INHERITANCE IN BARLEY.

II. THE AWN AND THE LATERAL FLORET.

[For I. see Bibliography (1).]

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SOME interesting contributions to this subject have appeared during the past three years. They contain somewhat discordant ideas and it has therefore been concluded that the present time is suitable for a brief review of the whole matter and for the publication of further experimental results. A striking susceptibility to environmental change is evinced by both the awn and the lateral floret, and it is part of the purpose of this paper to describe the nature of the fluctuations involved and to indicate the extent to which they militate against the reliable determination of genetic ratios.

A retrospect of genetic investigation—over the period 1900 to 1920—compels the question: "What has been discovered and where does the knowledge lead?" The bulk of the investigation has, quite naturally, taken the form of the establishment and confirmation of "genetic ratios." Segregation, as a bare phenomenon, has been proved to characterise the processes of reproduction but little has been achieved in the

elucidation of the precise morphological and physiological "characters" which behave as "units" when segregation is in process. The pre-Mendelian systematist was content to define floret-characters almost exclusively in two general terms—present (i.e. apparent to the eye) and absent. So long as the duty of building up a satisfactory general confirmation of Mendel's original discovery yet remained, genetics had no need to attempt greater precision than this. That such a need exists now and that the quest of ratios based upon simple "eye-judgment" characters may be in some cases disappointing and unreliable, is one of the indications of the experimental work to be described. Some attention has, in consequence, been devoted to that aspect of the observations which suggests—for these two experimental characters at any rate—the desirability of trying to raise one of the common present-day forms of genetic experiment to a different plane, a plane upon which genetics and plant physiology co-operate very closely.

To appreciate the different aspects of the situation it is necessary to devote a certain amount of consideration to the purely botanical nature of the experimental characters and for this reason, in the case of each of them, a descriptive paragraph has been set apart.

§ I. THE AWN IN BARLEY CONSIDERED AS A GENETIC CHARACTER.

In many genera of the Gramineae the outer palea (also called the flowering glume or lemma) and, more rarely, the glume (also called the empty glume) bears a bristle-like appendage. This is called the awn. The cultivated forms of the genus *Hordeum* (= the barleys) bear an awn on the *glume* which is insignificant but—save in certain cases described below—the awn of the outer palea is very long and prominent. It gives to the ear the appearance of having a long "beard." Reference to the awn in what follows is always to the awn of the outer palea of the floret.

Barleys which are commonly accepted as "natural" varieties fall into groups whose awn characters are as follows:—

H. hexastichum (6-row and 4-row barleys) with long awns on both median and lateral florets [both sets of florets form fertile grains].

H. intermedium (*H. i. Haxtoni* and *H. i. transiens*) with long awns on the median florets, but with lateral florets which, though generally setting grains, have blunt tips to their outer paleae.

H. distichum is like *H. intermedium* in awns. The lateral florets never set grains and have smaller paleae than in *H. intermedium*.

H. decipiens is like *H. distichum* save that the paleae of the lateral florets are much reduced, being, in fact, mere vestiges.

There is a group of barleys indigenous to parts of the Himalayas, which differs from the other forms of the genus *Hordeum* in that it has "hoods" or "caps" (the Kaputzer of Körnicke) in the place of awns. In a "hood" may occur a small flower. Two downward sloping lateral projections from the base of the hood lend a triangular appearance and hooded barleys are commonly known as "trifurcate" forms. Among the naturally occurring cultivated barleys, *H. hexastichum* alone shows "trifurcate" varieties, but trifurcate "distichums," etc., can readily be bred.

That the awn and the hood are simply different developments of the same organ is shown by their broad similarity and by the inheritance results recorded by Biffen(7). Certain of his F_1 and F_2 plants in Awned $\times$ Trifurcate crosses had a hood borne on a short awn. To some extent, therefore, the awn and the hood are teratological, there being a series of possible developments—awn, hood, and awn-cum-hood. In such a character sharp fluctuations are perhaps to be expected. They occur in a most baffling manner and a brief account of them must be given later.

In the accepted "natural" races of barley wide fluctuations in awn-length do not appear. When, however, hooded and awned forms are crossed, sorting into types may be impossible owing to the vagaries of the hood-cum-awn form [cf. Biffen(7)]. To further the investigation of awn-inheritance "awnless" forms of barley must be used—forms in which the outer paleae of median and lateral florets alike bear neither awn nor hood. Two such forms are known to exist and they merit close attention. The first is a variety called "Nogenasi" described by Ikeno(8). It is a 6-row form. Apparently it is a "natural variety" in Japan. How it has arisen is not clear and, as will later be shown, its existence is of some botanical interest [cf. § III, p. 165, below]. Although it must be classed as unique—beardless 6-row—it by no means represents a "clean-cut" character, a perfect "absence." Ikeno's own words best illustrate the nature of the awn fluctuation [*loc. cit.* p. 263]: "Nogenasi où les arêtes font en général défaut; on y voit cependant très fréquemment la production des arêtes courtes chez un certain nombre des épillets appartenant au rang moyen et il importe de remarquer ici que même dans tels cas les arêtes ne se produisent jamais chez ceux placés à la partie supérieure de l'épi et qu'elles n'ont jamais une longueur suffisamment grande pour que leur extrémité supérieure puisse atteindre le niveau des épillets placés au sommet de l'épi." In connection with the final clause of this quotation it is to be noted that the protrusion of the awns beyond the tip of the ear is no guide (in an F_2) to awn-length type unless there

is absence of segregation of rachis-segment length. A set of awns which makes a "dense" ear look half-bearded, presents quite an unimpressive appearance on a very long, lax ear. Segregation of rachis length is commonly encountered in barley crosses. It has greatly added to the complexity of the awn-inheritance problem.

The other "awnless" barley is *Hordeum distichum inerme* (hereinafter "Inerme"). Rimpau (9) was the first to breed it—from the cross:

$$\begin{array}{l} \text{Steudel's Gerste} \times \text{Gabelgerste} \\ (H. \text{decipiens v. Steudelii}) \times (H. \text{hexastichum v. trifurcatum}) \\ = \text{median florets fully awned;} \quad = \text{all florets setting grain and} \\ \text{laterals vestigial} \quad \text{all bearing a hood} \end{array}$$

One of a number of segregates from this cross, "Inerme," was awnless median florets and semi-decipiens laterals. Its grain is poorly filled and rich in nitrogenous compounds, its straw deep chrome in colour and of marked strength. These characters have led to its employment in the endeavour to raise a "feeding barley." Usually the outer paleae of the median florets are bluntly rounded but fluctuation is common. "Awns" of 2-4 cm. in length may occur especially on late tillers of a plant. Quite commonly on one plant may be found—in order of earliness—the absolutely awnless ear, the ear with very short scurs, and the ear with 2-4 cm. long awns. For some unknown reason "Inerme" types extracted from F_2 's of certain Inerme $\times$ Awned crosses, fluctuate far more violently in respect of "awn" than does the pure parental Inerme itself. It seems that the "Inerme potentiality" responds readily to environmental differences (e.g. changes in time of emergence of the ear from the sheath) and that, placed in the novel circumstances afforded by various genetic types extracted from F_2 's, the "potentiality" is even more responsive than in those afforded by the pure strain known as "Inerme."

The photographs included in this paper illustrate the range of awn fluctuation, which has been met in a number of Inerme crosses. Specimen ears of a number of F_2 plants were preserved for comparison with F_3 because of the obvious magnitude of possible fluctuations.

Fig. I $\left\{ \begin{array}{l} (a) \text{ An } F_2 \text{ plant with awns 2.5 cms. in length.} \\ (b), (c), (d) \text{ } F_3 \text{ plants from the progeny of } (a). \text{ All are completely awnless as were} \\ \text{all the eighteen members of this } F_3 \text{ family.} \end{array} \right.$
The cross was *H. i. Haztoni* $\times$ *H. d. inerme*.

Fig. II. Ears from one F_3 plant of the cross *H. h. parallelum* $\times$ *H. d. inerme*.

Fig. III. Ears from one F_3 plant of the cross *H. d. (v. Chevallier)* $\times$ *H. d. inerme*.

Figs. II and III illustrate tiller to tiller fluctuations on a single plant. Körnicke (16) has recorded a great number of interesting cases of awn fluctuation, the most striking being Hoffmann's case [see (16), p. 135, vol. 1], in which a strain of 2-row barley bore in some years awned ears and in others awnless ones.

The "awn" of barley is thus a most difficult character to observe in genetic work. Classification of an F_2 is usually impossible save by the raising of the F_3 families and even if this be done the way to reliable sorting is far from open. Judgment has to be based on the F_3 family as a whole and due regard has to be paid to the fact that late tillers of genetic "Inermes" may bear short awns. If the F_3 family be large, classification can be effected with confidence, but families of only one, two, or three plants occur. It is dangerous to throw them away and, perhaps, equally dangerous to sort them.

§ II. VIEWS UPON THE INHERITANCE OF THE AWN IN BARLEY.

Ikeno's observations(8) may be thus represented:

Kinukawa	×	Nogenasi
(Awned 6-row)		(Awnless 6-row)
<i>AA.EE.ii</i>		<i>aa.ee.II</i>

A and *E* have awn-producing powers, *I* inhibits awns. The F_2 contained 321 plants and a complete F_3 was grown from it. Of the F_2 plants 4 gave entirely Kinukawa progeny and 6 entirely Nogenasi. The mean of 4 and 6 is 5; $5/321 = 1/64$; therefore three factors are involved (as represented above). The F_2 was further classified by judgment of its F_3 families, but it was not found possible to attempt a sorting more elaborate than that represented by the following grouped types:

$$ii : Ii : II$$

This sorting gave the result:

$$69 : 164 : 88$$

The expectation on the three-factor theory is:

$$80.25 : 160.50 : 80.25$$

The error of 69/321 instead of 80.25/321 is about 2.2 times the probable error due to fluctuations of sampling.

