OBSERVATIONS ON TASSELS OF TEOSINTE MALFORMED BY SCLEROSPORA [1]

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INTRODUCTION

One of the most striking and commonly reported effects on cereals and other gramineous hosts resulting from attack by Sclerospora is the malformation of the inflorescence. This feature usually has been emphasized as conspicuous by many investigators during the last 50 years, who described these diseases on an extensive list of hosts, both cultivated and wild, comprising representatives in all but one or two of the less important tribes of the Gramineae. Of the tribe Maydeae (Tripsaceae), maize (*Zea mays*) has been found in Java, India, Formosa, and the Philippines to be seriously attacked by five separate species of conidial Sclerospora (*6, 35, 38, 45, 46, 54, 56*),[3] at times with some concomitant malformation of the inflorescence. Yet in the case of teosinte (*Euchlaena* spp.), although it is perhaps the closest relative of maize and (as might be expected therefore) also is susceptible to these downy mildews, no instances of deformation have been reported hitherto. In the Philippines, however, while studying the Sclerosporas chiefly destructive to maize but also attacking teosinte, the senior writer, during two years of investigation and among many teosinte plants relatively unaltered by such attack, did encounter certain cases of abnormalities developing as a result of inoculation with *Sclerospora philippinensis.* It is with the hope that their rarity, their remarkable structure, and their possible significance may render them of interest that these cases are described in the present paper.

HISTORY OF THE CASES

The first planting of teosinte at the College of Agriculture of the Philippines was a small experimental plot started in July, 1917, with seed of *Euchlaena luxurians* Schrad. obtained from a New York seedsman. With seed from this a second planting was grown from June to November, 1918. In this second plot, and among the volunteer plants which sprang up around the maize then planted in the first, many instances of infection by *Sclerospora philippinensis* were noticed, but only a few were at all deformed and these but slightly (*54, p. 104*). With healthy seed from this plot seedlings were grown in pots protected in the laboratory. Beginning January 25, 1919, when they were 9 days old, with two leaves and about 3 inches high, the seedlings were placed for seven successive nights under young

[1] Received for publication Nov. 20, 1928; issued December, 1929.
[2] To G. N. Collins for his kindness in critically reading this manuscript the writers wish to acknowledge their indebtedness; also, to the Milton Research Fund of Harvard University the senior writer wishes to acknowledge his gratitude for aid which, by lessening some of the demands of class work, has expedited the long-delayed preparation of parts of this paper.
[3] Reference is made by number (italic) to "Literature cited," p. 833.

maize plants infected with *S. philippinensis* and showing abundant nocturnal production of conidia. To prevent extraneous infection the seedlings were covered each night with large cans. After being thus subjected to certain infection, they were allowed to develop in the laboratory until, on February 6, several of them (now 5 inches high and with the third leaf developing) showed the first paling leaf areas that precede production of conidia (*57*). Sixty of these seedlings were then planted in a corner of an isolated abaca and tobacco patch far from any other cases of downy mildew, and the progress of the disease on individual plants and in the plot as a whole was followed.

By the end of March many plants had died, under these crowded conditions, leaving only nine living, of which three were still healthy and remained so. In late April and early May, 1919, when conidiophore production on the six diseased plants had ceased save on young leaves of shoots recently put out, the male inflorescences (tassels) both on the main axes and on side shoots were found to be developing into abnormal, malformed structures, in contrast to the normal ones of the three still healthy survivors. These tassels, instead of producing pollen and becoming passé, remained green, the deformed glumes and lemmas of the hypertrophied spikelets continuing to grow excessively into contorted, elongate, bractlike structures which gave them a most bizarre appearance. A representative specimen was photographed (fig. 1) and preserved in copper acetate solution for future study; the others were kept under further observation.

During June a few additional tassels, also malformed, continued to develop from the later suckers of the diseased plants. This isolated plot was not visited during July, as in the latter part of that month there began a series of successive and severe typhoons that raged as one intermittent storm for six weeks. When visited on August 6 the plants were found to have been blown over and beaten down into the mud by the violence of the storms. The plants themselves had responded indomitably to this severe treatment by taking root and sending up new shoots at each node, but of the remarkable malformed tassels only a few survived, the several others, already old, having been beaten and soaked to pieces. These few survivors were collected, and from two of them were taken the peculiar rooting plantlets which, as herein described, were planted in the endeavor to foster their independent growth. As these malformed tassels seemed to present features of unusual interest, all possibly pertinent information concerning them was recorded, various illustrative photographs were taken, and the specimens themselves were preserved in formalin and in alcohol for more thorough examination later.

BEHAVIOR OF THE MALFORMED TASSELS

When the few plants whose malformed tassels had survived the severe storms were collected on August 6 it was with the intention of making a complete record of each one by means of photographs and notes, and this was carried out in part. The storms, however, became so violent that they prevented the completion of the work, and two remaining plants were left in the shelter of a tree on the lawn. These showed remarkable behavior, for when they were examined on August 13, during a lull in the storm, the upper portions with only slightly deformed spikelets were found to have rotted apart and disintegrated, while the strikingly malformed spikelets of the more basal portion of the tassels had remained green and sound. Indeed, several of the

