

Defective inheritance-ratios in *Bursa* hybrids.

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Several years ago (1905—1907) I was making extensive cultures of *Bursa* (*Capsella*) *bursa-pastoris*, of *Bursa Heegeri*, and of hybrids between these two species. *Bursa Heegeri* is generally conceded to have originated from *B. bursa-pastoris* by a recent mutation and has been found in nature only once in a situation which would warrant the belief that it had not been derived from a near-by experimental culture. Although a number of specimens were found by Professor Heeger at the original locality on the market-place at Landau, Germany, in 1897, so far as is now known these represented a single elementary form or biotype. *Bursa bursa-pastoris*, on the other hand, is of almost world-wide distribution, and presents an unknown number, but certainly a large number, of distinct biotypes.

In my cultures of the latter species I found four forms of rosette which were related to one another as the four terms of a Mendelian di-hybrid. These four biotypes were named and described as follows:¹⁾

Type (a). *Bursa bursa-pastoris heteris* has the leaves divided to the mid-rib, the terminal lobe being usually separated from the nearest lateral lobes by clean, deep incisions. The lateral lobes consist essentially of two features, an elongated proximal portion, the „primary lobe“, and a more or less rounded or

¹⁾ „Results of crossing *Bursa bursa-pastoris* and *Bursa Heegeri*“. 6 pp. Proceedings Seventh International Zoological Congress, Boston Meeting, August 19—24 1907. „Advanced reprint“ issued in 1910.

„*Bursa bursa-pastoris* and *Bursa Heegeri*: Biotypes and hybrids“. 57 pp., 23 text-figs., 4 pls., Publ. No. 112, Carnegie Institution of Washington, 1909.

angular portion, the „secondary lobe“, in the distal axil of the primary lobe.

Type (b). *Bursa bursa-pastoris rhomboidea* has the leaves divided to the mid-rib as in *B. bp. heteris*. The lateral lobes have an incision on the distal margin setting off the secondary lobe from an *unelongated* primary lobe. There is usually a corresponding incision on the proximal margin of the primary lobe. In the best developed specimens these incisions set off a small terminal portion of each lateral lobe, which is rather blunt or angular at the apex, being generally of rhomboidal form. Less perfectly developed specimens have the incisions very shallow or nearly wanting, but retain the characteristic deep sinuses extending to the mid-rib.

Type (c). *Bursa bursa-pastoris tenuis* differs from both (a) and (b) in that the sinuses do not usually reach the mid-rib. The terminal lobe is not separated from the nearest lateral lobes by deep, clean-cut sinuses, these more distal sinuses being relatively shallow, so that one can with but scant propriety speak of the terminal lobe as a definite morphological structure. All the lateral lobes tend to be elongated and sharp, and no incisions are present to set off a secondary lobe, though in particularly vigorous specimens there may be a slight expansion of leaf-tissue in the region occupied by the secondary lobe in *B. bp. heteris* and *B. bp. rhomboidea*.

Type (d). *Bursa bursa-pastoris simplex*, like *B. bp. tenuis* is scarcely ever divided nearly to the mid-rib, and the lateral lobes are mostly obtuse, sometimes more or less acute, but never long and attenuated. No secondary lobing appears except occasionally a slight denticulation on the margins.

These descriptions refer to the characters of the climax-leaves in well-grown specimens, as all of these types have juvenile leaves entirely unlobed and indistinguishable from the juvenile leaves of the other forms, and the late rosette-leaves and stem-leaves likewise generally lack distinctive features. Under poor cultural conditions plants frequently complete their development, flower, and ripen their seeds, without exhibiting any but these juvenile and senescent characters. The complete procession of leaf-forms in typical specimens of the four described biotypes are shown in the plates I—IV.