What, in effect, has been accomplished is therefore a classification of the F_2 plants (by means of a complete F_3) on a basis which agrees—and not in a conspicuously accurate degree—with a theory of unifactorial difference between the awned and awnless parent forms.

So far the justification for the 3-factor theory rests solely upon the rather slender evidence that the number of true-breeding parental-type plants in F_2 is 5/321 ($4 + 6/2 = 5$). Further justification was sought by determining the proportions of F_2 plants in the groups

$$ii : Ii : II$$

which bred true to type in F_3 . The results were (in numbers of plants):

$$21 : 0 : 23$$

and the expectation:

$$17.25 : 0 : 22$$

Here the agreement is certainly good. The 3-factor theory emerges better from this sub-proof than from the proof-general already considered.

Since the behaviour of partially and completely awnless forms is so erratic, more ample information is desirable for nothing is said as to the numbers of plants in the F_3 families, nothing is said as to the existence of tiller to tiller fluctuations and but little is said as to plant to plant fluctuations in a genetically uniform population. Dominating all these considerations is yet another—personal bias. In respect of this, investigators doubtless differ; but in the handling of a considerable number of F_2 's and F_3 's involving different awn types it has never been possible to remove the fear of "bias." No method of check—e.g. by co-variant characters, such as might be based on an exact knowledge of the homology of the awn—has so far been devised to vindicate awn-sorting by eye. Safety rests only in very large numbers. That 4 plants (no more and no less) out of 321 breed true to the awn-characters of one of the parents is, in view of the circumstances which have been alluded to, a most difficult decision to make even if all four gave large F_3 families.

v. Ubisch(10) has worked very extensively upon the inheritance of barley awns. Comment has been made in a previous paper (Engledow(1), p. 102) upon the recognition of palea types such as "Spitz," and "Spitz verlängert." Paragraphs III and IV of his (v. Ubisch) paper deal respectively with the inheritance of beard-length and the "korrelation" (in the sense of coupling or linkage) between density of ear and beard-length.

In his own words, beard-length is thus defined: "Als Grannenlänge ist hier die Differenz Ähre mit Granne—Spindellänge bezeichnet." That is to say the length of the beard is judged by the greatest amount of protrusion of any one of its constituent awns beyond the tip of the rachis (Spindel) of the ear. How profoundly the density of the rachis is responsible for this amount of protrusion has been explained already. The data of v. Ubisch consist entirely of "protrusion" measurements. Not to observe the three variables obviously concerned—lengths of individual awns, rachis length, and number of internodes of the rachis—seems an indirect treatment of the problem. A "korrelation" (coupling) is established between density of rachis and beard-length, but it is perhaps a justifiable comment that since beard-length depends to some extent

upon rachis-density something in the nature of a correlation is almost bound to be observed between these two variables. In the absence of data of parental, F_1 , F_2 and F_3 rachis characters, further examination of the results is impossible.

§ III. SOME EXPERIMENTAL RESULTS ON THE INHERITANCE OF THE AWN IN BARLEY.

The results to be described are all derived from a series of crosses of various "awned" barleys with "Inerme." Although raised primarily for plant-breeding purposes, the F_1 's, F_2 's and F_3 's have been utilised as far as possible for genetic observation. In many cases it has not been possible to raise a complete F_3 , for every such F_3 (containing 5-8000 plants) involves a great deal of work and there were 27 complete F_2 's to be considered. The F_3 growings—partial and complete—were arranged so as best to meet, within the limitations of available time, the requirements of both plant-breeding and genetic experiment. It is clearly explained in every cross dealt with below, whether the evidence is that of a partial or a complete F_3 . The F_2 results in all cases are derived from complete F_2 's. In harvesting all the F_2 's every tiller of every plant was gathered, a separate bunch of ears was thus made for every plant. Thus all possible precautions were introduced to counteract the danger of the misleading "tiller to tiller" fluctuations.

The crosses fall into groups characterised by the botanical classes of the awned parents and the results are recorded under these groups.

GROUP I. *H. HEXASTICHUM* (AWNED) $\times$ INERME.

Cross E. 30 = *H. hexastichum* (var. Praecox) $\times$ Inerme.

Praecox is a lax-eared 6-row and in other characters connected with the awn and lateral floret it appears to be typical of the *H. Hexastichum* class. Inerme has been fully described in § I (above).

F_1 = 14 plants. The awns of the median florets were of about "half-length" so that none of their tips protruded much above the level of the tip of the rachis of the ear. The lateral florets were occasionally fertile (i.e. they set a grain), there being one or two such fertiles on every ear. All the F_1 plants appeared to answer the above description and no more precise account of awn characters was possible. The grain from eight of the fourteen plants was sown—the remaining plants being kept for reference—and in the tables below these plants are designated E.30.A, E.30.B, ... E.30.H.

F_2 = 688 plants. Repeated independent sortings were made, every plant, however small and poor, being included. The results of the repeated sortings did not agree. Quite clearly, if a number of awn-types existed, the eye was unable to detect them with certainty. Only one classification led to consistent results on repetition—that of (α) plants in all respects resembling the parent *Praecox* and (β) plants not resembling it. The latter class contained many degrees of awn and lateral floret form. If the classes be designated 6-row and non-6-row the results may be thus expressed:

Table I. $F_2.E.30$.

	6-row		Non-6-row		Total
	Number	%	Number	%	
Observed	164	23.84	524	76.16	688
Expected (1 : 3 basis) ...	172	25.0	516	75.0	688
Actual errors	—	1.16	—	1.16	—
Standard error of expectation ¹	—	1.65	—	1.65	—

Full-length awns appeared to be present only in plants of 6-row type; and plants which set six rows of grain appeared always to have full-length awns. It is, therefore, concluded from the F_2 evidence that the two characters, (i) six rows of grains set on the ear, (ii) full-length awns, are controlled together and that the control is unifactorial (the above 3 : 1 ratio is statistically satisfactory). No further deduction could be made from the F_2 since the two-fold classification was alone possible.

Of the 688 F_2 plants, 522 provided a reasonable amount of grain likely to be germinable. Owing to loss by wire-worm only 505 F_3 families were finally raised and harvested.

F_3 = 505 families. These families were sorted into three classes, viz.:

(α) All plants in the family fully awned. The plants proved to be all of parental *Praecox* (6-row) type.

(β) Families showing segregation for the awn. 6-row type, *Inerme* type, and partially bearded types with laterals of varying forms were found in these families.

(γ) All plants as "awnless" as the *Inerme* parental form.

¹ The standard error is thus calculated. Let p and q be the expected percentages (here = 25 per cent. and 75 per cent.) and n = number of observations. Then standard error of expectation as a percentage = $\sqrt{\frac{p \cdot q}{n}}$. The probable error is, of course, obtained by multiplying the standard error by 0.6745.

The results of the sorting are contained in Tables II and III.

Table II. $F_3.E.30$.

F_1 progenitors of F_3 families	Classification of F_3 families			Total
	(α)	(β)	(γ)	
$E.30.A$	18	47	17	82
$E.30.B$	10	34	9	53
$E.30.C$	23	42	19	84
$E.30.D$	6	17	13	36
$E.30.E$	15	36	21	72
$E.30.F$	22	42	24	88
$E.30.G$	11	12	7	30
$E.30.H$	15	29	16	60
Total	120	259	126	505

Table III. *Résumé of Table II with errors, etc.*

	Pure 6-row families i.e. (α)		Splitting families i.e. (β)		Pure Inerme families i.e. (γ)		Total
	Number	%	Number	%	Number	%	
Observed ...	120	23.76	259	51.29	126	24.96	505
Expected (1:2:1 basis) ...	126.25	25.00	252.50	50.00	126.25	25.00	505
Actual errors ...	—	1.24	—	1.29	—	0.04	—
Standard errors of expectation* ...	—	1.93	—	2.22	—	1.93	—

* See footnote to p. 166 (above).

Since the classification of 505 F_3 families is equivalent to that of an equal number of F_2 plants, it is concluded that the F_3 results support those of the F_2 . There is a one-factor difference for "awn" between Praecox and Inerme.

Discussion of the significance of the apparent inseparability of (i) 6 rows of grains set on the ear, and (ii) full awns, is postponed to § VI below, where data are given concerning the lateral floret types of this cross. Meantime the requirements of statistical safeguards have been provided (see Table III) and the one-factor awn may be accepted.

Cross $E.28 = H. hexastichum$ (v. parallelum) $\times$ Inerme.

Parallelum is a dense-eared 6-row barley.

$F_1 = 5$ plants. Like those of $F_1.E.30$ described above, the ears were "half-awned" in the median florets and awnless in the laterals.

$F_2 = 235$ plants. As in $F_2.E.30$ (above) a two-fold classification was all that could be performed consistently. Results were obtained as set forth in Table IV.

Table IV. $F_2.E.28$.

	6-row		Non-6-row		Total
	Number	%	Number	%	
Observed	55	23.40	180	76.60	235
Expected (1 : 3 basis)...	58.75	25.00	176.25	75.00	235
Actual errors	—	1.60	—	1.60	—
Standard error of expectation*	—	2.82	—	2.82	—

* See footnote to p. 166 (above).

Thus, again, a unifactorial awn-difference between a 6-row barley and Inerme is indicated. Again, too, the 6-row habit and the full-awn habit prove to be inseparable.

