Carpellody in the Wheat Flower and Its Inheritance.

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THE term carpellody signifies sex-reversal in the direction of male to female organs in plants.

An interesting abnormality of the wheat flower was noticed in a plant among the wheat plots at Lincoln College in 1924. The plant first attracted notice because the glumes remained expanded for from seven to ten days giving the head a conspicuous transparent effect. The abnormality has been investigated and certain experiments have been conducted to determine its behaviour on breeding. The present paper is a progress report of the results.

Carpellody has been reported in various plants and consists of partial or complete transformation of stamens to carpel.

De Candolle reported carpellody in the wallflower (*Cheiranthus cheiri* and he gave the plant the varietal name *C. cheiri gynanthus.* This case has been investigated by Nelson in the *Publications of the Royal Society of Tasmania* in 1928. The stamens adhere together and form a closed ring round the normal carpel. Ovules are produced within this ring and when pollinated produce viable seeds. Nelson crossed a carpellodic form with a normal. The F1 from the cross were normal and segregation occurred in the F2 in the proportion of 3 normal to 1 carpellodic showing that it was a simple mendelian recessive character.

Weatherwax, in the *Proceedings of the Indiana Academy* in 1925 reported carpellody in Maize, where the rudimentary anthers of the pistillate flowers were transformed into carpelloid structures. In this case, however, he states that there is no true ovarian cavity and no ovules are formed although style and stigma are similar to the normal.

Shaffner, in the *American Naturalist* in 1925, when discussing sex differentiation and determination in higher plants, states that sex-reversal is primarily dependent on physiological states, and these are subject to change and reversal through ecological factors.

The wheat flower is considered extremely stable few abnormalities having been reported.

Anthony, in the *Journal of Heredity,* 1918, reports an abnormality in which the anthers bore a few stigmatic hairs and the filament united with the anther as one piece.

Leighty and Sando, in the *Journal of Heredity* in 1923, reported pistillody in the wheat flower and from their description the abnormality is the same as the one here described. They did not give any anatomical description and they state that the character is not

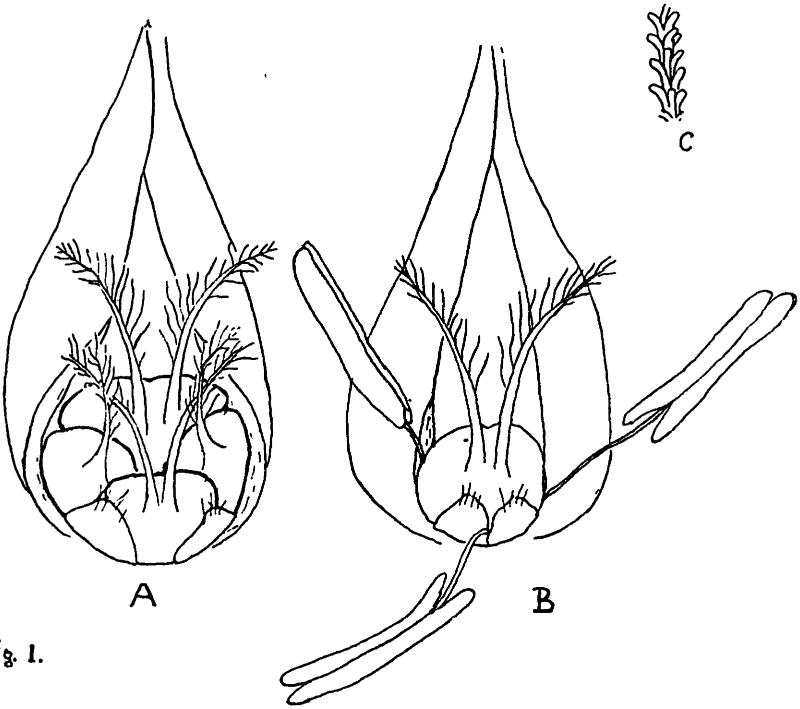

Fig. 1.

