GENETICS AND GENE DISTRIBUTION IN
TRITICUM VULGARE Vill.
and OTHER TRITICUM SPECIES.

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PREFACE

The work described in this dissertation is original except where specific acknowledgement had been made in the text to other workers. It has not been previously submitted for any degree in any university.

I am much indebted to Mr A.E. Watkins, M.A. for suggesting the problem dealt with in Part I of the dissertation — a study of the genetics of awn types in *Triticum vulgare* undertaken with the ultimate object of clarifying the story of the origin and spread of the species. I am also greatly indebted to Mr Watkins for much helpful criticism and advice throughout the course of the work and for genetic material of a few of the crosses studied.

Sydney Ellerton
3rd May 1939

I. INTRODUCTION

A great many genetic studies have been made relating to the characters of beardedness and beardlessness in wheat, but their mode of inheritance is still far from being fully understood. This is chiefly because none of the work so far done has been based on a careful study of the awn types to be found throughout the range of the wheat species. Most workers have determined the mode of inheritance of the character in some isolated cross or crosses which happen to have been made for plant breeding purposes. The description of the parental types used has usually been quite inadequate, the contrasting phenotypes being loosely termed "bearded" and "beardless". In some of the more recent work and in one or two early papers, true beardless forms have been distinguished from those with very short awns (awn tips) and "half-awned" types have also been recognized. Even here, however, no distinction has been made between certain pairs of genetical types which are easily distinguishable phenotypically and it is difficult to tell, except in cases where good illustrations or exceptionally good descriptions of the wheats used are given, precisely which types have been used as parents.

There are several reasons why the bearded character in wheat has received so much attention from geneticists; it is an obvious and striking character, with simple inheritance in the first crosses studied, though it ~~is~~ later proved to be very complicated; it is important agriculturally and therefore to the breeder; it is the first of an hierarchy of characters used by systematists for classifying the hexaploid wheat species into "botanical varieties" and, lastly, it proved to be connected with the speltoid mutations which have been so extensively studied by geneticists and cytologists.

With regard to the classification of wheats into botanical varieties, four awn classes were recognized by Vavilov (1923) — *aristatum* (awned), *muticum* (awnless), *Breviaristatum* (half-awned) and *inflatum* (hooded). Later Hosono (1934) suggested that the *inflatum* class should be divided into two, *aristoinflatum* and *mutinflatum*, which will be called hooded bearded and hooded beardless for the purposes of the present paper. It will be shown by the present work that these five classes, while distinguishing some of the major awn types which may be recognized by the systematists, do not in most cases represent a single genetical type but a group of unrelated but superficially similar types, some of which may be distinguished accurately by visual inspection alone.

As pointed out above, the literature on wheat awn genetics is confused in that the exact types used are rarely accurately described. It therefore seems advisable to give first a careful description of the major awn types occurring in the genus. It may then be determined in a majority of cases, from descriptions and photographs given by the author, which genetic types are involved and the earlier literature may thus be summarized on an exact basis.

II. THE TYPES OF GENETIC DETERMINATION OF AWN LENGTH IN WHEAT.

Before going on to describe the various awn types which form the basis of the present genetical and distributional study, it must be pointed out that the character of awn length in wheat is subject to several distinct types of genetical influence. These may be classified under four headings as follows:

(i) Chromosome number
(ii) Modifying factors
(iii) Genetic factors that have their most striking effect in influencing some other character, but also have a marked effect on awn length.
(iv) The major awn factors proper.

The effect of chromosome number is very striking. The tetraploid wheat species in general have very much longer awns than the hexaploid types. Very long awns are found in <u>T</u>. <u>dicoccum</u> and <u>T</u>. <u>turgidum</u>, and <u>T</u>. <u>durum</u> contains types with longer awns than any other wheat. Percival (1921) gives the awn length of the two tetraploid species <u>T</u>. <u>durum</u> and <u>T</u>. <u>turgidum</u> as 11 to 23 cm. and 8 to 16 cm., while the corresponding figures for <u>T</u>. <u>vulgare</u> and <u>T</u>. <u>Spelta</u>, two hexaploid species, are given as 5 to 10 and 6 to 8 cm. respectively.

In the segregates from pentaploid hybrids this effect of chromosome number is equally striking. The tetraploid segregates of every awn type have longer awns or awn points than the corresponding hexaploid segregates. The exact mechanism of this effect is not known.

Even within one species and within the types which would be classified without hesitation as "fully bearded", there are considerable variations in awn length. These are presumably due to modifying factors. The magnitude of their effect may be judged from the following figures quoted from Percival (1921) for the awn length of different forms of various species, all of which would be classified as fully bearded. A few widely different lines have been selected to give an idea of the extent of the range. Awn lengths are in centimetres.

TABLE I.

Awn Lengths (Cm.) in Fully Bearded Wheats.
(Data from Percival (1921)).

TETRAPLOID			HEXAPLOID
T. dicoccum	*T. durum*	*T. turgidum*	*T. vulgare*
6-8. *farrum* (White Emmer) 7-9. *farrum* (Large white Emmer) 12-15. *liguliforme* 15-17. *majus*.	12. *murciense* (form 3) 11-13. *apulicum* ("Cawnpore 18") 14. *murciense* (Santa Marta) 15-16. *melanopus* (Trigo Andaluze) 17-18. *erythromelan*. (Medea)	8-9. *dinurum* (Red Rivet) 9-10. *dinurum* (Nonette de Lausanne) 12-13. *dinurum* (Trigo focense) 12-14. *iodurum* (Petianelle noire de Nice)	4-6. *ferrugine* (Carman) 5-6. *meridional* (Form 1) 7-8. *ferrugineu* (Hsu Hsu Mai) 8-9. *erythroleu* (Perle de Nuisement).

Plate I shows the extreme forms of fully bearded vulgare and a form with average awn length is shown in Plate II A.

Corresponding differences in the length of the awn tips are found in tip-awned and half-bearded wheats, occasionally making the exact classification of a particular form difficult.

It has been shown conclusively by Stewart and his co-workers (S., 1926, 1928a; S. & Bischoff 1931; S. & Heywood, 1929) that factors which modify ear density also, at least in all the cases tested, modify the awn length of fully awned wheats. Correlation between rachis internode length and awn length was highly significant, e.g. + 0.6500 ± 0.028 in the cross Kanred x Sevier, both fully awned forms. It may be noted that the compactum factor reduces awn length appreciably, in the same way as the other spike density factors tested.

This correlation doubtless accounts for some of the differences in awn length between different forms of the same species shown in the above table, though there are undoubtedly other modifying factors too.

None of these modifying factors has been studied in the present work.

Thirdly, we have a number of factors or very closely linked factor groups which have their most marked effect on some plant character other than awns, but which at the same time influence awn development to a marked degree.

Plate I.

Extreme types of Bearded T. vulgare

A. Form with exceptionally long awns (Persia VII/52). B. Form with exceptionally short awns, approaching the half-bearded condition (China V 14/81). x $\frac{1}{2}$.

Among the most striking of these factors (or, more probably, closely linked factor groups) are those which distinguish *T. polonicum* from *T. durum* and *T. sphaerococcum* from *T. vulgare*. Both these have a very marked effect in reducing awn length.

Triticum polonicum, according to Percival (1921), has an awn length of 7 to 12 cm., as compared with the 11 to 23 cm. given for the nearly related *T. durum*. In crosses with other species the long glume *polonicum* factor *P* is seen to cause a marked shortening of the awns; e.g. Matsumura (1936) in the cross bearded *T. polonicum* x tip-awned *T. Spelta* shows that both tip-awned and bearded *polonicum* segregates have shorter awns than the corresponding *Spelta* types.

Triticum sphaerococcum shows an even more marked reduction in the length of the awn, the genetically fully bearded types having awns only 1.5 to 2 cm. long, as compared with a length of 5 to 10 cm. in *T. vulgare*. This factor group has an effect on awn length as great as that of several of the major factors which influence awn length alone. It will be discussed at length in the third part of this thesis. Comparative pictures of typical fully bearded *vulgare* and *sphaerococcum* forms are shown in Plate II.

The fourth class, the factors which have their major effect in ~~modify~~determining the length of awn, are the ones with which the main part of the present genetical work is concerned. The phenotypes to which they give rise are described in the next section.

A B

<u>Plate II.</u>

Reduction of Awn Length due to the <u>sphaerococcum</u> Factor.

Typical fully-awned types of <u>T</u>. <u>vulgare</u> (A) and <u>T</u>. <u>sphaerococcum</u> (B). Note the reduction in awn length and ear size in the latter. (Natural size).

III. AWN TYPES OCCURRING IN THE WHEAT SPECIES.

The diploid wheats exhibit no major variation with respect to awn type ; all forms are fully bearded, and the group therefore has little interest in the present connexion and may be left out of consideration.

The tetraploid species are also uniformly fully bearded, except for the shortening of the awns in *T. polonicum* already referred to and for a very distinct group of wheats confined to certain regions of Abyssinia. These were first studied in detail by Vavilov *et al* (1931) and referred by them to special subsections of *T. durum* and *T. turgidum*. Among them several distinct awn types are found. Fully-bearded forms exist as everywhere else, but "hooded", half-awned and tip-awned types also occur.

A hooded Abyssinian wheat (*T. turgidum abyssinicum* Vav.) is illustrated in Plate III. The character is somewhat complex in its effects. The length of the awns in the main tillers is considerably less than in bearded forms, and the awns are often bent at the base in a characteristic way. The glumes are inflate In the late tillers the awns are still further reduced to a hook, or are bent round on themselves to form a close spiral. They are very much thickened and in some forms have prominent lateral membranous outgrowths. All these wheats have considerably

Plate III.

A Hooded Bearded Abyssinian Tetraploid Wheats.

Main and subsidiary tillers from the same plant, showing difference in awn expression. (x 1½).

shorter straw than the more typical T. durum and T. turgidum forms from the Mediterranean region.

The difference between the early and late tillers of one and the same plant in these hooded forms is very striking. In general, the tillers developed latest show the strongest effect of the factor. The character is more strongly exhibited in material sown late in spring than in autumn-sown material.

The half-awned Abyssinian tetraploid wheats do not exhibit this difference between the early and late tillers. All the ears have long awns at and near the apex, but the awn length is progressively reduced as one approaches the base of the ear, where there are awn tips only a few millimetres long.

The tip-awned forms described by Vavilov et al (1931) have awnlets 1 cm. or so long at the apex of the ear and very short awn tips towards the base. The type is very like the ordinary "beardless" vulgare wheats of Western Europe in this respect.

In Vavilov's paper a number of wheats are figured which are hooded, but which have much shorter awns than the hooded type figured in Plate III. They present much the same appearance as the late tillers of that type. If the ears figured are actually main tillers, then we have another category "hooded beardless", which would be expected to occur where the factors for the hooded and for the half-awned or tip-awned condition occur together. None of these forms actually exists in the collection of some 200 Abyssinian wheats at Cambridge, though all the other types are represented. Their existence would, however, be expected. In the following discussion of the genetics of the various awn types, the ordinary hooded type will be called "hooded bearded" in contradistinction to "hooded beardless". "Hooded bearded" wheats are those that contain the factor for the hooded condition and no other major factors that reduce awn length; they differ from fully bearded only by a single factor pair.

The hexaploid wheats show even greater variation in awn type than the tetraploids. The full range of types is shown in <u>T. vulgare</u>, and this species will be discussed first. In it we can distinguish completely beardless wheats, two distinct forms with short awn tips, half-bearded types and forms that may be described as "hooded bearded" and "hooded beardless", as well as the usual fully awned wheats. This makes seven types in all, which are described separately below.

(1) <u>Tipped 1</u>.

The two different types of tip-awned wheats may be designated as Tipped 1 and Tipped 2. Tipped 1 is the type of "beardless" wheat familiar in England, and which was studied by Biffen (1905) and other early workers. Wheats of this type have very short awn tips on the paleae at the base of the ear and in the centre, but towards the apex they become increasingly longer, and in the apical quarter of the ear may be 1 cm. long or even longer, though in most types the longest tips do not reach this length. These awn tips are usually quite straight and not bent at the base, but sometimes there is a sharp angle at the junction of awn and ~~glume~~ palea or just above it. Even in these cases, however, the distal part of the awn is straight or nearly so, and not hook-like. The distribution of the awn tips with the longer awns confined to the apex of the ear is characteristic of this type. The type of bent awn tip sometimes found in this category is shown in Text-fig. 1A.

(2) Tipped 2.

The other type of tip-awned wheat, Tipped 2, is quite different. Here the awn tips are much more nearly equal in length all along the ear. If there is any difference, the longest tips are to be found near the centre of the ear and not at the apex. The awn tip is often curved in this type, the most common form of curvature being shown in Text-fig. 1B. It is never curved right round on itself as in "hooded beardless" wheats, and it never has membranous lateral outgrowths. Text-fig.2 shows a comparison between the distribution of awn tips in typical ears of the Tipped 1 and Tipped 2 categories and also of beardless T. vulgare. Measurements were made of the length of the longest awnlet in each spikelet on one side only of three typical ears of each class, and the average values represented in the diagram.

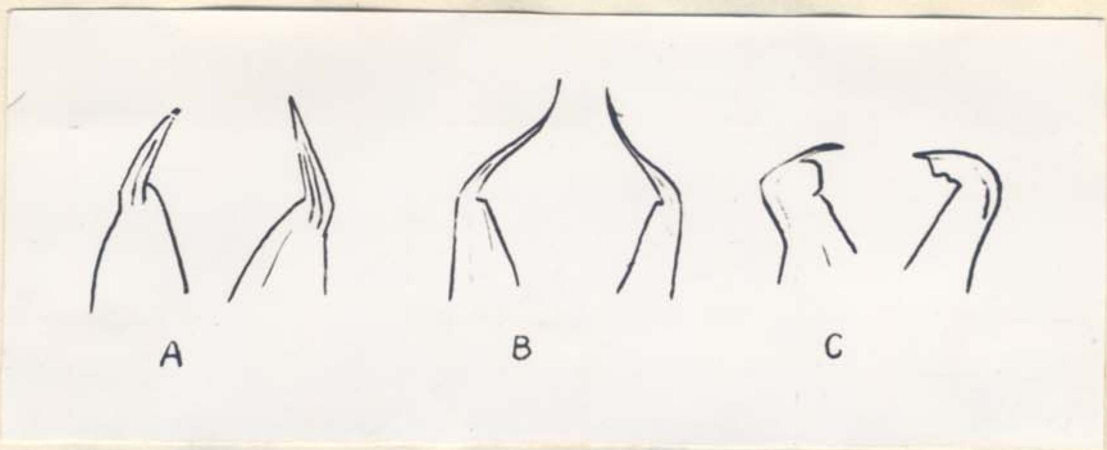
(3) Beardless.

Completely beardless wheats are comparatively infrequent. Here the awn tips are reduced almost to extinction. They are very little if any longer than the short blunt teeth found on the empty glumes, at most one or two millimetres.

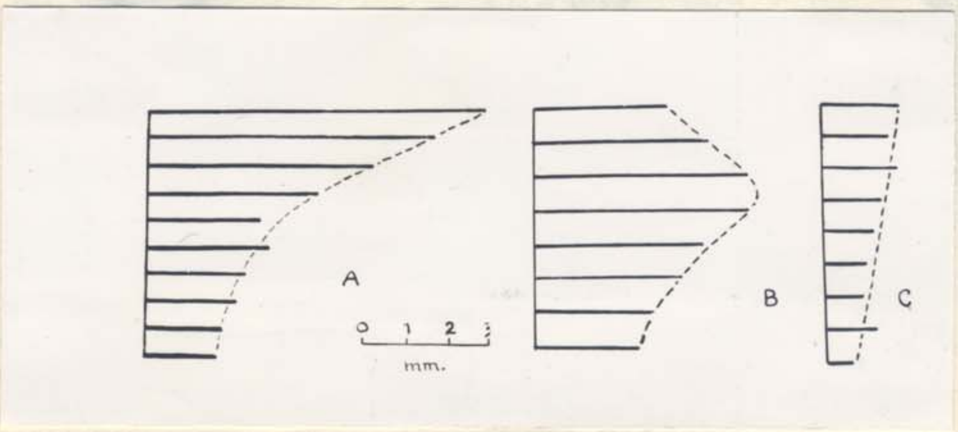
Plate IV shows typical wheats of the Tipped 1, Tipped 2 and beardless categories.

(4) Half-awned.

The half-awned vulgare wheats vary considerably among themselves and the character may be determined by at least two different genes. In most cases (Cf. Plate V) the awns in the apical portion of the ear are relatively long, but they become progressively shorter towards the base, where they may be reduced to quite short awn points. Some forms, however, have short awns of practically equal length (usually an inch or so) from the apex and the base of the ear, while others show extremly long awns in the apical four or five spikelets with very short ones below. No exact classification of these types was possible on the basis of visual examination, as they showed all gradations from one to another. All of them differ sharply from the next class by the fact that there is no marked difference in awn expression between the main and subsidiary tillers of the same plant



Text-fig. 1.
Characteristic Forms of Awn Tips in *T. vulgare*
A. Tipped 1 (var. Swedish Iron)
B. Tipped 2. (var. M.V.)
C. Hooded Beardless (var. Chinese White)



Text-fig. 2.
Average length and distribution of awn tips in tip-awned and beardless *T. vulgare*.

A. Tipped 1. (var. Squarehead's Master).
Note lengthening of tips towards apex of ear.

B. Tipped 2. (var. M.V.)
The awn tips are more uniform in length, but longest just above the centre of the ear, not at the apex.

C. Beardless (var. Australian 6)
The awn tips are very short throughout, increasing very slightly towards the apex.

A B C

Plate IV.

Awn Types of T. vulgare

A. Tipped 1 (apical awnlets), var. Swedish Iron. B. Tipped 2 (awnlets not confined to the apex), var. India V 2/133. C. Beardless, var. Australia 6. (Natural size).

Plate V.
A Typical Half-Awned T. vulgare
Var. Persia V 41/9
(Natural size)

(5) Hooded Bearded.

The hooded bearded type in T. vulgare is that classed by Hosono (1934) as aristoinflatum. It corresponds quite closely to the condition already described in Abyssinian tetraploid wheats. The awns of the main tillers are reduced in length in much the same way as in the half-awned wheats. They are, however, curved and deformed, usually with a marked inflection at the base; often they resemble a shepherd's crook in shape (see Plates VI and VII B). Frequently, though not always, the awn is considerably broadened at the base and has membranous lateral expansions, giving an appearance rather like that of the hooded barleys. This characteristic is shown in Text-fig. 3.

The glumes have a peculiar shape which Vavilov (1923) calls "inflated", but which is difficult to describe adequately. The glume is more markedly convex than in most wheats, and is rather tough, so that the ear is often difficult to thresh. The most striking and apparent difference is that the spikelets seem to have a U-shaped outline, the midribs of the two empty glumes lying almost parallel to each other for the distal two-thirds of their length, instead of diverging to give a more V-shaped outline (cf. Plate VII B). This distinction in outline is not, however, apparent in most Chinese hooded wheats, owing to the large number of grains per spikelet present (Plate VI).

A B

Plate VI.

Hooded Bearded T. vulgare

(A) Main and (B) subsidiary
tillers from the same plant.
(var. China V 2/146, natural size).

Sometimes, in spite of the above differences, it is a little difficult to distinguish between the main tillers of hooded and half-awned types, at least until the eye has become accustomed to the rather subtle difference in the shape of the glumes. The infallible test is then to look at the late tillers. Here the half-awned types show no marked difference from the main tillers, while in the hooded plants the expression of hoodedness is considerably exaggerated: the awns are reduced in length to a strongly recurved awn-tip which usually has very marked membranous lateral outgrowths (Plate VI B).

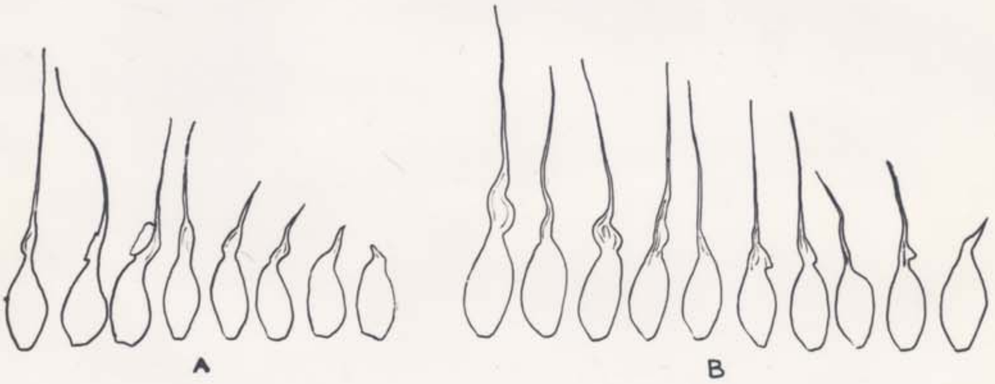
(6) Bearded.

The fully awned wheats need no special description; they are easily distinguished from the foregoing two types by the fact that the awns towards the base of the ear are long, as well as those at the apex.

(7) Hooded Beardless.

There is still one other category to be described; that of "hooded beardless". This resembles the hooded bearded type except that the awn length is still further reduced, the awn being represented by a short hook usually with membranous lateral outgrowths. The variety Chinese White (Text-fig. 1 C and Plate VII A) is typical of this class.

Thus we have in all seven different easily recognizable categories of awn development in *vulgare* wheats. It will be



Text-fig. 3.

The "Hooded" Character in Hexaploid Wheats.

A. Paleae of different races of T. compactum Host. from Afghanistan.
B. Paleae taken from the middle of the ear of different forms of T. vulgare Vill., group inflatum Flaksb.

Slightly larger than natural size.

Redrawn from Kobelev (1928).

A

B

Plate VII.

Hooded Beardless and Hooded Bearded T. vulgare.

A. var. Chinese White, B. var. Persia 368
(main tillers in each case, natural size).

shown later that three of these types (Tipped 1, Tipped 2 and Hooded bearded) are each due to a single gene difference from the recessive fully bearded. The half-awned wheats also have a single gene difference from bearded, but the same gene is not involved in every case — two genetically different types within the class have been established. The remaining two types, beardless and hooded beardless, are due to various combinations of two (or possibly in some cases three) of the genes responsible for the other types: in all the cases studied they show a two factor difference from bearded.

The geographical distribution of the above seven types has been studied in some detail and will be described below. Although the difference between types are in general very clear-cut, an occasional difficulty in classification does arise. A very few wheats have the distribution of their awn tips intermediate between typical Tipped 1 and typical Tipped 2, and it is difficult to decide whether certain forms with very short awn-tips should be described as tip-awned or beardless. These doubtful plants, however, form an extremely small proportion of the whole and are certainly not sufficiently frequent to vitiate the following study of the geographical distribution of the types.

In Triticum compactum tip-awned, hooded, half-bearded and bearded forms occur, corresponding exactly to the similar forms in T. vulgare. All the forms, however, have rather shorter awns or awn-tips than the corresponding *vulgare* type, owing to the effect of the *C* factor in reducing awn length. As far as I am aware, no completely beardless forms of *compactum* have been specifically reported, and the literature does not enable one to distinguish between Tipped 1 and Tipped 2 — they are classed together as '*muticum*'. It is probable, however, that a complete parallel series actually exists. The species shows its greatest diversity in Afghanistan, and half-awned and hooded forms were first discovered there by Vavilov and Bukinich (1929) (see also Kobelev, 1928). Owing to this parallelism between *vulgare* and *compactum*, and to the fact that a much larger and more varied amount of *vulgare* material was available at Cambridge, genetic experiments were confined to the former species ~~only~~. It seems unlikely that *compactum* contains any major factor for awnlessness not studied in *vulgare*.

