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THE PHYTOMER IN RELATION TO FLORAL HOMOLOGIES IN THE AMERICAN *MAYDEAE*

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THE structure of the inflorescences in the American *Maydeae* (maize or *Zea Mays* L., teosinte or *Zea mexicana* (Schrad.) Reeves and Mang.¹, and *Tripsacum* spp.) may be the result of developmental modifications to a repetitious pattern of organs, the "phytomer," which is basic throughout the entire plant. The parts of this pattern, as described later, have been recognized in vegetative form as an internode, a leaf, and an axillary bud (Gray, 1879 and others), and, recently (Galinat, 1956), as another organ, the prophyll.

If the phytomer and its components have a floral manifestation, then their basic homologies might be revealed by anatomical comparisons within any plant and with close relatives. Such comparisons have been successful in demonstrating the evolutionary development and homologies of certain floral structures such as carpels, compound ovaries and inferior ovaries.

We have already had some such studies in maize. The arrangement of large and small bundles has been de-

¹This new name was proposed in 1942 and has been used regularly by its authors in a recent series in these Leaflets (Vol. 18, Nos. 7, 8, 9 and 10).

scribed in the ear (pistillate rachis) and in the tassel (staminate rachis) by Reeves (1946, 1949) and Laubengayer (1948, 1949); in the tassel alone by Kumazawa (1939); and in the culm (stalk) by Esau (1943) and others. Certain bundles in the ear have been suggested as representing those of a lateral organ (the prophyll) which is fused to the main axis or rachis (Nickerson, 1954). These previous studies are largely descriptive, interpretations being difficult because the tissues and vascularization in maize was not compared with those of its close relatives; nor was the anatomy of the rachis considered as a possible reflection of the structure of the culm. The present study attempts to examine the evolution and development of the maize plant in terms of modifications, according to function, of the organs in a single basic pattern, the phytomer.

In addition to typical maize (sweet corn inbred Purdue 39) and its relatives, teosinte (race Durango) and *Tripsacum dactyloides*, two special maize-types were included in this study. One of these is a derivative from a maize-teosinte hybrid specifically bred for a simplified version of the vascular system which could be represented in three dimensions. This breeding was done by selecting a slender, four-ranked ear with greatly accentuated cupules² which were free from the usual crowding and distortion. Reduced condensation to remove vertical compression between the cupules was derived from Guarany maize. Enlargement of the lateral wings of the cupules, a character associated with spikelets oriented in the same plane as that of the rachis (Galinat, 1956), was introduced from teosinte. Pairing of the spikelets, a characteristic of maize, further accentuated the cupules by spreading out the lateral wings. The other special

²Corneous alveoli of the maize cob immediately above the attachment point of each pair of pistillate spikelets (Sturtevant, 1899).

maize type was a heterozygous tunicate (*Tu/tu*) strain of Argentine popcorn.

The material was prepared for staining by two techniques. One of these is a somewhat unusual method similar to that suggested by Cutler and Cutler (1948) as follows:

Intact spikes (ears) were stained at the time of style emergence by placing their freshly cut bases in an aqueous solution of safranin. In a few seconds this red stain had traveled up through the vascular system and had colored all of the xylem elements. Attempts to preserve this stained material by fixing it in (3:1) absolute alcohol: glacial acetic acid and then clearing it in a cedar wood oil series were unsuccessful because the color always diffused out from the bundles and into the adjacent, highly lignified rind; but, in less lignified material, such as that of typical maize, this clearing technique was successful in revealing the vascularization of specimens stained intact. It was later discovered that, if our stained specimens were immediately dried by warm, circulating air, the red color then remained in the bundles. Free-hand, three-dimensional drawings were then made from studies of the vascular system, as revealed on the exterior of these dried and intact specimens and as reconstructed from cross-sections of the same material.

The other method used is a classical one. The material was fixed eighteen days after pollination, then dehydrated in an ethyl-alcohol series and embedded in paraffin for cross-sectioning and eventual staining. Although no difficulty was encountered with microtome sectioning in the case of the maize, the teosinte and *Tripsacum* specimens were too highly lignified at this age for easy cutting. However, a few excellent free-hand sections of only about one cell-width in thickness were obtained from the embedded material of these relatives of maize. All sections

were stained by the safranin-fast-green technique. A projection apparatus was used in making tracings from comparable slides.

Pulvini swellings from the axils of tassel branches of P39 maize were also sectioned, stained and projected in a manner similar to that used for the ears, because these small axillary protuberances appeared to represent another possible homologue of the prophyll. They were at maximum swelling when collected at the time of anthesis.

THE NATURE OF THE PHYTOMER

Continuity of the phytomers. The phytomer, like the cell, was once considered to be the "true individual." But now the plant as a whole is usually recognized as the individual, and the term "phytomer" is used to describe the level of organization represented by one repetition of its specialized regions or organs. The boundaries of the phytomer, and of the organs which compose it, are only approximate. Neither vascularization nor disarticulation delimit a discrete phytomer (Arber, 1934). Also such a unit is not necessarily delimited by the order of maturation, as in the classical segmentation of the phytomer used by Evans and Grover (1940) and others, because the degree and order of development of its various organs differ during vegetative and floral growth.

In order to simplify comparison of its various manifestations, we have chosen a phytomeric cycle comprising the group of organs which are adjacent to a given node or apparent node, as in the inflorescence where the nodes are usually obscure. This combination includes the leaf borne just below the node and its axillary bud with associated prophyll just above the node, as well as the adjacent internode (Plate I). The more classical delimitation of the phytomer at the nodes includes a leaf and bud

which are isolated at opposite sides and opposite ends of an internode. Our grouping is more convenient for floral comparisons, especially when the internodes are telescoped: the axillary buds are either closely associated with or fused to their subtending leaf or leaf rudiment, and the lateral organs are whorled, as in the maize ear.

Repetition of the phytomer. Control over the number of repetitions of the phytomer, as well as their individual manifestation, usually seems to follow a functional pattern which is characteristic for a certain portion of the plant. In the lower parts of the plant, all organs of the phytomer are large, photosynthetic structures (Plate I, A), while in the highly compacted inflorescences, their counterparts may be reduced or entirely obliterated (Plate I, B through F).

The typical course of repetition by the phytomer in a given area of the maize plant may be changed by unusual genetic and/or environmental conditions. In short-day maize, as in other photoperiodic plants, the number of repetitions by vegetative-type phytomers and the time of change to a floral-type of manifestation is controlled by length of day. Also the production of vegetative phytomers by axillary buds, as well as the abruptness of their ultimate shift to a floral manifestation, seem to be controlled by the corn-grass (*Cg* gene) locus. At least four other genes control the production of phytomers at specific points in the inflorescence, as follows:

The primary branches (rachids), *ramosa* 1, 2 (*ra*₁, *ra*₂) on chromosomes 7 and 3;

The spikelets, branched-silkless (*bd*) on chromosome 7;

The florets, polytypic (*Pt*) on chromosome 6.