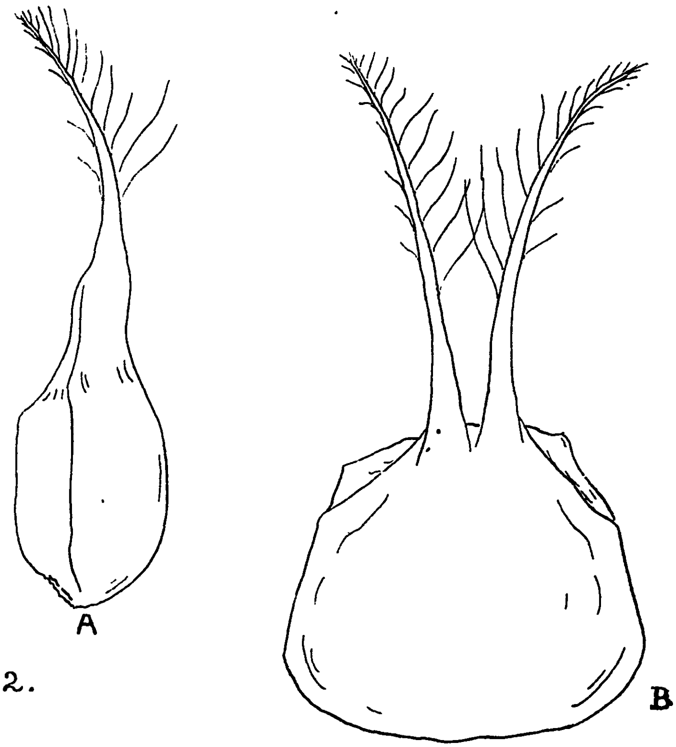

Fig. 2.

inherited as it did not appear among eighteen plants grown from seed of the abnormal plant the next year. They suggest some environmental cause.

In the present paper the anatomical description is given and definite proof that the character is inherited is produced.

In the normal wheat flower there is a central carpel, consisting of a single ovary in which there is a single ovule. There are two distinct style branches which are covered with long stigmatic hairs. Outside the carpel are three stamens—two lateral and one anterior. The stamens have distinct filaments which elongate rapidly at flowering and support definite linear oblong anthers which are devoid of hairs. Outside the stamens are two whorls of structures representing the normal two whorled perianth of Monocotyledons. The inner whorl is represented by two scale like structures in front at the base called lodicules. The outer whorl is represented by a single large member posteriorly—the palea. The above constitutes the flower proper. In addition there is present in front a large bract or glume, the lemma. There are three to five such florets in a spikelet attached alternately to a rachilla and subtended by two empty glumes. The spikelets, of which there are fifteen to twenty-five, are attached on alternate sides of a somewhat flattened zigzag rachis. This inflorescence is called the head or spike of wheat.

DESCRIPTION OF THE ABNORMALITY.

The abnormality involves the transformation of the stamens into carpelloid structures with no resemblance to anthers, or into structures that are partly anther and partly carpel, or involves simply the addition of a few stigmatic hairs at the apex of an anther. The degree of transformation extended over this very wide range. In some flowers only one anther was affected, in others two, but in the majority of cases all three showed some degree of transformation.

The greatest degree of transformation usually occurred in the lowest floret of a spikelet. The second floret was usually somewhat less abnormal and the third floret still less so.

Those stamens which were only slightly abnormal always produced pollen while some which were almost completely carpelloid showed a small portion of pollen bearing tissue usually at the distal end. Others produced no pollen at all. Any floret which did not produce pollen would not as a rule set seed. Thus the lowest florets of the spikelets which were the most abnormal, produced fewer grains than did the upper florets. For example:—

Seven heads were examined and found to contain ninety spikelets. The following table shows the number of grains that would usually be found in each floret of such spikelets and the actual number found.