F_3 = partial only (for strong-strawed types).

GROUP II. *H. INTERMEDIUM* × INERME.

Cross $E.37 = H. intermedium$ (var. Haxtoni) × Inerme.

Haxtoni is a typical "intermedium" barley (see § I above) with a lax ear [i.e. median florets fully awned, laterals usually setting grain, but with blunt ended outer paleae].

F_1 = 10 plants. The awns of the median florets were of "half-length," being never more than 2-2.5 ins. in length. The lateral florets were, without exception, quite awnless.

F_2 was an unsortable complex. Many of the plants were imperfectly developed and very considerable tiller-to-tiller (same plant) fluctuations were found. In a few cases, very late tillers had lateral florets whose outer paleae bore short awns. Of the total F_2 579 plants provided seed.

F_3 = 558 families (from 579 separate sowings). Disregarding the lateral florets—they are fully described in § VI below—the families were sorted into three classes, viz.:

(α) All plants in the family fully awned.

(β) The plants of the family showing "splitting" for awns (three types of awn were seen, viz.: full awns as in Haxtoni, half-awns [various, but not separable degrees of awning], and awnless like Inerme).

(γ) All plants in the family as awnless as Inerme.

"Full-awn," "half-awn," and "awnless" types are shown in Figs. VII, VIII and IX respectively.

Tables V and VI give the results of the sorting:

Table V. F_3 . E . 37.

F_1 progenitors of F_3 families	Classification of F_3 families			Total
	(α)	(β)	(γ)	
E . 37. A	19	36	25	80
E . 37. B	18	53	29	100
E . 37. C	35	78	34	147
E . 37. D	15	33	14	62
E . 37. E	11	20	6	37
E . 37. F	10	27	7	44
E . 37. G	25	36	27	88
Total	133	283	142	558

Table VI. *Résumé of Table V with errors, etc.*

	Families with full awns (α)		Families splitting for awn (β)		Families of Inerme type (γ)		Total
	Number	%	Number	%	Number	%	
Observed ...	133	23.83	283	50.72	142	25.45	558
Expected (1 : 2 : 1 basis) ...	139.5	25.00	279.00	50.00	139.5	25.00	558
Actual errors ...	—	1.17	—	0.72	—	0.45	—
Standard errors of expectation* ...	—	1.83	—	2.11	—	1.83	—

* See footnote to p. 166 (above).

Again, with statistical security, it may be said that the parent types—Haxtoni and Inerme—differ in respect of awn by one factor. By growing a complete F_3 it has been possible to establish the existence of segregation in F_2 on a 1 : 2 : 1 basis.

Between this cross and those described under Group I (above) an interesting difference exists. "Full awns" are not here inseparable from six rows of grain on the ear (i.e. from six rows as exemplified by the *H. intermedium* type of barleys). Quite definitely there occur plants having six rows of grain ("intermedium" pattern), but entirely devoid of awns. Such (F_2) plants breed true in F_3 . Further details are reserved to § VI below.

GROUP III. *H. DISTICHUM* (AWNED) $\times$ INERME.

For this group it was not possible, owing to restrictions upon time, to raise any complete F_3 's. The evidence is consequently less full than in the case of Groups I and II above.

Cross E . 31 = Russian Chevallier No. 6 $\times$ Inerme.

The Chevallier parent is typical of the well-known variety of which the most noticeable features are the lax ear and the woolly rachilla.

In other respects the variety is morphologically strictly comparable with the other kinds of the sub-variety "nutans" of *H. distichum*.

F₁ = 20 plants. The ears were even laxer than those of the Chevallier

parent. Awns were confined to median spikelets in the "lower quartile" part of the ear and they were only $\frac{1}{2}$ in.-1 $\frac{1}{2}$ ins. in length. All lateral florets were completely awnless.

F₂ = 631 plants and, for some unaccountable reason, sorting into awn types was comparatively a simple matter—in fact repetition gave consistent results. "Half-awned" forms seemed never to approach the full-awns and "Inermes" were definitely separable from the half-awns.

Table VII contains the results of the sorting, the classes being:

(α) Fully awned like Chevallier.

(β) "Half-awned," i.e. not so fully awned as (α)—an eye-judgment class, but in this cross, a practicably distinguishable one.

(γ) As awnless as Inerme.

Table VII. $F_2.E.31$.

	Fully awned (α)		Half-awned (β)		Inerme type (γ)		Total
	Number	%	Number	%	Number	%	
Observed ...	157	24.88	298	47.22	176	27.89	631
Expected (1:2:1 basis) ...	157.75	25.00	315.50	50.00	157.75	25.00	631
Actual errors ...	—	0.12	—	2.78	—	2.89	—
Standard errors of expectation* ...	—	1.72	—	1.99	—	1.72	—

* See footnote on p. 166 (above).

The errors here are far more considerable than in the cases recorded above, but even so, it may be remarked that, when the general fit (all three classes, α , β and γ) to expectation is tested by Pearson's χ^2 method (see (11) Table XII, p. 26) there proves to be a one in five chance of getting a worse fit by random sampling (i.e. by raising an F_2 of limited size).

F₃. A large F_3 was grown for plant-breeding purposes. In an indirect way it afforded further evidence for awn-inheritance. Batches of (α), (β) and (γ) F_2 plants were sown. Before harvest those F_3 families were destroyed which proved not to belong to the group (α), (β) or (γ) in which they were growing—the F_2 progenitors had, of course, been incorrectly classified. The remaining families—those from F_2 plants

which had been correctly classified—were harvested. The facts proved to be:

(i) Of the F_2 plants classified as fully awned, 119 were sown; but in six cases the F_3 family proved not to be homozygous for "full-awn." Thus the proportion of accurately sorted plants in F_2 was $(119-6)/119 = 113/119$. It may therefore be assumed that $113/119 \times 157 = 149$ F_2 plants were certainly of the full-awn type.

(ii) Similarly $\left(\frac{265-12}{265}\right) \times 298 = 285$ F_2 plants were certainly heterozygous for awn. [Their F_3 families contained all the types (α), (β) and (γ).]

(iii) Similarly $\left(\frac{133-27}{133}\right) \times 176 = 140$ F_2 plants were homozygous for the "awnless" character (i.e. of Inerme type).

Summarising, the results are as contained in Table VIII:

Table VIII. $F_2.E.31$ as classified by the F_3 .

	Fully awned (α)		Half-awned (β)		Inerme type (γ)		Total
	Number	%	Number	%	Number	%	
Observed ...	149	25.96	285	49.65	140	24.39	574
Expectation (1 : 2 : 1)	143.5	25.00	287.0	50.00	143.5	25.00	—
Actual errors ...	—	0.96	—	0.35	—	0.61	—
Standard errors of expectation* ...	—	1.80	—	2.08	—	1.80	—

* See footnote on p. 166 (above).

The reliability of the results is limited by the method of working (explained above), but, within these limitations, a one-factor difference for awn between Chevallier and Inerme is proved with satisfactory numerical exactness.

Cross $E.32$ = Russian Chevallier No. 7 $\times$ Inerme.

A complete F_2 was raised and sorted, results being as in Table IX.

Table IX. $F_2.E.32$.

	Fully bearded	Remainder	Total
Number	115	378	493
Percentage	23.3	76.7	—

No more detailed F_2 classification was attempted and in F_3 but twenty families were raised, these being the only selections possessing apparent economic value. As far as it goes, the evidence accords with that of Cross $E.31$ —a unifactorial effect is again indicated.

Cross *E.34* = Russian Goldthorpe No. 9 × Inerme.

This cross deserves to be placed on record for the reason that it furnished an instance of that neglected type of coincidence wherein are allied statistical security and error of inference. In the F_2 , sorting appeared to be a safe undertaking, giving the result:

	Fully awned	Half-awned	Inerme
$F_2 =$	226	224	181

Here, clearly, two or three factors had to be invoked. Factors *A* and *B* were entrusted with the duty of producing awns and factor *I* with that of awn-inhibition. As is common in multifactorial explanations, assumptions were made, viz.:

- (i) The awn is completely inhibited if *II* be present.
- (ii) *Ii* does not noticeably inhibit the awn if *AA* be present.
- (iii) *AA*, *Aa*, *BB*, and *Bb* produce full-length awns in the presence of *ii*.

The factorial representation therefore became:

F_0	Goldthorpe × Inerme (<i>AA.bb.ii</i>) (<i>aa.BB.II</i>)
F_1	Half-awned <i>Aa Bb Ii</i>
$F_2 = ii$	(<i>AABB</i> + <i>2AABb</i> + <i>AAbb</i> + <i>2AaBB</i> + <i>4AaBb</i> + <i>2Aabb</i> + <i>aaBB</i> + <i>2aaBb</i>) = 15
	= <i>2IiAA</i> (<i>BB</i> + <i>2Bb</i> + <i>bb</i>) = 8
	i.e. fully awned plants = (15 + 8)/64 = 23/64
	= <i>2Ii</i> (<i>2AaBB</i> + <i>4AaBb</i> + <i>2Aabb</i> + <i>aaBB</i> + <i>2aaBb</i>) = 22
	i.e. half-awned plants = 22/64
	= <i>II</i> (<i>AABB</i> + <i>2AABb</i> + <i>AAbb</i> + <i>2AaBB</i> + <i>4AaBb</i> + <i>2Aabb</i> + <i>aaBB</i> + <i>2aaBb</i> + <i>aabb</i>) = 16
	= <i>2Ii.aa.bb</i> = 2
	= <i>ii.aa.bb</i> = 1
	i.e. awnless plants = 19/64

The expectation is therefore:

	Fully awned	Half-awned	Awnless
$F_2 =$	23/64 = 35.94 %	22/64 = 34.37 %	19/64 = 29.69 %

Table X shows the observed results:

Table X. $F_2.E.34$.							
	Fully awned (α)		Half-awned (β)		Inerme type (γ)		Total
	Number	%	Number	%	Number	%	
Observed ...	226	35.83	224	35.49	181	28.68	631
Expected (theory ...							
above) ...	—	35.94	—	34.37	—	29.69	—
Actual error ...	—	0.12	—	1.12	—	1.01	—
Standard error of expectation ...	—	1.91	—	1.89	—	1.82	—

Statistically, therefore, the results are safeguarded.