GROSS STRUCTURE AND MANIFESTATION OF THE PHYTOMER

Evidence of homologous relationships based on gross

structure must rely largely on a study of developmental and evolutionary variations in the manifestation of the phytomers. Discussion of such variations will orient the floral expression of the phytomer and, thereby, aid in identifying the vestiges of certain reduced parts.

Leaves. Although the leaf of the vegetative phytomer is enlarged for maximum photosynthetic activity, the floral homologue is reduced and modified according to the protective device characteristic of the species, as well as according to the order of the axis on which it is borne. At the base of the maize tassel as a whole, or sometimes at the base of each tassel branch, the subtending leaf is usually reduced (Plate I, D-1), although it may undergo all degrees of development (Galinat, 1954a). In the "central spike" of the tassel or rachis and corresponding axis of the ear, the leaf initials are usually inhibited except for a possible rudimentary leaf, the "glume cushion," at the base of the glumes. But this leaf may be well-developed in certain bamboos (Holtum, 1956), in *Coix* (where it has a protective role) and in the corn grass and teopod mutants of maize (Galinat, 1956). On the spikelet axes or rachillas, the blade-parts (laminas) of the first two leaves (glumes) are rudimentary, but in the case of the third and fourth leaves (lemmas), single genes may cause the blades to develop as awns in the "bearded" varieties of small grains, or the blades may be stimulated to complete development in proliferated spikelets.

Axillary buds and internodes. The axillary buds represent the starting points for the internodes of new axes of lesser orders. Certain variations in their derivatives (tillers, ear-shoots, tassel-branches, spikelets, florets) demonstrate the homology of the buds concerned and of the internodes of their ultimate axes. This is especially apparent in the various intergrading branches of the mutant "corn grass," which is characterized by a gradual

transition from a vegetative shoot to a reproductive one rather than the usual abrupt change (Galinat, 1954b). Spikelets may be converted into "tassel-plantlets" as an "after-effect," resulting from an insufficient number of short-days during the early floral development of short-day maize (Galinat and Naylor, 1951). The growing point of the spikelet-axis or rachilla may shift from "cutting-off" floret primordia to that of initiating spikelets as this axis becomes the rachis of an ear enclosed by husks modified from glumes and lemmas (Weatherwax, 1925). Finally, during the evolution of the maize ear, either a tassel branch or a spikelet from the tassel seems to have been modified as a tiny, sub-tassel ear which later descended to a more efficient position on the stalk, where it could increase in size (Mangelsdorf, 1958).

Prophylls. The prophyll-part of the phytomer is a two-keeled, leaf-like organ which develops at or near the axil of a lateral bud. Its two-keeled form may result from its being pressed between the branch axis and parent axis during early development (Arber, 1934). Pressure between binding leaf-sheaths and their expanding axillary buds and associated prophylls is known to be responsible for the initiation of permanent grooves in the internode of the parent axis, and, in some bamboos, this channel retains the imprint of the prophyll, even after it has been left behind by the elongation of the internode (Arber, 1934). It is apparent that the prophyll occupies the most crowded position in the phytomer, especially along the rachis, where it is either absent or highly modified and reduced. But when the position of the floral prophyll is moved away from the rachis to a less crowded position in the ultimate branches (florets), it then develops fully as the so-called "palea."

The problem then is to identify the anatomical remains of the prophyll at or near the axil of a branch within the

phytomers of the rachis. Two independent theories have been proposed for the role of the prophyll in the development of the ear and tassel of maize. Nickerson (1954) suggested that the cupule in the ear was formed by a prophyll depressed into and adnate to the rachis, except for the auricles which produce laterally as "rachis-flaps." In the tassel of maize, which lacks cupules, as well as in the paniculate rachises of other grasses, the primordial prophyll may have been contained as an axillary swelling (the pulvinus) which has become specialized to function in spreading the primary branches at the time of anthesis (Galinat, 1956). Arber (1934) has noted that the inflorescence branches of many grasses have such axillary pulvini, which expand at the time of anthesis so as to force the branches outwards; and, after anthesis, the swellings usually wilt as the branches again rise.

INTERNAL ANATOMY AND MANIFESTATION OF THE PHYTOMER

Although the homologies of certain reduced and modified organs in the floral phytomer may not be apparent externally, their basic nature may lie hidden in some part of the internal anatomy, such as that of the vascular system. An anatomical study, therefore, may help to establish the anatomical remains of the prophyll at certain of its potential positions which are occupied by other excrescences, such as the cupule in the ear and the pulvinus in the tassel.

Vascularization in maize. The homology of the floral and vegetative internodes is reflected by a close similarity in their vascular systems. Certain modifications in vascularization of the ear are caused by the reduction and compaction of lateral organs. Since vascularization in the tassel is so similar to that of the culm (Kumazawa, 1939), it will be excluded, except in regard to the pul-

vinus, from these comparative studies. The bundles of both axes tend to be of two distinct diameters which are separated into two locations (a "meristele" arrangement). Those bundles with the smallest diameters lie adjacent to the rind or lignified periphery of the axis which, in the case of the (pistillate) rachis, is repeatedly parted into the wings of numerous cupules (Plate II, fig. 1). The bundles of the large diameter are scattered throughout the pith of the culm, but, in the rachis, they are usually concentrated near the margins of the pith, where they supply the longitudinal rows of traces to the lateral spikelets, even though a few "cauline" bundles may be isolated in the center of the pith.

The diameter and position of an individual bundle is different in various parts of the plant. The larger trace-bundles, which extend horizontally from a leaf, curve downward from the leaf-node and then extend through about six internodes as they decrease in thickness and slope outward before connecting to the peripheral bundles. In the smaller trace-bundles, on the other hand, such connections occur progressively earlier in the descent, the smallest bundles remaining free for only one internode or less. As these leaf-traces descend, they supply the axillary buds along the way by means of lateral connections to a network of horizontal bud-traces slightly above each leaf node.

The glume cushions, which seem to be rudimentary leaves of the rachis, are vascularized by small bundles descending to the rind-bundles in the cupule wings below. Inasmuch as the apical end of these bundles connects with the vascular supply to the outer glumes of its axillary spikelets (Plate II, fig. 1) rather than terminating as stubs, they would appear at first to be "rind-bundles"; on the other hand, they could be rudimentary leaf-traces which have become folded inward and fused

to the glume supply. In any case, the actual elaboration of the glume cushion into a well-developed leaf under certain conditions mentioned previously seems to leave little doubt about the homology of this rudiment.

