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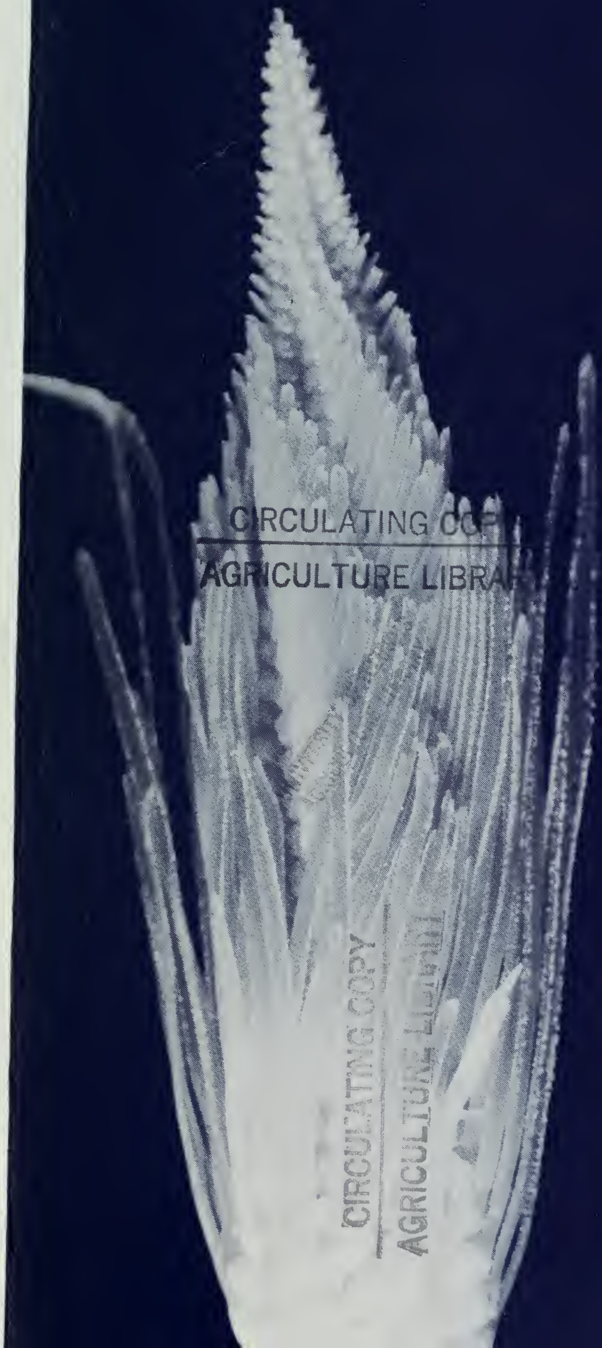
## EIR INITIATION AND DEVELOPMENT

O. T. BONNETT



# *Inflorescences of Maize, Wheat, Rye, Barley, and Oats:*

## THEIR INITIATION AND DEVELOPMENT / O. T. BONNETT

UNIVERSITY OF ILLINOIS COLLEGE OF AGRICULTURE AGRICULTURAL EXPERIMENT STATION BULLETIN 721

# *Contents*

# *Preface*

THIS PUBLICATION BRINGS TOGETHER PAPERS BY THE AUTHOR ON THE development of the inflorescences of the major cereal crops. The series was started in 1935 with a description of the development of the barley spike published in the Journal of Agricultural Research. There followed papers on the development of the wheat spike (1936), oat panicle (1937), the hood and supernumerary spike in barley (1938), and the ear and tassel of sweet corn (1940). Other publications by the author dealing with developmental morphology of cereal crops are listed in the literature citations that accompany each paper. The citations also include publications by others on the developmental morphology of the inflorescences of cereal grains.

The original papers have been somewhat revised and enlarged, and many illustrations have been added. Two new sections have been written, one on the development of the rye spike and one comparing the developmental patterns of the different inflorescences.

Certain major changes in form and in the time and sequence of development of the parts of the inflorescences will be noted in the descriptions that follow. The principle ones are: the transformation of the vegetative shoot as it gives rise to the floral structures; the location of the initial primordia of the parts of the inflorescence; the sequence, time of initiation, and order of development of the spikelets and their parts.

Only two kinds of parts are initiated by the developing inflorescence. They are the shoot and shootlike parts and the leaf and leaflike parts. The shoot and shootlike parts are the spikelet, floret, lodicules, and stamens. The leaf and leaflike parts are the leaf primordia, which subtend the branch primordia, the empty glumes, the lemma, the palea, and the carpel, which gives rise to the styles. Within the ovary are two leaflike parts, the outer and inner integuments.

Even at the earliest stages in the development of an inflorescence, the principal members of the two kinds of parts can usually be distinguished from each other. The leaves and leaflike parts are usually the first to be initiated and subtend the shoot or shootlike parts that develop in their axils. The leaves that subtend the branch primordia arising from the main axis or lateral axis may be suppressed to the point that they are present only as a slight ridge, and it may be difficult to identify them by an external examination. On the other hand, shoot or shootlike parts usually attain sufficient size that they can be identified at early stages of development. However, a cytohistological study of the developing inflorescence and its parts will show clearly the distinguishing differences in the two kinds of parts so that they can be identified. Two such studies have been published by the author: Developmental Morphology of the Vegetative and Floral Shoots of Maize (Illinois Agricultural Experiment Station Bulletin 568, 1953) and The Oat Plant — Its Histology and Development (Illinois Agricultural Experiment Station Bulletin 672, 1961).

*O. T. Bonnett, Professor of Plant Morphology, Emeritus*
*November, 1966, Urbana, Illinois*

# *Development of the Staminate and Pistillate Inflorescences of Maize*

STUDIES OF THE MORPHOLOGY OF THE CORN PLANT HAVE LED, ACCORDING to Weatherwax (1919), to clearer and simpler explanations of the results of certain experiments with corn. Variations from the normal sequence of development that lead to abnormalities of the tassel and ear and variations in such characters as length of ear, number of rows of kernels on the ear, irregularities in the straightness of the rows of kernels, and correlation in the development of the ears of multiple-eared types, to mention a few examples, can be better understood by studying the developmental morphology. By means of frequent observations during the development of the shoots, it is possible to see whether the variations observed in the mature plant are the result of variation in the pattern of differentiation and development or are the result of growth responses to changes in the environment.

While excellent descriptions of the morphological development of certain of the parts of the inflorescences have been written, some of which will be cited later, few workers have attempted to describe and illustrate all of the steps in the ontogeny of the staminate (tassel) and pistillate (ear) inflorescences as is done in this paper.

## LITERATURE REVIEW

Only a few of the publications dealing with the morphology of the corn plant will be reviewed. Most of the authors cited have made extensive reviews of the literature. In this connection special attention is called to the publications of Weatherwax (1916), Miller (1919), Randolph (1936), and Arber (1934).

The general morphology of the tassel and ear of the corn plant has been described by Collins (1919), Weatherwax (1916, 1917), and Arber (1934). A clear understanding of the developments of the pistillate spikelet was given by Miller (1919), and Randolph (1936) described and illustrated the development of the pistillate spikelet and the caryopsis. Schuster (1910) described and illustrated some of the early stages of spikelet development.

Noguchi (1929) is the only one of those cited who described some of the beginning stages in the development of the ear and tassel, and he illustrated a few of these stages with drawings.

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First published in 1940 in Journal of Agricultural Research 60:25-38. Revised and enlarged.

Descriptions of many-flowered spikelets, seeds in the tassel, and other variations from normal development in the inflorescences have been published by Kempton (1913), Stratton (1923), and Weatherwax (1925).

Papers by Bonnett (1948, 1953, 1954) also deal with the morphology and development of the maize inflorescences.

## MATERIALS AND METHODS

First-generation hybrids, Golden Cross Bantam (Purdue Bantam 39 × Purdue 51) and a Country Gentleman hybrid (Illinois 8 × Illinois 6), were used in these studies. Sweet corn (*Zea mays* var. *rugosa* Bonafous) was used because it could be easily grown in the greenhouse and, with an early-maturing type like Golden Cross Bantam, it was possible to get the various stages of development in a relatively short time. Another reason for using hybrids was that there would probably be less variation in development among individual plants, which would make it easier to follow the developmental sequences.

In a study of the developmental morphology of the caryopsis, Randolph (1936) found no significant differences among dent, flint, and sweet corn. Likewise, no essential differences were noted in the morphological characteristics of the inflorescences of dent and sweet corn. Therefore it seems reasonable to expect that whatever is found out regarding the ontogeny of the inflorescences of sweet corn would also apply to dent corn.

The corn plants were grown in the greenhouse, without artificial lights, in glazed 2-gallon jars, filled with a mixture of sand, soil, and well-rotted stable manure.

Shoots at successively later stages of development were removed from the plants and photomicrographs were taken. The photographic set-up was essentially the same as that described on pages 59 and 60. Photomicrographs were taken with an upright camera and special microlenses having focal distances of 16, 24, 32, and 48 mm. Light for photographing was obtained from a microscope lamp fitted with a 200-watt bulb. A Florence flask filled with distilled water was used as a condenser.

In order to bring out the morphological details in some of the specimens, a stain composed of a mixture of 90-percent alcohol, a small amount of glycerin, and basic fuchsin was applied. The alcohol quickly evaporated, leaving the stain and glycerin in the folds of the various structures which made them more easily seen.

## TASSEL AND STAMINATE SPIKELET DEVELOPMENT

Usually when the plants had 8 to 10 leaves, the ear shoot and tassel had begun to form (Fig. 1). However, the number of leaves that a plant has is not a reliable guide to the stage of development of the inflorescence. Plants with the same number of leaves may differ to a considerable extent in the degree of development of the shoot apexes owing to differences in growing conditions, differences in variety, and other factors.

Tassel and shoot development in greenhouse-grown plants with eight or nine leaves is illustrated in Fig. 1, *A* and *B*. The tassel has formed, the axillary shoots from which the ears will develop (Fig. 1, *A*, *sh*, and *B*, *sh*) can be seen on the upper part of the stem, and the basal internodes of the stem have begun to elongate (Fig. 1, *A*, *in*, and *B*, *in*).

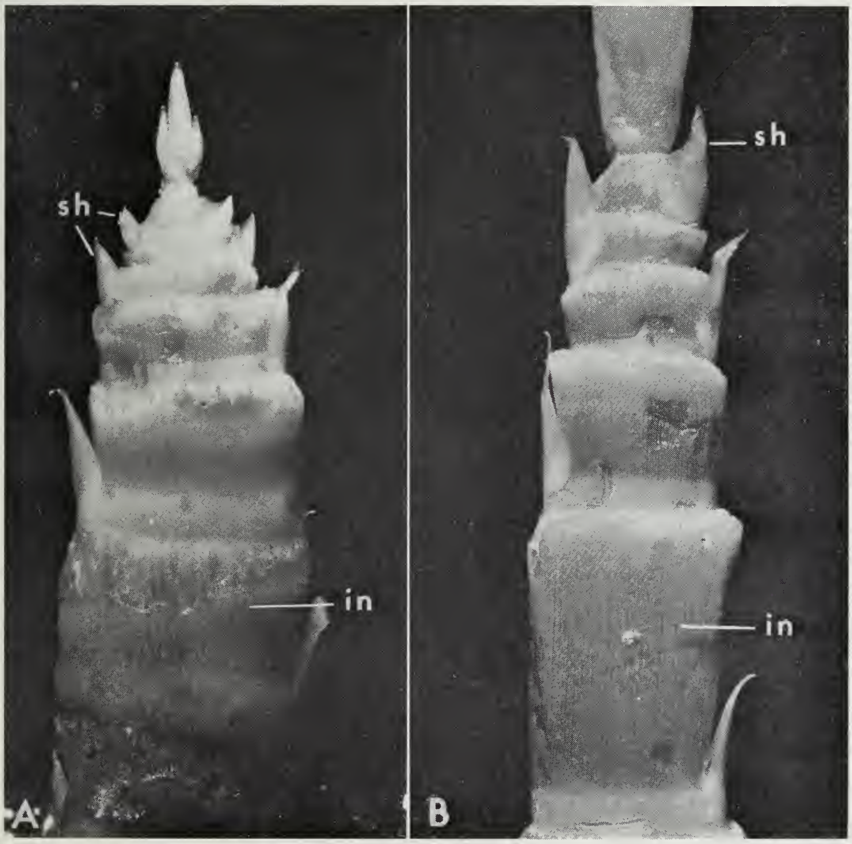

**Fig. 1. Stems of Golden Cross Bantam sweet corn with leaves removed to show the tassel, shoots, nodes, and internodes.**

**A.** Ear shoots and a tassel at the stage shown in Fig. 2, F. ×5.

**B.** Internodes are longer than in *A*, indicating a more advanced stage of development. Ear shoots and tassel are inclosed by leaves. ×5.

(*in* = stem internode; *sh* = ear shoot)

The shoot of the corn plant, like that of other cereals (Bonnett, 1935, 1936, 1937) and grasses (Weber, 1938), passes through two stages in its development from germination to the dehiscence of the anthers. During the first stage, leaf fundaments, leaves, and axillary shoots are produced, and the internodes of the stem remain short. During the second stage the internodes of the stem elongate, the tassel and its parts differentiate and develop, and the axillary shoot or shoots (ear or sucker) pass through their various stages of development.

Two shoot apexes (Fig. 2, *A* and *B*) represent the appearance of the shoot in the first stage of development. The shoot apex (Fig. 2, *A, sa*) is partly enclosed by two leaf primordia. At this stage of development the shoot apex is much smaller in relation to the diameter of the stem than the shoot apex of either wheat, oats, or barley at a similar stage of development.

Two processes, which occcur simultaneously, indicate the beginning of the second stage of development: (1) The internodes of the stem begin to elongate (Fig. 1, *A, in,* and *B, in*), and (2) the shoot apex elongates in preparation for the differentiation of the tassel and its parts. During the second stage the growth activities are internode elongation and the differentiation of the tassel and its parts. Tassel development is completed when the anthers dehisce.

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**Fig. 2. Initiation and development of the tassel.**

**A.** Shoot apex of a corn plant having four leaves visible. ×22.

**B.** Beginning of the elongation of the main shoot just before tassel differentiation. ×22.

**C, D.** Differentiation of the branches of the tassel. ×22.

**E.** Elongation of the basal branches of the tassel. ×22.

**F.** Beginning of the differentiation of the spikelet initials on the central axis of the tassel. ×22.

**G.** A stage similar to F with some of the basal branches removed to show spikelet differentiation on the central axis. ×22.

**H.** Differentiation of spikelets and empty glumes on a portion of the central axis of the tassel. ×35.

**I.** Portion of the tip of the central axis of the tassel. ×25.

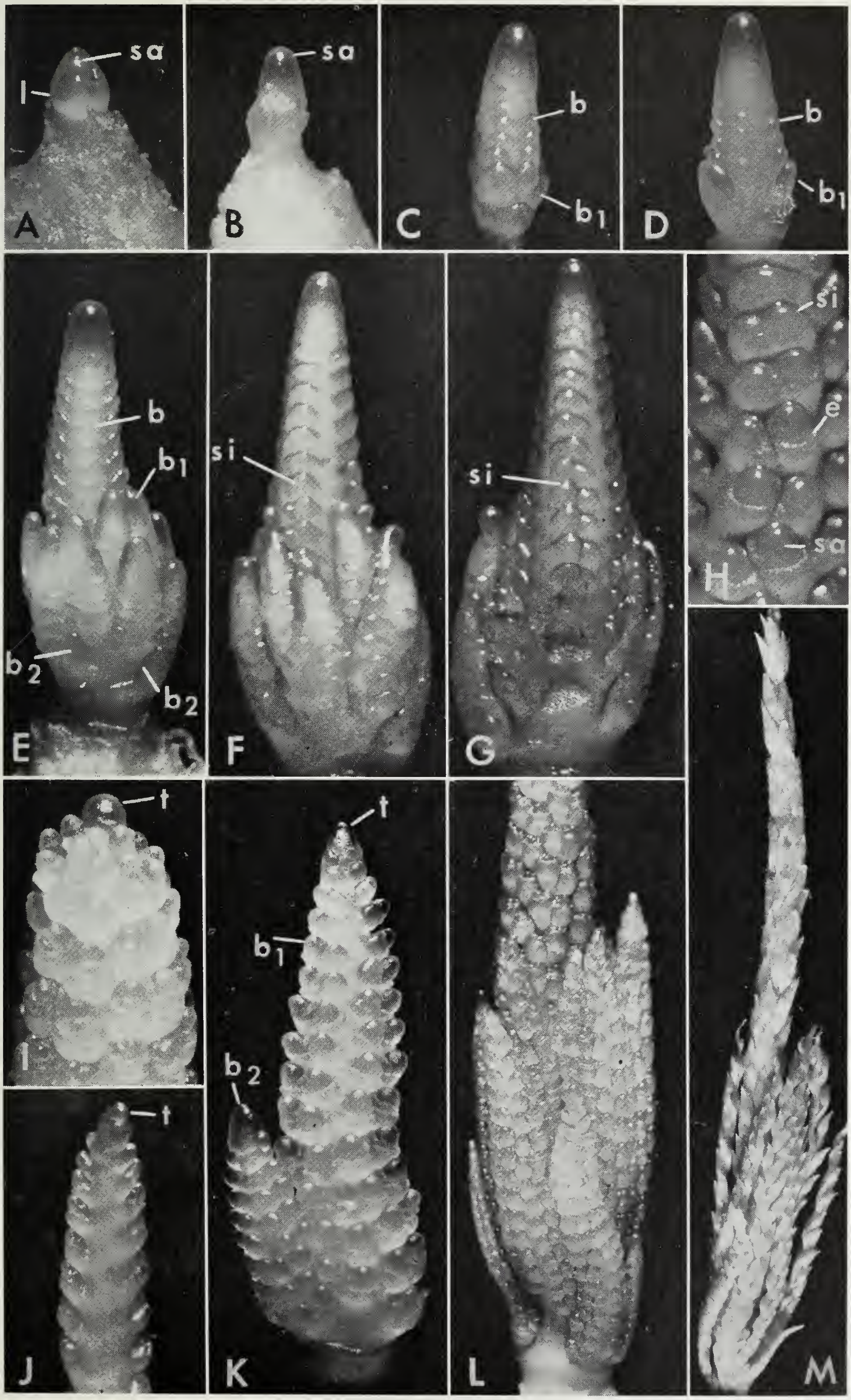
**J.** Adaxial side of a branch of a tassel. ×22.

**K.** Abaxial side of tassel branches of the first and second orders. ×25.

**L.** A more advanced stage of tassel development. ×25.

**M.** A fully differentiated but not full-sized tassel. ×8.

(*b* = branch primordium; $b_1$ = basal branch of the first order; $b_2$ = branch of the second order; *e* = empty glumes; $fl_1$ = upper floret; $fl_2$ = lower floret; *l* = leaf primordium; *sa* = shoot apex; *sa′* = shoot apex of a spikelet; *si* = spikelet primordium; *t* = undifferentiated tip of an axis)



(Fig. 2)

Branch primordia are the first of the tassel parts to differentiate (Fig. 2, *C, b,* and *D, b*). They arise in acropetal succession as lateral projections from all sides of the elongated central axis. Some of the branch primordia at the base of the central axis elongate and become the lateral axes of the tassel (Fig. 2, *E,* $b_1$). The other primordia arising from a point higher on the central axis are the primordia from which the spikelets originate (Fig. 2, *C, b*; *D, b*; *E, b*; *F, si*; and *G, si*).

It should be noted that, in the early stages of development of the tassel, so far as external appearances indicate, there are no differences between those primordia that become the lateral branches of the first order and those from which the spikelets differentiate. Therefore all of the first primordia to appear are branch primordia.

As is true for oats (see pages 94 and 95), branches of the second order may rise from the base, and at the lateral margins, of the branches of the first order (Fig. 2, *E,* $b_2$, and *K,* $b_2$). As has already been stated for the central axis, those initials of the lateral axes above the most basal ones are the primordia from which the spikelet initials differentiate.

With wheat, barley, and oats (see pages 36, 61, and 95) there is always an indication of leaf primordia on the central axis in the axils of which the lateral shoots of the inflorescence are formed. There is, however, no indication of leaf primordia subtending the initials of the lateral shoots of the tassel, but, as will be pointed out later, there are structures apparently homologous with leaf primordia, subtending the lateral shoots of the ear (Fig. 4, *C, l*).

All the branches of the tassel are indeterminate. Neither the central axis (Fig. 2, *I, t*) nor the lateral axes (Fig. 2, *J, t,* and *K, t*) of the tassel terminate in apical spikelets. Primordia from which the spikelets differentiate are produced acropetally as long as the axes increase in length.

In the beginning of spikelet development, the branch primordium divides into two unequal parts, the spikelet primordia (Fig. 2, *F, si*; *G, si*; and *H, si*). The spikelet that develops from the larger spikelet primordium is pediceled (Fig. 3, *E, sp′*) and the spikelet from the smaller spikelet primordium is sessile (Fig. 3, *E, sp*). The larger primordium is always in advance of the smaller in its development. This is shown by the beginning of development of the empty glume on the larger primordium in Fig. 2, *H, e,* and the lack of such development in the smaller primordium and by the beginning of stamen differentiation in the larger spikelet in Fig. 3, *C, sp′,* and the lack of anthers in the smaller spikelet Fig. 3, *C, sp.*

Several of the early stages of development of the spikelets can be seen in Fig. 2, *H,* which shows a group of spikelets from the central axis of the tassel. The stages of development beginning at the top of the photograph range from an undifferentiated lateral shoot primordium, through the various stages of division into spikelet primordia, to the beginning of development of the empty glumes. The empty glumes are the first of the spikelet parts to form and are first seen as transverse ridges across the spikelet primordium (Fig. 2, *H*, *e*). They grow in length and finally enclose the florets (Fig. 3, *I*).

Spikelet primordia develop from all sides of the central axis of the tassel (Fig. 2, *G*) but only on the abaxial side of the lateral branches. The abaxial side of branches of the first and second order is shown in Fig. 2, *K*, $b_1$, $b_2$ and the adaxial side of a branch is shown in Fig. 2, *J*. Two rows of lateral shoot primordia develop, and they divide into two pairs of spikelet primordia.

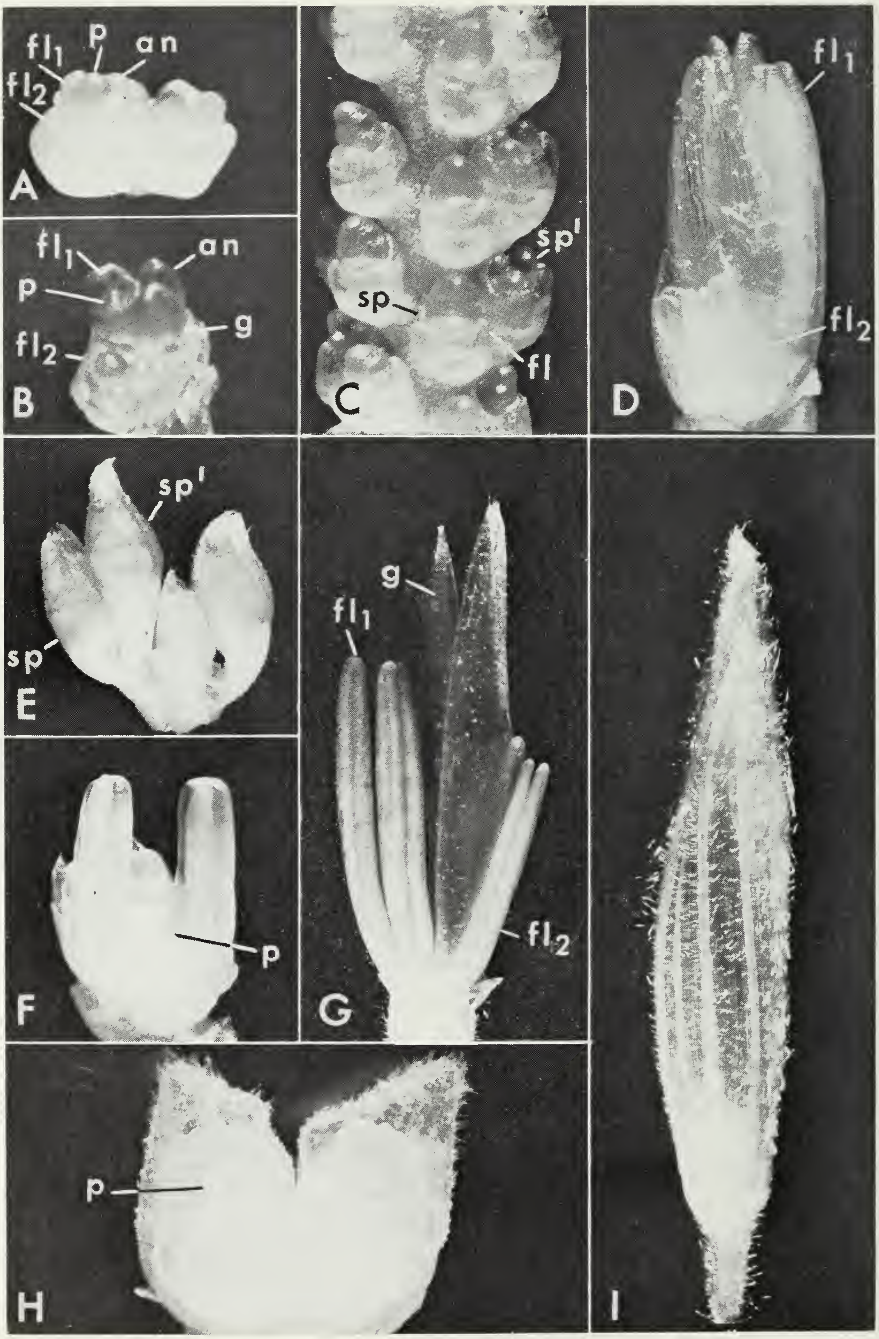
At any stage of development the central axis of the tassel is in advance of the branches (Fig. 2, *F*, *L*, and *M*). This is what should be expected since the central axis is formed first and the branches differentiate from it. The branches increase considerably in size before the primordia from which the spikelets differentiate are produced.

In each staminate spikelet two florets develop from the floral shoot apex located above the empty glume (Fig. 2, *H*, *sa′*). The shoot apex divides into two unequal parts. The larger part gives rise to the upper floret (Fig. 3, *A*, $fl_1$, and *B*, $fl_1$) and the smaller part develops into the lower floret (Fig. 3, *A*, $fl_2$, and *B*, $fl_2$). These florets differ in their rates of development. The stamens of the upper floret (Fig. 3, *A*, $fl_1$; *B*, $fl_1$; *D*, $fl_1$; and *G*, $fl_1$) differentiate first and in their development are always ahead of the corresponding parts of the lower floret (Fig. 3, *A*, $fl_2$; *B*, $fl_2$; *D*, $fl_2$; and *G*, $fl_2$). As the florets approach maturity the stamens of the lower floret attain nearly the same size as the stamens of the upper florets (Fig. 3, *G*, $fl_1$, and $fl_2$).

Stamen primordia are the first of the floret parts to differentiate (Fig. 3, *A*, *an*, and *B*, *an*). Since the tassel florets are staminate, the differentiation and development of the stamens are the principal growth activities within the floret.

Pistils may develop from the meristem located above the stamens (Fig. 3, *A*, *p*) but they usually remain rudimentary (Fig. 3, *B*, *p*). Under certain conditions of growth the pistil may show considerable development (Fig. 3, *F*, *p*) and become fully developed and functional (Fig. 7, *E*, *p*).

Flowering glumes develop for each floret, but they are so thin (Fig. 3, *G*, *g*) that they are difficult to distinguish at the beginning of their development. The lemma and palea begin their development as thin ridges at a point on the meristem just below the stamens (Fig. 3, *B*, *g*) at about the same time that the stamens begin to differentiate.


fl$_1$
p
an
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A
fl$_1$
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E
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fl$_1$
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G
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H
I

(Fig. 3)

Deviations from the normal development under field conditions are often seen in plants grown in the greenhouse. Normally one spikelet is sessile and the other pediceled (Fig. 3, *E*), but both spikelets may be sessile (Fig. 3, *H*). Another type of deviation, which will be described later, is the development of functional pistils in the tassel.

### EAR AND PISTILLATE SPIKELET DEVELOPMENT

In the early stage of stem development a shoot is produced in the axil of each leaf (Fig. 1, *A*, *sh*, and *B*, *sh*), but at a later stage of development axillary shoots are no longer produced. The cessation of axillary shoot development seems to be associated with the elongation of the internodes of the stem and the development of the tassel. This is in agreement with observations made by Percival (1921) on the cessation of axillary shoot (tiller) development in wheat and the same thing has been observed regarding axillary shoot development in barley (Bonnett, 1933).

Ears develop from the upper one or more axillary shoots of the stem. Those shoots formed at the base of the stem may remain nonfunctional or develop into suckers. At the time the topmost shoots are producing ear primordia, the basal shoots are producing only leaf primordia; but they are more and more advanced in development from the base to the top of the stem.

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**Fig. 3. Spikelet development in the tassel.**

**A.** Two spikelets at the beginning of the development of the florets. The upper (pedicellate) florets are more advanced in their development than the lower (sessile) florets. ×56.

**B.** Two florets of a spikelet also show the more advanced development indicated by the primordia of the stamens and pistil. ×56.

**C.** Part of a tassel in a more advance stage of spikelet development. The florets are partly covered by the glumes. ×40.

**D.** Staminate spikelet with the empty glumes removed to show the difference in the size of the stamens of the upper and lower florets. ×20.

**E.** Two pairs of spikelets. The empty glumes have been removed from one spikelet. ×25.

**F.** Staminate floret with one stamen removed to show the partly developed pistil. ×20.

**G.** Later stage of spikelet development in which the stamens of the lower floret are approaching the size of those of the upper floret. ×10.

**H.** A pair of staminate spikelets, both sessile. ×28.

**I.** A fully differentiated staminate spikelet. ×10.

(*an* = stamen; *fl* = floret primordium; $fl_1$ = upper floret; $fl_2$ = lower floret; *g* = palea; *p* = pistil; *sp* = sessile spikelet; *sp′* = pediceled spikelet)

Axillary shoots develop in acropetal succession and during the early stage of stem development the axillary shoots became larger in succession from the apex to the base of the stem (Fig. 1, *A*). Later when the ears begin to develop, the size sequence changes, so that the topmost shoot is the largest and the shoots become smaller from the top to the base of the plant (Fig. 1, *B*). The topmost shoot or the topmost two or three shoots, depending upon whether they are single- or multiple-eared types, in turn take precedence in their development or they may inhibit the development of the shoot immediately below. This difference in development is shown by the length of the ears in Fig. 4, *I*, *J*, *K*, and *L*, which are the ears from the topmost, second, third, and fourth shoots, respectively.

The axillary shoot is enclosed in a strongly keeled prophyllum (Fig. 4, *A*, *pr*, and *B*, *pr*) which may be entire or divided. Leaf primordia that develop into the husks are covered by the prophyllum.

Ear differentiation is indicated by an elongation of the shoot apex of the axillary shoot and the differentiation of lateral projections from the central axis of the ear primordium (Fig. 4, *C* and *D*). The lateral projections are the primordia from which the spikelet primordia differentiate and correspond to the primordia that first appear on the central axis and branches of the tassel. Subtending each primordium, as has already been mentioned, are ridges (Fig. 4, *C*, *l*) which are similar to the subtending leaf primordia that appear in the differentiation of the inflorescences of barley, oats, and wheat. These ridges increase in size and form the cuplike depressions in which the spikelets occur (Fig. 6, *B*, *rf*).

