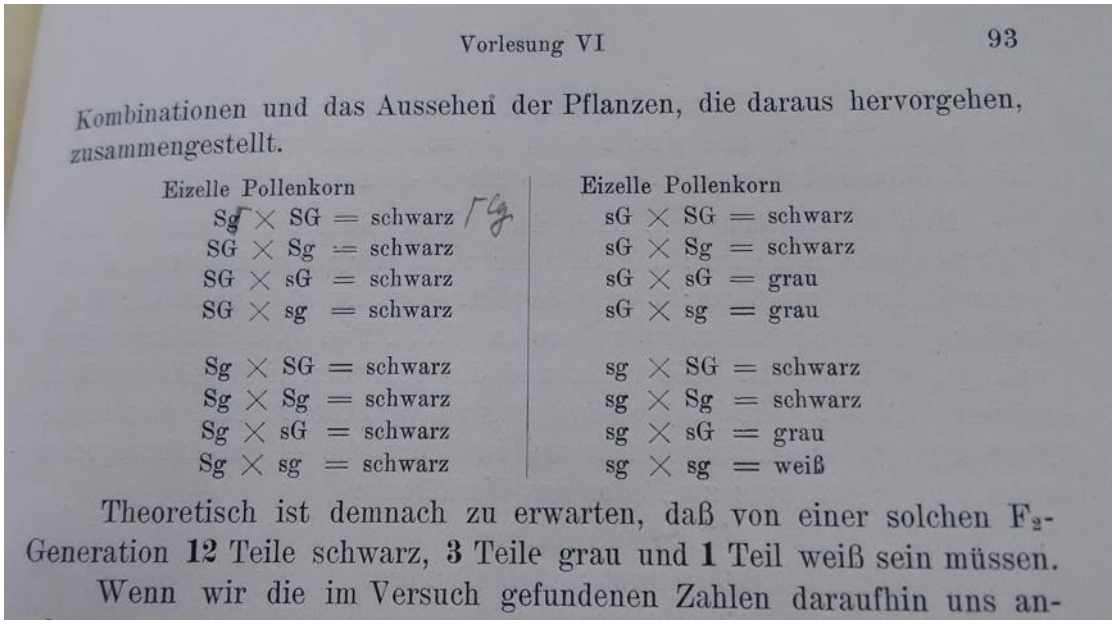
primarily upon the
factors that existed
to its building. Now
able variation and e
large, of more or les

Fig. 4: Annotation by Wilhelm Johannsen in his personal copy of the third edition of Punnett's *Mendelism*. Punnett explains on the page that '[i]n the simple case where the homozygous and heterozygous conditions are indistinguishable in appearance the number of possible forms is 2, raised to the power of the number of factors concerned […]. If the heterozygous form is different in appearance from the homozygous form, there are three possible forms connected with each factor […].' Johannsen proceeds to calculate the first six members for 2^n (2-4-8-16-32-64) and for 3^n (3-9-27-81-243-729). With kind permission of the Royal Danish Library, Copenhagen, Call no. 8° N. hist. 20481, p. 126.



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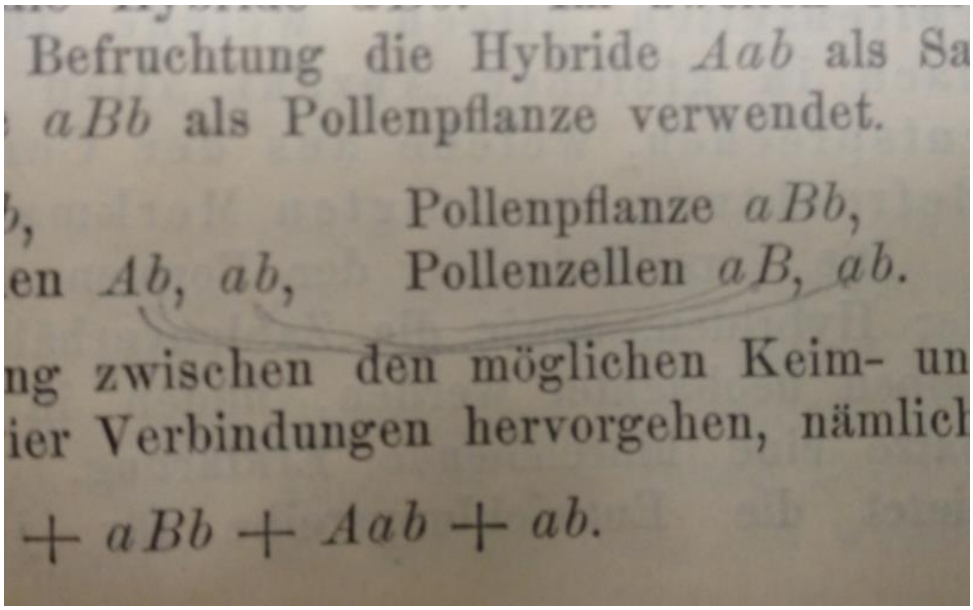
Kombinationen und das Aussehen der Pflanzen, die daraus hervorgehen, zusammengestellt.