The suppression of the primary leaves along the rachis is associated with a loss of the nodal plates and differences in trace connections from the axillary buds. These traces from the binate spikelets of the rachis fan out to the nearest group of "common" bundles (Plate II, fig. 1) rather than connecting through a vascular network extending to the entire meristele, as with the axillary buds along the culm.

Nature of the bundles in the cupule wings. The evidence from vascular anatomy does not support the suggestion of Nickerson (1954) that the bundles in the cupule wings are those of a prophyll adnate to the rachis. Although the bundles located near the lateral edges of the out-folded wings of a typical cupule do have a xylem-phloem orientation opposite to that of the larger bundles within the rachis, if one follows inward along the series of bundles in such wings, the orientation of each bundle is found to twist gradually, so that the innermost ones have the same orientation as the larger bundles (Plate III, fig. 1). This twisting of bundles suggests that the cupule wings are formed in part by a gradual folding out of flaps dislocated from the rind of the rachis. Further evidence in support of this view comes from the two-ranked spikes of our teosinte-derivative of Guarany maize. The wide spacing of the cupules in this stock reveals that the rind from the barren rachis has exactly the same vascular pattern as that in the cupule wings, and that the tissue at the back of the cupule is devoid of these small bundles (Plate IV, fig. 2). It seems, therefore, that the portion of the cupule wings which includes the vascularization is derived from the rind of the rachis.

The cupule lining in relation to the pulvinus. Evidence that the wings of the cupule consist of more than just a flap of the rind comes from the experimental in-folding of these structures. When these wings are bent over into the cavity, as can be seen in the diagram of the teosinte derivative (Plate IV, fig. 2), the reconstituted axis resembles more closely the structure of the pulvinus and associated axis (fig. 1) than it does that of the culm (fig. 3). The resemblance of this wing-filled cupule to the structure of the pulvinus is revealed by close similarities in size, position and numbers of cells in the areas concerned of a sweet-corn inbred (Purdue 39). Although the total number of cells extending from the large (common) bundles outward through the center of the cupule combined with those through a folded-in wing exceeds by about thirty cells the growth which occurs between the large bundles and the epidermis of the barren rachis between the cupules (Plate III, fig. 1), it nonetheless corresponds almost exactly in number and size of cells with those which occupy the corresponding position through the pulvinus (Plate V).

Evidence of a relationship between the pulvinus and cupule lining may also be shown by a hypothetical manipulation of the pulvinus into a cupule. Starting with the pulvinus (Plate IV, fig. 1), if one visualizes a central split perpendicular to the epidermis extending inward to a point just beyond the small bundles and then diverging in both directions along a line parallel to the epidermis for the width of the pulvinus, then the flaps therein dissected will resemble in-folded wings of a cupule. By folding these wings out laterally and away from the cavity, one may produce the structure of a cupule (such as in fig. 2) in which all of the small bundles are removed to lateral wings and in which there is a layer of small cells (represented by cross-hatching) exposed over the

EXPLANATION OF THE ILLUSTRATION

PLATE I. Manifestation of the phytomer in different parts of the maize plant.

		<i>i</i>	<i>l</i>	<i>p</i>	<i>ab</i>
Six different phytomeric cycles	A	internode	leaf	prophyll	axillary bud (ear)
	B	rachilla segment	glume cushion	cupule-lining	binate spikelets
	C	rachilla segment	lemma	palea	pistil +
	D	rachis segment	leaf rudiment	pulvinus	tassel-branch
	E	rachid* segment	glume cushion	rachid* scab	paired spikelets
	F	rachilla segment	lemma	palea	3 anthers +

* axis of a tassel branch

Drawn by WALTON C. GALINAT

PLATE I



EXPLANATION OF THE ILLUSTRATION

PLATE II. The vascular systems in the pistillate rachis of the American *Maydeae* in three-dimensional aspect. For simplicity, only that vascularization which is in the outer glume of the spikelet and in the rachis tissue adjacent to the observer is shown. Individual lines represent individual bundles except in the main bundles which are thicker and shaded when overlapped by other tissue, such as that of glumes and rind.

1. Vascularization of the maize-type rachis as represented in simplified form by a derivative from a maize-teosinte hybrid. A slight degree of twisting has been incorporated into the drawing in order to illustrate the vascular arrangement from several angles.

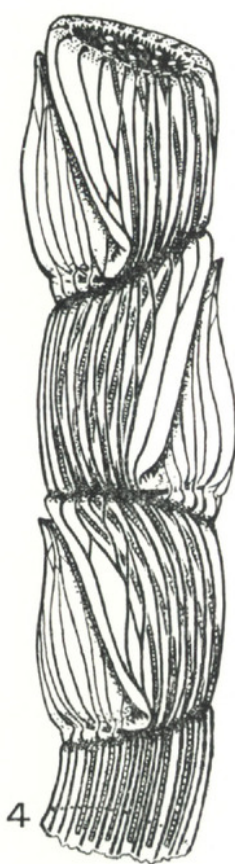
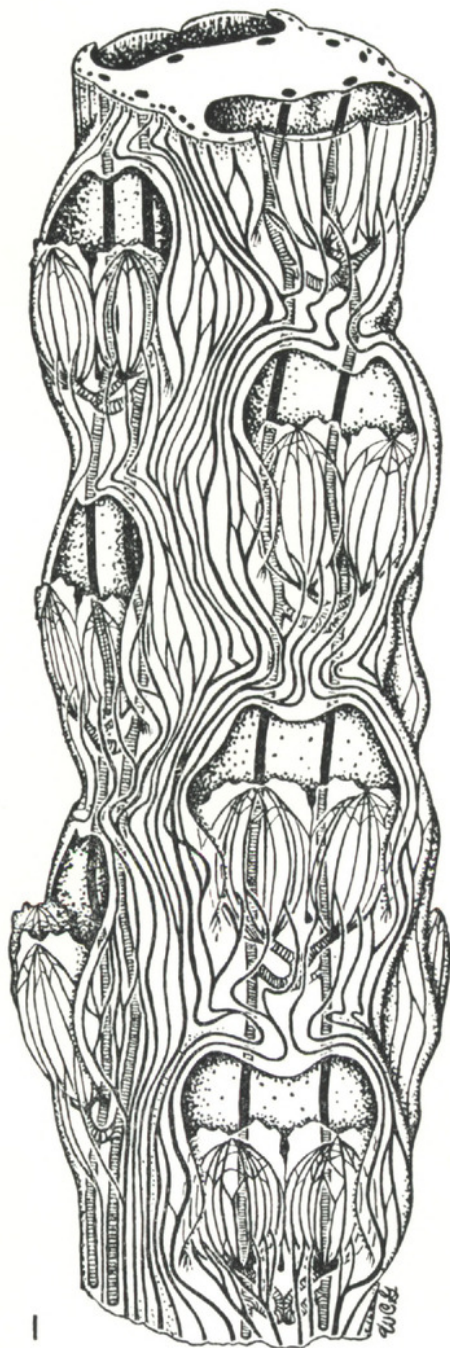
2, 3. Separate front and side views of the fruit case of Durango teosinte.