Spikelet primordia are produced in pairs by the division of the preceding initial into two unequal parts (Fig. 4, *E*, *si*). While the parts of the

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**Fig. 4. Development of the ear.**

**A.** Axillary shoot in which the ear develops, enclosed by the prophyllum. ×13.

**B.** Side view of an axillary shoot. ×17.

**C.** Beginning of the differentiation of the ear. ×25.

**D.** Ear development, showing a more advanced stage in the differentiation of spikelet-forming branches. ×25.

**E.** Beginning of spikelet differentiation by unequal division of the spikelet-forming branch. ×22.

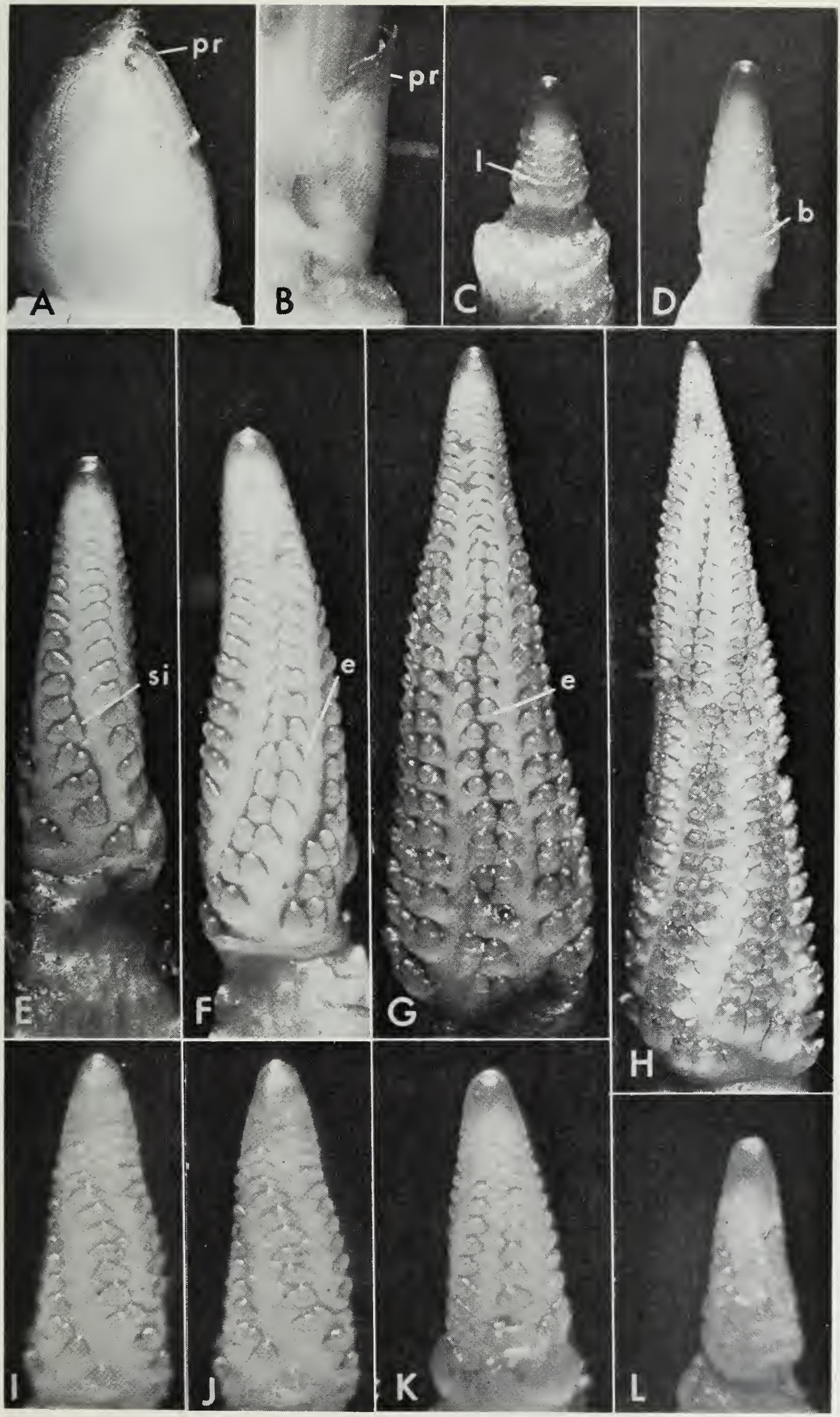
**F.** Development of the empty glumes shown by the transverse ridge on the spikelet primordia at the base of the ear. ×22.

**G.** Paired rows of spikelet primordia in the basal two-thirds of the ear. ×17.

**H.** Silk primordia developing on the florets of the basal spikelets. ×17.

**I, J, K, L.** Topmost, second, third and fourth ear primordia, respectively. ×17.

(*b* = spikelet-forming branch primordium; *e* = empty glume; *l* = subtending leaf primordium; *pr* = prophyllum; *si* = spikelet primordium)



(Fig. 4)

larger of the pair of spikelet primordia begin to differentiate before those of the smaller spikelet primordium, the difference in their development is not so great as was pointed out for the spikelet primordia of the tassel.

The empty glumes are the first of the spikelet parts to form and can be seen at transverse ridges across the spikelet primordium (Fig. 4, *F*, *e*, and 5, *A*, *e*). More advanced stages of development of the glumes are shown in (Fig. 4, *G*, *e*). As the empty glumes increase in length, they enclose the ovary, but the silk extends beyond them (Fig. 5, *K*, *e*).

Straightness of row and the number of rows of kernels per ear are characteristics of the ear that are determined when the spikelets differentiate. Variations in the straightness of row can be seen in Fig. 4, *E, F, G,* and *H*. The rotation to the left or right (Fig. 4, *E* and *F*) and the regularity or irregularity in the placement of the spikelets (Fig. 4, *H*) can be seen. Row number is determined by the number of rows of spikelet-forming branch primordia around the ear (Fig. 4, *D*, *b*) from which a pair of spikelets differentiates. Each spikelet has a fertile floret from which the kernels are produced.

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**Fig. 5. Differentiation of pistillate spikelet.**

**A.** Pair of pistillate spikelets at an early stage of development. ×40.

**B.** Initiation of stamens in the upper florets of a pair of pistillate spikelets. ×40.

**C.** Differentiation of the carpel as a ridge around the floral apex, the first stage of pistil development. ×40.

**D.** Another view of carpel initiation. ×40.

**E.** The carpel partly incloses the ovule. ×40.

**F.** Silk development from the adaxial side showing two points, the beginning of the biparted tip of the silk. ×40.

**G.** Spikelet with the glumes removed to show the upper (terminal) floret and the lower (lateral) floret. The upper floret is fertile and the lower floret is sterile. This is the usual situation in maize. ×40.

**H.** Functional upper floret and sterile lower floret of a spikelet. ×40.

**I.** A pair of spikelets of Country Gentleman sweet corn. In this type both florets are functional. ×40.

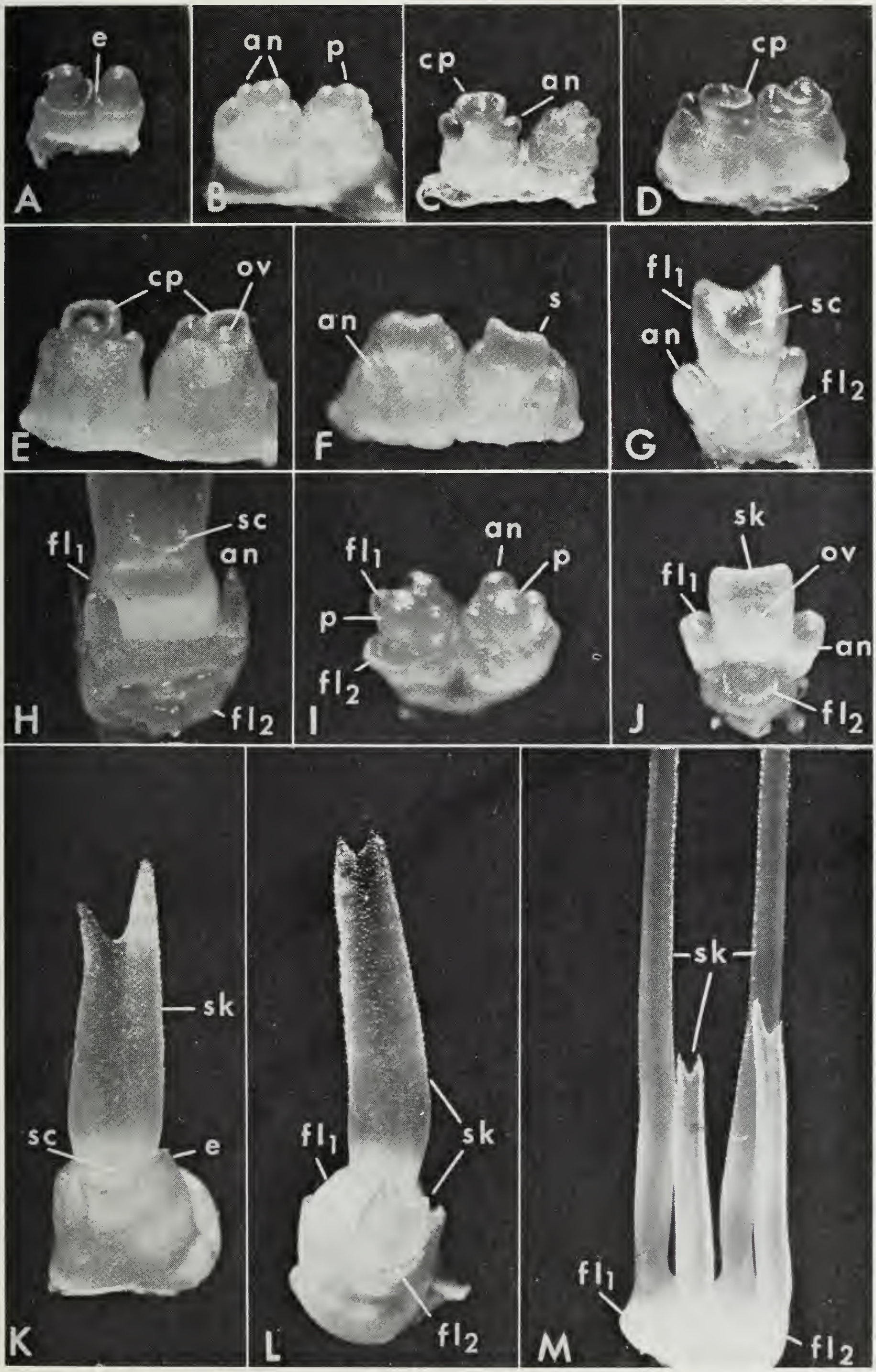
**J.** Spikelet of Country Gentleman, glumes removed, comparing the development of the florets. ×40.

**K.** Silk development of the upper floret of a spikelet having only one functional floret. ×28.

**L.** Spikelet of Country Gentleman showing silk development in the two florets. ×28.

**M.** A more advanced stage in the development of spikelets having two functional florets. ×10.

(*an* = stamens; *cp* = carpel; *e* = empty glumes; $fl_1$ = upper floret; $fl_2$ = lower floret; *ov* = ovule; *p* = pistil; *sc* = stylar canal; *sk* = silk)


A
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(Fig. 5)

The ear as well as the tassel is indeterminate in its growth and continues to elongate at the tip (Fig. 4, *H*), but many of the florets at the tip of the ear remain rudimentary (Fig. 6, *C*). Since the spikelets arise in acropetal succession, they are successively younger from the base to the tip of the ear (Fig. 4, *G* and *H*).

Two floret primordia are produced in each spikelet, but in most corn varieties only one floret is functional. In a few types like Country Gentleman sweet corn both florets are functional.

The two florets of the ear develop from an unequal division of the meristem of the spikelet just as was pointed out for the florets of the tassel. The floret differentiating from the larger mass of meristem (the upper floret) takes precedence in its development over the floret from the smaller mass of meristem (the lower floret). The larger floret is the functional floret in those types of corn that have only one functional pistillate floret per spikelet. In types of corn having two functional pistillate florets per spikelet, the larger floret is more advanced at every stage in its development than the smaller floret.

Primordia of the stamens are the first of the reproductive parts of the floret to differentiate (Fig. 5, *B*, *an*). In the pistillate floret the stamens begin differentiation but usually remain small and nonfunctional. Under certain growth conditions and in the genetic type, anther ear, the stamens of the pistillate floret may attain full development. Stamens well enough developed to show the locules of the anthers are shown in Fig. 5, *G*, *an*, and *J*, *an*.

The pistil develops from the apex of the floral shoot which is located between the stamen primordia (Fig. 5, *B*, *p*, and *I*, *p*). Development begins with the formation of a ridge, the carpel, which partly encircles the tip of the floral shoot (Fig. 5, *C*, *cp*, and *D*, *cp*). The ovule differentiates from the meristem, which is partly enclosed by the developing carpel (Fig. 5, *E*, *ov*, and *J*, *ov*).

**Fig. 6. Development of the corn silk and pollen on the silk.**

**A.** Ear showing different stages of silk development, most advanced at the base and least advanced at the tip. ×6.5.

**B.** Portion of an ear. ×19.

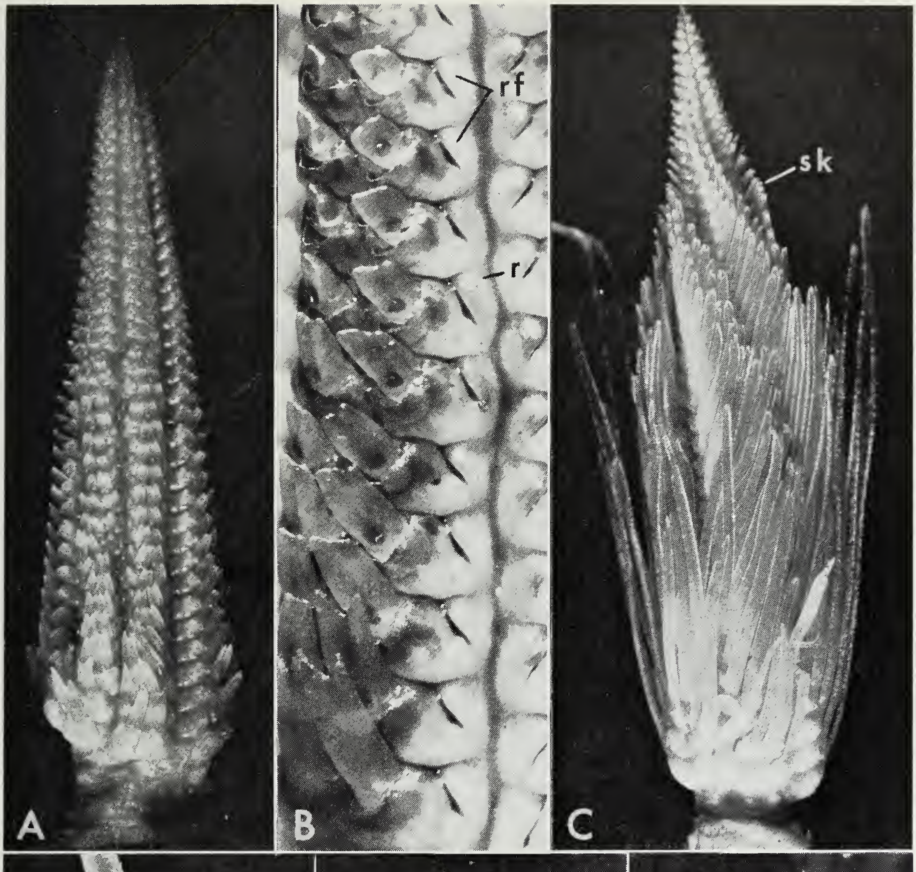
**C.** Variation in silk development; the silks are longest at the base where they are first initiated and shortest at the tip where they are last initiated. ×6.5.

**D.** A pistil from the tassel. ×14.

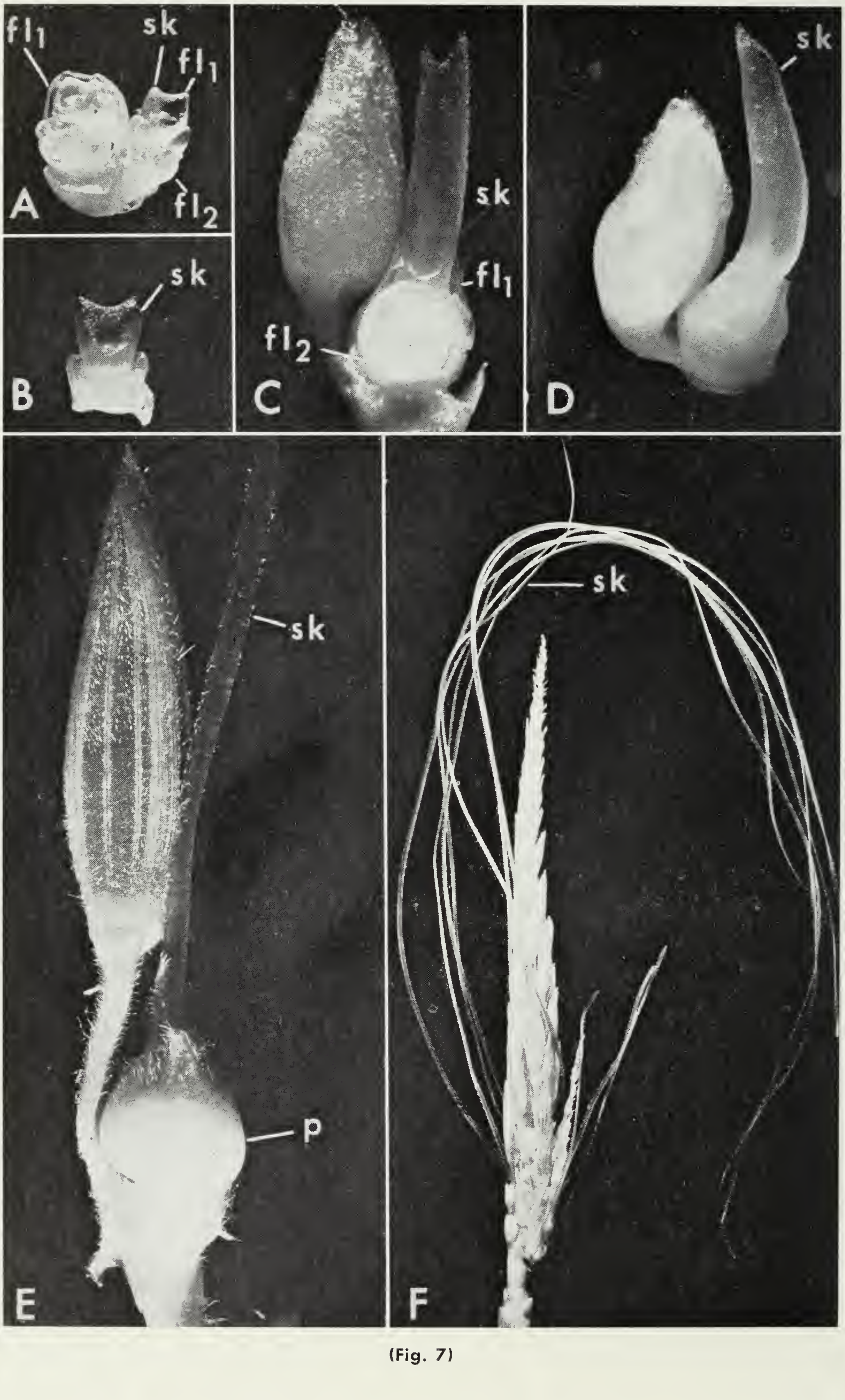
**E.** Tip of a mature silk with pollen grains germinating on it. ×38.

**F, G.** Pollen grains germinating on the silk. ×38.

(*e* = empty glumes; *o* = ovary; *po* = pollen grain; *r* = rachis; *rf* = rachis flap; *sk* = silk)



(Fig. 6)



(Fig. 7)

In Golden Cross Bantam only one floret, the upper one, of the spikelets of the ear is fertile and the same is true of the pistillate spikelet produced in the tassel. Consistent with the development of the florets of the ear of this type, the upper floret (Fig. 7, *A*, $fl_1$, and *C*, $fl_1$) developed and the lower floret aborted (Fig. 7, *A*, $fl_2$, and *C*, $fl_2$).

Pistil differentiation and development were the same as previously described for the pistillate floret of the ear. The various stages in the development of the silk are shown in Fig. 7, *A*, *sk*, to *F*, *sk*, inclusive, and it can be seen that they are essentially the same as already described.

The development of the florets of the staminate spikelet shows no deviation from normal development except that the pistil is a little further developed than in the tassels having only staminate spikelets. But the example shown in Fig. 7, *A*, should not, perhaps, be considered as typical because even in those plants that did not have pistillate spikelets, a considerably greater degree of pistil development was noted (Fig. 7, *E*, *p*) than would be expected in plants grown in the field. However, this is what should be expected of corn plants grown in the greenhouse under certain conditions of temperature and light.

## EAR TYPES

Tassels and ears of four different ear types, at early stages in their development, are shown in Figs. 8 and 9. Two flint types, four-row and eight-row, are shown in Fig. 8 and fasciated and ramosa types in Fig. 9. These ear types are of interest because they deviate from the ear type of commercial dent or sweet corn.

In four-row flint the spikelets are in two ranks on opposite sides of the rachis. The term four-rowed has been used by Laubengayer (1948) to designate this type. However, the number of rows of spikelets in a rank on the same ear may vary from two to three or more (Fig. 8, *D*), and the variation from ear to ear may range from two to four rows. The rows of

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**Fig. 7. Staminate and pistillate spikelets in the tassel.**

**A.** Staminate (left) and pistillate (right) spikelet from the tassel. ×20.

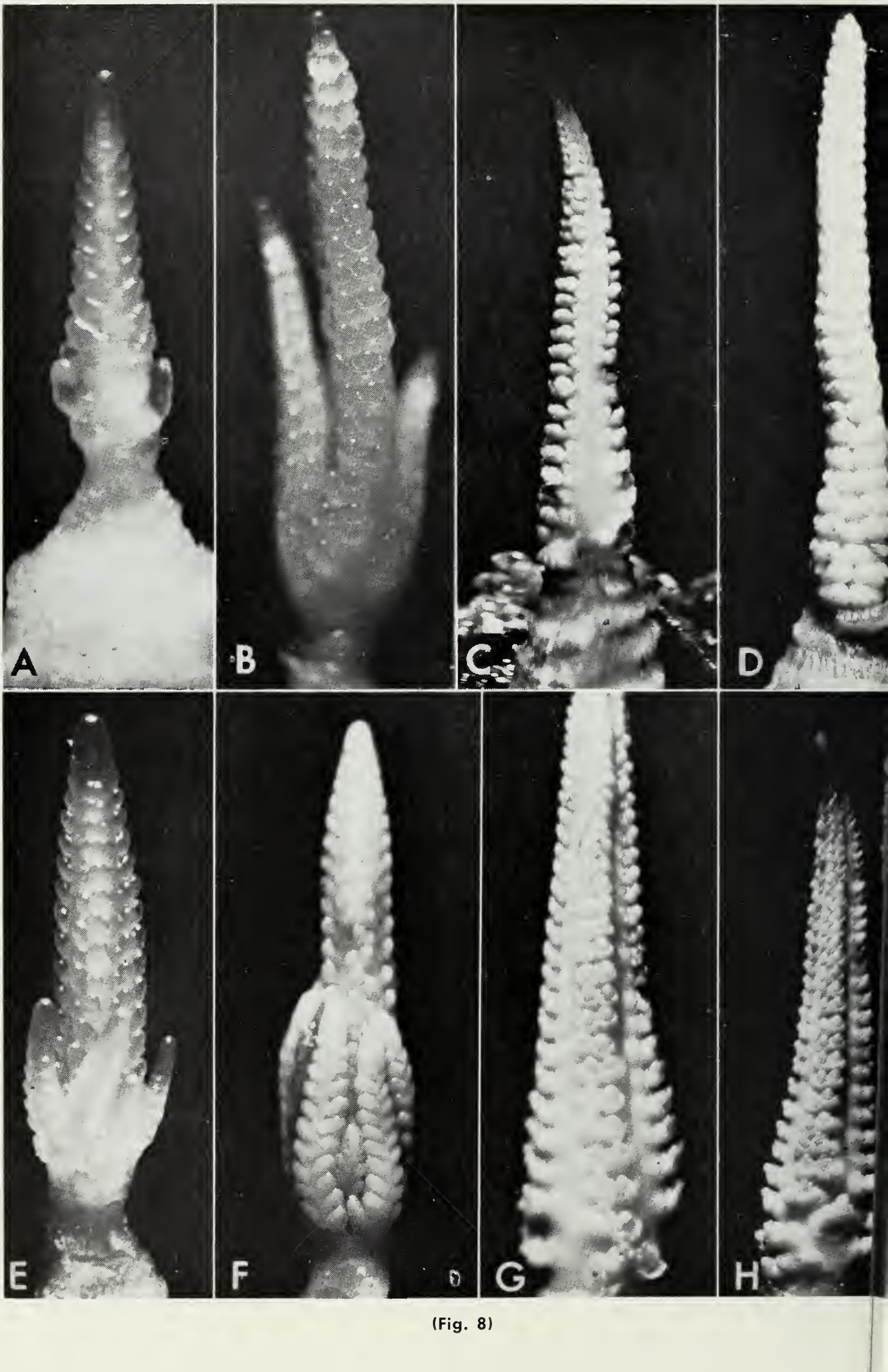
**B.** Silk development in a pistillate spikelet from the tassel, glumes removed. ×28.

**C.** Glumes removed from the pistillate spikelet to show the abortive lower floret. ×20.

**D.** Staminate and pistillate spikelets. ×15.

**E.** A fully differentiated staminate and pistillate spikelet of the tassel; the pistillate spikelet is sessile and the staminate spikelet is pediceled. ×10.

**F.** A tassel showing silks from pistillate spikelets at the base of the tassel. ×10.
($fl_1$ = upper flower; $fl_2$ = lower flower; *p* = pistil; *sk* = silk)



(Fig. 8)

spikelets may be easy to identify, or they may be so irregular that the rows cannot be distinguished. The characteristic that distinguishes this type is the two-ranked (distichous) arrangement of the spikelets and the bare rachis between the ranks, not the number of rows of spikelets or kernels. In fact, the term four-row corn is incorrect.

The spikelet-forming branches and the long branches of the tassel of the four-row type originate on either side of the shoot and develop acropetally. The meristematic area from which the spikelet-forming branch is initiated occupies nearly half of the circumference of the shoot. There is an area between the two opposite spikelet-forming branches, consisting of evacuolated dividing cells, from which the vascular bundles, rachis structure, and ground tissue are formed. Spikelet initiation and spikelet development follow the same pattern and sequence of development as in other maize.

The spikelets on the ear and central axis of the tassel of Longfellow flint, an eight-row type, are in four ranks (Fig. 8, *E* to *H*). In its early stages of development this gives the ear or tassel the appearance of being four-cornered. The ear and central axis of the tassel of Longfellow flint are long, slender, and sharply pointed at the tip. In the tassel there are two pairs of spikelets opposite each other at a node. The spikelets are at right angle to the spikelets immediately below and immediately above, a decussate arrangement. In contrast to the four-row type, a spikelet-forming branch primordium occupies only about one-fourth of the circumference of the shoot. As the number of ear rows increases, the circumference of the shoot increases but the area used in the differentiation of the spikelet-forming branch decreases.

Two fasciated types of the maize ear are shown in Fig. 9: Mexican Long Kernel, a dent type, in *A* and *B*, and Japanese Hull-less, a popcorn, in *C* and *D*. Fasciation is defined as broadening and flattening of a stem. In maize, several types have been observed. In one type the tip of the ear may be narrow and flat or broad and flat but not divided. A second type may be divided above the middle into two or three round elongated branches, sometimes called twin- or triplet-eared. A third type may be divided into many flattened points at the tip of the ear. The points are not uniform in width. They vary from narrow, flattened points to those

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**Fig. 8. Tassels and ears of the four-row and eight-row ear types.**

**A, B.** Tassels of four-row flint. ×25.

**C, D.** Ears of four-row flint. ×25.

**E, F.** Tassels of eight-row Longfellow flint. ×35.

**G, H.** Ears of eight-row Longfellow flint. G, ×20; H, ×15.

that partly encircle the tip of the ear. These few to many flattened tips produce an ear that at the tip may be nearly twice the diameter of the base of the ear and when viewed from the tip appears to be hollow. The flattened tips and bands develop spikelets on the interior and exterior surfaces, and seed is produced on both surfaces.

At the stage of development shown in Fig. 9, the ear and central axis of the tassel of fasciated maize are short, thick, and blunt at the tip. The ear of Mexican Long Kernel has either a broad and flat tip (Fig. 9, *A*) or a triparted tip (Fig. 9, *B*). In Japanese Hull-less fasciation is indicated only by the blunt tip of the tassel (Fig. 9, *C*). The many blunt flattened points on the ear of Mexican Long Kernel develop after the stages shown in Fig. 9, *A* and *B*.

Two stages in the development of the ramosa ear are illustrated in Fig. 9, *E* and *F*. *Zea ramosa* was discovered in 1909 at the Illinois Agricultural Experiment Station in a plot of Leaming, a yellow dent corn (Gernert, 1912). The ramosa ear is a branched inflorescence like a tassel. The ear has many short branches extending from the base nearly to the tip where it terminates in a short central axis (Fig. 9, *F*).

The characteristics of the tassel, not shown, are similar to those of the ear. The tassel has many long branches at the base and the branches gradually decrease in length upward. The tassel, like the ear, terminates in a short central axis (Gernert, 1912; Collins, 1917). Fig. 9, *E* shows a ramosa ear, husks removed at the beginning of the development of the lateral branches. In Fig. 9, *F*, the branches have elongated and overlap from the base upward. Spikelets are shown on the branches and the central axis.

The branches of the ear are asymmetrical with the spikelet primordia along the edge on the abaxial side of the branch the same as in the tassel of normal dent corn (Fig. 2, *F* and *K*). Kernels are found on the exterior

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**Fig. 9. Ears and tassels of fasciated and ramosa ear types.**

**A, B.** Early stage in the development of Mexican Long Kernel, a fasciated type. Note the broad tip and the high number of rows of spikelets. ×20.

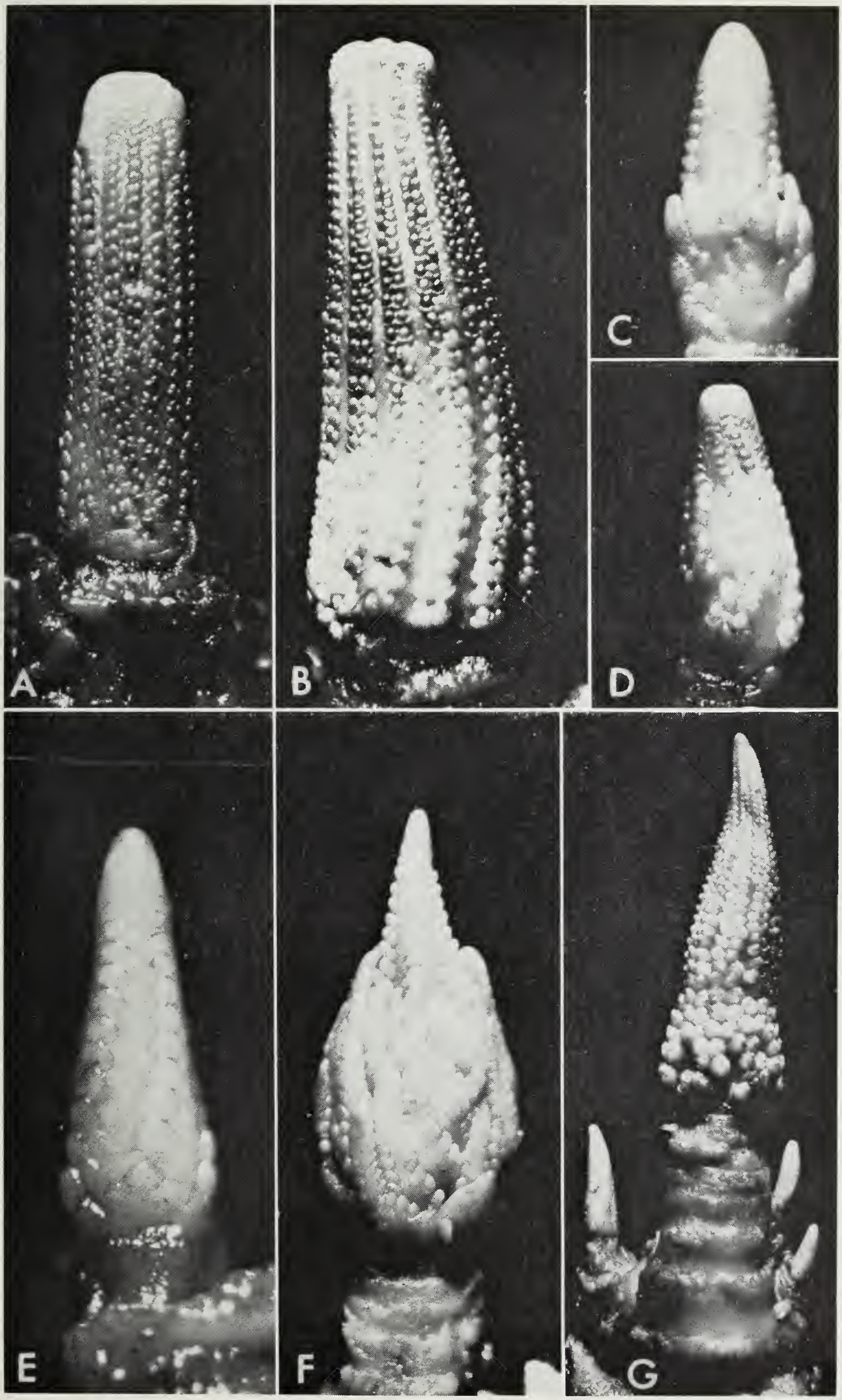
**C.** Tassel of Japanese Hull-less. The central axis is blunt and thick. ×35.

