STRUCTURE OF THE MAIZE EAR AS INDICATED IN ZEA-EUCHLAENA HYBRIDS

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INTRODUCTION

In attempting to trace the origin of maize (*Zea mays* L.) the center of interest is the evolution of the peculiar form of inflorescence, especially the pistillate inflorescence, or ear.

Since Euchlaena (*Euchlaena mexicana* Schrad.) or teosinte, the nearest known relative of maize, has a very different type of pistillate inflorescence, it may be instructive to compare the two genera and trace the successive changes that would be required in passing from the Euchlaena form of pistillate inflorescence to the maize ear.

Euchlaena and maize cross freely, resulting in intermediate hybrids which in subsequent generations grade back to the parental forms (Pl. 16). It is therefore possible to present a complete series of intermediates, graduated to any desired degree of minuteness. It should be kept in mind that although we may be able to arrange a continuous series of forms ranging from Euchlaena to maize, these forms may not represent the course of evolution. A study of these intermediate hybrids may be expected, however, to throw light on the morphology of the ear and to explain its evolution, at least in a mechanical sense.

DESCRIPTION OF MATERIAL

The forms here described as intermediate between maize and Euchlaena appeared for the most part among the descendants of a cross between Florida teosinte and a diminutive variety of popcorn called "Tom Thumb." Of this cross six first-generation plants were grown and from the self-fed seed of one of these a second generation consisting of 127 plants was produced. Several hundred third-generation plants from open pollinated seed were also examined.

Although in general appearance the pistillate inflorescences of maize and Euchlaena are so unlike that comparisons are difficult, the structure of the flowers is practically identical. The chief differences are therefore to be sought in the structure of the inflorescence and the arrangement of the spikelets.

To avoid circumlocution it is necessary to consider as a morphological unit the association represented by a sessile and pedicelled spikelet, as they occur in the staminate inflorescence. It would be misleading to refer to this unit as a pair of spikelets, because the same unit must also be kept in mind in considering the pistillate inflorescence where one of the spikelets may be suppressed. The two spikelets of a pair probably arise from a single metamer, at least they seem never to become separated. In the pistillate inflorescence, however, the individual metamers can be distinguished with difficulty and the pairs of spikelets become so profoundly and diversely modified that a general term is needed to designate this structural unit in all its forms.

In the pistillate inflorescence the members of this morphological unit, whether it is represented by one or two spikelets, occupy a single alveolus, and the complex might be described as the contents of an alveolus. In the staminate inflorescence, however, the depression in which the spikelets are borne is usually too slight to be termed an alveolus. It seems desirable, therefore, to derive the general term from some word that carries the same implication as alveolus but which has not been used in a specific morphological sense. The word *alicole* [1] is proposed and will be used in the following description to designate the spikelet or spikelets, whether staminate or pistillate, that are borne in a single alveolus or at a single point on the rachis, considered as the axil or point of attachment of a reduced branch.

The principal differences between the pistillate inflorescences of Zea and Euchlaena may now be contrasted as follows:

Euchlaena	*Zea*
Single spikelets	Paired spikelets
Two-ranked alicoles	Many-ranked alicoles
Separate alicoles	Yoked alicoles

SINGLE AND PAIRED SPIKELETS

The difference between single and paired spikelets will be best understood by considering first the arrangement of the spikelets in the staminate inflorescence of Euchlaena, which is identical with that of the lateral branches of the staminate inflorescence of maize. Since Euchlaena lacks the specialized central spike of the maize tassel it may be taken to represent the primitive arrangement of the spikelets.

In these staminate inflorescences each alicole consists of two spikelets—one sessile, the other pedicelled. The alicoles are disposed on the two sides of the branch, leaving the lower, and, to a less extent, the upper side of the branch, naked. The sessile spikelet is borne slightly below the pedicelled, that is, toward the abaxial side of the branch. Thus when viewed from the end of the branch the arrangement of the spikelets would be such that instead of an alternation between pedicelled and

[1] *Ala*, armpit+*colo*, inhabit.

sessile spikelets, the two sessile spikelets would stand next each other as would the two pedicelled spikelets (see fig. 1, A). This lack of radial symmetry will be shown to be a very persistent and important feature.