4, 5. Separate front and side views of the fruit case of *Tripsacum dactyloides*.

All about five times natural size.

Drawn by WALTON C. GALINAT

PLATE II

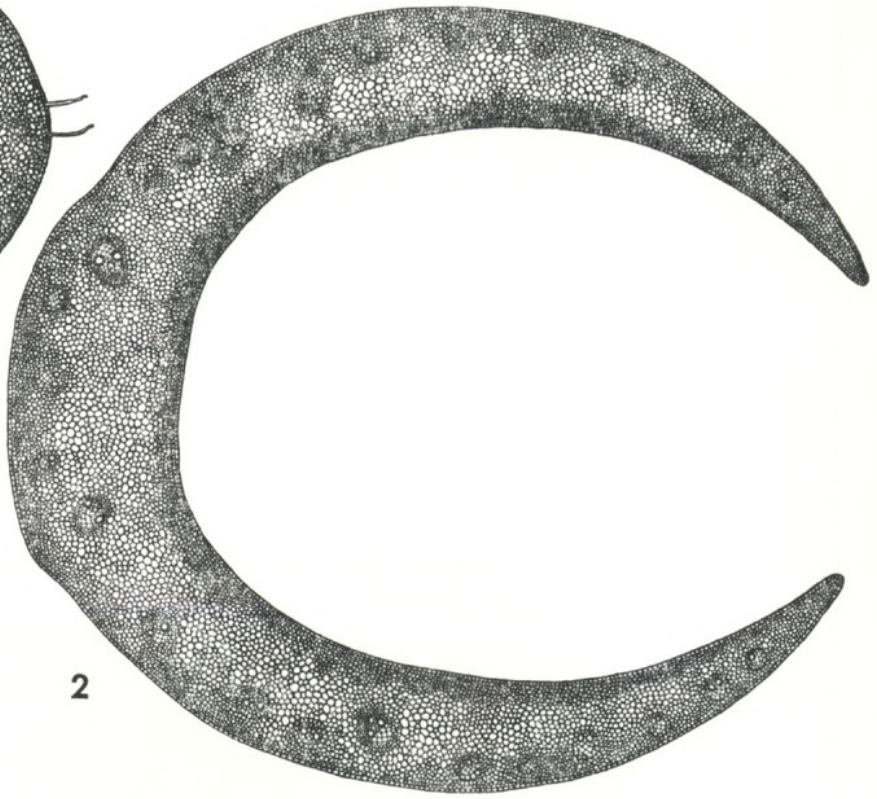
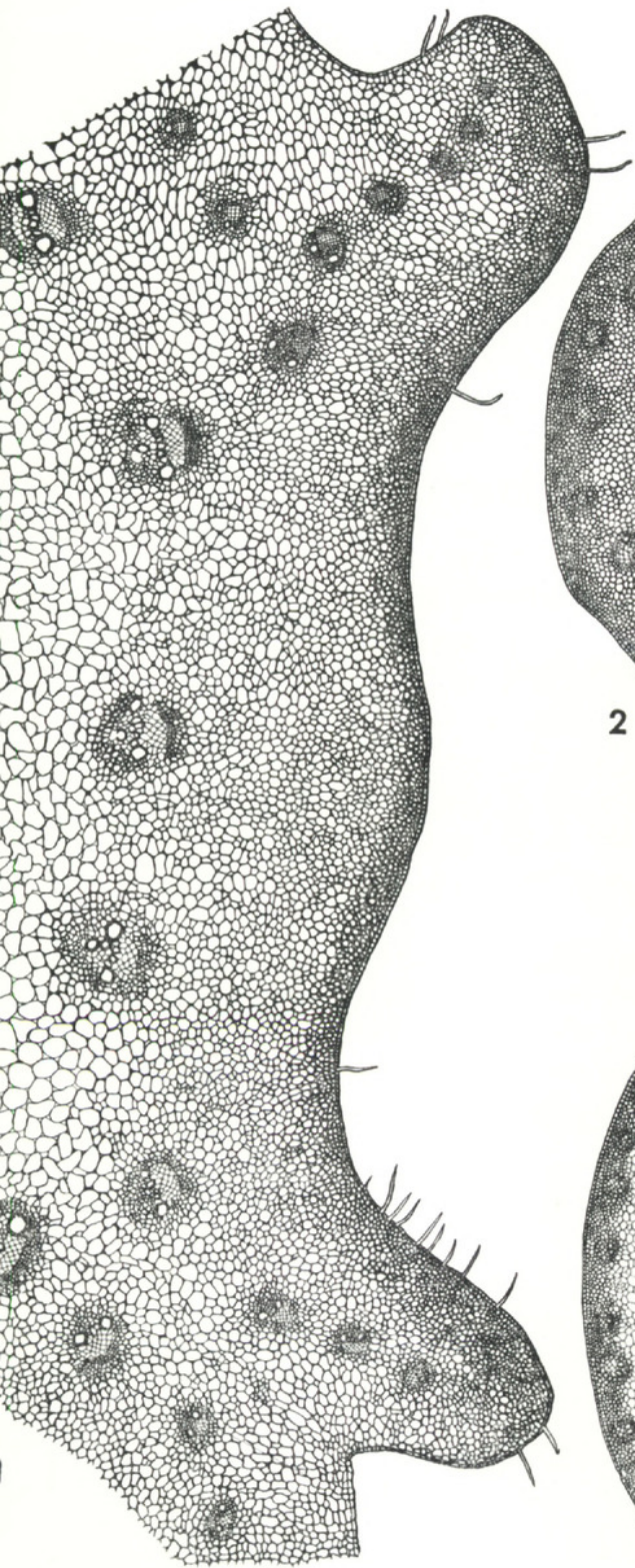