**D.** Ear of Japanese Hull-less. The ear and tassel have blunt tips and a high number of rows of spikelets as do other fasciated types. ×35.

**E.** Ear of ramosa at the beginning of branch initiation. ×70.

**F.** Ear of ramosa showing the proliferation of lateral branches. Lateral branches are similar to those of a tassel but in greater numbers. ×20.

**G.** Development of ears in the axils of the husks on the ear shoot. The husks have been removed to show the axillary ears and main ear. ×10.



(Fig. 9)

branches and on the interior branches covered by the exterior branches and on the central axis, wherever fertile florets are produced.

In some varieties of corn, ear shoots are initiated in the axil of the husks (Fig. 9, *G*). In this photograph the husks have been removed from the shank to show three ear primordia. Another shoot above the largest ear primordia at the left was broken off when the husks were removed. Shoots originating in the axils of the husks seldom produce seed.

## SUMMARY

The developmental morphology of the tassel, the ear, and their parts was studied by dissecting them from the stem of the corn plant at different stages of development. Photomicrographs were taken of the various stages.

From germination to the dehiscence of the anthers, the shoot of the corn plant passes through two stages of development. In the first stage leaves and axillary shoots are produced, and in the second stage the internodes of the stem elongate, and the tassel, ear, and their parts differentiate and develop.

Tassel differentiation begins with the appearance of lateral projections, branch primordia, which arise acropetally from the shoot apex of the central axis. The first primordia to appear at the base of the central axis elongate to produce branches of the first order. Those above develop into two spikelet primordia.

Branches of the second order arise from the base and at the margins of the branches of the first order.

Differentiation of the ear also begins with the appearance of lateral projections which arise acropetally from the shoot apex.

In both the tassel and the ear the spikelet-forming branch primordia divide into two unequal parts to form the spikelet primordia and in turn the spikelet primordia divide into two unequal parts to form the floret primordia.

In the tassel the spikelet developing from the larger division of the branch primordium is pediceled and the spikelet from the smaller division is sessile. In the ear and tassel the larger primordium begins the development of its parts ahead of the smaller primordium.

Differences in the size of the floret primordia in the tassel are correlated with a difference in the size and rate of development of the stamens. The stamens of the larger (upper) floret are ahead of, and larger than, the stamens of the smaller (lower) floret, but as the flowers approach maturity the stamens of the lower floret are almost as large as the stamens of the upper floret.

In the ear the floret developing from the larger (upper) of the two floret primordia becomes the fertile floret and the smaller (lower) floret primordium becomes the abortive floret in those types of corn that have only one fertile floret per spikelet. In those types that have two fertile florets per spikelet, the floret from the upper primordium is larger and develops before the floret from the lower primordium.

The empty glumes are the first of the spikelet parts to differentiate in the spikelets of the tassel and the ear.

Parts of the floret of the tassel and of the ear differentiate in the following order: Lemma and palea, stamens, and pistil. In the pistil the ovary, silk, and hairs on the silk develop in the order named.

Pistillate spikelets that develop in the tassel follow the same sequence in their development as the pistillate spikelets of the ear.

When two fertile florets develop in the pistillate spikelet of the ear both florets follow the normal sequence of development, but the upper floret develops ahead of the lower floret.

Because they do not terminate in apical spikelets, the ear and tassel are indeterminate inflorescences.

Four-row, ramosa, and fasciated are ear types that differ from the normal and each type is described.

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# *Development of the Wheat Spike*

ALL PARTS OF A WHEAT STEM ARISE FROM ITS SHOOT APEX. IN THE EARLY stages of growth only leaves are produced, while in later stages the spike and its parts are produced. The time of the transition from the early, or vegetative stage, to the later, or reproductive stage, of development has a bearing upon the earliness and lateness of heading of wheat varieties (Fig. 6). The effect of low-temperature germination (vernalization) in bringing about earlier heading in certain varieties of wheat is related to the effect of such treatment upon earliness of spike differentiation.

Some studies of the development of the wheat spike have been published, but more attention has been given to the development of the kernel than to that of the spike. An early contribution to a better understanding of the development of the wheat plant was made by Carruthers (1892). Jensen (1918) cited a number of publications dealing with certain phases of morphological development of the wheat plant, and he described and illustrated various phases of spike and floret development. Percival (1921), Kiesselbach and Sprague (1926), and Noguchi (1929) described and presented line drawings of certain phases of spike and spikelet development. McCall (1934) studied the developmental anatomy and morphology of the embryo and seedling of wheat. Barnard (1955) described the morphogenesis and histogenesis of the wheat plant.

This article describes and illustrates with photomicrographs, the principal stages in the development of the shoot, the spike, and the spikelet of the wheat (*Triticum aestivum* L.) plant.

## MATERIALS AND METHODS

The methods used in handling the dissected material and in taking most of the photomicrographs were the same as those described in the paper on barley (pages 59 and 60). Some of the photographs were taken with a 32-mm. Micro Tessar lens.

The plants from which the shoot apex and spikes were dissected were grown in the field. Collections were made from time to time during the growing season. Most of the plants used were Purkof, a beardless, semihard, red winter variety of wheat.

## DESCRIPTION OF SPIKE DEVELOPMENT

The shoot of a head-bearing wheat stem in its growth from germination to pollination passes through two stages of development. The first is

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the vegetative stage, which extends from seeding in the fall through the winter to late March or early April. In this stage the internodes of the stem remain short and only leaf initials are produced from the shoot apex. The shoot apex elongates somewhat but remains nearly smooth in outline. This is also the stage of active tiller development. The beginning of the second, or reproductive stage, is indicated by the appearance of double ridges, the upper member of which develops into the spikelet primordium. During the reproductive stage certain of the internodes of the stem elongate and the spikelet parts differentiate and increase in size. The vegetative stage is shown in Fig. 1, *A*, *B*, and *C*, and the reproductive stage in Fig. 1, *D*, to Fig. 2, *F*, inclusive. The developmental stages of the wheat plant are thus very similar to those of barley (see page 61).

The embryo of the mature wheat kernel consists of two major parts, the scutellum and the embryonic axis. The scutellum is in contact with the endosperm. The embryonic axis, which is slightly embedded in the scutellum, consists of the shoot and the primary root or radicle. Associated with these major parts are the epiblast on the anterior surface of the embryo opposite the scutellum, the coleohriza, a sheath covering the radicle, and two, sometimes four, adventitious roots originating from the first internode.

The coleoptile is the only part of the shoot that can be seen in Fig. 3. In Fig. 3, *A* the seed has just begun to germinate. Fig. 3, *B*, *C*, and *E* show seedlings after 24 hours of germination. The shoot and radicle and one or two adventitious roots can be seen extending laterally. After 48 hours of germination (Fig. 3, *D*), the shoot has elongated, and the root

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**Fig. 1. Spike initiation and development.**

**A.** Leaf primordia and shoot apex of a two-leaved wheat plant. ×35.

**B.** Shoot apex from the main stem of a volunteer plant of winter wheat. ×30.

**C.** Elongated shoot apex just before spikelet initiation. ×30.

**D.** Beginning of spikelet formation shown by double ridges on the spike. ×20.

**E.** Early stage of spikelet formation. ×25.

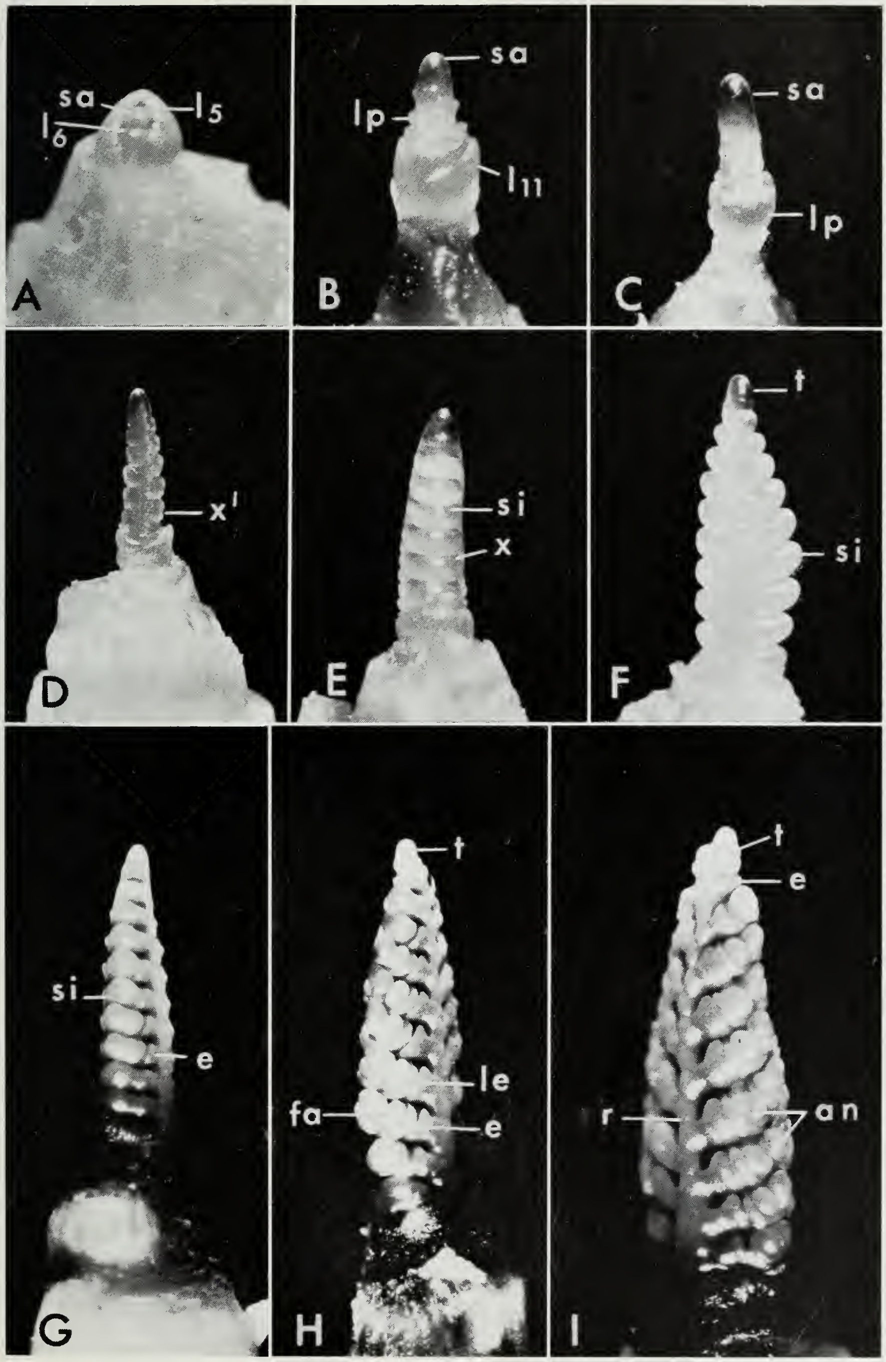
**F.** Spikelet-forming branches just before the differentiation of the spikelet parts. ×25.

**G.** Beginning of the differentiation of the empty glumes. ×20.

**H.** The basal florets have been initiated in the middle of the spike. The empty glume, lemma, and apex of the floral shoot are shown. ×20.

**I.** The florets of all of the spikelets have been initiated. Stamen primordia appear as three papillae in one of the spikelets. ×20.

(*an* = stamen primordia; *e* = empty glume; *fa* = floret apex; *le* = lemma; *lp* = leaf primordium; $l_5$ = primordium of fifth leaf; $l_6$ = primordium of sixth leaf; $l_{11}$ = primordium of eleventh leaf; *r* = rachis; *sa* = shoot apex; *si* = spikelet primordia; *t* = terminal spikelet; *x* = upper ridge; $x'$ = lower ridge)



(Fig. 1)

hairs have developed on the radicle. Root hairs may (Fig. 3, *C, E*) or may not (Fig. 3, *D*) develop upon the coleohriza.

The shoot of the embryo of a wheat kernel has only a few parts. They are the coleoptile, the first, second, third, and fourth leaf primordia, the shoot apex and a tiller bud in the axil of the coleoptile. The coleoptile completely encloses the leaf primordia and the shoot apex. In the axil of the coleoptile, opposite the scutellum, a tiller bud with its first (prophyllum) and second leaf primordia, and the shoot apex can be located. The first leaf is slightly shorter than the coleoptile, which also encloses the shoot apex, and its fold is on the side next to the scutellum. The second and third leaf primordia only partly enclose the shoot apex. The fold of the second leaf initial is on the side opposite the scutellum, and the fold of the third leaf is on the same side as the first leaf. Across the shoot apex on the side next to the scutellum is a ridge, which is the beginning of the fourth leaf. A more detailed description of all the structures mentioned has been given by Percival (1921).

By the time a wheat plant has two leaves, the sixth leaf primordium can be easily seen as a ridge beneath the shoot apex (Fig. 1, *A*, $l_6$). The rest of the leaves range in size from the fifth leaf primordium, which nearly encloses the shoot apex, up to the fully matured first leaf. The shoot apex at this time is short and hemispherical (Fig. 1, *A, sa*).

Leaves begin their development as lateral, alternate ridges (Fig. 1, *B*) beneath the shoot apex. The leaf initials arise in acropetal order, become larger on passing farther from the tip, and nearly encircle the shoot apex. Each ridge is most prominent on the side opposite the leaf initial just beneath it. The more prominent side of the ridge forms the apex of the young leaf (Fig. 1, *A*, $l_5$, and Fig. 2, *C, l*), and this is the oldest portion of the leaf since grass leaves elongate by basal growth.

**Fig. 2. Spike and spikelets at certain stages of development.**

**A.** A spike with spikelets at early floret development. ×30.

**B.** Spikes of an awnless and awned variety of wheat, at the beginning of the elongation of the peduncle. ×2.5.

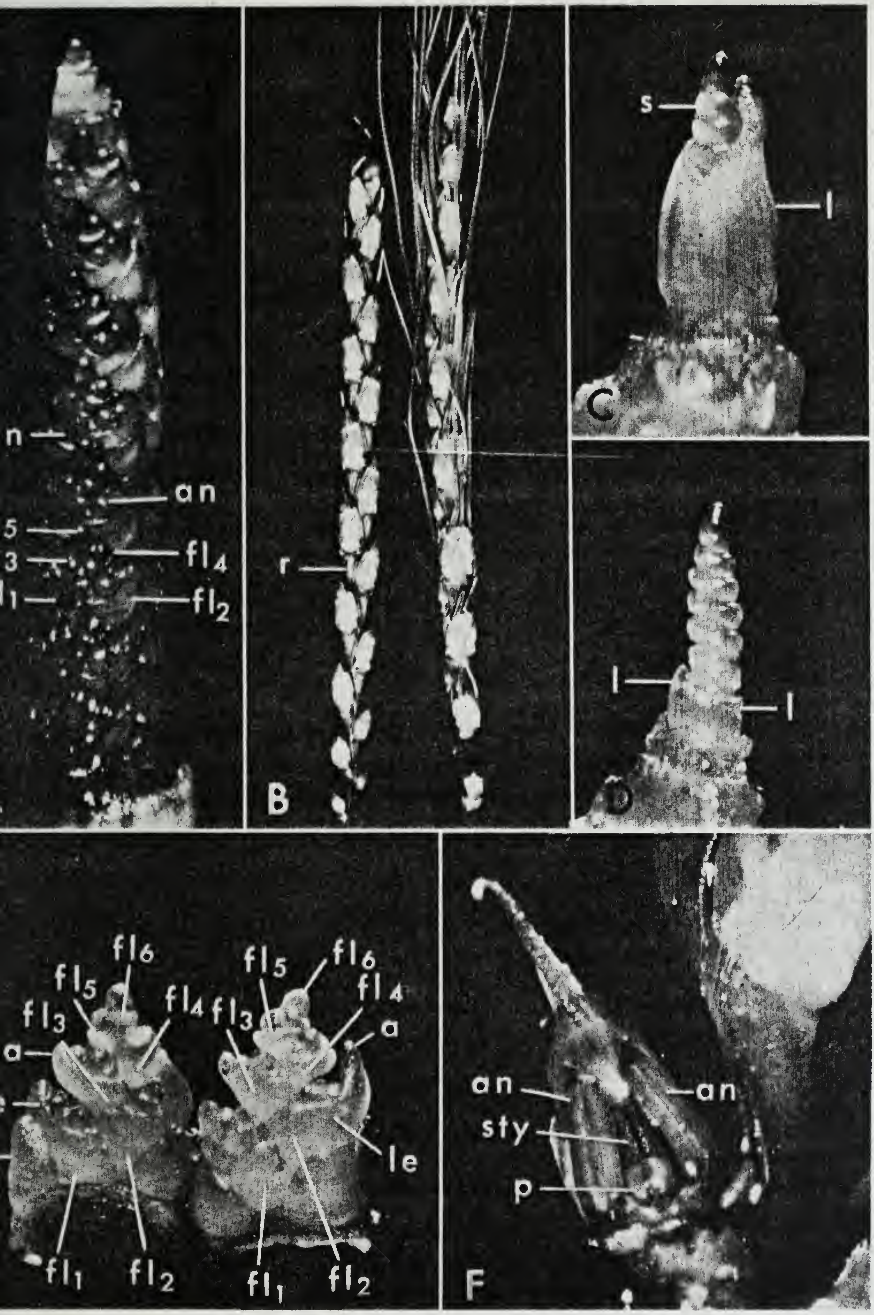
**C.** A spike of wheat, showing the way the leaves grow up over the spike. ×44.

**D.** Same spike as C, but with the large leaf removed to show the size of the next leaves and the stage of spike development. ×44.

**E.** Ventral (left) and dorsal (right) views of spikelets of wheat at an early stage of floret development. ×20.

**F.** A floret with the lemma removed to show a stage of pistil development. ×20.

(*a* = awn; *an* = stamens; *e* = empty glume; $fl_1$ to $fl_6$ = florets in succession from the base to the apex of the spikelet; *l* = leaf; *le* = lemma; *p* = pistil; *r* = rachis; *s* = spike; *sty* = style)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(Fig. 2)

Each leaf in succession grows up over the shoot apex or the spike and inside of the preceding leaf. A leaf partly enclosing the spike is shown in Fig. 2, *C*. This leaf was removed and a photomicrograph was taken to show the spike and the size of the succeeding leaves (Fig. 2, *D*, *l* and *l′*). The next leaf (Fig. 2, *D*, *l*) has just started to elongate. The two leaf primordia appear to be the last primordia formed on this stem.

The vegetative stage of stem development in winter wheat is shown clearly in Fig. 1, *B*. This shoot was removed on October 17 from one of the largest stems of a volunteer wheat plant 50 to 60 days old. The shoot apex is short. Ten leaves were removed to expose the shoot apex and there still remained four well-developed leaf primordia at the base and four ridgelike leaf primordia farther up on the shoot.

When active growth starts in the spring the shoot apex begins to elongate in preparation for spike differentiation (Fig. 1, *C*, *sa*). Leaf primordia can be seen at the base of the shoot apex and there is some indication of ridges higher up, but in contrast with the shoot apex in Fig. 1, *B*, *sa* it is relatively smooth in outline. When this plant was sampled on March 28, the internodes of the stem had not begun to elongate.

After the elongation of the shoot apex, the first indication of spike development is the appearance of double ridges (Figs. 1, *D*, *x*, and *E*, *x*, and 6, *B*, *C*, *D*, and *J*). As is pointed out in the discussion of barley (page 61) the double ridge is also the first indication of spike development in barley. The upper ridge of the pair enlarges and becomes the spikelet-forming branch (first-order branch) (Fig. 1, *F*) from which the florets (called second-order branches by Hitchcock, 1950) are produced (Figs. 1, *H*, *I*, and 4, *C*, *D*). The lower ridge of the pair represents a leaf primordium (as labelled by Bonnett, 1937; Bremer-Reinders, 1958; and Purvis, 1934). At the base of the spike the lower ridge develops into the collar (term used by Wiebe and Reed, 1961) or collar-leaf (as termed by Arber, 1934) (Figs. 4, *E*, *G*; 5, *B*, *C*) but at higher nodes of the rachis its devel-

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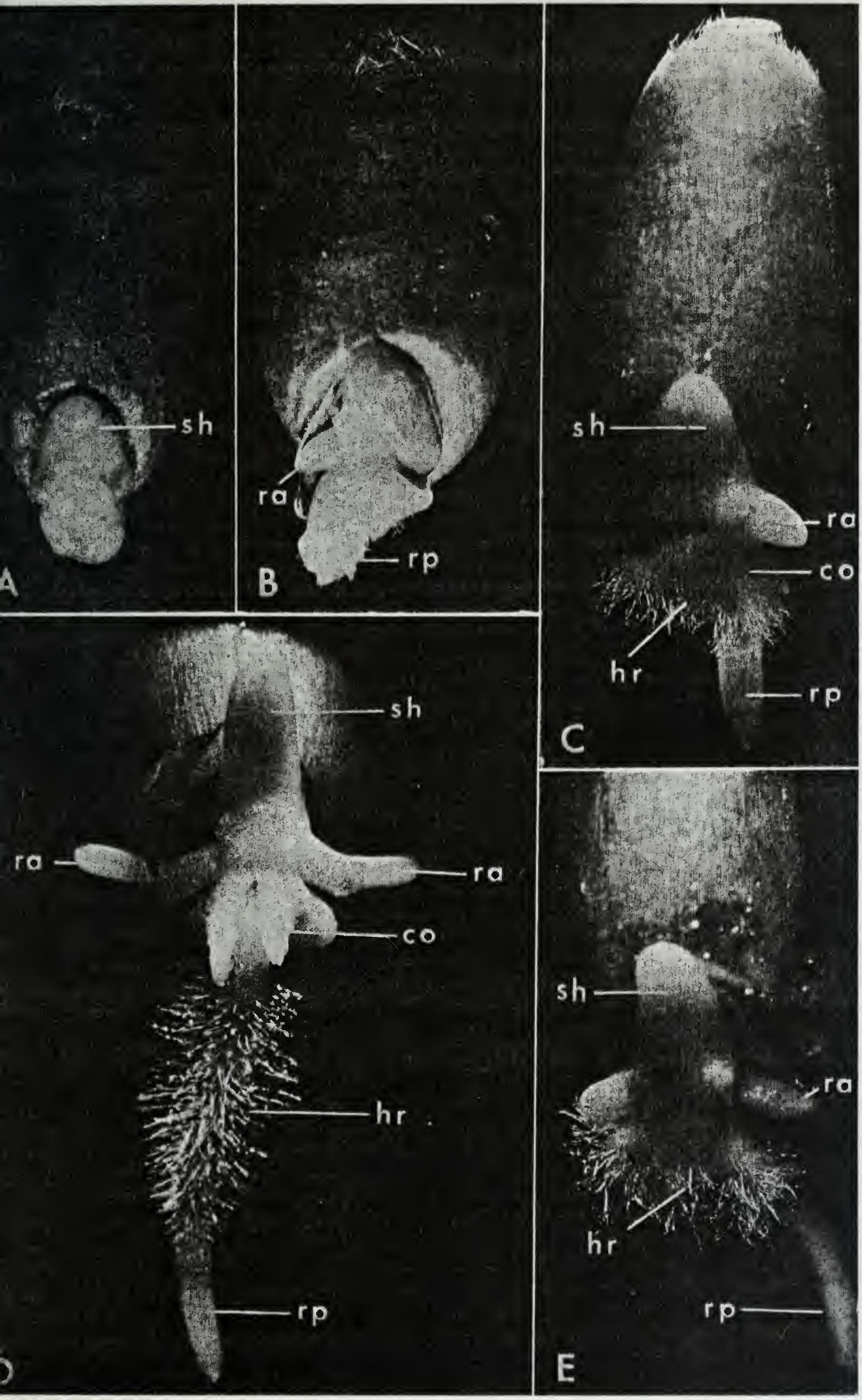
**Fig. 3. Germination of the wheat kernel.**

**A.** Beginning of germination is indicated by the enlarged embryo. Part of the pericarp has been removed. ×10.

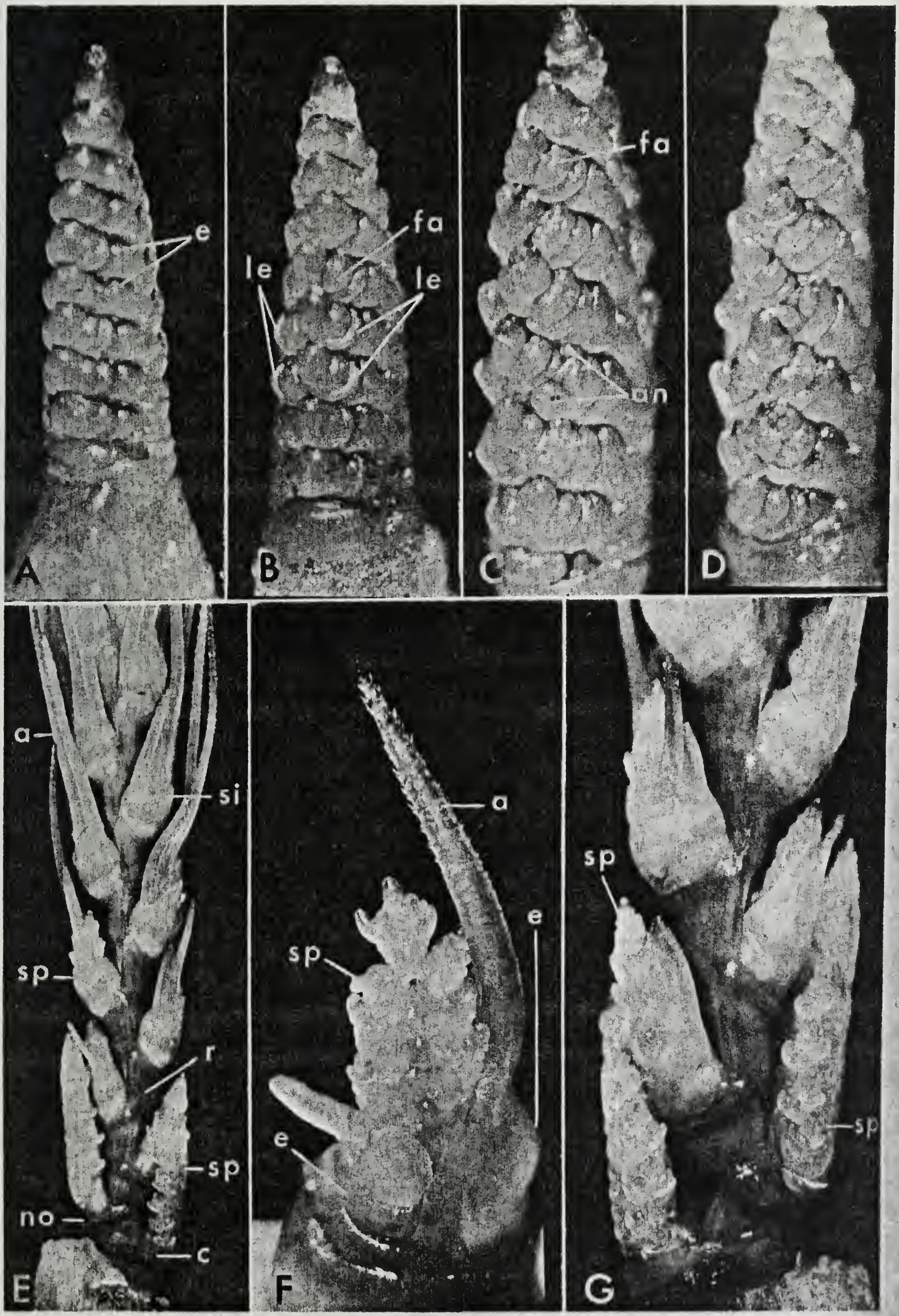
**B, C, E.** Various stages of development found in wheat seedlings after 24 hours of germination. Root hairs have developed on the coleohriza of the seedlings in C and E. Two lateral adventitious roots as well as the radicle are shown. All ×10.

**D.** Forty-eight hours after germination the plumule is more than twice as long as after 24 hours. The radicle has a well-developed root-hair zone. The coleohriza of this seedling does not have root hairs. ×10.

(*co* = coleohriza; *hr* = root hairs; *ra* = adventitious root; *rp* = primary root or radicle; *sh* = shoot)



(Fig. 3)



(Fig. 4)

opment is completely suppressed (Figs. 4, *E*, *G*, and 5, *B*, *no*). Longitudinal sections of wheat spikes, about 15 mm. long, show that above the basal two or three spikelets the lower ridge is only a small protuberance of the node beneath the basal empty glume.

It is of interest to note the changes in the shape of the spike and the difference in the size of the spikelet primordia in either direction from the middle (Fig. 1, *F*). The shape of the spike at this stage is lanceolate. The spikelet primordia show the greatest elongation in the middle of the spike (Fig. 1, *F*, *si*). From the middle toward the base and tip of the spike, the spikelet primordia are successively shorter, but the tip spikelets are not as long as those at the base.

Differentiation of each of the spikelet structures begins first in those middle spikelets that show the greatest elongation (Fig. 1, *F*, *si*), and in succession in other spikelets of the spike basipetally and acropetally. The terminal spikelet (Fig. 1, *F*, *t*) is the last to differentiate. This sequence of development among the spikelets is maintained throughout the development of the spike, including anthesis and kernel development. In the mature spike the order of the average kernel weight of a spikelet is the same as the order of spikelet differentiation — the heaviest kernels are in the spikelets in the middle of the spike where differentiation first begins, and they decrease in weight from this point toward the base and the tip.

Wheat spikelets are attached directly to the nodes of the rachis (sessile). Their arrangement on the rachis is alternate and distichous (Fig. 5, *A*, *B*). They lie flat against the concave internode of the rachis. The rachis terminates in a single spikelet, which is at right angle to the plane of the spikelets beneath it. At the base of each spikelet are two alternate, empty glumes that partly enclose it (Figs. 2, *E*, *e*; 5, *C*, *D*, *E*, *e*). In each spikelet are many florets each composed of a lemma, palea, two lodicules, three stamens, and a pistil. Six florets are in each of the spikelets in Fig. 2, *A*, *E* and 5, *C* to *G*. The arrangement of the florets on the rachilla is alternate and distichous, as shown in the ventral (Fig. 2, *E*, left) and dorsal

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**Fig. 4. Early stages in the development of spikelets and of supernumerary spikes.**

**A, B.** Beginning of the initiation of empty glumes and the lemma of some of the basal florets. ×40.

**C, D.** The empty glumes and the lemmas of the basal and higher florets have been initiated. The stamens are shown in some of the florets. ×40.

**E, G.** Lateral view of the base of spikes of Kota spring wheat, showing supernumerary spikes located where spikelets are normally found. E, ×10; G, ×30.