The production of a considerable number of hybrid families representing the various possible combinations of these four biotypes has demonstrated that their gametic formulae may be aptly represented by the conventional Mendelian symbols, as follows:

| | | |
|--------------------------|-----|-----------|
| <i>B. bp. heteris</i> | . . | <i>AB</i> |
| <i>B. bp. rhomboidea</i> | . . | <i>aB</i> |
| <i>B. bp. tenuis</i> | . . | <i>Ab</i> |
| <i>B. bp. simplex</i> | . . | <i>ab</i> |

By comparing these formulae with the descriptions of the different forms it will be seen that *A* is responsible for the long, sharp character of the primary lobe in *B. bp. heteris*, and the attenuation of the lobes in *B. bp. tenuis*, while *B* produces the division of the leaf to the mid-rib and the resultant definiteness of the terminal lobe in both *B. bp. heteris* and *B. bp. rhomboidea*, the rounded secondary lobe of *B. bp. heteris*, and the proximal and distal incisions of *B. bp. rhomboidea*.

Bursa Heegeri has the *heteris*-form of rosette, *i. e.* with the gametic formula *AB*, but differs so fundamentally from *Bursa bursa-pastoris* in the characters of the capsules, that if its relationship to the latter species were not so obvious on other grounds, its capsules would cause it to be placed unquestionably in a separate genus. The flat, triangular or cordate form of the *bursa-pastoris* capsule is too familiar to need description. The spur-like valves are firm, and fall readily at the slightest touch when the seeds are ripe. The capsules of *B. Heegeri* are of oval form, surmounted by the short, strong, persistent style, and the valves are thin membranous, not the least inflated, and do not fall when the seeds are mature. The seeds are liberated by an irregular break in the central region of each valve.

When this original genotype of *B. Heegeri* was crossed reciprocally with *B. bursa-pastoris simplex*, the rosette-characters segregated in the F_2 , into the four types described above, but the *Heegeri*-type of capsule appeared in only 111 specimens among 2540. The distribution of the several characters in the F_2 are shown in the following table:

Table I.

| | | <i>Bursa bp. simplex</i> (abC) | | | | × | <i>Bursa H. heteris</i> (ABc) | | | | | |
|----------|---------|--------------------------------|--------|---------|---------|------------|-------------------------------|--------------------|----------|--|--|--|
| | | Ped. No. 056.64 | | | | | Ped. No. 059. | | | | | |
| | | | | | | ↓ | | | | | | |
| | | <i>Bursa bp. heteris</i> (ABC) | | | | | | | | | | |
| | | Ped. No. 0564.88 | | | | | | Ped. No. 059.89 | | | | |
| | | Bursa-pastoris Series (C) | | | | | | Heegeri Series (c) | | | | |
| Ped. No. | heteris | rhomboidea | tenuis | simplex | heteris | rhomboidea | tenuis | simplex | C : c | | | |
| 06196 | 98 | 32 | 36 | 13 | 5 | 2 | 1 | 1 | 19.9 : 1 | | | |
| 06197 | 1032 | 302 | 331 | 78 | 45 | 13 | 13 | 1 | 24.2 : 1 | | | |
| 06212 | 317 | 67 | 102 | 21 | 19 | 4 | 7 | 0 | 16.9 : 1 | | | |
| Total | 1447 | : 401 | : 469 | : 112 | 69 | : 19 | : 21 | : 2 | 21.9 : 1 | | | |
| Expected | 1368 | : 456 | : 456 | : 152 | 63 | : 21 | : 21 | : 7 | 3.0 : 1 | | | |

The deficiencies seen to be consistently present in all these pedigrees in the number of *rhomboidea* and *simplex* were probably due at least in part to an error of classification, those *rhomboideas* having the greatest elongation of the terminal segment of the lobes having doubtless permitted their classification as minus-fluctuations of *heteris*, and the sharpest-lobed *simplex* as minus-fluctuations of *tenuis*. The greatest surprise was occasioned by a ratio of about 22 : 1 in the form of the capsules, as it was thought probable that the difference between the two forms would be found to be dependent upon the presence and absence of a single gene, the expected ratio on this assumption being 3 : 1.

At the close of the second generation the cultures were necessarily discontinued, and could not be resumed until in the autumn of 1910. The appearance of a paper by Nilsson-Ehle¹⁾, showing that certain characters of wheat and oats are independently determined by two or more distinct units or genes, gave the suggestion that the capsule-character of *B. bursa-pastoris* might be determined in like manner by two genes, the absence of both of which produces the *Heegeri*-type of capsule, although the observed ratio 22 : 1 is a bad approximation to the expected ratio

¹⁾ Nilsson-Ehle, H., Kreuzungsuntersuchungen an Hafer und Weizen. pp. 122. 1909. Lund: Hakan Ohlssons Buchdruckerei.