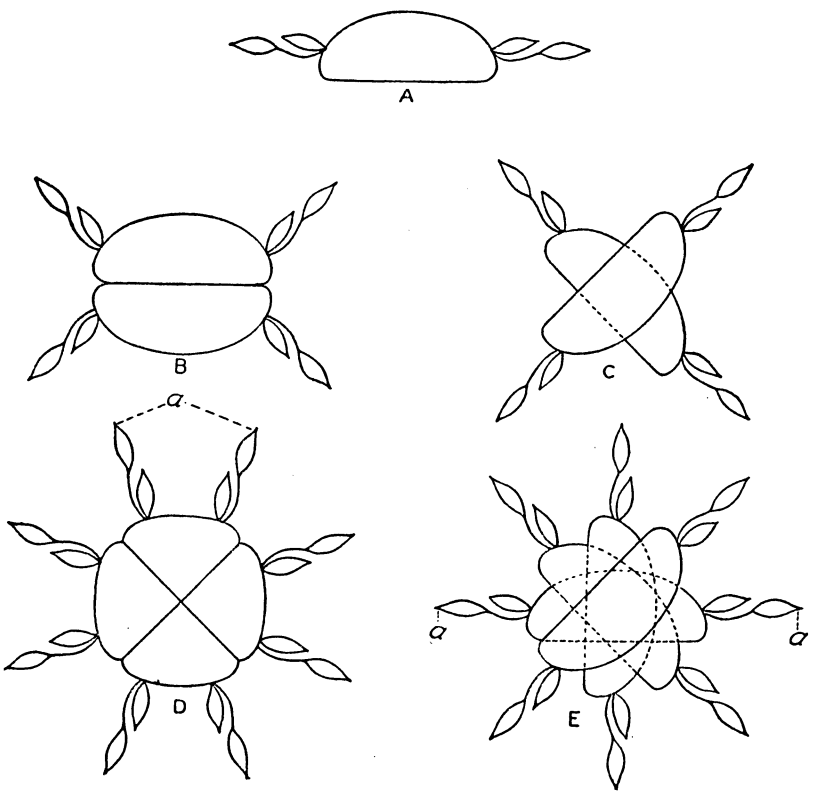


FIG. 1.—Diagram showing arrangement of pedicelled and sessile spikelets in A, undifferentiated four-rowed branch; B, eight-rowed ear, the result of the fasciation of two undifferentiated branches; C, eight-rowed ear the result of twisting a single undifferentiated branch; D, 16-rowed ear, the result of fasciation; E, 16-rowed ear, the result of a further twisting of "C."

Turning now to the pistillate inflorescences a striking contrast appears. Both spikelets are sessile in Zea, and it is usually impossible to determine which of the pair is the homologue of the pedicelled spikelet. In the pistillate inflorescence of Euchlaena, the spikelets are borne singly instead of being paired. It is the pedicelled spikelet that is suppressed, as is clearly shown in the hybrid plants where all stages of suppression can be observed (Pl. 17, A). Furthermore, in pure Euchlaena staminate branches frequently have pistillate spikelets at the base. In such specimens at the place where the transition occurs, rudiments of a pedicelled staminate spikelet can often be seen by the side of a sessile spikelet bearing a well-developed seed.

TWO-RANKED AND MANY-RANKED ALICOLES

The manner by which the number of rows has been increased in the pistillate inflorescence of maize has been the subject of much controversy. Two ways of developing additional rows have been suggested—by fasciation of long lateral branches of a compound inflorescence like the tassel,[1] or by the reduction of branches until each branch is represented by a single pair of spikelets.

The fasciation theory would explain the ear and the central spike of the tassel in the same way, by assuming that a many-rowed spike has resulted from the fusion of simple spikes or branches. In the terminal inflorescence of pure Euchlaena there is no indication of a central spike, all the branches being similar, except that the lower are again subdivided. If two of the upper branches of such an inflorescence were to coalesce, an eight-rowed spike would be formed, and if then the pedicelled spikelets should become sessile and all the spikelets pistillate, an eight-rowed ear would result.