Triticum Spelta is a recent form almost confined to mountainous regions of Central Europe (Flaksberger, 1930); it contains bearded forms and beardless forms with apical awnlets (Tipped 1).

T. sphaerococcum contains forms with short awns (1.5 to 2 cm.) which are genetically fully bearded. It also contains beardless forms; in all these the awn tips are very shor owing to the marked shortening effect of the *sphaerococcum* factor complex, and it is impossible to distinguish different phenotypes within them. In the forms tested genetically, the beardless type has proved to be Tipped 2. I have not seen any hooded forms of <u>sphaerococcum</u>, and they have not been reported in the literature.

IIIa. EARLIER INVESTIGATIONS OF AWN INHERITANCE

As stated above, it is intended here to interpret earlier literature on the basis of the awn types described in t foregoing section. No reference is found in the literature to studies of the awn types found in Abyssinian tetraploid wheats, so that the following discussion refers only to those found in the hexaploid group.

The cross Tipped 1 x bearded has been studied by Biffen (1905), Clark & Quisenberry (1929), Gaines (1917), Gaine & Singleton (1926) and many others (cf. Matsuura, 1933). In each case the F_1 resembled the tip-awned parent more nearly than the bearded one, so that the tipped condition may be regarded as dominant. The F_1 plants of different crosses were not of exactly the same awn type, however. In some cases they had awn tips distinctly longer than those of the Tipped 1 parent and it was possible to classify the F_2 into a 1 : 2 : 1 ratio. In others, the heterozygotes could only be accurately distinguis from the pure Tipped 1 plants by their breeding behaviour and the F_2 was classified in the ratio 3 tip-awned : 1 bearded. It appears that the various wheats used differ in certain genes which modify the dominance of the Tipped 1 gene.

Kajanus (1923, 1927) reported crosses between Tipped 1 and bearded in which there was a deficiency of bearded segregates in F_2 and F_3. He attributed this to differential viability of the bearded plants, particularly with respect to their cold resistance. Watkins (1928) also found a deficiency of bearded segregates in a *T. Spelta* x *T. vulgare* cross.

The gene determining the Tipped 1 condition is known to be linked to the genes for keeled glumes, the squarehead ear type and for pubescent nodes. Kajanus (1923) reported 33% of crossing-over with the keeled glume factor. Watkins (1928) found the value to be 28% in a *Spelta* x *vulgare* F_2 and 39% in a Rivet x *vulgare* back-cross. Nilsson-Leissner (1925) gave the cross-over value as 35% and Nilsson-Ehle (1927) recorded a gametic ratio of 1 : 2.8 : 2.8 : 1, equivalent to 26% of crossing-over. Philiptschenko (1934) found that the cross-over value between Tipped 1 and the gene *S*, determining the keeled glume or speltoid condition, was 33%, while there was 35% of crossing-over between Tipped 1 and the gene *q* for the squarehead ear type. The Tipped 1 gene lay between the other two genes, *S* and *q*.

For the linkage with pubescent node, Gaines & Carstens (1926) obtained a cross-over value of 5%, while Love & Craig (1924) found almost complete linkage.

It may be deduced from the results of Biffen (1905) and other workers who have examined crosses between Tipped 1 *T. vulgare* and bearded tetraploid wheats, ~~shew~~ that the Tipped 1 gene is located in the A or B chromosome set of *T. vulgare* and not in the "extra" *vulgare* chromosomes.

In the cross Tipped 1 x beardless, Clark & Hooker (1926) found a 3 : 1 ratio in F_2 for the segregation of the major factors concerned, and also found evidence of the segregation of a modifying factor. Stewart and Tingey (1928) obtained transgressive segregation due to the presence of modifying factors in this combination, Tipped 1 segregates being obtained which had longer awn tips than the Tipped 1 parent Marquis.

The Tipped 2 type has been studied in crosses to a much smaller extent. Love & Craig (1926) reported a 15 : 1 ratio for tip-awned and beardless to bearded in a cross between Sonora (Tipped 2) and a Tipped 1 wheat. A similar cross involving Sonora was made by Quisenberry & Clark (1933) who obtained an F_2 ratio of 104 awned: 1710 intermediate : 276 awnless. In the F_3 only half of the awnless group bred true, the others segregating tipped plants. The true ratio therefore corresponded closely to the 1 : 14 : 1 expected on the basis of independent segregation of two factors. The Tipped 1 and Tipped 2 genes in combination clearly produce a true beardless type.

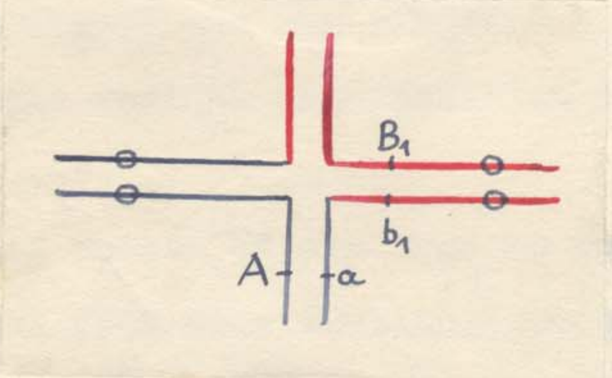
The same authors crossed Sonora with a bearded wheat and obtained an abnormal single factor ratio with a deficiency of Tipped 2 segregates in the F_2.

The genetics of completely beardless wheats has been studied by several authors. The above crosses with Sonora suggest that some such wheats may differ from bearded by two gene pairs, which separately determine the Tipped 1 and Tipped 2 conditions. The variety Supreme studied by Quisenberry & Clark (1933) appears to have been of this constitution, as in crosses with Sonora (Tipped 2) a single factor segregation for beardless v. tip-awned was obtained and no half-awned or other new types appeared.

The beardless wheats studied by other authors, however, all seem to have differed from bearded by two genes which individually determine a half-awned and the Tipped 1 conditions. This is true of the beardless Indian wheats, Pusa 4 and A 88, used in crosses with bearded by Howard & Howar (1912, 1915) and the varieties Federation (Stewart and Heywood, 1929), Hard Federation (Stewart & Judd, 1931 ; Clark, 1924; Clark _et al_, 1928) and Bobs (Clark _et al_, 1928). In each of these cases the factors for Tipped 1 and half-awned segregated independently.

A very odd result was obtained by Stewart (1926, 1928 who in crosses between Federation and the bearded varieties Sevier and G-149 found that the two awn factors of Federation were linked with 35% of crossing-over. The same two factors showed independent inheritance in the Federation cross studied later by the same author (S. & Heywood, 1929) and in the other beardless x bearded crosses reported above. Stewart regards the bearded character as being dominant and attributed the difference between the behaviour of Federation in the various crosses to differences in gene content between the bearded parents used. He gave Federation the formula *aa bb tt* and th two differing bearded types as *AA tt BB* and *AA TT bb*, the factors *A* and *T* being linked while *B* segregated independently. If this were so, then crosses between the different fully bearded types would give a proportion of *AA tt bb* plants, which would be half-awned according to the scheme proposed by Stewart This has never been known to occur; a great many crosses between bearded wheats have been recorded in the literature and none of them has given anything but bearded progeny. Further, all of the many thousands of bearded segregates obtained in a large variety of crosses by the writer and other workers bred true to the bearded condition; all bearded wheats may thus be regarded as recessive and genetically equivalent as regards their major awn factors. The probability of the correctness of Stewart's hypothesis is rendered still more remote by the fact that the supposedly different bearded parents (held to differ by two genetic factors) were very closely related. The lines G-149 and IIIc-18, the former of which showed linkage and the latter did not, were both pure lines from a Sevier x Dicklow cross. The variety Sevier itself behaved like G-149. Furthermore, the factors *T* and *B* had precisely the same effect.

The most probable explanation of Stewart's anomalous results appears to be that the different bearded wheats used differed not in gene number or kind but in gene arrangement. Using the symbols to be used later in this paper, Federation may be represented as $\underline{B_1B_1}$ $\underline{AA}$ and all the bearded wheats as $\underline{b_1b_1}$ $\underline{aa}$, $\underline{a}$ and $\underline{b_1}$ being the bearded allelomorphs of the half-awned and Tipped 1 conditions respectively and being situated normally in different chromosomes, thus segregating independently. If, now, the chromosome segment containing one of these recessive genes is involved in a reciprocal translocation with the chromosome containing the other, we should have a type of bearded wheat which would show a linkage between $\underline{a}$ and $\underline{b_1}$ in crosses with Federation. An association of four would be formed at pachytene in the F_1 as follows:



(The exact position and arrangement of the two genes in the above diagram is of course not known - the diagram is intended for illustration of the mechanism only).

It has been shown by Smith (1939) that a ring of four due to a reciprocal translocation segregates disjunctionally in a large proportion of cases in *T. monococcum* and there is good evidence (see Part III below) that this is also the case in other wheats. Smith found a gametic sterility caused by the presence of a ring of four of only some 10%, which might easily have been overlooked in some of Stewart's crosses, which were not examined cytologically.

The ring of 4 shown above would therefore give a preponderance of gametes of the constitution $\underline{ab_1} + 0$ and $\underline{A} + \underline{B_1}$, with a lesser number of the cross-over types, $\underline{Ab_1} + 0$ and $\underline{a} + \underline{B_1}$. The mechanism would thus account for the linkage found by Stewart.

The half-awned condition discussed in all the foregoing crosses ~~is shewn in~~ clearly depends on a single factor difference from bearded, the factor not normally being linked with Tipped 1. The cross half-awned x Tipped 1 (Pusa 7 x Pusa 6) was studied by Howard & Howard (1915) and the expected 1 : 14 : 1 segregation of beardless : various intermediates : bearded was obtained.

Half-awned wheats of the type so far dealt with are apparently different from others which have been recorded from time to time as rare admixtures in the wheat varieties of north-western Europe. These have been reported by Jenkin (1925) in Hen Gymro and by Nilsson-Ehle (1920) in Extra Squarehead II, Panzerweizen and Sommerperlweizen. The latter half-awned types were studied genetically by Nilsson-Ehle, who showed that they arose by mutation and bore a multiple-allelomorphic relationship with the factor for Tipped 1. The crosses half-awned x bearded, half-awned x Tipped 1 and Tipped 1 x bearded all gave 3 : 1 ratios, the type with the shorter awns being dominant in each case.

Nilsson-Ehle (1927) studied the linkage between this half-awned type and the keeled character. The linkage obtained (a gametic ratio of 1 : 1.4: 1.4 : 1, equivalent to 42% of crossing-over) corresponds roughly with the average linkage value of about 35% found by various authors between Tipped 1 and keeled glumes and gives another indication of the multiple allelomorphic relationship between the half-awned gene concerned and Tipped 1.

There therefore appear to be two factors which determine half-beardedness, as is also the case with the tip-awned condition. In the latter case, the two types may be distinguished phenotypically with accuracy; in the former they can not.

This survey covers all the major awn types described in the foregoing section except those of the Abyssinian tetraploid wheats and the hooded bearded and hooded beardless <u>vulgare</u> types. No reference to crosses involving these types occurs in the literature.

IV. NEW GENETIC DATA

(1) Introduction and List of Parents and Crosses.

The genetic behaviour of the hooded awn type found in Abyssinian tetraploid wheats and of all the awn types found in *T. vulgare*, with the exception of half-awned, was studied in the crosses to be described in this section. The omission of half-awned *vulgare* was unfortunate. It was due to the fact that in 1936, when most of the crosses were made, the author had not properly appreciated the distinction between the half-awned and hooded bearded types, and several forms used as parents and thought to be half-awned at the time, actually proved to be of the other type.

The following parental forms were used. Most of them were un-named varieties taken from the wheat collection grown in Cambridge and are designated by the collection numbers.

A. Hexaploid Species

Bearded.
1. Persia 170 (*T. vulgare* var. *ferrugineum* Al.)
2. *T. sphaerococcum* var. *rubiginosum* Perc.

Tipped 1.
3. Squarehead's Master (*T. vulgare* var. *milturum* Al.)
4. Swedish Iron (" " *lutescens* Al.)
5. Benefactor (" *leucospermum* Körn

Tipped 2.
6. M.V. (= Mesopotamian *vulgare*)(*T. vulgare* var. *leucospermum* Kör
7. Persia 465 (*T. vulgare* var. *pyrothrix* Al.)
8. India 742 (*T. sphaerococcum* var. *tumidum* Per
9. India 740 (" " " "
10. India 39 (*T. vulgare* var. *lutescens* Al.)
11. China 29 (" " " ")

Beardless.

12. Australia 6 (*T. vulgare* var. *albidum* Al.)

Hooded Bearded

13. Persia 357 (*T. vulgare* var. *rufinflatum* Flaksb.
14. Persia 413 (" " *albinflatum* "
15. Persia 368 (" " *khorassanicum* Vav.)

Hooded Beardless

16. Chinese White (*T. vulgare* var. *huangyangense* Hosor

B. *Tetraploid Species.*

Bearded

17. Indian Runner (*T. durum* var. *provinciale* Al.)
18. Cambridge Rivet (*T. turgidum* var. *iodurum* Körn)
19. Emmer (*T. dicoccum* var. *farrum* Körn)

Hooded Bearded

20. Hooded Abyssinian (*T. turgidum abyssinicum* Vav.)

The following is a list of the crosses between these forms which were studied (the female parent is placed first in each case):-

A. Crosses involving awn factors of *T. vulgare* or *T. sphaerococcum*

Tipped 1 x Bearded

1. (Swedish Iron x Rivet) F_1 back-crossed to both parents
2. (Swedish Iron x Emmer) F_1 back-crossed to Emmer and to Rivet.

Tipped 2 x Bearded

3. Persia 465 x Persia 170
4. (M.V. x Rivet) F_1 back-crossed to both parents.

Tipped 1 x Tipped 2

5. M.V. x Squarehead's Master
6. India 740 x Squarehead's Master

Tipped 2 x Tipped 2

7. Persia 465 x M.V.
8. M.V. x India 742 and reciprocal

bearded
Hooded/ x Bearded
9. Persia 357 x Persia 170

Hooded bearded x Tipped 2
10. India 39 x Persia 368
11. Persia 413 x India 39
12. China 29 x Persia 368
13. Persia 357 x Persia 465

Hooded beardless x bearded
14. Chinese White x *T. sphaerococcum* var. *rubiginosum*
15. (Chinese White x Rivet) F_1 back-crossed to both parents.

Hooded beardless x Tipped 2
16. Chinese White x M.V.

Hooded beardless x Tipped 1
17. Chinese White x Squarehead's Master

Beardless x Bearded
18. (Australia 6 x Indian Runner) F_1 x Indian Runner

B. Crosses involving the hooded Abyssinian tetraploid type.

Hooded bearded x bearded
19. Abyssinian Hooded x Indian Runner.

Hooded bearded x Tipped 1
20. (Benefactor x Abyssinian Hooded) F_1 back-crossed to both parents.

(2) Dominance Relations

Most authors have regarded the beardless or tip-awned condition in wheat as being dominant to bearded, though the opposite view has also been taken (Howard & Howard, 1912, 1915; Stewart, 1926, etc.). Actually, none of the awn factors is completely dominant nor completely recessive. The F_1 plants of crosses between Tipped 1 or Tipped 2 and bearded have awn tips distinctly longer than the tip-awned parent, but much nearer to it than to the bearded parent. The same applies to crosses between beardless or hooded beardless and bearded forms. It is therefore clear that the bearded type should receive the recessive symbol in each of these cases. As indicated above, the exact degree of dominance of the beardless or tip-awned condition varies from cross to cross, although the F_1 is invariably much nearer to the parental type with the shorter awns. This variation may be regarded as being due to dominance modifiers.

Crosses between the hooded bearded and bearded types show a curious state of affairs. The main tillers of heterozygous plants are practically indistinguishable from bearded, whereas the late tillers appear hooded. This is due to the fact that the effect of the hooded factor is much more strongly exhibited in the late tillers than in the main tillers of the same plant (see above pp. 13 and 22). The hooded condition may therefore be practically dominant and practically recessive in different parts of one and the same plant. This applies equally to the hooded type found in Abyssinian tetraploid wheats and to that found in T. vulgare. For the sake of uniformity, the bearded type will be symbolized as being recessive to hooded in the following treatment.

In crosses between tip-awned vulgare wheats and bearded T. sphaerococcum, the short beards (1.5 to 2 cm long) of the latter type appear in F_1 to be completely dominant.

This, however, is due to the fact that short-awned *T. sphaerococcum* is genetically fully bearded, the recessive *sphaerococcum* factor *s* itself reducing awn length; a bearded *sphaerococcum* plant roughly resembles a heterozygous bearded/tip-awned *vulgare* plant in length of awn, as two *s* genes or a single tip-awn gene reduce awn length to about the same extent. In F_2, in the *vulgare* and *sphaerococcum* segregates taken separately, the tip-awned condition is dominant as is usually the case.

There seems little doubt that the awned condition should be regarded as the basic or primitive one in wheat; ~~since~~ it is found in all species and is the only ~~awn~~ condition ~~one~~ in diploid and tetraploid wheats with the exception of the Abyssinian group of tetraploids. The other types have very probably been derive from the bearded form by a series of incompletely dominant mutations.

(3) Genetic Analysis of Crosses involving Awn Types of *T. vulgare* and *T. sphaerococcum*.

I. Tipped 1 and Bearded.

This combination has been studied in crosses 1 and 2, the results of the former of which have already been reported in considerable detail by Watkins and Cory (1931). In both cases, the F_1 plants were back-crossed to one or other of the parental forms, by which means very regular segregations were obtained. As many more plants of the first of these crosses have been grown and classified since the original publication, the segregations for the characters Tipped 1 v. bearded and keeled v. round glumes will be given here (Table II), together with similar results for the second cross. (I am indebted to Mr Watkins for most of the data presented in this table, though the later plants of each cross were classified by me. The statistical analysis is mine).

TABLE II

Segregation in the Crosses Iron x Rivet and Iron x Emmer

1. Iron x Rivet

	Bearded keeled	Tipped 1 keeled	Bearded Round	Tipped 1 Round	Total	χ^2	Degrees of freedom
F_1 ♀ x Rivet ♂	104	75	79	110	368	10.065	3
F_1 ♀ x Iron ♂	27	23	18	24	92	1.826	3
Iron ♀ x F_1 ♂	35	23	24	33	115	3.922	3
Rivet ♀ x F_1 ♂	30	17	16	27	90	6.622	3
						22.435	12
Total	196	138	137	194	665	19.903	3

Analysis of χ^2

	χ^2	Degrees of freedom	P
Linkage (390:275)	19.887	1	<.01
Keeled:round(334:331)	0.014	1	.90—.95
Tipped 1:bearded(332:333)	0.002	1	.95—.98
Heterogeneity	2.532	9	.98
Total	22.435	12	

Recombination value = 41.35 ± 1.94%

TABLE II (Contd.)

2. Iron x Emmer

	Bearded keeled	Tipped 1 keeled	Bearded Round	Tipped 1 Round	Total	χ^2	Degrees of freedom
F_1 x Emmer	53	41	41	61	196	5.877	3
F_1 x Rivet	10	2	11	14	37	8.514	3
						14.391	6
Total	63	43	52	75	233	9.867	3

Analysis of χ^2

		χ^2	Degrees of freedom	P
Linkage	(138:95)	7.936	1	<.01
Keeled:round	(115:118)	0.038	1	.80—.90
Tipped 1:bearded	(127:106)	1.893	1	.10—.20
Heterogeneity		4.524	3	.20—.30
Total		14.391	6	

Recombination value = 40.77 ± 3.28%

These results show that the Tipped 1 type differs from bearded by a single factor pair. The tip-awned type will be denoted as B_1B_1 and the bearded form as b_1b_1. This factor pair shows significant linkage with the character keeled v. round glumes in each of the above crosses, the cross-over percentages being 41.35 ± 1.94 and 40.77 ± 3.28 respectively, i.e. roughly 41% in each case.

II. Tipped 2 x Bearded.

This segregation was studied in crosses 3 and 4. In the former there was an unusually sharp distinction between the heterozygote and both parental types in the F_2, so that complete classification for awn type was possible. The observed segregation was:-

	Bearded	Heterozygous	Tipped 2	Total
Observed	65	230	108	403
Expected	100.75	201.50	100.75	403

$\chi^2 = 17.24$ D.F. = 2 $P = < .01$

A single factor segregation is therefore indicated, but there is a significant deficiency of the bearded type. In this cross, only 73.0% of the F_2 grains sown produced mature plants, so that there may have been a selective elimination of bearded plants. A heavy late spring frost and a severe spring drought occurred during the season (1938) in which the family was grown.

Cross 4 gave the following back-cross ratios for the segregation of the factor pair for Tipped 2 v. bearded:-

	Tipped 2	Bearded
(M.V. x Rivet)F_1 x M.V.	17	24
(M.V. x Rivet)F_1 x Rivet	19	25
Total	36	49

$\chi^2 = 1.694$ P = .19 approx.

In this case there was no evidence of linkage between the factors for Tipped 2 v. bearded and round v. keeled glumes, there being 41 parental combinations and 42 recombinations of these two factor pairs.

III. Tipped 1 x Tipped 2.

This combination was studied most extensigely in cross 5. This was carried through to F_3 by Mr A.E. Watkins, but the records were unfortunately lost. However, a random sample of the F_2 had been kept, and was classified by the writer. This family consisted of fully bearded forms, completely beardless ones and various intermediate tip-awned types that were not accurately classifiable. The distinction between fully bearded ears and other types was sharp, but accurate separation of completely beardless ears was not possibl

The segregation was:-

	Bearded	Intermediate	Beardless	Total
Observed	13	192	23	228
Expected	14.25	199.5	14.25	228

χ^2 for bearded v. others = 0.042. D.F. = 1. P = .80—.90

This is therefore a very good fit to a 15:1 ratio for beardless and intermediate to bearded, indicating a two factor difference between the parents. The apparent excess of beardless plants in F_2 was due to the classification difficulty — some of them were observed by Mr Watkins to segregate for one or other of the tip-awn factors in F_3 and there was every indication that the true ratio was normal.

If the Tipped 2 factor is designated as $\underline{B_2}$, we may now represent the types so far studied as:-

Tipped 1	$\underline{B_1B_1b_2b_2}$
Tipped 2	$\underline{b_1b_1B_2B_2}$
Beardless segregates	$\underline{B_1B_1B_2B_2}$
Bearded	$\underline{b_1b_1b_2b_2}$

The above combination was also studied in cross 6, in which the F_2 segregation was:-

	Bearded	Beardless and intermediate	Total
Observed	46	806	852
Expected	53.25	798.75	852

χ^2 = 0.913 D.F. = 1 P = .30—.50

Here, again, we get a normal 15:1 ratio.

IV. Tipped 2 x Tipped 2.

Crosses between the Tipped 2 form M.V. used in cross 5 and the forms Persia 465 and India 742, the latter a beardless *T. sphaerococcum*, gave no segregation for awn type in the F_2, thus indicating that both these wheats were also of the Tipped 2 constitution, $b_1b_1B_2B_2$.