15 : 1, considering the number of individuals involved in the F_2 cultures and the consistent results yielded by three different pedigrees involving reciprocal crosses. After the pedigrees were all arranged in the spring of 1910 for the testing of this hypothesis, Baur¹⁾ suggested the same possible explanation in a review of one of my papers.

The demonstration of two independent genes for the determination of the same external character is to be found in the composition of the F_3 families grown from self-fertilized F_2 individuals possessing the dominant character in question, — in this instance the *bursa-pastoris* type of capsule. Letting the two supposed genes for the triangular capsule be represented by the symbols *Cc* and *Dd*, the gametic composition in F_2 and the expectation in the F_3 is indicated in the following table:

Table II.

| Number of F_2 plants in 16. | Gametic Composition in the F_2 | Expected Results in F_3 |
|-------------------------------|----------------------------------|----------------------------------------------------|
| 1 | <i>CD CD</i> | All <i>bursa-pastoris</i> . |
| 2 | <i>CD Cd</i> | All <i>bursa-pastoris</i> . |
| 2 | <i>CD cD</i> | All <i>bursa-pastoris</i> . |
| 4 | <i>CD cd</i> | <i>Bursa-pastoris</i> and <i>Heegeri</i> , 15 : 1. |
| 1 | <i>Cd Cd</i> | All <i>bursa-pastoris</i> . |
| 1 | <i>cD cD</i> | All <i>bursa-pastoris</i> . |
| 2 | <i>Cd cd</i> | <i>Bursa-pastoris</i> and <i>Heegeri</i> , 3 : 1. |
| 2 | <i>cD cd</i> | <i>Bursa-pastoris</i> and <i>Heegeri</i> , 3 : 1. |
| 1 | <i>cd cd</i> | All <i>Heegeri</i> . |

The facts shown in this table may be summarized in the statement that among fifteen families raised from F_2 plants having the *bursa-pastoris* type of capsule, there will be on the average seven (1 *CD CD* + 2 *CD Cd* + 2 *CD cD* + 1 *Cd Cd* + 1 *cD cD*) which will breed true to that type, four (*CD cd*) will produce *bursa-pastoris* and *Heegeri* in the ratio 15 : 1 as in the F_2 , and four (2 *Cd cd* + 2 *cD cd*) will give these two types of capsules in the ratio 3 : 1. As in all other recessive types, the offspring of F_2 plants having *Heegeri* capsules should produce no plants with *bursa-pastoris* capsules in the F_3 .

¹⁾ Zeitschrift für Induktive Abstammungs- und Vererbungslehre 3 : 341—342, Je 1910.

Eleven families were grown during the winter of 1910—11 from seeds of F_2 plants having *bursa-pastoris* capsules, and five families from plants having *Heegeri* capsules. The results are brought together here in the form of a table.

Table III.