Eizelle	Pollenkorn		Eizelle	Pollenkorn	
Sg	× SG	= schwarz	sG	× SG	= schwarz
SG	× Sg	= schwarz	sG	× Sg	= schwarz
SG	× sG	= schwarz	sG	× sG	= grau
SG	× sg	= schwarz	sG	× sg	= grau
Sg	× SG	= schwarz	sg	× SG	= schwarz
Sg	× Sg	= schwarz	sg	× Sg	= schwarz
Sg	× sG	= schwarz	sg	× sG	= grau
Sg	× sg	= schwarz	sg	× sg	= weiß

Theoretisch ist demnach zu erwarten, daß von einer solchen F_2-Generation **12** Teile schwarz, **3** Teile grau und **1** Teil weiß sein müssen. Wenn wir die im Versuch gefundenen Zahlen daraufhin uns an-

Fig. 5: Correction in a table from Baur's *Einführung* (1919). The table reproduces the crossings for an experiment on the transmission of colours in hybrid oat plants. Unlike the reader, the typographer did not pay attention to the overall structure of the table, where the first entry in each column is the same throughout each block. This must have been a typographer's oversight, because a correct version of this table is printed in the previous edition of Baur's book. With kind permission of the Library of the Botanic Garden and Botanical Museum Berlin, Call no. 575 Bau <4>, p. 93.



Befruchtung die Hybride *Aab* als Sa
aBb als Pollenpflanze verwendet.

Pollenpflanze *aBb*,
en *Ab*, *ab*, Pollenzellen *aB*, *ab*.

ng zwischen den möglichen Keim- un
ier Verbindungen hervorgehen, nämlich

+ *aBb* + *Aab* + *ab*.

Fig. 6: Lines drawn by Wilhelm Johannsen in Tschermak's edition of Mendel's *Versuche* in order to visualize possible combinations between factors in germ and pollen cells respectively. Although a bit untidy, it seems clear that the connecting lines produce the combinations Aa, Bb and ab, which reappear in the series that Mendel derives below. Gregor Mendel, *Versuche über Pflanzenhybriden: Zwei Abhandlungen, 1865 und 1869* (eds.) Erich Tschermak, Ostwalds Klassiker der exakten Wissenschaften, Nr. 121, Leipzig: Wilhelm Engelmann, 1901, p. 28. With kind permission of the Science Library of the University of Copenhagen, Call no. 80-33.