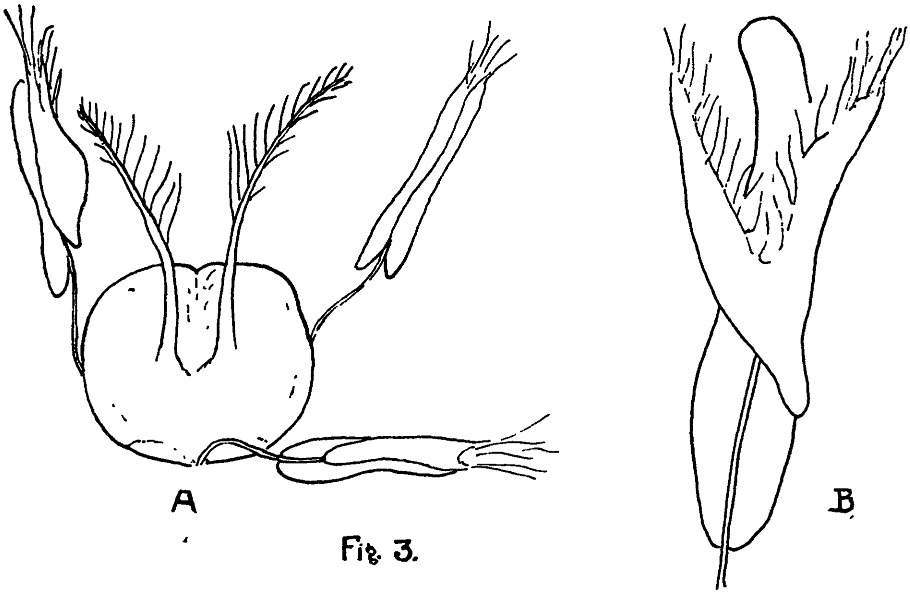

Fig. 3.

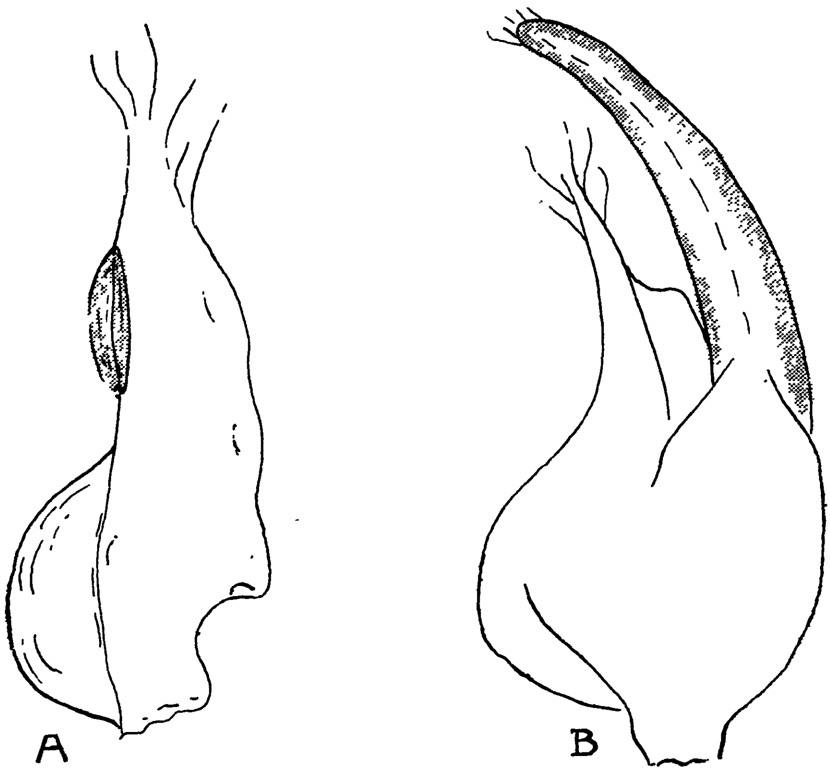

Fig. 4.