V. Hooded bearded x bearded.

The F_2 segregation for cross 9 was as follows:-

	Bearded	Hooded and Heterozygous	Total
Observed	91	267	358
Expected	89.5	268.5	358

$\chi^2 = 0.0149$ D.F. = 1 P = .90 approx.

Hooded bearded *T. vulgare* therefore differs from bearded by a single factor. The results of crosses 10 to 13 and 17 reported below show that this factor is not allelomorphic with either B_1 or B_2, so that it may be denoted by a fresh symbol Hd, hooded bearded being Hd Hd, and bearded hd hd.

VI. Hooded bearded x Tipped 2.

This segregation was studied in F_2 populations of crosses 10 to 13, the results of which are presented in Table III (expected values based on a 15:1 ratio are put in brackets throughout). Only the bearded segregates were accurately distinguishable in F_2, the remaining plants containing hooded bearded, Tipped 2, hooded beardless and various unclassifiable intermediate types.

TABLE III

Segregation in Hooded bearded x Tipped 2 crosses

Cross	Bearded	Others	Total	χ^2	Degrees of freedom
10	20(14.25)	208(213.75)	228	2.063	1
11	28(40.6)	622(609.4)	650	3.860	1
12	21(26.69)	406(400.31)	427	1.076	1
13	24(34.1)	522(511.9)	546	2.896	1
				9.895	4
Total	93(115.7)	1758 (1735.3)	1851	4.539	1

Analysis of χ^2

	χ^2	D.F.	P
Deviation	4.539	1	.02—.05
Heterogeneity	5.356	3	.10—.20
Total	9.895	4	

The above 15:1 segregation shows that the "hooded" factor <u>Hd</u> and the Tipped 2 factor $\underline{B_2}$ are not allelomorphic. There is a slight deficiency of bearded plants in the above families, which may be due to pollen competition or to differential viability in the severe spring of 1938. The percentages of F_2 grains sown which produced mature plants in the above families were 47.2, 70.7, 59.9 and 65.9 respectively, so that the possibility of selective elimination certainly exists. Alternatively, the deficiency may be due to a weak linkage between the factors *Hd* and B_2, since bearded is a recombination type in the above crosses. This latter possibility is, however, ruled out for two reasons (1) the factors *Hd* and B_2 show no significant linkage in crosses 14 and 15 and (2) a similar deficiency of bearded plants occurs in certain other crosses involving B_2 where single factor ratios were examined, viz. crosses 3 and 14.

The cross hooded bearded x Tipped 1 was not made, but the factors *Hd* and B_1 are involved together in cross 17.

VII. Hooded beardless x Bearded.

Cross 14, which involves hooded beardless *T. vulgare* and bearded *T. sphaerococcum*, is described at length in the third section of this thesis. Complete classification for awn type was only possible in the *vulgare* segregates, but it was shown that the hooded beardless type carries the factors *Hd* and B_2, which are independently inherited, so that 1/16 of the progeny were fully bearded. The F_2 segregations, based on F_3 progeny tests, for these *vulgare* segregates were as follows:-

	Hd Hd	Hd hd	hd hd
Observed	96	163	72
Expected	82¾	165½	82¾

$\chi^2 = 3.556$ D.F. = 2 P = .10—.20

	B_2B_2	B_2b_2	b_2b_2
Observed	97	176	56
Expected	82¼	164½	82¼

$\chi^2 = 11.827$ D.F. = 2 $P = < .01$

The F_2 contained hooded beardless, hooded bearded, Tipped 2 and bearded forms in addition to the various expected intermediate heterozygotes. The F_3 results show a significant deficiency of b_2b_2 plants, a result similar to that shown in cross 3 and suggested in crosses 10 to 13. The deficiency was shown to occur equally in the SS (pure vulgare) and Ss (heterozygous vulgare/sphaerococcum) segregates, so that it cannot be due to linkage with the s factor.

The combination hooded beardless x bearded was also studied in cross 15, which is an inter-group cross in which normal segregations were obtained by back-crossing the pentaploid F_1 to the parents.

The segregations in this cross, based on progeny tests of the back-cross plants, are shown in Table IV. Only the awn factors B_2 and Hd and their linkage with K (keeled glume) are considered.

TABLE IV

Segregation of Awn Factors in Chinese White x Rivet Back-crosses

(a) Single Factor Ratios

Combination	$\underline{B_2}$: $\underline{b_2}$	Degrees of freedom	χ^2	$\underline{Hd}$: $\underline{hd}$	Degrees of freedom	χ
(C.W. x Rivet) F_1 x C.W.	32 : 46	1	2.167	47 : 33	1	2.11
(Rivet x C.W.) F_1 x Rivet	29 : 17	1	2.399	22 : 24	1	0.02
(C.W. x Rivet) F_1 x Rivet	69 : 62	1	0.275	61 : 70	1	0.48
		3	4.841		3	2.62
Total	130 : 125	1	0.063	130 : 127	1	0.01

(b) Analysis of χ^2

	$\underline{B_2}$: $\underline{b_2}$			$\underline{Hd}$: $\underline{hd}$		
	χ^2	Degrees of freedom	P	χ^2	Degrees of freedom	P
Deviation	0.063	1	.80 approx.	0.016	1	.90 appr
Heterogeneity	4.778	2	.05—.10	2.608	2	.20—.30
Total	4.841	3		2.624	3	

(c) Linkage Relations.

Factor Pair	Parental Combinations	Re-Combinations	χ^2	P
$\underline{B_2}$ & $\underline{Hd}$	135	120	0.769	.30 - .50
$\underline{B_2}$ & $\underline{K}$	94	102	0.250	.50 - .70
$\underline{Hd}$ & $\underline{K}$	100	98	0.005	.90 - .95

The above results therefore confirm those of cross 14, Chinese White differing from bearded Rivet by two awn factors Hd and B_2. The factors Hd and B_2 do not show any significant linkage with each other and it also appears that both factors segregate independently of the factor K for keeled glumes. The absence of linkage between Hd and B_2 is further shown in cross 14 above.

The three different back-cross families in the above table do not show significantly different segregations for Hd or B_2. With respect to B_2, however, the value of χ^2 for heterogeneity approaches significance and there is a suggestion that there is again a disturbance due to a deficiency of b_2b_2 plants. The back-crosses to Rivet, in which the ratio should be 1 B_2b_2 : 1 b_2b_2, actually give a total of 98 B_2b_2 : 79 b_2b_2. This is not a significant deviation from a 1 : 1 ratio but it certainly cannot be asserted, on the basis of these data, that the deficiency of b_2b_2 plants found in cross 14 does not also occur in the present cross. The loss may have been due to differential viability of the young plants, as by no means all of the seeds sown in this cross produced mature plants.

VIII. Hooded beardless x Tipped 2.

Cross 16 showed only hooded beardless and Tipped 2 segregates in F_2, together with the expected intermediate heterozygotes. The ratio appeared to be roughly 1 : 2 : 1, but accurate classification proved impossible. The absence of bearded or hooded bearded segregates in this progeny shows conclusively that the tip-awned factor carried by Chinese White is actually B_2, a fact which had already been deduced from the phenotypic appearance of the tip-awned segregates in crosses 14 and 15 above.

IX. Hooded beardless x Tipped 1.

The behaviour of cross 17, Chinese White x Squarehead's Master, may now be predicted on the basis of the above results. Chinese White has the constitution $b_1b_1B_2B_2$Hd Hd, while Squarehead's Master is $B_1B_1b_2b_2$hd hd. One would therefore expect 1/64 of the progeny to be fully bearded, the remaining types including hooded bearded, Tipped 1, Tipped 2, hooded beardless and ordinary beardless wheats together with all possible intermediate heterozygotes. This was actually the case. In F_2 only the fully bearded segregates could accurately be distinguished, the segregation being as follows:-

	Bearded	All others.	Total
Observed	13	1095	1108
Expected	17.3	1090.7	1108

$\chi^2 = 0.853$ D.F. = 1 P = .30 - .50

The result is a good fit to the expected 1:63 ratio.

X. Beardless x Bearded.

The only cross in which this combination was studied, cross 18, was an inter-group cross in which inheritance proved to be very complicated owing to disturbances due to partial sterility. The results served to show, however, that the beardless parent, Australia 6, differed from bearded in two factors, which separately determined the Tipped 1 and half-awned condition. Bearded, half-awned, Tipped 1 and beardless pure-breeding *durum* segregates were isolated. The beardless *durum* plants were stunted and showed very considerable sterilit even after several generations of selection.

4. Genetic Analysis of Crosses Involving the Hooded Character of Abyssinian Tetraploid Wheats.

I. Hooded Bearded Abyssinian tetraploid x Bearded *durum*

This cross showed relatively high fertility and no genetic irregularity was observed in the inheritance of the hooded character.

The F_1 and the heterozygous F_2 plants resembled the bearded parent quite closely in their main tillers but had markedly hooded late tillers (see above, p. 11). It should therefore have been possible ideally to effect a complete classification of the F_2. This was impossible in practice, however, owing to the fact that many plants had single tillers or two nearly equal tillers only, so that they could not be classified definitely as either heterozygous or bearded. The F_2 classification was therefore made for the pure hooded plants v. all others. The result was:-

	Hooded	Bearded and Heterozygous
Observed	113	362
Expected	$118\frac{3}{4}$	$356\frac{1}{4}$

$\chi^2 = 0.070$ P = .70 - .80

All the F_2 plants which yielded enough grain to plant a row were grown on to F_3, where the F_2 classification was found to be substantially correct. The F_3 ratio for 415 F_2 plants which had been classified as 79 hooded : 236 bearded and heterozygous, was 77 : 238. Three heterozygous plants were wrongly classed as pure hooded and one hooded plant was classed as heterozygous in F_2. The single factor inheritance of the hooded character was fully confirmed in F_3.

The Abyssinian parent in this cross had considerably shorter straw than the bearded parent, so that measurements of the plant height of the parents, the F_2 and of a random sample of F_3 rows were made to determine whether there was any linkage between that character and the hooded factor. The results are expressed in Table V (the parent rows measured were growing next to the F_2 on an apparently uniform plot, so that the heights quoted may be regarded as comparable).

TABLE V

Relation between Hoodedness and Plant Height in the Cross Hooded Abyssinian x Indian Runner

		Plant height in cm.
Parents		
	Indian Runner	102.66 ± 2.22
	Hooded Abyssinian	69.18 ± 1.57
	Difference	33.48 ± 2.72
F_2		
	Bearded & heterozygous plants	104.01 ± 0.67
	Hooded	92.86 ± 1.24
	Difference	11.15 ± 1.41
F_3		
	17 pure bearded families	86.22
	24 segregating families	87.20
	17 pure hooded families	75.87

Difference between hooded families and others *ca* 11 cm.

It may be concluded from the above results that the hooded factor in Hooded Abyssinian is linked to a factor which reduces length of straw (the actual distance measured was from the rooting node to the tip of the ear, excluding the awns). The difference between the heights of the parents (33.5 cm.) was, however, much greater than that between the hooded segregates and the other two groups (11 cm.). It therefore appears likely that the parents differed by factors other than the one which is linked with the hooded gene, and which segregate independently. This possibility is confirmed by the measurements of heights of individual families in F_3, which showed clear differences due to the segregation of other height factors.

The closeness of the linkage between the hooded gene and the factor determining short straw cannot be determined without extensive biometrical studies, which were not carried out. The F_3 results suggested, but did not prove, that the linkage was not absolute. The mean plant heights in cms for 17 hooded families were as follows:- 99.6, 76.2, 82.9, 77.7, 67.8, 73.5, 73.3, 65.6, 65.9, 79.3, 90.3, 70.8, 71.4, 74.1, 79.1, 82.4, 74.0. The average standard error of these figures is around ± 3.75 cm. The two families with mean heights of 99.6 and 90.3 show a fairly marked discontinuity from the others, and compare with a mean height of 86.22 for all the bearded families taken together. These two may therefore have been cross-overs between the hooded gene and the short straw factor to which it is linked.

DISCUSSION

We are now in a position, on consideration of the above results taken in conjunction with those of previous workers, to make a more or less comprehensive statement of the mode of inheritance of awns in *T. vulgare*, as regards the major awn types. Bearded forms must be regarded as the bottom recessive in each case. There are five established major factors which, alone or in combination, lead to the production of the major awn classes. These, together with the phenotypes they produce when acting alone, may be denoted as follows:-

$\underline{B_1}$ —— Tipped 1
$\underline{B_1^a}$ —— ½-awned (allelomorphic with $\underline{B_1}$)
$\underline{B_2}$ —— Tipped 2
$\underline{A}$ —— ½-awned
$\underline{Hd}$ —— hooded bearded

In addition, it is possible that the half-awned types that have awns of practically equal length in all parts of the ear and occur but rarely, may be due to another factor — they were not studied in the present crosses and have not been reported upon elsewhere.

On the basis of the above five factors, the genetic constitution of the awn types of *T. vulgare* may be represented as follows:-

Bearded	$\underline{b_1b_1b_2b_2aa\ hd\ hd}$	
Tipped 1	$\underline{B_1B_1b_2b_2aa\ hd\ hd}$	
Tipped 2	$\underline{b_1b_1B_2B_2aa\ hd\ hd}$	
½-awned	$\underline{B_1^aB_1^ab_2b_2aa\ hd\ hd}$	or
	$\underline{b_1b_1b_2b_2AA\ hd\ hd}$	
Beardless	$\underline{B_1B_1B_2B_2aa\ hd\ hd}$	or
	$\underline{B_1B_1b_2b_2AA\ hd\ hd}$	
Hooded bearded	$\underline{b_1b_1b_2b_2aa\ Hd\ Hd}$	
Hooded beardless	$\underline{b_1b_1B_2B_2aa\ Hd\ Hd}$	= Tipped 2 hooded

The above types are those actually proved to exist. In addition, various other combinations would be expected to give the beardless and hooded beardless types, e.g. $\underline{b_1b_1B_2B_2AA\ hd\ hd}$ in the former case, and $\underline{B_1B_1b_2b_2aa\ Hd\ Hd}$ in the latter.

The only possible simplification of the above factorial scheme is that the factors $\underline{B_2}$, $\underline{A}$ and $\underline{b_2}$ may actually be multiple allelomorphs, just as are the factors $\underline{B_1}$, $\underline{B_1^a}$ and $\underline{b_1}$. No cross involving $\underline{A}$ and $\underline{B_2}$ has been studied genetically. That this multiple allelomorphic relationship may actually hold is suggested by three things. Firstly, one may expect a parallel series to the $\underline{B_1}$, $\underline{B_1^a}$, $\underline{b_1}$ series to be present in hexaploid wheats, on the basis of the law of homologous variation. Secondly, it is curious that all the beardless wheats containing $\underline{A}$ which have been studied, also contain $\underline{B_1}$ and not

B_2, and this in spite of the fact that several of them were of Indian origin and the B_2 gene is ten times as common in India as is B_1. This strongly suggests that a wheat of the constitution B_2B_2AA cannot exist, because B_2 and A are homologous. Thirdly, although a complete classification of half-awned wheats into sub-types was not possible, it seems to be true that those having the gene B_1^a have awns more definitely localized at the apex of the ear than those carrying the gene A. In other words, the difference between these two types corresponds to that between Tipped 1 and Tipped 2 wheats. If the factors B_2, A and b_2 are actually multiple allelomorphs, the series whould be represented as B_2, B_2^a, b_2, and the genetic constitution of the above types would be:-

Bearded	$b_1b_1b_2b_2\,hd\,hd$
Tipped 1	$B_1B_1b_2b_2\,hd\,hd$
Tipped 2	$b_1b_1B_2B_2\,hd\,hd$
½-awned	$B_1^aB_1^ab_2b_2\,hd\,hd$ or
	$b_1b_1B_2^aB_2^a\,hd\,hd$
Beardless	$B_1B_1B_2B_2\,hd\,hd$ or
	$B_1B_1B_2^aB_2^a\,hd\,hd$ or (presumably)
	$B_1^aB_1^aB_2B_2\,hd\,hd$
Hooded bearded	$b_1b_1b_2b_2\,Hd\,Hd$
Hooded beardless	$b_1b_1B_2B_2\,Hd\,Hd$ (or, presumably, Hd with B_2^a, B_1 or B_1^a).

The latter factorial scheme is regarded by the writer as being much the more probable. The crucial cross necessary to distinguish between the two schemes will be made at the earliest opportunity.

In addition to the above, we have certain other information about these factors. $\underline{B_1}$ is linked with the factors for pubescent node, squareheadedness and keeled glumes (speltoid). All the factors are contained in the *A* or *B* genoms, as all may be transferred to tetraploid wheats and there segregate regularly. None of these awn factors appears to be linked with any other in normal wheats, the only exception being the unusual linkage between $\underline{B_1}$ and *A* recorded by Stewart (1926, 1928b) in two Federation crosses.

As regards the Abyssinian wheats, only one factor, the hooded factor, was studied. This has a similar effect to the gene *Hd* formed in *T. vulgare* and has the same very curious dominance relations. The cross between hooded Abyssinian and a hooded *vulgare* wheat has now been made to establish the identity of the two genes, but it seems extremely probable that the same gene is involved in each case.

Having established a classification of the awn types occurring in wheats and having obtained a clear view of their mode of inheritance, we may now proceed to discuss their geographical distribution in Eurasia.

V. THE GEOGRAPHICAL DISTRIBUTION OF AWN TYPES IN TRITICUM VULGARE.

Our present knowledge of the distribution of awn types in *T. vulgare* is largely a consequence of the extensive plant explorations made by Vavilov and his Russian co-workers. The distribution of the four main types recognized by the systematist for the purpose of classification into botanical varieties, i.e. *muticum*, *breviaristatum*, *inflatum* and *aristatum* is fairly well known. It will be realized from the above genetic work, however, that two of these types, *muticum* and *inflatum* may be divided into genetically different sub-types, viz. Tipped 1, Tipped 2, beardless, hooded bearded and hooded beardless. Very little is known of the distribution of these types. Further, none of the previous studies has been concerned with the relative frequency of occurrence of the various genes in different regions; they have mostly been confined merely to recording the presence or absence of specified botanical varieties in the regions studied.

For the present purpose, the distribution of *T. vulgare* types in Europe and Asia only will be considered. Most *vulgare* wheats found in North Africa are recently imported forms and, of course, the same is true of all the wheats in North and South America, Australia and South Africa. Only the regions of old cultivation of wheats are of interest for a study of the geographical distribution of genes.

Our present knowledge of the distribution of awn types in T. vulgare is summarized by the distribution ~~of~~ map facing page 16 in Vavilov's "Theoretical Bases of Wheat Breeding (1935). It may be briefly summarized as follows: The types aristatum and muticum (bearded and "beardless") are found throughout the range of wheat cultivation. The inflatum type (including hooded bearded and hooded beardless) is more restricted. It occurs in Asia Minor, the Caucasus region, Iraq, Iran, Afghanistan, Turkestan, India, central Siberia, and China. It is absent from Europe, including European Russia, and from the more northerly and north-easterly parts of Siberia, Manchuria and Japan. Breviaristatum (half-awned) has a range almost identical with that of the inflatum type — both are absent from the regions of Europe and Asia farthest removed from the supposed centre of origin of hexaploid wheats.

For more detailed accounts of the Russian plant explorations, the reader is referred to Kobelev (1928), Stoletova (1930), Vavilov (1923, 1931) and Vavilov and Bukinich (1929).

In order to study the geographical distribution of the seven major awn types described in the previous section, the author classified two large collections of vulgare wheats, totalling some 3,~~5~~700 forms from nearly all parts of Europe and Asia. The larger of these, consisting of some ~~2,900~~ 3,100 forms was assembled by Mr A.E. Watkins, who obtained his material chiefly through the co-operation of the British consular service and also in part from agricultural experiment stations throughout Europe and Asia. This collection consisted principally of Asiatic forms. It was classified from ears stuck on cards and from material grown in the field. A large part of the material was grown on and re-classified in ~~the~~ a second~~ing~~ season as a check.

The smaller collection, of some 600 forms, was assembled by Professor J. Percival and was classified exclusively from ears stuck on cards. It was predominantly of European origin and therefore largely complementary to the other collection. Since very few wheats (if any) were common to both collections, they may be added together without any serious overlapping. Although Percival's collection was classified only from single ears on cards, ~~one may have every confidence in the accuracy of~~ the classification may be regarded as highly accurate, since it was ~~.~~ They were classified carried out after the author had carefully studied the larger collection for two years and had become thoroughly accustomed to distinguishing the differences between types. Classification of European forms is in any case relatively simple, since very nearly all of them proved to be either fully bearded or very obviously Tipped 1.

A few words of explanation must be given with regard to the exact method of assembling the larger collection.

The "samples" which were obtained were representative of the crops of the districts where they were collected and were often mixtures of several types. They were grown in Cambridge in 10-row plots and observed carefully. A specimen of every recognizably distinct type occurring in the mixture was then picked out and in the following years these types were grown on as "lines". These selected pure lines and not the original samples were studied by the author. In general, a close correlation between the proportion of different awn types found in th "lines" from a particular region and the proportion in the original population may be expected, as the lines were picked out on the basis of differences in any observable character and not merely in awn type. The method of selection would, however, tend to exaggerate the importance of any form which occurred in small proportions ~~of~~ as an admixture throughout the wheats of a region. It would, in fact, tend to some extent to level any difference in the proportions of the various awn types.

The results of the classification of the collections into the seven awn types is shown in Table VI, the lines being grouped by countries. In the table the countries have been arranged as far as possible in the order of their longitude, starting with the most easterly and proceeding westwards. The political sub-divisions used are those of August, 1938.

The geographical distribution of the four types

TABLE VI

Geographical Distribution of Awn Types in Triticum vulgare

	Bearded	Tip 1	Tip 2	B'less	½-awn	Hood B'd	Hood B'less	Total
Japan	12						1	13
China	252	23	78	19	9	18	16	415
Burma	15			2				17
India	441	22	214	50	23	34	11	795
Afghanistan	58	4	1		16	5		84
Iran	398	7	10	1	79	122		617
Iraq	50		13	1	1	1		66
Syria	33	1						34
Palestine	2							2
Turkey	53	3			2			58
U.S.S.R.	181 ~~68~~	96 26	7 ~~3~~		1	4 ~~2~~		289 ~~99~~
Cyprus	3							3
Crete	36	5	1					42
Bulgaria	45	7						52
Rumania	23	1						24
Greece	93	3						96
Yugoslavia	87	26			3			116
Hungary	30	2						32
Poland	17	15						32
Italy	24	16			4			44
Germany	11	47		1				59
Austria	12	15						27
Denmark		3						3
Sweden	1	18						19
Switzerland		13						13
Holland	1	12						13
Spain	334	103	3		4			444
Portugal	153	38	5			1	1	198
France	15	72						87
Great Britain	2	39						41
	2269	521	328	74	141	183	29	3545

which show single gene differences from bearded is shown further in Text-figs 4 to 7. In these maps an attempt has been made to show the distribution within the larger Asiatic countries (China, India and Iran) and within the U.S.S.R. In the case of the western European countries, no such attempt has been made, as the countries themselves are so small that an even distribution of the requisite number of dots within their boundaries is precise enough for present purposes. In all four maps, each dot represents a single pure line.