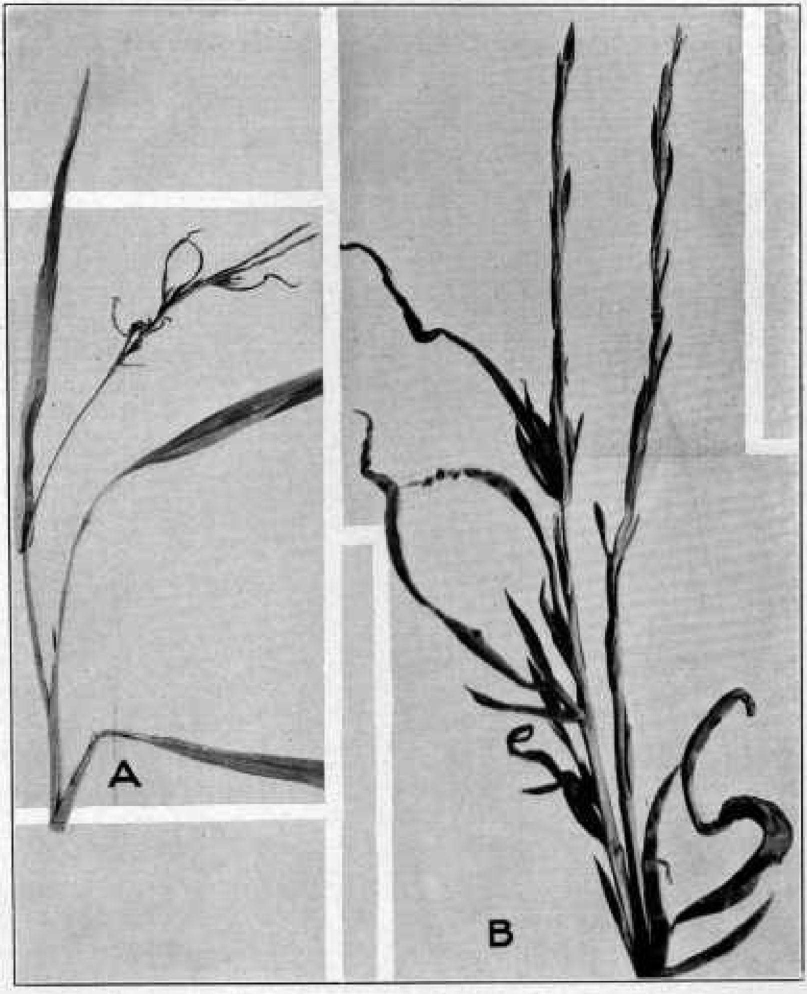

FIGURE 1.—Malformed tassel of teosinte: A, Upper portion of a plant of teosinte infected by *Sclerospora philippinensis*, showing the malformed tassel in position. This plant was one of a lot sprouted from seed planted in pots on January 17, 1919, inoculated as young seedlings with conidia of *S. philippinensis* from maize during the nights of January 25 to 31, planted on February 6 in an isolated plot, where, supporting the disease with little apparent effect beyond the striping of conidiophore-bearing areas of the leaves, the excessive production of tillers, and the suppression of the female inflorescence, the plants in late April developed the tassels. In June, when this specimen was photographed, the infected tassels were still flourishing vigorously, in marked contrast to the already passé tassels of comparable healthy plants. B, The same tassel more highly magnified to show its structure in greater detail. It consists of two long, approximately equal branches bearing spikelets, all of which are sterile, but most of them superficially relatively unchanged, although a few, as the one spikelet at the base of the right-hand branch and the six spikelets in the lower half of the left-hand branch, show malformation into striking, contorted outgrowths involving especially hypertrophy of the glumes and lemmas. The illustration is from two smaller photographs pasted together. About three-quarters natural size

more elaborately hypertrophied spikelets, resembling deformed seedling plantlets, had actually sent out roots from their bases (fig. 2, A, B, C, D) as though they were capable of independent existence; whereas some, as shown in Figure 2, A, *a*, *c*, and *d*, had practically separated from the prostrate tassel and had changed their orientation with relation to it until they had almost assumed the upright position which would be natural to young seedling plants of their size. Several of these, including those illustrated in Figure 2, B and D, were planted in a pot. Although they remained vigorous and continued to grow for more than a week longer, they were unable (probably in part because in the continuing storms they had almost no sunlight and were constantly far too wet and exposed) to establish themselves as independent plants and ultimately became water-soaked and rotten.

The development of the branchlets of these deformed tassels into entities comprising leafy shoots, giving rise at their bases to roots, orienting themselves like young plants, and for a time continuing to grow when quite separated from the tassel of which they had been a part, seems to justify regarding these as cases of apogamy. This holds, of course, only if the term is used in its general application, that is, to instances in which new plants develop nonsexually from parts that normally produce sexual organs, and not if the term is used in its more restricted cytological application. The behavior of these specimens, therefore, is of some interest, for in the Gramineae cases of apogamy in general are rare, whereas cases resulting from the attack of parasitic fungi have not been reported, as far as the writers are aware. As might perhaps be expected from the close relationship of the two genera, the examples of apogamy in maize (healthy, not parasitized) described by Collins (*9*) show striking resemblance in structure to those of teosinte now under consideration, although it should be noted that the plantlets which developed in the maize tassels terminated in small female inflorescences, whereas those of teosinte, if not completely sterile, showed only male rudiments. Moreover, the plantlets from the maize tassels when transplanted by Collins, even though they did not reach maturity, grew in an apparently normal way for nearly two months, producing roots more than a foot in length, thus far exceeding the amount or extent of the continued growth of the teosinte plantlets. The growth of these teosinte plantlets, however, even though scanty, was enough to show certain interesting aspects, for their development apparently resulted from attack by the Sclerospora, or at least followed it, and if they had lived they would have transmitted a novel type of primary infection to the plants into which they matured, since as long as the plantlets persisted they harbored within their tissue mycelium that remained living and apparently quite capable of renewed growth.

GENERAL STRUCTURE OF THE TASSELS

The appearance of the tassels as a whole was more or less striking, depending on the degree of malformation, but in all cases it was enough to arrest attention. In contrast to the normal graceful tassel with its several slender digitately diverging branches set with regular rows of small, smoothly fusiform, tapered spikelets of appressed florets, the inflorescences were frequently telescoped with reduced branching to bunchy, tufted heads, or rendered unsymmetrical and bizarre in contour by flaring, uncouth, sprawling outgrowths.

In the bunchy type, representing one extreme of the forms encountered, the branching was suppressed, the whole inflorescence being