Pressure of other work necessitated the growing of none but economically promising F_3 families. Three groups of families were raised—from F_2 plants sorted as fully awned, half-awned, and awnless respectively. That the F_2 sorting had been unreliable became at once apparent. Families that should have been homozygously fully bearded were splitting for awn and so on. The reason for the error is believed to be the influence on "beard appearance" of the density of the rachis—an influence which was not fully realised until the F_3 was handled. All F_3 families which were clearly "splitting" for awn were put together and sorted plant by plant. Two types of beard were recognised: (α) , $[(\beta) + (\gamma)]$ of Table X, and a sorting on this basis gave:

$$\begin{array}{rcl} (\alpha) & : & [(\beta) + (\gamma)] \\ 68 & : & 195 = 1 : 3? \end{array}$$

The numbers are small but in the past even smaller ones have established a "ratio"; they serve, at any rate, to refute the *ABI* theory for which the F_2 so accurately vouches.

The facts of this singular case are published solely as an illustration of the dangers which may attend the genetic investigation of what the human eye is sometimes satisfied to accept as a "plant-character."

Cross *E.41* = Plumage $\times$ Inerme.

Plumage is a popular cultivated form of the broad-ear (dense rachis) type of *H. distichum*.

The F_3 was treated in the manner described under Cross *E.34* above with the result:

$$\begin{array}{rcl} (\alpha) & : & [(\beta + \gamma)] \\ 40 & : & 121 \end{array}$$

[The numbers are of single plants in F_3 families which were clearly "splitting for awn."]

Here, again, is an indication of unifactorial difference for awn between an ordinary *H. distichum* barley and Inerme.

The derivation of Inerme in itself suggests this unifactorial difference. Rimpau's cross (described in § I above) may be represented:

$$\begin{array}{c} \text{Hooded 6-row} \times \text{Awned 2-row} \\ (AA\ bb) \mid (aa\ BB) \\ \hline F_2 \text{ contains } aa.bb = \text{Inerme} \end{array}$$

The existence of an awnless 6-row, "Nogenasi," (see Ikeno(8) and § I above) is of interest. For the "removal" of awns in 2-row barleys a

cross between "hooded" and "awned" forms proved to be necessary. Unless a hooded barley occurs in Japan and out-pollination of barleys is possible there, "Nogenasi" is, perhaps, to be regarded as a "mutation."

§ IV. SOME GENERAL CONCLUSIONS UPON THE INHERITANCE
OF THE AWN IN BARLEY.

The general conclusion from the experimental evidence which has been recorded is that the presence of a full-length awn is due to the homozygous presence in the plant of one factor: the intermediate or half-awn corresponds to the heterozygous presence of the factor; the absence of the awn to the absence of the factor. Between this conclusion and those of v. Ubisch and Ikeno there is the wide distinction of unifactorial as opposed to bi- and tri-factorial constitutions. That there exists a considerable range of apparent awn-forms may be regarded as *prima facie* evidence of multifactorial arrangement: but against this must be urged the certain existence of pure fluctuation. Figures I and III illustrate small extracts from a large and well-tried mass of similar material exemplifying fluctuation of the awn. In so far as the usual statistical safeguards are a guarantee of reliability the unifactorial explanation is acceptable, but Cross *E*.34 (p. 172 above) makes it clear that fluctuation may, at times, conspire with statistics to mislead the investigator. It is to be noted that there is, save in Cross *E*.31, a constant small defect of the "fully awned" type. In amount the defect is not great enough to transgress the bounds of latitude allowed by "error due to random sampling," but it may nevertheless indicate an order of coupling which is so high that the single 1 : 2 : 1 ratio in F_2 is but little disturbed.

Confirmation of some kind is needed in the case of the awn where—as with many other plant characters—fluctuation compels the investigator to regard his statistically acceptable "ratios" with apprehension. Repetition of the investigation is unlikely to be helpful and some other form of confirmation has to be sought. It is well known that in some plants and animals, there exist a number of features any one of which might be—some actually have been—looked upon as separate plant-characters, but all of which are transmitted *en bloc* in inheritance. "Characters" of this kind may conveniently be called "genetic inseparables." Doubtless they are simply separate manifestations of one real "plant-character," of a single biological process. Examples of "genetic inseparables" have been recorded *inter alia* in oats [Surface⁽¹²⁾], in oats [Zinn and Surface⁽¹³⁾], in wheat [Engledow⁽¹⁴⁾], and in barley [Engle-

dow⁽¹⁾). In *Drosophila* the same phenomenon is well exemplified, and Morgan and his collaborators [(15) pp. 209 *et seq.*] have already emphasised its importance. If in the case of the awn in barley some character could be found which stood in the relation of a genetic inseparable, the behaviour of that character could be observed in order to test classifications based upon awn-forms. Considerable effort has been expended in the search for a character inseparable from the awn, but so far nothing has been found. It may be that such a one does not exist; but it may equally be simply that the search has been misdirected. Physiological anatomy should direct a search of this kind, but as far as the cereals are concerned this is a very neglected subject, having, in fact, scarcely reached its infancy. An appeal to pure morphology may be made to determine to what organ or kind of organ the awn is homologous, for in this way the search for a genetic inseparable (and therefore a co-fluctuant) of the awn might be approximately orientated. The view of Hackel⁽²⁾ upon the homology of the awn seems still to enjoy general acceptance. He opined that the awn corresponded to the lamella of the ordinary foliage leaf, the outer palea similarly being a modified leaf-sheath. It is well known that the awn has chlorophyll tissue, vascular bundles and stomata—features which are common not only to foliage leaves in general, but to herbaceous stems in general as well—and it has been demonstrated that the combined awns of a barley plant perform a large proportion of the total transpiration of the plant [see Zoebl and Mikosch⁽³⁾, Schmid⁽⁴⁾, and Perlitus⁽⁵⁾]. Against this somewhat general evidence for Hackel's leaf-homology is that derivable from the "trifurcate" barleys. In them the awn is in the form of a "hood" inside which may be a flower. Perhaps, therefore, there is more justification for regarding the awn, not as a modified leaf blade, but as part of a modified stem. The outer palea may similarly be regarded as a leaf-like stem [similar to those in the familiar cases of *Lemna* sp., *Ruscus aculeatus*, *Semele* (*Ruscus*) *androgyna*, etc.].

It thus appears that although wide fluctuation makes it indispensable either to discover some co-fluctuant of the awn or so to understand its botanical significance that the fluctuations may be interpreted, yet the means to both of these ends are at present lacking. The conclusion is therefore drawn that, although unifactorial inheritance is quite probable, there should be further investigation upon awn inheritance. Such investigation should deviate from the familiar path of eye-sorting of F_2 's and F_3 's and strike out upon the comparatively untrodden one of physiological anatomy.

§ V. THE LATERAL FLORET IN BARLEY CONSIDERED
AS A GENETIC CHARACTER.

Throughout the genus *Hordeum*, one type of inflorescence prevails. The "ear" is formed on a central rachis of flattened cross section and alternating up the two broad sides of this are "notches" or "nodes." Grouped at every node are three spikelets, so that the ear has six rows of spikelets. Every spikelet consists of two small glumes (in a few exceptional cases these are fused into one), inner and outer paleae, a rachilla, and sexual organs. The spikelet invariably contains only one flower. In all barleys (save *H. sylvaticum*, noted below) the median florets—i.e. the two rows which are placed one along the middle of each of the broad sides of the rachis—are large; they set large, well-filled grains. The lateral florets—i.e. the remaining four rows which are obliquely placed at the sides of the median rows—possess a very wide range of forms in the different species and sub-species. In *H. hexastichum* (see § I above) the laterals set grains, but these never attain the size of the median grains and are readily detected by the slight "twist" which they show. Like the medians the lateral florets possess an awn (or hood) on the outer palea. The *H. intermedium* barleys are capable of setting grains in their lateral florets, but not of bearing an awn. Actually, the percentage of grains set by the lateral florets in *H. intermedium* varies with the growing conditions. All other cultivated barleys and all wild ones save *H. sylvaticum* have lateral florets incapable (in general) of setting grains. The various forms of *H. distichum* and *H. decipiens* exhibit a series of different sizes and developments of the lateral floret. Hybridisation adds to this series. In a previous paper [Bibliography(1), pp. 98–100] there is an account of the types commonly found and Körnicke (16) describes in great detail the usual structure and many of the observed abnormalities of lateral florets. One of the wild barleys, viz. *H. sylvaticum* is unique in possessing small medians and large, fertile, laterals.