A certain amount of caution is necessary in the use of these maps. By comparing them, the relative frequency of different types in a particular region may be seen, and differences between the distribution of dots in the various maps indicate differences in the distribution of the types. A blank area in any particular map may, however, merely mean that no sample was obtained from that region; in other words, the maps should to some extent be used in conjunction with Table VI in order to determine whether the apparent scarcity of a particular type in a given region is real or due to inadequate sampling.

The types will now be considered seriatim.

1. Fully Bearded.

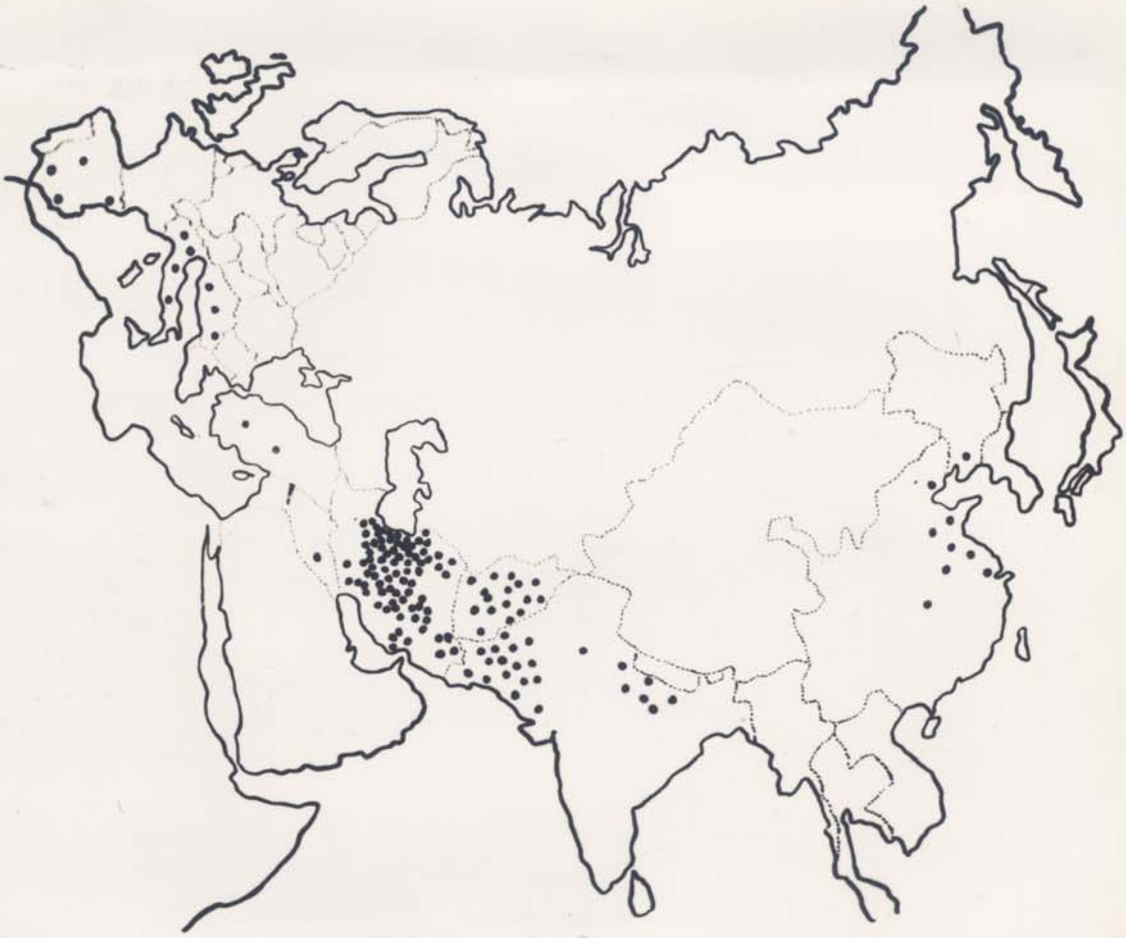
Bearded wheats are seen in Table I to occur throughout the range of *T. vulgare*, and form the most frequently

Text-fig. 4.

Distribution of Tip-awned 1 T. vulgare

Text-fig. 5.

Distribution of Tip-awned 2 *T. vulgare*

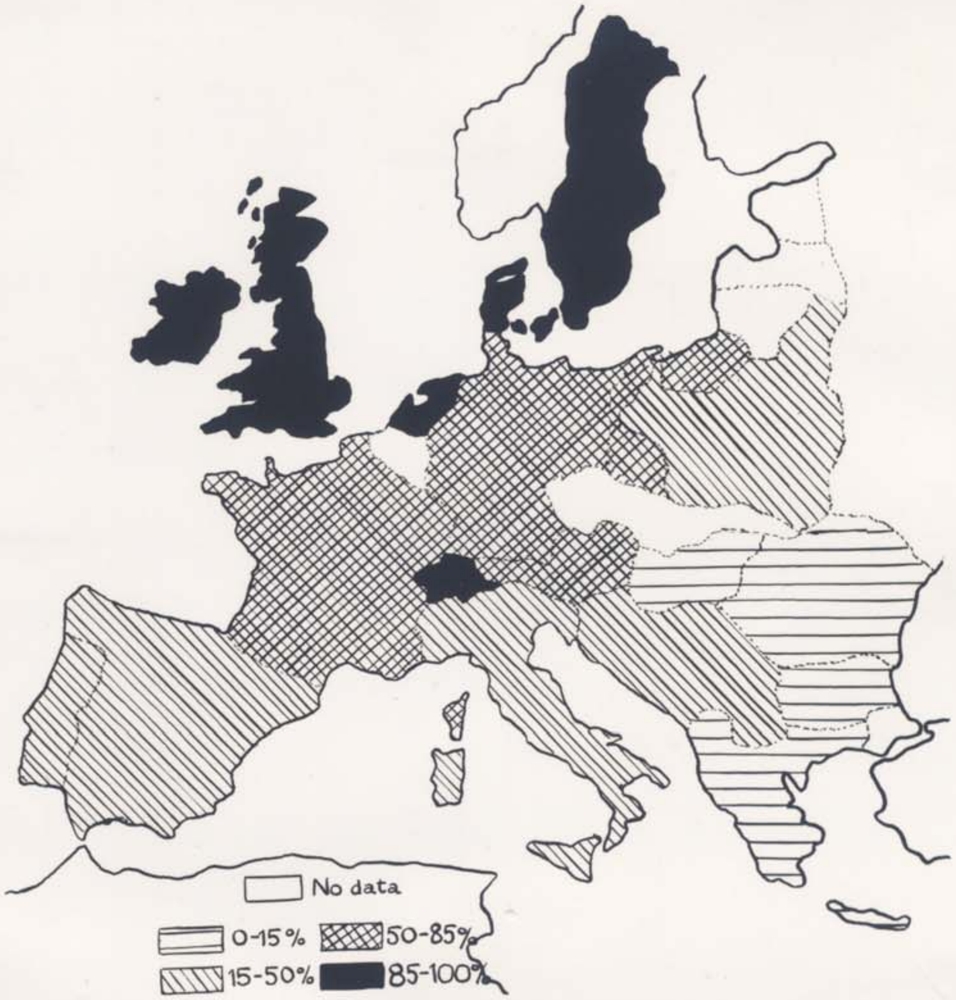


Text-fig. 6.

Distribution of Half-awned T. vulgare

Text-fig. 7.

Distribution of Hooded Bearded T. vulgare



Text-fig. 8.

Frequency of Tip-awned 1 *T. vulgare* forms
in Europe (excluding U.S.S.R.), expressed
as percentage of total

occurring type in most regions. It is only in north-western Europe that they are relatively infrequent. It was not thought necessary to plot the distribution of this type, since it would merely coincide with the regions from which samples were obtained.

2. Tipped 1.

It is shown in Table VI that, apart from certain countries from which an inadequate sample was obtained, Tipped 1 wheats also occur throughout the area of cultivation of T. vulgare. In the case of the Chinese forms, there was some suspicion that the types may have not been indigenous; American and other foreign wheats have fairly recently been introduced into China in appreciable numbers and it was possible that they may have included all the Tipped 1 wheats found there. A careful examination of the Tipped 1 Chinese wheats, however, dispelled this idea. Some of them probably were introductions, but others were characteristically Chinese in other respects; they had, for instance, the association of thin, papery glumes, easily shattered ear, many grains per spikelet and very fine awn tips (corresponding to very fine-awned bearded wheats) often found in China and not found elsewhere. It may therefore be safely assumed that the Tipped 1 type has occurred in China for a considerabl time.

A glance at the later maps (Text-figs 5 to 7) will show that the Tipped 1 and bearded types comprise very nearly all of the wheats found in Europe, the Tipped 2, half-awned and hooded types being extremely rare. The concentration of Tipped 1 wheats found in north-western Europe is particularly striking. Text-fig. 8 shows this distribution in a different way — it shows the proportion of all the wheat lines obtained from each country which were Tipped 1.

It will be seen that in south-eastern Europe, viz. Greece, Bulgaria, Rumania and Hungary, bearded wheats are predominant — they form 191 out of a total of 204 lines, or roughly 94%. In northern Europe, viz. Britain, Holland and Scandinavia, bearded wheats were rare and Tipped 1 forms constituted 72 out of 76 lines, or some 95%, the remaining 5% being bearded. Between these two sections there is a very regular gradation with the possible exception of Switzerland which shows a very high proportion of Tipped 1 forms. The sample from that country was, however, very small.

The reason for this gradation is not clear — it may be one of several. It is possible that the Tipped 1 type shows some genuine adaptation to a cool, oceanic climate while the bearded type is better suited to continental conditions. Precise data establishing such an adaptation are lacking; the opinions on the function of the awn in wheat which have been expressed are so varied and conflicting that they will not be discussed here. If such adaptation exists, however, the bearded type would be favoured by natural selection in a mixed population in south-eastern Europe and the tip-awned type in northerly regions. Alternatively, the better adapted type may have been consciously selected in both regions.

This reason of specific regional adaptation of the two types does not, however, seem a very probable one. There is no evidence that parallel changes in the proportion of tip-awned and bearded wheats occur, for instance, when one passes from south-western China to the more oceanic regions to the north-east.

A more likely reason is that it is due to a difference between the amount of conscious plant selection which has been practised by the farming communities in different parts of Europe. One may assume that a mixture of bearded and tip-awned wheats was first introduced in all parts. The awns, however, are in general a disadvantage. They render harvesting unpleasant and lessen the value of the straw for feeding. The awned type would therefore be selected against by the farmers in the more progressive communities of the north and west, and by the early plant breeders in those countries. In the south and east the peasant farmers are clearly in many respects more conservative and less developed and have in the past probably been content to continue sowing the local mixture.

If the above theory is true, and there is no initial superiority of awned forms to particular climatic conditions, the growing of predominantly awned wheats in parts of Europe with hot, dry summers and of Tipped 1 wheats in regions with a cool, oceanic climate would naturally be followed by adaptation of the different types to the regions in which they grow. This adaptation is probably reflected in the present-day distribution of United States wheats, which of course are almost exclusively of European origin. In general, bearded wheats are there preferred to beardless in the regions with the most continental climates. This distribution need not necessarily reflect any real adaptation of the awned character as such to hot, dry conditions. If the farmer would prefer beardless wheats in any such regions in America, the plant breeder may do well to turn to the occasiona Tipped 1 wheats from such countries as Rumania for parent material for use in crosses.

It should be noted that in the wheat-growing districts of Australia, beardless and tip-awned wheats of predominantly Indian origin have been most successful, so that the correlation between hot, dry summers and awned wheats is by no means invariable.

3. Tipped 2.

A glance at Text-fig. 5 will show at once that the Tipped 2 type has a very different distribution from Tipped 1. It occurs commonly in China and India and westwards into Iran, Iraq and southern Russia. The illustrations of Stoletova (1930) show that it occurs in Armenia.

In Europe, the type is absent except for a few forms found in Spain and Portugal. It is extremely probable that these are importations of Asiatic wheats made by the early Portuguese and Spanish explorers and traders. Various other Asiatic wheat types are found in small quantities in the Iberian peninsula and presumably came in in this way — among them, a single example of a hooded bearded wheat to be mentione later.

The distribution of Tipped 2, then, appears to be roughly co-extensive with that of the hooded and half-awned types. It is, unfortunately, not known how far the type extends north-east into Siberia. It is certainly common as far north as southern Manchuria.

The Tipped 2 type never becomes as predominant in any one region as does the Tipped 1 type in north-western Europe. In India, where it is commonest, it forms only about a quarter of the total samples collected. It appears that in no other region has natural or artificial selection against the bearded type been so intense as in north-western Europe.

4. Half-awned.

This class, as indicated above, consists of two (or possibly more) distinct genetical types which are not classifiable without genetic analysis, ~~and~~ since they form an almost continuous series. The geographical distribution plotted in Text-fig. 6 confirms in general the distribution of the type recorded by Vavilov (1935), but it is seen to extend in small numbers into the Mediterranean region and it has also been reported by Jenkin (1925) and Nilsson-Ehle (1920) in north-western Europe.

Examination of the half-awned types from Europe indicates that though some of them have very long apical awns and very short awns lower down the ear and are presumably of the type which is allelomorphic with Tipped 1, others have the more even distribution of awns associated with the other half-awn gene (A). Without a more extensive genetical study, there is therefore no evidence that the distributions of the two half-awn types differ~~s~~ except for the extension of the B_1^a gene into north-western Europe, where A is not found.

Although the half-awned wheats are widely distributed in Europe, they are in all parts very rare, and are not grown extensively in any region. They are really important in quite a limited area only — in Iran, Baluchistan, Afghanistan and in the adjoining parts of Turkestan. In Iran 79 half-awned forms were recorded out of a total of 617 lines, an exceptional high proportion. In that country tip-awned wheats of both types are rare and the half-awned and hooded bearded types appear to replace them.

5. Beardless.

This type is considered here since it is due to various combinations of two of the genes which account for the tip-awned and half-awned types described above. As is to be expected, it is confined to those regions in which the genes $\underline{B_1}$ or $\underline{B_1^a}$, and $\underline{B_2}$ or $\underline{A}$ (? = $\underline{B_2^a}$) are commonly found together. In the collection examined it was recorded in China, India, Burma, Iran and Iraq. Presumably it also occurs in Afghanista and the neighbouring regions and in Asia Minor and Armenia, though the samples from these regions were not large and did not contain it. A single form (of unknown genetical constitution) was found in Germany.

6. Hooded Bearded.

The distribution of this type, shown in Text-fig. 7, corresponds closely with its previously known range, except that, owing to the inadequacy of the sample, no specimens were recorded from Asia Minor or the Caucasus, where they are known to occur (Vavilov, 1935). According to Vavilov (1935 and earlier papers) hooded wheats also occur widely in Russian Turkestan and in the extreme north-west of China. No new knowledge, then, is obtained from Text-fig. 7 except that it emphasizes the extraordinary concentration of hooded bearded forms in Iran and in the neighbouring parts of Baluchistan. In Iran, the type constituted roughly 20% of 617 lines. The single form recorded from Portugal is, as stated above, presumably an importation from the east.

There is a considerable difference in appearance between hooded bearded Iranian and hooded bearded Chinese wheats. The former have in most cases rather tough glumes which closely envelope the grain and the markedly U-shaped outline of the spikelets referred to above (p.20). Membranous lateral "wings" at the base of the awn are not so common as in China. Most Chinese types do not have the characteristic U-shaped spikelet outline, as they have the many-grains-per-spikelet character so common in China, making the spikelet uncommonly broad. The glumes are papery and the ear easily shatters. Hosono (1934) regards China as a "secondary centre of distribution" of hooded wheats. Whether he means ~~by~~ that the form arose independently by mutation in China and did not spread from the west is not clear. It appears probable to the author that the differences between the hooded character of Chinese and Iranian wheats are merely due to the presence of the same gene in a different genetic background. The Chinese hooded wheats may then have spread from Afghanistan or Iran — there were undoubtedly early contacts between China and these countries as they lay on the overland silk routes from China to the west. There were also military expeditions into western Thibet from China. The peculiar dominance relations of the hooded character are identical in ~~both~~ Iranian and Chinese forms and their behaviour in crosses is the same. Hooded bearded forms from the two countries have not, however, been crossed together so that it cannot be asserted positively that two distinct genes are not present.

The hooded forms in Sikkim, the region between Nepal and Bhutan, have, judging by their other ear characters, reached there from China and not directly from the west. They closely resemble Chinese hooded wheats in their ear characters.

7. Hooded beardless.

This last type, like true beardless, is due to a combination of "beardless" genes — the hooded gene, Hd, together with B_2 or (presumably) B_1. Its distribution would therefore be expected to be confined to regions where these genes occur together. It is accordingly found in China and India, though in small quantities. It would be expected in Afghanistan, Russian Turkestan, Iraq and Asia Minor, but the samples recorded from these countries were inadequate and did not contain it. In the large collection from Iran it did not occur either, but in that country Tipped 1 and Tipped 2 wheats were very rare, forming together only 17 samples out of a total of 617. A single line was found in Japan, possibly an introduction from China, and there was also one from Portugal, almost certainly, like the other oriental types found there, an importation from the east (it may, however, have arisen from natural crossing between imported hooded bearded wheats and local Tipped 1 types).

DISCUSSION

To summarize, of the seven awn types recognized in wheat only two, fully bearded and Tipped 1, are found throughout the range of vulgare wheat cultivation in Eurasia. With the exception of rare and almost certainly imported forms, the Tipped 2, hooded bearded and hooded beardless types are absent from Europe. Half-awned wheats, probably of both genetic types, are found rarely in Europe, where they occur occasionally as new mutations (see p. 34 above) and also, possibly, in the Mediterranean region as descendants of ½-awned forms in the old wheat populations which spread westwards from the Asiatic centre.

So much for the total range. As regards relative frequency of the types, the most striking facts are (1) the concentration of Tipped 1 types and apparent selection against bearded wheats in north-western Europe (2) the predominance of Tipped 2 over Tipped 1 forms in most parts of Asia and particularly in India and (3) the enormous number of half-bearded and hooded bearded wheats in Iran, where they almost entirely replaced tip-awned forms.

Let us now discuss the results from the point of view of the region of origin of *vulgare* wheats. It cannot, of course, be assumed that each particular mutation occurred but once in *T. vulgare* or in one of its parental species of *Triticum* or *Aegilops*. In the case of the half-awn gene $\underline{B_1^a}$, new mutations are definitely known to have occurred (Nilsson-Ehle, 1920). In general, however, the regularities of the distribution of the awn genes indicates that most of the present-day distribution can best be accounted for as being due to the spread of types from a single or at most a few centres. All of the genes concerned might, in fact, have spread from a centre in south-western Asia.

The data of Vavilov and Bukinich (1929) show that the greatest amount of botanical diversity in *T. vulgare* is found in Afghanistan. As one passes outwards from this centre there is a steady and progressive diminution in the number of types (Vavilov, 1923). This might lead one to suppose that Afghanistan is the centre of origin of *T. vulgare* Actually, however, it is not possible on the basis of Vavilov's botanico-geographical method to fix the centre of origin quite so precisely. Part of the excessive diversity of Afghan wheats may be due to the topographical and climatic diversity of the country itself. The centre of origin therefore must be stated less precisely as "south-western Asia

(Vavilov, 1935). One may suppose that the region includes Iran, Afghanistan, the adjoining parts of Turkestan and north-western India.

The data for the distribution of awn types detailed above lend some support to Vavilov's hypothesis of the centre of origin of T. vulgare, though they do not give any definite proof of its correctness.

Inspection of the distribution maps (Text-figs 4-7) shows that there is a strong suggestion that the four awn types mapped might have originated in different areas. Tipped 2, for instance, occurs extremely commonly in the United Provinces of India and is relatively rare in Afghanistan and particularly in Iran, though it occurs eastwards in China in fair numbers. Hooded bearded, on the other hand, is extremely common throughout Iran but virtually absent in India except in the part of Baluchistan adjoining Iran. The forms occurring in Sikkim almost certainly came from China.

The commoner half-awned gene (A) also centres in Iran. The region of origin of Tipped 1 wheats is not so certain since it is shown above that their great concentration in north-western Europe is probably due to deliberate selection

Now it is possible, as Vavilov seems to suppose, that all these types may have arisen in one region, say Afghanistan, and one or another has been specially favoured by natural or artificial selection in the surrounding regions to which the original mixed population has spread. On the other hand, it is also possible that the original T. vulgare population consisted of bearded plants and that the various awn mutations arose subsequently in various distinct regions removed from the original centre.

If we accept the usual hypothesis (for which there is considerable evidence) that T. vulgare arose as an allopolyploid form from a hybrid between a tetraploid Triticum species and a species of Aegilops, it does seem likely that the original form was bearded, since all tetraploid wheats known (except some forms in Abyssinia where vulgare wheat is virtually absent) are of the fully bearded type. Further, it is clear from the foregoing genetical and distributional data that the bearded type is in a sense basic in T. vulgare. It is the most widespread type and almost everywhere the commonest, and it bears a simple recessive genetical relationship to all others.

We may therefore reconstruct the probable life story of T. vulgare as follows: Having arisen as an allopolyploid with bearded tetraploid Triticum and an Aegilops species as parents, the original entirely bearded population gradually spread outwards from its ~~original~~ centre of origin, which was probably in or near Afghanistan. During the course of thousands of years, awn mutations occurred in various parts of the extended range of the species — in northern India and in Iran, for instance, and perhaps further west, say in Armenia or Asia Minor, in the case of the Tipped 1 gene. These mutant forms became established in the populations and were perhaps in some cases consciously selected by the tribes wh~~o~~ich grew them. Each mutant population in turn spread outwards from its centre of origin — sometimes along peaceful trade routes, sometimes with a conquering tribe — and it has happened that all of them have spread back to the original centre of origin of the species. In this way, Afghanistan now has the greatest number of types of wheat, though originall it may have had an almost homogeneous population.

Ripple analogy.

There are, of course, other possibilities than the one outlined above. T. vulgare may, for instance, have originated independently in several different places, or much of its present diversity may be due to repeated natural backcrossing to one or other of the parents. A good deal more work will be necessary before the evolutionary history of T. vulgare is quite clear. The exact nature of the awn mutations is not at present known clear. They may have been "point mutations" or, perhaps more probably, they may have been due to structural changes following occasional irregular pairing between small duplicated chromosome segments or some other anomalous type of chromosome behaviour. Whatever the mechanism, it appears that a parallel series of changes has taken place in T. vulgare and in the Abyssinnian tetraploid wheats.

7/6 cross-connections. Other genes in vulgare.

It may be well to stress one fact which emerges from the above discussion, and that is the inadequacy of the method of studying the distribution of the wheat species purely on the basis of their accepted botanical varieties. Single genes must be studied wherever possible: as an example of the inadequacy of the former method it may be pointed out that the very characteristic and distinct distributions of Tipped 1 and Tipped 2 wheats would have remained unknown just as long as both were classed together with true beardless as "muticum".