Position of Spikelet.	Grains Expected.	Grains Found.	
Lowest	90	9	10%
Second lowest	90	18	20%
Third lowest	36	18	50%
Fourth lowest	7	7	100%

The decreasing percentage obtained from the fourth to the lowest floret is due to the increasing degree of transformation from the fourth to the lowest spikelet.

Fig. 1 B is a diagram of a normal floret; A, is a floret showing the greatest degree of transformation. The anterior abnormal carpel has two stigma branches. C is portion of a stigmatic hair.

Fig. 2 shows A, a lateral, and B, an anterior, abnormal carpel dissected out.

Fig. 3 A is a third floret of a spikelet showing three partly transformed anthers and B is an enlarged view of a single anther.

Fig. 4, two lateral abnormal carpels showing different amounts of carpel and anther tissue. Here the carpel tissue seems to develope chiefly from the filament at A or from both filament and anther at B.

Fig. 5 shows the carpel tissue developing from the anther (A) and from the filament (B).

The question whether the transformation ever extended to perfect carpels was tested by artifically pollinating all the abnormal carpels in one head. No grain set in any of these abnormal carpels thus demonstrating that they are infertile. Further, all the grain which formed in any abnormal head was produced from the central normal carpel. This was evident from the central position of the ripe grain and also from the fact that the ripe grain of the lowest florets, i.e., those in which the abnormality seemed sufficiently advanced to produce grain, had three scale like structures at the base. These represented the shrivelled remains of the abnormal carpels.

An interesting observation was the presence of Ergot in eighty per cent. of the sterile florets. This fungus is very rare on wheat in New Zealand. Adjacent plants in the plots showed no sign of it. Evidently, the fungus is able to gain entrance to the unfertilised ovary more readily than to normally fertilised ones.

Anatomical Description.

Fig. 6 shows, A, a transverse and B, a longitudinal section of a normal carpel. Externally is the massive carpellary tissue which is limited internally by the inner epidermis. Just outside the inner epidermis is a distinct layer of cells which forms the "cross layer" in the ripe grain. Within the inner epidermis is the nucellar cavity. The nucellus arises in the nucellar cavity from the carpellary tissue. It is bounded by a distinct epidermis with its cells elongated at right angles to the surface. Surrounding the nucellus is the two layered inner integument and outside this is the three to four layered outer integument. Occupying the bulk of the nucellus at maturity is the

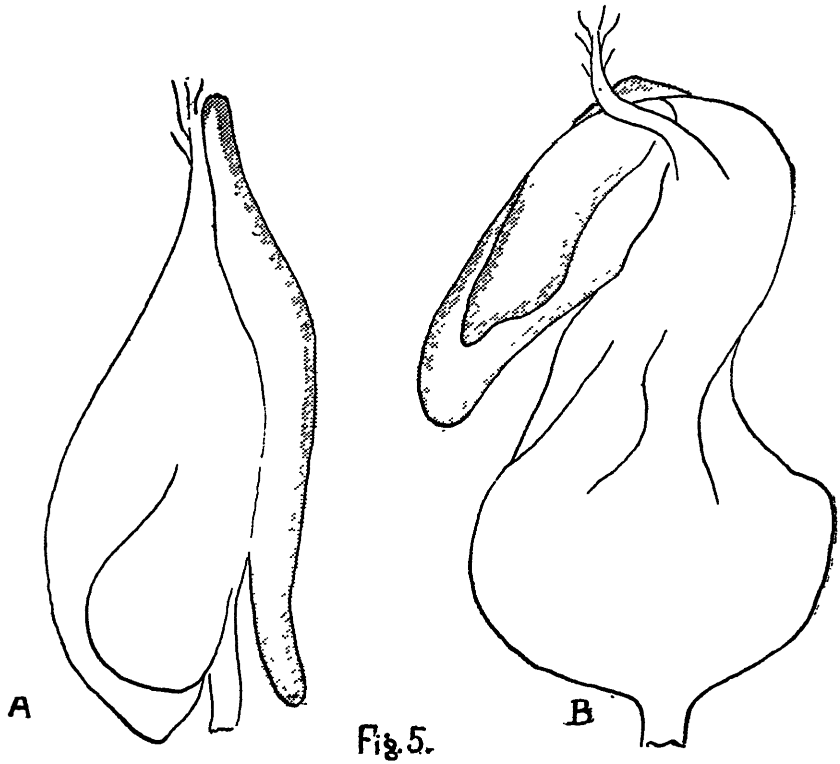

Fig. 5.