It is generally assumed that the lateral florets of those barleys whose medians alone set grains, are deficient in female reproductive organs only (*H. distichum*) or in both male and female (*H. decipiens*). Lateral florets of the size found in *H. distichum* (or the slightly larger more pointed forms of certain heterozygotes) are commonly assumed, wherever found to be staminate only: the extremely small laterals which characterise *H. decipiens* forms are likewise assumed to be entirely sexless. Size is, in fact, supposed to indicate stage of development of reproductive organs. This is a questionable supposition and the exceedingly puzzling

problem of "inheritance of lateral florets" is not likely to be solved without an attempt to separate "size" from "sexual development" in making observations. It has become quite clear that the sexuality of lateral florets cannot be properly studied without a detailed cytological investigation of the ear in successive stages of development. In the investigations here recorded a certain measure of success has attended the endeavour to distinguish "fertility" and "size" as separate characters but only by cytological study will final results be obtained. In, for example, "Archer" barley (a common cultivated form of *H. distichum*) stamens are certainly present and surrounded by the bases of their filaments is a small "organ" which nothing but careful sectioning can prove or disprove to be an ovary. The assumption that Archer laterals are staminate only, rests entirely on the quite unreliable judgment of the naked eye.

In attempting to classify the plants of an F_2 or the families of an F_3 (an F_3 family implying, of course, the progeny of a single F_2 plant) consideration has to be given to both size and general evidence of potential fertility of the lateral florets. The circumstances vary with the individual crosses concerned and in the paragraph of experimental results which follows, an account is given in the case of every cross, of the basis of judgment which was adopted.

The lateral florets of "Inerme" must be described since that form was one of the parents in all the crosses concerned. These laterals are in some respects unique. Their most noticeable feature is the relatively great length of their glumes [see Fig. V], whose actual "tips" (excluding the short "glume-awns") attain the level of the tip of the reduced outer palea. In other barleys [e.g. Haxtoni in Fig. VI] the glumes of the lateral florets are much shorter in relation to the size of the outer paleae. Inerme may, in fact, be said to possess "long" lateral-floret glumes, whereas most at any rate of the other barleys have short ones. Usually, the outer palea of the lateral floret is small, shrivelled and of "decipiens" type, but, at times, it attains a very considerable size and may even become fertile. In an ordinary growing, a very small proportion of ears is found among whose lateral florets—perhaps in three or four cases per ear—large size or even fertility is achieved. On such an ear the remaining lateral florets are usually quite normal (i.e. they have the usual reduced outer paleae).

"Fluctuation" among lateral florets is considerable in all crosses [cf. Engledow(1)], but it reaches a most acute stage in crosses of which one parent is "Inerme." In order that the difficulties may be realised

and that there may be no misapprehension as to the susceptibility of such investigations to error, an account is given of some of the more extreme cases of fluctuation. Harlan and Hayes⁽¹⁷⁾ have already recorded a case of lateral floret fluctuation. The photographs here published (see plate) need little comment:

- Fig. I { (a) = one ear of an F_2 plant; laterals very reduced.
 (b) (c) (d) = ears from plants of the F_3 progeny. In (d) the laterals resemble (a), in (b) they are somewhat larger, while in (c) [a late ear from an F_3 plant] many of them are fertile. (a) is a type which usually "breeds true," being in fact the "semi-decapiens" type which is characteristic of "Inerme."
- Fig. IV { (a) and (b) are ears from a single F_3 plant. In (a) median and lateral florets are both awned fully and fertile, while in (b) only the medians are awned and fertile. All the awns in both ears were removed to simplify the photograph. Thus on this plant one ear [(a)] presented the customary *H. hexastichum* appearance, while the other [(b)] simulated a typical *H. distichum*.
- Fig. III { (a) and (b) = ears from a single F_3 plant, (b) being from a very late tiller. Both its awns and its laterals are larger than those of (a).

The examples of fluctuation which have been photographed are, of course, extreme ones; but they indicate the nature of the phenomenon.

As in the case of the awn, so here, classification is a difficulty. The possibility of fluctuation must be borne in mind and the best safeguard against error is a wide experience of the range and nature of fluctuation in parent varieties and in their hybrid progeny. An F_3 family, even if it contains some late "fluctuant" plants, may be classified with fair confidence provided it is composed of not less than about six plants. Very small families are, as always, a danger—and some such families are bound to occur.

§ VI. VIEWS UPON THE INHERITANCE OF THE LATERAL FLORET IN BARLEY.

Some observations upon this subject have been made in a previous paper [Bibliography⁽¹⁾, pp. 102–108]. Since then has appeared an interesting publication by Harlan and Hayes⁽¹⁷⁾ in which is given evidence of the existence of two factors for the lateral floret [a two-factor difference between a *H. hexastichum* (of the vulgare kind) and a *H. distichum*]. The authors state (p. 578) that "Fertility is a definite, tangible, measurable condition..." They recognise classes of fertility which are characterised by certain percentages of fertile to total lateral florets on the ear, e.g. 0–79 per cent. and 80–100 per cent. in one division and 0 per cent., < 5 per cent. and 5–100 per cent. in another division. In

(a)

(b)

(c)

(d)

Fig. I

(a)

(b)

Fig. II

(a)

(b)

Fig. III

(a)

(b)

Fig. IV

an English climate Haxtoni (one of their parental forms) and the segregates from its crosses show such extreme fluctuation that percentage-fertility classes would be quite impracticable. It is almost certain that in a large F_2 of a Haxtoni cross there could be found some healthy plants any one of which would have tillers, exhibiting such divergences of percentage lateral fertility as would warrant the inclusion of the plant equally in any of three or even four such classes. The tendency to bring into existence such "mathematical" plant-characters for which there is no *prima facie* biological guarantee, appears to be dangerous. It has often led to elaborate investigation, the result of which has been a negative one [cf. Collins(18) and observations upon this reference in § IX, below].

Particularly perhaps in the case of lateral-floret fertility in barley, it seems undesirable to employ artificial "mathematical" characters without first carrying out a statistical investigation to vindicate the biological significance (tantamount perhaps simply to the constancy) of the numerical limits by which such characters are defined.

Despite the closeness of observation to expectation which the authors found, fluctuation was not absent as the following sentence shows: "Group 7 may be considered as composed of plants homozygous for 2-rowed, since with the exception of the two plants noted there was no fertility exhibited in the progeny." The F_2 numbered 87 plants and of these 5 fell into Group 7. It was in the F_3 progeny of one of the 5 (i.e. 20 per cent. of the whole) that the two aberrant plants were found. To demand that there should be no aberrants from a character so full of vagaries as the lateral floret, would seem like demanding the impossible; but the precision of sorting which differentiates between 0 per cent. and < 5 per cent. or between < 5 per cent. and 5-100 per cent. depends for its very existence upon a most strict observance by the plants of the prescribed limits.

§ VII. SOME EXPERIMENTAL RESULTS UPON THE INHERITANCE OF THE LATERAL FLORET IN BARLEY.

From data already published the conclusion has been derived that the four common types of lateral floret—those which characterise the four main groups, *H. hexastichum*, *H. intermedium*, *H. distichum* and *H. decipiens*—form a series of "multiple allelomorphs" or "alternative allelomorphs." Any two members of the four, when crossed, give an F_2 in which 1 : 2 : 1 segregation is shown. Crosses of members of these four types with Inerme, allowed a considerable body of F_2 data to be ob-

tained. This was withheld because wide fluctuation in both awn and lateral floret rendered the raising of F_3 's imperative. There was ground, too, for supposing that to some extent the fluctuations in these two characters were associated. The F_3 's—some partial and some complete—have now been raised and the results to be given are based upon them.

GROUP I. *H. HEXASTICHUM* × *INERME*.

Cross *E.30* = *Praecox* × *Inerme*.

It has been explained in § III above that the F_2 of this cross gave a ratio of fully awned to other types of 1 : 3, and that the F_3 families served to classify the F_2 plants thus:

(α) Plants indistinguishable from *Praecox* (the 6-row parent).

(β) Plants heterozygous for awn factor.

(γ) Plants as awnless as *Inerme* itself.

Moreover (α) : (β) : (γ) = 1 : 2 : 1.

An endeavour was made to detect different types of lateral in (α), (β) and (γ) respectively. The results were:

In the F_3 families of type (α) all the plants were like *Praecox*, the lateral florets always set plump grains and bore awns. Thus, in this case, the awn and the full fertility of the lateral floret appear to be inseparable. Possibly there were slightly different size-types in the laterals of the plants of this group, but the closest scrutiny failed to effect consistent sorting. It may be that there segregated—quite independently of the presumed awn-cum-fertility character—a purely morphological character which affected the size or shape of the outer palea of the lateral floret.

In the F_3 families of type (β) were three kinds of plant. The first was apparently identical with the *Praecox* (6-row) parent in both fertility and awn of the laterals; the record was best covered by the general designation "half-awned." This record type displayed a very big range of lateral floret forms, from "some florets of the ear fertile" to "all florets of the ear exactly like the 'normal' *Inerme*." Differences among the lateral florets of the same ear were in some cases extreme. The third kind—awnless save for the fluctuations which characterise *Inerme* itself—had in nearly all cases the "normal" *Inerme* lateral; but in a very few instances a fertile (grain setting) floret was seen, its companions upon the ear being "*Inerme*" in form. Thus it may be said that in this cross the absence of awn and the *Inerme*-lateral are apparently inseparable.