SUMMARY

1. The various ways in which awn length and type in wheat may be genetically influenced are detailed, with examples of each type of influence.
2. The awn types found in each of the important wheat specie are described.
3. On the basis of a careful study of the world's *vulgare* wheats, seven major awn types are recognized in the species.
4. Previous literature relating to the genetics of awn types in *T. vulgare* is interpreted on the basis of the above seven types.
5. Extensive new crosses of *vulgare* wheats were studied genetically. On the basis of these results the following factorial scheme is put forward for the seven main types:-

Fully bearded	$b_1b_1b_2b_2$aa hd hd
Tipped 1	$B_1B_1b_2b_2$aa hd hd
Tipped 2	$b_1b_1B_2B_2$aa hd hd
½-awned	$B_1^aB_1^ab_2b_2$aa hd hd
or	$b_1b_1b_2b_2$AA hd hd
Hooded bearded	$b_1b_1b_2b_2$aa Hd Hd
Hooded beardless	$b_1b_1B_2B_2$aa Hd Hd
Beardless	$B_1B_1B_2B_2$aa hd hd
or	$B_1B_1b_2b_2$AA hd hd

$\underline{B_1}$, $\underline{B_1^a}$ and $\underline{b_1}$ are multiple allelomorphs.

6. A possible, and indeed likely, simplification of the above scheme is that the factors $\underline{B_2}$, $\underline{b_2}$ and *A* may be multipl allelomorphs.

7. The geographical distribution of the above seven types was studied in two extensive collections of wheats from Europe and Asia and the detailed distribution of each type is discussed.

8. The distributional data so obtained are in accordance with Vavilov's hypothesis that *T. vulgare* originated in south-western Asia.

9. It is considered probable that the original *T. vulgare* population was fully bearded and that the various mutant awn genes arose subsequently in different regions after the awned type had spread outwards from its original centre.

10. A hooded bearded tetraploid wheat from Abyssinia was found to differ from the bearded form by a single gene.

11. This gene closely resembles in its effect the *Hd* gene of *T. vulgare* and is believed to be identical.

12. The hooded character of Abyssinian tetraploid wheat is linked (probably incompletely) to a factor for short straw.

PART II.

CHROMOSOME PAIRING IN PENTAPLOID WHEAT HYBRIDS.

I. Introduction

It has been shown by Watkins (1928) that when pentaploid hybrids between *Triticum vulgare* and *T. turgidum* are back-crossed to either parent, extremely regular segregations for the factors for keeled glumes (*K*) and beardedness (b_1) are obtained, as well as for several other factors located in other chromosomes. Extra data obtained by the author for the cross studied by Watkins and also for other *T. vulgare* x *T. turgidum* hybrids (see Part I above) confirm this contention. The same is also true of *T. vulgare* x *T. dicoccum* hybrids (p. 43 above). It was with some surprise, therefore, that Mr Watkins found that crosses between *T. vulgare* and *T. durum* (a species very closely related to *T. turgidum*) behaved entirely differently with respect to the keeled glume factor, extremely irregular genetic behaviour being observed. A large number of different *T. vulgare* x *T. durum* crosses were made, and all of them behaved irregularly.

Much of the genetic material obtained by Mr Watkins was handed over to the author in 1935, and some fresh crosses were also made. Unfortunately none of the back-cross families was large enough for a proper genetic analysis to be made.

The segregations were extremely irregular and their general features may be summarized as follows:-

(1) Whereas (*T. vulgare* x *T. turgidum*) F_1 x *T. turgidum* back-cross families could be classified for the keeled factor with considerable accuracy and gave 1:1 ratios, similar *T. durum* back-cross families could not be so classified. There was an almost continuous gradation from keeled plants like the *durum* parent to plants which appeared to be heterozygous for round glumes. A rather arbitrary classification could nevertheless be made, there being a considerable deficiency of obviously heterozygous round plants. Typical back-cross ratios of keeled : heterozygous round plants were 9:3, 9:3, 13:2, 18:4 (1:1 ratios expected).

(2) The progeny of heterozygous round *turgidum* back-cross plants segregated regularly in a 1:2:1 ratio. This was not the case for the *durum* families. The back-cross plants classified as heterozygous round almost invariably segregated with an excess of keeled and a deficiency of round plants, but in some cases the ratio was disturbed in the opposite direction. Typical ratios were 83 keeled : 70 heterozygous keeled : 17 round (usual type) and 5 keeled : 17 heterozygous keeled : 19 round (excess round type). Normal ratios were not found.

(3) In the case of *turgidum*, the progeny of keeled

back-cross plants invariably bred true to keeled. This was true of only some of the keeled *durum* back-cross plants. Others segregated keeled, heterozygous and round plants in a very irregular ratio with an excess of keeled and a great deficiency of round. A typical ratio in such a family was 37 keeled: 35 heterozygous keeled : 6 round.

(4) Back-crosses of the *durum* F_1 to *vulgare* showed an excess of round plants and a deficiency of keeled in the progeny of the heterozygous back-cross plants, e.g. 10 keeled 30 heterozygous keeled : 29 round.

(5) In spite of the above highly irregular behaviour for the *K* gene, the *b_1* gene for bearded, which is in the same chromosome as *k* in *T. vulgare*, segregated regularly or almost so in back-cross plants and their progeny. The same was also true of the gene for waxy epidermis.

It is not proposed to discuss the genetics of these *T. durum* crosses in detail here as the problem is one for further study. It seems, however, that no simple genetic scheme is adequate to explain the irregular segregation for keeled glumes, and it appeared that some specific chromosome structural rearrangement might be responsible. This suspicion was heightened by a survey of the literature (see below which revealed that irregularities of chromosome pairing had been observed by several authors in *T. vulgare* x *T. durum* crosses but such irregularities had not been reported in

T. vulgare x T. turgidum. It was therefore decided, in order to provide a clue to the genetic analysis of durum crosses, to conduct a comparative cytological study of F_1 hybrids of T. vulgare crossed with T. durum, T. turgidum and T. dicoccum, in the hope of detecting differences in behaviour.

At the same time, the author happened to have on hand an F_1 hybrid between T. vulgare and a hooded Abyssinian tetraploid wheat referred by Vavilov to T. turgidum s.sp. abyssinicum (Vavilov et al, 1931). Since such Abyssinian tetraploid wheats had not previously been studied cytologically (except for the determination of their chromosome number) and since they form a group widely separated in many respects from other tetraploids, it was decided to include the cross in the present studies.

The literature relating to chromosome pairing in these pentaploid hybrids may be briefly summarized as follows:-

Kihara (1919) reported that in various hybrids between tetraploid and hexaploid wheat species, 35 chromosomes were present as 14 bivalents and 7 univalents. This has been confirmed by Sax (1922), Watkins (1924) and others.

Kihara and Nishiyama (1928, 1930) reported in the cross T. vulgare x T. durum the occurrence of two types of deviation from this scheme. They found occasional nuclei with $1_{III} + 13_{II} + 6_{I}$, and a single cell with $2_{III} + 12_{II} + 5_{I}$.

These, they concluded, were due to occasional pairing between members of the *D* genom and their partly homologous partners in the *A* and *B* genoms. They found also some cells with $13_{II} + 9_{I}$, though these occurred only rarely.

Aase (1930) has reported as many as 11 univalents in the cross *T. vulgare* x *T. durum*, and also occasional trivalents and quadrivalents. No such deviations from the modal arrangement $14_{II} + 7_{I}$ have been reported in crosses of *T. turgidum* or *T. dicoccum* with *T. vulgare*, except for one rather anomalous variety of *T. dicoccum*, Khapli emmer (Hollingshead, 1932).

II. Material and Methods

Cytological preparations of the following F_1 hybrids were made:

144 F_1. *T. vulgare* var. Chinese White ♀ x
T. durum var, Indian Runner ♂

145 F_1. *T. vulgare* var. Australian 6 ♀ x
T. durum var. Indian Runner ♂

219 F_1. *T. vulgare* var. Benefactor ♀ x
T. turgidum abyssinicum Vav. var.
'Hooded Abyssinian' ♂

In addition, similar preparations of the following hybrids were kindly lent to me by Mr A.E. Watkins:

10 F_1. *T. vulgare* var. Swedish Iron ♀ x
T. turgidum var. Cambridge Rivet ♂

234 F_1. *T. turgidum* var. Cambridge Rivet ♀ x
T. vulgare var. Chinese White ♂

92 F_1. *T. vulgare* var. Swedish Iron ♀ x
T. dicoccum var. Emmer ♂

The method of making a preparation was as follows: An anther at the stage of the first meiotic division (as determined by examination of another anther from the same floret in Belling's iron aceto-carmine) was placed between a slide and a cover slip and the latter was given a sharp but gentle tap with the butt end of a dissecting needle. This caused the columns of pollen mother cells to exude slightly at the distal end of the anther and to stick to the slide or cover slip. The outer tissues were then quickly pulled away with a dissecting needle and the slide or slip, with the complete loculi of pollen mother cells adhering to it, was immediately inverted in La Cour's 2 B or 2 BE fixative, both of which gave good results. With practice, just the right strength of tap to make the pollen mother cells exude without damaging them could be given regularly and the whole procedure completed in not more than five seconds. After fixing and bleaching, the slides were stained by Newton's iodine- gentian violet method. Drawings were made with a camera lucida at a magnification of x 2900, using a Leitz 2 mm. apochromatic objective, and subsequently reduced to 2500 diameters.

Observations were made of the pairing at the first meiotic division, and the first anaphase was also examined for chromatin bridges. The preparations used were selected as having the best fixation and staining, and in them a critical analysis of the chromosome pairing of practically every metaphase plate was possible. A particular area of the smear was selected, and every plate within that area was examined, so that there was no selectinn likely to falsify the observed ratio of the various chromosome arrangements.

III. Observations at Meiotic Metaphase (excluding the cross Benefactor x Hooded Abyssinian)

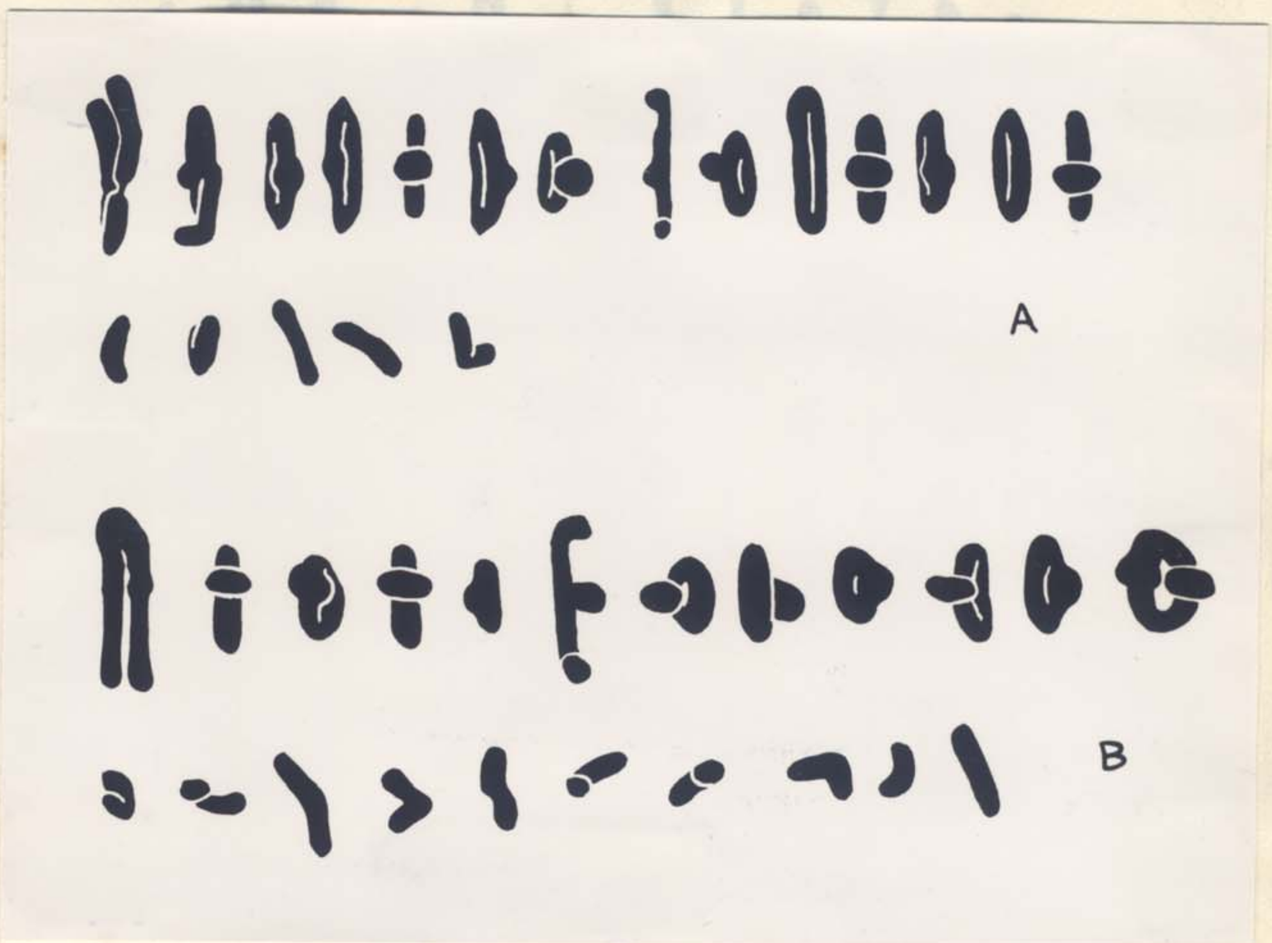
The results of the observations of metaphase pairing are shown in Table VII, except for the cross involving the Abyssinian form, which behaved differently from all the others and will be discussed later. The chromosomes of some cells of two of the crosses are shown in Text-figs 9 and 10.

It is at once apparent that various deviations from the $14_{II} + 7_I$ arrangement are found in the turgidum and dicoccum crosses as well as in the durum crosses, though they have not previously been reported. The only irregularity recorded above for durum and not for the other crosses is the quadrivalent occurring in one cell of 144 F_1. This, however, is a very rare configuration, and would quite probably be found in the other crosses if sufficient cells were examined. In any case, such a rare phenomenon could not upset the genetic segregations in F_2 to a detectable extent.

All the observed arrangements may be explained as being due to the interaction of three phenomena.

Chromosome Pairing in Pentaploid Wheat Hybrids

Cross	Preparation No.	1 IV 12 II 7 I	2 III 12 II 5 I	1 III 13 II 6 I	1 III 12 II 8 I	1 III 11 II 10 I	14 II 7 I	13 II 9 I	12 II 11 I	Total
T. vulgare x *T. turgidum* A. 10 F_1 (Iron x Rivet)	A	-	1	3	1	-	34	11	2	52
	B	-	-	-	-	1	10	1	-	12
	Total	-	1	3	1	1	44	12	2	64
B. 234 F_1 (Rivet x C.W.)	A	-	-	-	-	-	8	5	-	13
	B	-	-	-	1	-	11	-	-	12
	C	-	-	-	-	-	20	4	1	25
	Total	-	-	-	1	-	39	9	1	50
T. vulgare x *T. dicoccum* A. 92 F_1 (Iron x Emmer)	A	-	-	2	-	-	7	4	-	13
	B	-	-	4	-	1	18	1	-	24
	C	-	-	4	-	-	3	2	-	9
	Total	-	-	10	-	1	28	7	-	46
T. vulgare x *T. durum* A. 144 F_1 (C.W. x I.R.)	A	1	-	1	1	-	8	3	1	15
	B	-	1	-	2	-	4	4	2	13
	C	-	-	2	-	-	4	4	-	10
	D	-	-	1	-	-	10	10	2	23
	Total	1	1	4	3	-	26	21	5	61
B. 145 F_1 (Aus.6 x I.R.)	A	-	-	3	1	-	18	5	-	27
	B	-	-	-	-	-	1	-	-	1
	C	-	-	1	-	-	5	-	-	6
	D	-	-	1	1	-	13	2	2	19
	E	-	-	1	-	-	25	3	-	29
	Total	-	-	6	2	-	62	10	2	82
Total all	crosses	1	2	23	7	2	199	59	10	303



Text-fig. 9

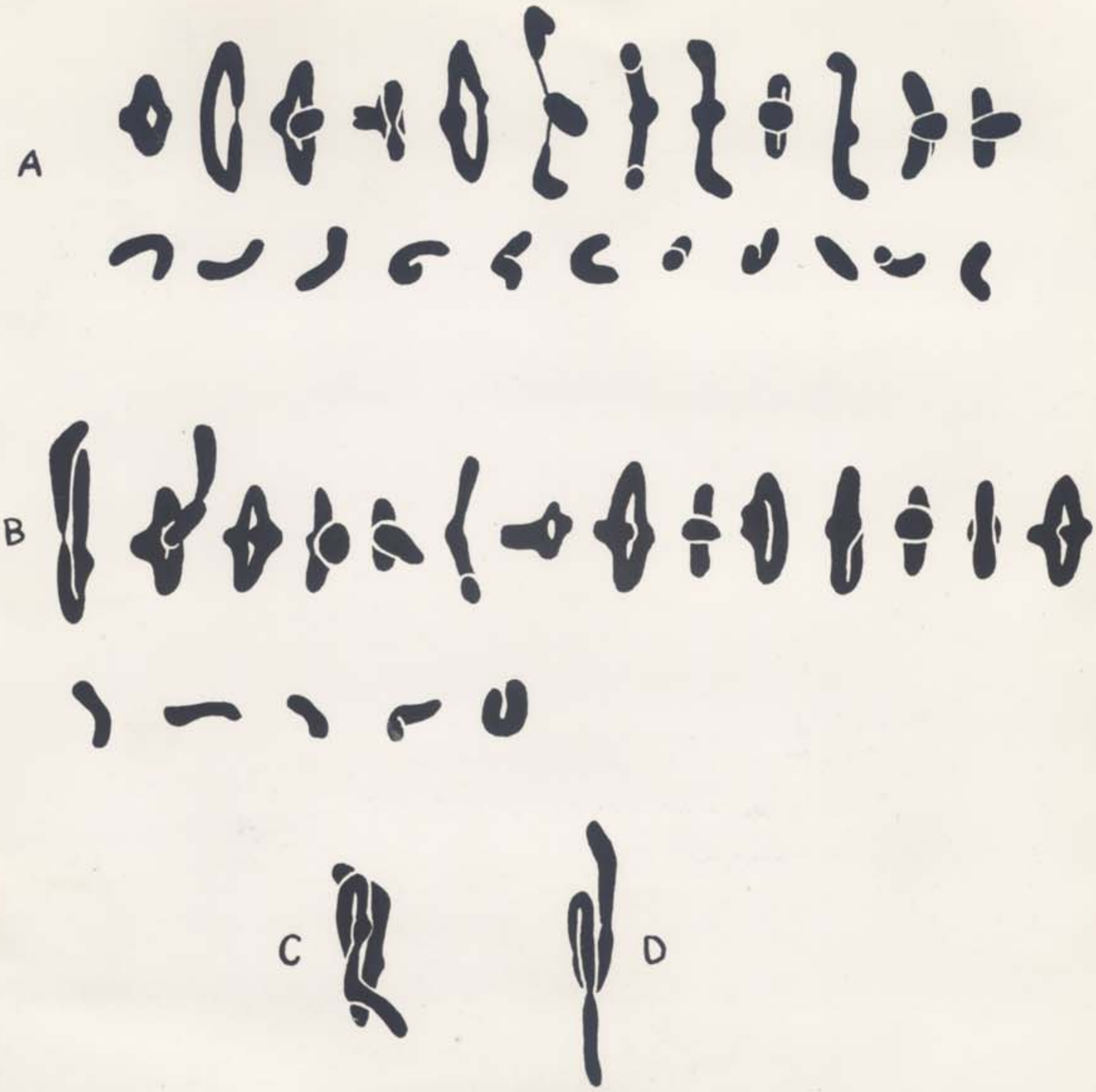
Chromosome Pairing at Metaphase I

in F_1 Swedish Iron x Rivet (10 F_1)

A. $2_{III} + 12_{II} + 5_{I}$

B. $1_{III} + 11_{II} + 10_{I}$

x 2,500

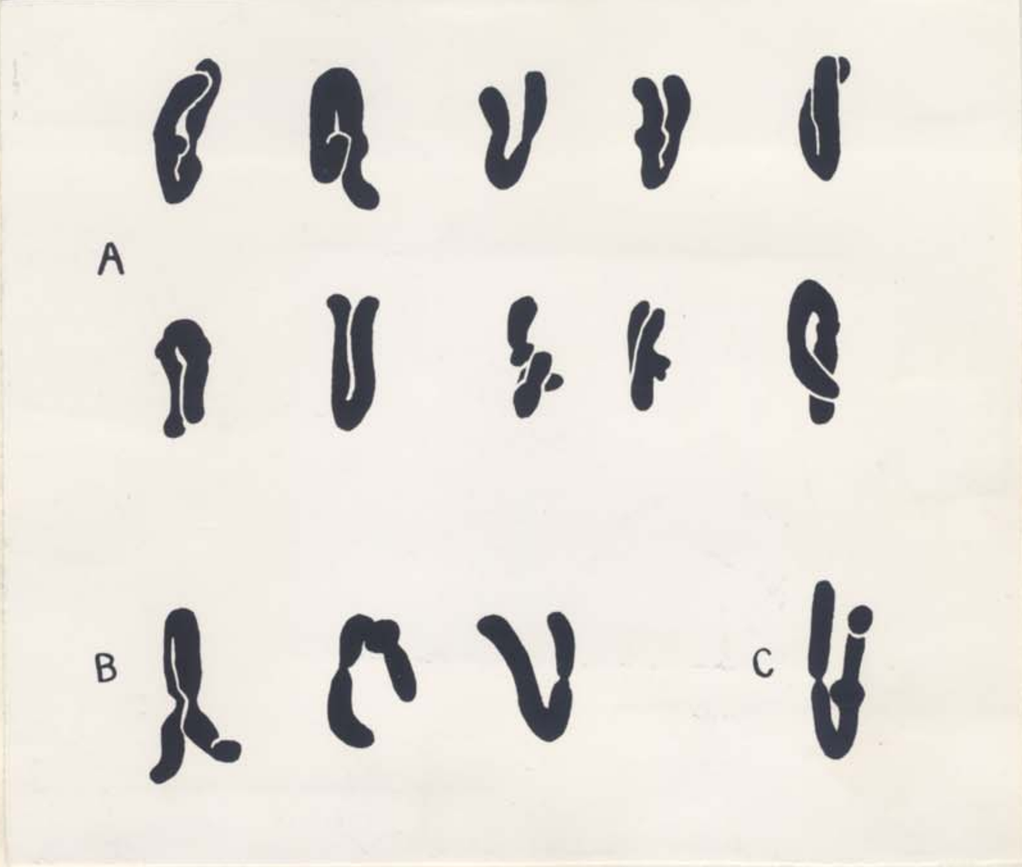


Text-fig. 10.
Pairing at Metaphase I in F_1
Chinese White x Indian Runner (144 F_1).
A. $12_{II} + 11_{I}$. B. $2_{III} + 12_{II} + 5_{I}$
C. & D. Quadrivalents
x 2,500

(i) Trivalent formation, giving $1_{III} + 13_{II} + 6_{I}$, $2_{III} + 12_{II} + 5_{I}$ etc. instead of $14_{II} + 7_{I}$. This must be due, as Kihara and Nishiyama (1928, 1930) concluded, to occasional pairing between one or more chromosomes of the extra set of seven '*vulgare*' chromosomes (the *D* genom) with their partial homologues in the *A* or *B* genom. Trivalents from the various crosses are shown in Text-fig. 11 and in Plate VIII.