| Pedigree Number | Capsule of parent | Rosette of parent | Result in F_3 | Ratio capsules | Ratio rosettes |
|--------------------|-----------------------|-------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------|----------------|
| 09258 | <i>bursa-pastoris</i> | <i>heteris</i> | 1 <i>H. heteris</i> | 0 : 1 | 1 : 0 |
| 09281 | <i>bursa-pastoris</i> | <i>heteris</i> | 307 <i>bp. heteris</i> | 1 : 0 | 1 : 0 |
| 09284 | <i>bursa-pastoris</i> | <i>heteris</i> | $\left\{ \begin{array}{l} 31 \text{ bp. } \textit{heteris} \\ 11 \text{ bp. } \textit{tenuis} \\ 5 \text{ } \textit{H. heteris} \\ 4 \text{ } \textit{H. tenuis} \end{array} \right\}$ | 4.67 : 1 | 2.47 : 1 |
| 09271 | <i>bursa-pastoris</i> | <i>rhomboidea</i> | $\left\{ \begin{array}{l} 175 \text{ bp. } \textit{rhomboidea} \\ 70 \text{ bp. } \textit{simplex} \end{array} \right\}$ | 1 : 0 | 2.50 : 1 |
| 09272 | <i>bursa-pastoris</i> | <i>rhomboidea</i> | $\left\{ \begin{array}{l} 96 \text{ bp. } \textit{rhomboidea} \\ 31 \text{ bp. } \textit{simplex} \\ 2 \text{ } \textit{H. rhomboidea} \end{array} \right\}$ | 63.5 : 1 | 3.16 : 1 |
| 09273 | <i>bursa-pastoris</i> | <i>tenuis</i> | 375 <i>bp. tenuis</i> | 1 : 0 | 1 : 0 |
| 09274 | <i>bursa-pastoris</i> | <i>tenuis</i> | $\left\{ \begin{array}{l} 224 \text{ bp. } \textit{tenuis} \\ 64 \text{ bp. } \textit{simplex} \\ 10 \text{ } \textit{H. tenuis} \\ 2 \text{ } \textit{H. simplex} \end{array} \right\}$ | 24.0 : 1 | 3.55 : 1 |
| 09283 | <i>bursa-pastoris</i> | <i>tenuis</i> | $\left\{ \begin{array}{l} 250 \text{ bp. } \textit{tenuis} \\ 16 \text{ } \textit{H. tenuis} \end{array} \right\}$ | 15.6 : 1 | 1 : 0 |
| 09275 | <i>bursa-pastoris</i> | <i>simplex</i> | $\left\{ \begin{array}{l} 443 \text{ bp. } \textit{tenuis} \\ 213 \text{ bp. } \textit{simplex} \end{array} \right\}$ | 1 : 0 | 2.08 : 1 |
| 09275 ¹ | <i>bursa-pastoris</i> | <i>simplex</i> | $\left\{ \begin{array}{l} 85 \text{ bp. } \textit{tenuis} \\ 35 \text{ bp. } \textit{simplex} \end{array} \right\}$ | 1 : 0 | 2.43 : 1 |
| 09276 | <i>bursa-pastoris</i> | <i>simplex</i> | 472 <i>bp. simplex</i> | 1 : 0 | 0 : 1 |
| 09282 | <i>bursa-pastoris</i> | <i>simplex</i> | 156 <i>bp. simplex</i> | 1 : 0 | 0 : 1 |
| 09278 | <i>Heegeri</i> | <i>heteris</i> | $\left\{ \begin{array}{l} 7 \text{ } \textit{H. heteris} \\ 3 \text{ } \textit{H. rhomboidea} \\ 1 \text{ } \textit{H. tenuis} \end{array} \right\}$ | 0 : 1 | 7 : 3 : 1 : 0 |
| 09288 | <i>Heegeri</i> | <i>heteris</i> | 1 <i>H. heteris</i> | 0 : 1 | 1 : 0 |
| 09289 | <i>Heegeri</i> | <i>heteris</i> | 1 <i>H. heteris</i> | 0 : 1 | 1 : 0 |
| 09277 | <i>Heegeri</i> | <i>tenuis</i> | $\left\{ \begin{array}{l} 167 \text{ } \textit{H. tenuis} \\ 79 \text{ } \textit{H. simplex} \end{array} \right\}$ | 0 : 1 | 2.11 : 1 |
| 09290 | <i>Heegeri</i> | <i>tenuis</i> | 10 <i>H. tenuis</i> | 0 : 1 | 1 : 0 |

¹ Second sowing.

Several of these families consisted of but one individual each, and these may be left out of account as having no significance. The most interesting is 09258 in which a *bursa-pastoris* parent produced a single *Heegeri* offspring, thus showing that this parent was heterozygous in respect to capsule-character. Six of the eleven families derived from *bursa-pastoris* parents bred true to the *bursa-pastoris* type of capsule, this being slightly in excess of expectation on the assumption that this character is determined independently by two genes, and considerably in excess of the one-third which should have bred true if but one gene differentiated the *Heegeri* capsules from the *bursa-pastoris* capsules of the P_1 . However the number of families is wholly inadequate to permit the attachment of any special significance to this closer agreement with the requirements of the two-gene hypothesis. All of the families from parents having *Heegeri* capsules have bred true to the parental character, as they should do to agree with Mendelian interpretation. The four families which split into the two parental types show the ratios, 4.67 : 1, 15.6 : 1, 24.0 : 1, and 63.5 : 1, all of these ratios differing in the same direction but in quite various degrees from the two available ratios 3 : 1 and 15 : 1. Two of the families show a suggestive approximation to the expected ratios, while the other two depart widely from the nearest available ratio 15 : 1. All of these families as well as the three families of the F_2 have shown a smaller proportion of *Heegeri* plants than required by the hypothesis that the *bursa-pastoris* capsules are determined independently by two genes.