According to the second or reduction hypothesis the development of the ear and the central spike of the staminate inflorescence is supposed to have been accomplished through a shortening of the branches in the upper part of an inflorescence similar to the staminate inflorescence of Euchlaena, the branches being reduced until each was represented by a single pair of spikelets. In apparent conflict with this view is the abrupt transition between the uppermost branch and the lowest spikelets of the central spike, that characterizes all normal varieties of maize. But in the mutation known as *Zea ramosa* the abrupt transition is lost, so that the branches become gradually shorter and pass by imperceptible gradation into simple pairs of spikelets like those of a normal tassel. Thus, *Z. ramosa* may be looked upon as representing an intermediate stage in the formation of a central spike, and as such constitutes the chief support of the reduction theory.

The evidence derived from hybrids of maize and Euchlaena does not support either of these theories. On the contrary, the hybrid plants provide an unbroken series of stages connecting the Euchlaena spike with the maize ear that clearly indicates a third method of increasing the number of rows and forming a central spike or ear. This is by shortening and twisting the rachis of a single spike of Euchlaena, accompanied by an increase in the number of alicoles. The stages in this process will be discussed in more detail later.

SEPARATE AND YOKED ALICOLES

In the pistillate inflorescence of pure Euchlaena the joints of the rachis, each of which bears a single alicole, stand almost directly above one another, resembling a string of triangular beads. One of the most

[1] The earliest published statement of the fasciation theory that has thus far come to light is an anonymous account (Sexual flowers in Indian corn), in Meehan's Monthly, v. 3, p. 105, 1893.

frequent and obvious indications of admixture with maize is a shortening of the rachis. The reduction in length, however, is not uniform but is more pronounced in alternate internodes, with the result that the alicoles become associated and yoked in pairs, the members of which stand nearly opposite to each other.

In the staminate inflorescence of either Euchlaena or the common varieties of maize there is little indication of this yoking of the alicoles. The pairs of spikelets stand on opposite sides of the rachis, but usually they are equally spaced with no indication of yoking, this tendency not even appearing in the pistillate inflorescence of the first generation of the hybrid between maize and Euchlaena. Yoking of the alicoles is, however, a striking characteristic of the second generation and appears in all the stages between the four-rowed spike and a well-formed ear. With the increase in the number of ranks of alicoles this yoking of the alicoles into pairs is obscured, but there are evidences that it still persists even in the fully developed many-rowed ear.

In addition to the sharply contrasted characters discussed above, the pistillate inflorescence of maize differs from that of Euchlaena in having the alicoles much more numerous and more closely crowded.

EUCHLAENA × MAIZE HYBRIDS

Having outlined the nature of the differences between the pistillate inflorescences of Zea and Euchlaena, the pistillate inflorescences of the hybrid plants may now be examined. In the first generation the spikelets are paired, the alicoles separate, and two-ranked. In number of alicoles and degree of crowding they are intermediate between the parents. This mixture of characters derived from both parents creates the general impression that the inflorescence is intermediate.

SECOND AND LATER GENERATIONS

Treating the three contrasted characters of maize and Euchlaena as alternative, there are eight possible combinations: (1) Spikelets single, alicoles separate and two-ranked; (2) spikelets single, alicoles separate and many-ranked; (3) spikelets single, alicoles yoked and two-ranked; (4) spikelets single, alicoles yoked and many-ranked; (5) spikelets paired, alicoles separate and two-ranked; (6) spikelets paired, alicoles separate and many-ranked; (7) spikelets paired, alicoles yoked and two-ranked; and (8) spikelets paired, alicoles yoked and many-ranked. With the exception of No. 6, all of these combinations have been found in second-generation plants and most of them in the descendants of a single cross. To class the individuals into the above eight combinations is, however, a very inadequate expression of the diversity. The dominance shown in the first generation was not followed by any clear-cut segregation in the second. On the contrary, a complete series of intermediates connected the parental forms with respect to each of the three contrasted pairs of characters.

TRANSITION FROM A TWO-ROWED SPIKE TO A MANY-ROWED EAR

The pistillate inflorescence of Euchlaena may be looked upon as a two-rowed ear. In hybrids between maize and Euchlaena the initial step from such a two-rowed ear to one with four rows may be made in two quite different ways. The more common method is for the pedicelled spikelets, which are suppressed in Euchlaena, to reappear. This converts the flat two-rowed spike into a flat four-rowed spike, the condition that obtains in the first generation of the hybrid (Pl. 17, B).