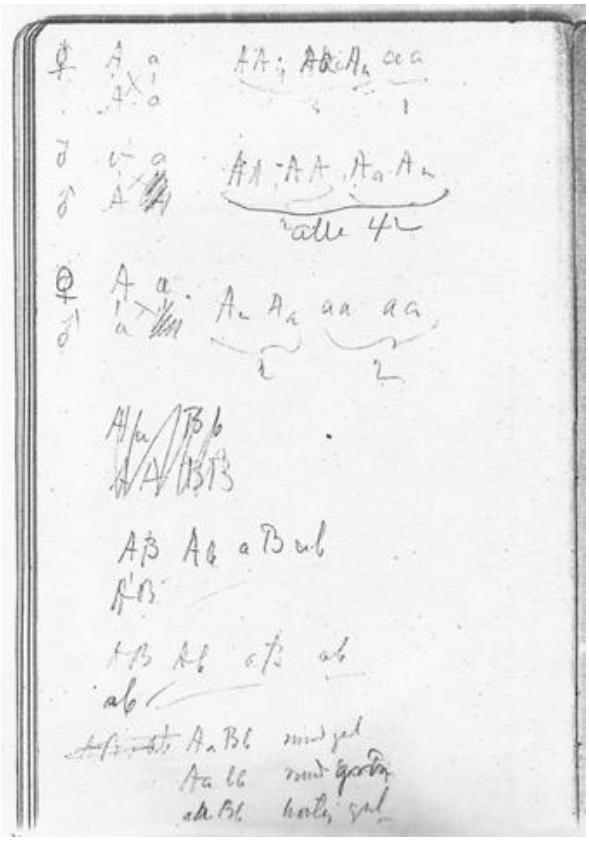
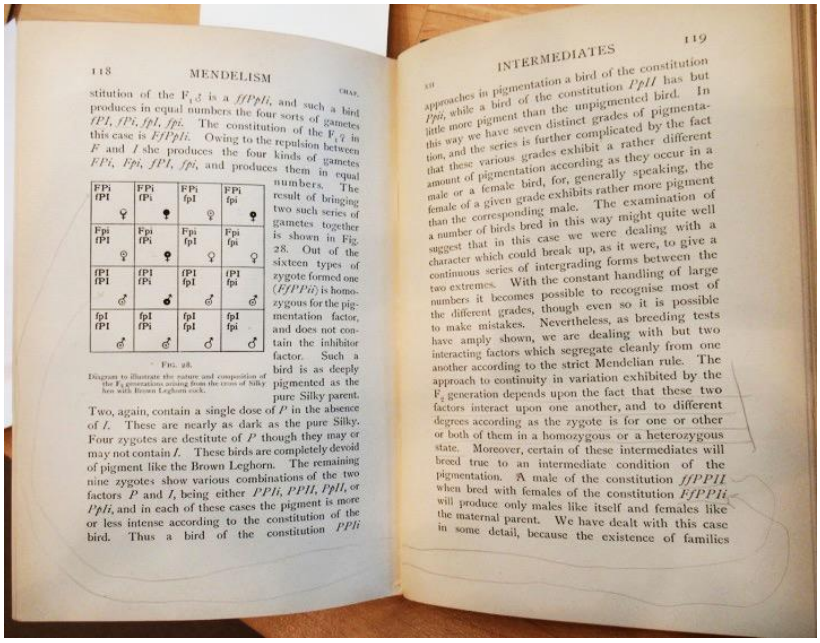


Fig. 7: Back flyleaf of Herman Nilsson-Ehle personal copy of Mendel's paper. Until recently, this copy was preserved in the library of the plant breeding station at Svalöf, Sweden. The station now belongs to the private company Lantmännen and we have not been able to ascertain the current whereabouts of the library. This reproduction is taken from a xerox in one of the authors' (SMW) private collection.



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stitution of the F_1 3 is a *ffPpIi*, and such a bird produces in equal numbers the four sorts of gametes *fPI*, *fPi*, *fpI*, *fpi*. The constitution of the F_1 ♀ in this case is *FfPpIi*. Owing to the repulsion between *F* and *I* she produces the four kinds of gametes *FPi*, *Fpi*, *fPI*, *fpi*, and produces them in equal numbers. The result of bringing two such series of gametes together is shown in Fig. 28. Out of the sixteen types of zygote formed one (*FfPpIi*) is homozygous for the pigmentation factor, and does not contain the inhibitor factor. Such a bird is as deeply pigmented as the pure Silky parent.

FPi fPI ♀	FPi fPi ♀	FPi fpI ♀	FPi fpi ♀
Fpi fPI ♀	Fpi fPi ♀	Fpi fpI ♀	Fpi fpi ♀
fPI fPI ♂	fPI fPi ♂	fPI fpI ♂	fPI fpi ♂
fpI fPI ♂	fpI fPi ♂	fpI fpI ♂	fpI fpi ♂

FIG. 28.

Diagram to illustrate the nature and composition of the F_2 generations arising from the cross of Silky hen with Brown Leghorn cock.