**F.** Dorsal view of a supernumerary spike partly enclosed by the empty glumes. ×30.

(*a* = awn; *an* = stamens; *c* = collar; *e* = empty glume; *fa* = floret apex; *lc* = lemma; *no* = node; *r* = rachis; *si* = spikelet; *sp* = supernumary spike)

(Fig. 2, *E*, right) views of the spikelets. Usually in the bread wheat varieties only the basal two or three florets are fertile, but under good growing conditions during spike development or in other wheat species more florets will set seed (Fig. 5, *C*, *D*). The size of the florets and their degree of development decrease from the base upward. Usually the basal floret, but sometimes the second one, has the largest and heaviest kernel. Development of infertile florets also decreases toward the spikelet apex until the apical floret may consist of only a rudimentary lemma (Fig. 5, *C*, *fs*).

At the beginning of spikelet initiation, the rachilla cannot be distinguished as a separate structure. The florets appear to arise from the lateral surfaces of the spikelet-forming branch (Figs. 1, *F* to *H*; 4, *A*, *B*). By the time the spikelet has reached the stage of development shown in Figs. 2, *E* and 5, *E* to *G*, the florets are separate and appear to be attached to a common axis. Serial sections of spikelets or cleared and stained spikelets at this stage of development show the rachilla as a continuous structure terminating in an apical floret. At maturity the rachilla is a very short, zigzag-shaped structure (Fig. 5, *C*). The internodes between the empty glumes and between the first and second floret are very short, but the internodes gradually become longer toward the tip of the spikelet (Fig. 5, *C*, *D*). The fourth internode is the longest.

Spikelet initiation proceeds from the base upward in acropetal order, and the same order is followed in each floret. The empty glumes are the first spikelet structures to differentiate (Figs. 1, *G*, *e*; 4, *A*, *e*). They appear as transverse ridges on both sides of the spikelet primordium nearly parallel with the long axis of the spike. A little later other ridges appear just above and parallel to the first. The second ridges are the primordia of the lemmas of the first and second florets (Figs. 1, *H*, *le*; 4, *B*, *le*). The

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**Fig. 5. Spikes and spikelets of awned and awnless wheat. Dorsal view.**

**A.** Mature spike of an awnless wheat. Natural size.

**B.** Lateral view of a mature spike of an awnless wheat with part of the spikelets removed to show the zigzag rachis. Natural size.

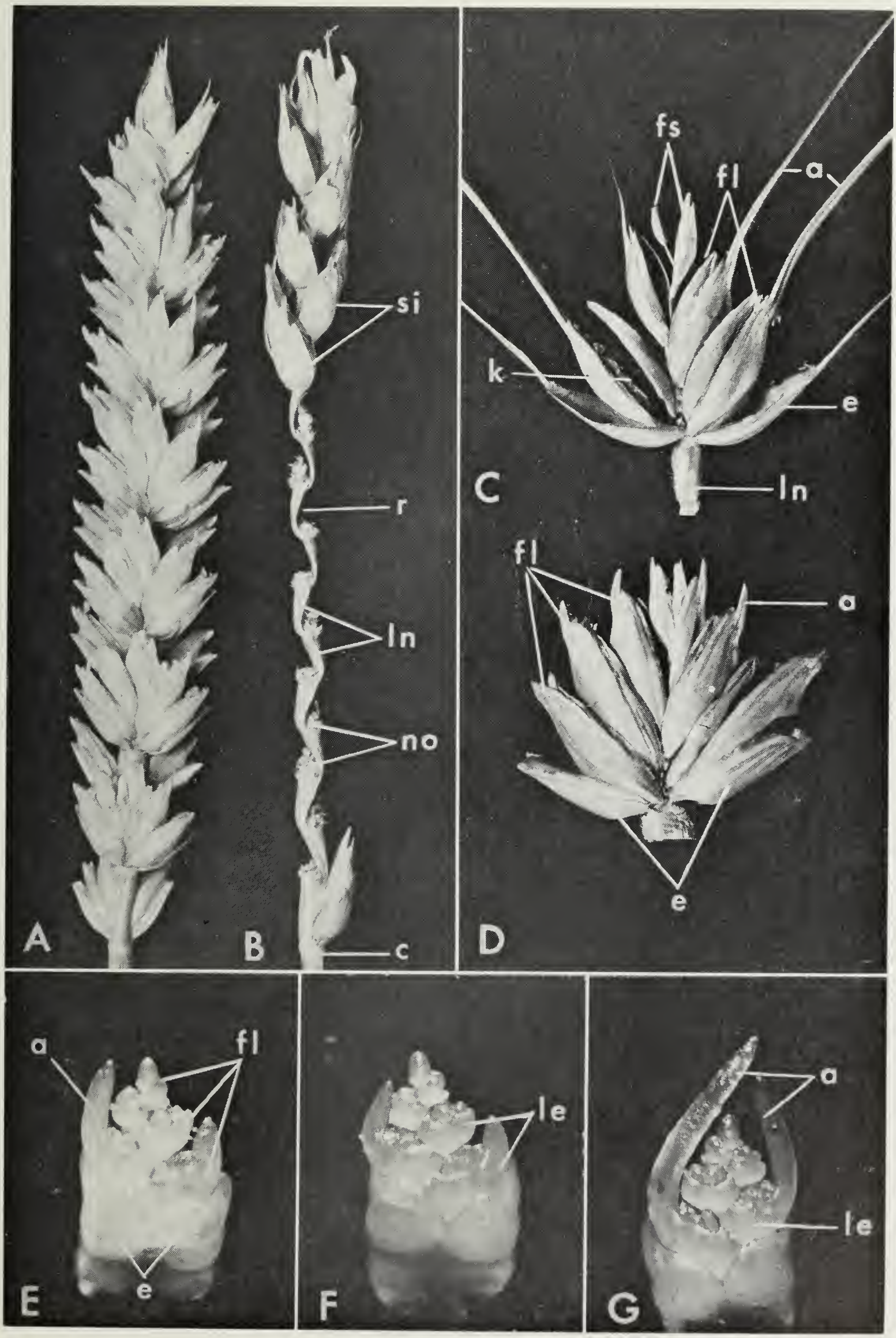
**C.** Mature spikelet of an awned wheat. ×2.

**D.** Mature spikelet of an awnless wheat. ×2.

**E, F.** Ventral view of spikelets of two varieties of wheat classified as having awnletted spikes. The awns on the lemmas of the awnletted type range from 3 to 40 millimeters in length at maturity. At the stage shown awnlets are present only on the two basal florets. ×35.

**G.** Ventral view of a developing spikelet of an awned variety of wheat showing awns only on the lemmas of the two basal florets. Awns seldom exceed 10 centimeters in length on the mature spike of common wheat. ×35.

(*a* = awn; *c* = collar; *e* = empty glume; *fl* = floret; *fs* = sterile florets; *in* = internode; *k* = kernel; *le* = lemma; *no* = node; *r* = rachis; *si* = spikelet)



(Fig. 5)

palea is initiated on the adaxial side of the floral axis soon after the lemma. It is hidden behind the developing stamens and is difficult to see in the early stages of development. However, the palea is shown in the third floret in the spikelet on the left in Fig. 2, *E*, *$fl_3$*. Development of the florets above the two basal ones proceeds in the same way as described above except that the infertile spikelets may only partially complete their development. The lemma arises from the rachilla, but the palea and the reproductive parts develop from the floral axis above the lemma (Figs. 1, *H*, *le*; 4, *B*, *le*).

Differentiation of the stamens begins in the basal flowers of the spikelets located about halfway up the spike (Figs. 1, *I*, *an*; 4, *C*, *an*) and proceeds toward the base and toward the tip. The anthers are the first part of the stamens to be initiated. The filament is formed later beneath the anther (Bonnett, 1961). The stamens appear as three papillae beneath the apex of the floral axis, but very soon the four locules are formed in each anther as shown in the basal florets of Figs. 2, *E* and 5, *E* to *G*. Two of the stamens are on either side of the floret in the keels of the palea and the third is opposite the lemma on the adaxial side.

The pistil is the last part of the floret to differentiate from the apex of the floral axis. It follows essentially the same pattern of development as described for the oat (see pages 98 to 101 and Bonnett, 1961). The carpel, a leaflike structure, is the first part of the pistil to differentiate. It is first observed as a crescent-shaped ridge around the floral apex. The ridge grows more rapidly opposite the two laterally placed stamens, forming two cone-shaped structures that elongate to produce the styles (Fig. 2, *F*, *sty*). The styles become covered with stigmatic branches to the base of the style on the inner surface but only about one-third of the way down from the tip on the outer surface. Only one stage of pistil development is shown (Fig. 2, *F*); a portion of the floret has been removed to show the pistil. At this stage the ovary and styles are well formed, but the stigmatic branches have not yet appeared.

The two lodicules are somewhat ovate structures attached to the rachilla just above the insertion of the lemma. They are on either side of the floret and anterior to the filaments of the laterally placed stamens. The filament of the stamen opposite the lemma (anterior) is between the two lodicules. The lodicules are thick from the base to about one-half of their length. Then they taper to a thin membranous portion only three to four cells thick. The thin portion terminates in a fringe of sharp pointed hairs. The thick base is grooved along the lateral margin. A thin, membranous, winglike structure extends laterally from the thick base and lies along the inner surface of the palea. The edges of the palea fit into the grooves of the lodicules. With the base of the lodicules firmly placed against the lemma and the edges of the palea in their lateral grooves and held in place by the wings of the lodicules, a mechanism is provided for forcing the glumes apart when the thick base of the lodicules swells to over twice its thickness at anthesis.

By the time the last internode (peduncle) of the stem begins to elongate, the glumes have enclosed the anthers and pistil (Fig. 2, *B*). The awns of the awned variety are long and show the presence of barbs.

It should be noted in Fig. 1, *H*, *t*, and *I*, *t*, that the wheat spike terminates in an apical spikelet, and may be classed as determinate. Before the spikelet and flower parts begin to differentiate (Fig. 1, *F*) the number of spikelets that a wheat spike will have has been determined.

## SUPERNUMERARY SPIKE DEVELOPMENT

Supernumerary spikes were found in Kota (C.I. No. 5878), a spring wheat variety, which was grown in the greenhouse in the fall and winter of 1940-41. Small spikes ranging from 10 to 12 spikelets in size developed at the base of the main spike (Fig. 4, *E*, *G*) at the point of origin of the spikelets. Empty glumes with a short awn or rudiments of empty glumes developed and enclosed the base of the supernumerary spike (Fig. 4, *F*, *e*). The supernumerary spike had all of the characteristics of a main spike at the same stage except that it had fewer spikelets (Fig. 6, *L*).

Supernumerary spike development was reported in Nepal barley grown in the greenhouse during the winter (see pages 84 to 86) and in Turkey wheat (Hurd-Karrer, 1933). The greenhouse conditions which were thought to be principally responsible for the formation of supernumerary spikes were a short day and a low temperature.

A branched spike is a characteristic of certain varieties of *Triticum turgidum L.* Arber (1934) pointed out that "wonder wheats" with branched spikes (ears) have been known for a long time. She published a woodcut from Lobel (1581) showing wheat with branched spikes. A variety of Poulard (*T. turgidum L.*) wheat, Alaska, which has branched spikes, was described by Clark and Bayles (1942). Percival (1921) described a variety of *T. turgidum, var. mariable, Korn.* called Miracle or Wonder wheat. In his description, the position of the supernumerary spike (secondary ears) corresponds to those shown in Fig. 4, *E*, *F*, *G*. Percival stated that a well-developed spike of Miracle wheat may have 115 to 120 spikelets and 140 to 150 kernels; an average spike has 85 to 90 spikelets and 80 to 100 kernels. Spikes of common wheats grown in the United States normally have 13 to 25 spikelets and 26 to 50 kernels. In spite of the size of the spike, which in part accounts for the names Miracle and Wonder wheat, its yield is low. It has been grown on a limited scale in the United States as a curiosity or as a feed crop.

## TIME AND RATE OF SPIKE FORMATION

Spike initiation in wheat varieties of the same maturity group occurs on different dates in different years. The stage of development shown in Fig. 1, *E* was found to occur in field-seeded midseason varieties on the following dates in seven successive years: April 18, April 10, March 28, April 17, April 21, April 15, and April 21. The earliest date was March 28 and the latest date was April 21. In five out of seven years the dates were from April 17 to April 25, a period of eight days.

Purkof (C.I. No. 8381), a midseason variety, was used for all the photomicrographs in Fig. 1 except Fig. 1, *B*. The plant in Fig. 1, *A*, was sampled October 19, 1935, seventeen days after planting. It had two leaves visible. Figure 1, *B* was from volunteer plants sampled October 17. Since volunteer plants started growth before those that were seeded, the shoot apex, while still in the vegetative stage, is more advanced in development. Plants shown in Fig. 1, *C* and *D*, were sampled March 28 and April 2, 1935, respectively. The dates of sampling of the other plants shown in Fig. 1 were as follows: *E*, April 10; *F*, April 21; *G*, April 28; *H*, April 28 and *I*, May 5, all dates in 1934. Although sampled on the same day, the plants in *H* and *I* in Fig. 1 are in different stages of development, *I* being more advanced. This much difference is no greater than normal among plants of the same population.

The time of initiation and rate of development of the wheat spike differ among maturity groups. Ten varieties of wheat, three early, four midseason, and three late, were sampled April 15, April 25, and May 1. The main stems of representative plants were dissected, and one of the spikes was photographed. Five of the varieties representing the different maturity groups are shown in Fig. 6. Early Blackhull (C.I. No. 8856) representing the early group, heading on May 21, is shown in Fig. 6, *A*, *F*, *K*. Two midseason varieties, Fulcaster (C.I. No. 4862) and Brill (C.I. No. 11853), headed May 26; Fulcaster is shown in Fig. 6, *B*, *G*, *L* and Brill in Fig. 6, *C*, *H*, *M*. The midseason variety Ukrainka (C.I. No. 8859), shown in Fig. 6, *D*, *I*, *N*, headed May 29, three days after Fulcaster and Brill of the same maturity group. Odessa (C.I. No. 4475), a late variety, shown in Fig. 6, *E*, *J*, *O*, headed June 10.

Spike development differed appreciably among the different maturity groups. On sampling date April 15 (Fig. 6, *A* to *E*), Early Blackhull

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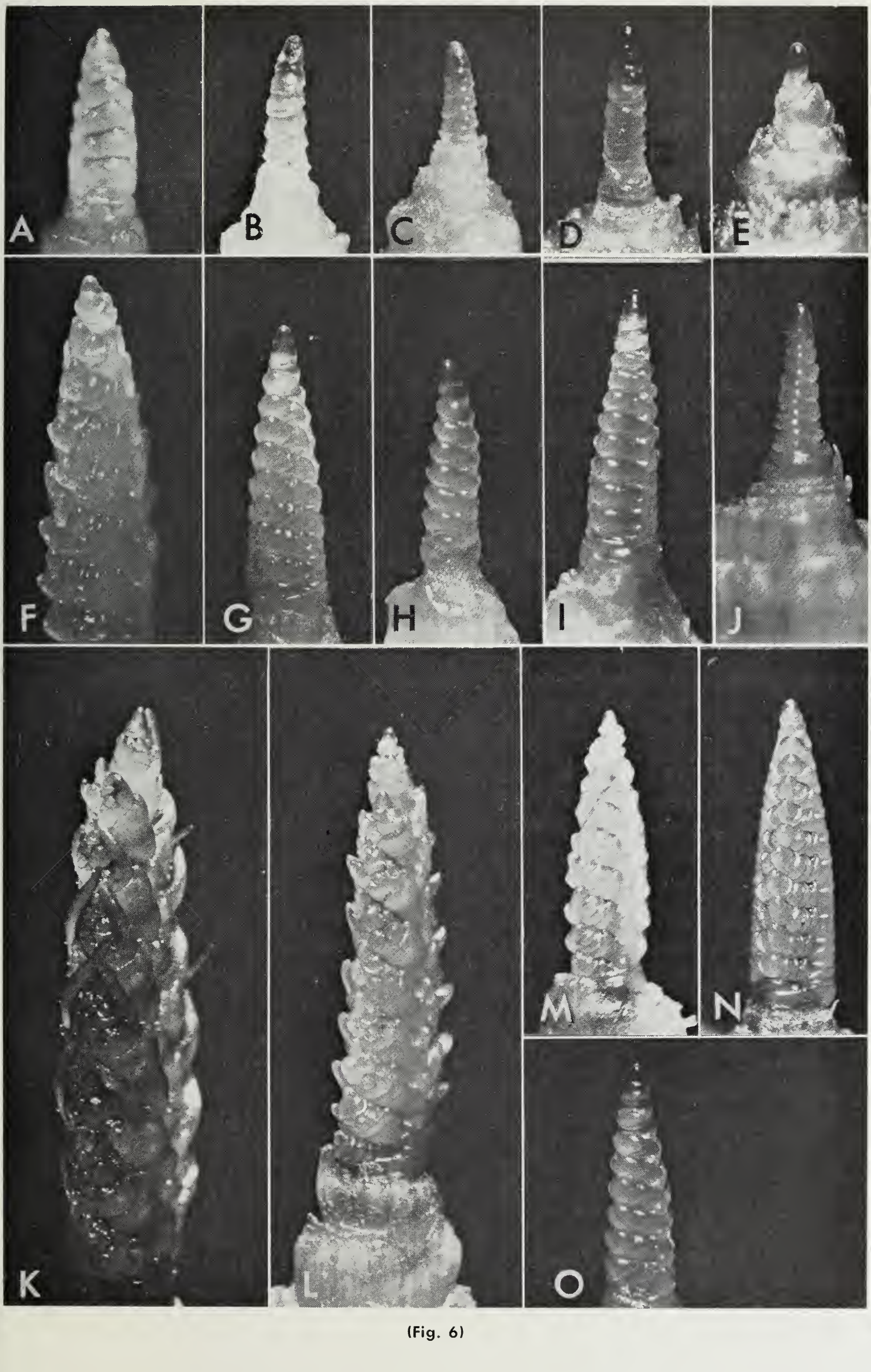
**Fig. 6. Spikes of wheat varieties of different maturity groups sampled at successively later stages of development.**

**A-E.** Sampled April 15. ×30.
**F-J.** Sampled April 25. ×25.
**K-O.** Sampled May 1. ×20.
**A, F, K.** Early Blackhull, early.
**B, G, L.** Fulcaster, midseason.
**C, H, M.** Brill, midseason.
**D, I, N.** Ukrainka, midseason.
**E, J, O.** Odessa, late.



(Fig. 6)

(Fig. 6, *A*) had well-developed spikelet-forming branches and an indication of the initiation of empty glumes on the left side of the spike. Odessa (Fig. 6, *E*), the late variety, showed the beginning of the elongation of the shoot apex, the transition stage, which precedes the appearance of double ridges, the first stage of spike initiation. The stage of development of the midseason varieties Fulcaster, Brill, and Ukrainka (Fig. 6, *B*, *C*, *D*) is between those of the early and late varieties. In this group the spikelet-forming branch has begun to enlarge, but the subtending ridge representing a leaf primordium can still be seen beneath the spikelet-forming branch.

All varieties sampled April 25 (Fig. 6, *F* to *J*) were advanced in development over the April 15 sampling. The early and late types were still markedly different. Early Blackhull (Fig. 6, *F*) was well advanced in floret development. The glumes of the basal florets are clearly shown, and the primordia of the stamens are present in many of the florets. The late variety, Odessa (Fig. 6, *J*), had double ridges like those of the midseason varieties sampled on April 15. The midseason varieties (Fig. 6, *G*, *H*, *I*) were between the early and late varieties in development. Spikelet-forming branches enlarged in all three varieties. Empty glumes and the lemma of the basal florets were initiated in most of the spikelets of Fulcaster (Fig. 6, *G*).

The difference in development among the maturity groups was greater at the May 1 sampling than at either of the previous dates. Early Blackhull (Fig. 6, *K*) developed to the point that all florets of the spikelets were formed, and the awns on the two basal florets of the spikelets were long enough to overlap the spikelet above. Fulcaster (Fig. 6, *L*) was much more advanced in development than Brill (Fig. 6, *M*) although they have the same heading date. Ukrainka (Fig. 6, *N*) headed three days later than Fulcaster and Brill but at the May 1 date it appeared to be at the same stage of development as Brill. Odessa (Fig. 6, *O*) was behind all other varieties in its development, as it was at the two previous sampling dates. Odessa was at the same stage of development as the midseason varieties were on April 25.

Which maturity group a variety belongs in — early, midseason, or late — can be determined at the time of spike initiation or at later sampling dates as well as at the time of heading. A variety initiates spike development in accord with its time of heading. Early Blackhull was at the first stage of spike initiation before the midseason varieties; it is estimated that this stage occurred for Early Blackhull on April 11 or 12 and that it headed 39 or 40 days later. The midseason varieties Fulcaster and Brill headed 41 days after spike initiation and Ukrainka 44 days after spike initiation. Odessas required 46 days to come into head after spike initiation.

Although the midseason varieties did not develop at the same rate, neither Fulcaster, which developed the fastest, nor Ukrainka, which developed the slowest, could be placed in an earlier or later maturity group. Of the ten varieties studied, none could be placed in a different maturity group on the basis of results in the sampling just described or of results from tests in other years. If a larger number of varieties was used, however, it is likely that some might, at later dates or at heading, shift out of the class in which they were placed on the basis of spike initiation.

## SUMMARY

A study of the morphological development of the shoot and spike of wheat was made by dissecting the shoots and spikes from stems at different stages of development. Photomicrographs of the principal stages are presented.

In the resting stage of the seed the stem portion of the wheat embryo consists of the coleoptile, first, second, third, and fourth leaf initials, the coleoptile tiller bud, and the shoot apex. Each of these parts can be dissected from a seed that has been soaked in water for a few hours.

Leaf primordia appear as alternate ridges which nearly encircle the shoot apex. The ridges are more prominent on the side opposite the leaf primordium just below or above it. The prominent portion forms the apex of the young leaf. Leaves elongate by basal growth and grow up inside the preceding leaf.

During the fall, winter, and early spring the shoot remains in the vegetative stage. In the fall the shoot apex produces only leaf primordia, while in early spring, in addition to the production of leaf primordia, the shoot apex elongates. The beginning of the reproductive stage is marked by the appearance of double ridges, the upper of which produces the spikelet and its parts. During the reproductive stage the spikelets and spikelet parts differentiate and increase in size.

Spikelet differentiation begins in the middle of the spike and proceeds toward the base and the tip of the spike. Likewise, each of the spikelet parts in the sequence of spikelet development appears first in the spikelets in the middle of the spike.

Within the spikelet, differentiation begins at the base of the spikelet and proceeds upward. Within the flower, the sequence of differentiation of its members proceeds from the outside inward. The pistil and its parts are the last to differentiate.

Spikelet parts differentiate in the following order: empty glumes, and florets 1, 2, 3, etc. Within the floret the order of differentiation is: lemma, stamens, palea, and pistil. The sequence of the pistil parts is: ovary, styles, and stigmas.

The wheat spike is a determinate inflorescence. It terminates in an apical spikelet at right angle to the plane of the rest of the spikelets. When the spikelets differentiate, the number is fixed, but adjustment to growth conditions may be made in the number of fertile flowers in a spikelet.

The time of initiation and rate of development of the wheat spike differ among maturity groups and in the same maturity groups. In the same maturity group the time of initiation of the spike occurs on different dates on different years.

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# *Development of the Rye Spike*

PUBLICATIONS GIVING DETAILED DESCRIPTIONS OF THE MORPHOLOGY AND development of the inflorescence of rye (*Secale cereale L.*) are limited in number. Hitchcock (1914, 1950), Gates (1936), and other authors on the taxonomy and classification of grasses have described only those characters used to distinguish rye from other cereal grains and grasses. Noguchi (1929) briefly described the early developmental stages of the rye spike and spikelet. A more extensive and detailed description of the development of the rye spike was given by Bremer-Reinders (1958). Because of this limited amount of information, a more complete account of the morphological characteristics and development of rye will be given than is given for the other cereal grains in this publication.

The rye inflorescence is a slender spike which has many spikelets (Fig. 1, *A*, *B*). The spikelets are sessile, alternate, in two ranks, and attached to a flattened zigzag-shaped rachis (Fig. 3, *A*). The spikelets lie flat against the rachis, so that the empty glumes and lemmas have an outer (abaxial) and inner (adaxial) margin with respect to the rachis. The rachis terminates in an apical spikelet, which is usually rudimentary and sterile (Fig. 3, *F*, *t*). The internode of the rachis is slightly concave on the side next to the spikelet (Fig. 3, *A*, *r*). Long silky hairs extend from node to node along the lateral margins of all of the internodes except the basal two or three, which have short hairs like the peduncle (Fig. 1, *C*). The hairs increase in length from the base of the internode upward and terminate in a tuft of hairs beneath the empty glumes at the node. There are no hairs beneath the node or on the surface of the internode between the margins, except that the first and second internodes are pubescent, as mentioned above.

The peduncle of the common winter rye used in this study is covered with short fine hairs just beneath the collar (Fig. 1, *A*, *pd*). The pubescence is thickest at the top of the peduncle and decreases downward for two to three inches and then the peduncle is glabrous. Some rye varieties, however, have a glabrous peduncle throughout their length (Gates, 1936).

As in other small-grained cereals, a modified leaf (called a collar by Wiebe and Reid, 1961) is found subtending the basal spikelet. A ridge representing a subtending leaf develops from the node beneath the second spikelet (Fig. 3, *A*, *B*, *C*) but rarely beneath the third. There is no indication of a subtending leaf at the higher nodes.

Taxonomic descriptions of the rye spikelet usually state that it has two florets (Hitchcock, 1950) or that it has two florets and a rudimentary

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This description has not been published elsewhere.

**Fig. 1. Spikes and spikelets of rye.**

**A.** A spike of rye showing the spikelets flat against the rachis. Natural size.

**B.** A spike of rye showing the spikelets from the edge. Natural size.

**C.** Two spikelets attached to the rachis and two kernels on either side. Natural size.

(*a* = awn; *pd* = peduncle)

third floret (Gates, 1936). Examination of the rudimentary portion of the spikelet above the two fertile florets, however, shows the remnants of more than one floret. In fact, early stages of spikelet development show six or more florets per spikelet (Fig. 3, *B*, *I*, *J*).

Examination of mature spikelets shows a marked difference in the development of the rudimentary florets. The third floret usually consists of a lemma, with a short awn, a palea, and remnants of the stamens. The florets above the third consist of shapeless remnants of the lemmas and paleas enclosed by the lemma of the third floret. The internode of the rachilla between the second and third florets is longer than any other internode. This internode has short, sharp hairs on the surface beneath the floret. The internodes beneath the rudimentary fourth and fifth florets are short, but they can be seen with a stereoscopic microscope at a magnification of ×50. The internodes of the rachilla between the empty glumes and the first and second florets are so short that they are difficult to identify even in cleared material where the origin and course of the main vascular bundles of the empty glumes and lemmas can be seen.

There are two empty glumes, one on each side at the base of the spikelet. They are subulate (awl-shaped) structures about two-thirds as long as the lemmas of the fertile florets above them. A scabrous keel extends from the base to the tip of the glume, terminating in a short awn. The middle vascular bundle extends throughout the length of the keel into the awn. Two thin margins, which curve inward toward each other, extend laterally from the keel. The outer (abaxial) margin is wider and slightly thicker in cross-section than the inner (adaxial) margin. There is a vascular bundle in each margin which terminates in the middle bundle. The lateral vascular bundle in the outer margin is larger than the one in the inner margin. A few small transverse (called commissural by Esau, 1960) vascular bundles connect the lateral vascular bundles with the middle bundle. A band of chlorenchyma (cells containing chlorophyll) on each side of the middle vascular bundle extends laterally almost to the vascular bundles in the margin. There is no chlorenchyma along the lateral vascular bundles on the side next to the edge of the margins. A row of stomata is present in the outer and inner epidermis over the collenchyma. When viewed in cross-section, the chlorenchyma is wider at the keel and tapers to the edge of the margins. In longitudinal section the empty glume is thick at the base and very thin at the apex. A cross-section shows that in the thin portion toward the apex, the glume consists of an outer epidermis of cells with thick, lignified walls and an inner epidermis of thin-walled cells. In the thicker portion of the base, there may be one or more thin-walled parenchyma cells between the epidermal layers. Near the edge of the margins is a band, several cells wide, that extends from the base to the tip of the lemma, consisting only of thick-walled cells of the outer epidermis and collapsed cells of the inner epidermis. On the keel are several rows of sharp, curved hairs that extend along the keel from the base of the glume to the tip and throughout the length of the awn. Sharp, curved hairs are present along the edge of the margins and also on the outer and inner surfaces. They are more numerous near the tip of the glume and on the outer than on the inner surfaces.

The outer and inner epidermis of the empty glumes consists of long cells (fundamental, Prat, 1948) which constitute the major part of the epidermis and short cells (specialized, Prat, 1948) of several kinds. The long cells have medium-thick, sinuous, parallel sidewalls. The end walls are shaped by the short cells with which they usually alternate. Otherwise, they are oblique or at right angle to the sidewalls. The short cells are silica-cork combinations; nearly round cells with thick sinuous walls with a short, rounded point; thick-walled, curved hairs with a sharp point; and the subsidiary and guard cells around the stomata. The essential differences in the outer and inner epidermis are that there are fewer short or specialized cells in the inner epidermis and the walls of the long cells are thinner and less sinuous.

The lemma is a lanceolate-shaped structure (Fig. 2, *B, le*). It terminates in an awn that is about one and one-half times as long as the lemma. The lemma has a keel that extends from the base to the tip. Rows of sharp, curved hairs extend throughout the length of the keel and into the awn. Lateral margins extend from the keel, curving inward and almost inclosing the palea, stamens, and pistil. The lateral margins are wider and thinner than those of the empty glumes. The outer (abaxial) margin is wider and thicker than the inner (adaxial) margin. There is no distinct tip to the lemma because the lateral margins extend upward, gradually merging with the awn. The lemma has five vascular bundles, one in the keel and two in each margin. Those nearest the keel are the largest and extend into the awn. The two vascular bundles in the margins nearest the edge terminate near the tip of the lemma. Small, transverse vascular bundles connect the two lateral vascular bundles and also connect the adjacent lateral vascular bundle with the middle vascular bundle in almost all of the lemmas examined. Occasionally transverse bundles are few or absent; this situation occurs only at the inner (adaxial) margin. Bands of chlorenchyma extend along each side of the middle vascular bundle throughout the length of the lemma and into the awn. Chlorenchyma is also present on either side of the lateral vascular bundles adjacent to the middle bundle, but it may not be present at the termination of the outermost vascular bundles or along the outermost vascular bundle of the inner margin. Stomata are present over the chlorenchyma

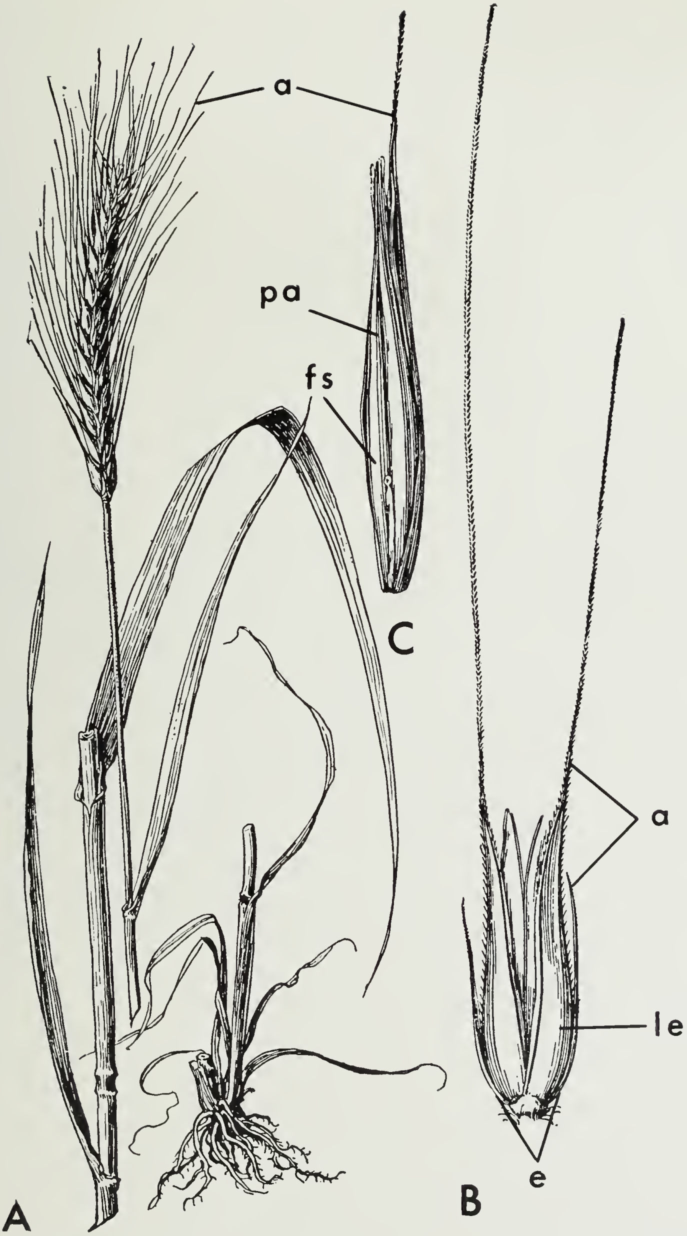

**Fig. 2. Plant, spikelet, and floret of rye (from Hitchcock, 1936).**

**A.** Rye plant. ×½.

**B.** Rye spikelet. ×3.

**C.** Rye floret. ×5.

(*a* = awn; *e* = empty glumes; *fs* = aborted florets; *le* = lemma; *pa* = palea).

in both the outer and inner surfaces of the lemma. Sharp, curved hairs extend halfway down the edge of the outer margin, but they are absent from the edge of the inner margin. Some sharp, curved hairs are present on the outer and inner surfaces of the lemma, but there are fewer than on the empty glumes. In cross-section the outer margin is thicker than the inner margin. The outer and inner margins taper from the keel to the edge where they may be only one cell thick. Both margins increase in thickness at the vascular bundles because of the band of chlorenchyma and the thick-walled fibers over the vascular bundles. The lemma also increases in thickness from the tip to the base. The cells of the outer epidermal layer have thick lignified walls, but those of the inner epidermis are thin-walled and usually collapse by the time the spikelet is mature. Bands of fibers (sclerenchyma) occur near the edge of each margin, but the band is thicker and wider in the outer margin. The kinds of cells in the epidermal layers and their histological characteristics are similar to those of the empty glumes.