(ii) Failure of chiasma formation between some pairs in the *A* and *B* genoms, giving one or more pairs of univalents where bivalents would normally be expected. This would give the arrangements $13_{II} + 9_{I}$, $12_{II} + 11_{I}$, etc., instead of $14_{II} + 7_{I}$. Where this phenomenon is superimposed upon the first, one would get $1_{III} + 12_{II} + 8_{I}$, $1_{III} + 11_{II} + 10_{I}$ and so on, instead of $1_{III} + 13_{II} + 6_{I}$, etc.

(iii) Quadrivalent formation. One cell out of 61 in 144 F_1 had a chain quadrivalent, giving the arrangement $1_{IV} + 12_{III} + 7_{I}$. A similar quadrivalent was observed in another cell which had been damaged, and could therefore not be analysed completely (Text-fig. 10, C,D). This phenomenon is evidently very rare (in the above table occurring in one cell out of 303), and is probably due to pairing between partly homologous members of the *A* and *B* genoms. This is the kind of behaviour which, according to Winge's (1924) hypothesis might give rise to 42-chromosome speltoids if it occurred in such a species as *T. vulgare*.



Text-fig. 11

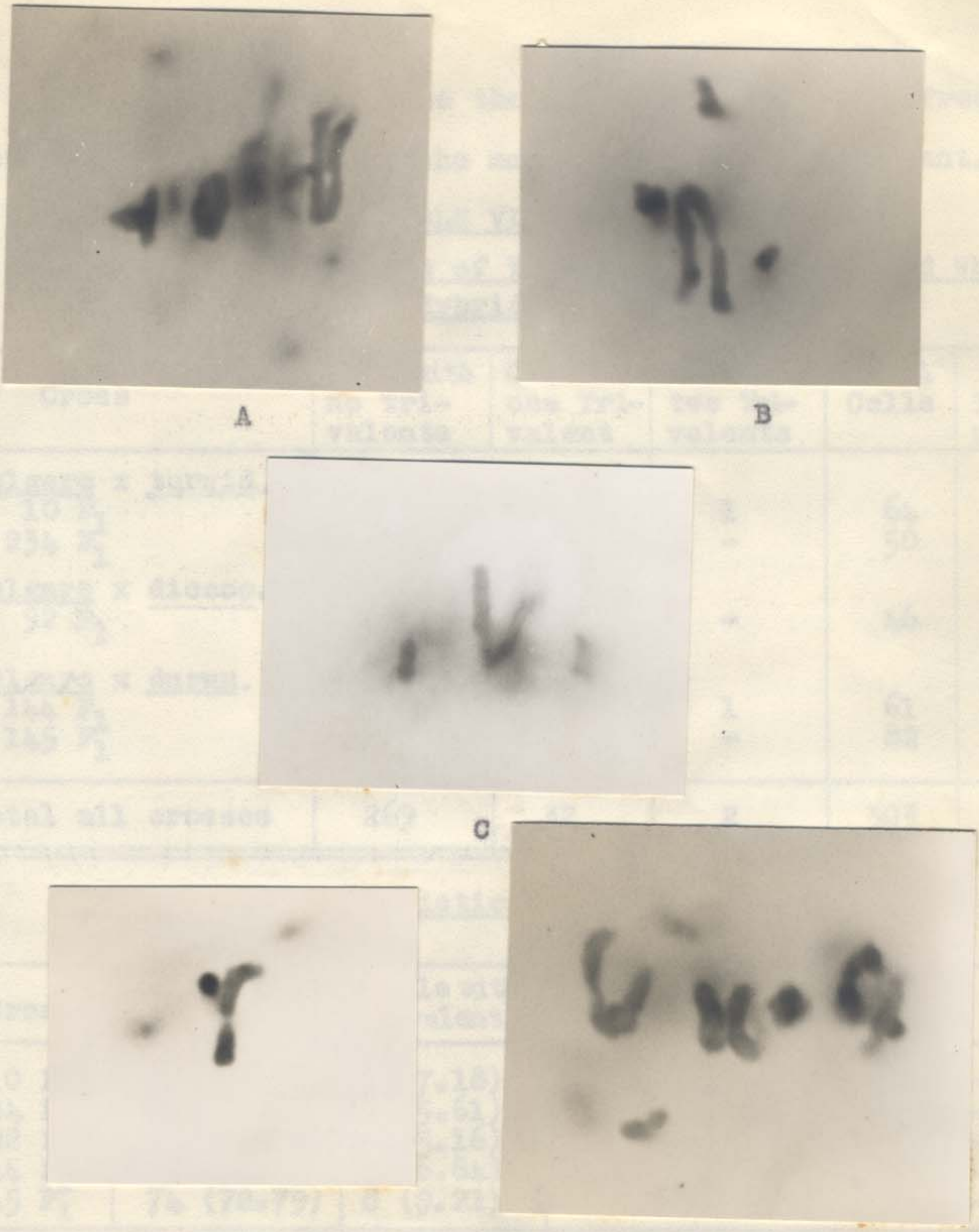
Trivalents due to Pairing of D Genom Chromosomes in Pentaploid Wheat Hybrids

A. F_1 Swedish Iron x Emmer (92 F_1)

B. F_1 Swedish Iron x Rivet (10 F_1)

C. F_1 Rivet x Chinese White (234 F_1)

x 2,500



A

B

C

D

E

Plate VIII.

Pairing of Members of the D genom in Pentaploid Wheat Hybrids, to give Trivalents

A & B. 145 F_1 (Australian 6 x Indian Runner)
C. 144 F_1 (Chinese White x Indian Runner)
D. 92 F_1 (Swedish Iron x Emmer)
E. 10 F_1 (Swedish Iron x Cambridge Rivet)

x 2,500 approx.

Now let us examine the frequency of the two frequentl occurring departures from the modal metaphase arrangement.

TABLE VIII

Frequency of Occurrence of Trivalents in Pentaploid Wheat Hybrids

Cross	Cells with no Trivalents	Cells with one Trivalent	Cells with two Trivalents	Total Cells	Mean Trivalen per ce
Vulgare x turgid.					
10 F_1	58	5	1	64	0.11
234 F_1	49	1	-	50	0.02
Vulgare x diccoc.					
92 F_1	35	11	-	46	0.24
Vulgare x durum.					
144 F_1	53	7	1	61	0.15
145 F_1	74	8	-	82	0.10
Total all crosses	269	32	2	303	0.12

Statistical Analysis

Cross	Cells with no trivalents	Cells with trivalents	Total cells	χ^2	P
10 F_1	58 (56.82)	6 (7.18)	64	0.0725	.70-.80
234 F_1	49 (44.39)	1 (5.61)	50	3.3803	.05-.10
92 F_1	35 (40.84)	11 (5.16)	46	6.2245	.01-.02
144 F_1	53 (54.16)	8 (6.84)	61	0.0717	.70-.80
145 F_1	74 (72.79)	8 (9.21)	82	0.0616	.80-.90
Total	269	34	303	9.8106	
Total	$\chi^2 = 9.8106$ D.F. = 4 P = .02-.05				

Analysis of these data by the χ^2 method, grouping the last two classes together because of their small size, and applying Yates' correction for discontinuous data, gives the results shown in the lower part of the table. The figures in brackets represent expected values, based on the observed ratio of the total for all crosses.

The various crosses are therefore significantly heterogeneous from the point of view of frequency of trivalent formation, though not highly so. It is obvious from the above table that this heterogeneity is due to the higher frequency for 92 F_1 (Swedish Iron x Emmer), the other four crosses not differing significantly among themselves.

Now let us consider the frequency of the other phenomenon - failure of homologous chromosomes of the A or B genom to pair. This is summarized in Table IX.

TABLE IX

Frequency of Failure of Homologous Chromosomes to Pair

Cross	No failures ($14_{II}+7_{I}$) etc.	One failure ($13_{II}+9_{I}$) etc.	Two failures ($12_{II}+11_{I}$) etc.	Total Cells	Mean per Cell
Vulgare x **turg.**					
10 F_1	48	13	3	64	0.30
234 F_1	39	10	1	50	0.24
Vulgare x **dicocc.**					
92 F_1	38	7	1	46	0.20
Vulgare x **durum**					
144 F_1	32	24	5	61	0.56
145 F_1	68	12	2	82	0.20
Total all crosses	225	66	12	303	0.30

Statistical Analysis.

Cross	Cells with no failures to pair	Cells with failures to pair	Total	χ^2	P
10 F_1	48 (47.52)	16 (16.48)	64	0.0000	1.0
234 F_1	39 (37.13)	11 (12.47)	50	0.1963	.50-.70
92 F_1	38 (34.16)	8 (11.84)	46	1.2688	.20-.30
144 F_1	32 (45.30)	29 (15.70)	61	14.0525	.01
145 F_1	68 (60.89)	14 (21.11)	82	2.7873	.50-.10
Total	225	78	303	18.3049	

Total $\chi^2 = 18.3049$ D.F. = 4 $P = < .01$

Here again, using the same kind of statistical analysis as in Table VIII, we find a significant difference between the crosses. 144 F_1 (Chinese White x Indian Runner) shows a significantly greater proportion of cells with $13_{II} + 9_{I}$, $12_{II} + 11_{I}$, and so on, than the other crosses. The latter do not differ significantly between themselves, though, of course, larger samples may have revealed real differences between them.

The high proportion of failures to pair in 144 F_1 is shown not to be a general phenomenon in *durum* x *vulgare* crosses, since the other *durum* cross, 145 F_1 does not show such a high frequency even though the same *durum* parent is involved. The differences found do not appear to depend upon which species are concerned, but rather upon the particula combination of pure lines.

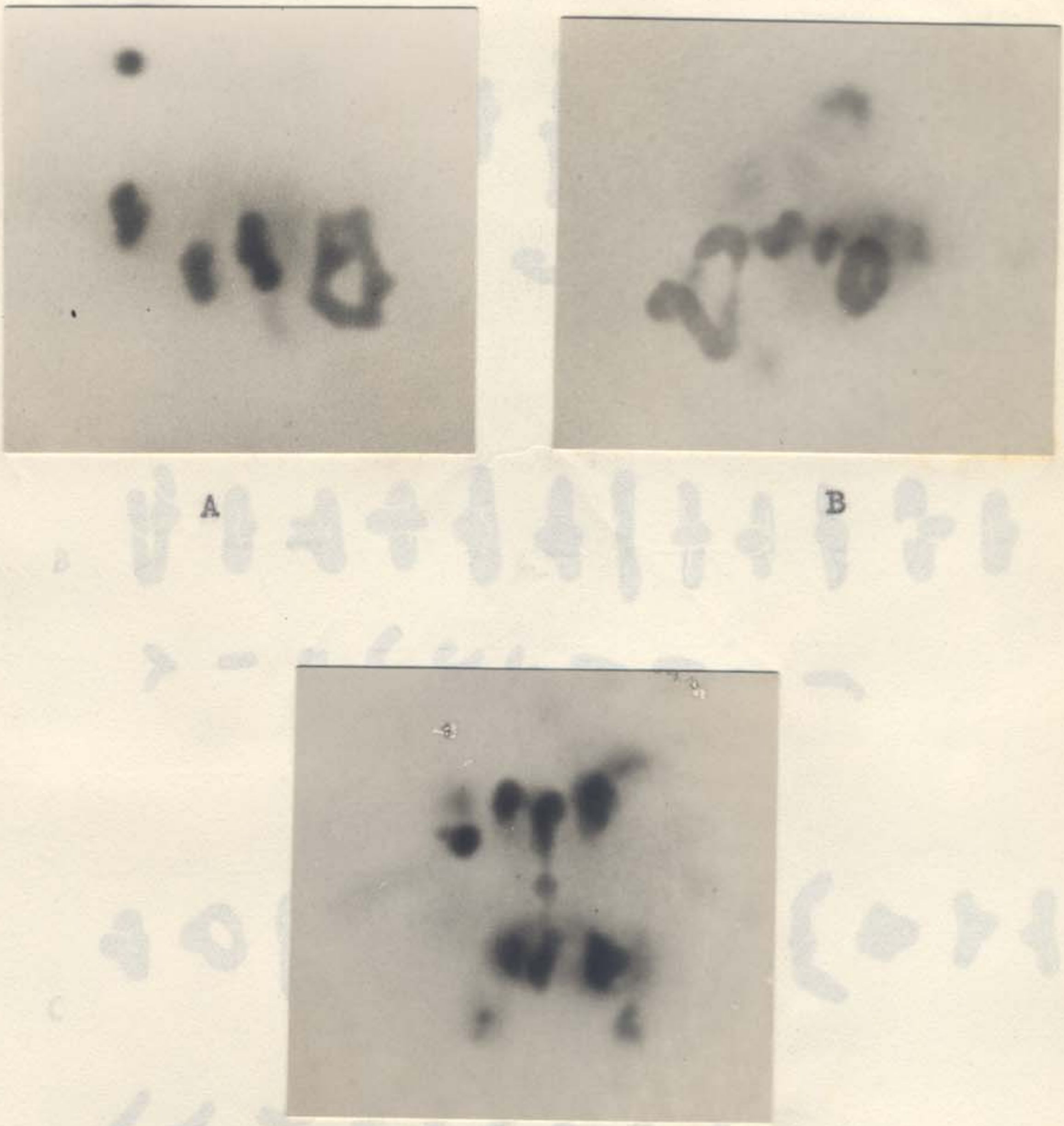
IV. Observations at Meiotic Metaphase in the Cross Benefactor x Hooded Abyssinian

The presentation of the results for this cross ~~will~~ is treated separately because it behaves differently from all the others so far discussed. The types of chromosome pairing found are summarized in Table X. The chromosome complements of three cells of this hybrid are shown in Text-fig 12, and in Text-fig. 13 ~~the~~ multivalent configurations from the same cross are shown. In Plate IX, A & B, photographs of cells containing rings of 4 chromosomes are shown.

TABLE X

Chromosome Pairing at Metaphase I in 219 F_1 (Benefactor x Hooded Abyssinian)

Pre-paration	1 V - - 12 II 6 I	- 1 IV 1 III 11 II 6 I	- 1 IV 1 III 10 II 8 I	- 1 IV - 12 II 7 I	- 1 IV - 11 II 9 I	- - 2 III 11 II 7 I	- - 1 III 12 II 8 I	- - 1 III 11 II 10 I	- - - 14 II 7 I	- - - 13 II 9 I	- - Total
A	-	-	-	5	4	1	3	1	2	-	16
B	-	-	-	2	-	-	-	-	-	-	2
C	1	1	1	18	1	-	3	-	3	3	31
Total	1	1	1	25	5	1	6	1	5	3	49
Mode of origin (see text)	b	b	b + c	-	c*	a(3+1) + b	a(3+1) *	a(3+1) + c*	a(2 + 2)	a(2+2) + c	



A

B

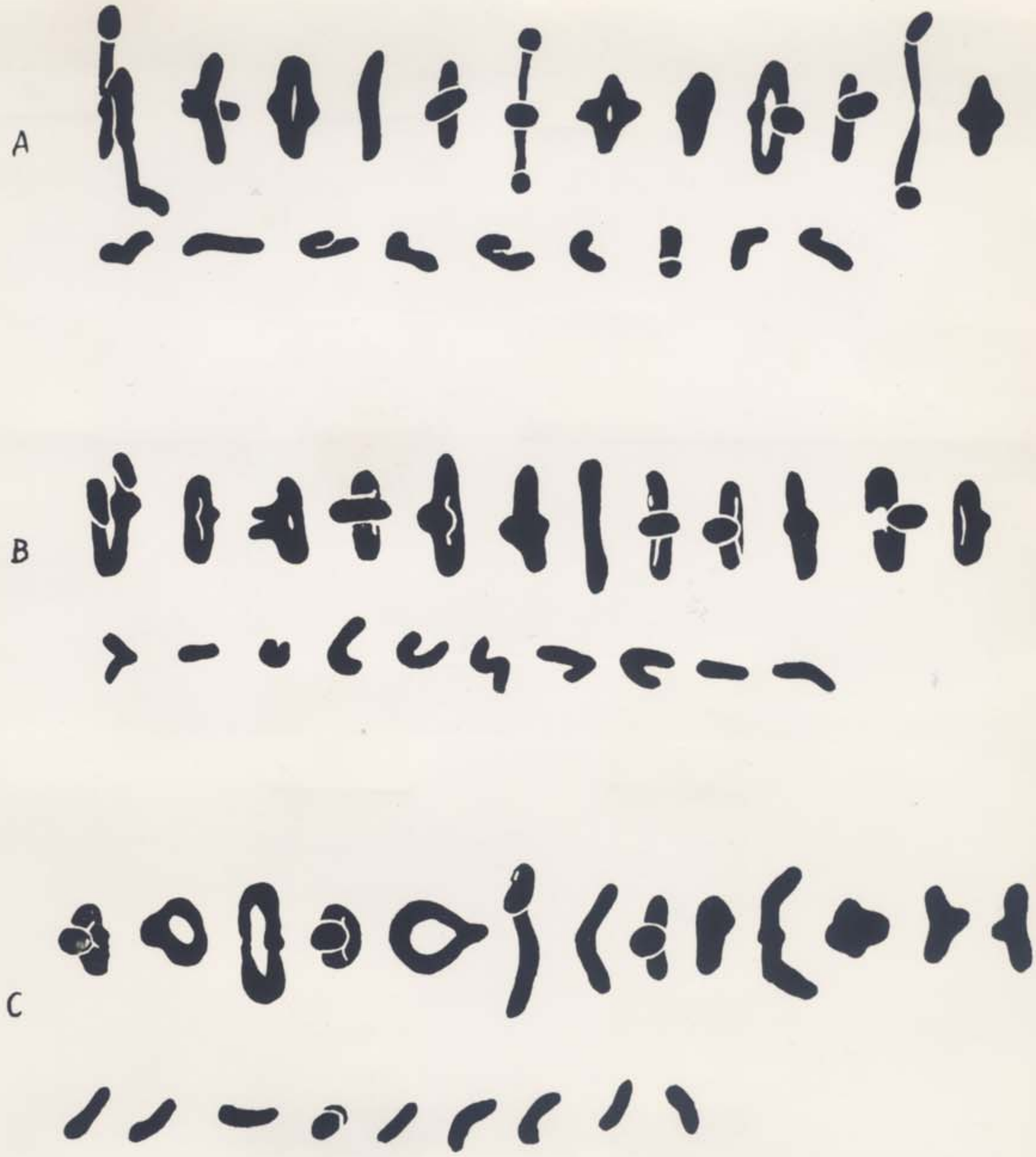
C

Plate IX.

Configurations in 219 F_1 (Benefactor x Hooded Abyssinian)

A. Open ring of four chromosomes.
B. Ring of four chromosomes assuming the zig-zag formation.
C. Chromatin bridge at first anaphase.

x 2,500 approx.

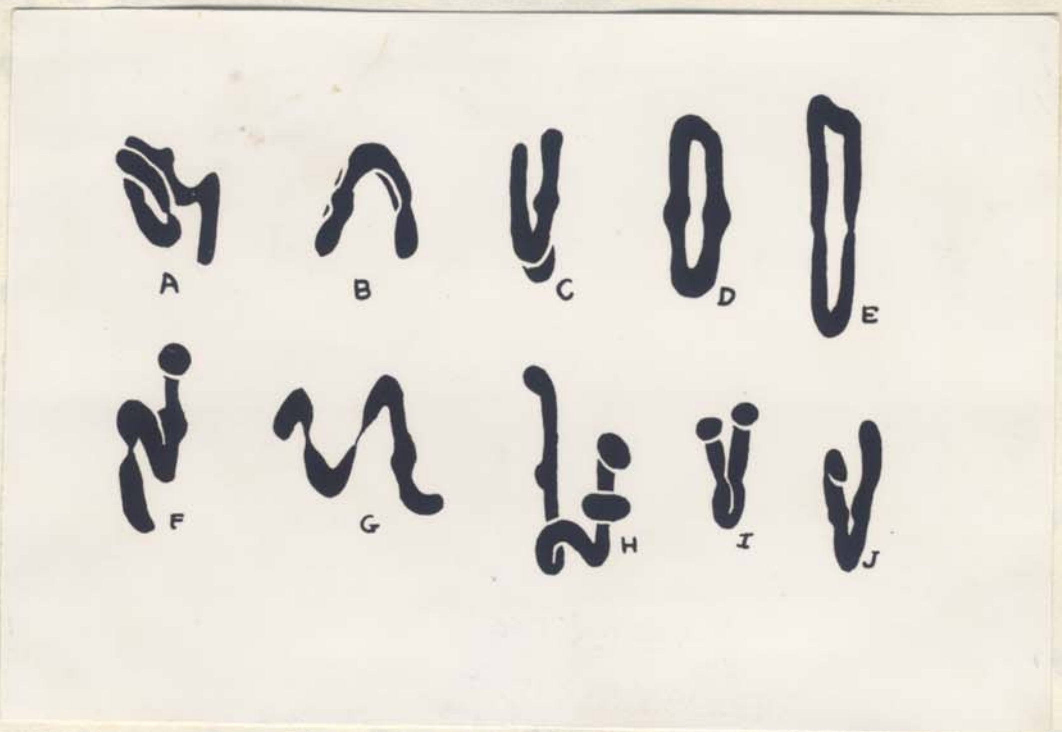


Text-fig. 12.

Pairing at Metaphase I in F_1
Benefactor x Hooded Abyssinian (219 F_1)

A. $1_{IV} + 11_{II} + 9_{I}$
B. $1_{III} + 11_{II} + 10_{I}$
C. $13_{II} + 9_{I}$

x 2,500



Text-fig. 13.

Multivalents in F_1

Benefactor x Hooded Abyssinian (219 F_1)

A. Quinquevalent. B-E. Rings of 4.

F-H. Chains of 4. I-J. Trivalents.

x 2,500

Here the modal arrangement is clearly $1_{IV} + 12_{II} + 7_{I}$, and we are dealing with a reciprocal interchange heterozygote.

The ring of four chromosomes is not complete in many cells, a chain of four being more usual. This configuration would be obtained if no chiasma were formed in one of the arms of two chromosomes concerned in the ring. Of the cells with quadrivalents, 13 had rings and 19 had chains of four. The other cells had the ring replaced by two bivalents and by a trivalent and a univalent, owing to failure of chiasma formation in more than one arm.

Disjunction of the quadrivalent did not appear to be at random. In 25 cases adjacent chromosomes of the ring or chain were going to opposite poles, giving genetically balanced gametes as far as these chromosomes were concerned, and in 6 cases adjacent chromosomes were orientated so that it appeared that they would go to the same pole, giving duplications and deficiencies of genetic material in the gametes. One configuration was doubtful in this respect. The ratio 25 : 6 is significantly different from 1 : 1 ($\chi^2 = 10.45$, D.F. = 1, $P = <.01$).

Pollen grain counts were made of this hybrid to show the effect of the ring formation on pollen fertility. The pollen was classified into morphologically perfect and morphologically imperfect (empty grains and grains with obviously deficient contents) by microscopical examination, after staining with iron acetocarmine. A number of other pentaploid F_1 hybrids were also examined for purposes of comparison and the results are shown in Table XI.