In the F_3 families of type (γ) some plants had most of their lateral

florets fertile, some had rather inflated but non-fertile laterals, some had all their laterals of normal *Inerme* form, and some had one (or two) fertile with the rest like the parental *Inerme*. The range of lateral-types was therefore greater than that shown by the "awnless" plants of the (β) families. It is difficult to suggest an interpretation of these results. To have attempted a classification based upon percentage of fertile laterals per ear would have led to no useful result for there was a whole range of sizes of non-fertiles. Perhaps the simplest explanation—purely hypothetical—is the one that, as sorting proceeds, thrusts itself upon the attention, viz. that the lateral florets of "*Inerme*" type are potentially fertile but that some morphological or possibly physiological condition presents the manifestation of the potentiality. This condition must, of course, be presumed to be linked with awnlessness and it must further be assumed that in the cases of certain florets the inhibiting condition is imperfectly developed so that these florets are able to set grains. Possibly two such inhibiting factors are involved. They may segregate independently and the awnless plants [members of (γ) families] which have a considerable proportion of their laterals fertile may have some specific genetic constitution in regard to the second of these hypothetical factors. Speculation such as this is, of course, rather primitive and not at all likely to lead to a furtherance of real knowledge; but it is the only form of speculation which is at present applicable despite the fact that a complete F_3 has been raised (containing some 4000 plants). Even were the formidable task of a complete F_4 undertaken, the hope of finality would still be very small. Here, as in the case of many other "eye-characters," a simple lesson is plainly pointed. The raising of successive generations and sorting by eye should be discontinued until the "eye-character" can be displaced by some positively observable character which, whatever its outward significance, has a real significance in the make up or functioning of the living plant.

A point of some interest remains. In all the crosses recorded in § III above, save one, there is a defect of the fully awned type as compared with 1 : 3 expectation. As already explained the defect is always too small to be statistically significant, but it may imply a very high coupling. If fertility of laterals (regular fertility as in *Praecox*) be not genetically inseparable from, but simply highly coupled with, full awn, a small percentage of fully-awned 2-row plants should appear. Such plants have never appeared in the F_2 's of 6-row $\times$ *Inerme* crosses, which have so far been bred, but in the F_3 of cross *E.30*, three such plants have been observed. They have typical distichum laterals and very lax

ears. So few in number (3 in 4000), so lax in rachis, and so completely unexpected (the type has long been sought in similar F_2 's and F_3 's), they arouse fears of an error (although past experience gives every confidence) in the methods of sowing, etc., employed. The full data of the cross, the existence of these "awned 2-rows," etc., has been recorded here because it is felt that a repetition of the cross on the lines already followed cannot lead to more precise results. To guard against possible errors and to allow an opportunity for the re-appearance of this rare type it is intended to raise an F_4 of 2000 families from the seeds set by plants of the (β) families.

Cross $E.28 = \text{Parallelum} \times \text{Inerme}$.

This cross has a general similarity to $E.30$ (just described) except that Parallelum has a denser rachis than Praecox. In the F_2 it was impossible to effect a consistent sorting of lateral floret classes and only a partial F_3 was raised (plant-breeding selections only). An interesting feature of the F_3 was that in the families bred from F_2 plants homozygous for "awnlessness," the laterals were all of "normal" Inerme type. This contrasts rather markedly, of course, with the case of Cross $E.30$, where deviations from the "normal" Inerme were found in corresponding families. Segregation of "density of rachis" evidently occurred and, in particular in awnless forms, rather curious shapes of ear resulted. Two or even three factors may have been involved in the production of these degrees of "rachis-density" (or differently regarded, of "ear-shape"), but to have sought to establish their existence would have been to add one more series of difficult "eye-judgments," and the endeavour was abandoned early in the investigation.

The form of cross considered in this group— $H. \text{hexastichum} \times H. \text{distichum}$ (in the above crosses, $H. d. \text{Inerme}$), has been made many times by a number of investigators. Until Harlan and Hayes(17) published their results it was accepted as a fact that the $H. \text{intermedium}$ form did not appear as a homozygote in the F_2 's of such crosses. These two authors found that in some cases the homozygote $H. \text{intermedium}$ did appear in the F_2 of the Hexastichum $\times$ Distichum cross; in others it did not. They consequently postulated *inter se* differences of the Hexastichum forms used as parents in the crosses.

Surprise is expressed that neither von Tschermak nor Biffen found homozygous $H. \text{intermedium}$ forms in the F_2 's of any of their numerous crosses of $H. \text{hexastichum} \times H. \text{distichum}$. It may well be that the very great fluctuations of the lateral florets allowed the homozygous "inter-

mediums" (if such did occur) to escape observation. Some crosses belonging to the same category have been described in a previous publication [Engledow⁽¹⁾, p. 100]. One of them, viz. *E.43* = *Praecox* × *Archer* was grown to a complete F_3 in 1920 (over 500 families containing about 5000 plants). The degree of lateral floret fluctuation was so extreme that no consistent result was obtainable; but certainly no F_3 family occurred from which the conclusion was to be drawn that there had been F_2 plants homozygous for the characteristics of *H. intermedium*. That the further raising of F_2 's and F_3 's should be deferred until a better understanding of "fertility" of lateral florets has been gained, seems once more to be clearly implied.

GROUP II *H. INTERMEDIUM* × *INERME*.

Cross E.37 = *H. intermedium* (var. *Haxtoni*) × *Inerme*.

The F_1 plants had, in some cases, a small proportion of fertile laterals (i.e. with grains set); in others of the same year, all the laterals failed to set grains but were more inflated and more pointed than *H. distichum* laterals; there was a considerable range of fluctuation. From F_2 no evidence for lateral-floret inheritance was derived. F_3 was raised complete and was classified as already described [§ III, Group II, above] on an awn basis into groups of families, viz.: (α) with all plants fully awned; (β) "splitting" for awns; and (γ) with all plants as awnless as *Inerme*. The result was (α) : (β) : (γ) = 1 : 2 : 1.

The next step was to examine (α), (β) and (γ) one by one for types of lateral floret. It will be recalled that the glumes of *Inerme* are relatively long while those of *Haxtoni* are relatively short [see § V, above, and Figs. V and VI], and the first fact disclosed by the examination was that extent of awn and relative size of glume were associated. Full-awn forms¹, i.e. plants of the F_3 families constituting class (α) had the relatively short glumes of the *Haxtoni* parent; in class (γ), where the awn was absent, the relatively long glumes of *Inerme* were found; while in (β), in addition to plants resembling (α) and (γ), were "half-awned" forms with glumes relatively of "intermediate" length. No measurements of glume-length were made and the observed "association" of awn and glume-length rests solely upon eye-judgment.

Once this "association" had been confirmed it was possible to devote attention to the evidence of segregation in other lateral floret characters. The time-honoured standards of "fertility," as judged by the eye, were employed. These standards are necessarily broad and elaborate—they

¹ The awn of the outer palea of the median floret is the one implied of course.

must allow for the known facts of fluctuation, such as one fertile lateral on an ear which is otherwise absolutely "normal" *Inerme* in its laterals. In fact, as in all such cases, the standards are almost intuitive; they represent an intuition arising from extended observation. Fluctuation is so prevalent in work of this kind and so little understood that eye-judgment cannot conscientiously be described as reliable. It is with this proviso that numerical results are set forth (Tables XI and XII, below). The F_3 families of awn-group (α) [and similarly of (β) and (γ)] were placed in three classes thus:

I. All plants with laterals as fertile as those of *Haxtoni*.

II. The plants of three types, viz. *Haxtoni*, *Inerme* and an "intermediate."

III. All plants with laterals of the type of *Inerme* (i.e. normally very reduced but now and then one or two small grains set on an ear).

Attention must be called to another small matter before the results of the classification are detailed. Although classes I, II and III could be made in both (α) = full-awn and (γ) = awnless, the reduction of the outer palea of III was less marked in (α) than in (γ). It seemed, in fact, that just as awns seem to be associated with relatively short glumes, so they are associated with a tendency to a rather large outer palea in the lateral floret [independently of fertility in the floret]. Figs. (text) VII-IX illustrate the types found in this cross and from them the "associations" of characters here described are apparent.

The numerical results are given in Tables XI and XII, in which, as in previous tables, the letters *A*, *B*, *C*,... designate individual F_1 plants or their progeny, according to the context.

Table XI. F_3 families of Cross *E.37*.

F_1 progenitors	Awn-types									Total
	(α)			(β)			(γ)			
	Lateral florets			Lateral florets			Lateral florets			
	(I)	(II)	(III)	(I)	(II)	(III)	(I)	(II)	(III)	
<i>E. 37. A</i>	5	10	4	4	18	14	4	13	8	80
<i>E. 37. B</i>	6	8	4	18	25	10	9	11	9	100
<i>E. 37. C</i>	9	19	7	28	32	18	5	22	7	147
<i>E. 37. D</i>	4	6	5	9	14	10	4	6	4	62
<i>E. 37. E</i>	3	7	1	4	11	5	2	2	2	37
<i>E. 37. F</i>	1	4	5	7	14	6	2	3	2	44
<i>E. 37. G</i>	4	18	3	5	22	9	8	14	5	88
Total	32	72	29	75	136	72	34	71	37	—
Total	133			283			142			558

The frequencies in the table are those of F_3 families and, from what has been said above, it will be observed that they may equally be treated as the frequencies of the F_2 plants from whose seed the F_3 was raised. Table XII sets forth the errors of observation, etc.

Table XII. *Résumé of Table XI with errors, etc.*

	(a)			(β)			(γ)			
	(I)	(II)	(III)	(I)	(II)	(III)	(I)	(II)	(III)	Total
Observed numbers ...	32	72	29	75	136	72	34	71	37	558
Expected numbers (1 : 2 : 1 basis) ...	33.25	66.50	33.25	70.75	141.50	70.75	35.50	71.00	35.50	558
Observed percentages	24.06	54.13	21.81	26.51	48.05	25.49	23.95	50.00	26.05	—
Expected percentages	25	50	25	25	50	25	25	50	25	—
Actual errors (%) ...	0.94	4.13	3.19	1.51	1.95	0.49	1.05	0.00	1.05	
Standard error of ex- pectation* ...	3.75	4.33	3.75	2.57	2.97	2.57	3.63	4.19	3.63	

* See footnote on p. 166 (above).