In some instances, however, another method is followed. Alternate internodes of the spike become shortened until the alicoles, each with a single spikelet, are yoked in pairs, the members of which stand opposite or nearly so. The rachis then twists until each pair of alicoles, instead of standing over the one below, stands at right angles with the pair immediately above and below (Pl. 16, D). This results in a square four-row ear. The pairs of alicoles are crossed and fitted into each other in a way that has suggested the name "saddleback" for this type of spike with four rows of alicoles.

In some instances still another step is taken before the spikelets are doubled in the alicole. The rachis is still further shortened and twisted, resulting in a six-rowed ear. Six-rowed ears are sometimes found in which both sessile and pedicelled spikelets are developed. In such cases it appears that the definite relation which ordinarily exists between yoked alicoles has been lost, and starting with the flat four-rowed ear every third alicole has slipped around so that it occupies a plane between the other two, which in turn are slightly displaced (Pl. 17, C).

Returning now to the more common form of a four-rowed ear, it is to be noted that the spike is four-rowed and the pedicels have been shortened, though the distinction between sessile and pedicelled spikelets can still be made out with certainty. The rachis also has been shortened and forced into a series of sharp angles and as a result of such crowding it has now begun to twist (Pl. 17, A).

The next clearly marked stage is the eight-rowed ear. The shortening of the rachis has continued, with increased crowding and twisting of the axil, forcing the alicoles, each bearing a pair of spikelets, to slip past one another into the unoccupied spaces of what were the upper and lower sides of the original horizontal branch. This is again a saddleback type, with the alicoles associated as in the square four-rowed ear described above, though each alicole contains two spikelets instead of one (Pl. 15, F). Intermediate stages between the flat four-rowed ear and the eight-rowed saddleback stage can sometimes be found where the twist is not quite a quarter turn, but all such appear to be unstable. The saddleback, on the contrary, is stable and will sometimes be shown consistently throughout a plant of the second generation (Pl. 18).

A further shortening of the rachis brings about the next stage, which is that of a 10-rowed ear. Intermediate stages are more common during the acquisition of this stage, and when they occur the seeds, as might be expected, are not arranged in regular rows.

With these facts in mind, the spike can be understood as composed of opposite or yoked alicoles, each with a pair of spikelets. These yokes are superposed, and as crowding increases there results a further twisting and the formation of a more complicated spiral. With seeds of a uniform size a compact spiral would result in the formation of longitudinal rows, though these might not run exactly parallel to the axis of the ear, as, indeed, they seldom do even in ears of maize.

MORPHOLOGY OF THE MAIZE EAR

It has been shown that the intermediate forms that appear in hybrids between maize and Euchlaena afford no support for the fasciation theory. Evidence from the ear of pure maize may now be presented.

If a number of four-rowed branches were forced together and their axes united, the conditions found in an ear of maize might result (see fig. 1, B). There is, however, evidence in the ear itself that it is not constructed in this way.

It is not an uncommon occurrence for an ear to drop rows. For example, there may be 12 rows at the base and only 10 rows at the tip. A study of how this transition is made throws light on the morphology of the ear. In the first place, the loss is almost invariably two rows, and both are lost at the same distance from the butt of the ear. There is no region with an odd number of rows. A normal ear is made up of a series of paired rows and this is usually accepted as an adequate explanation of the fact that the number of rows is always even. A pair of rows is looked upon as the fundamental structural unit of the ear, a view in accord with the theory of fasciation. Since two rows are dropped at once, it might be expected that the interrupted rows would be adjacent. This would follow from the suppression of a pair of rows representing the sessile and pedicelled spikelets arising from a single series of alicoles.

There is, however, abundant evidence to show that rows are usually interrupted by the abortion of pedicelled spikelets only. This can be seen in abnormal maize tassels in which the base of the central spike is pistillate, forming in reality a section of an ear. At the place where the transition occurs it can be seen that the sessile spikelets are more persistent and produce larger seeds.[1]

[1] With the idea of determining to what extent differentiation between pedicelled and sessile spikelets persists in the fully developed maize ear, the weight of each of the two seeds from individual alicoles was compared. An ear of flint corn was chosen in which the alicoles were clearly marked and the individual seeds were carefully weighed. There were 135 alicoles with two comparable seeds. The average weight of the individual seeds for all the seeds was 430 mgm. The average difference between the seeds of an alicole was 21.0 mgm. ±19.5.