An awn is present at the tip of the lemma and at each of the empty glumes (Figs. 1, 2, *a*; 3, *B*, *J*, *a*). The awn of the lemma is very much longer than those of the empty glumes. In each case the awn is an extension of the basal structure. The keel and the margins continue into the awn, forming a triangular-shaped structure with rounded corners. The middle vascular bundle and two lateral vascular bundles continue into the awn. A row of stomata is on each side of the main vascular bundle. Hairs from the margins and the keel continue along the corner of the triangular-shaped awn to the tip. The awn terminates with a group of four sharp-pointed hairs, one of which projects above the other three. The awn is a stiff, rigid structure. It is covered by lignified, thick-walled epidermal cells. Beneath the epidermis are several layers of thick-walled fibers, which inclose the vascular bundles and the chlorenchyma. The only openings through the mechanical tissue are at the stomata where the substomatal chamber extends into the chlorenchyma.

In contrast to the empty glumes and lemma, the palea has two keels. The keels lie on either side of the floret, touching the lateral margins of the lemma at the position of those lateral vascular bundles nearest the edge of the margin. The tip of the palea is divided into two obtuse-shaped apexes in which the keels and their vascular bundles terminate. Two margins, one from each keel, extend laterally, curve inward, and partly inclose the lateral stamens. At the base of the palea, the edges of the two margins are several cells thick and rounded where they fit into the lodicules. A thin membranous tissue connects the two keels. The tissue between the keels is folded inward, so that it separates and partially incloses the two lateral stamens. Two vascular bundles, one in each keel, are the only ones in the palea. A band of chlorenchyma and a row of stomata are on either side and beneath each vascular bundle. A few stomata are found in the inner epidermis. Pointed hairs, varying in length, are found throughout the length of the keels, along the edges of the margins at the apexes, and on the outer and inner surfaces of the palea. The palea does not have as much mechanical tissue as the lemma and the empty glumes. The mechanical tissue consists of lignified fibers over the vascular bundles and the thick-walled lignified cells of the outer epidermis. Except near the keels and at the base, the palea is thin in cross-section, consisting of the outer and inner epidermis and sometimes a third thin-walled parenchyma cell between them. Some of the cells of the inner epidermis near the keels are thin-walled and large in diameter as if inflated, as in the oat palea (Bonnett, 1961). At the apexes and at the edges of the margins, the palea is reduced to the two epidermal layers. Usually the inner epidermal layer and sometimes both layers collapse, leaving only the walls. The cell types in the epidermal layers are similar to those of the glumes and lemma, but the cell walls are not as thick. At the apexes and edges of the margins, the epidermal cells are long, thin-walled, and pointed at the ends, in contrast to those in the interior, which have medium-thick, sinuous, parallel side walls at right angle to the end walls. No hairs were found on the palea.

There are three stamens in each floret. One is opposite the keel of the lemma. The other two stamens are on either side of the pistil in the folds of the palea. A stamen consists of an anther and a filament. Each anther has four locules in which the pollen is contained, joined to a connective in the center. The filament is joined to the base of the connective and to the base of the floret just above the insertion of the lemma and palea. The filament of the stamen opposite the lemma is inserted between the two lodicules, and the filaments of the two lateral stamens are inserted just behind the lodicules.

The two lodicules are placed one on either side anterior to the pistil. They are thick and fleshy at the base but thin and membranous at the apex and margins. The thick fleshy base is in contact with the base of the lemma. There is a notch along the posterior edge of the thick base in which the thick, rounded edge of the palea is fitted. The thin, membranous margin extends from the notch along the inner surface of the palea. The lodicules swell at anthesis and force the lemma and palea apart so that the stamens can be exerted to shed pollen.

The pistil, as in other cereals and grasses, is composed of an ovary and two styles at the top. The ovary is oval in shape and terminates the floral axis. Long hairs cover the upper portion of the sides and the top of the ovary around the base of the styles. The styles extend from the top of

the ovary (Bonnett, 1937, 1961). They are larger at the base and taper to a blunt point. Stigmatic branches cover the exterior surface of the styles from the base to the tip, forming a plumelike group.

### SPIKE DIFFERENTIATION

Spike differentiation in rye follows the same pattern in all respects as in wheat (pages 36 to 43), except that the two basal florets are the only ones that produce kernels. The remaining three or four florets always remain rudimentary (Fig. 2, *C, fs*), but in wheat many of the florets may produce kernels.

The first indication of spike differentiation is the elongation of the shoot apex (Bremer-Reinders, 1958). Double ridges appear on the elongated shoot, which is a definite indication of spike initiation. As stated in the description of spike development of barley (page 61) and wheat (page 36), the upper ridge is the spikelet primordium. As in wheat, spikelet initiation occurs first in the middle of the spike and proceeds toward the tip and the base (Fig. 3, *C, D*).

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**Fig. 3. Stages in the development of the rye spike and spikelet.**

**A.** Base of a spike edgewise to the spikelets. ×20.

**B.** Base of a spikelet flatwise to the spikelet. ×20.

**C.** Early stages in the initiation of spikelets. The empty glumes are papillae at the right of the spikelet primordia. The spikelets at the tip of the spike have not developed as rapidly as those below. This difference continues during the development of the spike. ×35.

**D.** Spikelets in the middle of the spike show the primordia of the empty glumes and lemmas of the two basal florets as ridges parallel to the long axis of the spike. ×30.

**E.** Florets in the middle of the spike show primordia of the stamens as three papillae. ×25.

**F.** A spike showing the rachis and the apical spikelet at right angle to the plane of the spikelets below it. ×20.

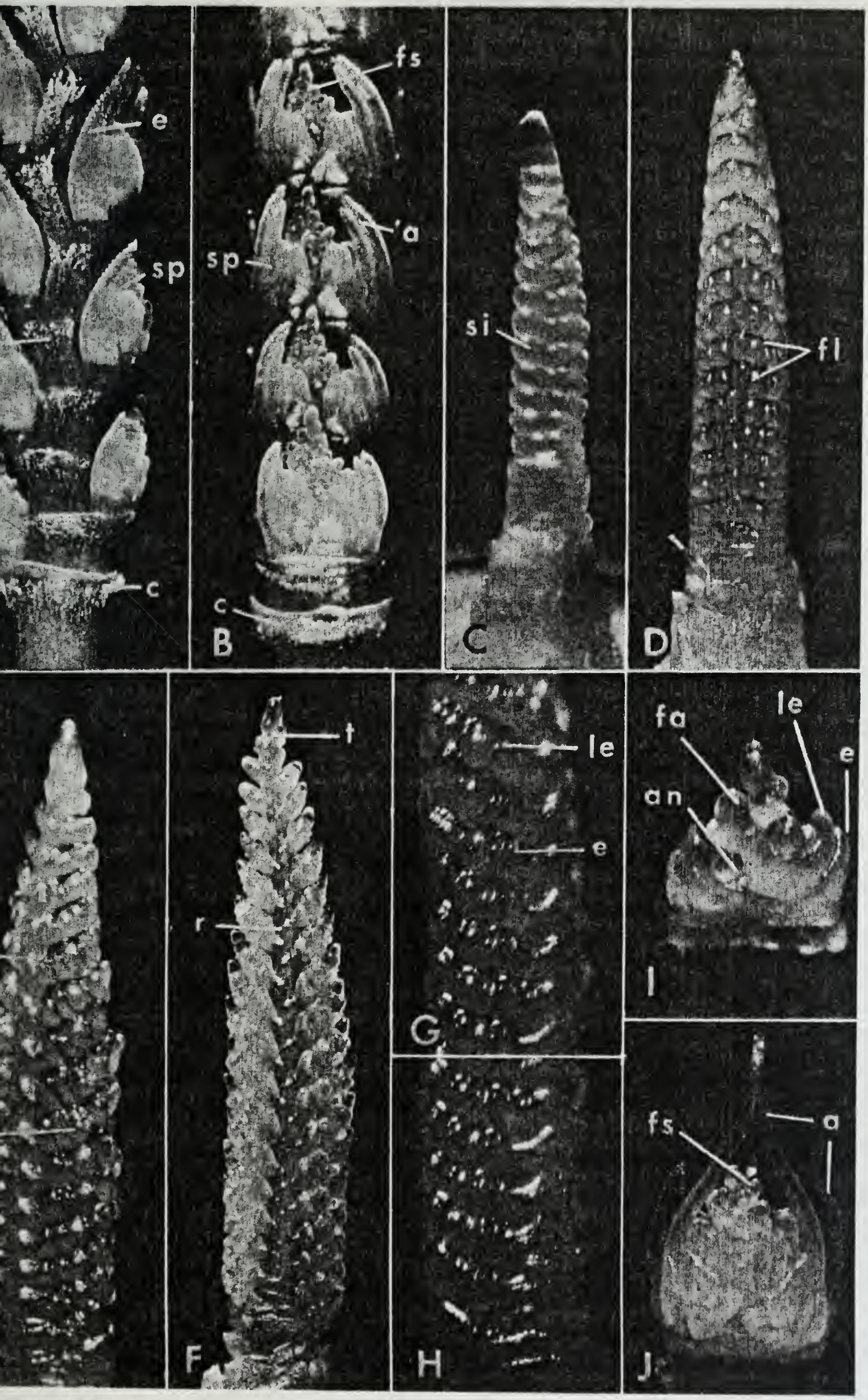
**G.** Part of the middle of a spike at the same stage as in D. ×40.

**H.** Base of a spike at the same stage as D. Spikelets at the base of the spike are not as far advanced in development as those in the middle. ×40.

**I.** An adaxial view of a young spikelet having (at this stage) five floret primordia. Early stages in the development of the glumes and lemmas of the two basal florets are shown. ×28.

**J.** Adaxial view of a rye spikelet showing awns, stamens, and six florets. The florets above the two basal ones appear to be retarded in development, indicating that they will abort. ×28.

(*a* = awn; *an* = stamens; *c* = collar; *e* = empty glume; *fa* = floret apex; *fl* = floret; *fs* = sterile florets; *le* = lemma; *si* = spikelet primordium; *sp* = spikelet; *r* = rachis; *t* = apical spikelet)



(Fig. 3)

The first indication of spikelet development is the appearance of the empty glumes as ridges on both sides of the spikelet primordium parallel with the rachis (Fig. 3, *C*). Soon the lemma of the two basal florets and the apex of the floral shoot are clearly delimited (Fig. 3, *D*, *G*, *H*). The florets above the two basal florets are initiated and develop acropetally. In the early stage of spikelet development, there is no indication that the florets above the basal two will abort (Fig. 3, *E*, *I*), but by the time the awns have begun to elongate the aborting florets can be easily identified (Fig. 3, *B*, *J*, *fs*). The awns elongate more rapidly than the basal part of the glumes or lemma (Fig. 3, *B*, *J*, *a*).

Initiation of the stamens and the palea occurs at about the same time. The stamens appear as three papillae above the primordium of the lemma (Fig. 3, *E*, *I*, *an*). The anthers grow rapidly and protrude above the inclosing lemma and palea (Fig. 3, *J*, *an*).

The pistil is the last part of the floret to develop. It follows the same pattern of development as described for oats (pages 98 to 101 and Bonnett, 1961).

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# *Development of the Barley Spike*

The inflorescence of cultivated barley is a spike. The spikelets are alternate and sessile, or nearly so, upon an elongated axis, the rachis. The axis does not terminate in a spikelet and so is classified as an indeterminate inflorescence. Barley differs from other members of the *Hordeae* in having three single-flowered spikelets at each joint of the rachis. Some of the florets are fertile and develop kernels and some are not. The florets are oriented so that the back of the lemma is away (abaxial) from the axis. The empty glumes are inserted on either side of the lemma at the node.

Publications dealing with the development of the barley stem from germination to pollination are few. Two that deal with the development of the barley spike from the earliest stages to complete differentiation should be mentioned. Schuster (1910) published a description and a set of drawings illustrating several steps in spike and spikelet development. Noguchi (1929) gave a brief description of the spike and spikelet development and illustrated some of the phases of development by drawings. He also gave data showing the length and breadth of the spike of 6-row and 2-row barley at different stages from 10 to 200 days old.

The illustrations accompanying the two publications are line drawings and hence present more or less diagrammatically what is shown in this article by photographs. In addition, this article shows several stages of development that are not included by Schuster and Noguchi.

## MATERIALS AND METHODS

Both 2-row and 6-row barleys were used in this study, and the photomicrographs that best showed the successive steps in spike and spikelet development were chosen without regard to type. This was justified because both types follow the same sequence of development, the only exception being that the side spikelets of the 2-row barley do not develop as rapidly or as completely as the central spikelets.

The plants were grown in pots in the greenhouse, and when they were 20 days old daylight was supplemented with electric light from 500-watt bulbs placed about 3½ feet above the bench on alternate nights. These conditions of growth produced normal plants except that the electric light hastened the development of the spike.

At intervals of a few days, plants were pulled, taken to the laboratory, and the shoots dissected from the stem under the low power of a binocular

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First published in 1935 in Journal of Agricultural Research 51:451-457. Revised and enlarged.

microscope. Dissecting needles ground flat and bent slightly at the tip were used. The shoot was easily exposed and removed for photographing by carefully cutting and removing the leaves enclosing it.

Photomicrographs were taken with an upright camera, adjusted to fit over one side of the binocular microscope. It was necessary to construct a special light-tight collar to connect the microscope and camera. The eyepiece was left in the microscope when exposures were made.

Light for photographing was obtained from a microscope lamp fitted with a 200-watt bulb. A Florence flask filled with water containing sufficient copper sulphate to produce a light blue-green color was used as a condenser. This set-up gave a light of sufficient intensity to produce a good negative on commercial orthochromatic film with about 10 seconds' exposure.

At first great difficulty was experienced in making photographs because of the very rapid drying of the dissected shoots. Later, the shoots when dissected were placed on moist blotting paper in a small preparation dish and stored in a Petri dish lined with wet paper towels and placed in a refrigerator at 40° F. over night. Material handled in this way could be kept for 24 hours without any apparent deterioration. It was also found that specimens stored in the refrigerator for a period of time did not dry out as rapidly as those that had just been dissected.

Two methods of mounting shoot apexes for photographing were used. In one the specimen was mounted on moist blotting paper over black paper placed in the bottom of a preparation dish. The preparation dish was covered with a watch glass for the preliminary manipulations and focusing and then the watch glass was removed for the final focusing. The other method was to place a drop of petroleum jelly on a glass slide, mount the specimen in the jelly, and then place the slide over a black velvet background. Both methods of mounting were satisfactory except that in using the latter method more speed was necessary to complete the photographing before the specimen dried.

Shoot apexes and spikes of barley are very difficult to photograph because they are colorless and nearly transparent. They were photographed against a black background with the light so placed that the highlights and shadows brought out the detail. In some cases in order to provide contrast, a stain composed of a mixture of 90-percent alcohol, a small amount of glycerin, and basic fuchsin was applied to the specimen with a camel's-hair brush. The alcohol quickly evaporated, leaving the glycerin and stain in the folds of the various structures. Since the red stain photographed black the details of the structures were clearly outlined.

## DESCRIPTION OF SPIKE DEVELOPMENT

In the resting stage of the barley grain the plumule of the embryo is composed of only a few structures. These are the coleoptile and first leaf, which are the largest of the structures, the second and third leaf primordia, the shoot apex, and a tiller bud in the axil of the coleoptile. The coleoptile and first leaf have been dissected from the embryo of the barley seed in Fig. 1, *A*, to show the second and third leaf primordia. The shoot apex, which is hemispherical, is partly enclosed by the third leaf primordium. By carefully removing the second and third leaves the primordium of the fourth leaf can be seen as a transverse ridge on the shoot apex.

By the time the second leaf is well grown nearly all of the leaves and leaf primordia that the main stem will have can be found. The leaves range in size from those fully grown to leaf primordia just distinguishable as ridges at the base of the shoot apex. At this stage of stem development the shoot apex has just begun to elongate in preparation for spike differentiation. Up to this time the shoot apex has been short and hemispherical.

The shoot apex of a stem in the three-leaf stage is shown in Fig. 1, *B*. The leaves that enclosed this shoot apex ranged in size from the fully grown first and second leaves with the third leaf about 2 inches long down to the sixth leaf that was just large enough to enclose the shoot apex. The seventh-leaf primordium is the basal one (Fig. 1, *B*, $l_7$), while the last prominent ridge (Fig. 1, *B*, $l_{12}$) is probably the last leaf that the stem would have produced. Above the twelfth-leaf primordium is the part of the shoot apex from which the spike is differentiated.

The first indication of spike differentiation is the appearance of double ridges (Figs. 1, *C*, *x*; 6, *A*, *B*) instead of single ridges as was noted previously. At first the ridges are nearly equal in size, but the upper ridge of each pair grows more rapidly and from it the spikelets are formed. The lower ridge of the pair is a leaf primordium subtending the spikelet primordium.

Spikelet differentiation is first indicated by the appearance of two slight depressions in the transverse meristematic ridge. The very earliest stages of spikelet differentiation can be noted in the two spikelet primordia at the base of the spike (Figs. 1, *D*; 6, *D*). Growth occurs in both sides and between the two furrows in preparation for the differentiation of the spikelet parts. Soon two little papillae, or empty glume primordia, appear on opposite sides of each spikelet (Fig. 1, *D*, *e*), but they appear first on the central spikelets.

Several stages of spikelet development are shown on the same spike (Fig. 1, *D*). In the center portion of the spike the spikelet primordia are

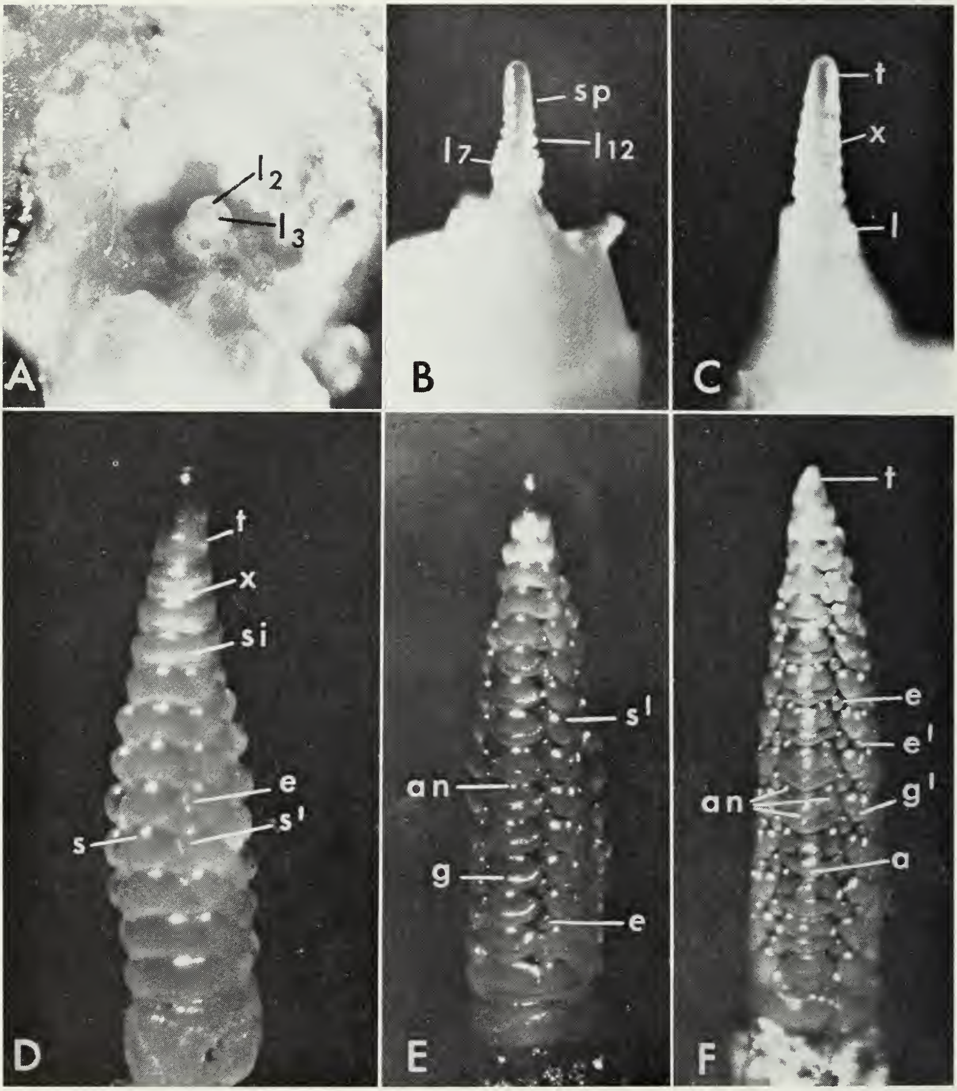

**Fig. 1. Early stages in spike development. (These stages are also shown in Fig. 6.)**

**A.** A part of the embryo of a barley kernel with the coleoptile and first leaf removed. ×27.

**B.** Shoot apex of a barley stem in the transition stage. The stem had three leaves visible. All leaves have been removed except the seventh to the twelfth leaf primordia. ×17.

**C.** Spike primordium of a 6-row barley stem in the four-leaf stage, showing double ridges, which mark the beginning of spike differentiation. ×25.

(Legend is continued on next page)

quite prominent. The two transverse ridges at the base of the spike and some of the ridges at the top of the spike show only the first evidences of spikelet differentiation. The very tip of the spike is smooth and shows little evidence of the formation of ridges, while in Fig. 1, *D*, *x*, the lower of a pair of ridges can be seen.

The lemma is the first structure of the flower to differentiate (Fig. 1, *E*, *g*). It appears as a distinct ridge across the spikelet primordia and forms first upon the central spikelets in the central portion of the spike. Differentiation of the palea occurs somewhat later than that of the lemma, but since it is hidden by the other spikelet parts its development cannot be followed in gross dissections.

Soon three papillae appear upon the meristem above the lemma (Fig. 1, *E*, *an*, and *F*, *an*). These papillae are the primordia of the stamens. The pistil is formed from that portion of the meristem located between the stamens, but it does not differentiate until considerably later than the stamens. The ovary differentiates first, followed by the styles and last, the stigma.

A side view of a young spike of barley is presented in Fig. 2, *A*, for the purpose of showing an early stage in the development of the rachis. In the early stages the internodes of the rachis are very short, but as the spike matures the internodes elongate. The degree of elongation determines spike density, a character used in the classification of barley varieties.

The awn begins its development as an outgrowth from the lemma (Figs. 1, *F*; 2, *B*; 4, *E*; 7, *C*, *D*, *a*). The awns and stamens grow quite rapidly and together with the empty glumes are soon the most conspicuous of the spikelet structures (Figs. 2, *B*, *C* and 3, *C*). The awn grows much more rapidly than the lemma and palea, which remain short with the stamens extending above them. About the time the last internode of the

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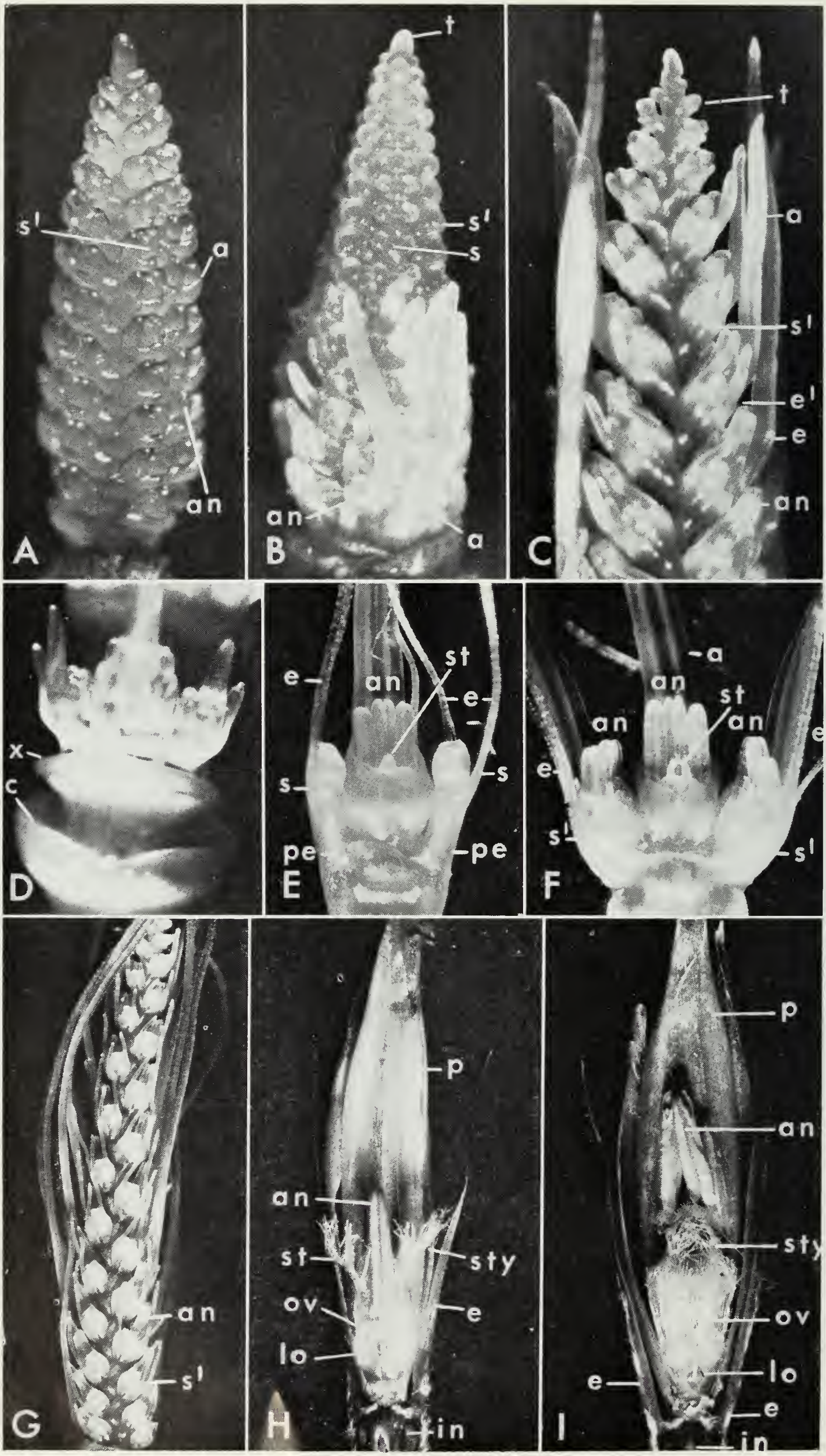
**Fig. 1. Continued.**

**D.** Spike of a 6-row barley stem in the five-leaf stage, showing the beginning of spikelet formation. ×40.

**E.** Spike of 6-row barley in the five-leaf stage, showing the initiation of the lemma and stamens. Stain has been used to outline the structures. ×25.

**F.** A spike of 2-row barley from a stem in the six-leaf stage, showing a more advanced stage of glume, stamen, and awn development. Stain has been used to outline the structures. ×25.

(*a* = awn; *an* = stamen; *e* = empty glume, central spikelet; *e′* = empty glume, side spikelet; *g* = lemma, central spikelet; *g′* = lemma, side spikelet; *l* = leaf primordia, subscript number indicates the leaf number from the base of the shoot; *s* = central spikelet; *s′* = side spikelet; *si* = spikelet forming ridge or primordium; *sp* = spike primoridum; *t* = tip of spike; *x* = double ridge)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(Fig. 2)

stem begins to elongate, the glumes begin their growth and finally enclose the stamens and pistil. It should also be mentioned that in barbed varieties of barley the barbs can be seen on the awn at an early stage (Fig. 4, *E*, *F*).

While the spikes of barley shown in Figs. 2, *B* and 4, *D* were chosen principally to show the early development of the awn, it also shows the differentiation of a 6-row barley at the 6-leaf stage. A difference in development at the base and tip of the spike should be noted as well as the relative stages of differentiation in the side and central spikelets.

The relative size and degree of development of the tip of the spike and the spikelets a little lower on the spike should be noted (Fig. 2, *C*, *t*). The very tip of the spike is at this stage a bit of undifferentiated meristem, and the spikelets at the uppermost 7 or 8 nodes of the rachis, as contrasted with the spikelets below, are much retarded in development. As has been pointed out, in the early stages of development the tip of the spike remains undifferentiated and smooth in outline. As the spike approaches maturity spikelet differentiation proceeds apically, but the last-formed spikelets never complete development, always remaining infertile and rudimentary. Rudimentary spikelets at the tip of the spike can be seen on any mature barley spike.

At the base of the spike is a structure called the collar (so designated by Wiebe and Ried, 1961) (Figs. 2, *D*; 4, *C*, *c*). This structure is a distinct ridge of tissue circling the stem at the first node of the spike. A similar but less prominent ridge of tissue is found at the first node above the collar

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**Fig. 2. Spikes, spikelets, and flowers.**

**A.** Spike of a 2-row stem in the six-leaf stage showing the rachis, stamens, awns, and side spikelet. ×35.

**B.** A 6-row barley spike from a stem in the six-leaf stage, illustrating awn development and comparative development of side and central spikelets. ×25.

**C.** Part of a spike of 2-row barley from a stem in the five-leaf stage, showing the differentiation of the tip of the spike. ×25.

**D.** Part of a spike from a stem in the six-leaf stage, showing the collar at the base of the spike. ×30.

**E.** Spikelet of a 2-row barley. ×15.

**F.** Spikelet of a 6-row barley. ×15.

**G.** Spike of a 2-row barley. ×8.

**H.** Spikelet before pollination. ×5.

**I.** Spikelet after pollination. ×5.

(*a* = awn; *an* = stamen; *c* = collar; *e* = empty glume, central spikelet; *e′* = empty glume, side spikelet; *in* = internode; *lo* = lodicules; *ov* = ovary; *p* = palea; *pe* = pedicel; *r* = rachis; *s* = central spikelet; *s′* = side spikelet; *st* = stigma; *sty* = style; *t* = tip of spike; *x* = node of rachis)

(Figs. 2, *D*; 4, *C*). So far as has been determined in these studies, the collar and the ridge at the node above are formed by two leaf initials that are just beginning to differentiate but are not far enough along to continue their development as leaves at the time spikelet differentiation begins. They are arrested in their development and form the structures mentioned. While spikelets develop at the collar, they are late and usually rudimentary and sterile (Fig. 4, *C*).