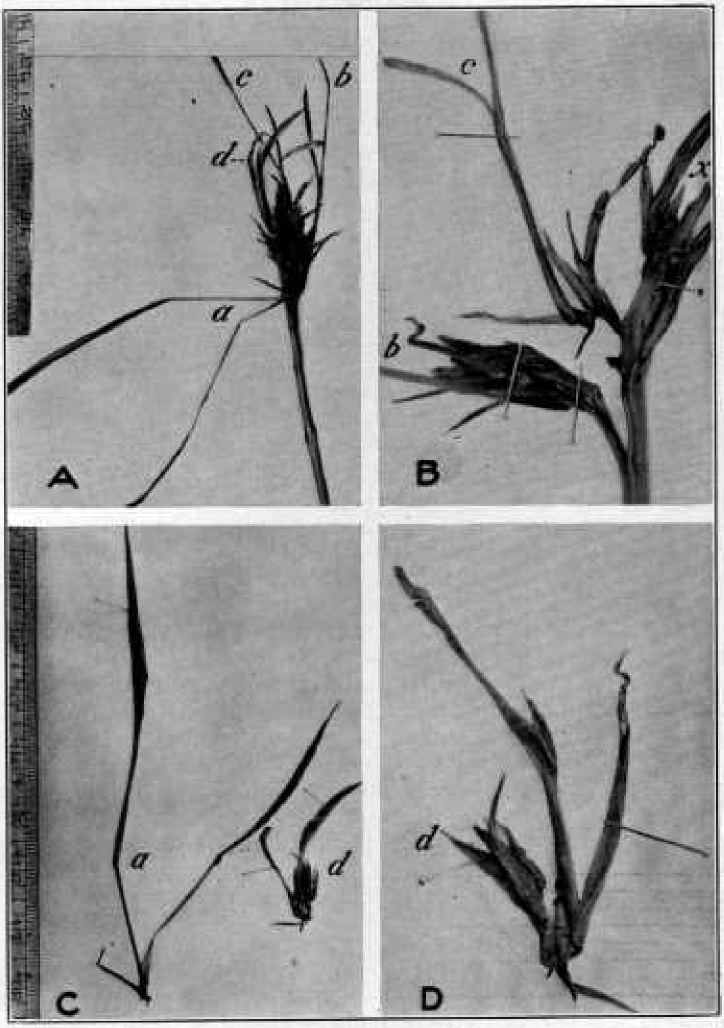

FIGURE 2.—Malformation and root development of parts of teosinte tassel: A, The basal portion of a male inflorescence of teosinte taken from a plant of the same lot and with the same history as the one illustrated in Figure 1. This plant, however, after surviving a long period of incessant storms until August 6, was pulled up and then left lying during an especially violent typhoon until August 13, when, although the top of the tassel had rotted apart and the less malformed spikelets of that portion had begun to disintegrate, the more elaborately malformed spikelets at the base of the inflorescence had continued growing and had sprouted roots at their bases. Scale in inches. B, The base of the same tassel with some of the seedlinglike branchlets removed and the remaining parts separated to show the general structure. The branchlet *c*, previously obscured by the lower clump of spikelets *b* now pinned down away from it, shows a general resemblance to a seedling plant with its base, almost separated from the tassel axis, having one short but obvious root growing down from it. The broken end of the main axis, from which the top of the tassel disarticulated, is shown at *x*. About two-thirds natural size. C, Two of the deformed parts, *a* and *d*, removed from the tassel shown in A. The slender one, *a*, is recognizable as a single spikelet with glumes and lemmas so overgrown into elongate leaflike structures (6 and 8 inches long) that the whole entity with its few short, poorly developed roots at the base resembles a sickly seedling plant of teosinte. The shorter one, *d*, is a compact clump comprising at least two spikelets, much malformed, rooting at the base. Scale in inches. D, The malformed branchlet, *d*, already shown in C after removal from its place (*d*) in the tassel of A, spread apart and photographed somewhat larger to show the general structural features of the several parts and the growth of the roots at their base. About two-thirds natural size

shortened and condensed into a single compact, clumped, bunchy head, superficially resembling the inflorescence of Setaria or Pennisetum, as is shown in Figure 2, A. Even the more open branching type, less completely deformed, less departing from the normal, and representing the other extreme encountered, showed more or less numerous striking, elaborate, twisted, curved outgrowths that, as shown in Figure 1, at once marked them as abnormal. In their gross structure these male inflorescences presented a striking contrast to those healthy ones illustrated and described by Collins (*14*, *16*), by Weatherwax (*53*), and by others. While more detailed morphology and histology of these malformations will be considered later, it is worthy of note that in general the spikelets of the tassel, especially the more basal ones (fig. 1), were strikingly hypertrophied, the lemmas particularly enlarging astonishingly into expanded leaflike structures (fig. 2), and the whole spikelet elaborated until in some cases it much resembled a somewhat deformed seedling plantlet (fig. 2, B, C, D) sprouting from the joints of the tassel branches. Moreover, the stamens were lacking entirely or else abortively developed, so that all the spikelets of the tassels were sterile. This was true not only in the badly deformed, more basal spikelets, as might be expected, but also in those usually nearer the tip, which appeared superficially unaltered.

In view of the elaborate development of these deformed spikelets, it is remarkable that all the cases showed no malformation except in the tassels. The plants themselves were not seriously injured and, like most of the Sclerospora-infected teosinte individuals already studied, described, and illustrated by the senior writer (*57*, *pl. 6*; *54*, *pl. 22c*), had shown during the period of conidiophore production relatively inconspicuous striping and stiffening of the leaves, had continued growing unimpeded, and at maturity, when production had ceased, were only faintly mottled, although the mycelium was still present in the leaf tissue. Moreover, these plants without exception did not develop any female inflorescence, thus lacking opportunity for the malformations that frequently occur in those structures in downy-mildewed maize plants.

DETAILED STRUCTURE OF THE TASSELS

The representative specimens which had been preserved in the Philippines eventually were brought to Harvard University, where a detailed study of the floral structure and the histology of the tassels was made by the junior writer. The floral parts of these malformed specimens were carefully unrolled, dissected, drawn under the camera lucida, and compared with one another and with healthy material. Also, critical structures and parts were embedded in paraffin, cut in several directions in sections of various thicknesses, and stained with various combinations, such as Flemming's triple, Pianese 3, or haematoxylin and Orange G.

As the general symptoms of this disease in teosinte plants have been described in earlier papers by the senior writer (*54*, *57*), attention was directed to the staminate inflorescence in which the malformations occurred.

The normal, healthy, staminate inflorescence of teosinte resembles that of Indian corn except that in the former the central spike is suppressed. The spikelets are 2-flowered and arise in pairs at each joint of the rachis and on one side of it. One spikelet of each pair is subsessile, the other one is pediceled. These features are well known from the descriptions and illustrations of Collins (*13*, *16*), Weatherwax (*53*), and others.

In the tassels of the diseased plants various gradations of transformation existed. As a rule, the sessile spikelets were more excessively malformed than were the pediceled ones, and those at the base of the spike more than those toward the tip. In some of the diseased plants the general appearance of the spikes was not greatly altered, but in other cases only a few joints of the rachis developed, and the spikelets here were generally contorted and excessively hypertrophied, so that they presented a "bunchy" appearance in which practically all semblance of a spike was lost. Each joint of the rachis, however, almost invariably bore its two spikelets. Sometimes both of these were pedicellate.