Observation may be called fairly close to expectation on the 1 : 2 : 1 basis.

For the cross *H. intermedium* (var. Haxtoni) × Inerme the following conclusions are therefore indicated:

(i) Relatively short glumes and a relatively large outer palea in the lateral floret, are associated with a full awn in the median floret and conversely.

(ii) "Fertility" of the lateral floret segregates on a 1 : 2 : 1 basis.

(iii) Sorting into fertility classes is made possible only by making allowance for fluctuations, such as observation has shown to occur in the parent varieties.

The genetic constitution of *H. intermedium* (var. Haxtoni) must consequently be supposed to be radically different from that of *H. hexastichum* (for var. Praecox and var. Parallelum at any rate) for in the latter form "fertility" of lateral florets was shown to be either quite inseparable from the full awn or coupled (linked) with it to a very high degree.

GROUP III. *H. DISTICHUM* (AWNED) × INERME.

For this group no detailed observations upon lateral florets are available. Partial F_3 's were raised in four crosses, the *Distichum* (awned) parents of which were:

For Cross E. 32.	Russian Chevallier No. 7	—ear very lax (narrow)
E. 34.	Russian Goldthorpe No. 9	—ear very dense (broad)
E. 35.	Russian Goldthorpe No. 10	—ear very dense (broad)
E. 41.	Plumage	—ear very dense (broad)

From the complete F_2 's and the partial (plant-breeding) F_3 's the following facts have become clear:

(i) The lateral florets of fully-awned plants are never reduced like those of *Inerme*. In Cross *E.32* little range of size was shown in the fully-awned extracts, but in the other crosses (the awned parents of which were broad-eared) distinct differences appeared. Density of ear clearly segregated, and the denser the ear the larger the lateral florets. Plants whose ears were as dense as those of the awned-distichum parent had laterals of parental size; those with lax (narrow) ears had laterals of the same size and of the same general appearance as in the "narrow-eared" 2-row barleys such as *Chevallier* and *Archer*, etc.

One homozygously-awned F_3 family of *E.32* was unique in that two of its plants had about 20 per cent. of their lateral florets fertile. The significance of these plants must remain an open question. Nowhere else in Group III (F_2 's or F_3 's) were there found awned plants with any fertile laterals.

(ii) Among the plants belonging to homozygously awnless families the lateral florets were always of *Inerme* type, i.e. reduced (semi-decapiens) but with one or two becoming fertile per ear in a very small percentage of the total number of plants (exactly as may happen in the *Inerme* parental form itself).

(iii) Half-awned plants showed a wide range of lateral floret forms—never quite as reduced as in normal *Inerme* and rarely as large as in the awned parent.

(iv) Relatively long glumes—as in Group I and II—appear to be associated with the *Inerme* type of lateral and conversely.

Conclusions. (i)–(iv) show a general agreement with those derived from cross *E.37* (described under Group II above) except that, of course, they do not bear upon the question of the fertility, but only on that of the morphology of the lateral floret. The fact that glume, outer palea of the lateral floret, and awn of the median floret appear to behave as if governed by one and the same genetic factor is interesting. It does not, however, furnish a very helpful means of checking the form and fluctuation of any one of the characters by observation of the other two. For this, some much more profound botanical inter-relationship will have to be discovered.

§ VIII. SOME GENERAL CONCLUSIONS UPON THE INHERITANCE
OF THE LATERAL FLORET IN BARLEY.

The preceding paragraph is heavily loaded with close descriptions of anatomical features. This is inevitable for the elusiveness of the character has led to the observation of every other character which might be of assistance. Shorn of side issues the main conclusions are that "fertility" of the lateral floret segregates on a 1 : 2 : 1 basis. In *H. hexastichum* crosses it is inseparable from "full awn" whereas in *H. intermedium* crosses this is not the case. Relatively long glumes are inseparable from "awnlessness" and conversely; while, finally, dense-rachis is similarly inseparable from a large outer palea (lateral floret).

Setting aside as a "fluctuation" the occasional but rather striking fertility of isolated laterals on otherwise Inerme ears, there yet remain complications. In § VII (Group I) the possibility of a high coupling (linkage) between "awn" and "fertile lateral" has been indicated; the two plants showing some fertile laterals in an F_3 derived from *E.32* (Chevallier $\times$ Inerme) are quite beyond explanation at present; and, though not connected with Inerme crosses, the bi-factorial effects alleged by v. Ubisch⁽¹⁰⁾ and the production of *H. intermedium* in a hitherto unrecorded manner by Harlan and Hayes⁽¹⁷⁾, must be added to the list of lateral floret "complications." The suggestion that the four commonly recognised forms of lateral floret constitute a series of multiple (alternative) allelomorphs, while giving no assistance in the solution of the general problem, adds to its interest.

By some means, the problem must be solved and the future line of attack is a debateable question. Repetition of the methods which have been carried on for fifteen years by several independent investigators is certainly a last resort—but it is no more. "Fluctuation" has been the bar to success of the method in the past and must always so remain. To ascertain the cause of the fluctuations—the reasons for the observed responses to environmental differences—must be the first step: and this implies a knowledge of the exact histology of the various forms of lateral floret and of the physiological factors by which they are affected. Few, if any, of the floral arrangements in other plants are comparable to e.g. the ordinary distichum barleys in which, with unfailing regularity, six rows of florets come into existence, but two only, and these two placed in an unvarying position on the rachis, are able to set grains. No one has yet determined at what stage in the life cycle these laterals fail. Possibly their failure is due to no fault of stamens or ovaries. It

may be that the paleae are too small to afford room for the full development and functioning of the reproductive organs. Rough hand-sections of the rachis appear to indicate the possibility that there may be a deficient vascular supply to the lateral florets in the various 2-row barleys. A third possibility is that the laterals develop later (chronologically) than the medians of the same ear. Usually, the medians effect self-pollination, while still protected from wind, sun, rain, etc., by the leaf-sheath, so that at the time of emergence of the ear from the sheath the laterals (if later in development) may not yet be sufficiently mature to allow of self-pollination. Lacking the sheltered conditions under which the medians effect self-pollination, the laterals may in this way have infertility forced upon them. This third explanation is not likely to apply to the ordinary "distichum" barleys such as Archer, etc., but may possibly be correct in the case of forms which, like *Inerme*, have "occasional" fertile laterals. Anthony and Harlan⁽²⁰⁾ have conceived the idea of classifying lateral florets by the germinability of their pollen (in the laboratory), but have not yet attained decisive results.

These questions are some of a number which point out untried lines of investigation. Fifteen years covered by the close observations of a number of workers have led to discordant views upon the genetic constitutions of lateral florets and one is forced to remark that an attack along a new line seems to be essential. The work that has been done has served to reveal a fascinating genetic problem, but it would be regrettable if a corresponding amount of endeavour were squandered in unpromising repetition instead of being diverted to the more hopeful but neglected line of physiological-anatomy. It is not suggested that barley-laterals are unique in requiring this change of direction of genetic inquiry; the change would be beneficial in connection with many plant-characters—in particular the "multifactorial" characters—but perhaps the need is here emphasised with uncommon clearness by the history and results of past investigation.

§ IX. SOME CONSIDERATIONS ARISING OUT OF THE FOREGOING PARAGRAPHS.

A few brief sentences suffice to describe the essence of the experimental results contained in the foregoing paragraphs. Some new 1 : 2 : 1 ratios have been established and their simplicity is out of concord with certain earlier findings of similar investigations. Fluctuation has been proved to be a serious obstacle, its limits of range have been explored, but its causes and significance have remained a mystery. In fact, the

investigations—both those recorded here for the first time and those published earlier and here reviewed—have yielded a tangled mass of observations from which may be gleaned certain interesting genetic conclusions. The conclusions are—in the main—genetic ratios, ratios which testify, as did Mendel's first ratios in 1865, to the occurrence of an ordered "segregation" of inheritance factors. This review of experimental results applies in full to many other of the numerous series of genetic records which have been published since 1900 but it is, perhaps, particularly applicable to the awns and lateral florets of barley for these are among the best known and best tried of the "genetic" plant-characters.

It is impossible, after weighing these facts, to evade the questions "What is the value of a continuance of this repeated establishment of 3 : 1 and other ratios?" and "Is sufficient attention being given to the raising of a superstructure on the foundation constituted by these ratios?"

At the outset, it must be made clear that these questions are looked upon as in no need of an answer in the case of those lines of investigation which relate to "Reduplication" (Linkage), "Gametic Contamination," "Multiple Allelomorphs" and all kindred phenomena, for investigations such as these have a definite goal beyond the mere establishment of "ratios." Much effort continues to be devoted, however, to experiments which terminate—and many experiments do so terminate—in further "ratios" and in nothing more. It is in connection with this kind of experiment that the above questions seem thoroughly pertinent.