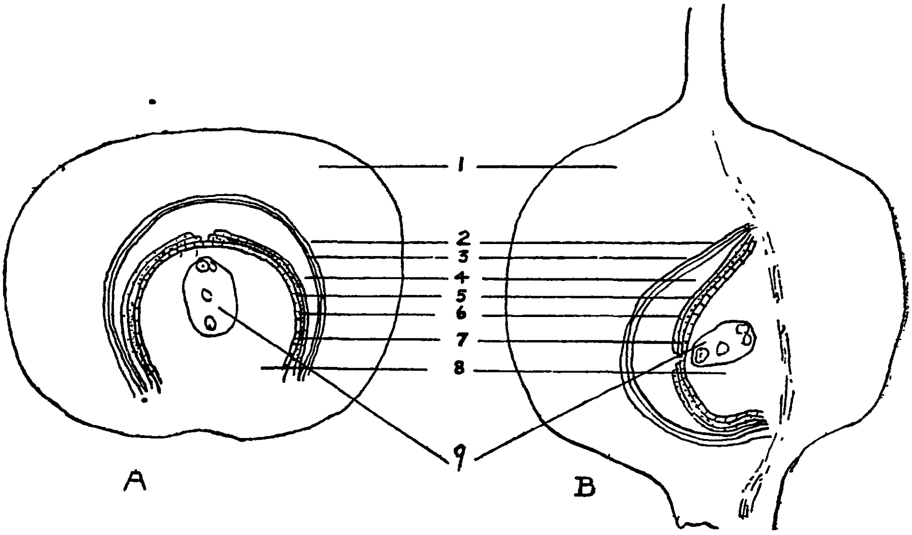

Fig. 6

embryo sac, which arises from a single cell of the nucellus, the megaspore. The embryo sac grows rapidly and is well grown by the time the integuments have closed over the nucellus. So that we have in a normal carpel the following tissues:

1. Carpellary tissue.
2. Cross layer.
3. Inner epidermis of carpel.
4. Nucellar cavity.
5. Outer integument.
6. Inner integument.
7. Nucellar epidermis.
8. Nucellus.
9. Embryo sac.

Fig. 7 is a longitudinal section of an anterior abnormal carpel showing two masses of nucellus with all the tissues one to eight present as in a normal carpel but the embryo sac is missing. The two nucellar masses developing in the abnormal carpel might be of importance in a discussion of the morphology of the grass flower.

Fig. 8 is a diagram of the tissues seen in the abnormal carpel of diagram 7. Exactly similar to those of a normal carpel.

Fig. 9 is another longitudinal section of an anterior abnormal carpel. There are the beginnings of two nucelli (X and Y). The embryo sac and the two integuments are missing, *i.e.*, tissues five, six and nine. The double nucellar masses are correlated with the two stigma branches.

Fig. 10 is a L.S. of a lateral abnormal carpel. Here the nucellus has one nucellar mass with an inner integument composed of several layers of cells and the rudiment of the outer integument. Also in the nucellar cavity are two other outgrowths of tissue without a defined epidermis and do not suggest nucellar tissue. There is no embryo sac *i.e.*, tissue nine is missing, five is rudimentary, six is massive instead of being two-layered.

Fig. 11. This is another L.S. of a lateral abnormal carpel. Here the nucellus has formed near the inner edge of the carpel so that in its growth it has broken through the wall and appears external to the carpel. The inner integument is present adhering close to the nucellus and a portion of the outer integument is present at the apex. There is no embryo sac. In the same diagram are seen stigmatic hairs and a portion of an anther lobe.