One case different from any of the others was observed. Two spikelets were raised on a short pedicel and inclosed by three glumes. (Fig. 3, H.) One of these glumes was somewhat larger than either of the other two, but there were no indications that it resulted from a fusion of two. That these spikelets were indeed spikelets and not florets is shown by the fact that each one possessed two florets whose composition and arrangement were identical with those of other diseased spikelets.

Gabotto (*19*) relates that in a study of maize infected with *Sclerospora macrospora* he counted 60 virescent staminate inflorescences of abnormal development and states that, since the plants did not produce ears, the parasite seemed to stimulate excessive growth of some parts at the expense of others. A somewhat similar effect was evident in this material. In those branches which retained their spikelike formation the excessive overgrowth of the spikelets on the lower portion of the rachis seemed to take place at the expense of spikelets higher up. Indeed, from the base to the tip of the rachis there was manifest a tendency toward the progressive reduction, and finally the suppression, of the several parts of the florets. The second floret of each spikelet was invariably smaller than the first floret and first suffered the loss of one or more of its floral elements. At a distance up the rachis of approximately one-third the entire length it lost its palea. Slightly higher a similar loss was sustained by the sessile floret. The lemmas of each of the florets were still present at that height, but about halfway up the rachis the lemma of the second floret usually disappeared, and somewhat farther up the first floret lost its lemma, so that in the topmost spikelets, more often than not, only the two glumes were present. (Fig. 3, F.) Occasionally the first glumes alone remained. As the spikes of diseased tassels differed much in length and were always shorter than those of healthy tassels, it can readily be understood that in extreme cases the upper portion of the spikes would fail to develop at all and the bunchy type of tassel already mentioned would result. In the more detailed account of the floral structure which follows, the features referred to will apply particularly to excessively hypertrophied spikelets, the applicability of the description diminishing proportionately as the spikelets approached normal development.

The glumes shared in the general overdevelopment of the spikelet, but rarely lost their glumelike character. Their increase in width and thickness was proportionate to their increased length, which in many cases exceeded three times that of the normal glume. (Fig. 3, A, B, H.) More vascular bundles were present than in the healthy glumes,

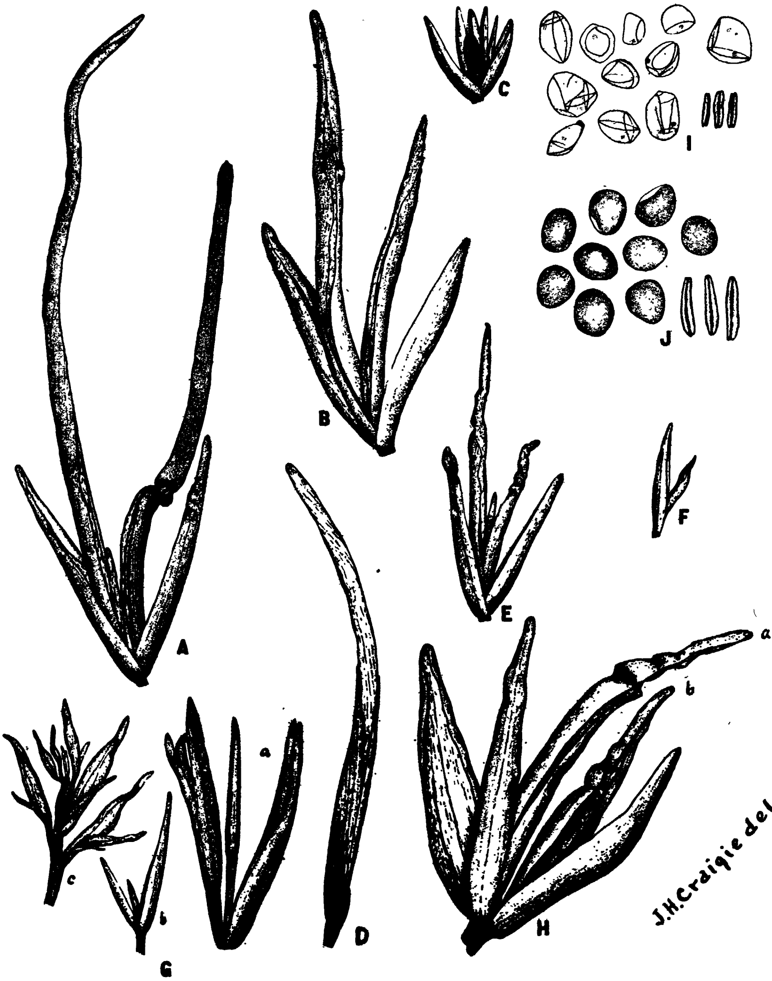

FIGURE 3.—Structure of malformed spikelets from tassels of infected teosinte: A, B, E., Staminate spikelets of teosinte hypertrophied and malformed by an attack of *Sclerospora philippinensis*. The tightly enwrapped floral elements were opened and spread apart to show the position and relative size of each. In A the lemma of the second floret had to be twisted from its original position in order to expose the palea. The portion above the knotlike formation was not enveloped by the other lemma. × 1½. C, Spikelet of healthy tassel, showing stamens in first floret, and affording an interesting comparison in size, proportions, and construction to those of the diseased. × 1½. D, Spikelet of diseased tassel showing hornlike form characteristic of many diseased spikelets. × 1½. F, Spikelet from tip of a diseased tassel, floral parts reduced to two. × 1½. G, *a*, Three spikelets which arose at one joint of a rachis; *b*, central spikelet opened, consisting of three floral parts; *c*, prolification of florets found within the glumes of the left spikelet of *a*. × 1½. H, Two spikelets, *a* and *b*, growing on a common short pedicel and inclosed by three glumes. × 2. I, Pollen grains and anthers from diseased florets. The grains are shrunken and collapsed, with variously wrinkled and infolded walls and with content almost devoid of protoplasm, so that the germ pores appear very distinct. The anthers from the diseased florets are small and poorly filled out. Pollen grains, × 78; anthers, × 2½. J, Healthy pollen grains and anthers, drawn to the same scales of magnification as I, in order that they may be compared with the pollen grains and anthers of the infected plants