It would appear, therefore, that if there was any consistent difference between the weight of the seeds borne in pedicelled and sessile spikelets in this ear, the difference must have been something less than 5 per cent of the weight of the seed.

With the recognition of the fact that the interrupted rows represent pedicelled spikelets instead of the pedicelled and sessile spikelets of a row of alicoles the position of the interrupted rows with respect to one another becomes of importance in studying the formation of the ear.

Following the fasciation theory, if both of the rows of pedicelled spikelets of a single branch aborted leaving the sessile, we should find the two interrupted rows separated by two remaining rows. (This may be illustrated by reference to fig. 1, D. If the two rows of pedicelled spikelets marked *a* were aborted the two missing rows would be separated by two rows.) This is not what occurs. In the examination of many ears in which rows were dropped no instance has been found where the dropped rows were either adjacent or separated by two rows. In cases where the location of the dropped rows can be determined with reasonable certainty the dropped rows are on opposite sides of the ear. Yet they are not exactly opposite, but missing it by just two rows. This is what should occur if the two pedicelled spikelets were dropped simultaneously from a pair of yoked alicoles. It will be recalled that the dorsoventral arrangement of the spikelets in the original four-rowed spike results in bringing the pedicelled spikelets not exactly opposite, but separated by two more rows on one side than on the other. (See fig. 1, E. The pedicelled spikelets of a pair of yoked alicoles are marked *a*. It will be seen that they are separated on one side by six rows and on the other by eight.)

The persistence with which ears of maize maintain an even number of rows is therefore more wonderful than has been supposed, for it can not be fully accounted for by the fact that the spikelets are born in pairs. It must, in addition, be recognized that when a pedicelled spikelet of one alicole is suppressed there is a simultaneous suppression of the pedicelled spikelet in another alicole. The further evidence afforded by Euchlaena hybrids is that the two alicoles are the members of a yoked pair which though standing on opposite sides of the ear, have not lost their identity as a structural and developmental unit.

SUMMARY

Before the pistillate inflorescences of maize and Euchlaena could be compared in detail it was found necessary to recognize as a morphological unit the organs borne by a single metamer of the rachis. This unit, whether staminate or pistillate, whether composed of one or more spikelets, has been called an alicole.

The stages between a Euchlaena spike and a maize ear as they appear in hybrids between the two genera may be summarized as follows:

(1) The suppressed pedicelled spikelet in each alicole reappears. (2) The alicoles become more crowded and their number is increased. (3) The alicoles associate themselves in pairs or yokes. (4) The axis twists, increasing the rows of alicoles.

The order in which these changes occur is by no means fixed, but taken together they comprise all the changes necessary in deriving the maize ear from the Euchlaena spike.

In this series of intermediate stages nothing was observed that affords support for either the fasciation or "reduced branch" theory of ear formation. There is also evidence from the maize ear itself that the association of alicoles into pairs is more fundamental than the linear arrangement.

In all the hybrids between maize and Euchlaena that have been observed there has appeared no suggestion of either pod corn or *Zea ramosa*. Since it can scarcely be doubted that the peculiar characteristics of both of these mutations represent the reappearance of ancestral characters common to the Andropogoneae, it would seem that in crossing maize and Euchlaena, and thus calling forth a series of intermediate forms, we are not returning to the point in the ancestry of maize where it became differentiated from the Andropogoneae.

Furthermore, if the stages shown in the hybrid plants were to be taken as indicating the path of evolution of the ear, it would be necessary to assume that the central spike of the staminate inflorescence or tassel had evolved separately and along different lines. The close homology between the ear and the central spike of the tassel makes such an assumption unreasonable.

In the present article emphasis has been placed on the shortening and twisting of the axis of a single spike as a possible method of deriving a structure like the maize ear from the inflorescence of Euchlaena. This has been done, not because the method is believed to represent the most probable course of evolution, but because the present discussion has been restricted to the evidence afforded by hybrids of maize and Euchlaena, which seems to require such an interpretation.