Fig. 12 is a L.S. of a similar abnormal carpel showing the nucellus more central but free from carpel enclosure at the apex. Also a portion of anther tissue with pollen grains. Tissues numbered two and three are much reduced.

Fig. 13. A L.S. of a lateral abnormal carpel showing the nucellar cavity appearing as a slit. The inner epidermis of the carpel and the cross layer are present. There is no nucellus or integuments, *i.e.*, tissues five, six, seven, eight, nine are missing.

Fig. 14 is a L.S. of an abnormal carpel showing a reduction in pollen bearing tissue and an increase in parenchyma.

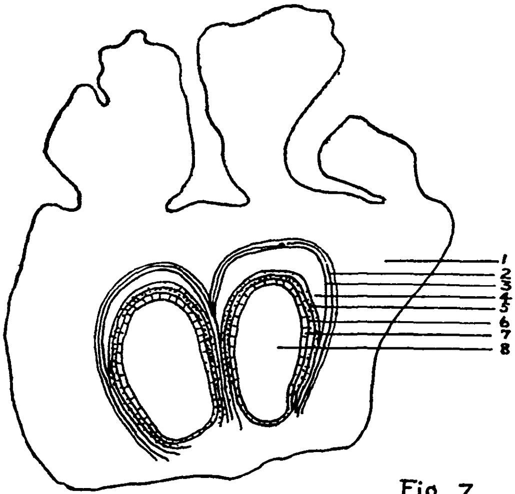

Fig. 7

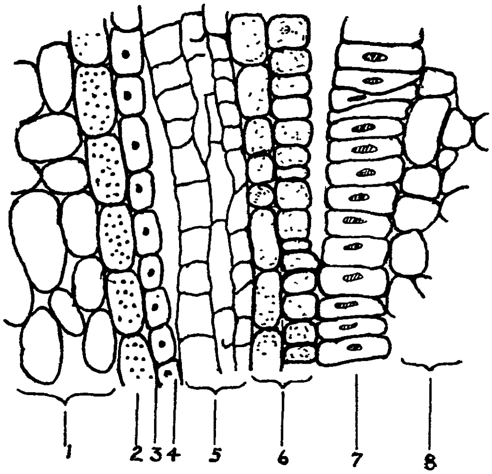

Fig. 8.