It appears to me that the explanation of these results is to be sought in some modifying influence acting upon the normal Mendelian processes. The ratio 4.67 : 1 may then represent a modified ratio of 3 : 1, and the other three ratios may be referred to the ratio 15 : 1. These three families taken together give a ratio of 22.2 : 1, essentially identical with the observed ratio 21.9 : 1 in the F_2 , and showing almost exactly the same proportional departure from 15 : 1, that 4.67 : 1 shows from 3 : 1, for $4.67 : 3 = 23.3 : 15$.

The nature of the modifying cause or causes which may be operating to produce these defective ratios need not be discussed at length here, as the matter is capable of experimental treatment and is being investigated; but it may be pointed out that either „selective fertilization“ favoring the union of unlike gametes,

or „selective elimination“ of the *Heegeri* homozygotes, would produce the observed results. Of these two sources of modified ratios, „selective elimination“ seems to be the more promising, because there appears to be at present no satisfactory evidence that „selective fertilization“ occurs in any other organism, while „selective elimination“ has been clearly demonstrated in *Antirrhinum*¹⁾ and in yellow mice.²⁾ In both of these, the one class of homozygotes is entirely eliminated, so that the normal ratio 3 : 1 (1 + 2 : 1) becomes 2 : 1. If „selective elimination“ is the source of the discrepancies between the theoretical and observed ratios in the capsule-characters of Bursa, its operation must differ from that in *Antirrhinum* and in yellow mice in two particulars, namely, there must be only a partial elimination of one homozygous class in Bursa, and this elimination must affect the negative, instead of the positive, homozygotes.

The ratios for the rosette-characters in several of the families also deviate considerably from the expected ratio 3 : 1, and it is a pertinent question whether any of these deviations is significant, or whether they may be accounted for by the errors of random sampling, due to the small size of the families. The fact that several of the ratios lie above 3 : 1 and others below, suggests that at least a considerable part of the variation in the ratios is due to purely chance causes of this kind. The ratio 3 : 1 is the ideal, but can be absolutely expected only when the number of offspring is infinite.

Too little attention is paid by students of genetics perhaps to the probable errors of their results. If we follow Johannsen³⁾ in computing the standard deviation in the case of alternative characters by the formula $\sigma = \sqrt{\%p_0 \cdot \%p_1}$, in which $\%p_0$ represents the percentage of individuals in the one class and $\%p_1$ the percentage in the alternative class, it is easy to determine within what limits a single observed ratio might be referred to 3 : 1 with a sufficient degree of probability. These limits for

1) Baur, E., Untersuchungen über die Erbliehkeitsverhältnisse in einer nur in Bastardform lebensfähigen Sippe von *Antirrhinum majus*. Ber. d. Deutsch. Bot. Gesell. 25 : 442, 1907.

2) Castle, W. E., and Little, C. C., On a modified Mendelian ratio among yellow mice. Science N. S. 32 : 868—870, 16 D 1910.

3) Johannsen, W., Elemente der exakten Erbliehkeitslehre. pp. VI + 516, 1909. Jena: Gustav Fischer. See p. 57.

families of various sizes from 100 to 1000 are given in the following table, and are calculated to allow a departure from the observed ratio, equal to three times the probable error. The adoption of three times the probable error as a criterion of significant differences is purely arbitrary, and about three families in one-thousand having the given number of individuals could be expected to transgress the limits indicated in the table, and such departures would still be due only to the errors of random sampling. Some biometricians accept 2.5 times the probable error as the limit within which results may not be confidently claimed to be significant.