and as a consequence of this and the greater thickness the glumes were quite rigid. The hispidness characteristic of the glumes was much more pronounced in these than in the healthy ones, The lemmas, on the other hand, underwent astonishing transformations and usually assumed a very extraordinary arrangement. Although in healthy florets the lemmas are membranaceous and hyaline, with any trace of hispidness visible only microscopically, several of the diseased ones were leaflike and virescent, while most of the others were distinctly hispid and rigid, resembling very much in texture the diseased glumes. These observations apply more particularly to the lemma of the first floret of each spikelet, for in most cases the arrangement of the floral parts seemed to forbid such extravagant development in the other parts as was permitted in this one. In practically every diseased spikelet examined, the lemma of the first floret tightly enwrapped its palea (and stamens when present) and the second floret either wholly or in part. In doing this it usually assumed a somewhat spiral course, so that when it completley enveloped the other floral elements it presented the appearance of a horn. (Fig. 3, D.) Occasionally this formation was quite regular, but more frequently it showed various degrees of torsion and wrinkling. (Fig. 1, B; fig. 3, E.) When the second floret was not completely encircled, the upper portion being sometimes uncovered, the exposed portion was very similar in appearance to the enwrapping lemma. (Fig. 3, A.)

In a few cases there were modifications of this general arrangement. The most interesting one of these was the differentiation in several cases of extremely enlarged lemmas into sheath and blade, as in a leaf. (Fig. 2, B.) The lower portion was tightly enrolled after the manner of a sheath, but the upper portion flattened out into a well-formed blade. (Fig. 2, A, B.) Just at the top of the sheath a ligule was almost invariably present. It never developed completely around, but extended inward from either edge for about one-third the width. The central portion of the ligule failed to develop. In the cases just mentioned the upper portion of the lemma of the second florets was left exposed, and two or three of them expanded into virescent blades, but no ligule formation was observed.

Toumey (*50*), in describing abnormalities in the inflorescence of *Phleum pratense*, mentions that some of the flowering glumes were changed into leaves. Butler (*5*) did not observe any transformation of this kind in *Pennisetum typhoideum* attacked by *Sclerospora graminicola*, although other abnormalities were produced. He states, however, that the lemmas were usually elongated, occasionally virescent, and softer than healthy ones.

Although each joint of the rachis regularly bore two spikelets, a case was observed in which three spikelets arose from the same joint (fig. 3, G, *a*), one of which was subsessile, the other two pedicellate. Of these last two, one was situated centrally and possessed but one floret (*b*), the other resembled in external characters the ordinary diseased spikelets, but when its glumes were removed it disclosed a very unique construction. The rachilla, which in other spikelets bore two florets, was elongated considerably and bore seven spikelets. (Fig. 3, G, *c*.) These were not arranged in quite the orderly manner that was evident in the ordinary spike. The first spikelet on this elongated rachilla was sessile, the next one above it pediceled. The fourth was raised on a comparatively long pedicel in the axis of the third, which was sessile. The three uppermost arose separately and were greatly reduced, two of them being represented by only a single glume each, the third one by two very diminutive glumelike structures. In this particular case the rachilla had evidently assumed the function of a rachis and bore spikelets instead of florets. The term "spikelet" is applied to these structures for the reason that the glumelike character of the outer element of each was very evident, and one spikelet consisted of three bracts, whereas, if it were a floret, it would have had but two—the lemma and the palea.

This aberrancy would seem to fall in teratological classification under "median prolification." Moquin-Tandon (*37*) speaks of prolification as "median" when an adventitious bud springs from the center of the flower as a direct continuation of the growing point. In describing prolification in flowers, Masters (*32*) states that in median prolification the adventitious bud springs from the center of the flower; the usual arrest of growth which occurs at this spot no longer holds good, but a new growth takes place, manifesting itself generally in the formation of a new flower bud, a new leaf bud, a branch, or even in the production of an inflorescence. Toumey (*50*) described a case in which some timothy spikelets had four glumes, some only two, and between the inner ones a long stipe, generally more or less twisted, arose and was surmounted by a perfect flower. This irregularity in structure Penzig (*44*) termed "central prolification."

The dissimilarities of the internal structure of healthy and diseased lemmas were not less marked than those of their outward form. Healthy lemmas, for the most part, were of a uniform thickness, mainly one cell thick, and therefore contained no mesophyll or well-defined vascular bundles. Diseased ones, on the other hand, were of uneven thickness, having well-developed mesophyll and fairly regularly spaced vascular bundles (fig. 4, F, H), some of which were quite perfect, with vessels, phloem, and sheath, while others perhaps, consisted of only two or three vessels, or presented gradations between these two extremes.

As the morphology of those portions which flattened out to form blades was considerably different from that of the rest, it will be mentioned first. A comparison of the two cross sections F and G of Figure 4 shows how closely the former approximated the regular leaf formation of the latter. In both cases the upper and lower external walls of the epidermis were of about the same thickness, although in the leaf, G, these were slightly thicker than in the bladelike lemma, F. Also, the leaf itself was somewhat thicker. The vascular bundles in the bladelike lemma were regularly spaced and were as complete as many of those in the leaf, yet at intervals the leaf possessed bundles which, above and below, were abutted by a group of thick-walled sclerenchymatous cells which extended to the epidermis. These were absent in the bladelike lemmas, but in general their structure corresponded very closely to that of the leaf.

The inrolled lemmas, on the other hand, differed quite materially from the flattened portions or from a leaf. As seen in cross section, their margins were thin, but a progressive thickening took place toward the middle, so that in this region there was a spongy mesophyll, as in the leaf. (Fig. 4, D.) There were present also more or less regularly spaced vascular bundles. Toward the edges, and therefore in the thinner portion, these were always incomplete, being composed usually of a few vessels. In the thicker portions some were quite complete (fig. 4, H) and others were imperfect like those in the thinner parts. The cell walls of the outer epidermis were thick and sclerenchymatous, and they frequently protruded, so that this surface was studded with short stout hairs. Stomata