Facts of other kinds are more easliy interpreted by the theories of fasciation and reduction of branches, but there are also facts that do not seem to accord with any of the theories yet proposed. Until the apparently contradictory evidence can be reconciled, it seems best to keep the several possibilities in mind and await additional evidence before attempting a complete interpretation.

PLATE 16

Intermediate stages between a simple spike of the pistillate inflorescence of Euchlaena and an ear of maize:

A.—Spike of pure Florida teosinte.

B.—Spike with slightly shortened axis.

C.—A still more compact spike with an increased number of seeds. A–C have single spikelets and separate two-ranked alicoles.

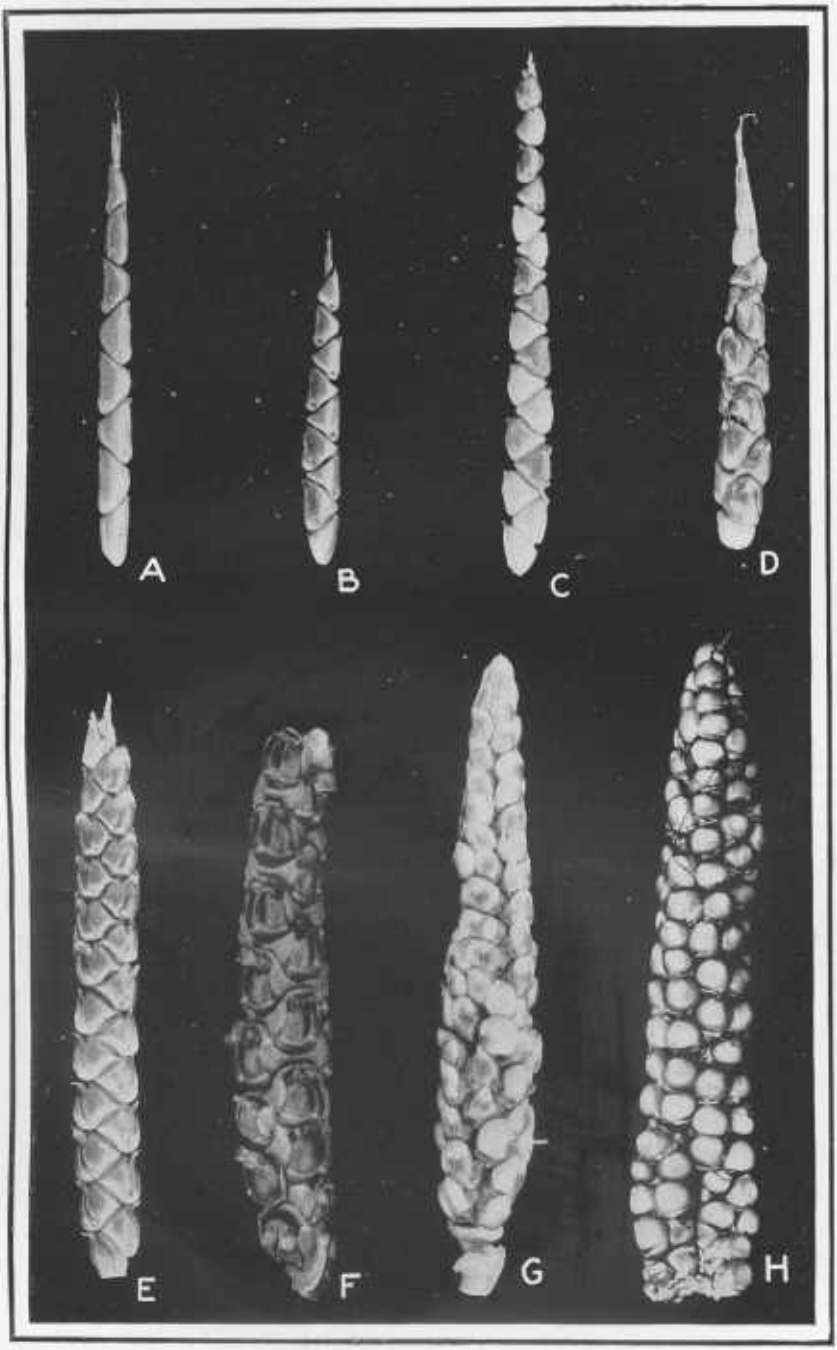
D.—Spike with single spikelets and yoked alicoles, irregularly four-rowed.