Table IV.

| Number of individuals | Observed percentages theoretically referable to 75 % | Observed ratios referable to ratio 3 : 1 |
|-----------------------|------------------------------------------------------|------------------------------------------|
| 100 | 60.34 % to 85.54 % | 1.52 : 1 to 5.91 : 1 |
| 200 | 64.87 % to 82.97 % | 1.85 : 1 to 4.87 : 1 |
| 300 | 66.84 % to 81.70 % | 2.02 : 1 to 4.46 : 1 |
| 400 | 68.00 % to 80.90 % | 2.13 : 1 to 4.23 : 1 |
| 500 | 68.78 % to 80.33 % | 2.20 : 1 to 4.08 : 1 |
| 600 | 69.35 % to 79.91 % | 2.26 : 1 to 3.97 : 1 |
| 700 | 69.80 % to 79.57 % | 2.31 : 1 to 3.89 : 1 |
| 800 | 70.14 % to 79.29 % | 2.35 : 1 to 3.82 : 1 |
| 900 | 70.43 % to 79.07 % | 2.38 : 1 to 3.77 : 1 |
| 1000 | 70.68 % to 78.87 % | 2.41 : 1 to 3.73 : 1 |

Only one of the ratios for the leaf-characters in the F_3 cultures transgresses the limits indicated in this table. The family 09275 in which 656 individuals gave a ratio of 2.08 : 1, clearly presents a defect not due to random sampling, and the cause of the deficiency was easily discovered. The parent of this family was classified as *Bursa bursa-pastoris simplex*, and was expected to produce only the parental characters in its offspring; but the progeny consisted of 443 *B. bp. tenuis* and 213 *B. bp. simplex*, thus demonstrating that the parent was a heterozygote in which the normally dominant *tenuis* characters failed to appear. The relative impotency of the *tenuis* character which allowed it to remain undeveloped in the parent, seems to have affected the offspring in a similar manner, so that without doubt many of the heterozygotes were classified as *B. bp. simplex*.

During the early development of this family, it appeared to consist of about three *B. bp. simplex* to one *B. bp. tenuis*, and

only much later did it become obvious that many of the supposed *simplex* plants were producing a greater elongation of some of the lobes than is to be found in pure *B. bp. simplex*. The ratio 2.08 : 1 here reported for this family, was derived by waiting until the flower-stems were about 5—10 centimeters high, and then calling everything *tenuis* which produced at least one lobe more elongated than those of pure-bred *B. bp. simplex*. Plate V shows the most highly developed leaf-characters attained in each of twenty-six individuals taken quite at random from plants in this family, which had been finally classified as *B. bp. tenuis*. In normal, well-developed specimens of *B. bp. tenuis* there is a long series of leaves in the middle („climax“) region of the rosette, in which there is marked elongation of the lobes (see plate III), but in family 09275 many of the plants which were finally regarded as *B. bp. tenuis*, had but one or two leaves in which recognized *tenuis* characters appeared. Thus the wide gap which ordinarily separates the dominant and recessive types in these hybrid families of Bursa, was in this particular family not only reduced to zero, but it appears certain that the heterozygous and recessive categories overlapped to such an extent that many individuals which belonged in the former were necessarily classified in the latter: hence the defective ratio is to be explained by the failure of dominance of the *tenuis* characters in the heterozygotes.

The cause of this failure of dominance is not apparent. The environment has a very considerable influence in determining the various features of Bursa plants, and especially in limiting the development of such distinctive characters as ordinarily appear only in the climax leaves. Crowding in the seed-pans, poor illumination, and other unfavorable conditions, have caused many plants in certain of my cultures, to develop flowers and ripen seeds without having developed their leaves beyond the early juvenile stages. While the rosettes in 09275 were not in any sense juvenile, the *simplex* characters do represent a less highly specialized type than *tenuis*, and therefore any influence which tends to abbreviate the cycle of development, might conceivably reduce *tenuis* plants to a form indistinguishable from *simplex*. This large family of 656 individuals was germinated in a single square seed-pan, 30 × 30 cm, and the young plants grew in this seed-pan for seven weeks before they were potted. Perhaps this long

crowding might be expected to have some such effect as that observed. So far as known, all other conditions under which these plants grew, were conducive to vigorous development. At any rate this culture was in all other regards on an equal footing with the other cultures which were being grown during the same period, and which gave normal development of the several biotypes.