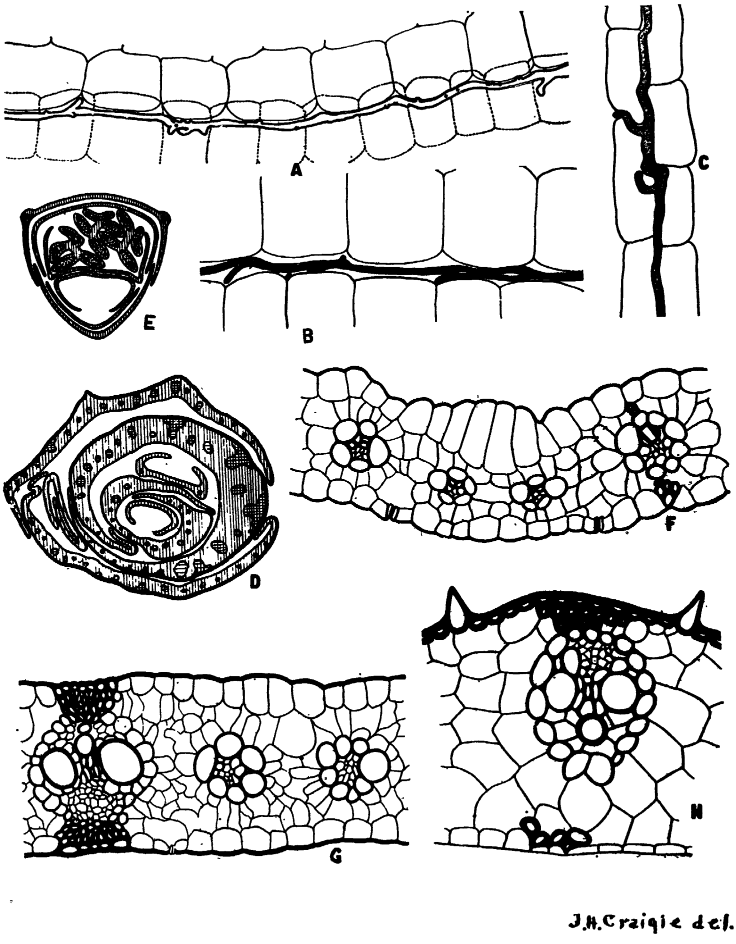

FIGURE 4.—Details of internal structure of malformed spikelets: A, Thick-walled strand of mycelium without cytoplasmic content, showing swellings and prominences which press against the cell walls. × 200. B, Thick-walled strand of mycelium with content. The host cells have been wedged apart by the mycelium. × 200. C, Portion of thin-walled hyphal strand with cytoplasmic content. × 200. D, Schematic representation of a cross section of a deformed spikelet, cut 3 mm. above the base, to show the inrolled nature of the lemmas. In this spikelet an additional abnormality appears in the form of an extra floral bract just inside the glumes. The vascular bundles and sclerenchymatous tissue are crosshatched. × about 14. E, Schematic representation of a cross section of a healthy spikelet. × about 14. F, Portion of a cross section of a virescent lemma, showing its similarity in internal structure to the normal leaf. × 200. G, Portion of a cross section of a healthy leaf. × 200. H, Cross section of a portion of strongly inrolled lemma at its thickest part, showing the external thick-walled epidermis, the sclerenchymatous reinforcement cells which connect with the bundle, and the thin-walled inner epidermis with its adjoining small group of thick-walled cells. × 200

occurred sparsely. Abutting on the epidermal cells and just over the bundles were one or more layers of thick-walled cells. Where the bundles were large and more complete, these cells bridged the space between the epidermis and the bundle sheath (fig. 4, H), but where the bundles were more or less imperfect, thin-walled cells usually intervened between these thick-walled cells and the bundle. On the opposite side of these bundles and lying adjacent to the inner epidermis there were usually a few thick-walled cells, but these never connected with the bundles. (Fig. 4, H.) The walls of the inner epidermis were thin, like those of the mesophyll cells, and few stomata or hairs were evident on this side. This condition—a firm outer epidermal layer, reinforced by clusters of thick-walled cells and opposed on the inside by only a thin-walled epidermis—seems to account satisfactorily for the inrolling that took place in so many of the diseased lemmas.

As already stated, the lemma of the second floret of the spikelet was either partly or wholly enveloped by that of the first floret, and as an apparent consequence (although it duplicated in a general way the features already indicated of the enwrapping lemma) these features were not so pronounced. The thick-walled outer epidermis, the strengthening clusters of fibers, and the vascular bundles were present, but less conspicuously developed. However, in those cases where its upper portion became uncovered and thus exposed to sunlight, it took on the characters of the enwrapping lemma, which seemed to indicate that if this lemma had had an exposure to sun and air it would have been identical with the one that inclosed it. The leaflike appearance of two or three of these has been mentioned.

The palea of the first floret participated somewhat in the general hyperplastic condition and became frequently three times its normal size, but in no case did it approach the extravagant dimensions of the corresponding lemma. In the second floret, the palea, surrounded as it was by two lemmas, was apparently stifled and only rarely attained the size of the other palea. As a rule, it was poorly developed, often only a vestige being present, and it was more frequently absent than any of the other floral bracts.

The stamens, more often than not, were suppressed. If present, the anthers appeared atrophied and were rarely more than two-thirds their normal size. The pollen grains varied greatly in size and shape, some being even larger than the normal healthy grains, while others, again, were reduced to half that size. (Fig. 3, I, J.) All of the pollen grains in a diseased plant were practically devoid of content, so that the walls became wrinkled and infolded, and the appearance of the grain was irregular and bizarre. (Fig. 3, I.) None of the modifications that Butler (*5*) described for the stamens of *Pennisetum typhoideum* attacked by *Sclerospora graminicola* (Sacc.) Schroet. was observed.

As the characteristics of the mycelium of this fungus have been described by the senior writer in a previous publication (*54*), it is unnecessary to repeat them here. It might be added, however, that the hyphal filaments that seem to serve for communication between different parts of the host were frequently, though not always, very thick walled, a condition resembling that observed by Butler (*5*) in *Sclerospora graminicola* on Pennisetum. Usually these filaments were devoid of cytoplasmic content. A portion of a thick-walled hyphal filament without content (A) and a portion of one with content (B) are shown in Figure 4, as well as a thin-walled portion of a filament (C).

DISCUSSION

These cases of malformation involve several points of interest. Not only are they remarkable because of their rarity in the Gramineae in general and in teosinte in particular, but also because of their elaborate structural overdevelopment in contrast to their complete sterility, their growth as independent plantlets, and their resulting abortive apogamy. Moreover, they present an interesting comparison to cases of malformations in other grasses and contribute to possible interpretations of such structures and their significance.