E.—Compact spike with two-ranked separate alicoles and single spikelets.

F.—Spike with paired spikelets and four ranks of yoked alicoles.

G.—Transition stage between four-rowed and eight-rowed ear.

H.—Ear of maize with eight rather poorly defined rows of seeds.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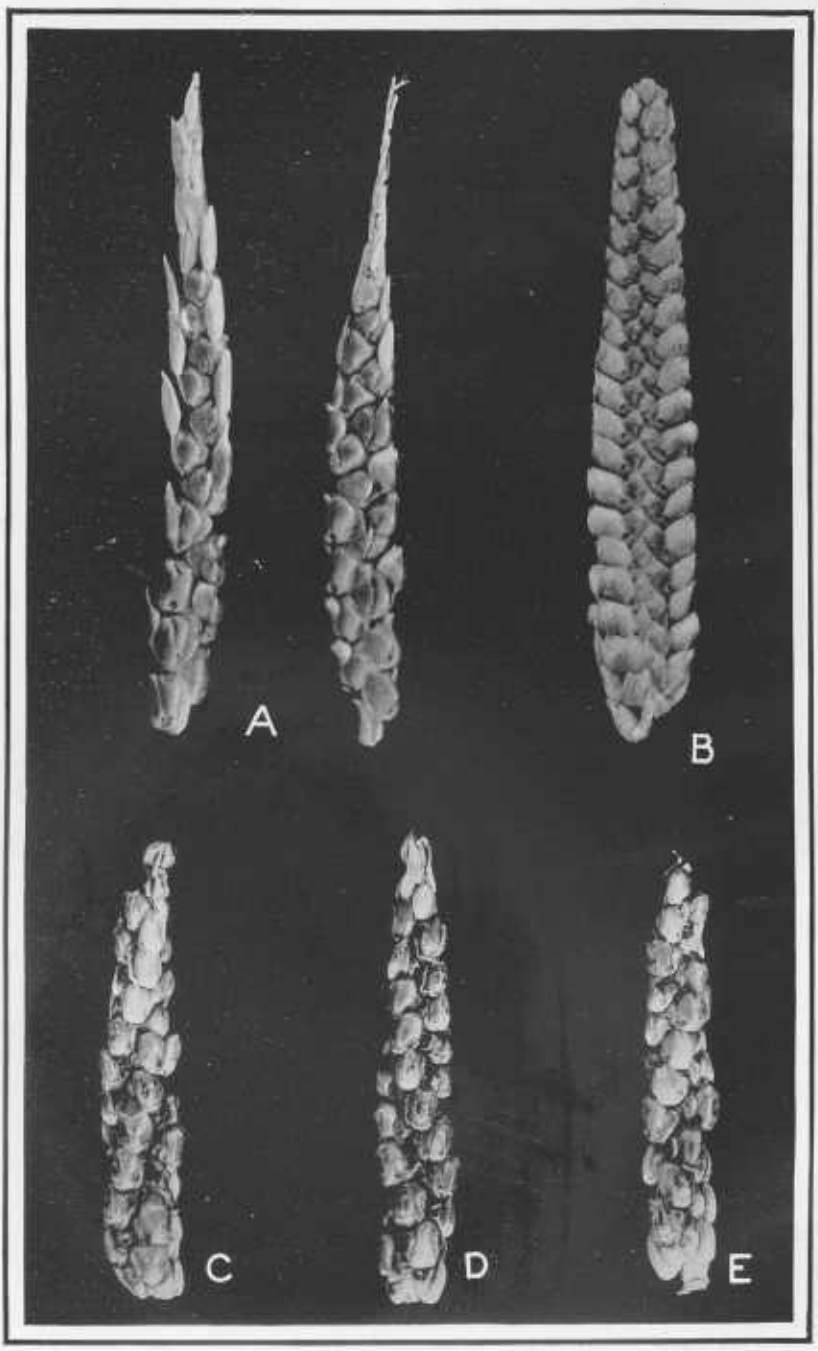
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PLATE 17