There is, undoubtedly, a growing tendency to select as "experimental characters" those which are of some economic importance and in attempting to vindicate repeated "ratio" experiments it is best, perhaps, to consider first the economic value that such experiments have had in the past and their possible future worth. More than a century before Mendel made his first cross, Robert Bakewell of Dishley had begun to improve British live-stock by carefully regulated breeding. Plant-hybridisation, though it remained for so long the speculative study of men such as Kölreuter, Knight, Herbert, v. Gaertner and Noudin was definitely and successfully brought to the assistance of Agriculture by Farrar in Australia and by the brothers John and Robert Garton in England. These last-named commenced their hybridisation work in 1880 and from that time onward they and their colleagues (at the present time Garton's Ltd., of Warrington) have continued to put new cereal varieties on to the market. A popular account⁽¹⁹⁾ of plant-

hybridisation, written in 1900, explains the procedure of the raising of new varieties in vogue in the year which brought Mendel's discovery out of obscurity. To employ a great number of widely different parents in the making of crosses and by eye-judgment and trial to select the most valuable plants of the progeny—this was the method then in use and, when the bare fact is exposed, it is the one still in use. Although eye-selection remains the prime agent, there has been a very marked change in outlook. Twenty or so years ago there prevailed an unaccountable optimism which held that if far-removed forms—the further the removal the better—were crossed in a great number of different combinations, then “discoveries,” “the ideal yielder,” the “ideal disease-resister” and so on *must* be made. Such would appear as the treasures among a huge dross of “types.” The advent of the scientific plant-breeder cast away this baseless optimism and in its place installed the principle that parents must be selected for their known specific values. For example, it was argued that to produce a “strong” wheat from a cross, it was essential to use “Fife” as one parent. What genuine “improvements” have been produced in this country must all be placed to the credit of this general principle—a principle which comes as a natural one to plant-breeders now. It will, however, be readily apparent that the introduction of this principle is a contribution rather of insight and clear thinking, than of experiment. Of what value then, from the economic standpoint, has been this repeated finding of ratios? The whole value is expressed by the single word “segregation.” When it became known that there were regularly segregating “unit characters,” plant-breeding received an immense impetus and to this impetus may be traced some of the best of the cereal varieties now in existence. The conception of “independent” (unit) characters removed the former fear of the “reversion” of hybrids to the inferior parental types and restored the long-lost hope of the possibility of “fixity” of type. In so far as it has confirmed Mendel's theory and established its applicability to agricultural plants, “ratio-finding” investigation has been of inestimable value. To-day, however, there is no doubt as to the general validity of the theory and therefore “ratio-finding” must seek some other economic justification. [Perhaps the safer form of statement is that Mendelism has a general validity which the coarse method of the ratio-determination of eye-characters is not likely to be able to challenge.]

Those who, since 1900, have raised new and better cereal and other varieties have, of course, consciously depended in their investigations upon the fact of segregation. Further than this, they have, in many

cases, conducted ratio-experiments in the early stages of the work which has had its fulfilment in the production of valuable new strains. It is, however, a most debateable question, whether they could not and would not, have produced precisely the same final result, if their academic interest had not led them to include a "ratio-determination" as part of their procedure.

The past indebtedness of plant-breeders to Mendelism is unquestioned; exactly how it was incurred is to a great extent a matter of opinion; and interest must now centre on the possible future value of simple "ratio-Mendelism."

In the cereals, at any rate, it will be of no economic advantage to establish further ratios in connection with simple, eye-judged, morphological characters. Many such are already on record and, except as confirmations of the very general theory of Mendelism, they have not been an aid to the plant-breeder. To discard such characters for those of direct practical importance seems the first step. The step has already been taken in connection with cotton, wheat, barley, oats, maize, potatoes, etc., but the achievements have been few. As long as the eye is allowed to determine the form of Nature's "hereditary-units" it will remain a just contention that the results achieved in work of this kind could equally well be achieved without calling upon mathematics to reinforce eye-judgment by "ratios" derived from eye-observation. Apart from this, is the fact that the economic features of prime importance—such as Yield and Standing Power in the cereals—are far more complex than awns and fertile lateral florets, etc. It is not likely to be of either academic or economic interest to know whether the eye-sorting of an F_2 on the basis of some morphological character requires two hypothetical factors to explain the observed ratio, or only one. In any case, the "eye-character" is only a manifestation and one depending in part for its precise form upon environment. Upon what else does it depend? The customary answer is, upon a "factor" or upon two or more "factors." Let this answer be accepted and let it further be accepted—as thanks to Morgan and his collaborators it now well may—that the factor is a "something" in a chromosome. That a "factor" exists and segregates is a helpful idea and a very well tried one, but in what manner does the factor operate? Its presence is responsible for a potentiality, the potentiality controlled by growth-environment produces a certain manifestation—but what is the exact physiological nature of the potentiality? This seems to be the enquiry upon which genetic effort—forsaking the simple ratio-quest—should now concen-

trate. If, in the case of a few readily recognisable eye-characters, the causative physiological potentialities could be exposed, it might be possible to undertake an investigation of the inheritance of such highly important attributes as "yield" with fair prospect of success. Up till now researches on yield-inheritance have employed only the unwieldy standards of physical and numerical plant attributes. Before any progress is made resort will have to be had, it is felt, to the fundamentals, the determining physiological potentialities, and these elusive features may, perhaps, best be sought by first making acquaintance with them in the simple eye-characters of plants the inheritance phenomena of which have been already investigated. A knowledge of the potentialities which lie behind the manifestations (for convenience called the plant-characters) represents the "superstructure" which, logically, ought to be building upon the foundation of the ratio. It is, perhaps, a justifiable comment, that the foundations are being monotonously extended while the superstructure suffers neglect.

As a first step in the endeavour to elucidate "potentialities," suitable forms of "character" will have to be decided upon. It is of interest briefly to trace the development of the choice of "characters" in genetic work. For a time the simple eye-judged characters such as "tall and short," "rough and smooth," etc., were alone observed. Measurements—first linear, then superficial, then of weight, etc.—came next. Chronologically, perhaps, the series was then extended by the "characters" *implied* by "multiple factors." A sub-extension was introduced by the still more highly imaginary "characters" demanded by the supposed existence of a great number of "minor multiplying factors." Ratios of various dimensions came to be adopted for the reason that, wisely chosen, they might help to eliminate the disturbances for which environmental differences are usually responsible in absolute-measurement characters (such as length of rachis, etc.). A novel and highly artificial character—best referred to, perhaps, as a "mathematical" character—has not infrequently been used. Collins(18) in one investigation sought the aid of this conception of a character because he found that in maize the facile recognition of "types" was not at all easy to achieve. The general argument was this. If, in some selected pure line population, every possible "character" of the plant be investigated—purely botanical and economic, eye-obvious and eye-elusive alike—and if correlations be found between certain economic characters and certain non-economic but readily observable ones, then the economic characters will be traceable in hybridising and selection by observation of the correlated ones. To

measure correlations, it was necessary to give numerical representation to all the experimental characters. One example of the procedure must serve for illustration. "Hairyness" was one of eleven selected characters and it was measured by:

- (i) The number of nodes per plant with completely hairy sheaths.
- (ii) The number of nodes per plant with a complete circle of hairs at the throat of the sheath.
- (iii) The length of the longest tuberculated hairs.

There is, perhaps, little room for surprise that an elaborate investigation of such characters as these led to a negative result—there was, in maize, a marked absence of "genetic correlations."

This brief survey of the history of development of the conception of plant-characters, has one very striking feature. There has been a steady departure from the ideas of character in which the systematic botanists used to trade—and still trade—and, bit by bit, very artificial, "mathematical," conceptions innocent of any biological basis, have come into vogue. It seems most improbable that the observation of characters of this kind—although their possible number is indefinite—will ever lead to a knowledge of physiological potentialities.

There remains an outline-consideration of the steps to be taken to glean a knowledge of physiological potentiality. To a great extent, the nature of the experimental "character" must direct these steps. For the awn and the lateral floret of the barleys four possibilities are readily apparent, viz.:

(α) A search may be made for other eye-characters that seem to be modified and to fluctuate *pari passu* with the awn or lateral floret. It has, for example, been suggested (§ VIII above) that the vascular bundle supply is a "co-variant" with lateral floret-form. Possibly it may prove to be causative rather than co-variant. If a group of co-variants can be found, the features they possess in common may point to some physiological activity as the "potentiality" of which they are, in part at any rate, manifestations.

(β) The botanical homology of the character may be important in indicating from what source to seek co-variants and of what nature the governing potentiality is likely to be. Paragraph (iv) (above) contains evidence that the accepted view of the homology of the awn needs examination.

(γ) In all cases a histological study of development is likely to be important. For the lateral floret it is certain to be indispensable. The difference of the developments which in *H. hexastichum* lead finally to

six rows of fertile florets and in *H. distichum* to two rows of fertiles and four of infertiles, offers a fascinating study and one that will have to be undertaken before the significance of the manifold floret forms can be properly assessed.

(8) The growing of experimental plants under a wide range of controlled environments may, perhaps, lead to a knowledge of the possible limits of "fluctuation." It may indicate the extent to which the different "manifestations," which are called varietal and sub-varietal "characters," can overlap. A knowledge of the bounds outside of which a manifestation cannot extend may cast light upon the nature of the potentiality of which that manifestation is an expression. Some of the F_2 "Inerme" extracts in which very occasional fertile lateral florets may appear (say one or two per ear) seem likely to be suitable material for work of this kind.

The present-day is indebted for its knowledge of Mendelism, in a measure almost too great for acknowledgement, to the "ratio-finding" experiments of the past; but the time seems now to have come when investigation should be raised to a new plane, the plane upon which physiological potentiality is, in place of eye-obvious manifestation, the acceptance of the phrase "the character of the plant."

Fig. V. Inerme parent.

Fig. VI. Haxtoni parent (tops of awns not shown).

Fig. VII. Fully awned types.

(a) Laterals not fertile; glumes short; outer paleae of laterals not extremely reduced.

(b) Laterals of intermediate size and usually fertile.

(c) Laterals all fertile though irregular in size.

Fig. VIII. "Half-awned" types. (a), (b), (c) as in Fig. VII.

Fig. IX. Absolutely awnless forms. Here in (a) a more complete state of reduction of the outer palea of the lateral floret occurs than in the fully awned forms [cf. Fig. VII (a)]. In (b) two fertile laterals occur with the remainder infertile.

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