A spike of a 2-row barley well advanced in its development is shown in Fig. 2, *G*. The awns on the central spikelets are well developed but not fully grown, and the anthers protrude well beyond the glumes. The side spikelets are small, without awns on the lemma, and rudimentary anthers extend slightly beyond the glumes. Empty glumes and the barbs on them can be seen. Barbs can also be seen on the awns.

A spikelet of a 2-row barley (Fig. 2, *E*) and a spikelet of a 6-row barley (Fig. 2, *F*) are shown for comparison. Both spikelets were taken from stems in about the same stage of development. The last internode of the stem (peduncle), the one to which the spike is attached, had just begun to elongate. The stamens and stigmas in the spikelets of the 6-row and in the central spikelet of the 2-row barley extend above the flowering glumes. However, just before the head emerges from the boot, the lemma and palea, which up to this time have grown slowly, begin to grow rapidly and soon enclose the stamens and stigmas. The stamens in the side spike-

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**Fig. 3. Early stages in the development of the pistil. All photographs taken from the adaxial side of the spikelet.**

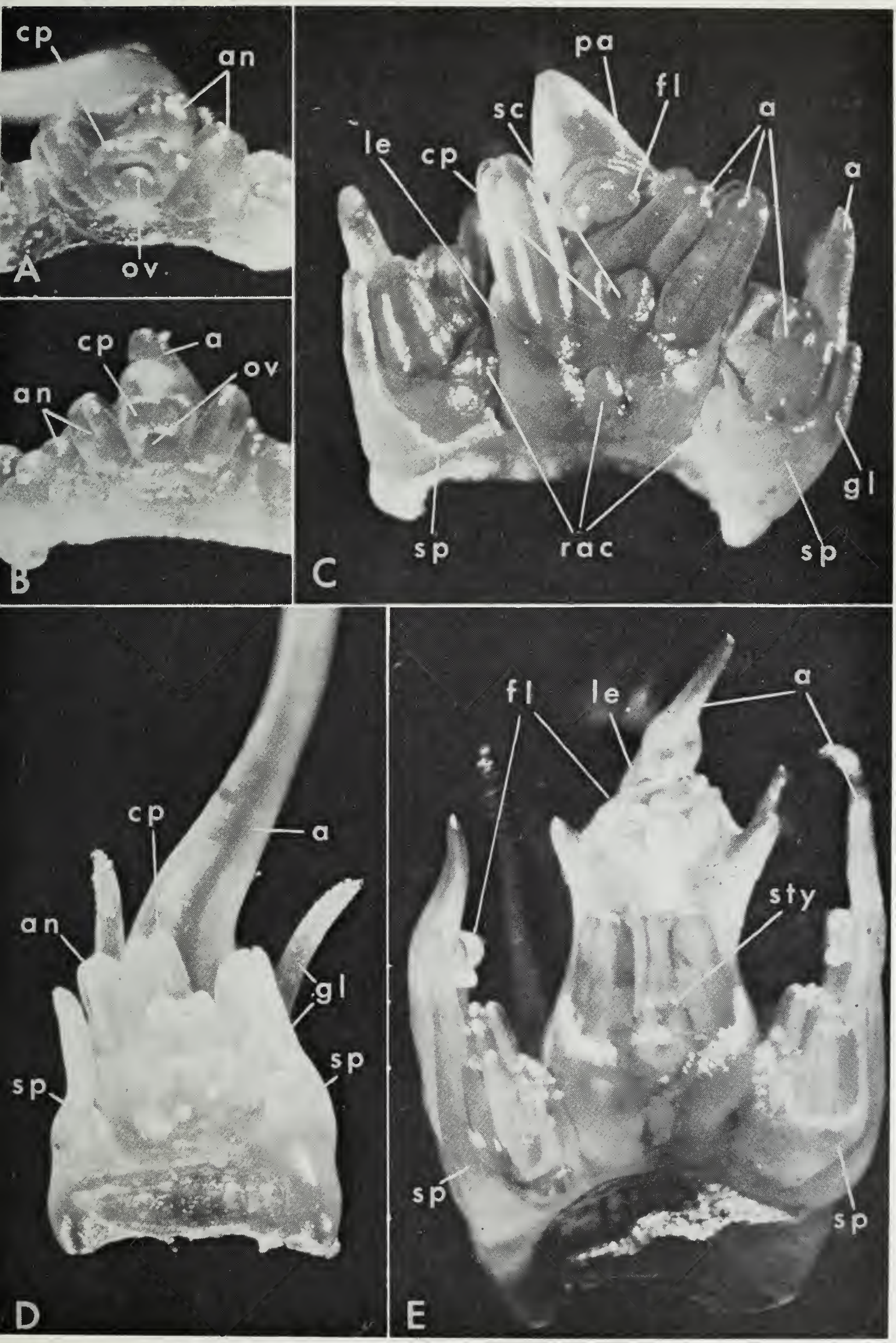
**A, B.** Central spikelet of a 6-row barley showing the carpel and the initiation of the styles as two points, each opposite to a laterally placed stamen. ×60.

**C.** Central and lateral spikelets of a 6-row, hooded barley. The stamens have not been enclosed by the lemma and palea. The pistil in the central flower is more advanced in its development than in A or B. The stylar canal is open. Initiation of the rachilla has begun at the base of the spikelets. The accessory flower on the lemma of the central spikelet shows three papillae, the beginning of initiation of the stamen. ×50.

**D.** Spikelets of *Hordeum deficiens,* a 2-row barley. The side spikelets are poorly developed compared with those of the 6-row type in C. Stamen and pistil do not develop in the side spikelets of this type. The stylar points of the pistil are more prominent than in A or B. ×50.

**E.** The styles have started to elongate on the pistil of the flower in the central spikelet. This is a hooded type. Initiation of flowers on the lemma of the central and lateral spikelets is shown. ×50.

(*a* = awn; *an* = stamen; *cp* = carpel; *fl* = flower; *gl* = empty glume; *le* = lemma; *ov* = ovule; *pa* = palea; *rac* = rachilla; *sc* = stylar canal; *sp* = spikelet; *sty* = style)


cp
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E

(Fig. 3)

lets of the 2-row barley have been enclosed by the flowering glumes. The stigmas in neither Fig. 2, *E*, nor Fig. 2, *F*, have branched.

Early stages in the development of the pistil are shown in Fig. 3. The carpel, which is the first part of the pistil to differentiate, originates as a crescent-shaped ridge (Fig. 3, *A*, *B*, *C*, *cp*) that forms beneath the apex of the floral shoot. The apex of the floral shoot becomes the ovule (Fig. 3, *A*, *B*, *ov*). At first the ridge is more prominent on the anterior side of the floral shoot, but it gradually extends laterally around each side to enclose the ovule; however, the opening over the ovule is never completely closed but remains as the stylar canal (Fig. 3, *C*, *sc*). The carpel grows more rapidly on either side opposite the laterally placed stamens and elongates to become the styles. More advanced stages in the development of the styles are shown in Fig. 3, *D*, *E*. The styles continue to grow in length, and at maturity they are covered with stigmatic branches which develop from cells of the epidermis (Fig. 2, *H*, *st*).

Mature flowers before pollination and after pollination are shown in Fig. 2, *H* and *I*, respectively. The lemmas have been cut away to show the flower parts. Only one stamen can be seen (Fig. 2, *H*). The other two stamens are hidden in the folds of the palea. Before pollination the anther is not dehisced, the stigmas are erect, branched, and feathery, the lodicules swollen and turgid, and the ovary small. After pollination the anthers are dehisced, the stigmas are collapsed, the lodicules are shrunken, and the ovary has increased in size. The fertilized ovary after a period of growth and differentiation becomes the barley kernel.

Aside from the pistil and palea mentioned previously, two other spike-

**Fig. 4. Tiller, rachis, and awn development.**

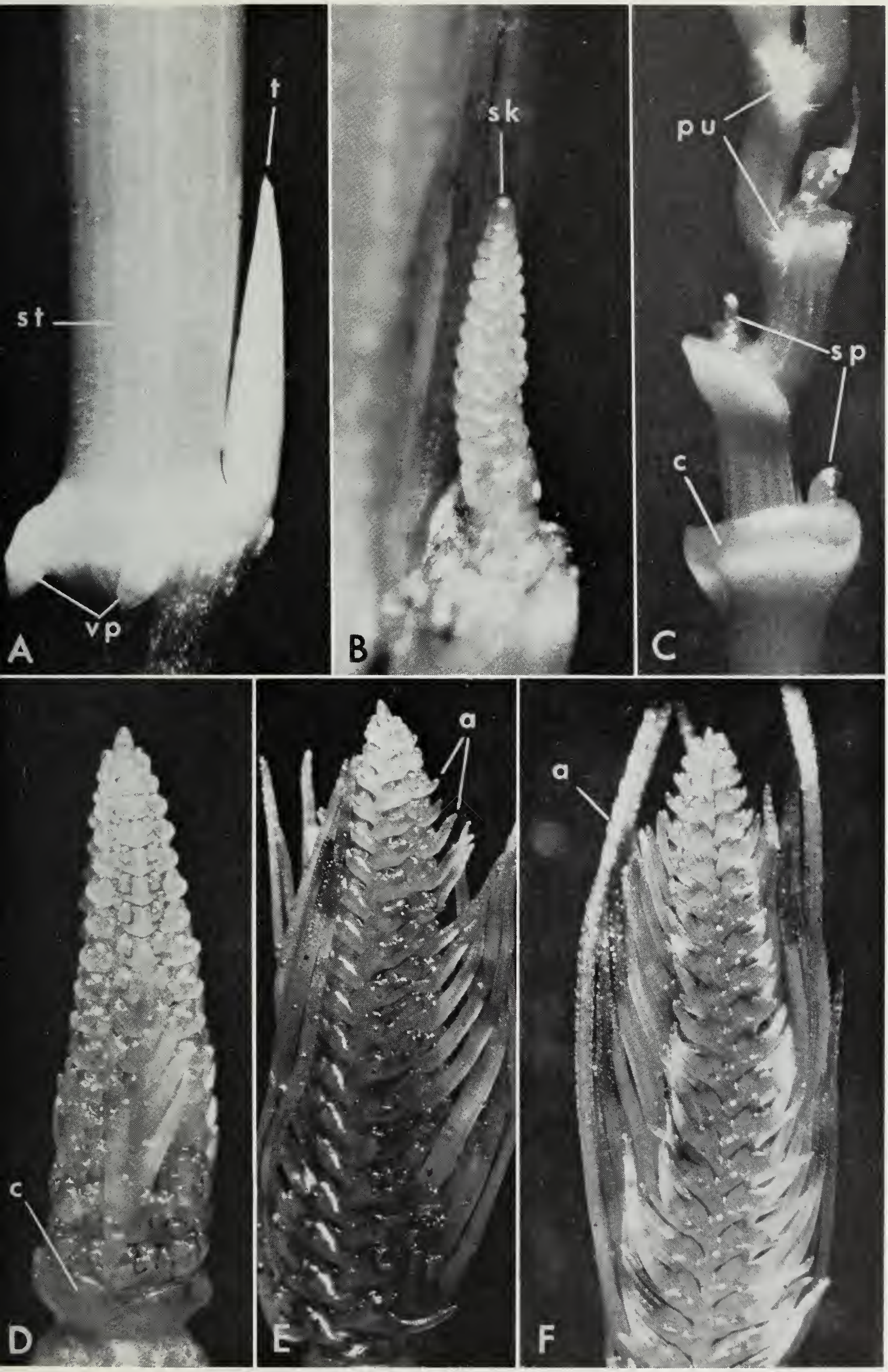
**A.** A tiller at the base of a head-bearing stem of barley. The leaf sheath was removed to expose the tiller. Adventitious root primordia extend from the base of the node. ×12.

**B.** The prophyll and leaves were removed from the tiller in A to show the spike that was enclosed. Spikelets have been initiated indicating that even in very small tillers spikes are formed the same as in the main stem and the larger stems of the plant. ×30.

**C.** Four nodes of the rachis showing the collar, a modified leaf, subtending the rudimentary spikelet at the basal node of the spike and successively smaller modified leaves at the nodes above. Pubescence is evident at the two upper nodes. ×20.

**D, E, F.** These spikes have awns in various stages of development ranging from initiation at the tip of the spikes in D, E, and F to awns with barbs in F. D, ×25; E, ×20; F, ×15.

(*a* = awn; *c* = collar; *pu* = pubescence; *vp* = root primordia; *sk* = spike primordium; *sp* = aborted spikelets; *st* = stem; *t* = tiller)



(Fig. 4)

let structures, the rachilla and the lodicules, have not been followed in their differentiation and development in this study. They are so located that their differentiation and development cannot be shown.

### DIFFERENCES BETWEEN 2-ROW AND 6-ROW BARLEY IN SPIKE DEVELOPMENT

Cultivated barley is classified into two major groups: 6-row, *Hordeum vulgare,* and 2-row, *Hordeum distichum* (Wiebe and Reid, 1961). The 6-row barley has three sessile, single-flowered spikelets at each joint of the rachis. All flowers are fertile (Fig. 2, *F*). In 2-row barley, only the flower of the central spikelet is sessile and fertile. The lateral spikelets are pediceled and infertile (Fig. 2, *E, pe*). There are two groups of 6-row barley and two groups of 2-row barley. The two groups of 6-row barley are separated on the basis of a difference in the size of the kernels of the lateral and central spikelets. In the typical 6-row barley the kernels of the lateral spikelets are nearly the same size as those of the central spikelets (Fig. 5, *A, E*), but the kernels of the lateral spikelets of intermedium 6-row barley are much smaller than those of the central spikelets and are usually without awns or hoods on the lemmas (Fig. 5, *B*). The 2-row barleys are also separated on the basis of size and of the degree of development of the parts of the lateral spikelets. In the typical 2-row barley, the lateral spikelets have two empty glumes, a rachilla, and a floret consisting of a lemma, palea, three rudimentary stamens, and a rudimentary pistil (Fig. 5, *C, F*). In the deficiens 2-row barleys, lateral spikelets are very small and the floret consists only of a lemma, rarely a palea, and no stamen or pistil (Figs. 5, *D*, and 3, *D*).

Early stages in the development of the 6-row and 2-row barleys are illustrated in Figs. 6 and 7. In Fig. 6 the typical 6-row barley is in the left-hand column (*A, E, I*); the second column is intermediate barley

**Fig. 5. Mature spikes and spikelets of barley species.**

Spikes of *Hordeum vulgare:* **A.** Six-row barley. **B.** Intermedium barley.

Spikes of *Hordeum distichum:* **C.** Two-row barley. **D.** Deficiens barley.

**E.** Mature spikelets of 6-row barley which has three sessile spikelets, each with a fertile flower located at each joint of the rachis.

**F.** Mature spikelets of a 2-row barley. Only the central spikelet has a fertile flower. The lateral spikelets are rudimentary and pediceled.

**G.** Mature spikelets of a 6-row, hooded barley. In this type an accessory flower develops on the abaxial surface of the lemma of the fertile flowers. A hoodlike structure develops at the point of origin of the accessory flower.

(*a* = awn; *e* = empty glumes; *sp* = central spikelet; *sp′* = lateral spikelet)

*All photographs in Fig. 5 were supplied by Dr. G. A. Wiebe, barley investigations, crops research division, Agricultural Research Service, U.S. Department of Agriculture.*

(Fig. 5)

(*B*, *F*, *J*) ; the third column is 2-row barley (*C*, *G*, *K*) ; and the fourth is deficiens barley (*D*, *H*, *L*). In Fig. 6 from the top down, each row of photomicrographs shows a successively more advanced stage in spike development. In Fig. 7, *A* shows a typical 6-row barley; *B* shows intermedium; *C* a typical 2-row barley; and *D* deficiens barley. The spikes in Fig. 7 are more advanced in development than those in Fig. 6.

Little difference in spike development can be seen among the four barley types at any of the stages illustrated in Fig. 6. Fig. 6, *A*, shows the beginning of spikelet initiation, indicated by the paired ridges. This is the earliest stage of spike development in this figure and is similar to that shown in Fig. 1, *C*. The subtending ridge, the lower ridge of the pair, is the most prominent feature; this stage is more advanced than in Fig. 1, *C*. In Fig. 6, *B*, *C*, the upper ridge from which the spikelet primordium is formed is the most prominent. Spikelet initiation is indicated in Fig. 6, *D*, by the formation of a small projection at the right of each of the two ridges in the middle of the spike. This is an earlier stage than shown in Fig. 1, *D*. There are no differences in the developmental pattern of the spikelets of the different types shown in Fig. 6, *E* to *H* and in *I* to *L*. The stage shown in Fig. 6, *E* to *H*, is very similar to that in Fig. 1, *E*, and those in Fig. 6, *I* to *L*, to that in Fig. 1, *F*.

Differences in the development of the spikelets between the 6-row and the 2-row types as well as between two 2-row types are shown in Fig. 7. Valid comparisons can be made since all types illustrated are at nearly the same stage of development, as shown by the degree of development of the stamens of the central spikelets. In all four types shown the stamens range in development from stamens having four lobed anthers at the base of the spike to papillae at the tip of the spike.

The two 6-row barleys look alike since the distinguishing difference between them is in the size of the kernels of the central and lateral spikelets, and this difference cannot be seen at this stage. However, the 6-row and 2-row types show distinct differences in the development of the lateral spikelets. Stamens in the lateral spikelets are clearly defined in the 6-row but not in the 2-row types. The rudimentary characteristic of the spikelet of the 2-row barleys, at maturity, is already indicated at this stage by its small size. It can also be seen that the lateral spikelets of the typical 2-row barley (Fig. 7, *C*) are slower in initiating stamens than the 6-row

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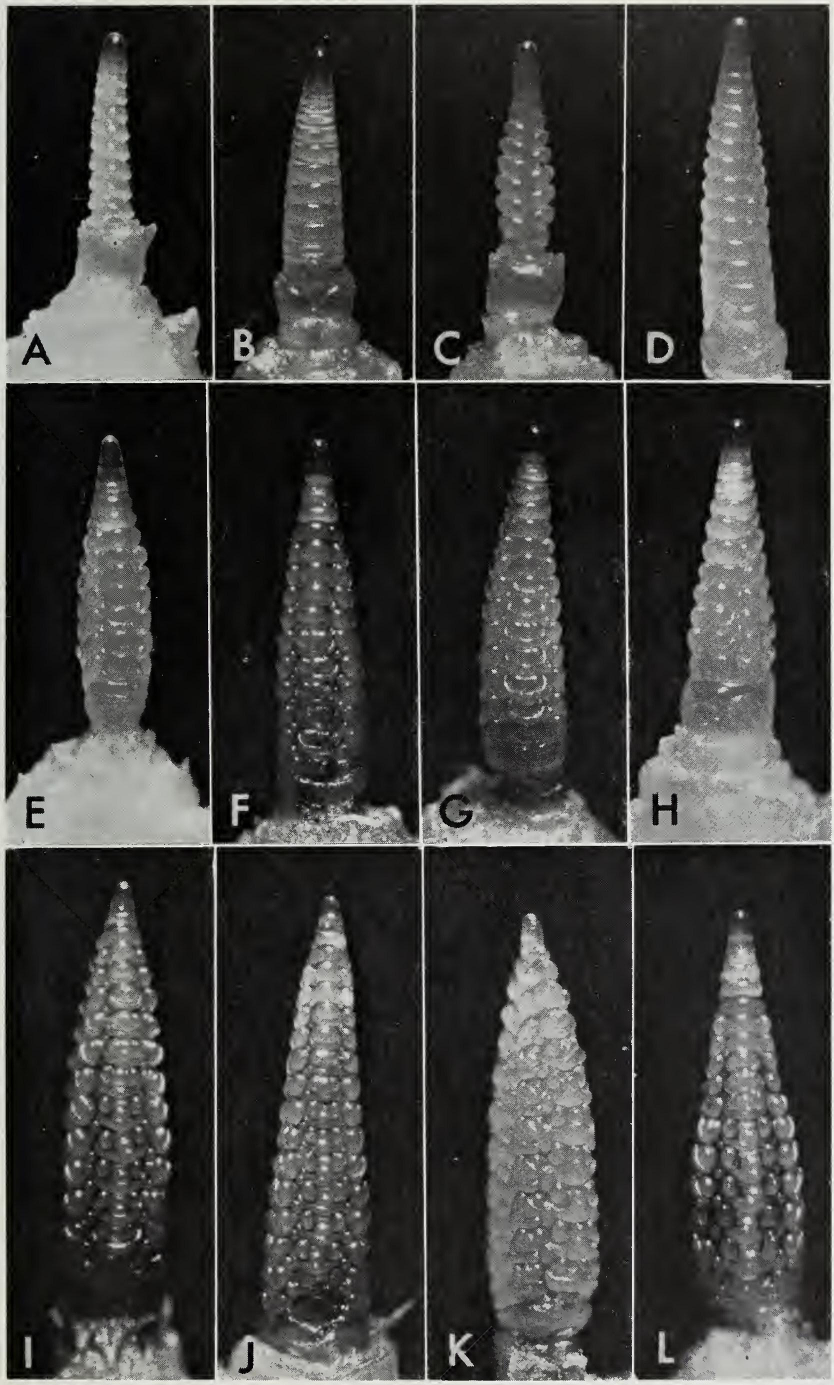
**Fig. 6. Early stages in the development of the spikes of barley species.**

**A, E, I.** Six-row barley. **B, F, J.** Intermedium barley.

**C, G, K.** Two-row barley. **D, H, L.** Deficiens barley.

All magnifications ×24 to ×30.



(Fig. 6)

barleys (Fig. 7, *A*, *B*). Except for two lateral spikelets near the base of the spike, stamens of typical 2-row barley have not been initiated as they have in more than half of the lateral spikelets in the spikes of the 6-row barleys. The lateral spikelets of deficiens (Fig. 7, *D*) are distinctly more retarded than typical 2-row barley. They lack the primordia of the empty glumes and stamens, but they have the primordium of a lemma. The pediceled characteristic of the lateral spikelets of the 2-row barleys, as illustrated in Figs. 2, *E*, and 5, *F*, is not exhibited at this stage of development.

## DISCUSSION

That period in the morphological development of a head-bearing barley stem extending from germination to pollination can be divided into two phases. These phases can be determined approximately by examining the stem and more accurately by examining the shoot apex. In the first phase of development, the internodes of the stem do not elongate, leaves grow, leaf initials are the only structures differentiated from the shoot apex, and the shoot apex above the base remains smooth in outline but increases in length. The changes in the stem and the shoot apex which mark the transition from the first to the second stage are shown by the beginning of internode elongation in the stem and the appearance of double ridges on the shoot apex. In the second phase of development, the internodes of the stem elongate and the spikelets and spikelet structures differentiate, increase in size, and complete their development in preparation for pollination.

It is interesting to note how the phases of stem development of a barley plant parallel each other not only in those stems that produce heads but in all stems even down to the tiller buds. When stems producing

**Fig. 7. Immature spikes of barley species.**

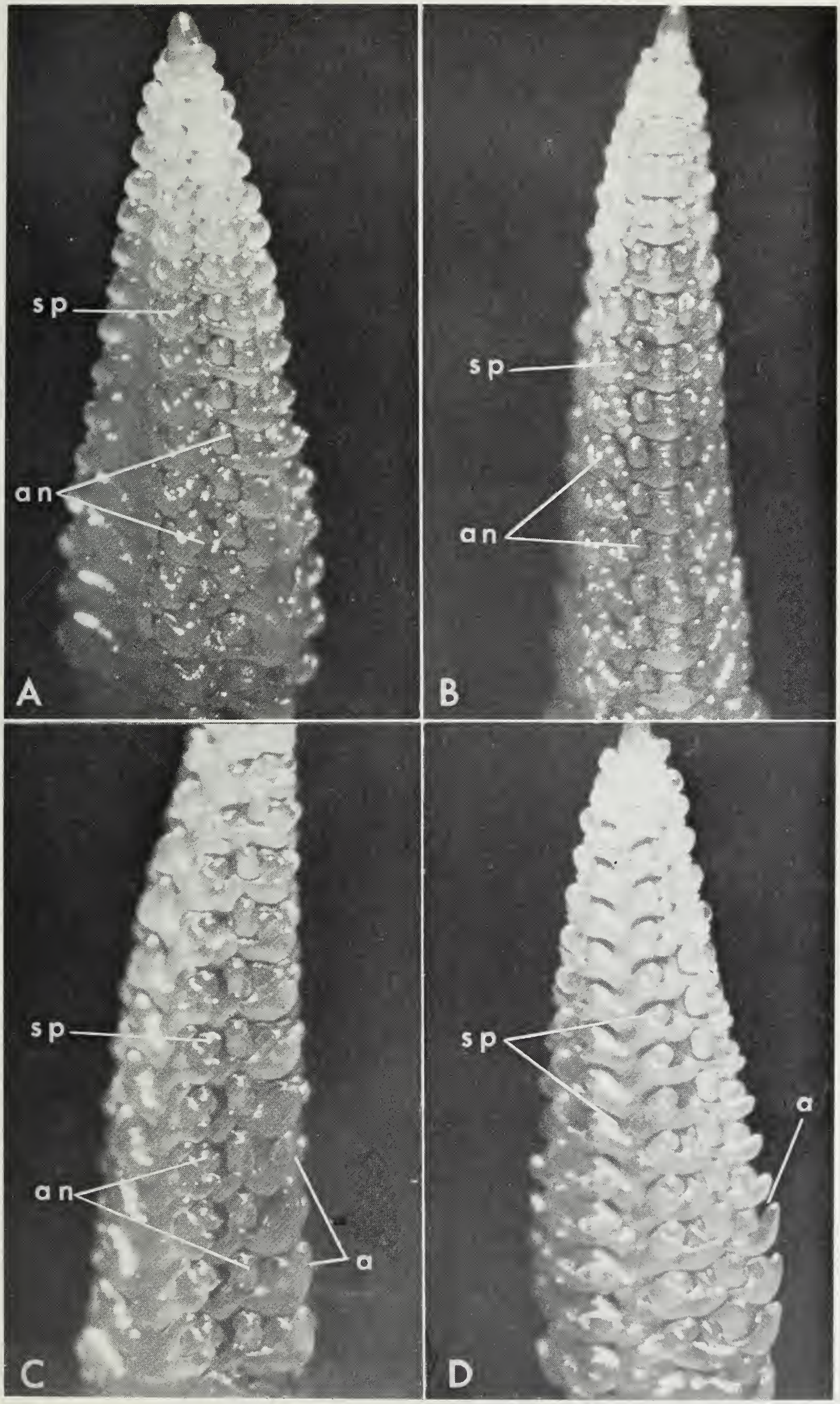
**A.** A typical 6-row barley taken to show a row each of lateral and central spikelets. Stamen primordia are present in the central and lateral spikelets in the lower half of the spike. ×40.

**B.** Intermedium, 6-row barley showing stamen development similar to that of the typical 6-row barley in A. ×40.

**C.** A typical 2-row barley, which at maturity has small, infertile lateral spikelets, which is indicated at this stage by the small size of the spikelets and absence of stamen primordia in all but a few of the basal spikelets. ×44.

**D.** Deficiens, a 2-row barley in which the lateral florets at maturity lack empty glumes, palea, stamen, and pistil. At the stage shown here the florets are small and lack the primordia of the parts listed above. ×37.

(*a* = awn; *an* = stamen primordia; *sp* = lateral spikelet)



(Fig. 7)

heads pass into the second phase, i.e., jointing and spike differentiation, it is not long before all stems on the plant follow in rapid succession. An examination of a plant in head shows even the shoot apex of the tiller buds to be in the process of spikelet differentiation.

Very early differences in the time of differentiation and rate of spikelet development are maintained and are reflected in the mature spike. The early differences can be seen in Fig. 1, *D*, *E*, *F*. The spikelets in the middle of the spike are in advance of the basal spikelets and the basal spikelets are in advance of the tip, which is the last portion of the spike to differentiate. The central spikelets are more advanced in development than the side spikelets in both the 2-row and 6-row types. All of these differences are reflected in the mature spike. The best-developed and heaviest kernels are in the middle portion of the spike, the basal kernels are next heaviest, and the tip kernels are the lightest of all. The kernels in the central spikelets of the 6-row barley are heavier than those in the side spikelets. While the spikelets progressively develop at the tip of the spike, the spikelets remain rudimentary and do not bear kernels. Thus those spikelets that have an initial advantage in differentiation maintain this advantage throughout spike development.

Since the number of spikelets at the joints of the rachis is fixed, response to the environment during early differentiation takes place principally at the tip of the spike. The barley spike is an indeterminate inflorescence and does not terminate in a single spikelet as wheat does. Within limits a certain amount of response to growth conditions is made at the tip of the barley spike in the number of fertile spikelets. Some response can be made at the base of the spike, but the capacity for responding at this point is much more limited.

Although the lemma differentiates before the awn, the awn grows more rapidly. It is not until well along in the development of the spikelet that the lemma and palea become long enough to enclose the stamens and other flower parts. A possible explanation for this behavior was suggested by Kennedy (1899), who stated that in the spikelet the awn corresponds to the leaf blade and that part of the glume below the insertion of the awn may be regarded as corresponding to the sheath of the leaf. He also stated that of the three parts of the leaf the sheath develops last by intercalary growth which pushes up the blade. If the leaf parts and the spikelet parts are homologous as stated, then the slow growth of the lemma is in accord with development of the leaf sheath.

Up to the time that the stamens begin to differentiate, so far as the varieties used were concerned, no difference could be noted between a spike of a 2-row and a spike of a 6-row barley. As development continues the discrepancy in the development of the central and side spikelets of the

2-row barley becomes more apparent. The side spikelets develop very slowly, and remain rudimentary without awns and infertile. On the other hand, while the side spikelets of the 6-row barley are always slower in development than the central spikelets, they finally attain nearly the same size, have awns, and are fertile.

## SUMMARY

The morphological development of the spike of a 2-row and a 6-row barley was studied by dissecting the shoot apexes from the stems. Photomicrographs of the various stages are shown.

Stem development from germination to pollination can be divided into two phases in each of which the growth response of the stem and shoot apex is different. In the first phase the internodes of the stem remain short, the shoot apex produces only leaf primordia, and the undifferentiated portion of the shoot apex elongates. The beginning of the second phase is marked by the elongation of the internodes of the stem and the appearance of double ridges on the shoot. In the second phase the internodes of the stem elongate and the spike and its parts differentiate and develop.

The order of differentiation of the various parts of the spike as far as could be seen in this study are: spikelet primordia, empty glumes, lemma, palea, stamens, awn, and pistil.

Early differences in the time and rate of differentiation of the spikelets in the different parts of the spike are maintained and account for some of the variation in size among the spikelets of the mature spike.

The barley spike is an indeterminate inflorescence, and with the number of spikelets at each joint of the rachis limited, some response to the environment can be made in the number of fertile spikelets at the tip of the spike.

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# *Hood and Supernumerary Spike Development in Barley*

The lemmas of Nepal barley (*Hordeum vulgare* L.) terminate in a trifurcated structure called a hood. The center lobe of the hood is an accessory floret having stamens and a pistil, but the lateral wings of the hood are only vegetative outgrowths of the margins of the lemma. When the hoods of mature spikes are examined, various degrees of development of the stamens and pistil can be found. Almost invariably the supernumerary florets of the hood are infertile, but Biffen (1905) stated that he found fertile florets in the hood and grew plants from the grain that they produced.

Hooded barley was found, according to Harlan (1931), in Nepal between the years 1830 and 1837. He believed that the hooded character probably originated as a mutation. This assumption was supported by the discovery of a hooded mutant in the $F_2$ of a cross of Everest × Manchuria, two awned varieties. If this hypothesis is correct, the hooded character is an example of a dominant mutation.

Biffen (1905), Hor (1924), and Robertson (1929) made crosses between hooded and awned varieties. In such crosses they found that hooded was dominant to awned, and that segregation occurred in the $F_2$ in the ratio of approximately 3 hooded to 1 awned.

The hooded character in barley is of interest for another reason. Arber (1934) stated that the origin of accessory spikelets from the lemma is contrary to one of the dicta of formal morphology, which is that the power of producing lateral shoots is confined to axes. However, in hooded barley, the spikelet, a modified shoot, is produced from the lemma, a modified leaf.