TABLE XI

Proportion of Good Pollen in Various Pentaploid Wheat Hybrids

F_1	Good pollen grains	Bad pollen grains	% bad	S.E.
Benefactor x Hooded Abyssinian (219 F_1)	444	314	41.4	± 1.79
Chinese White x Rivet(233 F_1) (*vulgare* x *turgidum*)	442	77	14.8	± 1.56
Mesopotamian *vulgare* x Rivet (235 F_1)(*vulgare* x *turgidum*)	364	61	14.4	± 1.70
Australian 6 x Indian Runner (145 F_1)(*vulgare* x *durum*)	332	82	19.8	± 1.96

Therefore the proportion of bad pollen found in the ring-forming hybrid is very much higher than in the other pentaploid F_1's examined. If, however, the ring of four segregated at random, one would expect the percentage of bad pollen to be well over 50. The observed amount, 41.4 ± 1.8% is significantly less than 50%, so that there is some suggestion that the ring segregates disjunctionally in more than 50% of cases, though it is possible, of course, that the percentage of germinable pollen is considerably less than that classed as morphologically normal.

These observations agree with those of Thompson & Thompson (1937) and Smith (1936, 1939), who both found comparatively little disturbance of the pollen in ring-forming wheat hybrids, and disjunctional separation of the ring in more than 50% of cases (approximately 80% in T. monococcum). Both Thompson & Thompson (1937) and Smith (1936) observed a significantly greater proportion of open rings at early metaphase than at late metaphase, indicating that most of the open formations change to zig-zag ones during this stage. The present work presents only fragmentary data on this point, but as far as they go they support this view (Table XII).

TABLE XII

Stage	Disjunctional orientation of ring or chain	Non-disjunctional orientation of ring or chain
Early metaphase (Slide C)	15	5
Late metaphase (Slides A & B)	10	1
	25	6

Plate IX B shows a ring of four which is apparently in process of assuming the zig-zag formation, having previously been an open ring.

All the deviations from the basic arrangement

$1_{IV} + 12_{II} + 7_I$ shown in Table X can be explained as being due to one or more of three causes.

(a) "Breakage" of the ring, giving a trivalent plus a univalent or two bivalents. (Denoted by the symbols a(3 + 1 and a(2 + 2) in the above table).

(b) Pairing of members of the D genom with their partial homologues in the A or B genoms, giving trivalents, or, where the ring of four is involved, quinquevalents.

(c) Failure of chiasma formation between homologous pairs of the A or B genoms, causing replacement of bivalents by pairs of univalents.

The symbols a(3 + 1), a(2 + 2), b and c in the above table show how the various arrangements have been derived from the basic arrangement. In the cases marked with an asterisk there are possible alternative ways of arriving at the same result, but the one shown has by far the greater degree of probability.

The three types of variation occur, then, in the following frequencies:-

(a)	Number of cells.
Ring of four	13
Chain of four	19
Chain of five	1
III - I	8
II - II	8
	49

(b)	Number of cells
No D genom chromosome paired	45
One D genom chromosome paired	4
	49

(c)	Number of cells.
No 'failures to pair'	39
One 'failure to pair'	10
	49

The mean number of trivalents, etc., due to D chromosomes pairing, is 0.08 per cell. The mean number of 'failures to pair' is 0.20 per cell. Both these figures are of the same order as in the other crosses already described.

Unfortunately, only the one cross involving an Abyssinian wheat was available in 1937, though further crosses have since been made. It is therefore not known at present whether the reciprocal interchange found in the form studied is characteristic of the peculiar group of Abyssinian tetraploid wheats in general, or only of particular forms.

V. Observations on the Meiotic Anaphase

Where suitable material was available, the first and second meiotic anaphases of the above crosses, and also some others, were examined for chromatin bridges.

All crosses involving _durum_ and _vulgare_ proved to be heterozygous for at least one inversion. The inversions were apparently not large in 144 F_1 and 145 F_1, since chromatin bridges were found only in a small proportion of cells (roughly 5%). A maximum of one bridge was found in these crosses (Plate X A). This does not, of course, necessarily mean that the F_1's were heterozygous for only one inversion. If there were a number of small inversions, each with a very small chance of a chiasma being formed in the lopp, a very large number of cells would have to be examined before a cell with more than one bridge was found. In very small inversions, chiasma formation would presumably be entirely suppressed.

Cross No.220 ((Swedish Iron x Durum 27/2)F_1 x Durum 27/2) was examined in the F_3. Some of the plants in this generation did not produce bridges, being presumably homozygous for all detectable inversions. Most, however, gave frequent bridges and acentric fragments, and a maximum of three bridges in one cell was found (Plate X B).

The presence of relatively inverted chromosome segments was not, however, confined to _durum_ crosses. The _turgidum_ cross 233 F_1 (Chinese White x Rivet) showed one bridge at the second anaphase fairly frequently (Text-fig.14 A

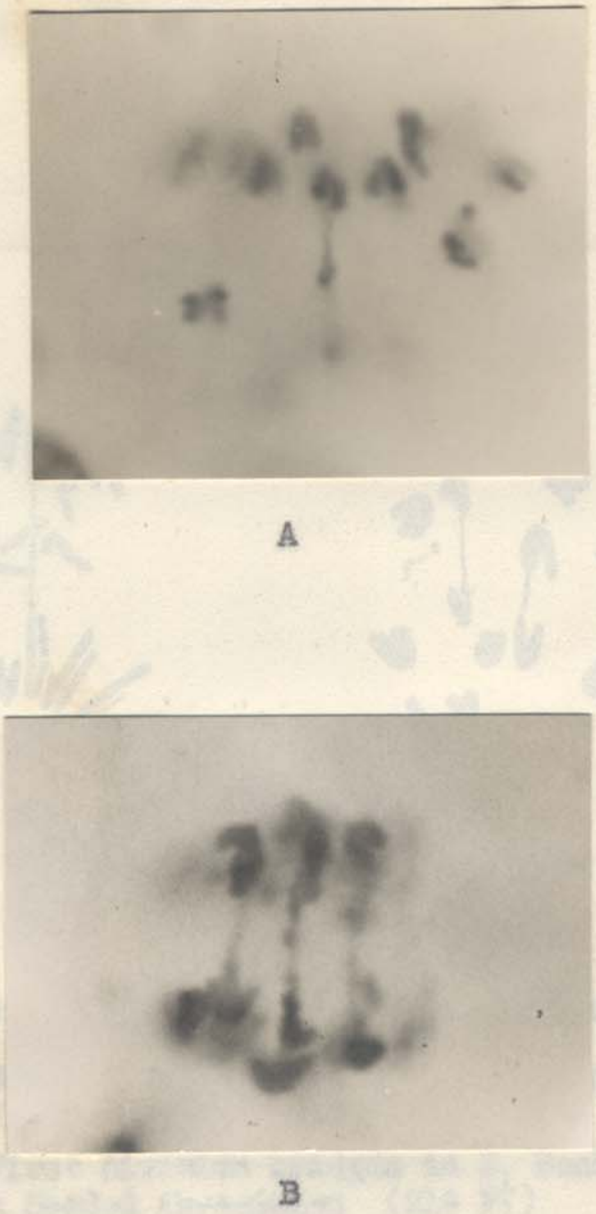


Plate X.

Chromatin Bridges in _T_. _vulgare_ x _T_. _durum_

A. Bridge with "strangled" fragment in 144 F_1 (Chinese White x Indian Runner)

B. Three chromatin bridges at anaphase I in 220 F_4 (Swedish Iron x D 27/2) x D 27/2.

x 2,500 approx.

Text-fig. 14.

Inversion Bridges at Meiotic Anaphase.

A. Second division bridge in F_1 Chinese White x Rivet (233 F_1)

B. First division bridges in F_1 Benefactor x Hooded Abyssinian (219 F_1)

For the sake of clarity, not all the chromosomes on the plates are shown. Plate B is lying obliquely to the field of view. f = acentric fragment.

x 2,500.

First anaphase material of this cross was not available. Another *turgidum* cross examined (10 F_1, Swedish Iron x Rivet) showed a single bridge at anaphase I in occasional cells. Sufficient anaphase material of *vulgare* x *dicoccum* was not available for study.

It may be said, therefore, that here again there was no clear difference in chromosome behaviour between those crosses which behave regularly genetically and those which behave irregularly.

The cross Benefactor x Hooded Abyssinian (219 F_1) gave frequent cells with anaphase bridges and up to two bridges per cell were found (Plate IX,C and Text-fig. 14,B).

VI. Discussion

These results, then, are completely negative in that no difference in cytological behaviour is demonstrable between *T. durum* x *T. vulgare* pentaploid hybrids on the one hand and *T. turgidum* or *T. dicoccum* x *T. vulgare* hybrids on the other. The differences in genetic behaviour between *T. durum* and the other species when crossed with *T. vulgare* cannot be explained on the basis of any observed cytological irregularit and the causes must be sought through further and more extensive genetical studies. It is possible, of course, that although the total amount of irregular behaviour was similar in each species, different chromosomes were involved in each case. The chromosomes containing the K factor may have been frequently involved in the *durum* crosses and not in the others. No evidence can be presented for or against this argument, but even if it holds true to some extent, it seems unlikely that the irregular behaviour would be sufficiently frequent to account for the extreme distunbance of the ratios fpund in *durum* crosses.

The results are, however, of interest in that they show that the extremely regular behaviour reported in *T. vulgare* x *T. turgidum* hybrids by several previous authors (the regular formation of 14 bivalents and 7 univalents) is illusory. Irregularities of the types previously reported by Kihara and Nishiyama (1928, 1930) in *durum* crosses were also found in *T. turgidum* and *T. dicoccum* hybrids. The exact frequency of these anomalies varied from cross to cross, but there was no clear difference in behaviour between the species.

Four types of irregular behaviour were found, viz. (i) pairing of normally univalent chromosomes of the D genom with their partial homologues of the other chromosome sets, giving trivalents, (ii) failure of chiasma formation in one or two chromosome pairs, so that bivalents were replaced by pairs of univalents, (iii) pairing between partly homologous chromosomes of the *A* and *B* genoms, giving quadrivalents and (iv) pairing in relatively inverted chromosome segments, giving dicentric chromatids and acentric fragments at anaphase I and II. The third of the above types of disturbance differs from the others in being very rare. It was only found in one cell out of a total of 303 and in another damaged cell not included in the total and both cases happened to be in one *durum* cross. There is no reason to suppose that it would not also be found in the other crosses if sufficient cells were examined. The other three types of disturbance are all common. The minimum number of relatively inverted segments in one *T. vulgare* x *T. durum* cross was three, but it is probable that the actual number of structural changes is much greater in every case.

The Hooded Abyssinian cross studied shows that this form, which belongs to *T. turgidum* s.sp. *abyssinicum* Vav. is closely related to the other tetraploid wheats studied as regards its chromosome homologies. It shows, however, a reciprocal interchange of segments between two chromosomes when compared with the common arrangement, so that a ring of four is found at meiotic metaphase. It is not at present known whether this interchange is characteristic of the Abyssinian tetraploid wheats as a group or whether it occurs only in a limited series of forms.

SUMMARY

1. The genetic irregularities found in *T. vulgare* x *T. durum* back-crosses are briefly outlined. A comparative cytological study of F_1 hybrids of *T. vulgare* x *T. durum*, x *T. turgidum* and x *T. dicoccum* was made in an attempt to discover a reason for these irregularities.

2. All the hybrids studied showed irregularities at meiotic metaphase and anaphase, in contrast to the regular behaviour previously reported in *T. vulgare* x *T. turgidum* crosses.

3. The irregularities were of four types. No clear difference between the three tetraploid species studied was found with respect to their occurrence and no clue to the explanation of genetical irregularities in *durum* crosses was obtained.

4. The cross *T. vulgare* x *T. turgidum* s.sp. *abyssinicum* Vav. showed the same irregularities as the above, but in addition proved to be an interchange heterozygote, forming a ring of four chromosomes at metaphase I.

5. Whereas the percentage of bad pollen in the other pentaploid hybrids studied was around 15%, in the above *T. turgidum* s.sp. *abyssinicum* cross it was 41.4%.

6. Evidence is presented to show that the ring or chain

of four chromosomes in the above cross disjoins regularly in a zig-zag manner in a majority of cells.

7. There is an indication that the proportion of "open" rings is higher at ~~diakinesis and~~ early metaphase than at late metaphase. Previously "open" rings became orientated in a regular zig-zag manner during metaphase.

PART III

THE ORIGIN AND GEOGRAPHICAL DISTRIBUTION OF TRITICUM SPHAEROCOCCUM PERC. AND ITS CYTO-GENETICAL BEHAVIOUR IN CROSSES WITH T. VULGARE VILL.

I. Introduction

The hexaploid wheat species Triticum sphaerococcum was first described as such by Percival (1921), since which time practically no study has been made of its geographical distribution or of its mode and region of origin, and only a very little work has been done to determine its genetical and cytological relationships with other wheats. It would therefore appear desirable to collect together the scattered information which is available about this species and to supplement it with new findings which lead to a more precise knowledge of its phylogeny and cyto-genetics.

Triticum sphaerococcum Perc. differs very strikingly from the other hexaploid wheat species in its short stature (averaging 60-70 cm. according to Percival (1921) and 54 cm. for the form of T. sphaerococcum var. rubiginosum grown by the author at Cambridge in 1936), its small ears and its characteristic, small, round grains and practically hemispherical, inflated glumes. It has a very characteristic tufted appearance when growing, usually being profusely tillered and having erect, stiff straw which is thick in proportion to its height. Bearded and beardless forms are known, the former never having long awns, but irregularly spreading ones 1.5 - 2 cm. long at the apex of the ear and much shorter at the base. It occurs with red or white and with glabrous or pubescent chaff, and may have red or white grains. For a full botanical description the reader is referred to Percival (1921) and to Howard and Howard (1910).

II. Geographical Distribution of T. sphaerococcum

(1) Literature.

According to Percival (1921), T. sphaerococcum was referred to by Duthie and Fuller in Field and Garden Crops of the North-West Provinces of Oudh (1882), who described "a curious round-berried wheat named 'Paighambari', apparently an introduction from Arabia". There is little doubt, however, that these authors were mistaken as to its origin, as the species does not appear to exist in Arabia.

Howard and Howard (1910) describe six botanical varieties of T. sphaerococcum under the name T. compactum. True T. compactum apparently does not exist in India (Cf. Percival, 1921, Vavilov, 1923). Of these six types, only one, T. compactum var. Humboldtii Kcke. of Howard and Howard (= T. sphaerococcum var. tumidum Perc.) appears to be an important agricultural variety, and is described as the common dwarf wheat of the Punjab. This is a beardless, white-grained form with white, smooth chaff. Howard and Howard state that dwarf wheats occur chiefly in the Multán and other western districts of the Punjab and also to a small extent in the Central Provinces and United Provinces. They are valued mainly for their drought resistance, are said to be good yielders and have a good reputation for bread making. Their cultivation is, however, rapidly declining, since their grain has no export value owing to its small size and can therefore only be used for local consumption.

In a later publication (1916) G.L.C. Howard records "*T. compactum* var. *Humboldtii* Kcke" (= *T. sphaerococcum* var. *tumidum* Perc.) from Baluchistan. She states that wheats of this type are not cultivated in a pure state in the Agency, but they were found in very small quantities as an impurity in two samples of wheat obtained from Gandava in eastern Baluchistan. This is quite near to the Punjab and but a small extension of the previously known range of the species. None of the Baluchistan wheats in the Cambridge collection belongs to *T. sphaerococcum*.

Percival (1921) reports *T. sphaerococcum* from the Punjab and from the Central Provinces and United Provinces. In addition, he found it in a sample of Kallak (little head) wheat obtained from Seistan (Iran). Vavilov (1923) did not, however, report this species from Iran and it does not occur in the large collection (approximately 600 forms) of Iranian hexaploid wheats which is grown in Cambridge. *T. sphaerococc* cannot, therefore, be of more than extremely rare occurrence in Iran, and it is probable that Percival's isolated sample was an importation from India. The wheat was of exactly the same type as the Indian *T. sphaerococcum* forms and occurred in the region of eastern Iran which adjoins north-western India and is in direct communication with it.

Vavilov (1923) did not record T. sphaerococcum except from India and did not find it later in his exploration of the putative centre of origin of hexaploid wheats, Afghanistan (V. and Bukinich, 1929), nor in Central Asia (V., 1931) nor Abyssinia (V. et al, 1931). Its absence from Afghanistan is particularly striking, since that country is the centre of botanical diversity of T. vulgare and T. compactum. This evidence strongly suggests that T. sphaerococcum has a centre of origin distinct from that of other hexaploid wheat species.

(2) Forms in the Cambridge Collection.

The Cambridge wheat collection is particularly rich in forms from India, Iran, China and other parts of Asia, so that it is unlikely that T. sphaerococcum can be at all widespread in any regions other than those from which it is recorded in this paper. All the botanical varieties described by Percival are present in the collection and also one new variety which is bearded and has glabrous, red chaff and white grain. The distribution of the forms is shown in Table XIII.

TABLE XIII

GEOGRAPHICAL DISTRIBUTION OF *T. SPHAEROCOCCUM* FORMS IN THE CAMBRIDGE COLLECTION

Variety.	No. of Forms	Source.
echinatum, Perc.	7	Sind 1*, Central Prov. 2, United Prov. 4.
spicatum Perc.	1	United Prov.*
new var. (see above)	4	Sind 1*, United Prov. 3*.
rubiginosum Perc.	6	Punjab 2, United Prov. 4*.
tumidum Perc.	4	Iraq 1*, Sind 1*, Punjab 2.
rotundatum Perc.	1	Punjab.
globosum Perc.	3	Sind 1*, Punjab 2.

* Not previously reported

(In addition to the above records, Howard and Howard (1910) report var. *spicatum* from the Central Provinces and var. *tumidum* is reported by Howard (1916) from Baluchistan and by Percival (1921) from the United Provinces).

The above data agree with previous records in demonstrating the occurrence of *T. sphaerococcum* in the Punjab, United Provinces and Central Provinces. The range is seen, however, to extend into Sind, from which the species has not previously been reported; four varieties were obtained from the province, all from the Agricultural Research Station at Sakrand, as "pure lines of Sind wheats". An isolated form was found in Iraq. This was originally collected in 1919 in the Euphrates region. It belongs to the variety tumidum commonly cultivated in the Punjab and the high probability that it was a recent importation from India is indicated by the following quotation from Wimshurst (1920), who describes the particular collecting expedition on which this wheat was found: "During the stress of war operations a considerable quantity of Indian wheat and barley seed was distributed all over the country[Iraq]....... The Indian wheat seed, however, was very mixed in variety and it is almost inevitable that in last year's survey odd ears originating from this war time seed import have been collected as local types and, in a way, such they have now become".

T. sphaerococcum, then, appears to be almost entirely confined to Northern India (Sind, eastern Baluchistan, the Punjab, United Provinces) and to the Central Provinces. The isolated occurrences in Iraq and Iran are almost certainl due to importation of wheats from India.

III. The Genetical Relationship between T. sphaerococcum and T. vulgare

(1) Literature.

Two crosses between T. vulgare and T. sphaerococcum and their reciprocals were studied by Miczyński (1930), who concluded that the whole complex of T. sphaerococcum characters was inherited as if it were determined by a single gene. He denoted the T. vulgare type as SS and the T. sphaerococcum type as ss. The sphaerococcum type was practically recessive to vulgare, but a few intermediate plants were found and the F_2 plants classified as "vulgare" varied somewhat in their characters. The segregation observed in the F_2 of the cross between the apically tip-awned T. vulgare variety Marquis and a bearded T. sphaerococcum variety was 9 variously tip-awned vulgare : 3 tip-awned sphaerococcum : 3 fully bearded vulgare (beards 4 to 8 cm. long) : 1 bearded sphaerococcum (beards 1.5-3.5 cm. long). Miczyński concluded from these results that the s gene has a direct effect in reducing awn length, the T. sphaerococcum parent with awns averaging 2 cm. long being genetically fully bearded. The alternative possibility that the s factor was closely but incompletely linked to another factor which reduced awn length was, however, by no means excluded.

- Miczyński's report only discussed inheritance in the F_2 and the subsequent behaviour of the intermediate plants was not determined. It is not clear from his results whether these plants were fluctuant heterozygotes or whether they represented cross-over types within a group of closely linked sphaerococcum genes. A further analysis therefore seems desirable.

(2) Inheritance in the Cross T. vulgare var. Chinese White x T. sphaerococcum var. rubiginosum.

In order to study further the mode of inheritance of the T. sphaerococcum character, a form of T. sphaerococcum var. rubiginosum was crossed with a hooded, beardless variety of T. vulgare, "Chinese White".

The F_1 of this cross closely resembled T. vulgare in type, though dominance was not absolutely complete. The spikelets were rather shorter and more inflated than in the vulgare parent, though the grains closely resembled those of Chinese White in shape.

In the F_2 the progeny could easily be classified into vulgare-like and sphaerococcum-like. Though the vulgare-like plants varied somewhat, the distinction between the two classes was sharp, and not a single F_2 plant was shown in F_3 to be classified wrongly in this respect. The F_2 segregation, as determined by the progeny test, was as follows:

	SS (vulgare-like)	Ss (heterozygote)	ss (sphaero.-like).
Observed	114	219	92
Expected	$106\frac{1}{4}$	$212\frac{1}{2}$	$106\frac{1}{4}$

$\chi^2 = 2.690$ Degrees of freedom = 2. P = .20-.30

There was therefore a reasonably close fit to the expected 1 : 2 : 1 ratio for a single gene difference. Within the segregating F_3 families themselves, the following ratio was observed:-

	S	:	s
Observed	2475	:	816
Expected	$2468\frac{1}{4}$	:	$822\frac{3}{4}$

$\chi^2 = 0.063$ Degrees of freedom = 1 P = .80 approx.

This is a very close fit to a 3 : 1 ratio.

Most of the Ss plants in the above family would undoubtedly be classified as typical T. vulgare. There was, however, some fluctuation, some of the heterozygotes being intermediate in character. In these cases, the plants often resembled T. sphaerococcum more closely in one respect than another. Plants were found, for instance, with short, hemispherical glumes almost like sphaerococcum but with large ears and oval, vulgare-like grain; with vulgare-like ears and round grain, and so on. It appeared in F_2 that some of these intermediate plants might be cross-overs, recombinations of the various characteristics of T. sphaerococcum and T. vulgare. In the F_3, however, all of them proved merely to be fluctuants. They all segregated in the ratio 3 *S* : 1 *s* in typical fashion and gave rise to families exactly similar to those of the more normal *Ss* plants.

Careful search was made throughout for one possible cross-over type, a tall-strawed *T. sphaerococcum* plant. The mean plant heights of the two parental varieties of this cross in 1936 were 93.9 cm. for Chinese White and 54.1 cm. for *T. sphaerococcum*. Forty exceptionally tall *sphaerococcu* segregates were found in the F_3, ranging from 75 to 95 cm. in height. These were grown on to F_4, where the highest family mean height proved to be only 66.3 cm. The mean height for the entire 40 F_4 families, totalling 493 plants, was 53.8 cm., i.e. no greater than that of the *sphaerococcum* parent.

The tall F_3 plants, then, were only fluctuants, plants particularly favourably placed with respect to the available food material and often only possessing single tillers. There was some evidence of segregation for minor factors affecting plant height, but not a single cross-over type with *sphaerococcum* type ear and tall straw could be found.