To test the suggestion that crowding might be responsible for the failure of dominance, a second sowing was made on February 25, 1911, each seed being sown separately and spaced in such a manner that the seed-pan contained only 120 plants. On April 7 these were potted and their growth has been continuously healthy and vigorous. They have not been subjected at any time to the least injurious crowding, yet they show the same tardy development of the *tenuis* characters as observed before. On April 22 only three of the 120 plants could be distinguished from *B. bp. simplex*, though nearly all were sufficiently advanced that if it had been a normal family representing the same hybrid combination, almost a complete separation of the alternative types might have been made. The final census of the plants derived from this second sowing, made on the same basis and with the same care as in the case of the first sowing, showed 85 *B. bp. tenuis* and 35 *B. bp. simplex*, — a ratio of 2.43 : 1. The conclusion is reached therefore that the low grade of the *tenuis* characters in this family is inherent, and not a direct effect of unfavorable conditions of the environment.

This result appears to furnish an illustration of the phenomenon known as „variable potency“¹⁾, but whether the gene *A* for the *tenuis* characters is really different in family 09275 from that in the other families must remain for the present an open question. It is conceivable that the relative inefficiency of *A* in this family is due to the operation of some other factor which acts as a partial inhibitor, so that although the actual character of *A* remains unchanged, it must meet a greater resistance, and therefore produces a less effect. To avoid a decision of the question whether the gene has less power or whether it must meet a greater resistance, I use the expression „relative

¹⁾ Davenport, C. B., Heredity and Mendel's law. Proc. Washington Acad. Sci. 9 : 179 187, 31 Jy 1907.

potency". The „inhibiting factor“, if such there be, need not even be genotypic in nature, but may be the result of some somatic quality of the parent (such for instance as its state of health) projected to the offspring through influences surrounding the latter during their embryonic development.

Summary.

Crosses between *Bursa (Capsella) bursa-pastoris simplex* and *B. Heegeri heteris* have demonstrated the existence of two genes, *A* and *B*, which determine the differentiating characteristics of the rosettes and which result in the production of four forms in the F_2 in the ratio 9 : 3 : 3 : 1.

They seem to indicate also the presence of two genes, *C* and *D*, each of which is independently responsible for the *bursa-pastoris*-type of capsule. The *Heegeri*-type appears only in the absence of both *C* and *D*. On this basis the two forms should appear in the F_2 in the ratio 15 : 1. The observed ratio was 21.9 : 1. In the F_3 , some families should give ratios of 3 : 1, and other families should again give ratios of 15 : 1. The observed ratios in F_3 were 4.67 : 1, and 22.2 : 1. These observed ratios show a corresponding deviation from the theoretical ratios, and are thought to indicate the action of some modifying influence, such as „selective elimination“, distorting the results of an otherwise normal Mendelian segregation.

A defective ratio in the rosettes of one family is shown to be due to failure of dominance, and certain facts are presented, which indicate that this failure of dominance is attributable to a less „relative potency“ of the gene *A* which determines the *tenuis*-character. This change in the relative potency of *A* may be due to a decline in the efficiency of the gene itself, or to the operation of some other factor or condition which offers an increased resistance to the development of the *tenuis*-characters.

Shull — Defective ratios in Bursa.

Plate I.



Ontogenetic succession of leaf-forms in *Bursa . . . heteris*.

Shull — Defective ratios in Bursa.

Plate II.



Ontogenetic succession of leaf-forms in *Bursa* *rhomboidea*.

Shull — Defective ratios in Bursa. Plate III.



Ontogenetic succession of leaf-forms in *Bursa tenuis*.

Shull — Defective ratios in Bursa. Plate IV.



Ontogenetic succession of leaf-forms in *Bursa*. . . . *simplex*.

Shull — Defective ratios in Bursa. Plate V.



Inflorescences of *Bursa bursa-pastoris* (at right) and of
B. Heegeri (left).

Shull — Defective ratios in Bursa. . Plate VI.



Climax leaves of twenty-six individuals classified as *B. bp. tenuis*, in a family (09275) which showed an unusually low grade of development of the *tenuis* characters.

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