A morphological study of the development of hooded barley is of interest from two standpoints. By studying the morphological development of the hood, it is possible, so far as external appearances will permit, to determine when the genes responsible for the development of the character begin to produce their effects, and to see what changes the genes produce. Furthermore, according to Arber (1934), some morphologists have questioned whether the accessory floret actually does arise from the lemma as its axis. By following the developmental sequence a better idea can be obtained of the points of origin and parts initiated than can be obtained by studying the mature parts. This is because many times parts

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are initiated that never complete development, and in the beginning of development the surrounding parts are not large enough to hide the point of origin of the parts being studied.

Supernumerary spikes were found on the stems of Nepal barley when the development of the hood was being studied. They had also been observed previously in greenhouse cultures of awned barley. The photomicrographs used to show this character were taken from awned barley.

## MATERIALS AND METHODS

Nepal (C.I. No. 595) was obtained from M. N. Pope, division of cereal crops and diseases, U.S. Department of Agriculture. This variety was used for a study of hood development.

The awned varieties in which supernumerary spikes developed were Spartan, Wisconsin Pedigree No. 5, and their $F_2$ progeny.

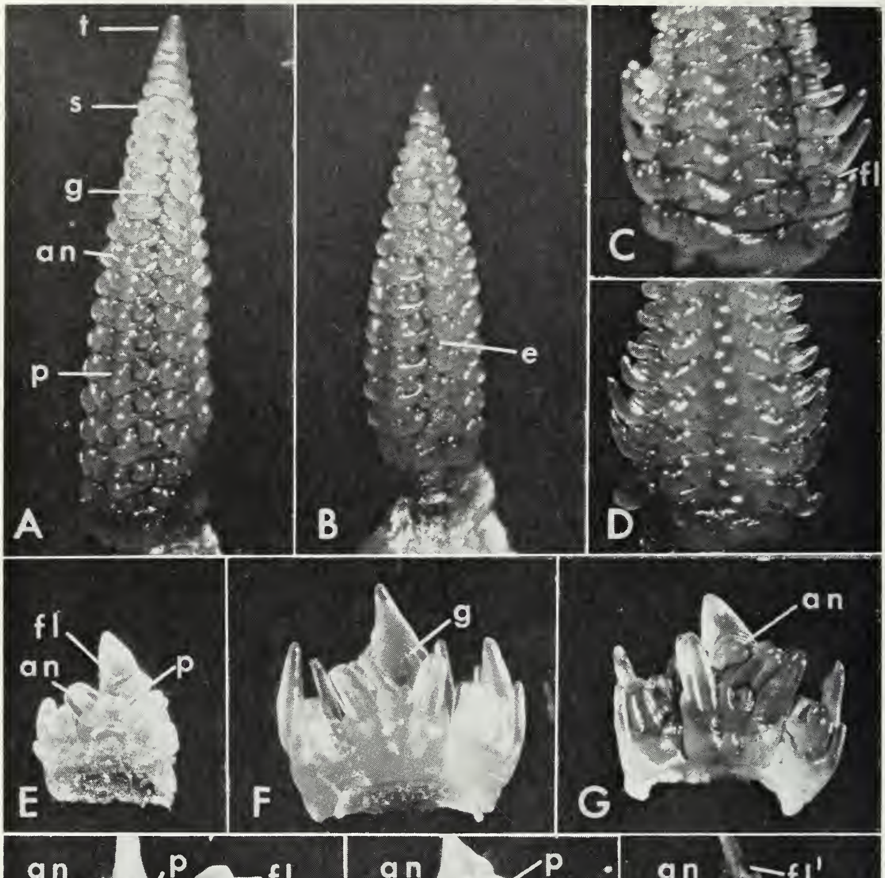
Supernumerary spikes were produced upon plants grown during the winter of 1935 and 1936 on a greenhouse bench filled with about 6 inches of soil. The plantings were made on November 22, 1935, and the plants from which the supernumerary spikes were dissected were sampled on February 21, 1936. The growing period extended through the short days of the winter, and during the period of spike differentiation, December 27 to February 21, the temperature was seldom above 65° F. and dropped to as low as 45° for short periods. The average minimum temperature was 53.2°, the average maximum temperature was 68.1°, and the average mean temperature was 60.8°.

The photomicrographic apparatus and the technique used in taking the photomicrographs were essentially the same as those described in an earlier paper on pages 59 and 60. One exception was that special microlenses having a focal distance of 24 and 32 mm. were used to take the photomicrographs instead of one side of a binocular microscope.

## DEVELOPMENT OF THE HOOD

Since the hood develops from the lemma, the lemma must differentiate and attain some size before the hood primordium appears. An early stage in the development of a spike of hooded barley is shown in Fig. 1, *A*, and a spike of an awned barley is shown in Fig. 1, *B*. In both cases the lemmas of the central spikelets have differentiated, and the tips of the lemmas have begun to elongate in the formation of the awn. At this stage the hood primordia have not differentiated, and no differences in the appearance of the spikelets of the hooded and awned types can be observed.

When the tip of the lemma of the hooded variety has elongated to the point where it begins to resemble an awn (Fig. 1, *C* and *D*) the hood



(Fig. 1)

primordia begin to appear (Fig. 1, *C, fl*). From this point, the development of the lemmas of hooded and awned barley is different.

The hood primordium first appears as a dome-shaped outgrowth on the adaxial side and near the tip of the lemma (Fig. 1, *E, fl*), and from this primordium the parts of the accessory floret differentiate. There is no indication of a leaf primordium subtending the accessory floret of the hood, as is true for normal florets.

When the hood primordium is first seen, the parts of the normally placed floret are not very far advanced in development. The stamens are short and show the development of the locules (Fig. 1, *E, an*), but the pistil is not far enough advanced to show any development of the styles (Fig. 1, *E, p*).

Differentiation of the flower parts of the accessory floret in the hood, with but one exception, follows the same sequence as for those of the normally placed floret. In the normally placed floret the first flower part to differentiate is the lemma (Fig. 1, *A, g*), but, since the tip of the

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**Fig. 1. Stages in the development of hooded barley, Nepal (C.I. No. 595).**

**A.** An early stage in the development of Nepal barley. ×25.

**B.** A spike of 6-row awned barley at about the stage of development as that shown in A. ×25.

**C.** Part of a spike of Nepal barley at the beginning of hood differentiation. A spikelet with an accessory floret is developing on the lemma on the right in the second spikelet from the base. ×20.

**D.** Part of a spike of an awned barley at about the same stage as in C. This is not a hooded type. ×25.

**E.** An adaxial view of the beginning of the development of an accessory floret on the lemma of the central spikelet. ×25.

**F.** Beginning of the development of the palea of the accessory floret on the lemma of the central spikelet. ×25.

**G.** Stamen differentiation of the accessory floret on the lemma of the central spikelet is shown as three papillae on the apex of the floral shoot. ×25.

**H.** Two accessory florets side by side; four stamens and the pistil primordium are clearly shown in the accessory floret at the left. ×25.

**I.** A more advanced stage of development of the stamens and pistil of the accessory floret. ×25.

**J.** An accessory floret showing four stamens and an accessory floret. The rudiment of a second accessory floret is shown above the first. ×25.

**K, L, M.** An abaxial view of the lemmas of the normally placed florets showing successive stages of hood development. ×25.

(*a* = awnlike appendage of the hood; *an* = stamen; *e* = empty glume; *fl* = floret; *fl′* = a second accessory floret; *g* = palea; *p* = pistil; *s* = spikelet; *t* = undifferentiated tip of the spike) lemma of the normally placed floret serves as the lemma of the accessory floret, no lemma is produced for the accessory floret. The first part to differentiate in the accessory floret is the palea, which appears as a ridge on the lemma of the normal floret above the accessory floret (Fig. 1, *F*, *g*). The palea, a leaflike structure, bears the flower parts (stamens and pistil) in its axil. This is the same relationship as in normal floret development.

It should also be pointed out that the accessory floret is not subtended by empty glumes as is the case with the floret of the normal spikelet in Fig. 1, *B*, *e*. Since there are no empty glumes present, the floral part of the hood cannot be classified as a spikelet, but must be considered as a floret.

Soon after the palea of the accessory floret differentiates, the stamens and pistil differentiate just as in normally placed florets. The successive steps in the anther differentiation are shown in Fig. 1, *G*, *an*; *H*, *an*; *I*, *an*; and *J*, *an*; and in Fig. 2, *C*, *an*. Successive stages of pistil development are shown in Fig. 1, *H*, *p*; *I*, *p*; and *J*, *p*. While functional pistils do not often develop in the floret of the hood, the pistil primordia are present and go through a part of their developmental cycle.

The description of accessory floret development has been for the central spikelets only. Hoods and their accessory florets also develop on the lemmas of the side spikelets (Figs. 1, *H*, and 2, *C*, *fl* and *fl′*). No hoods developed on the empty glumes of the plants grown for this study, but Harlan (1931) found them on the empty glumes of the progeny of certain crosses.

More than one floret may develop on the lemma. They may be located side by side (Fig. 1, *H*, *fl*) or above each other (Figs. 1, *J*, *fl′*; 2, *C*, *fl′*; 3, *A*, *B*, *fl*). The more basal floret is the one that attains the greatest development.

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**Fig. 2. Hoods and supernumerary spikes.**

**A.** Accessory florets on two side spikelets, showing the differentiation of pistils. ×25.

**B.** Base of a barley spike showing two supernumerary spikes; one in the position of the central spikelet and one in the position of the side spikelet. ×15.

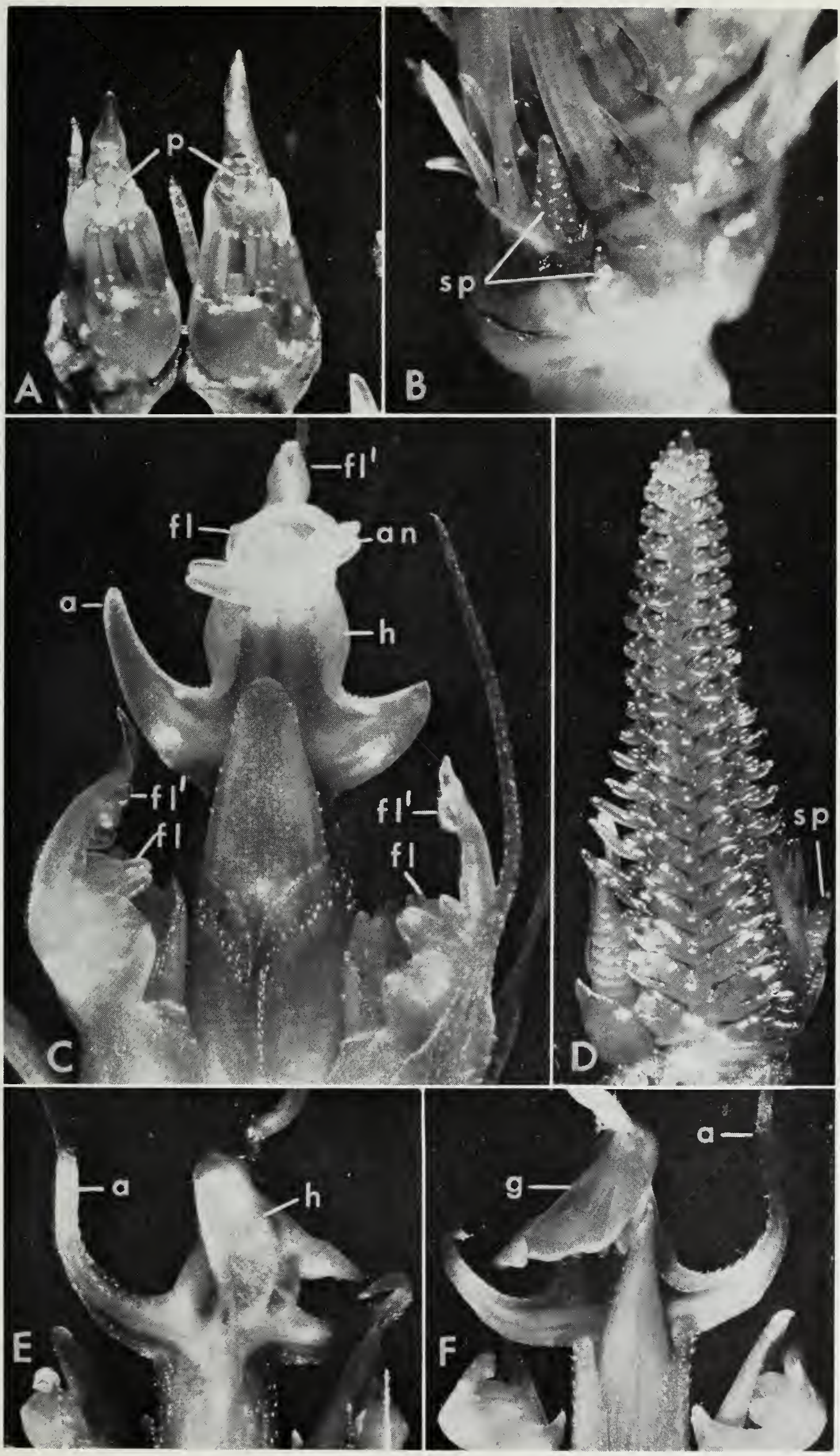
**C.** Adaxial view of central and lateral spikelets, showing two accessory florets on the lemmas, one above the other. ×17.

**D.** A spike of barley showing a supernumary spike on either side at the base. ×20.

**E.** An adaxial view of the hood of the accessory floret nearing complete development. ×8.

**F.** An abaxial view of the hood of an accessory floret. ×8.

(*a* = awn; *an* = stamen; *fl* = first-formed acccessory floret; *fl′* = second-formed accessory floret; *g* = glume; *h* = hood; *p* = pistil; *sp* = spike)



(Fig. 2)

Only three stamens develop in a normal floret and this is the usual number in the accessory florets. Some cases are shown (Figs. 1, *H*, *J*; 2, *A*; 3, *A*, *B*) where four stamens have developed.

Pistils begin development in the supernumerary florets of the side spikelets as well as in the central spikelets (Fig. 2, *A*, *p*). This observation is contrary to a statement made by Arber (1934) that the accessory florets of the side spikelets are male and only those of the central spikelets are complete.

Several stages in the development of the lemma into a structure resembling a hood are shown. In the earlier stages (Fig. 1, *K*) the abaxial side of the lemma resembles that of an awned variety except that the margins of the lemma protrude slightly at a point opposite the point of origin of the accessory floret.

The margins of the lemma continue to grow (Fig. 1, *L*, *a*, and *M*, *a*) and form a pair of awnlike points (Fig. 2, *C*, *a*; *E*, *a*; *F*, *a*). That portion of the lemma between the awnlike lateral projections continues to grow (Fig. 2, *C*, *h*) and serves as the lemma of the accessory floret. As maturity approaches, the tip of the lemma has the appearance of a hood (Figs. 2, *E*, *h*, and 3, *D*) with two lateral awnlike appendages (Figs. 2, *E*, *a*; *F*, *a*; 3, *C*, *D*).

### DEVELOPMENT OF SUPERNUMERARY SPIKES

Supernumerary spikes, in those barley varieties studied, differentiate at the basal nodes of the main spike (Figs. 2, *B*, *sp*, *D*, *sp*; 4, *A-F*; 5, *A*). They arise most frequently in the axil of the lemma of the central spikelets, but they may appear at the position of the side spikelets (Figs. 2, *B*, *sp*; 5, *C*, *D*).

Both the primary spike (Fig. 6, *sp*) and the largest supernumerary spike (Fig. 6, *sp′*) arise at the same node. At this node there is a normal leaf (Fig. 6, *l*). The spike (Fig. 6, *sp′*) is attached to a culm consisting of

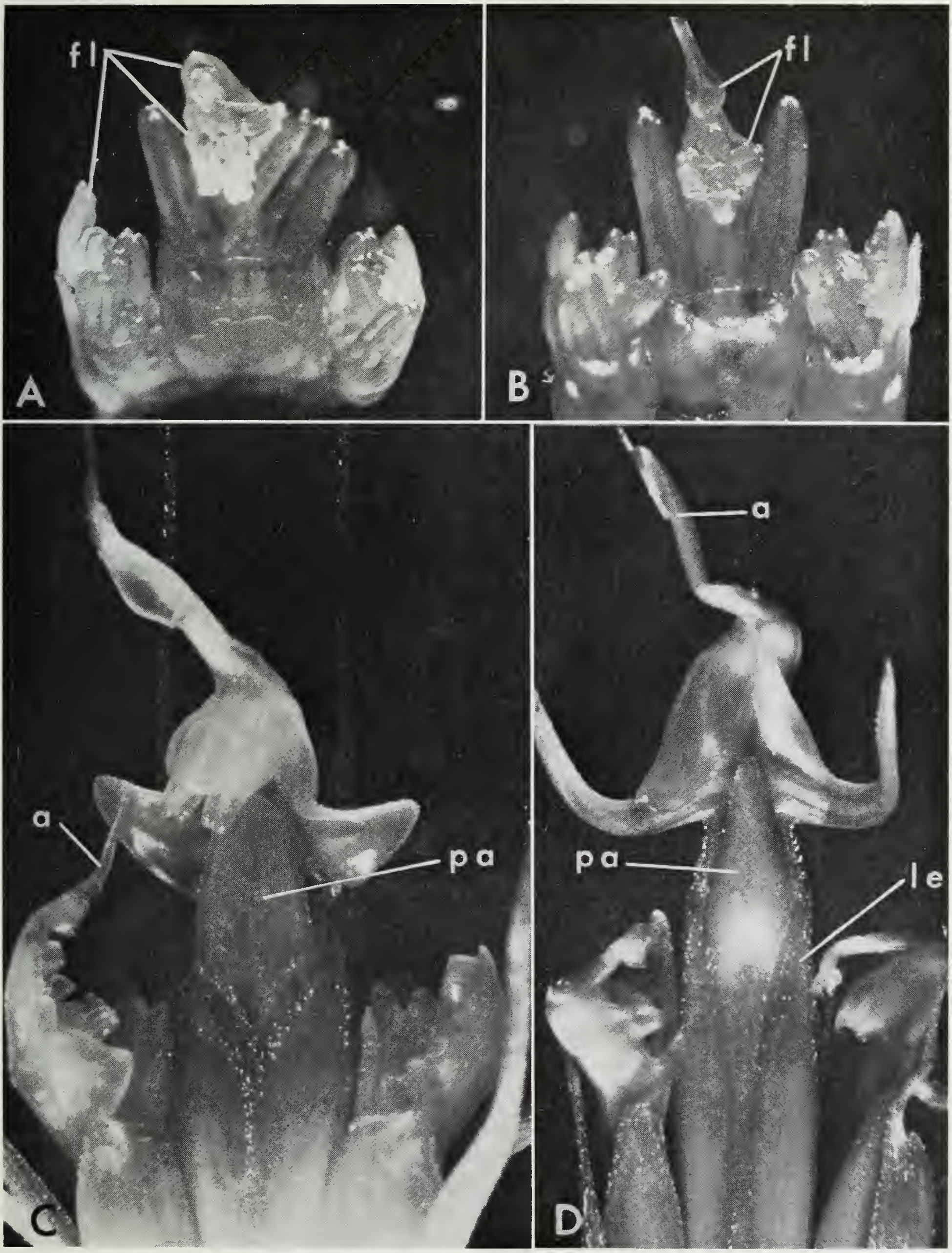
**Fig. 3. Hood development on the lemma of the florets of the central and lateral spikelets.**

**A.** Two accessory florets, one above the other, are shown on the lemma of the central spikelet. Initiation of accessory florets on the lemma of the lateral spikelets has begun. ×25.

**B.** The accessory floret on the lemma of the central spikelet has four stamen. ×25.

**C, D.** Advanced stages of hood development on the central and lateral spikelets. C, ×17; D, ×18.

All of the above photomicrographs are taken from the adaxial side of the spikelets. (*a* = awn; *fl* = flower; *le* = lemma; *pa* = palpa)



(Fig. 3)

three nodes. At the basal node the leaf is not normal but is biparted, one division of which resembles a prophyllum (Fig. 6, *l′*). Normal leaves are found at both the nodes above the basal one of the spike in Fig. 6, *sp′*.

The smallest supernumerary spike (Fig. 6, *sp″*) originates from the primary spike at the point usually occupied by the central spikelet (Fig. 2, *B, sp*). There is no indication of a prophyllum, but the empty glumes are present. On both sides of the smallest supernumerary spike (Fig. 6, *sp″*) are found the rudiments of spikes subtended by the empty glumes of the side spikelets.

The culm beneath the primary spike (Fig. 6, *sp*) is flattened and has three elongated internodes. The first internode of the primary spike has also elongated. No leaves were found at any of these nodes. The smallest supernumerary spike (Fig. 6, *sp″*) is attached at the second node.

## DISCUSSION

Opinions differ regarding the number of pairs of genes involved in the development of the hooded character. The majority of the investigators cited by Matsuura (1933) interpreted their results on a monogenic basis, but others said that two or more pairs of genes are involved. Regardless of the number of gene pairs, it may be of interest to discuss briefly what it seems would be necessary for the gene to do to produce the hooded character.

The description of the development of the accessory floret shows that it differs from the normally placed floret in its point of origin and in its pattern of development. The accessory floret originates as an outgrowth from the ventral surface of the lemma, a modified leaf, rather than from an axis. A normally placed floret has two flowering glumes, a lemma and a palea, but the accessory floret has only a palea since the tip of the lemma of the normally placed floret serves as the lemma of the accessory floret. Finally, at the point where the accessory floret differentiates, the lemma of the normally placed floret develops into a hoodlike structure with two lateral awnlike appendages.

If the pattern of development of the accessory floret were exactly like that of a normally placed floret, the gene action in the production of hoods could be rather easily explained. Every cell is believed to possess the same gene content as the fertilized egg, and since normal barley plants

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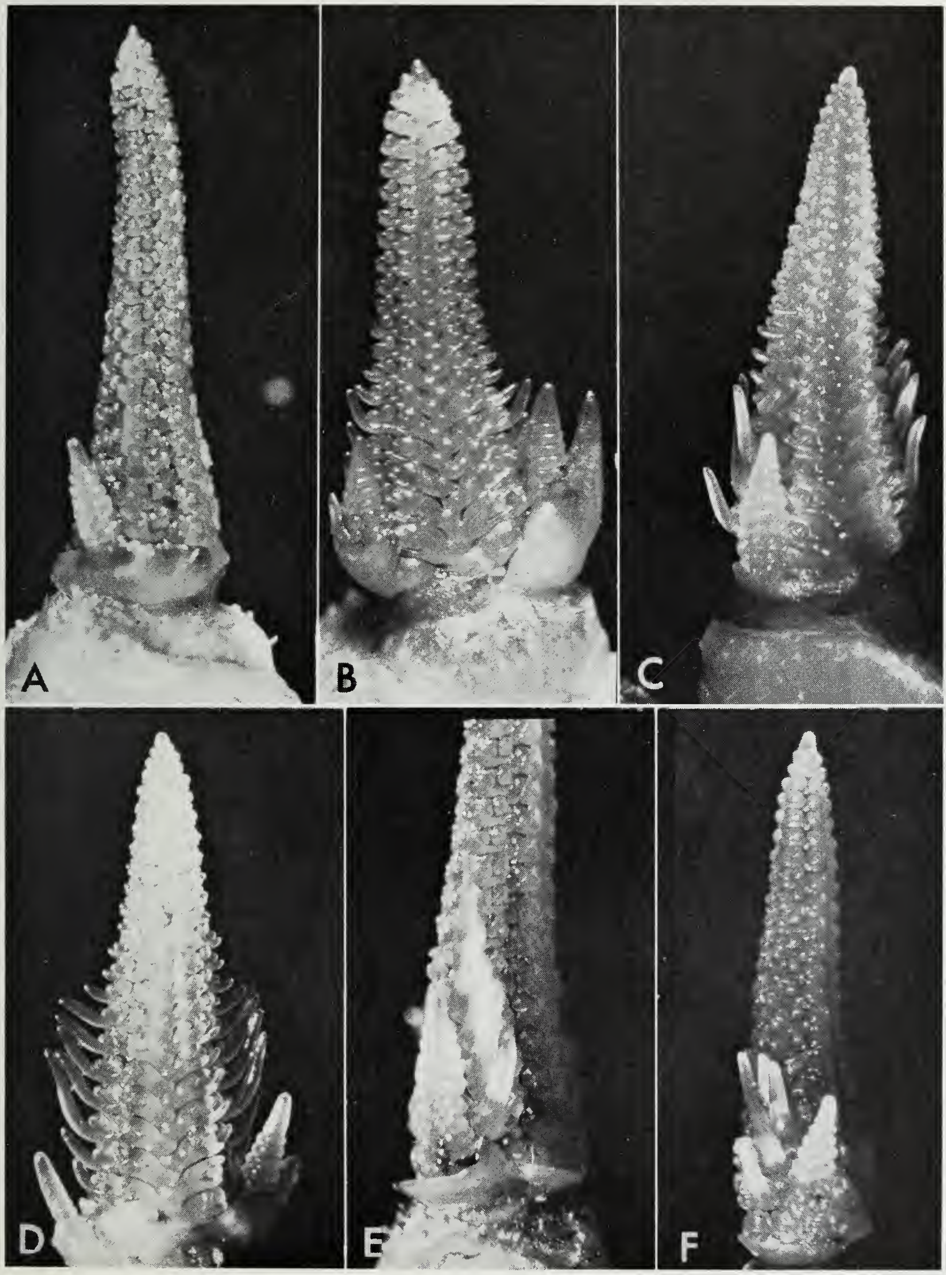
**Fig. 4. Early stages of supernumerary spike development.**

**A, B, E.** Photomicrographs of Spartan, a 2-row barley.

**C, F.** Spikes of Wisconsin Pedigree 5, a 6-row barley.

**D.** An $F_2$ progeny of a cross between Spartan and Wisconsin Pedigree 5.

A, B, D, ×20; C, E, F, ×23.



(Fig. 4)

have the ability to produce floral centers, all that the genes for hooded would need to do would be to initiate at the proper time, and at the proper point on the developing lemma, the production of a floral center. But, as has been pointed out, the accessory floret does not follow exactly the same pattern of development as the normally placed floret.

If a single gene or gene pair were responsible for the entire pattern of hood development, it would have to initiate the development of a floral center, inhibit the development of a lemma, and initiate the development of the hood and its appendages. While the explanation of the inheritance of the hooded character on a monogenic basis accounts satisfactorily for the ratio of the phenotypes in the $F_2$, the explanation does not fit so well in accounting for the morphological development of the character. It seems reasonable to require that the genetic assumptions account not only for the $F_2$ ratio but for the developmental processes as well.

Other deviations from the normal in the development of the accessory floret, such as more than one floral center on the lemma, four stamens instead of three, restricted pistil and awn development, need not be discussed. It is believed that these differences could be explained without the necessity of assuming the action of special genes.

The development of supernumerary spikes in the awned barley varieties previously mentioned is explained as the result of the action of environmental factors rather than as the result of the operation of special genes. During the period from December 19 to February 22 when the barley spike was differentiating, the temperatures were relatively low. The average maximum was 68.1° F., the average minimum 53.2°, and the average mean 60.8°. This period of time also included the short days of the year. It is believed that the low temperature and short days were principally responsible for the production of the supernumerary spikes. Such an assumption is in accordance with the results of the investigation of Hurd-Karrer (1933) with Turkey wheat; with an 8-hour day and low temperatures, Turkey wheat developed a branched head.

**Fig. 5. Supernumerary spikes at different stages of development.**

**A.** Base of a spike of Spartan, a 2-row barley, with a supernumerary spike on either side of it. Spikelet primordia are present in the supernumerary spike on the right but none is in the one on the left. ×35.

**B.** A portion of a normal leaf and spike. A prominent auricle, characteristic of the barley leaf, is shown at the base of the leaf blade, enlarged. ×2.

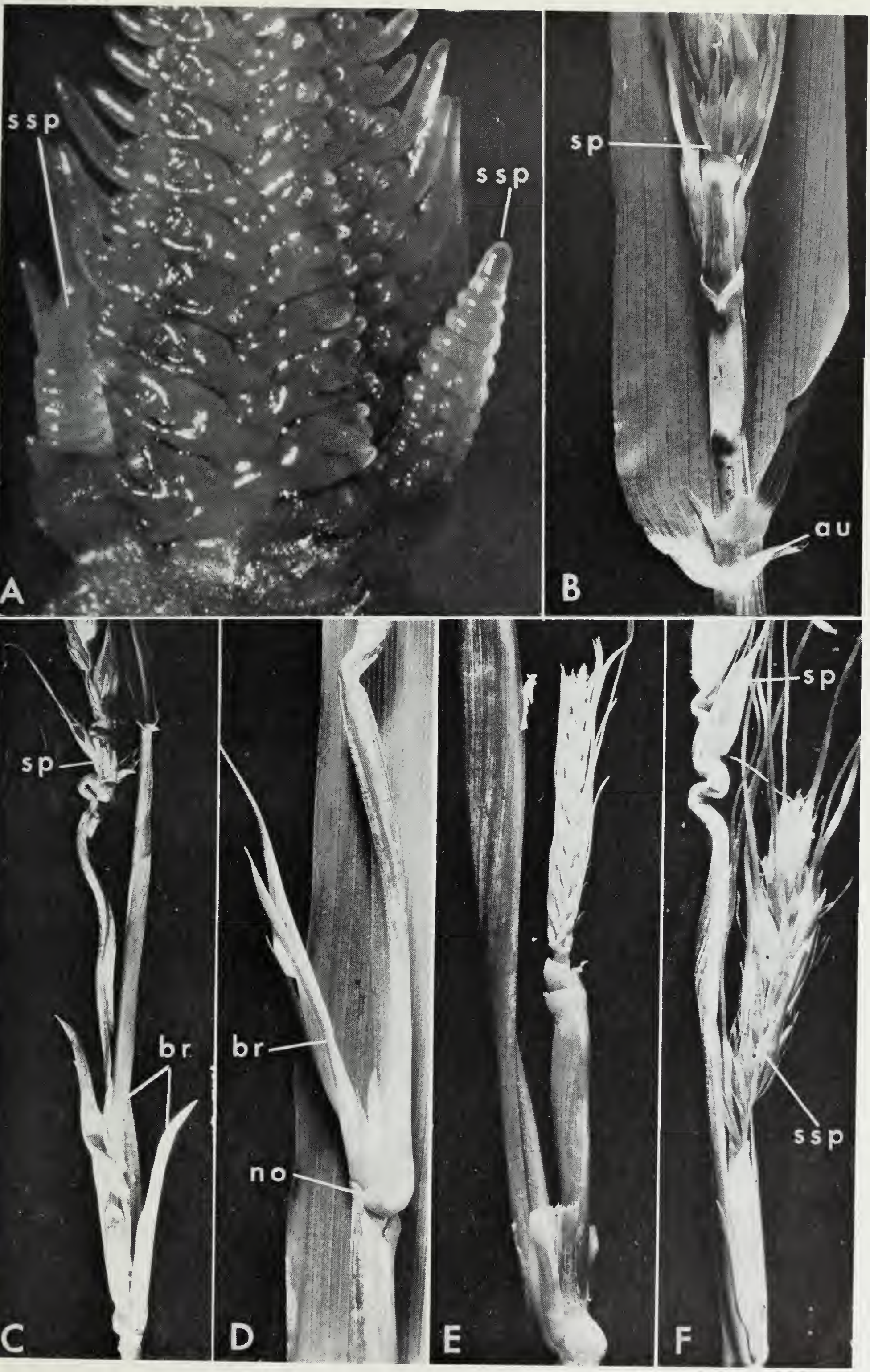
**C.** Branches at the first node beneath the spike. Natural size.

**D.** A branch containing the supernumerary spike shown in E. ×1½.

**E.** Supernumerary spike. ×1½.

**F.** Supernumerary spike with kernels in it. ×1½.

(*au* = auricle; *br* = branch; *no* = node; *sp* =spike; *ssp* = supernumerary spike)



(Fig. 5)

**Fig. 6. Primary spike and supernumerary spikes of barley at the mature stage.**
(*l* = normal leaf; *l'* = a biparted leaf; *sp* = primary spike; *sp'* = supernumerary spike originating at the same node as the primary spike; *sp''* = supernumerary spike originating at the second node of the primary spike)

## SUMMARY

The morphological changes which occur in the development of the hood in barley were studied by dissecting spikes at successive stages of development. Photomicrographs of the principal stages of development are shown.