In the first place, these malformations are of interest because in teosinte the occurrence of structural abnormalities of any kind, whether resulting from injury by downy mildew or from any other factor, is exceedingly unusual. Although numerous plantings of teosinte from several lots of seed obtained through the kindness of G. N. Collins and others from Mexico, Florida, and other localities were kept under observation for two years in the Philippines, the senior writer found exceedingly few and slight abnormalities either in healthy or in downy-mildewed plants with the exception of the present cases. Moreover, Collins, who has studied extensive plantings for many years, summed up his long experience in a lecture in 1918 (*12*) with the statement:

> Compared with maize, teosinte is absolutely constant. This is true whether looked at from the standpoint of fluctuating variations of a quantitative nature or the frequency of occurrence of abnormalities. We have had teosinte under observation every season for 10 years, and during that time, with the exception of some apogamous plants one season at San Diego, not a single pronounced abnormality has appeared.

Nine plants survived the crowded conditions in the senior writer's test plot in the Philippines. That the six infected ones of these all developed decidedly malformed tassels is therefore the more striking. It should be noted in this connection that from seed of representative plants in the parent plot Collins made certain that this teosinte was pure and free from contaminating hybridization with maize.

In the second place, these malformations are of interest in themselves because they show such remarkable modifications in structure. The elaborate overdevelopment of such floral parts as the glumes and lemmas; their hypertrophy to many times the normal extent and bulk; the formation of additional fibrovascular bundles within them; the marked alteration in size, position, arrangement, and relation of the florets and their parts; the local unevenness of growth with consequent crumpling and curling of mature organs; and the binding and restraint of rapidly expanding inner portions of the inflorescence by the adherent unexpanding outer parts enfolding them, with consequent contortion, buckling, and tearing—all these features mark these malformed inflorescences as noteworthy cases of abnormal growth. As such they may be of interest in the field of teratology, a branch of botany little emphasized at present, but one in which in the past Penzig (*44*), Masters (*33*), Moquin-Tandon (*37*), and others not only devised extensive classifications and terminologies, but also made comparative studies of the structural modifications in different groups of plants and worked out convergences and homologies that are still of some general significance. The extensive deformation of these teosinte tassels is of added interest because it seemingly was consequent to the irritation of the downy-mildew mycelium growing immediately within their tissues, an action which apparently in most cases was direct, as in very few instances did the apparent absence of hyphae within the deformed floral parts permit consideration of possible action at a distance.

In the third place, these malformed inflorescences are of interest because they were completely sterile. This was true not only in cases where the spikelets entirely lacked sexual organs and were profoundly modified, but also in cases where the florets in general appearance were almost normal and developed stamens, for the pollen was invariably abortive and nonfunctional. Moreover, they were sterile with respect to both sexes, for in no case did female branches develop. This sterility, however, was accompanied by unusual vegetative rejuvenescence. Uncommonly numerous shoots were developed continuously from the bases of the plants, and when during the heavy storms the plants were beaten down into the mud, they sent up many new sprouts from their nodes. The continued proliferation was so pronounced that during the six months they were under observation the plants, although of the annual species of teosinte, in general resembled the perennial type that occurs in Mexico and has been studied and described by Collins (*14*). That these plants should be sterile florally and yet have such unusually prolific vegetative growth gave rise to the rather anomalous situation that if the plants had been grown for seed or to furnish pollen for hybridization the effect of the downy mildew would have been regarded justly as very injurious, quite as it is in the case of other grain-bearing crops such as maize or wheat; whereas, if the plants had been wanted for their vegetative growth for fodder or stover, the effect of the mildew on the whole was beneficial, rendering them even more valuable than the less prolific healthy individuals.

It is of interest also that coincident with the sterility of these plants there took place an abortive apogamous reproduction through the temporarily independent growth of the seedlinglike spikelets, for although examples of this viviparous method of propagation have been observed in the Gramineae they apparently are rare in the tribe Maydeae. The cases of apogamy in maize reported by Collins (*9*) are the only ones in the tribe described hitherto, and the cases in teosinte (unfortunately not described but merely mentioned in the same paper) are the only ones ever even recorded in that genus, as far as the writers have been able to ascertain.

In the fourth place, malformations such as these in teosinte may perhaps have some structural or phylogenetic significance as traumatic reversions to ancestral conditions. The consistently leaflike structure of the abnormal growths which develop from diverse injurious agents in the several Gramineae considered probably may be interpreted as evidence for the theory that the leaf is the ultimate progenitor from which all floral organs have been evolved.

Is it possible to go still farther? In a comparable case—an intensive study of the malformations of maize following attack by corn smut (*Ustilago maydis*)—Iltis (*22*) has found structural evidence which he considers to indicate beyond doubt that Zea has been derived indirectly from the Andropogoneae. This might arouse expectations that these malformations of teosinte may offer some structural evidence of significance in the phylogenetic question of the ancestry of teosinte and even of the ancestry of maize, with which teosinte is more or less involved in the hypotheses advanced by Collins

(*10, 12, 15*), Montgomery (*36*), Weatherwax (*53*), and others. Yet toward a solution of the disputed question whether maize originated by slow evolution or as a mutation or sport from teosinte or some ancestral plant like it; or whether it arose as the result of hybridization between teosinte and some other grass; or whether pod corn, erroneously believed to grow wild in Paraguay, is the ancestor of cultivated maize quite separate from teosinte, these abnormal inflorescenses of teosinte seem to furnish no clear evidence.

To be sure, these malformed teosinte spikelets somewhat resemble those of pod corn (*Zea tunicata*) in the overgrowth of their glumes, a character well developed in this type of Zea, not only in the ear but also at times in the tassel. (Collins *11, pl. 13, B*). This resemblance, even though some consider pod corn as the type most primitive or most like ancestral maize, can hardly be of any special significance, however, for similar overgrowths of floral parts occur in such genera as Pennisetum and in other tribes too remote to furnish any evidence of ancestral characters or relationships in the Maydeae. Likewise, there seems to be no significance in the resemblance between the adherence and binding of the leafy parts in certain deformed teosinte spikelets (fig. 2, C, D) and that traced by Kempton (*27, fig. 16*) as an inherited feature in "adherent" plants of certain strains of maize, and between the lobing and consequent entanglement of parts in the deformed teosinte tassels and that which Kempton (*26*) has found in leaves, husks, and tassel glumes, not only in maize but also in teosinte and related grasses.