EXPLANATION OF THE ILLUSTRATION

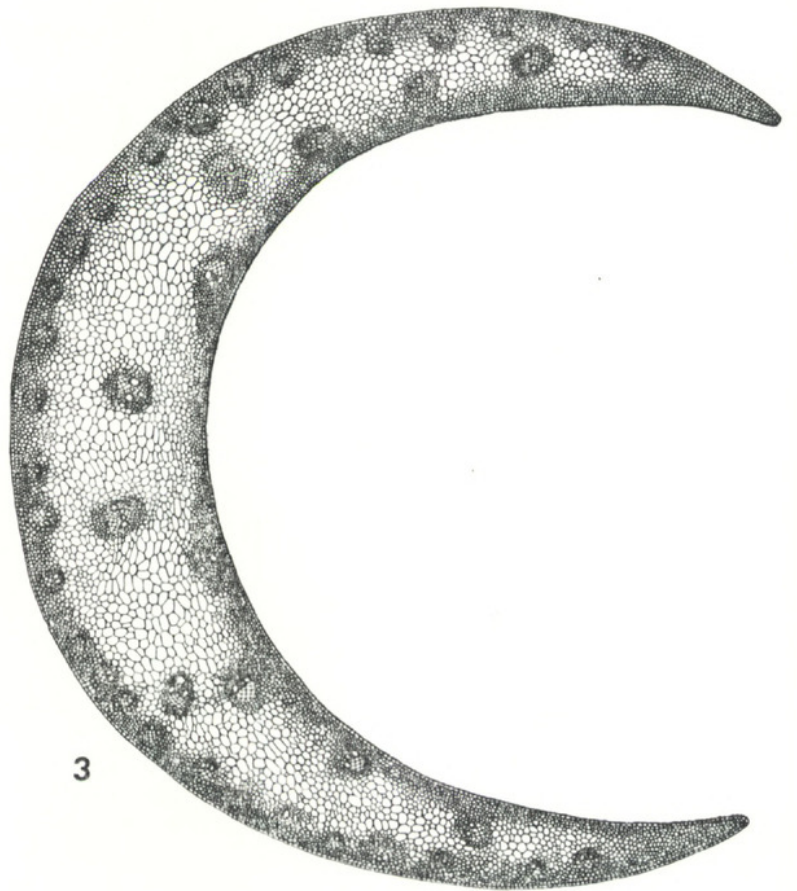
PLATE III. Projection tracings of cross-sectional views of the cupule and rachis segment in the American *Maydeae*.

1. The cupule and associated rachis tissue of maize as represented by the sweet corn inbred Purdue 39.
 2. The rachis segment of Nobogame teosinte.
 3. The rachis segment of *Tripsacum dactyloides*.
- All about twenty five times natural size.

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2



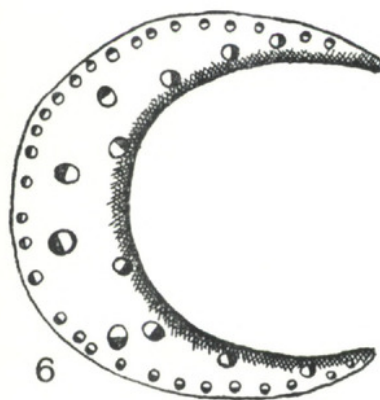
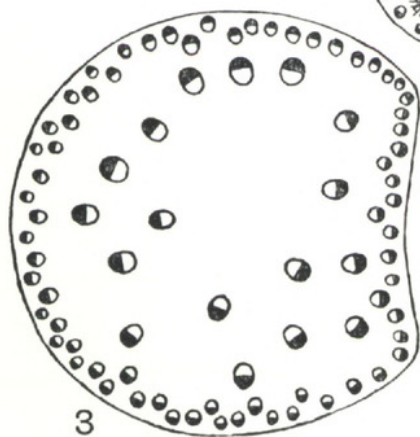
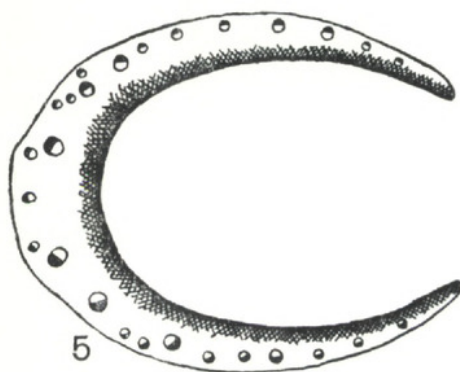
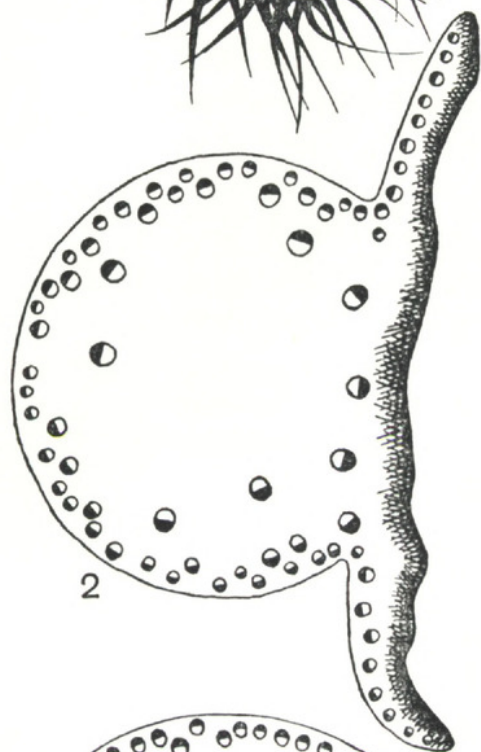
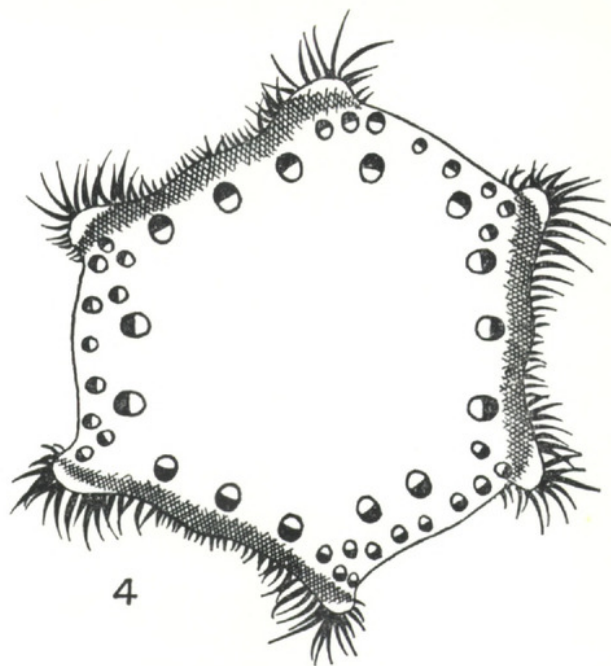
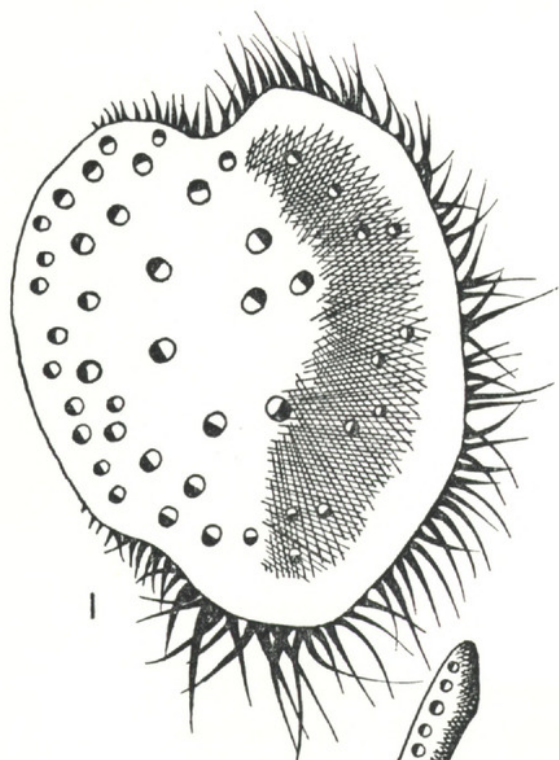
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EXPLANATION OF THE ILLUSTRATION