Two, again, contain a single dose of *P* in the absence of *I*. These are nearly as dark as the pure Silky. Four zygotes are destitute of *P* though they may or may not contain *I*. These birds are completely devoid of pigment like the Brown Leghorn. The remaining nine zygotes show various combinations of the two factors *P* and *I*, being either *PPIi*, *PPII*, *PpIi*, or *PpIi*, and in each of these cases the pigment is more or less intense according to the constitution of the bird. Thus a bird of the constitution *PPIi*

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approaches in pigmentation a bird of the constitution *PpII* while a bird of the constitution *PpII* has but little more pigment than the unpigmented bird. In this way we have seven distinct grades of pigmentation, and the series is further complicated by the fact that these various grades exhibit a rather different amount of pigmentation according as they occur in a male or a female bird, for, generally speaking, the female of a given grade exhibits rather more pigment than the corresponding male. The examination of a number of birds bred in this way might quite well suggest that in this case we were dealing with a character which could break up, as it were, to give a continuous series of intergrading forms between the two extremes. With the constant handling of large numbers it becomes possible to recognise most of the different grades, though even so it is possible to make mistakes. Nevertheless, as breeding tests have amply shown, we are dealing with but two interacting factors which segregate cleanly from one another according to the strict Mendelian rule. The approach to continuity in variation exhibited by the F_2 generation depends upon the fact that these two factors interact upon one another, and to different degrees according as the zygote is for one or other or both of them in a homozygous or a heterozygous state. Moreover, certain of these intermediates will breed true to an intermediate condition of the pigmentation. A male of the constitution *ffPPII* when bred with females of the constitution *FfPPIi* will produce only males like itself and females like the maternal parent. We have dealt with this case in some detail, because the existence of families

Fig. 8: Lines drawn by Wilhelm Johannsen in the third edition of Punnett's *Mendelism* (1911) to connect the allelic combinations mentioned in the text using Mendelian notation with the fields of the accompanying Punnett square. With kind permission of the Royal Danish Library, Copenhagen, Call no. 8° N. hist. 20481, p. 118–119.

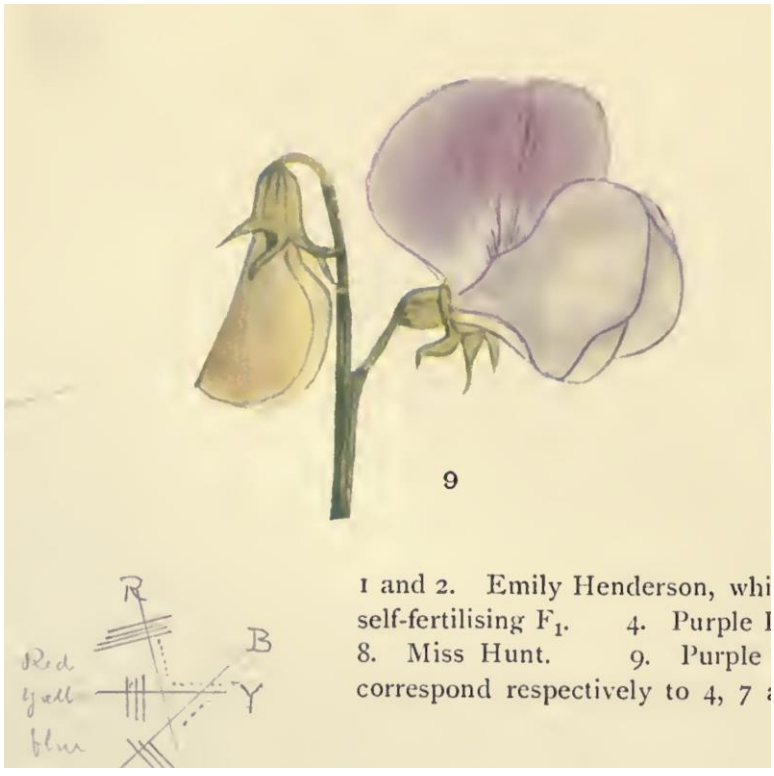

Fig. 9: Detail from a plate on the 'reversion' of colour in sweet peas from Bateson's *Mendel's Principles of Heredity*, Cambridge: Cambridge University Press, 1909). The plants here displayed are second generation types. A reader drew a scheme for colour mix in the bottom left margin. He was likely working out the possible combinations for obtaining purple as a mixture of red and blue or red, blue and yellow. With kind permission of the Library of the Marine Biological Laboratory, Woods Hole.