Hood primordia first appear as dome-shaped outgrowths on the adaxial side, near the tip of the lemma, and from these primordia the parts of the accessory floret differentiate.

A lemma is not produced in the differentiation of the accessory floret since the tip of the lemma of the normally placed floret serves as its lemma. The first floret part to differentiate is the palea, followed in turn by the stamens and pistil as in normally placed florets.

More than one floral center may develop. They may be placed one above the other or side by side.

Although stamens and a pistil of the accessory floret may begin development, they usually are nonfunctional.

The tip of the lemma of the normally placed floret develops into a structure resembling a hood, and from the lateral margins two awnlike appendages develop. While an awn begins to develop at the tip of the lemma, its growth is suppressed by the growth of the accessory floret.

Supernumerary spikes were found to arise from the base of the primary spike. They probably resulted from the effect of a combination of low temperature and a short day.

Although most investigators explain the inheritance of hoods in barley on a monogenic basis, such an explanation is not entirely satisfactory when an attempt is made to explain how a single gene or gene pair could bring about the morphological changes necessary to produce the hooded character.

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# *Development of the Oat Panicle*

OATS (*Avena sativa* L.) DIFFER FROM THE OTHER COMMONLY GROWN small grains by having an inflorescence in the form of a panicle, while the inflorescences of wheat, barley, and rye are spikes. The panicle consists of a main axis with subdivided branches grouped at the nodes of the main axis. The arrangement of the groups of branches is alternate and the spikelets are pediceled (Fig. 4). On the other hand, the spike is an unbranched inflorescence in which the spikelets are sessile on the main axis.

A panicle differs from a spike in the plan of differentiation and development as well as in form. However, it is not the purpose of this paper to compare or contrast the development of the panicle with the development of the spike, but to illustrate and describe the principal stages in the formation of the oat panicle and floret.

Few descriptions of the development of the oat panicle have been published. Cannon (1900) studied the spikelet development of *Avena fatua* L., describing and illustrating various stages in the development of the floret and floret parts. He also studied the formation of the male and female gametophytes, fertilization, and the subsequent development of the caryopsis. The description of the development of the oat panicle given by Noguchi (1929) is brief and the paper contains only three figures. In addition to other grasses, Arber (1934) discussed the morphology of several forms of *Avena*. Two other publications of Bonnett (1961A, 1961B) describe the development and the histology of the oat plant.

## MATERIALS AND METHODS

The methods used in taking the photomicrographs in this article are similar to those described for barley (pages 59 and 60) and wheat (page 31).

Plants were grown in the field and greenhouse. They were sampled from time to time to obtain successively advanced stages of development. The panicles were dissected for study and photographing.

## DESCRIPTION OF PANICLE DEVELOPMENT

The oat stem, like that of wheat and barley (pages 36 and 61), passes through two stages in its development. In the first stage the shoot apex remains short, the leaf primordia differentiate, leaves grow, and tiller buds

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develop in the axils of the leaves at the base of the stem. During the second stage the internodes of the stem elongate, and the branches, spikelets, and flower parts differentiate and develop.

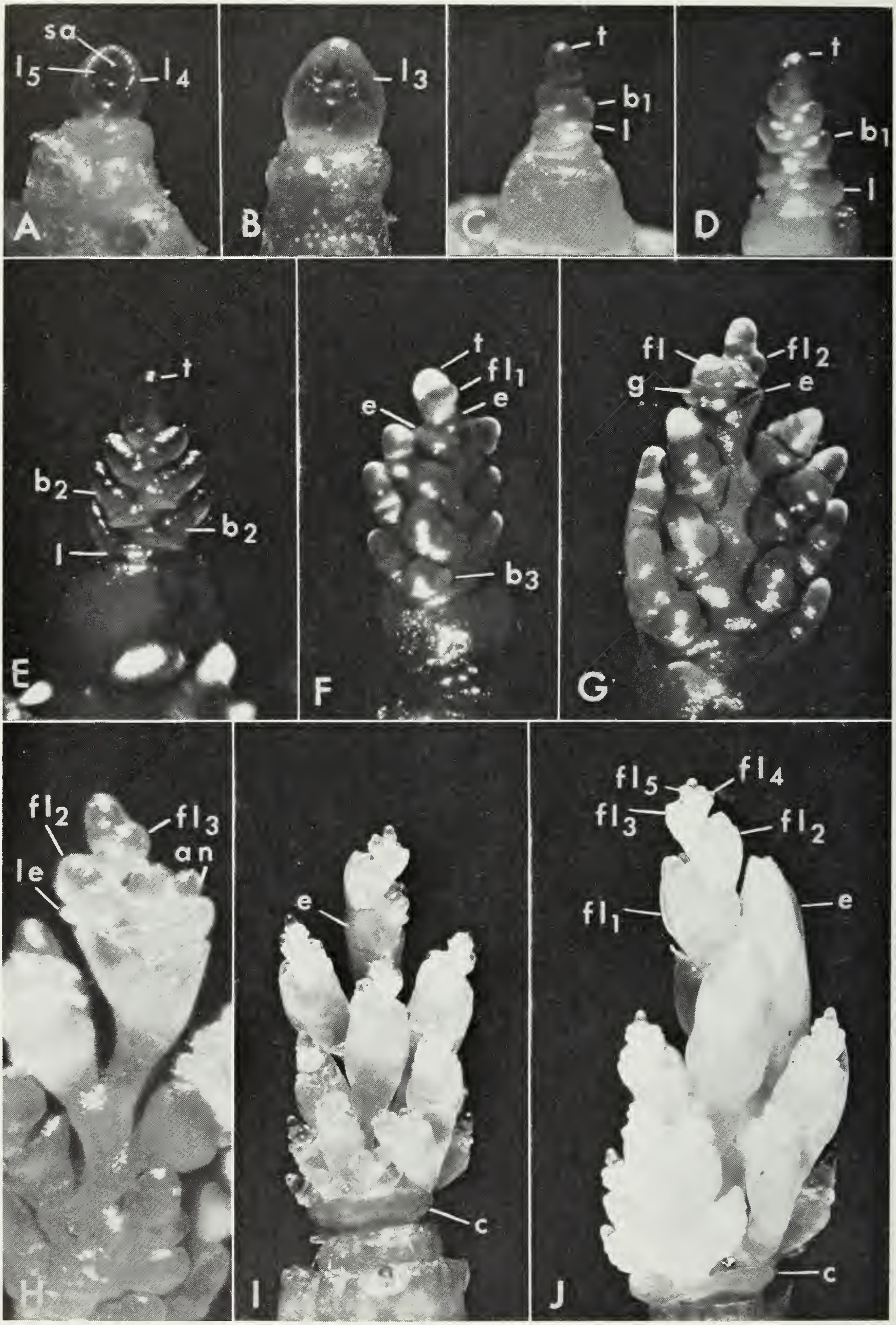
Two shoots (Fig. 1, *A*, *B*) show the first stage in the differentiation and development of an oat stem. The shoot apex in Fig. 1, *A* was removed from the stem of a plant showing two leaves. These two leaves and the third leaf primordium were removed to show the shoot apex and the position and size of the remaining leaf primordia. The fourth leaf primordium partly encloses the shoot apex, the fifth leaf primordium is seen as a ridge across the shoot apex, and the shoot apex itself appears as a smooth, rounded projection above the fifth leaf primordium (Fig. 1, *A*, $l_5$, and *sa*).

A more advanced stage in the development of a leaf primordium is presented in Fig. 1, *B*, $l_3$. The shoot apex with the fourth leaf primordium appearing as a ridge across it can be seen through the slit between the leaf margins. As growth continues one leaf margin laps over the other, and the blade becomes rolled.

An oat panicle, as above defined, is a many-branched determinate inflorescence consisting of a main axis from which arise lateral axillary branches which are grouped on alternate sides of the main axis at its nodes (Fig. 4). The main axis and each of the lateral branches terminate in a single apical spikelet. The oat panicle is therefore a determinate inflorescence. The branches have been designated as branches of the first, second, or third order depending upon their point of origin, i.e., whether they arise from the main axis (first order) or from the lateral branches (second or third order).

Previous to the differentiation of the branches of the panicle, the shoot apex elongates, but the elongation is not so marked as in barley or wheat. This difference between oats and barley or wheat lies, probably, in the difference in the number of nodes on the main axis of the inflorescence. The average number of "half whorls" of branches on the panicle of some oat varieties, according to Fore and Woodworth (1933), may range from 5 to 7, while a wheat or barley spike may have from 7 to 20 or more nodes. The averages mentioned vary according to variety and growth conditions.

Panicle formation is first indicated by the appearance of single, lateral, alternate projections (Fig. 1, *C*, and *D*, $b_1$) arising in the axils of leaf primordia (Fig. 1, *C* and *D, l*) beneath the apex of the shoot apex (Fig. 1, *C* and *D*, *t*). At first one or two and later several projections can be seen (Fig. 1, *D*). These are the primordia of the branches of the first order.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(Fig. 1)

The sequence of differentiation of the branch primordia of the different orders can be traced in Fig. 1, *C* to *F*. The differentiation of the branches of the first order has just been described. As the branch primordia of the first order increase in size at those nodes where many lateral branches are found, branch primordia of the second order appear beneath the apex and on alternate sides of the first (Fig. 1, *E*, $b_2$). In turn and in the same manner, primordia of the branches of the third order arise from the second (Fig. 1, *F*, $b_3$).

All the primordia of the lateral branches of the various orders arise in the axils of leaf primordia (Fig. 1, *C*, *D*, and *E*, *l*). The leaf primordia can be clearly seen at the basal nodes of the main axis (Fig. 1, *D* and *E*, *l*). The primordia become succcessively less distinct from the base of the main axis upward to the tip, and likewise they are less distinct on the branches of the second order.

It should be noted that all branch primordia arise beneath the apex of the parent axis (Fig. 1, *C* to *F*). The apex of the branch primordium is the region from which the spikelets differentiate; therefore new branches arise subapically from the parent axis. Branches elongate between the spikelet and their attachment to the parent axis.

Spikelet differentiation begins first with the spikelet at the tip of the central axis (Fig. 1, *F*, *t*) and proceeds basally in succession at the tips of

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**Fig. 1. Stages of panicle development.**

**A.** Leaf primordia and shoot of an oat plant in the two-leaf stage. ×40.

**B.** Leaf primordium nearly inclosing the shoot apex. ×40.

**C.** First stage of panicle development. ×35.

**D.** Early stage of panicle formation, showing several branch primordia. ×35.

**E.** A panicle at the beginning of the formation of branches of the second order. ×35.

**F.** A panicle at the beginning of the formation of branches of the third order. ×35.

**G.** A panicle at the beginning of spikelet differentiation. The primordia of the empty glumes and two florets of the apical spikelet are clearly shown. ×35.

**H.** The apical spikelet of the main axis enlarged. ×55.

**I.** Panicle showing spikelets in different stages of development. ×20.

**J.** The spikelets are partly enclosed by the empty glumes except the apical spikelet where the empty glumes have been removed to show the florets. ×20. (*an* = stamen; $b_1$-$b_3$ = branch primordia of first to third order; *c* = collar; *e* = empty glume, $fl_1$-$fl_5$ = first to fifth florets; *le* = lemma; *l* = subtending leaf primordium; $l_3$-$l_5$ = third to fifth leaf primordia; *sa* = shoot apex; *t* = tip of the central axis of the panicle) the primordia of the branches of the first order. At the nodes the sequence of spikelet differentiation is (1) branches of the first order, (2) branches of the second order, and (3) branches of the third order. To generalize, those branch primordia that differentiate first are the first to show the differentiation of spikelets.

The beginning of the sequence of spikelet differentiation can be seen in Fig. 1, *G*, by noting the more advanced stage of differentiation of the spikelet at the tip of the panicle in comparison with that of the two just below it. The branches at the base of the panicle have not yet shown any evidence of spikelet differentiation. Dehiscence occurs in the same order as spikelet differentiation.

Differentiation of the empty glumes is the first indication of spikelet development (Fig. 1, *F* and *G*, *e*). The pair of empty glume primordia first appear as prominent ridges, one slightly above the other and each half encircling the branch primordium just beneath the apex (Fig. 1, *F*, *e*). The meristem from which floret primordia are formed is irregular in outline and extends above the empty glume primordia. The empty glumes grow and enclose the developing florets (Fig. 1, *I* and *J*, *e*).

Within the spikelet the florets differentiate acropetally. The florets are alternate and attached to a short rachilla (Fig. 1, *H*, *J*, and Fig. 2, *F*). Floret primordia first appear as protuberances beneath the apex of the

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**Fig. 2. Stages in the development of the pistil, floret, and spikelet of the oat.**

**A.** An early stage of pistil and stamen development. ×50.

**B.** Stamens and the pistil at the beginning of the differentiation of the styles. ×50.

**C.** A pistil at the beginning of the elongation of the styles. ×35.

**D.** A later stage of pistil development. ×40.

**E.** A pistil showing the elongation of the styles and enlargement of the ovary. ×40.

**F.** A spikelet, empty glumes removed, to show the position and development of the florets and the awn on the first floret. ×20.

**G.** Floret with the lemma and one stamen removed. The styles have papillae, the primordia of the stigmatic branches, at their tips. ×40.

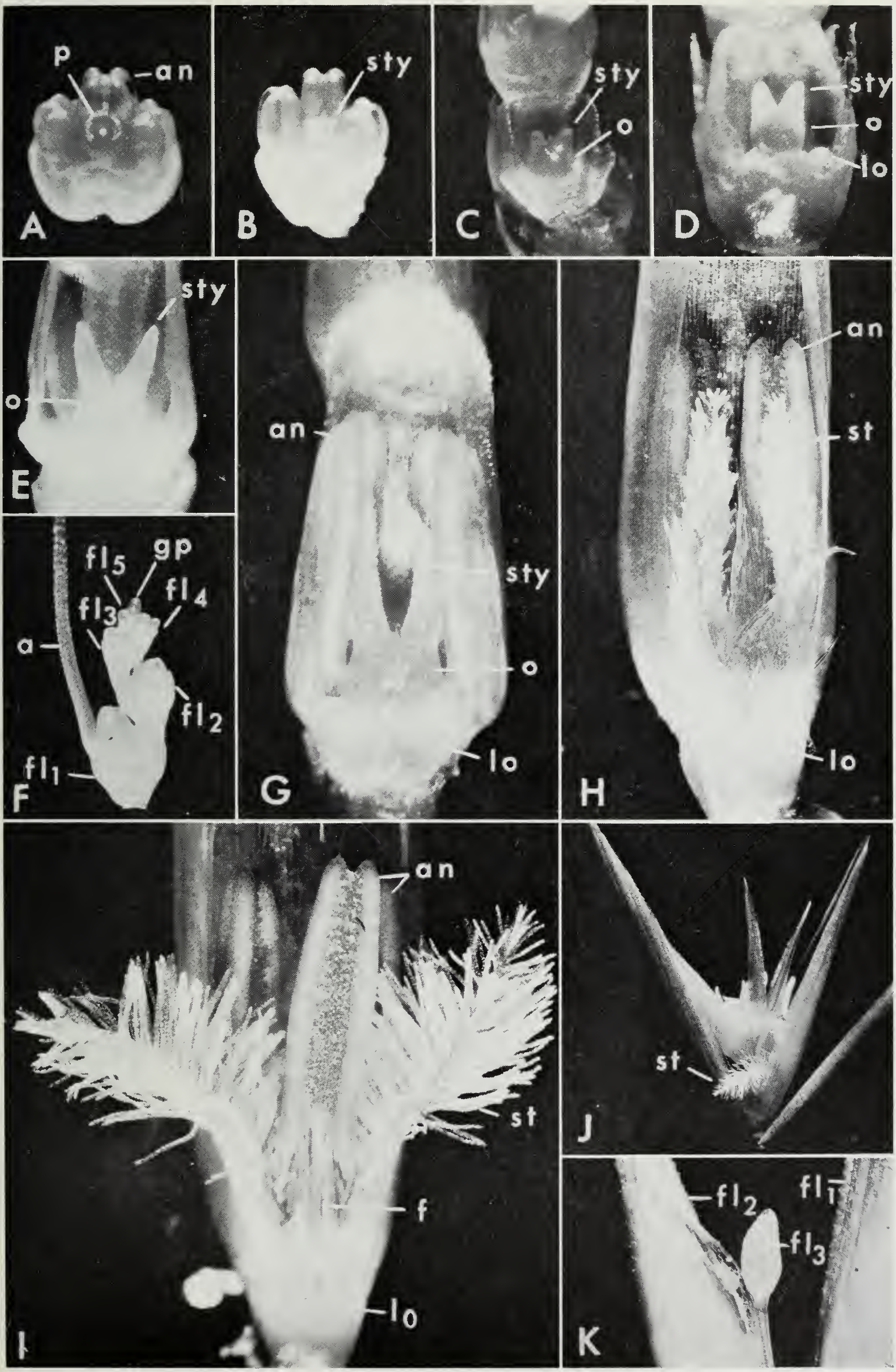
**H.** Oat flower, one stamen removed, showing the development of the lodicules and stigmatic branches. ×20.

**I.** A fully developed oat floret, lemma removed. ×15.

**J.** Unfertilized oat florets have opened for pollination. ×1½.

**K.** Sterile, rudimentary florets. ×8.

(*a* = awn; *an* = stamen; *f* = filament of the stamen; $fl_1$-$fl_5$ = first to fifth florets; *gp* = apex of floral axis; *lo* = lodicules; *o* = ovary; *p* = pistil; *st* = stigmatic branches; *sty* = style)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(Fig. 2)

shoot above the empty glume primordia (Fig. 1, *F*, *fl*$_1$, *G*, *fl*$_2$, and *H*, *fl*$_3$). The more basal floret is always more advanced in its development than those above it.

In the oat the basal floret and the next one above it are usually fertile, but the third floret does not often produce a kernel except for some varieties or in an especially good environment. While stamens and pistils differentiate in nearly all the florets, those stamens and pistils in all the florets above the second floret (Fig. 1, *J*, *fl*$_3$ to *fl*$_5$ and Fig. 2, *fl*$_3$ to *fl*$_5$) usually remain small and rudimentary. In Fig. 2, *K*, *fl*$_3$, the rudiment of the third floret is shown. The remainder of the infertile florets can be found in the folds of the lemma of the third flower.

The parts of the floret differentiate acropetally. First the lemma and then the palea appear as transverse ridges across the floret (Fig. 1, *G*, *g*, and *H*, *g*). Soon the stamens appear as small papillae above the glume primordia (Fig. 1, *H*, *an*) and finally the pistil differentiates from the meristem between the stamens at the apex of the floral shoot.

Very early in the development of the stamen the four chambers or locules can be identified. Even before the stage shown in Fig. 2, *A*, the anthers have separated from the meristem beneath them and filaments have formed. From this stage, as far as external appearances indicate, little change occurs in the anthers except an increase in size.

At the time that the three papillae or stamen primordia appear, a fourth papilla, the pistil primordium, can also be seen. At first the pistil shows no change except an increase in size.

Differentiation of the pistil begins with the formation of a ridge (Fig. 2, *A*, *p*). The ridge does not at first completely encircle the pistil primordium and is more prominent on the side next to the lemma. A papilla, the primordium of the ovule, can be seen in the opening between the ends of the crescent-shaped ridge.

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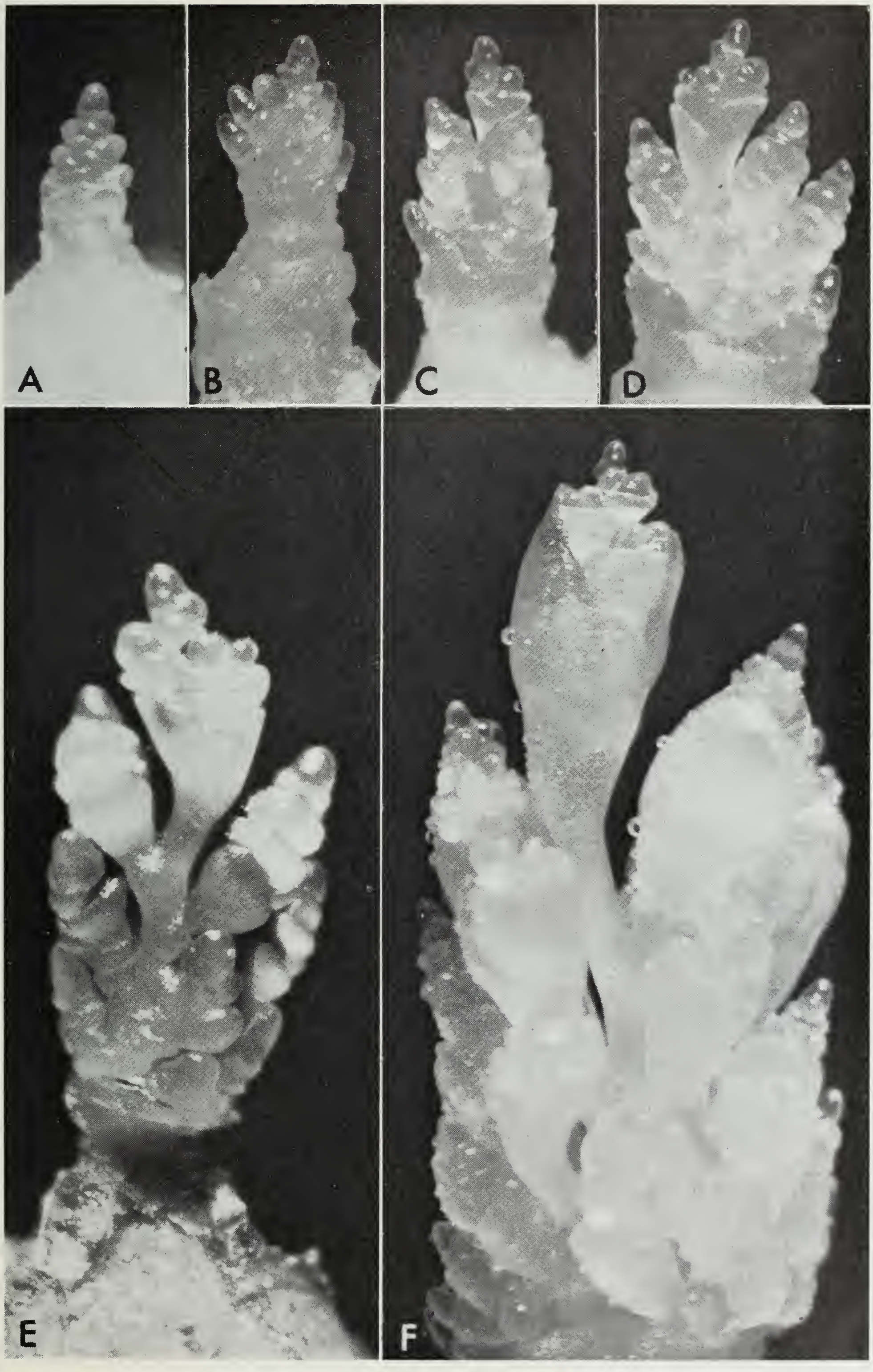
**Fig. 3. Stages of panicle development presented as a supplement to those of Fig. 1.**

**A.** Branches of the first order have been initiated. ×50.

**B, C, D.** Spikelet primordia are developing at the tip of the main axis and the branches of these panicles. Branches of the second order appear as rounded meristematic shoot apexes at the base of the panicles in C, D, and E. ×50.

**E.** Six groups of branches are shown in an alternate, distichous arrangement on the main axis. The apical spikelet is at right angle to the plane of the branches below it. ×80.

**F.** Spikelets at the top of the panicle are partly enclosed by the empty glumes. ×40.



(Fig. 3)

Pistil development is continued by the extension of the ridge entirely around the floral shoot, enclosing the ovule. The margins of the ridge on either side, opposite the laterally placed stamens, grow more rapidly than any other portions of the ridge. These two rapidly growing points are the style primordia (Fig. 2, *B*, *sty*).

Increases in the length of the style primordia and in the size of the ovary, and the closing of the opening above the ovule are shown in Fig. 2, *C*, *D*, *E*. The differentiation and development of the ovule cannot be followed in these illustrations, but the various stages of ovule development have been adequately described by Percival (1921) for wheat and Bonnett (1961) for oats.

**Fig. 4. A mature oat panicle. X½.**

The stigmatic branches are the last of the parts of the pistil to differentiate. They first make their appearance upon the styles as papillae (Fig. 2, *G*), increase in length (Fig. 2, *H*, *st*), finally attain full size and are covered throughout their length with projections which function as lodging points for pollen grains (Fig. 2, *I*, *st*).

Some of the stages in the development of the lodicules are shown, beginning with Fig. 2, *D*, *lo*. In the specimens shown in the photomicrographs of the earlier stages of floret development (Fig. 2, *A*, *B*, *C*) the lodicules were destroyed when the lemma was removed to expose the pistil. The lodicules first appear as blunt projections located on either side of the floret at the inner margins of the palea. They increase in size and become rounded at the base and pointed at the tip as shown in Fig. 2, *H*, *lo*, after which there is very little change.

The chief function of the lodicules is to force the lemma and palea apart and open the floret at anthesis by becoming turgid and thus increasing in size. This function is illustrated in Fig. 2, *J*, which is a spikelet taken from a plant grown in the greenhouse. Many times under certain greenhouse conditions viable pollen is not produced and unfertilized florets open day after day over a considerable period of time.

## SUMMARY

A study of the morphological development of the oat panicle was made by dissecting shoots and panicles from stems in different stages of development. The principal stages of development are shown in photomicrographs.

An oat stem passes through two stages of development. In the first stage leaves and tillers are produced, and in the second stage the internodes of the stem elongate and the panicle and its parts differentiate and develop.

Panicle formation is first indicated by the appearance of single, lateral, alternate projections arising in the axils of leaf initials beneath the shoot apex. These projections are the primordia of the branches of the first order.

Branches of the second and third order are produced from the parent axes in the same manner that the branches of the first order are produced from the main axis.

Spikelets differentiate from the tips of the branch primordia. Spikelet differentiation begins first at the apex of the main axis and proceeds basally on the branches of the first order and in sequence on the branches of the second and third orders.

The empty glumes are the first of the spikelet parts to differentiate. The florets of a spikelet differentiate acropetally.

Floret parts differentiate in the folowing order: lemma, stamens, palea, lodicules, and pistil.

Ovary, styles, and stigmas is the order of differentiation of the parts of the pistil.

Since the main axis and all branches terminate in spikelets, a panicle can be called a determinate inflorescence.

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# *Relation Between Numbers of Spikelets and Florets and the Developmental Pattern of the Inflorescence of Cereals*

THE TOTAL NUMBER OF FLORETS AND THE NUMBER OF FERTILE FLORETS that an inflorescence will have are determined to a large extent by the type and the developmental pattern of both the inflorescence and the spikelet. These relationships, which are described in more detail below, can be summarized as follows:

| | *Inflorescence* | | *Florets per spikelet* | | *Spikelet* |
|---|---|---|---|---|---|
| *Crop* | *Type* | *Growth*[a] | *Number* | *Number fertile* | *When number is determined* |
| Wheat | Spike | Determinate | Many | Two or more | At spike initiation |
| Rye | Spike | Determinate | Many | Two | At spike initiation |
| Barley | Spike | Indeterminate | One | One | Potential not fixed |
| Oats | Panicle | Determinate | Many | Two or more | Potential not fixed |
| Maize | Panicle-raceme | Indeterminate | Two | One | Potential not fixed |

[a] Determinate means main axis terminates in a spikelet; indeterminate, main axis does not terminate in a spikelet.

The spike is an unbranched inflorescence with a single spikelet at each joint of the rachis. The spikelets are alternate and arranged in two ranks. In some spikes the rachis terminates in an apical spikelet; such spikes are determinate. In other spikes it does not; these spikes are indeterminate. The spikes of wheat and rye are determinate. When the spikelets of wheat or rye are initiated, all the spikelets of the spike have been differentiated. The barley spike is an indeterminate spike. Barley spikelets are first initiated near the middle of the spike, and spikelet initiation proceeds toward the base and toward the tip of the spike. When the first spikelets are initiated near the middle of the spike, a portion of the tip is still undifferentiated. More spikelets can be initiated at the tip of the spike but the degree to which the potential can be realized has not, so far as known, been investigated. Sterile spikelets are found at the tip of the mature barley spike, but the variation in their number among different varieties or in different years is not known. Rudimentary sterile spikelets at the base of the spike are typical of wheat, rye, and barley; the number varies with the variety and with the growing conditions during the differentiation and development of the inflorescence.

The oat panicle is a branched inflorescence terminating in a spikelet at the tip of the main axis. The panicle develops from the tip downward. Branching starts with first-order branches originating on alternate sides of the central axis. First-order branches give rise to second-order branches, second-order branches to third-order branches, etc. Each branch, whatever the order, terminates in a spikelet. The amount of branching of the different orders increases from the tip downward, so that the greatest potential is in the branching at the base of the panicle. In some varieties of oats, the branches at the basal node may have one-third or more of the total number of spikelets in the panicle.

In maize the main axes of the ear and tassel and the lateral branches of the tassel are indeterminate. The ear is a thick, round symmetrical axis. Development of the ear begins with the initiation of spikelet-forming branches around the circumference of the base of the ear primordium. Each of the spikelet-forming branches divides to produce two spikelets. Development of the spikelets proceeds toward the tip of the ear (acropetally). The number of spikelets that an ear will have is determined first by the number of spikelet-forming branches, hence pairs of spikelets, formed around the base of the ear, and second by the number of spikelets per row. Both the row number and the spikelets per row will vary with the type and the growing conditions. The factors controlling row number other than genetic (8-row (flint), fasciated, etc.) are not clearly understood. The chief cause of variation in row number within a type is in doubt.

The developmental characteristics of the spikelet are also an important factor in determining the potential number of fertile florets that an inflorescence will have. In common wheat, the spikelet is multiflorous with the possibility of producing several fertile florets per spikelet, usually two but sometimes as many as five. Common rye also has a multiflorous spikelet with as many as six florets initiated, but only the two basal florets are ever fertile. Barley has a single floret in each spikelet and three spikelets at each node of the rachis. In 6-row barley all three spikelets at each node of the rachis have a fertile floret, but in 2-row barley the floret of the center spikelet is the only one that is fertile.

Cultivated oats initiate five or more florets per spikelet. Usually the basal two and sometimes three florets are fertile, and the remainder abort. The oat spikelet is similar to that of wheat and rye in that at initiation it is multiflorous. However, the potential number of fertile florets is more limited than in wheat but less than in rye.

In maize the number of fertile florets per spikelet is limited. A distinguishing characteristic of maize is that it produces only two florets per spikelet. Only the terminal floret is fertile, except in types like Country Gentleman sweet corn in which both florets are fertile.

In addition to the effect of the developmental patterns on the number of potential and functional spikelets and florets, there is a critical time period when the maximum effect of the growth factors occurs. Effective growth with respect to the number of spikelets and florets must take place within this time period.

The number of spikelets and florets is increased or decreased in conformity with the developmental pattern. Indeterminate inflorescences such as maize or barley can increase the number of florets by adding spikelets at the tip of the spike, but the number of florets per spikelet is fixed. Determinate inflorescences such as those of wheat and rye cannot increase the number of spikelets after spike differentiation; both initiate multiflorous spikelets but the number of fertile florets per spikelet in rye is two, leaving only wheat with the potential of having many fertile florets in a spikelet.

Oats have a determinate inflorescence, and the spikelet usually has only two fertile florets per spikelet. But oats have the ability to increase the number of spikelets by producing branches of a higher order from branches of a lower order. When adverse growing conditions occur after the spikelets and florets are differentiated, many of them fail to develop and set seed.

The rudimentary spikelets will be the last to be differentiated. They are the spikelets or florets with the least chance to produce seed. Rudimentary spikelets are found at the tip and base of wheat, rye, and barley spikes and among the higher-order branches at the basal node of the oat panicle and at the tip of the maize ear. As adverse growing conditions intensify, the order of sacrifice is in reverse order of initiation, so that the last to succumb are those that were first initiated.

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