PLATE IV. Diagrammatic cross-sectional representations of various axes to show structure, vascularization, pubescence, and distribution of an extremely small type of cell. The last is indicated by cross-hatching, while the phloem-region of the vascular bundles is indicated by solid black. 1, pulvinus and associated axis from a tassel branch of P39 sweet corn. 2, rachis with cupule from the distichous branch of a teosinte derivative of Guarany maize. 3, the shank associated with the spike of fig. 2. 4, the rachis of a 12-rowed ear of tunicate Argentine popcorn showing three cupules. 5, pistillate rachis of Nobogame teosinte. 6, pistillate rachis of *Tripsacum dactyloides*. All about fifteen times natural size.

Drawn by WALTON C. GALINAT

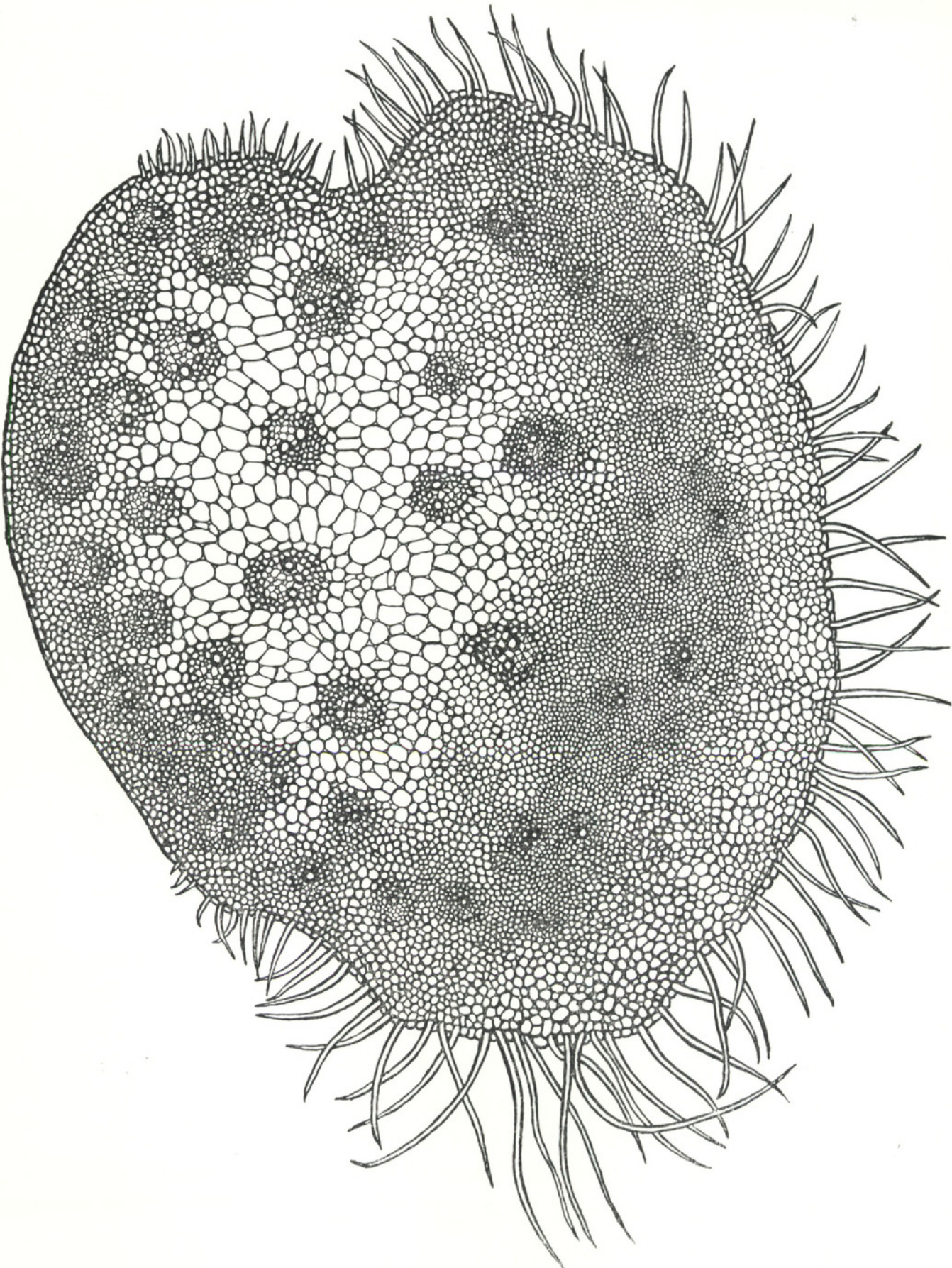
PLATE IV



EXPLANATION OF THE ILLUSTRATION

PLATE V. Projection tracing of cross-sectional view of the pulvinus and associated branch from the tassel of Purdue 39 sweet corn. Note that the tissues of this mature pulvinus suggest the primordium of an organ (such as the prophyll) in that the swelling results from a proliferation of many small cells, rather than an expansion in individual cell size. About forty five times natural size.

Drawn by WALTON C. GALINAT



surface or lining of the cavity. Such a process of cupule formation, by a hypothetical splitting of the pulvinus, serves to illustrate the similarities of the structures involved. It does not represent a plausible explanation for the origin of the cupule in terms of ontogeny, as will be noted later.