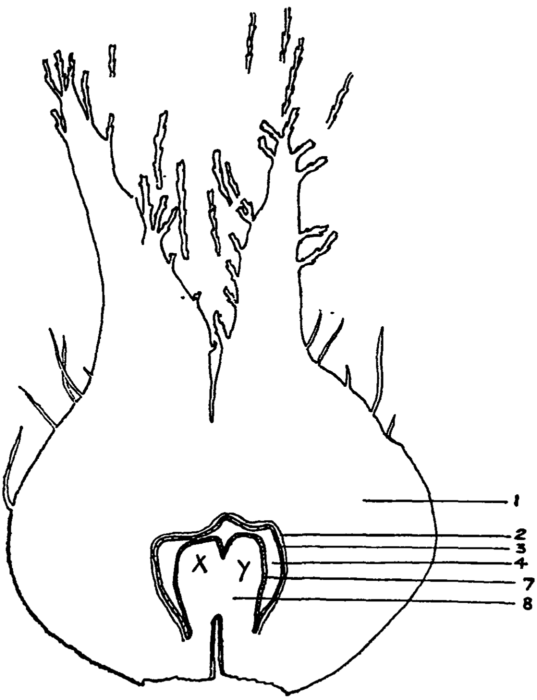

Fig. 9

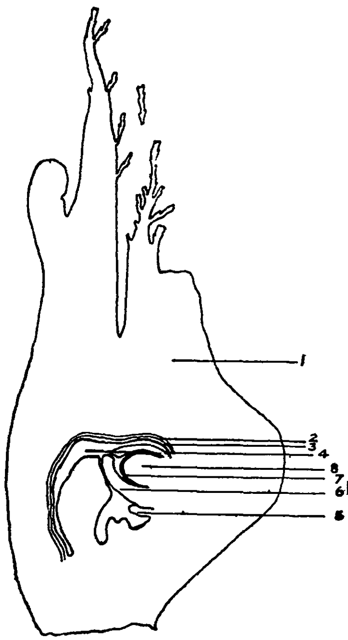

Fig. 10

SUMMARY OF ANATOMICAL STRUCTURE.

A section of the most completely transformed abnormal carpel shows all the tissues present as in a normal carpel with the exception of the embryo sac which was missing in all cases examined. In the anterior abnormal carpel two masses of nucellar tissue develop. Abnormal carpels with less degree of transformation show reduction and suppression of the various tissues numbered one to eight. Tissue nine the embryo sac, is always missing. Anther tissues and nucellus are present in the same structure in some cases. The anther may show an increase in parenchyma with a corresponding decrease in pollen tissue. This parenchyma may develop from the filament or from the anther or from both filament and anther. The lowest degree of transformation was the presence of a few stigmatic hairs at the apex of the anther. Some anthers of the abnormal plant appeared quite normal.

INHERITANCE OF THE ABNORMALITY.

The abnormal plant occurred as one among twenty-five F1 plants produced from a cross between Solid Straw Tuscan and a selected plant from the F4 generation of a cross between White Fife and Benefactor. The remaining twenty-four plants of the cross were normal.

The plant was first noticeable on account of the glumes remaining open throughout the flowering period. This is no doubt due to the extra bulk of the flower and it makes conditions very suitable for cross pollination, which is the only means of pollination in those flowers in which the stamens are sterile. The flower might be accommodating itself for cross pollination.

All of the grain produced by the abnormal plant was sown in the glass house. From fifty-nine grains, some of which were very shrivelled, thirty-nine plants were obtained. These were planted out in the birdcage in the spring and examined at flowering time. Five out of the thirty-nine were abnormal. These were particularly uniform as regards certain morphological characters: they had thin straw, were three to four inches shorter than the other plants of the row, the straw was solid and the heads were of one type. The five plants had the appearance of a pure line. The remaining plants of the plot were very heterogeneous suggesting cross pollination by different parents (this was likely to occur in the plots).

The original plant commenced to grow after harvest so it was transplanted to the green house over winter and planted out again the following spring. At flowering time the abnormality was again present. The plant was weak and no grain was formed. It died after harvest.

BREEDING RESULTS.

A. *Self-pollination.*

Seventeen heads of the five abnormal plants were enclosed in paper bags to ensure self-pollination. One hundred and forty-three grains were obtained and one hundred and thirty-two plants de-