Moreover, Collins (*14*) has suggested that the perennial type of teosinte is the more primitive from which the annual has been derived (possibly by crossing with its annual relative, maize). The unusually abundant and prolonged production of new shoots by the infected teosinte plants might be interpreted as a reversion to an ancestral condition. More probably, however, it is merely an example of the prolongation of vegetative growth which often follows tolerated parasitism of Sclerospora in other hosts (*57, pl. 5*).[4]

In the fifth place, these malformations in teosinte present interesting comparisons to those recorded in cases of infection by the other species of Sclerospora in numerous grasses. In the case of the common *Sclerospora graminicola*, for example, malformations of the inflorescence of an extensive list of grasses, chiefly in the tribe Paniceae, have been reported many times from Europe, Africa, China, Japan, and India. Also, the widely distributed *S. macrospora* has been found inducing deformities of the floral structures in some 25 hosts (including maize, wheat, rice, and many wild grasses) in 9 of the 11 gramineous tribes in many localities through Europe, Asia, Australia, and the United States. In the other species of Sclerospora, moreover, although less numerous, striking, and widespread, similar cases have been reported, so that in all more than 40 papers might be referred to as pertinent. From these facts it seems obvious that these plants of teosinte, in showing malformations of the inflorescence as the result of attack by downy mildews of the genus Sclerospora, were only behaving toward these parasites as many other genera of grasses have

[4] Further resemblances of possible phylogenetic significance might be noted, but realizing that such material can be better interpreted by others more familiar with the morphology, development, genetics, history, relationship, and agronomy of maize, teosinte, and their relatives, the writers will gladly turn over the remaining material, including slides, photographs, and notes, to those who will undertake further study.

been found to behave in the history of our knowledge of this group. On going over these cases and comparing the deformities in the tassels of teosinte with those developed in other male inflorescences, such as the tassels of maize (*17, 19, 23, 25*), and those formed in the perfect spikes or inflorescences of other grasses, such as Pennisetum (*5, 8, 29*), Setaria (*20, 21, 29, 34, 48, 49, 51, 58*), Triticum (*1, 2, 4, 39, 40, 41, 43, 47, 52, 55*), Oryza (*18, 59*), Agropyron, Phragmites, etc.(*42, 43*), it is noticeable that there is a general similarity, but that these in teosinte are on the whole more extensive in their growth, more elaborate and complex, and more profoundly altered in their structure. In their behavior, that is, in the partially successful growth of some of the more pronouncedly modified spikelets as if they were young independent plants, they are in some ways unique among the cases of abnormalities resulting from Sclerospora attack. It seems probable, however, that some of the elaborately malformed spikelets in the virescent tassels of maize infected with *S. macrospora* described in Italy by D'Ippolito and Traverso (*25*) and others would have made at least abortive attempts at independent apogamous growth if they had been given opportunity.

Finally, when the foregoing points have been considered, what seems to be the most probable interpretation of such malformations as these in teosinte? All deformed inflorescences in the case of wild and cultivated Gramineae are not occasioned, of course, solely by the growth of Sclerospora in the host tissue. Deformities with general resemblance to those just considered have been found, for example, to develop as the result of attack by nematodes in wheat (Leukel, *30*) and rice (Butler, *7*); of infestation by insects in wheat and Setaria (D'Ippolito, *24*); of chemical and mechanical injury in maize (Blaringhem, *3*); and even, apparently, of excessive moisture in wheat (Lo Priore, *31*); probably following the general principle emphasized by Knox (*28*) that most malformations such as phyllodies, multiplications, fasciations, torsions, or virescences arise from injuries and are not heritable. Also, in a few instances malformations of the inflorescences very similar to these of traumatic origin have been found by Kempton (*27*), Zapparoli (*60*), and others to develop in maize unassociated with any detectable injury and to persist as hereditary characters.

These points seem to suggest the following: Under normal conditions the floral parts of teosinte and other grasses have inherent possibilities of certain structural development regarded as usual, normal, or typical. Also, however, they have inherent potentialities for ways of development that are unusual, nontypical, or abnormal, but may be induced by the action of various factors that are injurious or that disturb the usual course of growth. Obviously, there are limits to the inherent capabilities for abnormal development; but within these limits they show great range in such structural excesses as remarkable leaflike elaboration, extensive overgrowth of floral envelopes, and suppression of sexual organs; and these abnormalities, agreeing in general, may be called forth in response to various diverse disturbing influences. Under ordinary conditions of growth in the field, however, such disturbing influences are encountered but seldom; consequently, such malformations develop only rarely. Under ordinary circumstances, also, cases of malformation attributable to chemical injury, to harmful environmental conditions, or to noxious insects are relatively infrequent.

Attack by Sclerospora, however, is a disturbing factor encountered in such a wide range of valuable and much-studied host crops, in so many different parts of the world, and it is so commonly followed by malformation of the inflorescence, that such deformation very naturally has come to be regarded as one of the distinctive symptomatic stigmata of these diseases.

SUMMARY

This paper considers the case histories, structural peculiarities, and possible interest or significance of malformed male inflorescences of teosinte (*Euchlaena luxurians*) infected with the downy mildew (*Sclerospora philippinensis*) in the Philippines.

The tassels were strikingly altered in appearance and structure; the spikes shorter, the rachis in extreme cases comprising only a few joints; the floral elements progressively reduced in size and number from base to tip of spikes, the tip spikelet in some represented by a single glume; the glumes, and particularly the lemmas, in reduced spikelets, excessively hypertrophied, the latter usually characteristically enwrapping although occasionally expanded above to a green blade, leaflike in gross structure and in histology; the paleas less hypertrophied, sometimes in the second florets only vestigial; the stamens generally wanting, but when present having atrophied anthers and abortive pollen. Not only were the tassels profoundly malformed, but the female inflorescences were suppressed, so that the plants were completely sterile. This sterility was accompanied by unusually prolific vegetative growth, the continued and abundant production of new shoots showing some resemblance to the growth habit of perennial teosinte.

In tassels left lying on the ground during heavy rains, deformed spikelets comprising leafy shoots resembling seedling plantlets remained green and vigorous, grew into an upright position, sent out roots from their bases, and when transplanted continued to develop independently for more than a week. Within their tissues the mycelium of the fungus remained living and apparently capable of continued growth had the plantlets lived. As such cases of apogamy or vivipary are unusual in the gramineous tribe Maydeae and exceedingly rare in teosinte, these are described and illustrated, and compared with those following infection by other species of Sclerospora in other grasses.

The possible bearing of these malformations on the general question of the interpretation of floral malformations is outlined and their possible significance is considered.

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