This relationship between pulvinus and cupule lining is also revealed by intergrades between these structures in tunicate (*Tu* gene) and other variants of maize. The tunicate cupules are usually shallow because of small wings and, in some cases, the "cupule" may be elevated above the adjacent rachis in such a way as to appear like a flattened pulvinus. One such type of tunicate cupule from a twelve-rowed ear of Argentine popcorn is illustrated in Plate IV, fig. 4. The hairiness and distribution of small cells in this type of cupule produce a striking resemblance to that of the pulvinus (Plate IV, fig. 1). This condition differs from the typical cupule (Plate III, fig. 1) in having all of the rind bundles crowded into corners between the cupules rather than dislocated into flaps. When tunicate cupules lack such vascularized wings, they may be "peeled" from the rachis.

Other circumstantial differences may appear during the development of the pulvinus and cupule lining. Fertilization is accompanied by a metaxenial stimulation for the deposition of lignin in the small cells of the cupule lining, while the corresponding cells of the pulvinus eventually shrink during aging of the plant. Further, the cupule or its lining is embedded into the main axis or rachis, while the axillary pulvinus usually expands along the axis of the primary branch. But the primary branches of the ear are reduced to binate spikelets which, in certain ears of tunicate maize, may be associated with pulvinus-like swellings rather than cupules. Finally, the pulvini in certain highly condensed and compressed tas-

sels, found in inbred P39, are partly formed by tissues from the main axis. Such modifications in structure are imposed by the different conditions of development in tassel and ear and do not detract from the important anatomical evidence of a close similarity between the lining of the cupule and the pulvinus.

The cupule lining and pulvinus as homologues of the prophyll. The pulvinus resembles a rudimentary prophyll in phytomeric position, in external appearance and in internal structure. The cell structure of the pulvinus suggests the primordium of an organ, such as the prophyll, in that the swelling results from a proliferation of many small cells rather than from an expansion in size of individual cells. It is rudimentary in development in being delimited by a zone of rapidly changing cells rather than by an abrupt boundary of cells such as might occur between elaborated organs which are fused (Plate V). Inasmuch as the anatomy and phytomeric position of the pulvinus is also similar to that of the cupule lining, as discussed previously, we conclude that these formations are different manifestations of the rudimentary prophyll-part of the phytomer. Therefore, it is necessary to modify our previous conception of the cupule lining as an adnate prophyll (Nickerson, 1954; Galinat, 1956) to the extent that we now believe that the cupule lining is only one of several possible manifestations of the rudimentary prophyll-part of the phytomer. Under other developmental conditions elsewhere in the plant, the tissue from this region has ultimately developed in the form of a prophyll, a pulvinus or a palea.

The role of pressure in cupule formation. The effect of pressure from constricting leaf sheaths upon floral development and floral evolution in the grasses has been recognized (Arber, 1934, and others). In maize, such pressure moulds expansion of a plastic inflorescence from the

time the plant is only a few weeks old and it continues throughout the development and maturation of the ear. Its role in cupule formation in maize and its relatives seems obvious. Here, in the position of maximum compression between two axes, the central portion of the rudimentary prophyll and associated rachis tissue seems to be depressed inward by penetration of the expanding spikelets. The resulting stresses have apparently inhibited development of the small rind bundles, while the larger bundles deeper within the rachis buckle under stress and bend inward in conformity to the depth of the depression (Plate II, fig. 1). Meanwhile, the lateral portions of the prophyllar tissue and associated rachis, which are free from pressure, bulge out as wings on either side of the penetrating spikelets. At this point in maize, lack of elongation by the internode or condensation forces the elongating spikelets to bend out and away from the cupule, finally diverging at right angles from it. This condition is in sharp contrast to that of teosinte and *Tripsacum*, as will be discussed later, where a slight elongation of the internode, as well as the rigid, sessile and solitary condition of the spikelets, leave no alternative for the spikelets but to become embedded more deeply into the rachis segment as a result of pressure from constriction.

Teosinte and Tripsacum. The homology of the cupule lining to the prophyll is more obscure in teosinte and *Tripsacum* than it is in maize, because of reductions resulting from an extreme depression of the rachis segments in these relatives of maize. The lining of the hollowed rachis segments consists of very small lignified cells similar to those which line the cupule of maize, except that they are spread out more thinly over the surface of the cavity. As with the maize cupule, these cells of the lining are smaller and more highly lignified than those of the rind. In the relatives of maize, a reduction in the

thickness of this lining is probably an effect of increased compression (Plate III, figs. 1, 2, 3).

The extreme depression of the rachis segments affects their vascularization as well. In *Tripsacum*, the larger bundles adjacent to the cupule lining are twisted into a more space-conserving position so that their longest axis lies parallel to the surface rather than in the usual perpendicular orientation, as exemplified by both large and small bundles from the opposite or convex side of the segment. In teosinte, where the effects of compression seem even more extreme, there is an actual loss of some vascularization. There are fewer strong bundles, and these lie just lateral to the dorsal position, so that they may serve equally well either of the alternate positions of spikelets from successive rachis segments (Plate III).

This increased compression in teosinte and *Tripsacum* is likewise apparent in the character of the cells in the "pith" region. In *Tripsacum*, the pith cells tend to be flattened in a direction parallel to the surface, whereas, in teosinte, the cells are restricted from expansion and, as in the glumes, small cells become lignified during kernel development (Galinat, 1957).

The physical effects of pressure in producing the above differences may be visualized by an extension of the same process used previously to manipulate (hypothetically) the pulvinus into resembling the cupule of maize. These derivations may be seen in the figures of Plate IV as follows: Having depressed the pulvinus (fig. 1) into a cupule (fig. 2), as explained previously, further concentrated pressure from single spikelets at the center of the cupule would cause the lateral wings to assume a position at right angles to that of the cupule and the cavity to sink more deeply into the pith, as the general structure and anatomical reductions come to resemble those of the rachis segments in *Tripsacum* (fig. 6) or in

teosinte (fig. 5), depending upon the degree of depression.

The extreme depression of the rachis segments in teosinte and *Tripsacum* seems to require a rigidly erect and sessile condition of solitary spikelets in combination with a thickened rachis. In the staminate rachis, the spikelets are paired, the rachis is more slender and the cupule development is weak or absent. A condition somewhat similar to that of the staminate rachis may be produced in the pistillate region by introducing the tunicate (*Tu*) gene of maize. Thus, in tunicate teosinte, as in tunicate maize, the pistillate spikelets become more pedicellate and accentuated at the expense of a more slender rachis and they are able, thereby, to bend away from the rachis sufficiently early to leave little or no depression in it. Under such conditions, the would-be cupule lining assumes many of the aspects of a flattened pulvinus (Plate IV, figs. 1, 4).