The segregation for awn type in this cross and in other crosses involving Chinese White is described in Part I above. Chinese White differs from a bearded wheat by two awn factors, *Hd* and *B_2*. The above F_2 showed a wide range of awn type from fully bearded *vulgare* to the parental hooded beardless form. For each genotype, however, the *sphaerococcum* segregates had much shorter awns or awnlets than the corresponding *vulgare* form. Whereas the fully bearded *vulgare* segregates had awns 5 cm. or more in length, those of the corresponding *sphaerococcum* class had awns only 1.5 to 2 cm. long. In a very extensive F_3 population, not a single case was observed in which a *sphaerococcum* plant had the long awns of bearded *vulgare*, and there was also no case of a *vulgare* segregate breeding true for the short *sphaerococcum*-type awns.

The absence of cross-over types in the above cross shows that the whole complex of characters by which *T. sphaerococcum* differs from *T. vulgare* does actually behave as if determined by a single gene and not ~~as~~ by a group of closely but incompletely linked genes. The impossibility of obtaining cross-overs of the types looked for is further illustrated by their absence in nature. *T. sphaerococcum* has undoubtedly been exposed to natural crossing with *T. vulgare* for long periods and one would expect to find almost every type of possible recombination in the naturally occurring populations of the species. The magnitude and diversity of the effects of this single Mendelian factor are much greater than one would normally associate with a recessive mutation at a single locus, particularly in a hexaploid species. This suggests that we are dealing not with a "point mutation", but with a structural change involving a short section of a chromosome. One likely hypothesis is that the two species differ by a single deletion covering several loci, the general characteristics of the mutation suggesting that it is the effect of gene deficiency. Such a deletion would, of course, be preserved intact and would be inherited as a single Mendelian factor.

Another possible mechanism is that of inversion. A small inversion, too small to permit of the frequent formation of chromatin bridges at meiotic anaphase, might have made possible the isolation of a series of gene mutations in a short section of a chromosome. The deficiency hypothesis appears, however, to be the more probable, especially as short straw, small ears and profuse tillering, all characters of _T_. _sphaerococcum_, are frequently found in 40- and 41-chromosome _T_. _vulgare_ plants, where they are undoubtedly caused by gene deficiencies. It is also the simplest mechanism, as it requires merely a simple structural change and not a structural change plus a complicated series of subsequent mutations.

A number of other _T_. _sphaerococcum_ x _T_. _vulgare_ crosses were studied by the author, but since their behaviour with regard to the _sphaerococcum_ character was exactly the same as in the above cross, no detailed results will be presented. The F_2 segregations for the Ss gene pair alone will be given. Expected values are given in brackets below ~~by~~ the observed segregations in Table XIV.

TABLE XIV.

Segregation in Further T. vulgare x T. sphaerococcum Crosses

Cross.	S	s	χ^2	P
T. vulgare var. Swedish Iron x T. sphaero. var. rubiginosum	1166 (1153½)	372 (384½)	0.499	.30-.50
T. vulg. var. Squarehead's Master x T. sphaero. var. rubiginosum	448 (466½)	174 (155½)	2.772	.05-.10
T. sphaero. var. rubiginosum x T. vulgare var. Swedish Iron	416 (413¼)	135 (137¾)	0.049	.80-.90
T. sphaero. var. tumidum x T. vulg. var. Squarehead's Master.	688 (639)	164 (213)	14.667	$<.01$

The segregations in the first three crosses does not deviate significantly from the expected 3 : 1 ratio, whereas in the fourth cross there is a significant deficiency of sphaerococcum segregates, the cause of which cannot be determined from the data available.

IV. The Cytology of Interspecific Crosses Involving T. sphaerococcum

(1) Literature.

~~Literature.~~ Vakar (1932) appears to have been the first to have studied the cytology of hybrids between T. sphaerococcum and other wheat species. He studied meiosis in the F_1 of two T. sphaerococcum x T. turgidum crosses and one cross of T. sphaerococcum x T. pyramidale Perc. In the first of the two turgidum crosses, 14 bivalents and 7 univalents or, rarely, 13 bivalents and 9 univalents were observed. No multivalents were reported, but in his Figure 66 he shows a chromatin bridge and acentric fragment, indicating that the hybrid was heterozygous for an inverted chromosome segment. The second T. sphaerococcum x T. turgidu cross and the T. sphaerococcum x T. pyramidale cross both showed a high degree of regularity, 14 bivalents and 7 univalents apparently being found in all the cells analysed. The chromosome behaviour was typical of that normally found in T. vulgare x T. turgidum hybrids and the author concludes from his observations that T. vulgare is very closely related to T. sphaerococcum and T. turgidum to T. pyramidale.

Kihara (1937), in a preliminary report, summarizes the cytological behaviour of a cross between T. sphaerococcu and T. vulgare. He reports that Lilienfeld and Kihara in

1934 found in both *T. vulgare* x *T. sphaerococcum* and the reciprocal cross a modal arrangement of 21 bivalents with apparently normal closeness of pairing. Occasional multivalents were also observed. The fertility of these two crosses is given as 91.51 and 94.84 per cent respectively. No further details are presented.

Percival (1930) describes an *Aegilops ovata* ($2n = 28$) x *T. sphaerococcum* cross in which he finds a maximum of four bivalents. He found 2 to 3 bivalents in the cross *Ae. ovata* x *T. compactum* and 1 to 3 bivalents in *Ae. ovata* x *T. vulgare*, so that the behaviour of *T. sphaerococcum* is very similar to that of other hexaploid wheat species in combination with *Ae. ovata*.

These cytological findings show clearly that *T. sphaerococcum* is very closely related to *T. vulgare*, a result to be expected on the basis of the genetical behaviou described above. It forms a modal number of 21 bivalents with that species and behaves similarly to it in crosses with other species. The occasional formation of multivalents observed by Lilienfeld and Kihara (Kihara, 1937) in crosses between *T. vulgare* and *T. sphaerococcum* is worthy of note, in view of similar occurrences which are to be reported and discussed below.

(2) Material and Methods.

Cytological preparations of the F_1 of the cross T. sphaerococcum var. tumidum (Cambridge collection number F 50/1) x T. vulgare var. milturum (Squarehead's Master) were made in the spring of 1937. The cytological technique employed was the same as that described above (p.94) except that La Cour's 2 BE fixative was used in all cases, and the camera lucida drawings were made at an initial magnification of X 3750 and subsequently reduced, as before, to X 2500.

(3) Experimental Results.

The types of chromosome arrangement found in the above F_1 are summarized in Table XV. It will be seen that the modal arrangement is that of 21 bivalents, as reported by Kihara (1937) in his material. In some cells (10 out of 68) two univalents replaced a bivalent and in one cell four univalents were found. This degree of disturbance, however, is no greater than that frequently found in crosses between different varieties of T. vulgare (Hollingshead, 1932b and author's unpublished results).

TABLE XV.

Chromosome Arrangements at Metaphase I in the Cross *T. sphaerococcum* x *T. vulgare*

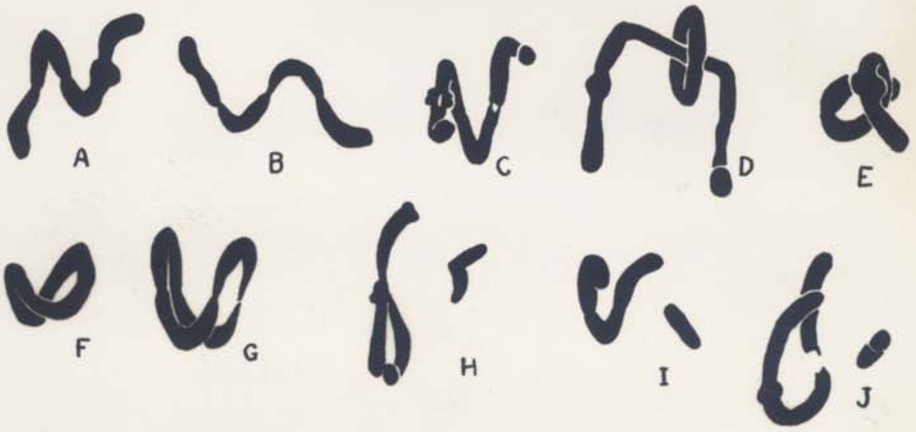
Arrangement.	No. of cells
$2_{IV} + 16_{II} + 2_{I}$	1
$1_{IV} + 19_{II}$	15
$1_{IV} + 18_{II} + 2_{I}$	1
$1_{III} + 19_{II} + 1_{I}$	4
21_{II}	38
$20_{II} + 2_{I}$	8
$19_{II} + 4_{I}$	1
Total	68

The general closeness of pairing in this material (as shown in Text-fig. 15) and the modal arrangement of 21 bivalents, again indicate that the chromosomes of *T. sphaerococcum* show a very high degree of homology with those of *T. vulgare*. The unusual feature of the cross is the high proportion of cells with multivalent associations. Out of 68 cells, 4 had a trivalent and a univalent, 16 had one quadrivalent and one (shown in Text-fig.15) had two quadrivalents. Some of these multivalent associations are shown in Text-fig. 16. Only two cells had closed ring

Text-fig. 15

Chromosomes at meiotic metaphase in the F_1 of the cross T. sphaerococcum x T. vulgare.

A cell with $2_{IV} + 16_{II} + 2_{I}$. x 2,500



Text-fig. 16

Multivalents in a T. sphaerococcum x T. vulgare F_1

A - E. Chains of four chromosomes (D with interlocked bivalent).

F - G. Rings of four.

H - J. Trivalents with univalents.

x 2,500.

quadrivalents, the remaining 15 quadrivalents being of the open chain type. It is to be noted that a large proportion of the multivalents are arranged in a regular zig-zag (disjunctional) manner, a condition observed by Thompson and Thompson (1937) and Smith (1939) in other Triticum material. The non-disjunctional quadrivalent in Text-fig. 16 D is clearly so arranged because its normal orientation was prevented by interlocking with a bivalent.

The multivalents* observed in this cross may be due to one of three causes, (1) pairing in reduplicated chromosome segments, (2) reciprocal interchange of segments between chromosomes or (3) a combination of both. One would naturally expect reduplicated segments to occur in an allopolyploid form where there are three chromosome sets which must show a considerable amount of homology. The frequent occurrence of multivalents due to this cause in a hybrid would, however, imply that some relatively long homologous, reduplicated segments were present, and almost equally frequent multivalent formation would be expected in the parents. Multivalent formation undoubtedly occurs in pure lines of wheat, but only rarely. One of the parents actuall

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*) Some cytologists prefer not to use the terms 'quadrivalen 'hexavalent', etc. for ring and chain formations caused by reciprocal interchange, but use the terms 'associations of four','association of six', etc. The terms are here used in their widest sense to denote any primary association of chromosomes.

involved in this cross, Squarehead's Master, was studied from this point of view and two chain quadrivalents are found in 74 cells. In the pentaploid wheat hybrids studied by the author and ~~to be~~ reported in Part I above, one chain quadrivalent attributable to pairing in a reduplicated segment was observed in 303 cells. This mechanism may therefor have led to the production of a small proportion of the observed multivalents in the <u>sphaerococcum</u> cross, but the alternative mechanism of reciprocal interchange must be chiefly responsible. The evidence obtained from the occurrence of speltoids detailed below also supports the reciprocal interchange hypothesis. All the configurations observed except that in Text-fig. 16 H are of the types to be expected on this basis, either rings of four or chains of three or four. The exception may be due to pairing in a reduplicated segment or to chiasma formation in a segment proximal to the interchange in the chromosomes involved in th ring.

We may accept, therefore, the fact that reciprocal interchange is responsible for nearly all the observed multivalents; what is not clear is how many reciprocal interchanges are involved. It may be that there is only one and that the second quadrivalent shown in the cell in Text-fig.15 is due to pairing in a reduplicated segment. In view of the comparative rarity of naturally occurring reciprocal interchanges in wheat, this hypothesis would appear to be a likely one. On the other hand, it cannot be shown from the present data that there are not two or even more reciprocal interchanges, in each of which, chiasma formation occurs in the interchanged segments in only a small proportion of cases.

In the above cross, the frequency distribution of rings and chains of four and of the configurations which may replace them is as follows:-

1 cell with two chains of 4
2 cells with one ring of 4our
15 cells with one chain of 4
2 cells with a chain of 3 and a univalent
1 cell with a Y univalent
47 cells in which bivalents replace the ring or rings of 4

(possibly in some of these cases, two univalents may be present instead of a bivalent).

The large proportion of cells with incomplete or "broken" rings of four chromosomes in this material shows that the reciprocally interchanged regions must be relatively short, so that chiasma formation in them fails frequently. The position of the "breaks" in the ring is by no means at random. Two breaks giving a trivalent and a univalent are relatively rare, whereas two breaks giving two bivalents are extremely common. This is clearly to be expected. The replacement of a ring of four by two bivalents depends upon failure of chiasma formation in two short interchanged segments, a relatively likely event, whereas the production of a trivalent and a univalent depends upon failure of chiasma formation in a single interchanged segment and also in a pair of chromosome arms which are not involved in the structural change and which are presumably completely homologous or very nearly so. The latter event is relatively unlikely.

It should be noted that no heteromorphic bivalent was observable in the present material, indicating that the deletion by which, it has been suggested above, T. sphaerococcum differs from T. vulgare is not large enough to be detectable at meiotic metaphase.

V. The Occurrence of Speltoid Mutations in *T. sphaerococcum* Crosses.

Miczyński (1930) reported the occurrence of a few plants "resembling *T. Spelta*" in the F_2 of his *T. vulgare* x *T. sphaerococcum* cross. Such speltoid mutations were also found with exceptional frequency in the present material. The results are summarized in Table XVI.

TABLE XVI

The Frequency of Speltoid Mutations in the F_2 of *T. sphaerococcum* x *T. vulgare* Crosses.

Cross	No. of Plants in F_2	No. of heter zygous spel toid mutan
T. vulgare var. Chinese White x *T. sphaero.* var. *rubiginosum* (1936)	425	4*
ditto (1938)	349	24
T. sphaero. var. *rubiginosum* x *T. vulgare* var. Swedish Iron	551	0
T. vulgare var. Squarehead's Master x *T. sphaero.* var. *rubiginosum*	290	17
T. sphaero. var. *tumidum* F 50/1 x *T. vulgare* var. Squarehead's Master	852	6**
Total	2467	51

* confirmed in F_3.

** the cross studied cytologically above.

Normally, speltoid mutants in wheat occur but rarely, so that there would appear to be some special reason for their frequent occurrence in the above crosses.

Winge (1924) first postulated that speltoid mutants in wheat were due to pairing between corresponding chromosomes of different chromosome sets, followed by irregular segregation. If the normal *vulgare* type is represented as $\frac{ABC}{ABC}$, then the heterozygous speltoid is $\frac{ABB}{ABC}$ and the homozygou speltoid $\frac{ABB}{ABB}$. Watkins (1927, 1928) found that speltoid formation need not depend upon irregular segregation of whol chromosomes, but on the segregation of a specific gene or block of genes which determines the keeled glume condition. If we represent typical *T. vulgare* as $\frac{k_1K_2}{k_1K_2}$, then the form $\frac{K_1}{k_1}$ is a heterozygous speltoid and $\frac{K_1K_2}{K_1K_2}$ a true speltoid. Presumably the form $\frac{K_2K_2}{K_2K_2}$, which would be produced by the mechanism postulated by Winge, would be of a similar speltoi type, K_1 and K_2 being regarded as duplicate factors.

If, in a particular hybrid form, the chromosome pairs carrying the genes k_1k_1 and K_2K_2 are involved in a reciprocal interchange, then in a proportion of cases the ring of chromosomes (or its derivative chain of four or trivalent and univalent) will segregate irregularly, giving K_2K_2 and k_1k_1 gametes instead of the usual k_1K_2 form. This mechanism would give rise to an exceptionally high proportion of heterozygous speltoids in the F_2 generation, and in view of the fact that at least one reciprocal interchange occurs in the above T. sphaerococcum x T. vulgare hybrid, it appears to be a very likely one to explain the observed genetical results. It should be noted here that, a priori, reciprocal interchanges in polyploid wheats are most likely to occur between corresponding chromosomes of different sets, since the simplest mechanism for their production is occasional pairing between such chromosomes, followed by crossing over.

In most plants, it appears that non-disjunctional gametes derived from a ring of four by the passing of adjacent chromosomes to the same pole do not function, owing to the occurrence of duplications and deficiencies. Here, however, the interchange is short and involves chromosomes which are themselves more or less homologous, so that non-disjunction would not cause a serious disturbance of the genetic balance.

The proportion of speltoid mutations observed in the above crosses is in good agreement with this hypothesis of non-disjunctional separation of a ring or chain quadrivalent. Smith (1939) has presented evidence which indicates that in the case of T. monococcum a ring of four chromosomes disjoins regularly in about 80% of cases, and non-disjunctionally in the other 20%. The proportion of non-disjunction appears to be rather less in this material; although the number of quadrivalents observed is not great enough to form a precise estimate, the figure of 10% of non-disjunction may be taken as being not very far wrong. Now in the cross studied cytologically above, 21 cells out of 68 formed multivalents and the remaining 47 had presumably regular segregation of two bivalents. The proportion of speltoids to be expected is therefore 1/10 x 21/68, or roughly one in thirty if only one reciprocal interchange is present, involving the K chromosomes. If two reciprocal interchanges are present and pairing in them occurs with roughly equal frequency, then the expected proportion of speltoids would be one in sixty. The observed proportion, 51 out of 2467, or about one in fifty, is therefore of the order which is to be expected.

After the above hypothesis of speltoid formation had been formulated, the writer discovered that Huskins (193 had already made the suggestion that the mechanism of reciprocal interchange occurring between partly homologous chromosomes may lead to the production of races of oats which give a high proportion of fatuoid mutations, so that the case in oats would appear to be enitely parallel to that in wheat.

VI. Discussion

These geographical, genetical and cytological data enable us to trace the story of *Triticum sphaerococcum* in considerable detail. First of all, it is clear that it is an allohexaploid species which arose secondarily from *T. vulgare* and not directly from a sterile hybrid between *Triticum* and *Aegilops*. It arose as a result of a single mutation in a plant of *T. vulgare*, which very probably took the form of a deletion of a short chromosome segment. This mutation is only known to have occurred once in the history of the species *T. vulgare*. It may, of course, have occurre at other times and in other places, but at any rate it only became established in the wheat population in one region, the Punjab and the neighbouring parts of India. Probably its persistence and spread into that region were determined by its marked drought resistance, which enabled it to compet on advantageous terms with *T. vulgare*.

We must regard it as highly probable that at first only one plant of *T. vulgare* was affected and that all the *T. sphaerococcum* plants in existence to-day are descendants of it. *T. sphaerococcum* is found to-day, however, in a number of different "botanical varieties" and it contains a large number of alternative pairs of genes. Some of these new forms may, of course, have arisen by mutation, but it is clear that the present-day diversity of the species has very largely been attained by repeated natural crossing with *T. vulgare*. By now, most of the alternative characters associated with the latter species have been transferred to i

The strains of *T. sphaerococcum* tested were found, when crossed with western Europe *T. vulgare*, to be associated with one or more reciprocal translocations. This association, however, is purely a matter of chance, as the *sphaerococcum* character is determined solely by a single Mendelian factor and does not in any way depend on segmental interchange. This translocation may have occurred in the population of *T. vulgare* forms from which *T. sphaerococcum* arose or to which it has been exposed in repeated natural crosses, or, alternatively, in *T. sphaerococcum* itself after the inception of the species. Crosses between western European wheats and a wide range of Indian *sphaerococcum* and *vulgare* forms would be required to determine the distribution of the reciprocal interchange or interchanges involved.

This occurrence of interchange, though not essential a feature of *T. sphaerococcum*. leads to interesting results. "Pure lines" of *vulgare* wheats never breed true, but produce a variety of mutants caused by irregular chromosome pairing. The speltoid type of mutant is the most widely known of these, and it is known that different pure lines give rise to it in widely differing frequencies. The variety Yeoman, for instance, produces speltoids very much more frequently than most wheats. The present study shows clearly that a wheat which is heterozygous for a small reciprocal interchange involving the chromosomes which carry the $\underline{K}_2$ and $\underline{k}_1$ factors may behave regularly in a large percentage of cases and would, if inbred and suitably selected, be regarded as a "pure line". The only difference between its behaviour and that of wheat in which reciprocal translocation was not present would be that it would give rise to an exceptionally high proportion of speltoid mutants. Reciprocal interchange therefore, can be looked upon as an important factor in the determination of differences between "pure lines" on the proportion of speltoid mutants to which they give rise. The frequency of speltoid formation would be directly correlated with the length of the interchanged segment or, more correctly, with the frequency of chiasma formation in it.

Systematists may hold that a form like _T. sphaerococcum_, which differs from its parent form only by a single Mendelian factor and which is still very highly fertile in crosses with it, does not merit the distinction of specific rank. It is not proposed to discuss this question at length, but it may be pointed out that _T. sphaerococcum_ is very distinct from _T. vulgare_ in phenotypic appearance and that the difference is discontinuous, so that it is at least desirable to retain the name sphaerococcum for convenience in description. From a systematic point of view, it may be that *T. vulgare*, *T. compactum*, *T. Spelta* and *T. sphaerococcum*, the latter three of which each differ from the first only by a single Mendelian factor, should be regarded as sub-species of a single species. From the point of view of practical convenience, however, the present nomenclature is satisfactory, providing that the real nature of the differences between the "species" is understood.

SUMMARY

1. *Triticum sphaerococcum* is confined in its geographical distribution to Sind, eastern Baluchistan, the Punjab, Central Provinces and United Provinces of India, with the exception of isolated forms recorded from Iran and Iraq, which are probably recent introdutions from India. The species does not occur in Afghanistan, where *T. vulgare* and *T. compactum* are found in their greatest diversity.

2. *T. sphaerococcum* differs from *T. vulgare* only in a single "gene", the *vulgare* type being dominant. *T. sphaerococcum* may be denoted as *ss*, and *T. vulgare* as *SS*. Occasional heterozygotes are intermediate and appear in F_2 to be cross-over types representing a breaking up of the *T. sphaerococcum* complex. Progeny tests, however, reveal that these are only fluctuants and they behave like other *Ss* plants when grown on.

3. Owing to the complex effect of the *s* gene, and the improbability of a recessive mutation at a single locus having such a large effect in a hexaploid form, it is considered likely that the change involves a block of genes, and is probably a deletion.

4. The F_1 of a cross between *T. sphaerococcum* and *T. vulgare* was studied cytologically. The behaviour resembled that in an intervarietal cross in *T. vulgare*, except

that the F_1 was heterozygous for one or more reciprocal translocations.

5. An exceptionally high proportion of heterozygous speltoid mutants was observed in several F_2 populations of T. vulgare x T. sphaerococcum. This can be explained on the assumption that the chromosomes which carry the speltoid character are involved in one of the above reciprocal translocations, so that non-disjunctional separation of the ring or chain of four gives rise to heterozygous speltoids.

6. T. sphaerococcum apparently arose as the result of a deletion in the population of T. vulgare forms which spread into north-western India, probably from Afghanistan.

7. The present-day diversity of T. sphaerococcum arose almost entirely by natural crossing of the original mutant population with forms of T. vulgare.

8. The association of one or more reciprocal interchanges with certain T. sphaerococcum forms is purely accidental and is not an essential characteristic of the species.

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