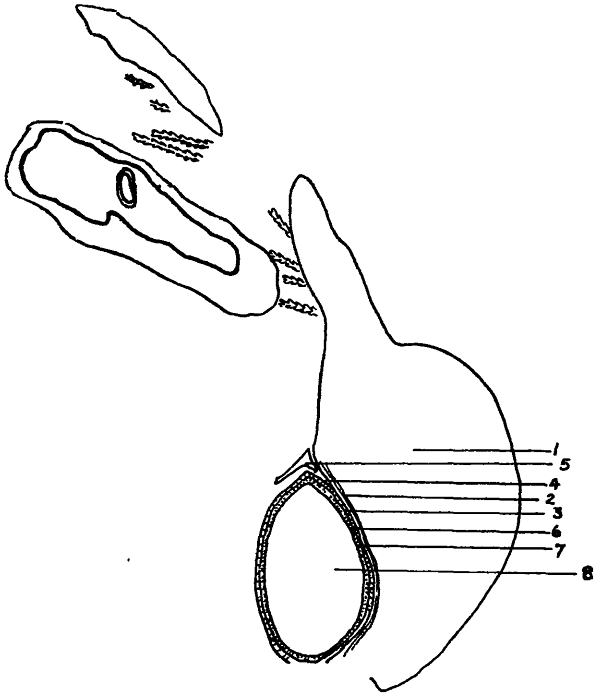

Fig. 11

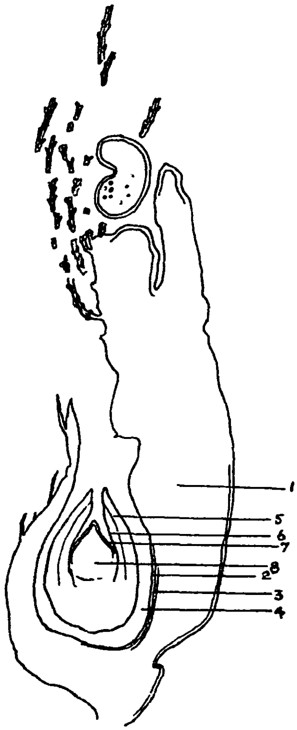

Fig. 12

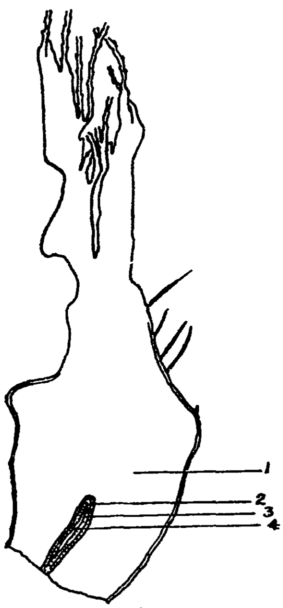

Fig. 13

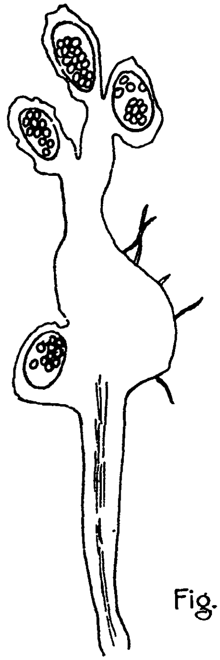

Fig. 14

veloped. Of these, one hundred and twenty-six were abnormal and six were normal. All these one hundred and thirty-two plants (normal and abnormal) were alike morphologically, *i.e.*, they were all short, had solid straw, thin straw, and had similar head type. The presence of the six normal plants is accounted for as follows: As the abnormality was known to vary over a wide range it was thought that these six plants might be masked abnormals. So the seed was sown the next year along with seed from ten abnormal plants. The abnormality occurred among the offspring of five of the six plants to the same extent as it occurred among the offspring of the ten abnormal plants showing that they were masked abnormals. If this is so then the results of self-pollination of the abnormal plants is abnormal offspring. This has enabled the abnormality to be carried on for four generations.

B. *Cross-pollination.*

Five heads of abnormal plants were pollinated with pollen from velvet wheat. Thirty-seven grains were obtained and thirty-four plants developed. These thirty-four F1 plants were normal and had velvet chaff (a dominant character of the male parent). All the grain of these thirty-four plants was sown and 2016 F2 plants developed. Velvet chaff appeared in the proportion of three velvet to one smooth, but not a single plant of the 2016 showed any sign of the abnormality. The abnormality occurred in adjacent plots where the plants were obtained from selfed seed.

The results of the breeding indicate that the character is inheritable and is recessive. It is not a simple recessive as it does not segregate in the F2. It is fairly clear that it is not due to environmental causes. The fact that it also occurred in a single plant in America suggests that it is due to a definite alteration in the chromosomal complex.

The correlation of certain morphological characters with the abnormality are very suggestive of a linkage group and in view of the fact that linkage groups have not yet been definitely located in wheat this abnormality might be of importance in this direction.

Further work on its inheritance is in progress.