The identification of the small bundles from near the outer or convex surface of the rachis segments as rind bundles is more obvious in the relatives of maize than it is in the cupule wings of maize, because the two-ranked condition of the former, as compared to the many-ranked condition of the latter, simplifies comparison with its counterpart in the culm, which is also a two-ranked axis (Plate IV, figs. 2, 3, 5, 6). The course of these rind bundles, as well as those of the stronger inner bundles in all members of the American *Maydeae*, tends to be strictly vertical, even though in the cases of teosinte and *Tripsacum*, the spikelet positions alternate between opposite sides of the rachis. Consequently, in these relatives of maize, the small bundles from the wing area of one segment extend upwards into a dorsal position in the next segment above as they assume a position identical to those in the rind of the culm. Finally, in the third segment, some of these bundles merge with those from the

glume cushion (Plate II). The branching and fusion of small bundles is most frequent in the wing area, but such changes in the degree of vascularization may occur elsewhere in the rind. There is little doubt that these small wing bundles are actually rind bundles.

Certain extreme features of teosinte, as already noted, seem at first to be exceptions to the usually intermediate position of teosinte between its putative parents, maize and *Tripsacum*, as might be expected if teosinte be a derivative from a hybrid between these other two species (Mangelsdorf and Reeves, 1939; Reeves, 1953). These extreme features of teosinte are a more slender peduncle, a shorter spike with less pith, fewer vascular bundles, and deeper, more highly lignified cupules, as well as more numerous pistillate spikes arranged in compact clusters. But, on final analysis, all seven of these new characters seem to be a hybrid product of combining two other characters from maize and *Tripsacum*.

The derivation of these new characters might be as follows; If the erect sessile spikelets of *Tripsacum* should be combined with increased lateral compression from the tightly binding husks characteristic of the maize ear, the spikelets would become more deeply embedded in the rachis segment. Reductions in the pith, the vascular system and in cell size would follow such extreme compaction, and the smaller cells would accumulate lignin during kernel development (Plate III, fig. 2).

The "clusters" of numerous pistillate spikes in teosinte may also be explained as a recombination of two other characters: condensation in the shank (peduncle) of maize, which has lateral buds at every node, and the small, two-ranked spike of *Tripsacum*. Although the potential for the production of ears at every node along the shank occurs in most varieties of maize, it seldom develops, because the energy is concentrated into the

formation of a single large spike, the ear; but in teosinte, where the individual spikes are small, there is sufficient energy for the development of clusters of spikes.

DISCUSSION AND SUMMARY

The structure of the entire plant of maize and its relatives results from various controlled manifestations of a basic pattern of organs, the phytomer. The parts of the phytomer have been recognized in vegetative form as an internode, a leaf, an axillary bud and a prophyll. These organs, as well as their organization in the phytomer, constitute specialized regions without exact boundaries. Nevertheless, the phytomer represents a fundamental design which occurs repetitiously throughout the entire plant. A comparison of its various manifestations is simplified, if we select a cycle comprising the group of organs which are adjacent to a given node rather than to use the classical delimitation which includes lateral organs at opposite ends of a given internode.

The reduction of parts of the phytomers which have internodes along the rachis is usually extreme. For example, the leaves which potentially subtend the spikelets are usually reduced to glume cushions or swellings at the base of the glumes, although certain genes (*Tp*, *Cg*) may stimulate their development as typical leaves. These glume cushions are vascularized by small-bundles which might be regarded as rind-bundles rather than the vascular remains of rudimentary leaves, because they connect with the vascular supply to the outer glumes rather than terminating as stubs. More information is needed concerning vascularization of swellings associated with unsuccessful attempts at leaf development.

The prophyll is another phytomeric part which is highly reduced along the rachis. In the staminate rachis at the axils of tassel branches, it assumes the functional

form of a pulvinus, an axillary swelling which has become specialized for spreading these branches at the time of anthesis. The tissues of the mature pulvinus suggest the primordium of an organ such as the prophyll, in that the swelling results from a proliferation of many small cells rather than from an expansion in size of individual cells. A study of the ontogeny of the pulvinus would be of interest in that leaf primordia (which would complete development) are usually initiated in the dermatogen or outermost layer of cells, although this condition might not necessarily apply to reduced leaves. Vascular development in the pulvinus, like that of the glume cushion, appears to be a part of the rind of the rachis.

Higher up in the staminate rachis or central spike of the tassel where the axillary buds are manifest as binate spikelets rather than as elongated branches, the rudimentary prophyll usually appears as a scab-like growth on the rachis or may be entirely reduced.

In the pistillate rachis, it is the lining of the cupules which seem to represent the prophyll. The small cells of this lining are very similar to the small cells of the pulvinus, and the physical differences in the external shape of these structures may be attributed to differences in compression during development.

The depression of the rudimentary prophyll and associated tissue is even more extreme in the relatives of maize. The result is a deeply hollowed, cupulate rachis segment which is lined with a thinner layer of "prophyllar" cells and has a distorted and reduced vascular system. Such effects are extreme in teosinte rather than intermediate between its putative parents, as might be expected if teosinte is a derivative from a hybrid between these other two species, because the extreme compression responsible is a hybrid product of combining two other characters. Accordingly, when the erect and sessile

spikelets of *Tripsacum* are subjected to increased lateral compression from tightly binding husks of maize, the spikelets then become more deeply embedded in the rachis, and various reductions in the pith, vascular system and cell size follow.

It is curious that the vascularization associated with all three of the rudiments studied—the glume cushion, the pulvinus and the cupules or hollowed rachis segments—appears to be a part of the rind of the rachis, rather than to represent vascular vestiges of their apparent homologues. But the tissues of these rudiments, as well as the effects of unusual genetic or environmental conditions, reveal their homology to organs which correspond to that of their apparent phytomeric position.

In the ultimate axes or rachillas, the parts of the phytomer become obvious. The first two phytomers of the rachilla have reduced axillary buds and produce little more than the leaves or glumes. But, in more distal phytomers, the leaves (now called lemmas) subtend a bud of sexual organs and its associated prophyll or so-called “palea.”

The gross structure of the entire plant in maize and its relatives is organized upon a basic pattern of organs, the phytomer. The variations in expression which the phytomer has sought in different portions of the plant may (as Arber has suggested with respect to orders) be compared with the intrinsic beauty of a “theme with variations” as expressed in certain musical compositions. Both represent harmonious variations upon a repetitious design, and both obey the dictates of an overall plan.

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