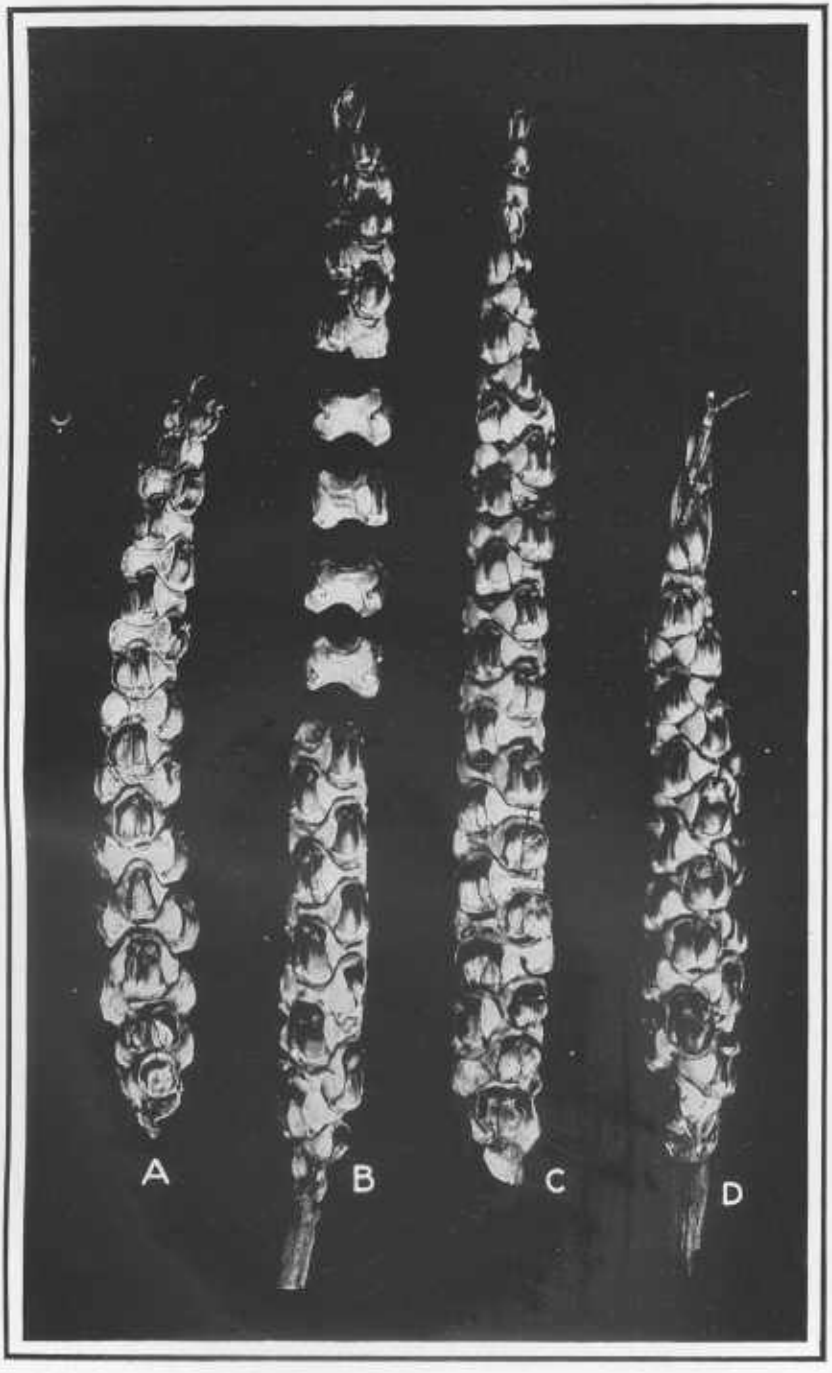
Pistillate inflorescences of hybrid between Euchlaena and maize:
A.—Showing pedicelled staminate spikelets with sessile pistillate spikelets.
B.—Closely compacted inflorescense with two rows of alicoles and four rows of seeds.
C–E.—Spirally twisted inflorescences, with three rows of alicoles.

PLATE 18

Pistillate inflorescences of hybrid between Euchlaena and maize, showing yoked alicoles:

A–C.—The alicoles are in four rows corresponding to an eight-rowed ear.

D.—The alicoles are in five rows, corresponding to a ten-rowed ear.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